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RESEARCH ARTICLE

Seed germination traits reveal naturalization potential: Global insights from temperate European herbaceous species

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Abstract

1. Seed germination is a key stage in a plant's life cycle, influencing regeneration from seed by determining the post-germination environment, plant fitness and evolutionary potential. Therefore, seed germination traits are expected to play a fundamental role in the naturalization of alien seed plants; yet broad-scale empirical evidence of this remains limited.
2. Using seed germination data for 1146 native temperate European herbaceous species, we tested whether species that have become naturalized outside their native range differ from non-naturalized species in overall germinability (final germination proportion) and in their germination responses to six environmental cues across temperate, tropical dry and tropical humid macroclimatic zones of naturalization. We also assessed whether germinability and responses to these cues are associated with the geographic extent of naturalization, using a phylogenetically informed meta-analysis that integrates 18,596 standardized laboratory germination records with global naturalization data.
3. Naturalization was a common phenomenon, with 60% of species having naturalized in temperate regions and over 30% having naturalized in tropical regions. Naturalized species showed consistently higher overall germinability, germination at lower temperatures and higher requirements for seed scarification compared to non-naturalized species, while other germination traits varied with the macroclimatic zone of naturalization. The extent of naturalization was also positively, though weakly, related to higher germinability and to the same germination traits that distinguished naturalized from non-naturalized species.
4. *Synthesis*. This study provides global-scale evidence that the naturalization of European herbaceous species is related to specific germination traits acquired in the native range. Our findings indicate that traits such as high germinability,

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low stratification requirements and responsiveness to scarification act as preadaptations that facilitate naturalization by increasing opportunities for establishment. They also show that standardized laboratory germination tests using seeds sourced from native populations represent a cost-effective tool for improving global risk assessments and for predicting naturalization potential under climate change through alterations in regeneration from seed.

KEYWORDS
alien species, GloNAF, macroclimate, plant invasions, regeneration niche, seed dormancy, seed germination, *SeedArc*

1 | INTRODUCTION

Invasions by alien plants introduced outside their native range are among the major human-induced drivers of global environmental change and biodiversity loss (IPBES, 2023), often interacting synergistically with other components of global change (Gioria et al., 2023; Pyšek et al., 2020). Plant invasions are characterized by two key stages: naturalization and invasion (Richardson et al., 2000). Naturalization refers to the ability of alien species to establish self-sustaining populations without further introduction of propagules (i.e. reproductive units), emphasizing the role of effective regeneration strategies, while invasion success refers to the subsequent expansion of naturalized populations (Richardson et al., 2000; Richardson & Pyšek, 2012). Unlike invasion success, naturalization is a binary measure of a species' success (Pyšek et al., 2017), representing a pivotal phase in the invasion process as subsequent population expansion hinders management and eradication efforts (Richardson & Pyšek, 2012).

Identifying the main drivers of naturalization success is therefore crucial for predicting which species are more likely to become naturalized, for enabling proactive management and for preventing future invasions. Climate and reproductive traits play a critical role in the successful naturalization of alien plants (Gioria et al., 2023; Lavoie et al., 2016; Pyšek et al., 2015; Richardson & Pyšek, 2012). To become naturalized, an alien species must overcome environmental and reproductive barriers or filters (Richardson et al., 2000; Richardson & Pyšek, 2006). Environmental filtering is considered a key mechanism driving naturalization, which is expected to occur when the fundamental ecological niches of alien species match the environmental conditions in the introduced ranges, through preadaptation (e.g. climate matching; Thuiller et al., 2005) or preintroduction selection, that is, the intentional introduction of species with desirable traits for various purposes (Briski et al., 2018; Colautti & Lau, 2015). This prediction forms the basis of the 'preadaptation hypothesis' (Cadotte et al., 2018; Ricciardi & Mottiar, 2006) and is supported by empirical evidence that alien species often occupy similar ecological niches in the native and introduced ranges, while evidence of climatic niche expansion in the latter is limited (Liu et al., 2020). However, under intense resource competition from resident species, naturalization may be facilitated if alien species occupy distinct or 'empty' ecological niches (competition-relatedness hypothesis; Daehler, 2001; Park et al., 2020). These include vacant phenological niches, that is, windows of opportunity generated by temporal mismatches in phenological events (Gioria et al., 2018; Gioria & Osborne, 2014; Park et al., 2024; Wolkovich & Cleland, 2014).

Germination traits are expected to play a central role in the successful establishment of alien seed plants in non-native ranges (Gioria et al., 2018, 2023). Seed germination, in fact, determines the post-germination environment (Donohue et al., 2010), influencing early resource acquisition, competitive interactions (Gioria et al., 2018) and subsequent phenological events (de Rubio Casas et al., 2012) in both native and alien species. These factors, in turn, affect the fitness, persistence and evolutionary potential of seed plants and, ultimately, their distribution (Baskin & Baskin, 1989; Donohue et al., 2010; Hoyle et al., 2015; Pausas et al., 2022; Rosbakh et al., 2023; Verdú & Traveset, 2005).

Seed germination occurs in response to environmental cues that define a species' 'seed germination niche' (Grubb, 1977), that is, the set of conditions that ensures a successful transition from seeds to seedlings (Donohue et al., 2010; Larson & Funk, 2016). The germination niche is associated with dormancy-breaking requirements and the conditions required for germination in non-dormant seeds (Baskin & Baskin, 1989, 2014). Germination traits have evolved to minimize the risk of emergence under unfavourable conditions for seedling survival and growth, in response to local environmental constraints and uncertainty (Baskin & Baskin, 1989; Donohue et al., 2010; Finch-Savage & Leubner-Metzger, 2006; Pausas et al., 2022; Rosbakh et al., 2023), and to climatic selection pressures (Baskin & Baskin, 2014; Carta et al., 2022; Fernández-Pascual et al., 2021; Zhang et al., 2022).

As germination–climate relationships strongly influence regeneration from seed (Baskin & Baskin, 2014, 2022), an important question is whether preadaptation in seed germination traits to the climatic conditions of the regions of introduction favour the naturalization of alien plants. In this respect, seed plants may adopt a range of strategies to mitigate the negative effects of unfavourable abiotic conditions and antagonistic biotic interactions with resident species. These include opportunistic germination through broad dormancy-break requirements, allowing the exploitation of phenological windows of opportunity under low competition from resident species (Gioria et al., 2018; Wolkovich & Cleland, 2014). Another strategy, not mutually exclusive (Gioria et al., 2018, 2021), is delayed germination through dormancy mechanisms that promote the formation of persistent soil seed banks (sensu Gremer & Venable, 2014; Thompson et al., 1997; Venable & Brown, 1988; Walck et al., 2005). Both strategies have been linked to naturalization success (Gioria et al., 2018, 2021).

Comparisons between naturalized and non-naturalized species, using species trait data from the native range, can reveal potential mechanisms that underlie successful naturalization in alien plants and improve global risk assessments (Gioria et al., 2021; Richardson & Pyšek, 2012). While several studies have examined the germination characteristics of individual alien species or small groups of species, often contrasting them with germination patterns in co-occurring native species or non-invasive congeneric species (Gioria & Pyšek, 2017), broad-scale relationships between germination traits and naturalization success are lacking.

In this study, we used a comparative approach to evaluate whether the germination responses to key environmental cues, measured as the final germination proportion reached in standardized laboratory germination tests, are related to the naturalization occurrence (yes/no) and geographic extent of naturalization of 1146 native European temperate herbaceous species. To do so, we integrated seed germination records extracted from *SeedArc*, a global database of seed germination data (Fernández-Pascual et al., 2023), with global naturalization data from the Global Naturalized Alien Flora database (GloNAF; van Kleunen et al., 2019). We focused on herbaceous species to minimize the variability associated with substantial differences in regeneration strategies between herbaceous and woody species (Baskin & Baskin, 2014) and because woody species were underrepresented in *SeedArc*.

We addressed three main research questions. First, we tested whether germinability, that is, the final proportion of germinated seeds, differs between naturalized species and non-naturalized species, and whether it is positively related to naturalization extent, defined as the number of GloNAF regions (van Kleunen et al., 2019) where a species has become naturalized globally. We hypothesized that naturalized species exhibit higher germinability than non-naturalized species as a greater proportion of germinated seeds may increase the probability of successful regeneration from seed (see Gioria & Pyšek, 2017). Second, we tested whether naturalized species differ from non-naturalized species in their responses to six key environmental cues, based on data from the native range, and whether these differences vary between the macroclimatic zones of naturalization, that is, temperate, tropical dry and tropical humid zones. Because germination is strongly climate-dependent (Baskin & Baskin, 2014), we expected naturalized species to differ in at least some germination traits that may confer advantages in non-native ranges under specific macroclimatic conditions, such as lower dormancy-breaking requirements potentially resulting in priority effects (Gioria & Pyšek, 2017; Wolkovich & Cleland, 2014) or stricter requirements that improve synchronization with favourable or disturbed conditions or that promote the formation of persistent soil seed banks. Third, we asked whether germination traits influence the geographic extent of naturalization within each macroclimatic zone of naturalization. As the extent of naturalization is strongly influenced by human activities (e.g. Hulme, 2021; Pyšek et al., 2015), we did not formulate an a priori hypothesis on potential relationships between germination traits and naturalization extent.

Ultimately, the findings of this study can provide valuable insights into the role of seed germination in the process of naturalization of herbaceous species and into whether germination traits from native populations observed under controlled laboratory conditions can improve predictions of naturalization potential across contrasting climatic conditions.

2 | MATERIALS AND METHODS

2.1 | Seed germination data

To evaluate whether the naturalization success of European herbaceous species is related to seed germination traits acquired in the native range, we extracted germination records from *SeedArc* (Fernández-Pascual et al., 2023), a global compendium of primary seed germination data. In this database, each record represents the final germination proportion observed in a test conducted under controlled environmental conditions, with germination defined as radicle protrusion of 1–2 mm. A primary record refers to a specific seed lot, that is, a collection of seeds from a geo-referenced wild population collected at a specific date. Each record includes information on species identity, the number of sown and viable germinated seeds, the institution (seed bank or research group) where the test was carried out and country of collection.

From this database, we extracted germination data for 2571 species native to temperate Europe, based on experimental trials using seeds collected from their native range in Europe. Species names were standardized using the 'World Checklist of Vascular Plants' (WCVP; Govaerts et al., 2021). We obtained the phylogeny by pruning the Smith and Brown (2018) megaphylogeny as implemented in *U.PhyloMaker* (Jin & Qian, 2023) to our study list.

We applied four filters or inclusion criteria to minimize potential biases and ensure comparability across species: (1) a phylogenetic filter, retaining only those species present in the *U.PhyloMaker* megaphylogeny, ensuring consistency between the phylogeny and the trait dataset. This conservative approach avoids uncertainty from inferred placements and ensures consistency with the published reference phylogeny (Smith & Brown, 2018); (2) a life-form filter, selecting only herbaceous species (versus woody species) based on the life form categories available in WCVP (Govaerts et al., 2021); (3) a data-sufficiency filter, retaining only those species with at least three primary seed germination records to allow for a more accurate characterization of the germination traits adopted by each species;

and (4) a methodological filter, including only records from experiments conducted on agar or filter paper rather than soil, to minimize potential systematic effects associated with different experimental conditions.

The final dataset comprised 18,596 germination records for 1146 herbaceous species across 68 families and 26 orders, representing the major angiosperm clades. These records were derived from 4933 seed collections originating from temperate Europe and neighbouring regions, involving a total of 690,584 seeds collected from 52 countries. In this dataset, four families accounted for over 45% of all the species in the dataset: Asteraceae (13.1%), Poaceae (12.8%), Fabaceae (11%) and Caryophyllaceae (9%). Besides being some of the most common plant families in Europe, the Asteraceae, Poaceae and Fabaceae are the dominant contributors, in the same order of magnitude, to the naturalized alien flora globally (Pyšek et al., 2017), indicating that the final dataset is highly representative of global floristic trends.

This dataset includes the final germination proportion observed in response to six experimental cues simulating key environmental cues for dormancy release or germination (Baskin & Baskin, 2014): (1) Temperature: germination trials were conducted at temperatures ranging between 0 to 40°C (on average, 18°C), with 95% of tests being in the range 7°–26°C; (2) Alternating temperature (binary: constant vs. diurnally alternating); (3) Light (binary: diurnal light versus darkness); (4) Cold stratification (binary: yes/no, based on exposure >4 weeks to cold wet stratification at <6°C); (5) Warm stratification (binary: yes/no, based on exposure >4 weeks to warm stratification at >20°C); and (6) Scarification (binary: yes/no), depending on whether the seed coat had been treated to promote water imbibition.

Stratification and scarification are dormancy-breaking treatments. Scarification is a pretreatment aimed at breaking or altering the seed coat to make it permeable to water and gases, thereby promoting dormancy break in seeds with physical dormancy (Baskin & Baskin, 2014). Because seed mass can influence various aspects of seed germination, such as sensitivity to light (Carta et al., 2017; Milberg et al., 2000), we also compiled seed mass data extracted from the Seed Information Database (SER, INSR, RBGK, Seed Information Database, 2023) and TRY v5 (Kattge et al., 2020).

2.2 | Species naturalization data

Biogeographic data on naturalization success were extracted from the 'Global Naturalized Alien Flora' database (GloNAF v2.02, Davis et al., 2025), a global compendium of naturalization data providing information on whether a plant species is considered as naturalized in a specific region or geographic area (van Kleunen et al., 2015). GloNAF covers 1343 TDWG (Working Group on Taxonomic Databases) level 4 regions, following the standard World Geographical Scheme for Recording Plant Distributions (Brummitt, 2001). These regions are hereafter referred to as GloNAF regions. In our study, naturalization success was quantified using two variables: (1) naturalization occurrence (naturalized vs. non-naturalized), indicating whether a species has been recorded as naturalized at least in one GloNAF region; and (2) naturalization extent, defined as the number of non-overlapping GloNAF regions in which a species is naturalized. Across all species in our dataset, we identified 472 GloNAF regions of naturalization.

2.3 | Macroclimatic zones

To identify which germination trait may promote naturalization under different macroclimatic conditions, we assigned each GloNAF region of naturalization to a predominant macroclimatic category (zonobiome), based on the classification of Walter and Breckle (1991), as adapted by Essl et al. (2019). Using this classification, we grouped the regions of naturalization represented in our dataset into three broad macroclimatic zones: (1) temperate zone; (2) tropical dry zone, characterized by high seasonality in precipitation; and (3) tropical humid zone, with warm temperatures and consistently high humidity throughout the year. No additional categories were represented in our data. The number of species unique to each macroclimatic zone of naturalization and those shared within zones are represented in Figure 1. For species naturalized in more than one macroclimatic zone, naturalization extent was calculated as the number of regions within each zone.

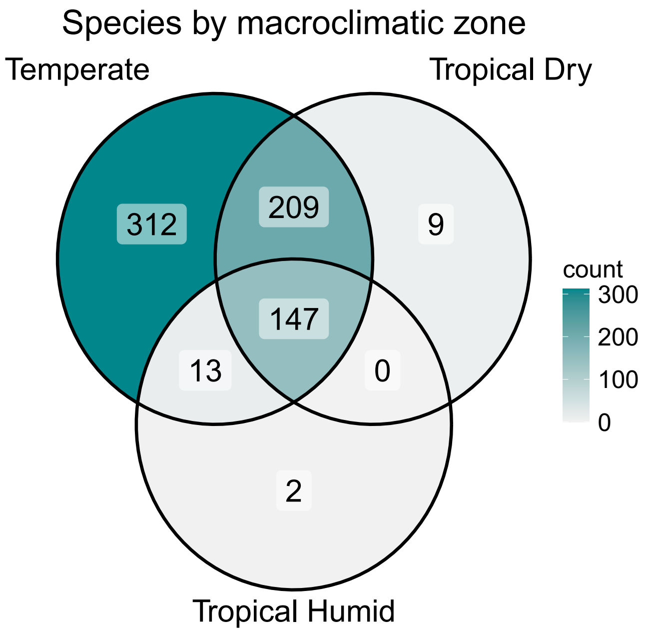

FIGURE 1 Venn diagram displaying the number of species naturalized in each of three macroclimatic zones (temperate, tropical dry and tropical humid) and overlap, for 692 temperate herbaceous species that have naturalized outside their native range in Europe. Circle areas are shaded on a gradient from light grey (fewer species) to steel blue (more species), with counts in each partition indicating the number of species unique to or shared among macroclimatic zones.

2.4 | Statistical analyses

To test our hypotheses, we conducted a phylogenetically informed meta-analysis of germination data using binomial phylogenetic generalized mixed models with Bayesian estimation via Markov chain Monte Carlo (MCMC), implemented in the R package *MCMCglmm* (Hadfield, 2010). To test whether germinability differed between naturalized and non-naturalized species (Hp1), germinability was modelled as the proportion of germinated to non-germinated seeds, with naturalization occurrence (692 naturalized species vs. 545 non-naturalized species) or naturalization extent (scaled) as the fixed effect. To account for the potential effect of seed mass on germination responses, we also tested interactions between seed mass ($\log(x+1)$ transformed) and naturalization occurrence or extent. However, seed mass had no significant effect and was thus excluded from the final models. Models of naturalization extent were run both including and excluding non-naturalized species, for which this extent equals zero. Both models provided similar results. We present only models including non-naturalized species because this allows testing the relationship between germinability and extent along the full gradient of naturalization extent.

To test whether the germination responses to environmental cues differ between naturalized and non-naturalized species, and whether they are related to the geographic extent of naturalization, we modelled germinability as a function of the interaction between naturalization occurrence or extent and each of the six experimental cues. To evaluate whether different traits contribute to naturalization in different macroclimatic zones, we performed separate models for each macroclimatic zone of naturalization (temperate, tropical dry and tropical humid). This resulted in six models per germination cue, for a total of 36 models. Only records from the relevant macroclimatic zone were included (species and record counts are provided in Appendix S1). Macroclimatic zone was not used as an explanatory factor in full species models because many species were naturalized in more than one macroclimatic zone and models in each zone were characterized by a different number of species (1135 species in the temperate region, 819 in the tropical dry region and 616 in the tropical humid region).

All models included the following random effects: (1) phylogeny, to account for the statistical non-independence of data points due to shared evolutionary history among related species; (2) species identity, to capture within-species variation in germination responses and potential measurement errors; (3) seed lot and (4) country of collection, to account for between-study variation among seed lots in the seed physiological status and storage time, as well as differences in experimental conditions across laboratories.

All continuous predictors were centred on their means and scaled to unit variance, to allow direct comparisons of effect sizes. In all relevant models, we ran analyses using both log-transformed and scaled (mean = 0, SD = 1) values of naturalization extent. As the results were similar, we present the scaled values because they allow direct comparison of effect sizes with those of other predictors. We used weakly informative priors and parameter-expanded priors for the random effects. Each model was run for 1,300,000 MCMC steps, with an initial burn-in phase of 100,000 and a thinning interval of 100, resulting in an average of 10,000 posterior distributions per model. From the resulting posterior distributions, we calculated mean parameter estimates and 95% credible intervals (CIs). Effects were considered significant if the CIs did not overlap zero. All data processing and statistical analyses were conducted in R v. 4.5.0 (R Development Core Team, 2025).

3 | RESULTS

Of the 1146 species considered in this study, 60.4% (692 species) had naturalized in at least one GloNAF region globally, while 39.6% (454 species) had not been reported as naturalized. Among naturalized species, 681 had naturalized in the temperate zone (60% of the total), 365 in the tropical dry zone (32% of the total) and 162 in the tropical humid zone (14% of the total) (Figure 1). The Poaceae, Fabaceae and Asteraceae were the most frequently represented families, although their relative importance varied with the macroclimatic region of naturalization (Figure 2).

3.1 | Germinability and naturalization success

Consistent with our first hypothesis, germinability was significantly higher in naturalized than in non-naturalized species ($p_{\mathrm{MCMC}} < 0.001$) and was positively associated with naturalization extent ($p_{\mathrm{MCMC}} = 0.005$) (Figure 3). In both models (naturalization occurrence and extent), random effects indicated that germinability was influenced by evolutionary history and exhibited both intra- and interspecific variability. Phylogeny had the strongest effect (naturalization occurrence: 3.88, CI [2.51–5.43]; naturalization extent: 3.56, CI [2.28–4.58]), followed by seed lot (naturalization occurrence: 2.74, CI [2.49–3.00]; naturalization extent: 2.75, CI [2.51–3.03]) and species identity (naturalization occurrence: 1.73, CI [1.37–2.11]; naturalization extent: 1.79, CI [1.38–2.17]). Country of collection had the weakest effect (naturalization occurrence: 1.31, CI [0.69–2.01]; naturalization extent: 1.29, CI [0.70–2.03]).

3.2 | Germination and naturalization occurrence in the temperate zone

In support of our second hypothesis, species naturalized in the temperate zone showed distinct responses to most germination cues compared to non-naturalized species (Figure 4a). Naturalized species germinated at lower temperatures ($p_{\mathrm{MCMC}} < 0.001$) and had lower requirements for cold stratification ($p_{\mathrm{MCMC}} = 0.032$) and warm stratification ($p_{\mathrm{MCMC}} < 0.001$), while they were more responsive to seed scarification ($p_{\mathrm{MCMC}} < 0.001$) (Figure 4b). However, no significant differences were observed in their responses to alternating

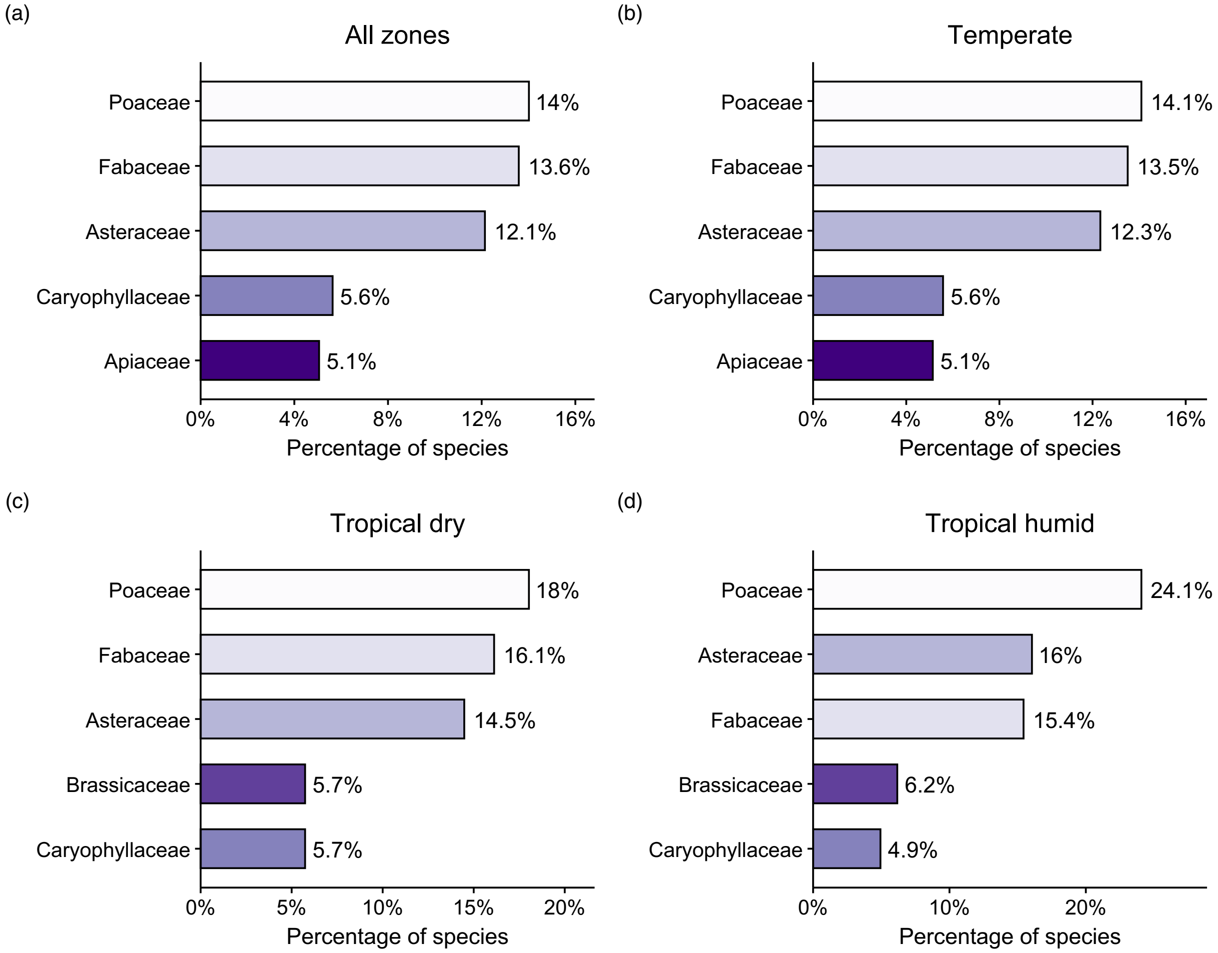

FIGURE 2 Relative contribution of naturalized plant families across climatic zones. Bar charts show the percentage of species represented by the six most speciose families of naturalized species in (a) all macroclimatic zones combined (692 species), (b) temperate zone (681 species), (c) tropical dry zone (365 species) and (d) tropical humid zone (162 species). Percentages are calculated within each zone and are displayed beside the bars.

temperatures or light. Among random effects, phylogeny had the strongest effect on germination responses, followed by seed lot, species identity and country of collection (Appendix S2).

3.3 | Germination and naturalization occurrence in tropical zones

Species naturalized in tropical GloNAF regions exhibited distinct germination responses depending on whether they occurred in the tropical dry or tropical humid zone. Those naturalized in the tropical dry zone had similar responses to non-naturalized species, except for a negative response to high temperature ($p_{\text{MCMC}}<0.001$) and a positive effect of scarification ($p_{\text{MCMC}}=0.005$; Figure 4b). Those naturalized in the tropical humid zone, in contrast, differed in all germination responses except for light, showing negative responses to temperature ($p_{\text{MCMC}}=0.002$), alternating temperatures ($p_{\text{MCMC}}=0.002$) and cold stratification ($p_{\text{MCMC}}<0.001$), but positive responses to warm stratification ($p_{\text{MCMC}}<0.001$) and scarification ($p_{\text{MCMC}}<0.001$) (Figure 4c). As in the temperate zone models, phylogeny had the strongest effect on germination responses, followed by seed lot, species identity and country of collection (Appendix S2).

3.4 | Germination responses and naturalization extent

Patterns observed for naturalization extent were broadly consistent with those associated with naturalization occurrence (Figure 4). For species naturalized in the temperate zone, naturalization extent was negatively associated with temperature ($p_{\text{MCMC}}<0.001$), alternating temperatures ($p_{\text{MCMC}}=0.012$), cold stratification ($p_{\text{MCMC}}=0.003$) and warm stratification ($p_{\text{MCMC}}<0.001$), while it was positively associated with scarification. For species naturalized in tropical macroclimatic zones, naturalization extent was negatively related to a requirement for cold stratification and positively related to requirements for warm stratification and scarification (Figure 4b,c). As with naturalization occurrence, phylogeny had the strongest effect on seed germination responses among the random factors tested (Appendix S3).

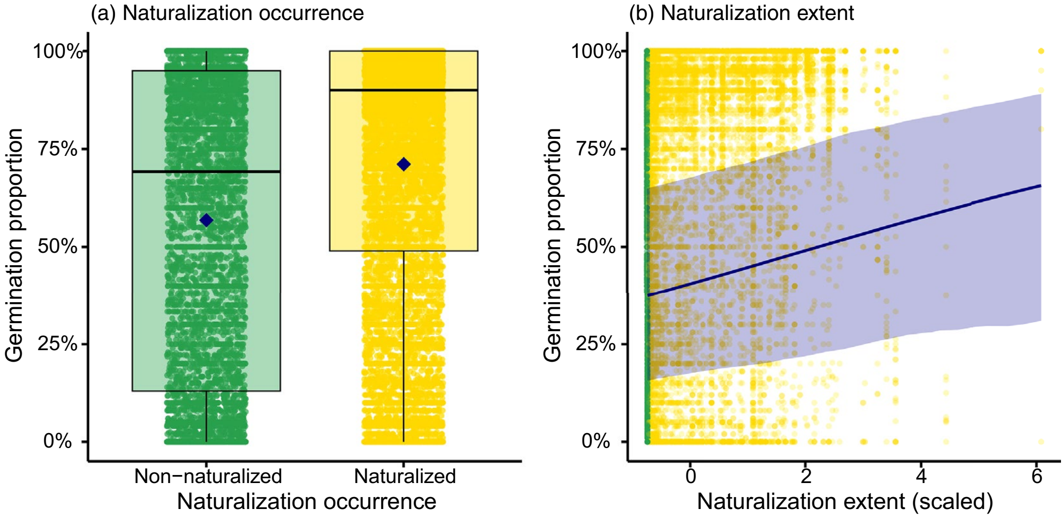

FIGURE 3 Germinability, that is, the final germination proportion in 18,596 records for 1146 native European temperate herbaceous species that have been reported as naturalized outside their native range (692 naturalized species, in 6307 records; gold) or have not been recorded as naturalized in non-native ranges (454 non-naturalized species in 12,289 records; green), based on naturalization data extracted from the GloNAF database (Davis et al., 2025). (a) Boxplots showing differences in germinability between naturalized and non-naturalized species, with mean values plotted as blue diamonds. (b) Relationship between germinability and naturalization extent, that is, the scaled number of regions of naturalization, with fitted model lines and credible intervals from Bayesian phylogenetically informed models. Primary germination data are represented as jittered points (naturalized species in gold and non-naturalized species in green).

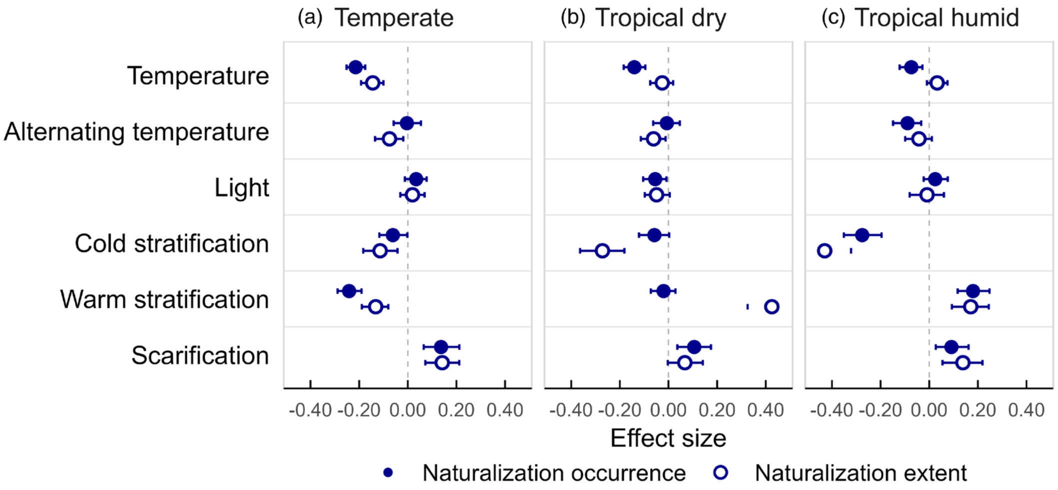

FIGURE 4 Results of binomial Bayesian generalized linear mixed models testing relationships between the germination responses of 1146 native European (18,596 records) to six environmental cues and their naturalization occurrence (naturalized vs. non-naturalized species; solid dots) or naturalization extent (scaled number of regions; empty dots), in each of the three macroclimatic zones of naturalization: (a) Temperate, (b) Tropical Dry, and (c) Tropical humid. Naturalized species are those reported as naturalized outside their native distribution range in the GloNAF database (Davis et al., 2025). Dots represent posterior means of interaction effect sizes with 95% credible intervals. The dashed vertical line indicates no effect. A negative effect of temperature indicates that naturalized species germinated at lower temperatures than non-naturalized ones. Analyses were conducted separately for species naturalized in temperate (681 species, $n = 1135$), tropical dry (365 species, $n = 819$) and tropical humid zones (162 species, $n = 616$), with non-naturalized species (454) included in each comparison. For species naturalized in more than one macroclimatic zone, naturalization extent was calculated separately as the number of GloNAF regions within each zone. Across macroclimatic zones, some traits showed ordered patterns (temperature and warm stratification: temperate < tropical dry < tropical humid; cold stratification: temperate > tropical dry > tropical humid). Naturalization was consistently promoted by germination at cool temperatures and responsiveness to scarification across all zones, while strong responses to warm stratification were positively related to naturalization extent in tropical regions.

4 | DISCUSSION

This study provides the first global evidence that seed germination traits acquired in the native range influence the naturalization success of European herbaceous species native to temperate Europe in non-native regions within temperate, tropical dry and tropical humid macroclimatic zones. Naturalized species consistently showed higher germinability, the ability to germinate at lower temperatures and greater responsiveness to seed scarification, while other responses varied with the macroclimatic zone of naturalization. These traits were also associated, although to a lesser degree, with the geographic extent of naturalization, indicating that preadaptation in germination traits contributes to establishment success in non-native regions.

4.1 | Germination traits promoting naturalization success

Higher germinability in naturalized species supports the hypothesis that high germination success favours naturalization by increasing opportunities for successful regeneration from seed. This advantage likely arises because a greater influx of seedlings into a system increases the probability that some encounter favourable environmental conditions, occupy empty ecological niches or escape natural enemies (Gioria et al., 2023; Gioria & Pyšek, 2017). In this sense, germinability represents a functional component of propagule pressure, a variable that refers to the number and frequency of propagules introduced in a system over time (Colautti et al., 2006) and that is recognized as a key driver of naturalization (Cassey et al., 2018; Pyšek et al., 2015). For seed plants, propagule pressure should thus be more accurately estimated by integrating information on both seed production and germinability, as successful recruitment depends on the product of these two components. Yet, many non-naturalized species showed high germinability, suggesting that this trait alone is not a sufficient condition for naturalization in non-native ranges, even where macroclimatic conditions are similar.

Two additional germination traits distinguished naturalized from non-naturalized species, that is, germination at cooler temperatures and a positive response to seed scarification, although the magnitude of their relationship with naturalization success varied between macroclimatic zones. Germination at lower temperatures broadens phenological windows of opportunity for germination, potentially generating priority effects (Gioria et al., 2018; Wolkovich & Cleland, 2014) that can favour naturalization, especially in the temperate zone. This hypothesis was supported by the fact that species naturalized in temperate regions germinate at lower temperatures than those naturalized in tropical regions.

A requirement for seed scarification reflects several potential benefits that physical dormancy may provide in non-native ranges, such as the optimization of germination timing under local environmental conditions that may differ from those found in the native range; a physical protection against natural enemies (Parker & Gilbert, 2007) such as local pathogens and seed predators (Paulsen et al., 2013; Willis et al., 2014); greater seed dispersal and/or germination through interactions with native frugivores (Baskin & Baskin, 1989; Chama et al., 2013); the exploitation of disturbance-driven dormancy release (Baskin & Baskin, 2000; Pausas et al., 2022); and the formation of persistent soil seed banks (sensu Baskin & Baskin, 2014; Gioria et al., 2020; Thompson et al., 1997). Moreover, by providing resistance to fungal infections (Dalling et al., 2011), physical dormancy may increase survival during long-distance dispersal from native to non-native regions. These processes collectively increase opportunities for seed establishment (Gioria et al., 2021). The environmental cues that terminate physical dormancy occur in different macroclimatic zones, explaining the frequent association of this dormancy type with naturalization success (Gioria et al., 2021) and the colonization of disturbed habitats by invasive alien plants (Davis et al., 2000; Gioria et al., 2023; Lear et al., 2022).

Zone-specific comparisons revealed additional patterns, whose ecological significance and management implications are discussed below for each macroclimatic zone of naturalization.

4.2 | Germination traits in the temperate zone

Naturalization was most frequent in temperate regions, especially within the Poaceae, Fabaceae and Asteraceae. Naturalized species germinated at cooler temperatures and had lower requirements for both cold and warm stratification compared to non-naturalized species, suggesting that reduced dependence on seasonal germination cues and broader thermal germination ranges favour naturalization even where climatic conditions are similar to those in the native range.

These traits are consistent with climate–germination relationships typically observed in the native range of temperate species (Baskin & Baskin, 2014). Most seeds in temperate soil seed banks have physiological dormancy (Baskin & Baskin, 1989, 2014; Finch-Savage & Leubner-Metzger, 2006; Rosbakh et al., 2023), which is typically broken by low winter temperatures (e.g. in summer annuals) or warm summer temperatures (e.g. in winter annuals) (Baskin & Baskin, 1989; Soltani et al., 2022). An ability of naturalized species to germinate at cooler temperatures and lower dependence on cold stratification suggests that an early-spring germination phenology favours naturalization in temperate regions by conferring competitive advantages through priority effects (Gioria & Osborne, 2014; Verdú & Traveset, 2005). These effects include exploiting periods of low competition from resident species (Gioria & Osborne, 2014), resource pre-emption leading to asymmetric competition (Gioria et al., 2018) and reduced exposure to seed predation and pathogens, which may improve overall fitness (Long et al., 2015). The importance of germinating at cooler temperatures as a trait favouring naturalization is consistent with evidence that many invasive alien species in temperate regions germinate earlier and faster than native species (Gioria & Osborne, 2014; Gioria & Pyšek, 2017; Wolkovich & Cleland, 2014), with even short-term mismatches in germination timing (or seedling transplanting) affecting the outcomes of competitive interactions with resident species (Gioria et al., 2018).

A scarification requirement for germination was strongly associated with naturalization success, reflecting the benefits of physical dormancy in optimizing germination timing, protecting from natural enemies and promoting the formation of persistent seed banks that provide increased opportunities for regeneration (Baskin & Baskin, 2014). These functions are consistent with the frequent association of physical dormancy with naturalization success (Gioria et al., 2021) and with requirements for seed scarification observed in European fabids from climates with high temperature seasonality (Carta et al., 2022).

Species naturalized in the temperate zone did not differ in their requirements for light and alternating temperatures from non-naturalized species. Light signals the depth of seed burial or canopy openness, that is, the occurrence of 'safe sites' (Harper, 1977), and is strongly dependent on the characteristics of the habitats where a species typically occurs (Baskin & Baskin, 2014; Finch-Savage & Leubner-Metzger, 2006), while temperature fluctuations prevent germination at unsuitable times in seasonal climates and also signal seed burial depth (Baskin & Baskin, 2014). Comparable responses to these cues suggest that most temperate species colonize similar habitats in both native and non-native ranges and are indicative of the importance of microsite cues in preventing germination at unsuitable times.

From a management perspective, species able to germinate at cool temperatures with low requirements for stratification should be prioritized in risk assessments. Examples of widely naturalized, early germinating species in our dataset include *Stellaria media* (L.) Vill., *Cerastium fontanum* Baumg, *Plantago major* L., *Senecio vulgaris* L. and *Veronica arvensis* L. Species requiring scarification should also be prioritized, as they may accumulate persistent seed banks that hedge against environmental unpredictability and increase the probability of germination at safe sites or after disturbance events, thus hampering control efforts.

4.3 | Germination traits in the tropical dry zone

About one-third of the species in our dataset have naturalized in tropical dry regions, which are characterized by strong precipitation seasonality. These species germinated at lower temperatures compared to non-naturalized species, providing further evidence that broad germination thermal niches are advantageous preadaptations in non-native regions (Gioria & Pyšek, 2017). In contrast, naturalized and non-naturalized species did not differ in their cold or warm stratification requirements. Similar responses to these cues likely reflect the weak temperature seasonality of these regions, indicating that winter-like cues are weak predictors of favourable windows of opportunity for establishment, while cues related to rainfall, including changes in seed permeability in species requiring scarification, play a greater role. Moreover, similar requirements for warm stratification confirm the importance of this trait in species from warm, seasonally dry regions (Baskin & Baskin, 2014), since it prevents germination during dry seasons. Examples of widely naturalized species in our dataset not requiring stratification for germination in this macroclimatic zone include *Plantago lanceolata* L., *Senecio vulgaris* L. and *Silene gallica* L.

Requirements for alternating temperatures also did not differ between naturalized and non-naturalized species, reflecting the importance of diurnal temperature fluctuations not only in temperate but also in tropical seasonal habitats (Wyse & Dickie, 2018). Species naturalized in the tropical dry zone were, in contrast, less dependent on light for germination, a preadaptation that may be advantageous under the strong moisture constraints typical of tropical dry systems, allowing seeds to germinate in shaded microsites such as beneath litter layers, grass tussocks or nurse plants, where evapotranspiration and exposure to consumers are reduced (Flores & Jurado, 2003).

A strong response to scarification in naturalized species reflects the benefits of physical dormancy in seasonal rainfall climates, including seed persistence in the soil during dry seasons and synchronized germination with the onset of the rain season (Jaganathan et al., 2016; Rosbakh et al., 2023). These adaptations buffer against the strong temporal variability in rainfall that is typical of tropical dry systems (Baskin & Baskin, 2014; Fenner & Thompson, 2005). Moreover, a requirement for scarification is frequently associated with disturbance or dispersal processes such as fire, soil abrasion or animal gut passage (Moreira & Pausas, 2012), which are frequent in these regions (Jurado & Westoby, 1992). Species requiring scarification that have naturalized in this zone include fabids such as *Lathyrus pratensis* L., *Lotus subbiflorus* Lag., *Medicago lupulina* L. and other *Medicago* species.

From a management perspective, two groups of species are at high risk of naturalization in tropical dry regions, that is, those germinating in the native range at cool temperatures with flexible requirements for cold and warm stratification, and those requiring scarification, which promotes the formation of persistent seed banks that can respond rapidly to disturbance events or rainfall pulses.

4.4 | Germination traits in the tropical humid zone

In tropical humid regions, where seasonality is weak, 14% of native European temperate herbs have become naturalized, again most frequently in the Poaceae, Asteraceae and Fabaceae. Naturalized species differed from non-naturalized ones in all traits except their response to light, showing lower requirements for cold stratification but stronger responses to warm stratification, which is frequent in species native to warm, humid regions (Baskin & Baskin, 2014). These findings suggest that species from warm temperate Europe are especially preadapted to become naturalized in this macroclimatic zone. Conversely, a requirement for cold stratification is not advantageous in this zone because of the absence of prolonged low temperatures, so that species relying on a period of chilling for the breaking of dormancy may fail to establish.

Naturalization was associated with lower requirements for alternating temperatures, suggesting that reduced dependence on diurnal temperature fluctuations for germination favours naturalization in warm, humid conditions, where soil temperatures are characterized by low diurnal amplitudes. Thus, species better adapted to more stable thermal conditions are more likely to establish than those with strict requirements for temperature fluctuations (Pearson et al., 2002).

A requirement for seed scarification was a key trait associated with naturalization also in this macroclimatic zone, where seeds without dormancy are prone to rapid germination upon dispersal and high pressure from herbivores or pathogens (Garwood, 1989). In this zone, physical dormancy may favour naturalization by mitigating the effects of the high biotic pressure typical of tropical systems (Baskin & Baskin, 2014), while promoting seed persistence in the soil until favourable or disturbed conditions create safe sites for establishment.

From a management perspective, high-risk species in this zone are those from warmer regions with strong responses to warm stratification and low dependence on cold stratification and diurnal temperature fluctuations, as well as species with seed scarification requirements. These trait combinations indicate a high potential for germination and establishment under the relatively constant, warm and humid conditions characteristic of tropical humid regions.

4.5 | Germination traits and naturalization extent

The number of regions of naturalization is a variable influenced not only by biological species traits and ecosystem properties but also by extrinsic factors such as international trade (Hulme, 2021; Humair et al., 2015), native range size (Guo et al., 2024), residence time (Pyšek et al., 2015), introduction history, propagule pressure (Colautti et al., 2006; Pyšek et al., 2015) and ornamental popularity (Chrobock et al., 2011; Lavoie et al., 2016). These extrinsic factors affect both the occurrence and the extent of naturalization, but their relative importance differs. Naturalization extent is typically more influenced by human activities, as species that are widely traded, repeatedly introduced, or cultivated for ornamental purposes tend to become established in multiple regions. In contrast, naturalization occurrence, especially for species restricted to a single region of naturalization, such as many species naturalized in the tropical zones, is more strongly dependent on species traits that either promote or constrain successful establishment. As species not yet reported as naturalized in a region may do so in the future, we made no a priori predictions. Despite these differences, naturalization extent and occurrence were generally related to the same germination traits and in the same direction, providing further evidence that preadaptations in these traits increase the probability of naturalization of native European herbs.

Yet, two exceptions emerged. In tropical dry regions, naturalization extent was strongly associated with warm stratification, likely reflecting the widespread ornamental use of species requiring this cue, such as *Campanula rapunculoides* L. and *Narcissus pseudonarcissus* L. In both tropical dry and humid regions, the relationship between naturalization extent and germination temperature was weaker than in temperate regions, probably because germination at lower temperatures is more critical in temperate climates and because naturalization was more frequent in temperate than tropical regions.

4.6 | Preadaptation in seed traits and naturalization

Our results show that seed germination is a critical stage mediating the naturalization of native European herbs, with macroclimatic conditions acting as filters that influence the probability of naturalization in non-native regions. Many species introduced intentionally, such as ornamental and forage species, possess beneficial germination traits in their native range, such as broad thermal germination niches, weak responses to cold stratification (e.g. *Centaurea stoebe* and *Achillea millefolium* L.), or strong responses to scarification (e.g. *Lathyrus* species and *Galega officinalis* L.), consistent with the pre-introduction selection hypothesis (Briski et al., 2018; Colautti & Lau, 2015). Our findings, however, indicate that even unintentionally introduced species benefit from preadaptations in germination traits acquired in the native range that facilitate naturalization, with these advantages varying among macroclimatic zones of introduction. These preadaptations are likely critical during the early stages of naturalization before post-introduction adaptive changes in seed traits can influence germination responses (Gioria et al., 2023; Hierro et al., 2020). Using germination data from the native range thus allowed us to identify key germination traits promoting naturalization independently of potential post-introduction evolutionary changes.

The success of certain germination traits in non-native ranges was driven primarily by responses to climate-related cues, as postulated by the 'climate matching' hypothesis (Gallagher et al., 2010), while light and alternating temperature showed little difference between naturalized and non-naturalized species, especially in temperate regions. This suggests that naturalized species tend to establish in similar habitats and microsite conditions as in their native range, while responses to stratification and scarification play a stronger role in determining naturalization in non-native ranges.

Although vegetative propagation may contribute to determining naturalization success in some species with both sexual and asexual modes of reproduction, available evidence indicates that post-introduction establishment in non-native ranges is primarily driven by regeneration from seed, while vegetative propagation plays a more significant role in population maintenance and range expansion (Gioria et al., 2023). That the same germination traits were related to both the occurrence and extent of naturalization provides strong support for the central role of germination traits in the naturalization process.

4.7 | Management implications

These findings have important management implications. We showed that combining germination data from the native range with information on the regions where a species has become naturalized represents a simple yet powerful framework for identifying herbaceous species with high naturalization potential and for informing risk assessment and management. Risk assessments and early detection programmes could benefit from integrating information on germination traits with naturalization data from different climatic zones, with particular attention to families that are disproportionately represented among naturalized species in this study as well as globally (Pyšek et al., 2017).

Relating germination traits to naturalization success in different macroclimatic zones also provides valuable insights into how projected climatic changes may alter naturalization processes by promoting or constraining regeneration from seed. Climate warming is expected to influence regeneration from seed differently among climatic zones (Baskin & Baskin, 2022; Gioria et al., 2022). In temperate regions, warmer winters could favour early germinating species with low stratification requirements or those capable of germinating at cooler temperatures, although the benefits of these traits will depend on the tolerance of seedlings to suboptimal conditions, including late frosts (Gioria et al., 2018, 2022). In seasonally dry climates, altered precipitation regimes could accelerate the release of physical dormancy, increasing mortality risks for some species but benefiting others with persistent seed banks (Gioria et al., 2022). Because species in arid or seasonally dry systems often rely on seed coats that respond to rainfall pulses, changes in the timing, intensity or predictability of precipitation could alter the balance between the risk of and opportunity for rapid establishment. In tropical humid regions, warming could strengthen the advantage of species requiring warm stratification for dormancy break, potentially broadening their thermal germination window (see Just et al., 2023). Overall, climate change is likely to promote or constrain naturalization by altering opportunities for regeneration from seed.

4.8 | Caveats and limitations

While our study provides robust evidence that seed germination traits contribute to the naturalization success of herbaceous species, some caveats should be acknowledged. Our study focused on herbaceous species native to Europe because the most reliable germination data were available for this group and region, and because germination traits in herbaceous plants differ substantially from those of shrubs and trees. Although this focus allowed rigorous testing of the role of germination traits in determining naturalization success, it also limited the generality of our conclusions. The use of primary germination records from standardized laboratory germination experiments made it possible to compare germination responses among many species under controlled conditions but may not fully capture responses under field conditions.

5 | CONCLUSIONS AND FUTURE DIRECTIONS

Future research should broaden the scope of germination studies to include a wider range of species, life forms and climatic zones. A key priority is to link germination responses to local conditions and clinal variation in both native and non-native ranges. This information is essential to improve predictions of the realized species distributions of native species in their native ranges and the potential range expansion in non-native regions. Progress in this field also requires germination experiments under broader and more realistic temperature and moisture regimes, including simulations of climatic extremes, to improve predictions of how global environmental changes may affect naturalization dynamics via regeneration from seed. Finally, integrating laboratory germination data with field experiments and soil seed bank studies will be essential for predicting naturalization trajectories and for detecting post-introduction adaptive changes in germination traits in non-native ranges.

AUTHOR CONTRIBUTIONS

Margherita Gioria, Petr Pyšek and Angelino Carta conceived the idea and designed the methodology. Angelino Carta, Eduardo Fernández-Pascual, Diana María Cruz Tejada, Sergey Rosbakh, Katalin Lukacs, Lorenzo Pinzani and Markus Wagner provided seed germination data. Wayne Dawson, Franz Essl, Holger Kreft, Jan Pergl, Mark van Kleunen, Patrick Weigelt and Petr Pyšek compiled the Global Naturalized Alien Flora database. Angelino Carta and Margherita Gioria performed the analyses of the data. Margherita Gioria wrote the manuscript with inputs from all authors.

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CONFLICT OF INTEREST STATEMENT

Sergey Rosbakh is an Associate Editor of the *Journal of Ecology* but took no part in the decision-making processes for this paper.

DATA AVAILABILITY STATEMENT

Germination data and information on the naturalization status of the species considered for this article, in each macroclimatic region of naturalization, are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.nk98sf86v (Gioria et al., 2025).

STATEMENT OF INCLUSION

Our study is based on a global synthesis of seed germination and naturalization data, combining secondary data with germination data personally collected by members of the authorship team. While the analysis did not involve new local data collection for this study, team members contributed both germination data, collected through standardized laboratory protocols and naturalization records, compiled from regional and local sources. The authors are based in different European countries that represent the core regions of interest in the study. We are committed to inclusive, collaborative and responsible research practices and to the transparent use of ecological data across regional and global contexts.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Number of species and germination records extracted from *SeedArc*, categorized by naturalization occurrence: non-naturalized temperate species, species naturalized in temperate regions, species naturalized in tropical dry regions and species naturalized in tropical humid regions.

Appendix S2. Models of naturalization occurrence. Results of binomial Bayesian generalized linear mixed models for the germination responses of naturalized and non-naturalized species to six environmental cues in temperate, tropical dry and tropical humid regions.

Appendix S3. Models of naturalization extent. Results of binomial Bayesian generalized linear mixed models for the germination responses to six environmental cues as a function of naturalization extent in temperate, tropical dry and tropical humid regions.

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