Fire as a regeneration filter: contrasting effects of heat and smoke on Arctic seed germination.

Running title: Fire and Arctic Seed Germination

Jerónimo Vázquez-Ramírez[1,2*] (0000-0001-6421-5594), Margherita Tognela[3*] (0009-0004-0836-3110), Natasha de Vere[4] (0000-0001-9593-6925), Barbara Gawlak[5] (0009-0007-8587-6982), Julia Kemppinen[6] (0000-0001-7521-7229), Daniel Kępski[5] (0000-0001-7903-2942), David Kniha[7] (0009-0004-9287-0181), Simone Iris Lang[8] (0000-0002-6812-2528), Petr Macek[9,10] (0000-0002-4792-9461), Maija-Susanna Sujala[11] (0009-0003-2101-7709), Otso Suominen[12] (0000-0002-7209-6078), Anne Tolvanen[13] (0000-0002-5304-7510), Brandon Samuel Whitley[4] (0000-0002-5954-282X) and Sergey Rosbakh[14, 1] (0000-0002-4599-6943).

[1]Department of Plant and Environmental Sciences, University of Copenhagen, Denmark.

[2] Department of Biology, University of Copenhagen, Denmark.

[3] Department of Earth and Environmental Sciences, University of Pavia, Italy.

[4] Natural History Museum of Denmark, University of Copenhagen, Denmark.

[5] Institute of Geophysics, Polish Academy of Sciences, Poland.

[6] Botany and Mycology Unit, University of Helsinki, Finland.

[7] Division of Environment and Natural Resources, Norwegian Institute of Bioeconomy Research, Norway.

[8] Department of Arctic Biology, The University Centre in Svalbard, Longyearbyen, Norway.

[9] Institute of Hydrobiology, Biology Centre of Czech Academy of Sciences, Czech Republic.

[10] Department of Biodiversity and Nature Tourism, Estonian University of Life Sciences, Estonia.

[11] Kilpisjärvi Biological Station, University of Helsinki, Finland.

[12] Kevo Research Station, Biodiversity Unit, University of Turku, Finland.

[13] Natural Resources Institute Finland, Finland.

[14] Institute of Earth System Sciences, Leibnitz University Hannover, Germany.

*These authors contributed equally to this work.
Correspondence: Jerónimo Vázquez-Ramírez (vasq@plen.ku.dk) | Margherita Tognela (margherita.tognela01@universitadipavia.it).

Abstract. The rapid warming of the Arctic is increasing the frequency, intensity, and spatial extent of fires. Because fire has historically been rare in this region, most Arctic plant species are unlikely to have evolved traits that confer tolerance to fire, and the consequences for early life-history stages such as seed germination remain largely unknown. Here, we experimentally tested the effects of two key fire-related cues, heat shock and smoke exposure, on the germination traits of 25 widespread Arctic plant species. Seeds collected across the Arctic were subjected to four treatments: (i) high-heat (110 °C for 4 min, simulating surface fire exposure); (ii) low-heat (50 °C for 10 min, simulating soil seed bank conditions); (iii) smoke water produced from Arctic plant biomass; and (iv) a combination of low-heat and smoke water. We analysed germination responses at three levels: overall, across functional groups (forbs, graminoids, and woody species), and at the species level. High-heat treatment almost completely inhibited germination, reducing the final percentage of germination from ~78% to ~2%, with only three species showing any germination, two of them graminoids. Low-heat treatment produced no overall or functional group changes in final germination but reduced germination speed and germination synchrony in 20% of the species. Smoke water did not alter the final germination percentage but accelerated overall germination speed by ~9–11%. Together, these results suggest that most Arctic species are not adapted to survive the temperatures experienced at or near the soil surface during fires; however, buried seeds may remain viable after low heating and be stimulated by smoke, creating an ecological filter that favours species with persistent soil seed banks. As Arctic fires become more frequent and intense, seed-based regeneration will likely play a growing role in shaping post-fire recovery and will influence the diversity and composition of plant communities.

Keywords. Arctic tundra, climate change, fire ecology, seed germination, smoke cues, heat shock, post-fire recruitment.

1. Introduction

Wildfires are emerging as a rapidly intensifying disturbance across the Arctic (Descals et al., 2022; Gosden et al., 2022). Historically rare and typically of small spatial extent (Masrur et al., 2018), Arctic fires are now increasing in frequency, intensity, severity, and spatial coverage (French et al., 2015; McCarty et al., 2021). This phenomenon is mainly driven by the region warming nearly four times faster than the global average (Rantanen et al., 2022) and by increasingly longer, drier, and more lightning-prone growing-seasons (He et al., 2022). When they occur, Arctic fires burn vegetation and organic soils disrupting carbon dynamics (Mack et al., 2011), accelerating permafrost thaw (Virkkala et al., 2025), and altering plant community structure, diversity, and composition (Heim et al., 2025).

In contrast to other high-latitude ecosystems, such as boreal forests, where fire is a natural and recurring ecological disturbance that shapes vegetation dynamics (Kasischke & Turetsky, 2006), fire has likely not been a recent ecological and evolutionary driver for most Arctic species due to its rarity in the region. Consequently, emerging fire regimes can produce disruptive and divergent ecological outcomes, with multiple post-fire vegetation trajectories and alternative states (see for instance, Chen et al., 2021; Gaglioti et al., 2021; Heim et al., 2025). While frequent Arctic fires can lead to graminoid-dominated communities (e.g., in Bret-Harte et al., 2013; Hollingsworth et al., 2021), they can also lead to shifts towards shrub-dominated landscapes (Chen et al., 2021; Jones et al., 2013; Landhausser & Wein, 1993; Liu et al., 2022; Racine et al., 2004). These contrasting trajectories highlight the complexity of the recovery of Arctic vegetation after a fire, which appears to be shaped by the fire regime (i.e. frequency, intensity, severity; Heim et al., 2025), vegetation type (e.g. low or high tundra; Gaglioti et al., 2021), and site-specific abiotic factors (e.g. soil properties and nutrients, near-surface permafrost, and soil moisture; Chen, Hu, et al., 2021).

Following a low intensity fire event, Arctic vascular plant vegetation can recover to near pre-fire levels within four to ten years (Heim et al., 2025). Much of this initial recovery is attributed to plants that resprout from surviving below-ground structures (Bret-Harte et al., 2013; Racine et al., 1987), particularly after low-severity fires that leave surface moss and peat intact, favouring vegetative regeneration over seedling establishment (Frost et al., 2020). However, deep-burning fires that consume the organic soil layer can create post-fire conditions where recruitment from seeds, either from the soil seed bank or via dispersal, is the primary source of vegetation recovery (Bret-Harte et al., 2013; Liu et al., 2022; Racine et al., 2004, 1987).

Despite evidence that seed-based regeneration contributes to post-fire vegetation recovery, Arctic seed responses to fire remain poorly understood. More quantitative evidence is needed to determine the extent to which Arctic seeds tolerate fire-generated temperatures; whether exposure to smoke-derived compounds (e.g. butenolides; Light et al., 2009) affects germination; or which species and functional groups may be fire-sensitive versus fire-tolerant. Insights from fire-prone ecosystems with related taxa (e.g. European heathlands with *Empetrum nigrum* L. and *Vaccinium* spp.; Bargmann et al., 2014; or boreal forests with *Luzula* and *Rumex* spp.; Granström & Schimmel, 1993) suggest that some Arctic species may respond to heat or smoke cues, but this remains unclear and calls for systematic, empirical evaluation. The absence of such data limits our ability to predict how emerging fire regimes will shape recruitment and vegetation dynamics in a warming Arctic.

Here, we address this knowledge gap by conducting a geographically, functionally, and taxonomically comprehensive experimental test of Arctic seed responses to fire-related cues. We simulated key aspects of Arctic fire to examine how two heat-shock levels, representing soil surface (110 °C for 4 min) and subsurface (50 °C for 10 min) temperatures, and smoke exposure, influence the germination traits of 25 widespread Arctic vascular plant species. These species represent a variety of functional groups (graminoids, forbs, and woody plants), allowing us to detect ecologically meaningful variation in responses. Based on the historically low fire frequency in the Arctic, we hypothesised that (H1) any heat shock will reduce overall germination, (H2) smoke exposure will not significantly affect germination, but (H3) species will differ in the magnitude and direction of their responses, potentially reflecting phylogenetic or functional trait patterns.

2. Materials and Methods

2.1. Study species and seed collection

We selected 25 widespread Arctic plant species (Table 1) representing three functional groups: forbs (12), graminoids (4), and woody species (9, including trees, tall shrubs, and dwarf shrubs). Seeds were collected during their natural dispersal period (July–September 2023 and 2024) from >20 individuals within a single population per species across multiple Arctic sites (Figure S1). After collection, seeds were air-dried at room temperature and transported in paper bags under ambient conditions to the laboratory in Copenhagen, Denmark. On arrival, seeds were cleaned and stored at 5 °C, 35 ± 4% (mean ± SD) relative humidity, and dark conditions until the germination experiment commenced in November 2024. Viability tests conducted prior to the experiment confirmed that seeds were not physiologically dormant; therefore, no conventional wet-cold stratification was applied.

Table 1. Family, functional group, and seed collection site for all species included in this study. Additional details on habitat, collection date, collectors, and collection geographical coordinates are provided in Table S1. Species names follow the International Plant Names Index (IPNI, 2026).

Family	Species	Functional group	Collection site
Asteraceae	*Taraxacum bracteatum* Dahlst.	Forb	Odindalen, Svalbard
Betulaceae	*Betula nana* L.	Woody plant	Kilpisjärvi Biological Station, Finland
	Betula pubescens Ehrh.	Woody plant	Kilpisjärvi Biological Station, Finland
Brassicaceae	*Arabis alpina* L.	Forb	Låktatjåkko Mountain, Abisko, Sweden

	Cochlearia groenlandica L.	Forb	Odindalen, Svalbard
Caryophyllaceae	*Cerastium alpinum* L.	Forb	Polish Polar Station Hornsund, Svalbard
	Silene acaulis (L.) Jacq.	Woody plant	Endalen, Svalbard
	Silene involucrata (Cham. & Schltdl.) Bocquet	Forb	Odindalen, Svalbard
Cyperaceae	*Eriophorum scheuchzeri* Hoppe	Graminoid	Adventdalen, Svalbard
Ericaceae	*Cassiope tetragona* (L.) D.Don	Woody plant	Nuolja Mountain, Abisko, Sweden
	Kalmia procumbens (L.) Gift, Kron & P.F.Stevens ex Galasso, Banfi & F.Conti	Woody plant	Kevo Research Station, Finland
	Phyllodoce caerulea (L.) Bab.	Woody plant	Kilpisjärvi Biological Station, Finland
Fabaceae	*Hedysarum alpinum* L.	Forb	Churchill Rocket Research Range, Canada
Juncaceae	*Luzula confusa* Lindeb.	Graminoid	Polish Polar Station Hornsund, Svalbard
Onagraceae	*Epilobium angustifolium* L.	Forb	Svanvik, Norway
	Epilobium anagallidifolium Lam.	Forb	Låktatjåkko Mountain, Abisko, Sweden
Plantaginaceae	*Veronica alpina* L.	Forb	Latnjajaure, Sweden
Poaceae	*Anthoxanthum odoratum* L.	Graminoid	Nuolja Mountain, Abisko, Sweden
	Phleum alpinum L.	Graminoid	Låktatjåkko, Abisko, Sweden
Polygonaceae	*Bistorta vivipara* (L.) Delarbre	Forb	Qeqertarsuaq, Greenland
	Oxyria digyna (L.) Hill	Forb	Odindalen, Svalbard
Rosaceae	*Dryas integrifolia* Vahl	Woody plant	Churchill Rocket Research Range, Canada
Saxifragaceae	*Micranthes nivalis* (L.) Small	Forb	Polish Polar Station Hornsund, Svalbard
	Saxifraga cernua L.	Forb	Polish Polar Station Hornsund, Svalbard
	Saxifraga cespitosa L.	Forb	Odindalen, Svalbard

2.2. Fire-related treatments

Seeds were subjected to four treatments that simulated Arctic fire and post-fire conditions: (i) high-heat (110 °C for 4 min), (ii) low-heat (50 °C for 10 min), (iii) smoke water, and (iv) a combination of low-heat and smoke. Three replicates of 10–20 seeds (depending on availability) were used per treatment, with untreated seeds serving as controls (22 °C).

The two heat treatments were based on temperature data from an experimental Arctic fire conducted in Greenland (Hermesdorf et al., 2022). The high-heat treatment reflects conditions at the soil surface, or for seeds still attached to standing vegetation, whereas the low-heat treatment represents temperatures experienced in the soil seed bank (~2 cm deep). Treatments were applied in a pre-heated electric oven (Binder GmbH, Germany), with four to five species processed simultaneously. Seeds were placed in preheated glass Petri dishes arranged randomly in the centre of the oven to minimise edge effects. Internal dish temperatures were monitored using a digital thermometer (Huato Electric Co., S220-T8, China). After heating, seeds were transferred to unheated Petri dishes and allowed to cool to room temperature prior to further processing.

For the smoke exposure treatment, seeds were immersed in an aqueous smoke solution, an effective and convenient substitute for airborne smoke (see Brown, 1993; Dixon et al., 1995). The solution was prepared using biomass from Arctic shrub and herbaceous plants collected in Abisko, Sweden, in August 2024. Three replicates of 20 g of plant material were heated separately in aluminium containers in an oven at 200 ± 1 °C for 30 minutes, following Jäger et al. (1996). After heating, 200 ml of distilled water was added to each replicate and left to steep for 10 minutes. The resulting extracts were filtered and combined to produce a single smoke solution. Seeds were imbibed in this solution for 24 h at room temperature (~22 °C). Control seeds were treated with distilled water for the same duration.

The combined low-heat and smoke treatment involved first applying the low-heat treatment, followed by a 24 h imbibition in smoke water. Preliminary trials showed that the high-heat treatment was lethal to most species; therefore, its interaction with smoke water was not investigated further.

2.3. Germination trials

After fire-related treatments, seeds were placed on a double layer of filter paper soaked in demineralised water in 60 mm Petri dishes. The dishes were incubated in a climate chamber (Buch & Holen, Panasonic, Japan) under conditions previously identified as optimal for germination of Arctic species (25/15 °C and a 12/12 h light/dark photoperiod). Dishes were not tightly sealed, and demineralised water was added as required to maintain consistent moisture levels throughout the experiment. The trial lasted four weeks. Germination (radicle emergence ≥ 2 mm) was scored three times per week for the first three weeks, and twice during the final week. After each count, germinated seeds were removed to prevent potential allelopathic effects. At the end of the experiment, all non-germinated seeds were cut to assess embryo presence or emptiness, and the initial number of viable seeds was adjusted accordingly.

2.4. Data Analysis

All analyses were conducted using R software version 4.4.3 (R Core Team, 2025). Germination counts were used to calculate three indices: (i) final germination percentage (FGP); (ii) germination speed (GSP), expressed as the germination speed coefficient, which reflects the rate of germination over time, with higher values indicating faster germination; and (iii) germination synchrony (SYN), which measures the temporal clustering of germination events and ranges from 0 (completely asynchronous) to 1 (fully synchronised). All indices were calculated using the "GerminaR" package version 2.1.4 (Lozano-Isla et al., 2019). These indices were then used to assess treatment effects at three levels: overall (all species pooled), functional groups (graminoids, forbs, and woody species), and species level. Functional-group classification was based on growth form and life-history characteristics (Table 1).

2.4.1 High-heat

Most species failed to germinate following the high-heat exposure treatment, so only final germination percentage was analysed. Germination speed and synchrony were not calculated, as these indices require germination values greater than zero.

To quantify the overall effect of the high-heat treatment, we modelled final germination counts (germinated vs. non-germinated seeds per dish) using a binomial mixed-effects model fitted with the "glmmTMB" package (Brooks et al., 2017). Treatment (control vs. high-heat) was included as a fixed effect, and we included random intercepts for species and for replicates nested within species (1|Species/replicate) to account for dish-level and interspecific variation. Fixed-effect estimates were evaluated with Wald z-tests and back-transformed to obtain germination probabilities.

To test whether functional groups differed in their sensitivity to high-temperature exposure, we extended the model by adding functional group and its interaction with treatment as fixed effects. The significance of the interaction was evaluated using likelihood-ratio (LRT) tests. Functional group level estimated marginal means and pairwise treatment contrasts were obtained on the response scale using the "emmeans" package (Lenth, 2023).

To estimate species-specific responses for the three species that germinated under high-heat treatment, we fitted separate binomial mixed-effects models at the seed level. Because only three Petri dishes per species and treatment were available, each seed was treated as an independent observation rather than modelling dish-level counts. Seed counts within each dish were expanded into one row per seed with a binary outcome of "germinated" (1) or "not germinated" (0), and a random intercept for Petri dish ID was included to account for within-dish non-independence. The resulting model (germinated ~ treatment × Species + (1 | Petri Dish ID), family = binomial) increased statistical power while appropriately modelling dish-level clustering.

All high-heat models used a logit link and Laplace approximation for estimation. Model fit was assessed using simulation-based diagnostics (i.e., dispersion, zero-inflation, KS tests, and Q–Q plots) with the "DHARMa" package (Hartig, 2024). No violations of assumptions were detected.

2.4.2 Low-heat and smoke

To quantify the effects of low-heat, smoke, and their combination on final germination percentage, we fitted binomial mixed-effects models using the same fixed and random effects structure described above (i.e. treatment as a fixed effect; species and dish nested within species as random effects). Functional-group differences were evaluated by adding functional group and its interaction with treatment as fixed effects, while species-specific responses were assessed using a model that included treatment and species as fixed factors. Estimated marginal means and treatment contrasts were used to summarise both functional-group and species-specific responses.

Germination speed was analysed using a linear mixed-effects model fitted to log-transformed values with the "lme4" package (Bates et al., 2015). Treatment was included as a fixed effect, and random intercepts for species and for replicates nested within species accounted for interspecific and dish-level variation. Residual diagnostics confirmed that assumptions of normality and homoscedasticity were met. Estimated marginal means were back-transformed to the original scale, and Tukey-adjusted pairwise comparisons were used to test for treatment differences relative to the control. Functional-group- and species-specific patterns were examined using models that included the relevant interaction terms (functional group × treatment or species × treatment) as described above.

Germination synchrony values are bounded between 0 and 1 and can include zeros, so we used a Tweedie mixed-effects model with a log link in the "glmmTMB" package (Brooks et al., 2017) to analyse the data. For the overall model, treatment was included as a fixed effect, and replicates nested within species were included as random intercepts. Estimated marginal means (on the response scale) were back-transformed to the original 0–1 scale, and Tukey-adjusted pairwise contrasts were used to compare synchrony among treatments. As above, functional-group- and species-specific responses were obtained from models that included the relevant interaction terms.

All models were checked using simulation-based diagnostics, and no violations of model assumptions were detected.

3. Results

3.1. High-heat

3.1.1. Final germination percentage

Exposure to high-heat caused a pronounced reduction in final germination percentage, dropping from 78.4% under control conditions to just 2.1% ($p < 0.001$; Fig. 1a). This represents extreme sensitivity to high temperatures across species (logit estimate = –5.14 ± 0.27, $z = -19.3$).

Functional groups differed in their responses (treatment × group interaction: LRT = 80.3, $p < 0.001$; Fig. 1b). Forbs exhibited near-complete germination failure, with only 1 of 14 species germinating (odds ratio = 0.001, $p < 0.001$). Graminoids were less affected, with 2 of 4 species showing any germination (odds ratio = 0.12, $p < 0.001$). Woody species did not germinate under high-heat exposure; although model contrasts could not be estimated due to complete separation, raw germination percentages confirm zero germination.

Only three species germinated following high-heat exposure, and their responses were contrasting (Table S2, Fig. S2). *Epilobium angustifolium* L. declined from 94.7% to 26.9% (odds ratio = 0.02, $p < 0.001$); *Phleum alpinum* L. showed no detectable change (92.9% vs. 89.3%; odds ratio = 0.64, $p = 0.58$); and *Anthoxanthum odoratum* L. exhibited a small, non-significant increase (29.8% vs. 39.3%; odds ratio = 1.52, $p = 0.38$).

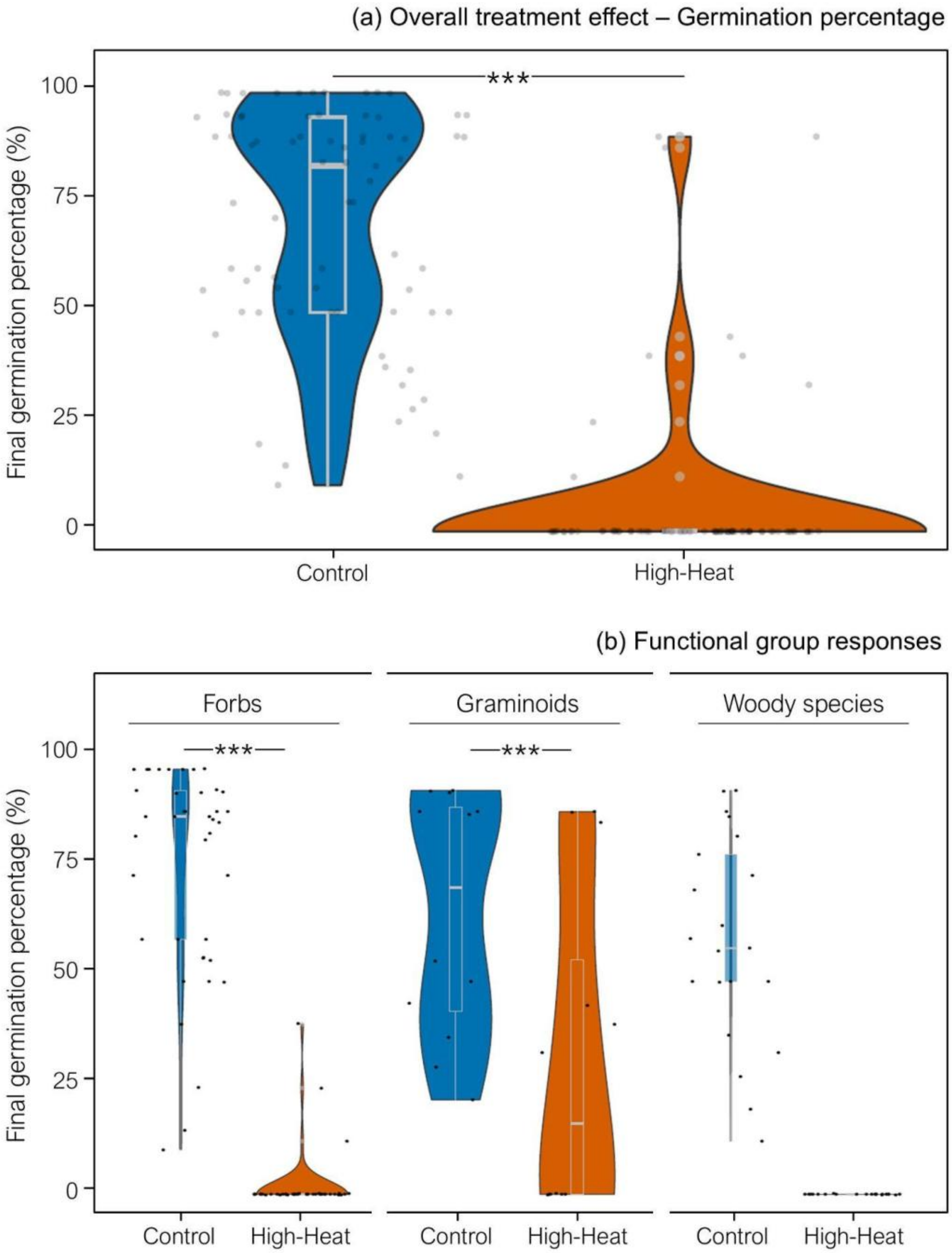

Figure 1. Effects of high-heat treatment on the final germination percentage across 25 Arctic vascular plant species. (a) Overall reduction in germination following high-heat exposure. (b) Responses by functional group. In this and subsequent figures, violin plots depict the distribution

(kernel density) of dish-level germination values; embedded box-and-whisker plots show the median and interquartile range; points represent individual Petri dishes. *** = $p < 0.001$.

3.2. Low-heat and smoke

3.2.1. Final germination percentage

Low-heat, smoke, and their combination did not significantly affect overall germination proportions (Fig. 2a). Germination remained high under all treatments (76–80%), and none differed from the control: low-heat (model estimate = –0.08 ± 0.10, $p = 0.43$; 76 % predicted germination), smoke (+0.13 ± 0.10, $p = 0.20$; 80 %), or smoke × low-heat (+0.10 ± 0.10, $p = 0.34$; 79 %). Pairwise contrasts confirmed the absence of treatment effects (all $p > 0.40$).

Functional groups showed similarly consistent responses, with no evidence of a treatment × group interaction (LRT = 5.07, df = 6, $p = 0.53$). Forbs maintained high germination (82.9–85.1%), graminoids ranged from 73.7–80.4%, and woody species from 59.2–67.8% (Fig. 2b).

At the species level, only one of the 75 contrasts tested (i.e. three treatments vs. control per species) was statistically significant: *Hedysarum alpinum* L. showed higher germination under the smoke × low-heat treatment than under the control (odds ratio = 3.18, 95% CI: 1.14–8.87, $p = 0.022$). No other species displayed evidence of treatment-related changes in final germination (Table S3, Fig. S3).

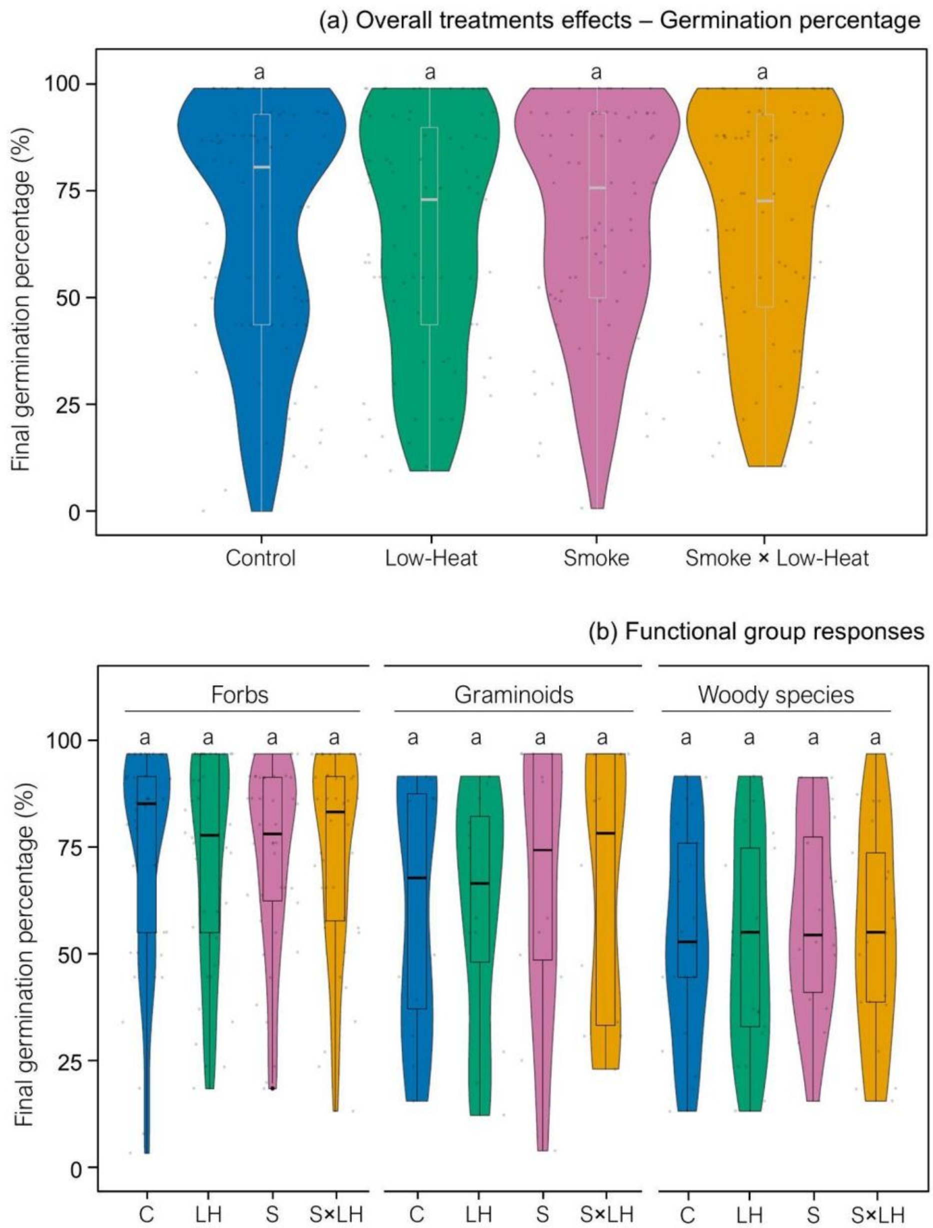

Figure 2. Effects of low-heat and smoke treatments on germination across 25 Arctic vascular plant species. (a) Final germination percentage under low-heat (LH), smoke (S), and combined smoke × low-heat (S×LH) treatments. (b) Functional group responses showing broadly similar patterns across forbs, graminoids, and woody species. Different letters indicate statistically significant differences among treatment groups.

3.2.2. Germination speed

Smoke treatments modestly but consistently accelerated germination, whereas low-heat alone had no effect (Fig. 3a). Back-transformed estimates were similar in the control and low-heat treatments (12.6 vs. 12.0; $p = 0.18$), but higher under smoke (13.8; $p = 0.004$) and smoke × low-heat (14.0; $p < 0.001$).

Different functional groups responded similarly to the treatments (treatment × group interaction: $F = 1.16$, $p = 0.33$; Fig. 3b). Across all groups, low-heat did not influence germination speed, whereas smoke and smoke × low-heat generally increased it. Forbs ($\Delta\log(GSP) = 0.10$, $p = 0.015$) and woody species ($\Delta\log(GSP) = 0.14$, $p = 0.024$) exhibited the strongest acceleration under smoke × low-heat, while graminoids showed only weak, non-significant trends in the same direction. Back-transformed means indicated modest increases in germination speed under smoke treatments across all groups.

Responses of germination speed to the treatments (Low-heat, Smoke, and their combination) varied across species (Fig. S4) and did not cluster by functional group. Ten of the 25 species showed at least one significant contrast (17 of 75 contrasts, $p < 0.05$). Low-heat slowed germination in five taxa: *Arabis alpina* L., *Dryas integrifolia* Vahl, *Micranthes nivalis* (L.) Small, *Phleum alpinum* L. and *Saxifraga cespitosa* L. ($\Delta\log(GSP) \approx -0.12$ to -0.29, i.e. GSP ≈ 10–25 % slower; Table S3). By contrast, smoke, either on its own or combined with low-heat, commonly accelerated germination in seven species, including *Betula nana* L., *Eriophorum* *scheuchzeri* Hoppe, *Luzula confusa* Lindeb., *Silene involucrata* (Cham. & Schltdl.) Bocquet and *Taraxacum bracteatum* Dahlst. (Δlog(GSP) ≈ 0.18–0.70, i.e. GSP ≈ 20–100% faster; Table S3).

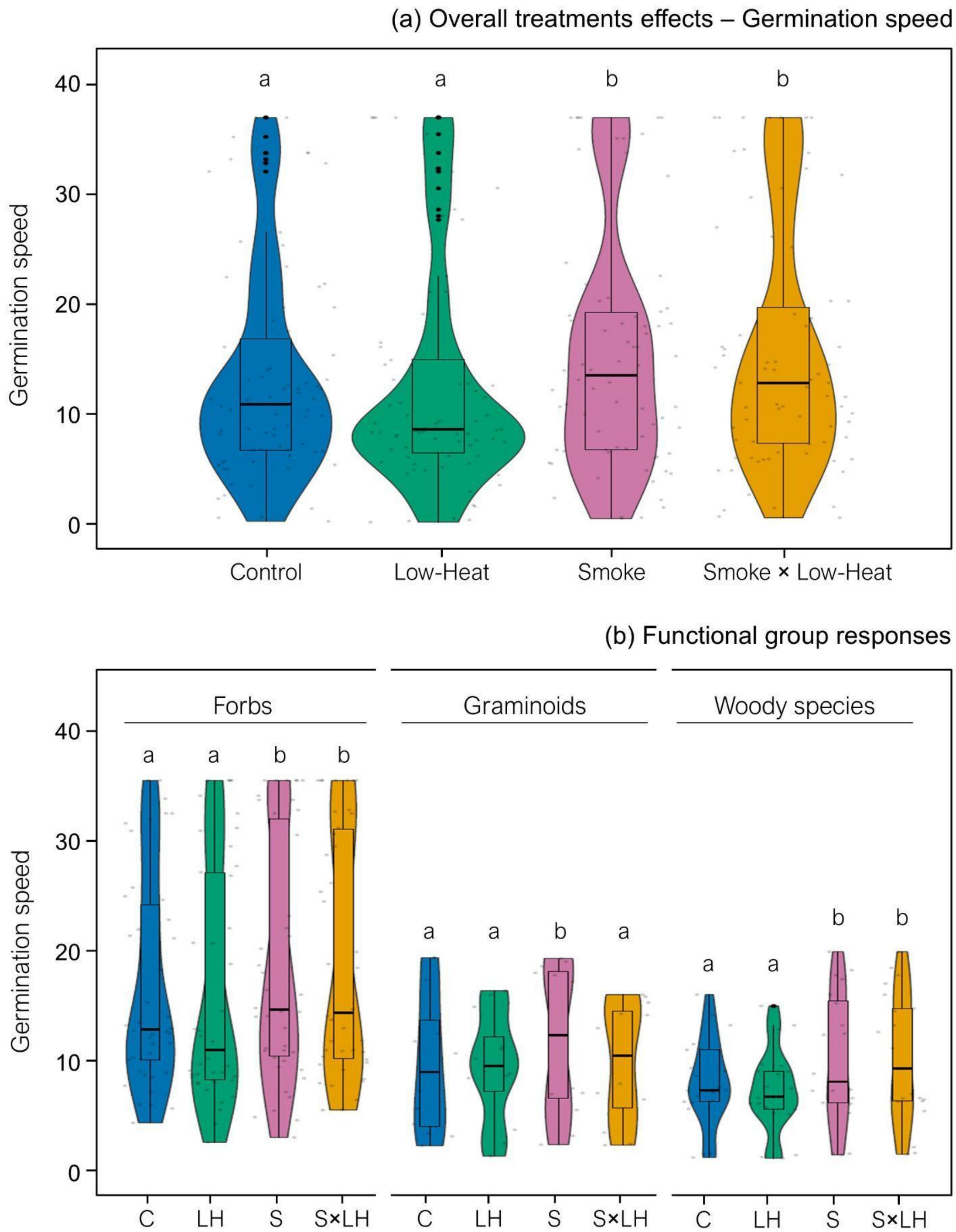

Figure 3. Effects of treatments on germination speed across 25 Arctic vascular plant species. (a) Overall germination speed under low-heat (LH), smoke (S), and combined smoke × low-heat (S × LH). (b) Functional group responses showing similar patterns across forbs, graminoids, and woody species. Values are back-transformed means (±95% CI) from linear mixed models. Different letters indicate statistically significant differences among treatment groups.

3.2.3. Germination synchrony

Overall germination synchrony was not affected by any of the experimental treatments (Low-heat, Smoke, and their combination). Mixed-effects models detected no effect of low-heat, smoke, or their combination (all $p > 0.32$). Estimated synchrony values were similar across treatments, ranging from 0.40 in the control to 0.43 under smoke. Pairwise comparisons and Dunnett tests confirmed that none of the treatments differed significantly from the control (all $p > 0.61$; Fig. 4a).

Functional groups showed the same pattern. The treatment × functional group interaction was non-significant (LRT: $F_{6,215.63} = 1.28$, $p = 0.27$; Figure 4b), indicating that synchrony responses did not differ among forbs, graminoids, and woody species. Dunnett-adjusted contrasts also showed no significant deviations from the control in any group (all $p > 0.26$).

By contrast, species-level responses were more variable. Nine of the 25 species showed at least one significant difference from the control (Fig. S4; Table S3). Synchrony increased under smoke exposure in seven species (*Bistorta vivipara* (L.) Delarbre, *Epilobium angustifolium* L., *Eriophorum scheuchzeri* Hoppe, *Luzula confusa* Lindeb., *Saxifraga cespitosa* L., *Silene involucrata* Cham. & Schltdl. Bocquet, *Taraxacum bracteatum* Dahlst) and decreased in response to low-heat in two species (*Arabis alpina* L., *Phleum alpinum* L.). These species-specific effects indicate that low heating and smoke can alter germination synchrony in some taxa even when community-wide averages remain unchanged.

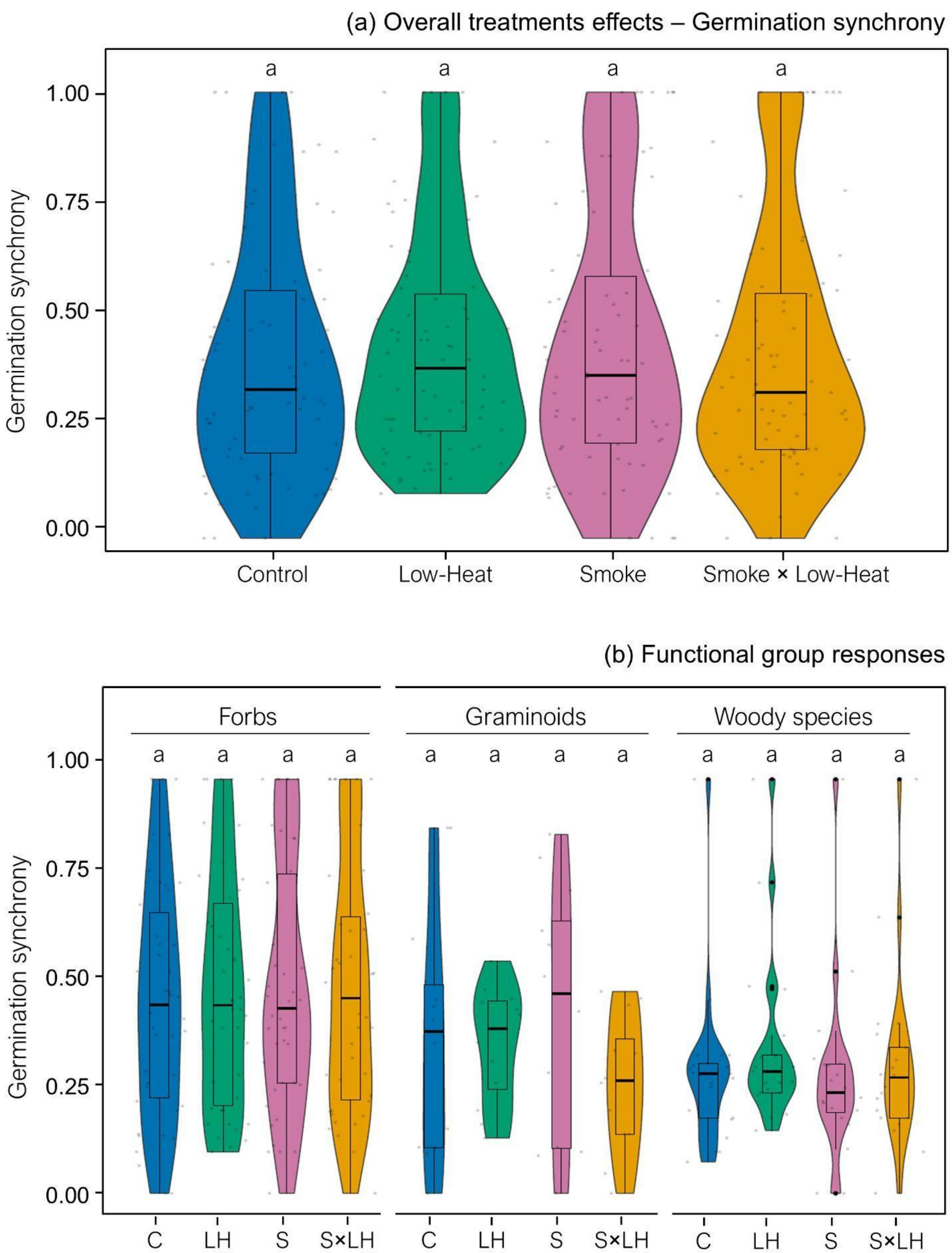

Figure 4. Effects of experimental treatments on germination synchrony across 25 Arctic vascular plant species. (a) Germination synchrony under low-heat, smoke, and combined smoke × low-heat treatments. (b) Estimated marginal means (±95% CI) for forbs, graminoids, and woody species.

4. Discussion

This study provides a geographically, functionally, and taxonomically comprehensive experimental assessment of how seeds of Arctic species respond to fire-related cues. High-heat exposure caused near-complete germination failure across species, whereas low-heat exposure had little effect on overall germination but did alter germination speed and synchrony in some taxa. Smoke water exposure accelerated overall germination, but without affecting final germination proportion. Together, these results suggest that seeds of the studied Arctic species exhibit limited fire-adaptive traits: they are highly sensitive to high temperatures and show no increase in germination in response to low heat or smoke cues.

4.1. Fire-heat acts as a strong ecological filter on Arctic seeds

Our results show that fire-induced temperatures at or near the soil surface, reflected by our high-heat treatment, are lethal for almost all studied species. This lack of physical or physiological tolerance is not surprising from an ecological and evolutionary perspective, because fire has played only a minor role in the recent history of Arctic ecosystems (Descals et al., 2022; Gosden et al., 2022; Masrur et al., 2018) and has therefore not acted as a selective force shaping seed traits. In contrast, in fire-adapted regions such as temperate ecosystems of Australia (Hodges et al., 2021; Tangney et al., 2025) or tropical grasslands in Brazil (Paredes et al., 2018; Ramos et al., 2019), heat levels comparable to our high-heat treatment (~110 °C) are generally not lethal to seeds.

Graminoids were less negatively affected than forbs or woody species, a pattern that aligns with graminoid-dominated post-fire trajectories in the Arctic (Heim et al., 2025) and suggests that their seed-level heat tolerance may complement their well-known capacity for resprouting (Bret-Harte et al., 2013; Hollingsworth et al., 2021). Nevertheless, this interpretation requires caution, as it is based on a limited number of graminoid species (n=4), and expanded sampling across taxonomic, intraspecific, and regional diversity is needed to assess whether this pattern is consistent.

Only three species germinated following high-heat exposure. *Epilobium angustifolium* L.and *Phleum alpinum* L. are well-known pioneers of fire-affected boreal and tundra sites (Bret-Harte et al., 2013; C. Racine et al., 2004; C. H. Racine et al., 1987), while *Anthoxanthum odoratum* L. is a dominant invasive in post-fire alpine grasslands in Australia (Verrall & Pickering, 2019). Their tolerance may reflect phylogenetic heritage rather than local adaptation, as they belong to lineages with fire-responsive traits (e.g. Poales; Lamont et al., 2019). However, this explanation is not consistent across all taxa, as some study species that are members of typically fire-adapted families, such as Ericaceae or Fabaceae (Lamont et al., 2019) failed to germinate, despite the fact that close relatives have shown fire-related responses in European heathlands (Bargmann et al., 2014) and boreal forests (Granström & Schimmel, 1993).

In contrast to high-heat, the low-heat treatment, representing subsurface temperatures during a fire, was non-lethal for the study species and produced only modest, species-specific shifts in germination speed or synchrony. These results align with findings from both fire-adapted ecosystems (e.g. boreal forest: Granström & Schimmel, 1993; temperate grasslands in Australia: Hodges et al., 2021; Mediterranean shrublands in South Africa: Hall et al., 2017) and non-fire-adapted ecosystems (e.g. tropical wetlands: Soares et al., 2021), where moderate heating (~60 °C) is generally not lethal to seeds. However, unlike such fire-prone floras, where comparable temperatures often stimulate germination by breaking physical dormancy, we detected no increase in germination proportion. Instead, some species germinated more slowly or less synchronously, suggesting an absence of heat-responsive dormancy mechanisms, which reinforces the hypothesis that fire has not shaped the germination traits of Arctic plants.

From an ecological perspective, Arctic fires are likely to kill surface seeds, whereas those buried in the soil may survive. Fire may therefore act as a strong ecological filter, favouring species with traits that enhance seed burial and promote the formation of permanent soil seed banks (e.g. small and spherical seeds; see Wang et al., 2024), while disadvantaging species with transient or aerial seed banks. This filtering effect is likely to be amplified by the interaction between site moisture, soil fertility and the depth of the organic layer throughout the Arctic. Dry tundra sites, for example, typically have thinner organic soil layers that can burn more intensely and uniformly, thereby increasing the probability of seed bank mortality. Seed dispersal phenology will also shape vulnerability to fire, with late-dispersing species (i.e. those releasing seeds in autumn or winter) at greater risk because fires are projected to occur more frequently in late summer and autumn (French et al., 2015).

4.2. Smoke cues may facilitate post-fire recruitment

The accelerated germination observed after exposure to smoke-water for many of the species shows that Arctic vascular plants can respond to smoke-derived chemical cues despite the historical rarity of fire in the region. The lack of change in final germination percentage, a common effect of smoke in fire-prone environments such as European heathlands (Bargmann et al., 2014) or Australian grasslands (Hodges et al., 2021), suggests that smoke compounds (e.g. butenolide) may have stimulated metabolic activity or relaxed residual physiological constraints on germination, rather than breaking fire-related dormancy (Light et al., 2004, 2009; Staden et al., 2000). This indicates a non-evolutionary response to smoke, similar to effects reported for species in other low-fire frequency environments, such as arid zones (Merritt et al., 2006), alpine herbfields (Vázquez-Ramírez & Venn, 2023) or wet rainforest (Ferraz et al., 2013).

From an ecological perspective, faster germination following smoke exposure could enhance post-fire recruitment by allowing seedlings to establish earlier before they are outcompeted by resprouting plants. Such rapid establishment may be particularly advantageous where fire has removed moss and litter layers, exposing mineral soil, increasing soil temperature, and temporarily enhancing nutrient availability (Racine et al., 2004, 1987). Faster germination would give seedlings a competitive advantage, as it would enable them to accumulate sufficient biomass before winter begins, thereby increasing their chances of survival (Milbau et al., 2009). However, the ecological benefit of accelerated germination ultimately depends on the availability of viable seeds after the fire (i.e. whether enough seeds survived the fire heat shock) and the presence of suitable microsites for establishment (Graae et al., 2011).

In this context, while the overall pattern indicates that smoke generally accelerates germination across taxa and functional groups, some modest species-level differences were found (see e.g., table S3 and Figure S4). Smoke-related cues produced the strongest phenological shifts in a subset of early-successional forbs and sedges (e.g. *Eriophorum scheuchzeri* Hoppe, *Silene involucrata* Cham. & Schltdl., Bocquet and *Taraxacum bracteatum* Dahlst.) whereas species that typically occur on dry, wind-exposed ridges and fellfields (e.g. *Micranthes nivalis* L. Small, *Saxifraga cespitosa* L. and *Cerastium alpinum* L.) showed little or no response. These differences may influence which species are able to capitalize on the brief post-fire recruitment window, contributing to shifts in post-fire vegetation composition.

From a management perspective, the stimulatory effect of smoke water on germination speed (and synchrony in some species) could be used to pre-treat seeds prior to seed-based restoration activities in the Arctic, thereby potentially enhancing the success of these efforts.

4.3. Study limitations and future directions

Our results provide geographically and taxonomically comprehensive insights into the potential impact of fire on Arctic seed-based regeneration and, thus, our findings can be generalised to similar ecosystems and taxa. Yet, it is always important to consider limitations, and we note that the following aspects could be further extended in future study designs. First, our study focused on 25 widespread species, and we sampled only one population per species, and we did not account for potential effects of fire history. Seed stress tolerance can vary among populations, and seeds from previously fire-affected sites may differ in their sensitivity to heat (Zaki et al., 2021) and smoke (Manela et al., 2019). To better understand how fire influences Arctic seeds, future studies should broaden the taxonomic scope to rare species and include multiple populations along a fire-history gradient, thereby enabling tests of potential local adaptation or transgenerational plasticity in seed responses to heat and smoke.

Second, we used a single concentration of smoke-water. Seed responses to smoke vary depending on the concentration and exposure time, and can shift from stimulatory to inhibitory (see Light et al., 2004; Merritt et al., 2006). Future studies should therefore test a broader range of concentrations and exposure durations. Furthermore, our smoke solution was produced from a mixture of Arctic plant biomass, and because smoke chemistry differs depending on the type of fuel, smoke generated from different types of vegetation (e.g. graminoid-dominated or shrub-dominated tundra) may result in different germination responses (Jäger et al., 1996). Future studies should aim to produce smoke from single-species fuels or community-specific fuel to test how biomass composition influences smoke chemistry and seed responses.

Finally, to our knowledge, there is no published information on the temperatures reached during Arctic fires (although we did not conduct a systematic literature review), representing an important knowledge gap that must be addressed to better understand how seeds respond to fire-related heat. Although our heat treatments were based on *in situ* measurements from an Arctic experimental burn (Hermesdorf et al., 2022), the large temperature variation between the low- and high-heat treatments prevented us from determining lethal temperature thresholds for our study species. Future work should therefore record temperature profiles during real fire events to inform experimental designs more effectively and also expose seeds to continuous temperature and heating duration gradients to determine their lethal thresholds (see the pyro-niche framework proposed by Tangney et al., 2025). Such experiments would also allow comparisons with other high-latitude systems, such as boreal forests, where fire is an important ecological driver.

5. Conclusion

We provide a geographically and taxonomically comprehensive experiment on the fire tolerance of Arctic seeds. We found that 88% of species were unable to withstand high temperatures, and neither moderate heat nor smoke-related cues increased overall germination proportion. Our findings suggest that fire-related heat exposure acts as an ecological filter in the Arctic: high surface temperatures kill seeds, while elevated subsurface temperatures have no effect on seed viability and germination. Thus, species with permanent soil seed banks may be better adapted to cope with future fire regimes. Smoke accelerated overall germination, suggesting that surviving seeds may be able to take advantage of short recruitment windows following fire. As fire frequency, intensity, severity, and extent increase due to rapid Arctic warming, seed-based regeneration is likely to play an important role in vegetation dynamics. Understanding how these processes scale across landscapes and interact with changing fire regimes is essential for predicting the resilience of Arctic ecosystems and for informing seed-based restoration in a rapidly transforming Arctic.

Author contributions.

Jerónimo Vázquez-Ramírez: visualization, writing – original draft, writing – review & editing. **Margherita Tognela:** investigation, methodology, writing – review & editing. **Natasha de Vere, Barbara Gawlak, Julia Kemppinen, Daniel Kępski, David Kniha, Simone Iris Lang,**

Petr Macek, Maija Sujala, Otso Suominen, Anne Tolvanen, and Brandon Samuel Whitley: resources (seed collection); writing – review & editing. **Sergey Rosbakh:** conceptualization, formal analysis, visualization, writing – review & editing. **Jeronimo Vazquez-Ramirez** and **Margherita Tognela** contributed equally to this work.

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Conflicts of interest.

The authors declare no conflicts of interest.

Data availability statement.

Data and analyses, diagnostics, and figure generation were scripted to ensure reproducibility, and full code is archived and available at https://doi.org/10.5281/zenodo.18302947

Supporting information.

Additional supplementary material accompanies this manuscript and includes: **Table S1.** Taxonomic identity, functional group, habitat, and collection metadata of the studied species. **Table S2.** Pairwise contrasts comparing the effects of low-heat, smoke, and combined low-heat + smoke treatments against the control on final germination percentage. **Table S3.** Pairwise contrasts comparing the effects of low-heat, smoke, and combined low-heat + smoke treatments against the control on final germination speed. **Table S4.** Pairwise contrasts comparing the effects of low-heat, smoke, and combined low-heat + smoke treatments against the control on final germination synchrony. **Figure S1.** Seed collection sites for all species included in the study. **Figure S2.** Final germination percentage for each species under control and high-temperature treatments. **Figure S3.** Species-specific effects of low-heat, smoke, and their combination on final germination percentage. **Figure S4.** Species-specific effects of low-heat, smoke, and their combination on germination speed. **Figure S5.** Species-specific effects of low-heat, smoke, and their combination on germination synchrony.

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