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Seed Bank and Ashfalls: The Ecological Resetting Effect of the Recent Tajogaite Volcano Eruption in the Canary Pine Forest (La Palma, Spain)

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ABSTRACT

Question: Tephra deposition is one of the most critical sudden alterations caused by volcanic eruptions in ecosystems. Tephra accumulation on the ground decreases with distance from the crater. The effect of ash deposition on the seed bank and its subsequent germination success has previously been studied by removing the tephra from the soil. However, conducting controlled experiments on the effect of tephra thickness on the seed bank and its seedling emergence capacity is a new approach to tackle and quantify recruitment mechanisms. Here, we present the first experimental study of the impact of tephra layer thickness on the seed bank combined with field surveys on seedling emergence.

Location: Tajogaite volcano, Cumbre Vieja Ridge, La Palma, Canary Islands.

Methods: The study includes a controlled experiment and a field survey along a gradient from the volcano crater to the perimeter within the Canary Island's pine forest. In the experiment, six tephra thickness categories were used to bury seeds (1, 5, 10, 45, 75 and 150 cm) based on observatory evidence corresponding to the distance away from the crater (7, 4, 2, 1.5, 0.75 and 0.15 km, respectively). Seeds were collected from the four most characteristic endemic pine forest species, representing different seed sizes and growth forms: *Pinus canariensis* (Pinaceae, tree), *Chamaecytisus proliferus* (Fabaceae, shrub), *Lotus campylocladus* (Fabaceae, forb) and *Cistus symphytifolius* (Cistaceae, shrub). One hundred seeds of each species were used per treatment (2800 seeds). In the field survey, we randomly established six quadrats (30 × 30 m) at the same distance from the crater as indicated above. Seedlings (< 5 cm in height) from natural regeneration were counted every three months.

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Results: After 18 months under ash, germination in the experiment was only detected in the treatments of control (germination rate of *P. canariensis* = 71%, *Ch. proliferus* = 13%, *L. campylocladus* = 24%, *C. symphytifolius* = 1%), and at 1 cm (51%, 18%, 11%, 1%) and 5 cm (5%, 4%, 0%, 0%) of ash depth.

Conclusions: The massive ashfall during this eruption completely and suddenly dysfunctionalized the seed bank as a reservoir of recruitment in areas within a radius of approximately 5 km from the crater (still buried under a 5 cm thick ash layer to date). Therefore, we provide evidence for the hypothesis that the recent volcanic eruption will profoundly change plant community dynamics and composition within large areas of the Canary Island's pine forest.

1 | Introduction

Volcanic eruptions are considered extreme natural disturbances that cause substantial changes in biological communities, depending on their intensity, size, and frequency (del Moral and Grishin 1999; Crisafulli et al. 2015; Jentsch and White 2019; Burton et al. 2020). Furthermore, these catastrophic events affect areas near the eruption site with different magnitudes of impacts and types of deposits, such as toxic gases, lahars, lava, tephra, and volcanic bombs. These substantial disturbance impacts strongly affect ecosystem response, particularly vegetation, recruitment, and its subsequent successional trajectories (del Moral and Grishin 1999; Antos and Zobel 2005; Irl et al. 2019).

Tephra deposition is one of the most widespread volcanic legacies (del Moral and Grishin 1999; Kent et al. 2001; Yeloff

et al. 2007). Airborne pyroclastic material deposited as tephra includes a broad spectrum of particle sizes, such as fine ash ($\phi < 2$ mm), intermediate lapilli ($2 < \phi < 64$ mm) and large volcanic bombs ($\phi > 64$ mm). Fine ash can reach considerable distances from the volcano, eventually covering a great surface area. The thickness and grain size of tephra decrease with the distance from the volcanic cones (Judd 1888; Titus and Tsuyuzaki 2003). The responses to this gradient differ in terms of the size and growth forms of plants affected by ash-falls (del Moral and Grishin 1999; Grishin et al. 1996; Kent et al. 2001; Antos and Zobel 2005; Paredes-Mariño et al. 2022; Beierkuhnlein et al. 2023).

On September 19, 2021, the Tajogaite volcano eruption began on the western slope of the Cumbre Vieja volcanic ridge on La Palma (Canary Islands) (Figure 1). The eruption was classified as fissural basaltic, dominated by strombolian activity, and was

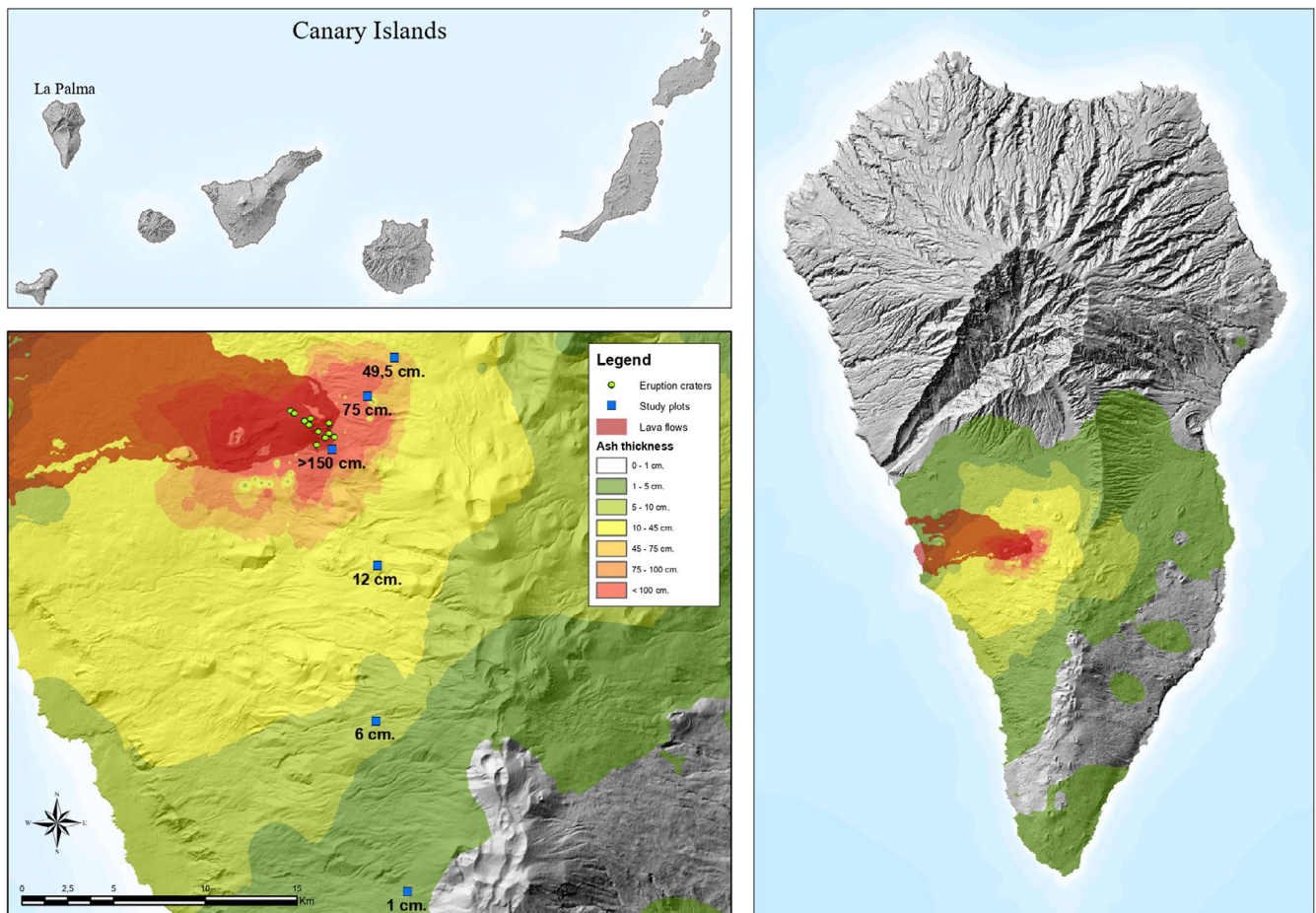


FIGURE 1 | Location of Tajogaite volcano and distribution of ash blanket and lava flows after the 2021 eruption (La Palma, Canary Islands).



FIGURE 2 | Massive tephra deposits on La Palma (Canary Islands) after the Tajogaite volcano eruption in 2021. Photos by Anke Jentsch.

moderately explosive (Longpré 2021; Carracedo et al. 2022). Ending on December 13, 2021 (González 2022), the 85 days of eruption gave rise to a 34 Mm^3 edifice, piling up 200 m high around the craters (Cívico et al. 2022). The volcano emitted more than 200 Mm^3 of lava and pyroclastic material (Cívico et al. 2022; Plank et al. 2023). From this ejected material, approximately 23 Mm^3 was deposited as tephra (Bonadonna et al. 2022; Shatto et al. 2024), ranging from $< 1 \text{ cm}$ in tephra depth in remote areas to several metres in tephra depth close to the volcano (Figures 1 and 2) (Copernicus 2021; Longpré 2021; Bonadonna et al. 2022, 2023; Nogales et al. 2022; Shatto et al. 2024). Additionally, toxic gases such as carbon monoxide (CO) and sulphur dioxide (SO_2) were emitted in large amounts (e.g., 2 Tg of SO_2) (Weiser et al. 2022; Milford et al. 2023).

Overall, studies on how tephra deposition affects the survival of species, revegetation dynamics, emergence responses, and primary succession have shown that plant cover and survival decreased with increasing tephra thickness (Antos and Zobel 1985, 1986; Black and Mack 1986; Tsuyuzaki 1989, 1991a; Whittaker et al. 1999; Hotes et al. 2004; Tsuyuzaki and Hase 2005; Ayiris and Delmelle 2012).

The selective survival of previously established plant species, including trees, woody plants, and herbaceous species, is essential for seedling recruitment and plant establishment in areas affected by volcanic ash deposition (Wood and del Moral 1987; Dale, Delgado-Acevedo, and MacMahon 2005; Crisafulli et al. 2015; Talbot et al. 2010). This is particularly important in most tephra burial scenarios where plants with established roots have better chances of thriving under these conditions (Zobel et al. 2022; Beierkuhnlein et al. 2023). In Kamchatka (Russia), Korabev and Neshataeva (2016) found that vegetation structure and composition varied strongly with distance to surviving communities and tephra thickness 30 years after a strong eruption. Sites with over 100 cm of tephra were inhabited only by pioneer species on the new soil surface, mainly grasses, mosses, and lichens dispersed from nearby populations. Rees (1979) reported that two herbaceous plant species and three grasses were found to survive 50 cm of ash cover after the Parícutín eruptions in Mexico (1943–1952), but only because of their tubers or adventitious roots.

However, few studies examine the effect of buried seed banks and their impact on the natural regeneration of vegetation (Tsuyuzaki 1991b, 1994; Whittaker et al. 1995; Tsuyuzaki et al. 1997; Tsuyuzaki and Goto 2001; Hotes et al. 2004; Ghermandi et al. 2015). In most cases, seeds were collected from the seed bank after removing the ash layer from the former topsoil or even from ravines without ash cover, aiming to test the persistence and viability of the seed bank after the eruption (Tsuyuzaki 1991b, 1994; Whittaker et al. 1995; Tsuyuzaki and Goto 2001; Ghermandi et al. 2015). Other works considered the chemical composition, nutrient ratios, and size of ash particles deposited on vegetation (Hotes et al. 2004; Dale, Swanson, and Crisafulli 2005). Furthermore, the effects of microsite conditions, such as larger tephra particle size and high moisture content, have been recorded for their positive influence on seed germination and seedling emergence (Wood and Morris 1990; Tsuyuzaki et al. 1997). Hotes et al. (2004) buried seeds directly in the field to determine the degree of species loss caused by tephra cover. Although the soil seed bank—depending on the seed longevity of individual species—can remain dormant and viable for a long time under a deep volcanic ash layer, viability is reduced over time (Whittaker et al. 1995; Ghermandi et al. 2015).

The only experiment using “inorganic ash rich in black carbon” from a volcanic eruption was conducted by Frenzen and Franklin (1985). These authors focused on the effect of ash accumulation on the germination and emergence of seedlings from the former seed bank; they planted seeds on the ash surface in varying thicknesses to examine their establishment in the new soil.

Considering the global relevance of tephra deposits (Walker 1999), it is surprising that practically no experiments have ever been carried out on the effect of tephra thickness on the seed bank and its seedling emergence capacity. For this reason, we studied a 7 km cline of decreasing tephra thickness in the Canary pine forest of La Palma, from the crater to the south of the island (Figure 1), approximately coinciding with the prevailing east-northeast trade winds during the eruption (Bonadonna et al. 2022, 2023; Nogales et al. 2022; Beierkuhnlein et al. 2023; Milford et al. 2023).

The Canary Island pine (*Pinus canariensis*) is evolutionarily well adapted to withstand intense disturbances such as forest fires or volcanic eruptions (Climent et al. 2004; López de Heredia et al. 2014; Nogales et al. 2022). However, the pine forest can be severely affected by the destruction of the seed bank depending on the intensity of the disturbance, mainly by wildfires. A great wound-healing capability, resprouting, and the presence of serotinous cones of surviving pines favour the regeneration of the Canary Island pine (Chano et al. 2015, 2017, 2023; Climent et al. 2004; Méndez 2010; Otto et al. 2010; Wilkens et al. 2025). In the case of the understory, species such as *Cistus symphytifolius*, *Chamaecytisus proliferus*, and *Lotus campylocladus* are pyrophilous, showing seed dormancy and requiring thermal shocks to increase their germination rate (Baskin and Baskin 2001; Clemente et al. 2007; Pérez-García et al. 2008). However, these understory species do not resprout and are killed by fire; therefore, in the case of the Canary Island pine forest, the main way of recovery is through the re-establishment of seedlings from the seed bank (Otto et al. 2012; Méndez et al. 2015; Weiser et al. 2021; Wilkens et al. 2025).

This study presents a controlled experiment to study seedling emergence after sowing seeds at different ash depths. In addition, the presence of seedlings in the field was monitored in order to test the hypothesis that seedling emergence decreases with increasing tephra thickness.

2 | Material and Methods

2.1 | Study Area

La Palma is the second youngest of the Canary Islands, an archipelago located in the Atlantic Ocean 100 km off north-west Africa (28°25'–28°51' N, 17°43'–18°00' W). It is a medium-sized island (708 km²) reaching above the treeline (2426 m a.s.l., Roque de Los Muchachos), with steep slopes (Figure 1) clearly influenced by the humid north-east trade winds, altitude, and aspect (Afonso 1985). Its climate parameters lead to widely heterogeneous environments characterised by vertically successive bioclimatic vegetation series (for details, see del Arco et al. 1999).

The Canary pine forest, covering almost 250 km² at an altitude between 90 and 1850 m a.s.l., is an important and representative ecosystem of the island with predominantly natural dynamics (Santos 1983; Pérez de Paz et al. 1994). This habitat consists of an open-dry woodland dominated by a single endemic tree species, *P. canariensis* (Pinaceae).

The Canary pine forest tends to exhibit low herbaceous species richness. Herbs and grasses can emerge with high cover after periods of rain; the nitrogen-fixing endemic *L. campylocladus* subsp. *hillebrandii* (Fabaceae) can become highly abundant. Other perennial forbs persist only in places of sufficient soil moisture (Weiser et al. 2021).

The understory of the pine forest is characterized by shrubs such as *Ch. proliferus* (Fabaceae) and *C. symphytifolius* (Cistaceae) (del Arco et al. 1999). The scientific names of the plant species

have followed the nomenclature given by Plant of the World Online (POWO 2024) and the Biodiversity Data Bank of the Canary Islands (BIOTA 2024).

2.2 | Experimental Approach

The pine forest was the main habitat affected by the Tajogaite volcano eruption due to the effects of tephra fallout and sulphurous gases (Nogales et al. 2022; Weiser et al. 2022). Only woody species resisted the intense tephra fallout (Nogales et al. 2022; Beierkuhnlein et al. 2023). The most common native species surviving in the pine forest after the volcanic eruption were *P. canariensis*, *Ch. proliferus*, *L. campylocladus* subsp. *hillebrandii*, and *C. symphytifolius* (Nogales et al. 2022), and seeds were collected from these four species, representing different seed sizes and structures (Figure 3).

Around 2000 seeds from each species were directly collected from plants during July–September 2022 in pine forest areas approximately 5 km from the main crater. Seeds were stored in a stable atmosphere before planting under controlled nursery conditions. From a series of ash depths (thicknesses) (see Beierkuhnlein et al. 2023; Figure 1), six categories were considered (1, 5, 10, 45, 75 and 150 cm) representing different distances from the crater (7, 4, 2, 1.5, 0.75 and 0.15 km, respectively). In addition, two controls were established: (1) only inert substrate with seeds of the four target species and (2) only ashes without seeds to check for potential seed contamination. Containers with different sizes and depths were used to represent the varying thicknesses of the ashfall (Appendix S1). A six-cm-thick inert substrate base (1 cm of coconut fibre and 5 cm of peat-perlite mix in a 10:1 ratio) was used for sowing the collected seeds. The tephra used in the experiment was previously homogenised to avoid physico-chemical singularities, as recommended for germination experiments (Robinson 2005).

One hundred seeds per species and treatment (ashfall thickness categories and control 1), making a total of 2800 seeds, were sown using grades of mesh. The seeds of each species were sown independently in their own containers and immediately covered by tephra. The experiment was watered every 2 days from October to March, during the Canary Island rainy season, when seedlings mainly emerge (Rodríguez et al. 2007). Irrigation was set proportionally to the size of the container until the container was saturated with water. Seedling emergence was surveyed every 5 days from October 2022 until the end of March 2024, comprising an 18-month monitoring process. Categorical data analysis (*Chi-square*) was used to evaluate seedling emergence at the different ash depths tested in the experiments.

The tephra substrate used in this experiment was a sample from the 2021 eruption pyroclasts removed from the affected areas. In September 2022, 3 metric tons were sampled and transported to the Native Flora Nursery of the Cabildo Insular de La Palma, where the experiment was conducted. Ten kilogram of this material was sub-sampled and homogenised by mechanical mixing for physical and chemical characterisation of the substrate. In addition, an aliquot of 1.3 kg was wet sieved through a column of 9 sieves of mesh sizes 63 µm < Ø < 16 mm, with a 1 Krumbein phi

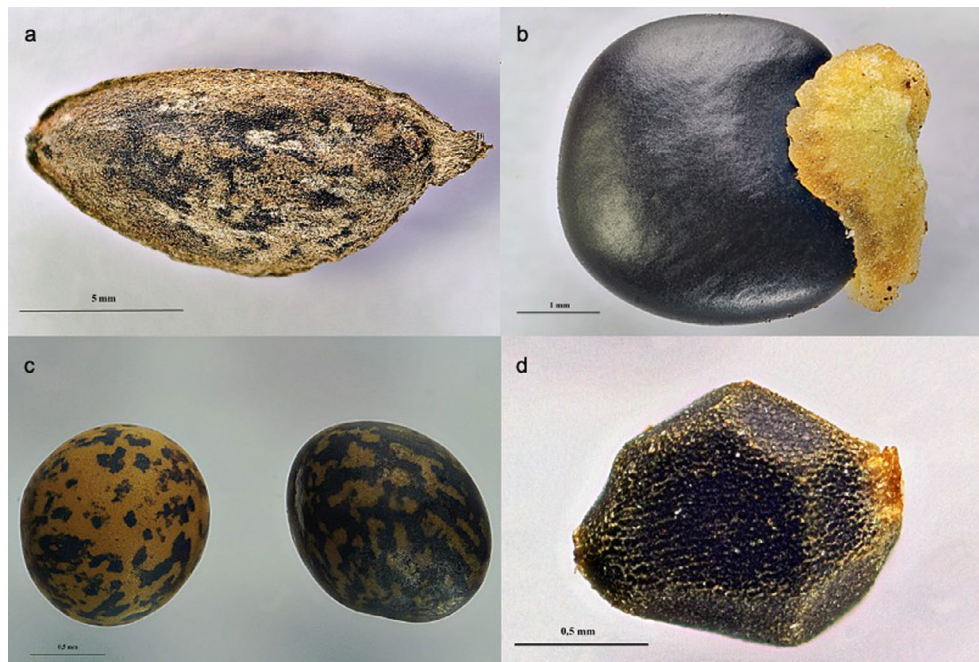


FIGURE 3 | Seeds from plant species of the Canary pine forest used during the experiment: (a) *Pinus canariensis*, (b) *Chamaecytisus proliferus*, (c) *Lotus campylocladus* subsp. *hillebrandii*, (d) *Cistus symphytifolius*. Photos by Rafael García Becerra.

scale Φ interval ($\Phi = -\ln 2[\phi]$, Krumbein and Sloss 1963), using an electromagnetic sieve shaker. The resulting granulometric fractions were weighed on a Radwag WLC 1/A2/C/2 precision balance (precision 0.01 g). The tephra used as substrate in the experiment granulometrically consists of a relatively poorly graded medium to coarse sand, with ~80 wt.% of the sample $0.25 < \phi < 4$ mm (Appendix S2).

We ensured that our substrate did not contain adhered volcanic salts that could damage the seeds by forming acids during watering. Therefore, following the Stewart et al. (2020) protocol, four leaching experiments were performed in the Soil Fertility and Plant Nutrition Laboratory at IPNA-CSIC with 10 g tephra desorbed in 200 mL Milli-Q water (1:20 ratio). Anion concentrations (F^- , Cl^- , SO_4^{2-} , PO_4^{3-}) in the leachates were measured by ion chromatography (883 Basic IC plus-Metrohm), and cation concentrations by ICP-OES (Perkin Elmer AVIO500). The repeatability of our analyses ($n=4$) was better than 0.5 ppm for all the anions and major cations, and better than 10 ppb for traces.

The chemical and physical analyses (Appendix S3) confirm that the substrate used in our experiment was essentially lixiviated naturally by ≈ 450 mm of rainfall between the end of the eruption and the mid-September sampling close to El Paso (Agencia Estatal de Meteorología EL PASO-C.F. station).

2.3 | Field Survey

To contrast the results obtained from the experiment, we monitored the seedling emergence in biodiversity monitoring plots following a gradient from the crater (Figure 1). A total of 6 plots (30×30 m) in the Canary pine forest were monitored every three months, starting at the end of the eruption and following the same spatial cline from the crater to 7 km south (one plot per

distance). The floristic composition of each plot, immediately after the end of the eruption, was characterised (Table 1). In the total surface of these plots, we systematically identified and counted all the seedlings by each species. Only those seedlings < 5 cm in height were recorded in each survey to avoid duplications. The total number of seedlings recorded in each survey was used in the analyses (Figure 4).

3 | Results

3.1 | Seeds and Experimental Emergence

The seeds selected for the experiment were of diverse sizes and weights among the species. Seeds from *P. canariensis* were the largest, whereas seeds from *C. symphytifolius* were the smallest (Table 2, Figure 3).

After 18 months of the experiment, a total of 200 seeds (7.14% of the total) emerged: 127 from *P. canariensis* (18.14%); 35 from *Ch. proliferus* (5.00%); 35 from *L. campylocladus* (5.00%); and 3 from *C. symphytifolius* (0.29%). By treatment, most seedlings emerged in the control with only an inert substrate and in the 1 cm-thick tephra ash layer, with significant differences between them ($\chi^2_1 = 5.78$; $p = 0.016$) (Figure 5). Furthermore, a striking decrease in seedling emergence was observed in the 5 cm ash depth ($\chi^2_1 = 64.90$; $p < 0.001$), where only those from the largest seed sizes emerged (*P. canariensis* and *Ch. proliferus* with 5 and 4 seedlings, respectively). No seedling emergence was recorded in treatments from 10 to 150 cm.

Regarding the seedling emergence per plant species, differences among years were observed. While *P. canariensis* showed a higher percentage during the first year (2022–2023) ($\chi^2_1 = 135.00$; $p < 0.001$), the germination rates in the two leguminous species

TABLE 1 | Floristic composition (% vegetation cover) in the studied plots after the end of the eruption process in the Tajogaite volcano.

Plant species	Ash depth (cm)					
	1	5	10	45	75	150
<i>Pinus canariensis</i>	29.67	25	20.22	37.25	28.48	—
<i>Aeonium spathulatum</i>	0.001	—	—	—	—	—
<i>Adenocarpus foliolosus</i>	—	1.91	—	—	—	—
<i>Lotus campylocladus</i>	0.076	0.30	—	—	—	—
<i>Echium webbii</i>	0.51	—	—	—	—	—
<i>Bystropogon organifolius</i>	0.06	—	—	—	—	—
<i>Scrophularia glabrata</i>	0.023	—	—	—	—	—
<i>Castanea sativa</i>	—	—	—	—	2.22	—
Total species	7	3	1	1	2	0



FIGURE 4 | Fresh pine seedling on raw tephra inoculated with mycorrhiza in April 2023, about one year after the end of the Tajogaite volcano eruption in December 2021 . Photos by Anke Jentsch.

TABLE 2 | Seed characteristics of the species used for the experiment.

Species (n = 40)	Size (mm)		Weight (g)
	Length	Width	
<i>Pinus canariensis</i>	11.63 ± 1.26	6.20 ± 0.57	0.10 ± 0.04
<i>Chamaecytisus proliferus</i>	4.74 ± 0.42	3.05 ± 0.45	0.02 ± 0.003
<i>Lotus campylocladus</i>	1.54 ± 0.11	1.34 ± 0.09	0.002 ± 0.0003
<i>Cistus symphytifolius</i>	1.15 ± 0.12	0.97 ± 0.10	0.0004 ± 0.0002

Note: Values: Mean ± SD.

(*Ch. proliferus* and *L. campylocladus*) were higher during the second year (2023–2024) ($\chi^2_1=6.59$; $p=0.010$ and $\chi^2_1=28.20$; $p<0.001$, respectively). However, no significant differences between years were recorded in the case of *C. symphytifolius* ($\chi^2_1=2.01$; $p=0.157$) (Figure 5).

3.2 | Seedlings' Emergence in the Monitored Field Survey Plots

The number of seedlings that emerged by natural regeneration within the 6 plots monitored in the pine forest of La Palma

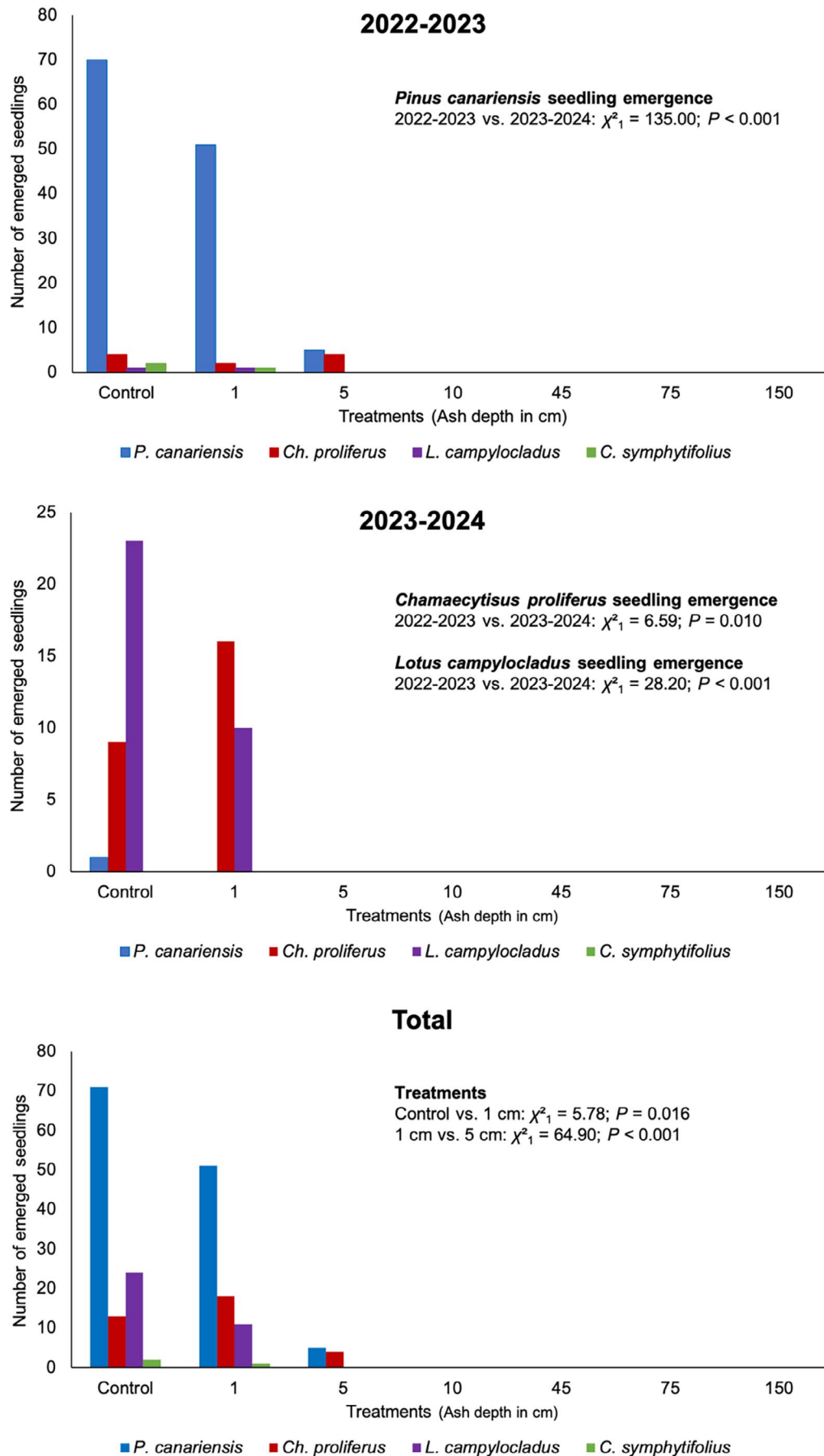


FIGURE 5 | Number of emerged seedlings of the four species planted in the seed bank and ash deposition depth experiment. Only significant comparisons are included.

TABLE 3 | Seedling emergence recorded in the six plots (30 × 30 m) located along the pine forest cline (from the crater to 7 km away), following the ashfall depth to the south from the Tajogaite volcano.

Plant species	2022						2023					
	Ash depth (cm)											
	1	5	10	45	75	150	1	5	10	45	75	150
<i>Pinus canariensis</i>	358	18	151	—	—	1	51	23	45	13	320	78
<i>Aeonium spathulatum</i>	5	—	—	—	—	—	7	—	—	—	—	—
<i>Adenocarpus foliolosus</i>	—	—	—	—	—	—	—	102	—	—	—	—
<i>Chamaecytisus proliferus</i>	—	—	2	—	—	—	—	—	2	—	—	—
<i>Lotus campylocladus</i>	—	5	7	—	—	—	78	151	1	—	—	—
<i>Vicia disperma</i>	—	—	33	—	—	—	—	—	58	—	—	—
<i>Echium webbii</i>	53	—	—	—	—	—	11	—	—	—	—	—
<i>Bystropogon organifolius</i>	6	6	30	—	—	—	1	—	—	—	—	—
<i>Scrophularia glabrata</i>	24	—	—	—	—	—	15	—	—	—	—	—
Poaceae indet.	—	—	—	—	—	—	3	—	—	—	—	—
Total species	5	3	5	0	0	1	7	3	4	1	1	1
Total seedlings	446	29	223	0	0	1	166	276	106	13	320	78

coincided with the ash layer thickness used in the experiment (Table 3). Most of the seedlings targeted in this study were observed in the thinner layers of tephra deposition, where a greater number of other plant species were also recorded. While germination of *P. canariensis* seeds predominated in the first year, one of the two leguminous species, *L. campylocladus*, reached the maximum germination rate in the second year. The other leguminous species, *Ch. proliferus*, was present in low frequency in our plots, while *C. symphytifolius* was absent. However, in those plots where the tephra layer was thicker, the emerged seedlings belonged to the only tree species present, *P. canariensis* (Figure 4).

4 | Discussion

Physical disturbance is one of the most critical factors affecting plant regeneration (Jentsch and White 2019; Burton et al. 2020; Wohlgemuth et al. 2022), particularly after volcanic eruptions, mainly due to burial by tephra deposition (del Moral and Grishin 1999; Yeloff et al. 2007; Crisafulli et al. 2015). This natural physical impact also affects the seed bank (Tsuyuzaki and Goto 2001). Nevertheless, volcanic ashes are rich in plant nutrients and trace elements and develop into highly productive soils (Robinson 2005; Fiantis et al. 2019). The volcanic ash and sterilised substrate used in this experiment were suitable for investigating post-eruption germination and vegetation recovery (Robinson 2005).

In this contribution, the fate of the seed bank buried under volcanic ashfall was studied experimentally for the first time after a recent volcanic eruption. However, other contributions have provided information on seed banks, mainly from observational studies (see Tsuyuzaki 1991b, 1994; Whittaker et al. 1995; Tsuyuzaki and Goto 2001; Robinson 2005; Ghermandi

et al. 2015). Our findings suggest that the seed bank was inactive (temporarily or definitely) within a distance of 5 km from the crater, where the tephra deposit was thicker than 5 cm.

4.1 | Seedling Emergence in the Experiment

Most of the emerged seedlings were from those species with larger seeds, mainly in *P. canariensis*. This can be explained by the absence of dormancy, thin seed coats, and a large endosperm (see Wood and Morris 1990; Baskin and Baskin 2001; Grundy et al. 2003). In the other three experimental species, seed dormancy could be the driver of reducing seedling emergence. The two legumes (*Ch. proliferus* and *L. campylocladus*) and the Cistaceae (*C. symphytifolius*) belong to families in which physical dormancy is widely prevalent (Baskin and Baskin 2001). Therefore, they require scarification by high temperatures (Thanos and Georgiou 1988; Baskin and Baskin 2001; Clemente et al. 2007), mycorrhizae (Baskin and Baskin 2001; Allen et al. 2005) or *Rhizobium* bacteria (e.g., Beringer et al. 1979; Lorite et al. 2018) to stimulate their germination. These different dormancy patterns among species could explain the differences observed in seedling emergence between years in our experiment.

Comparable results derived from experiments to find out how seed germination and seedling emergence are affected by the depth at which seeds are buried and using different substrates (see Chen and Maun 1999; Izhaki et al. 2000; Ren et al. 2002; Traba et al. 2004; Guo et al. 2010; Tao et al. 2022). In these studies, the highest percentage of seedlings emerged mainly through a sand cover from 4 to 8 cm, although some emerged from an ash thickness of 12 cm. This finding could principally be explained by the seed failing to germinate or the shoot not reaching the soil surface (Baskin and Baskin 2001), but also because seeds

may become dormant and form part of a longer-lived seed bank (Ren et al. 2002).

Profound changes in vegetation as a result of volcanic eruptions have been observed and documented in various field studies worldwide regarding both plant regeneration and subsequent plant community composition (Rees 1979; Andersen and Macmahon 1985; Clarkson and Clarkson 1994; Hotes et al. 2004; Tsuyuzaki 2009; Korablev and Neshataeva 2016). But to our knowledge, no controlled experiment has been available to test for thresholds of germination and regeneration. The experimental findings suggest that the seed bank in the buried soil becomes inactivated when the ashfall deposits are thicker than 5 cm (Figure 5). Linking this information with a fieldwork database on the ashfall thickness distribution, this substantial impact can be equated with areas within a radius of 5 km from the new volcano.

4.2 | Seedling Emergence in the Field Survey

Surviving plants from the pre-disturbance ecosystem can profoundly influence post-eruption ecosystem recovery (see Crisafulli et al. 2015, and references therein). Furthermore, the recovery of vegetation will be facilitated by the presence of seed banks depending on the timing of the eruption, as dormant plants are less likely to suffer adverse effects (Ghermandi and González 2012). However, vegetation recovery could be negatively affected because the burial of seeds at the above critical tephra depth results in a failure of germination or seedling emergence (Zobel and Antos 1997; del Moral and Grishin 1999; Kent et al. 2001; Tsuyuzaki and Goto 2001).

In the plots monitored in our study, the general seedling emergence pattern coincides with the results of the experimental treatments, suggesting that the thickness of the ash layer influenced seedling emergence. No seedlings were observed in treatments where the ash thickness exceeded 5 cm. As the ash layer deepened, both seed germination and seedling emergence declined, with a rapid reduction in seedling emergence above the 5 cm threshold. We can suggest that seedlings found in plots with an ash thickness > 5 cm likely originated from new seeds produced by surviving plants (see Table 1). Conversely, in plots where the ash thickness was < 5 cm, the emerging seedlings may have come from the pre-eruptive seed bank, surviving plants, or seed dispersal from outside the plots (Wood and del Moral 1987; del Moral and Grishin 1999; Crisafulli et al. 2015). Furthermore, a higher number of seedlings and species, including non-targeted ones, appeared in the 10 cm-thick ashfall layer (Appendix S4), which may correspond to the arrival of seeds by dispersion from nearby source populations (e.g., *Adenocarpus foliolosus* and *Vicia disperma*) (Table 3) (see Tsuyuzaki 1987; Tsuyuzaki and Hase 2005; Korablev and Neshataeva 2016).

In the specific case of *P. canariensis*, we found large accumulations of seedlings in all areas affected by volcanic deposits, even in those where ashfall thickness reached the maximum values (Table 3). *Pinus canariensis* produces serotinous cones that open and disperse seeds under the effect of heat (Climent et al. 2004; Nogales et al. 2022), acting as an aerial seed bank essential to increase seed availability under unfavourable

conditions. This enables high seedling densities, sometimes referred to as “seedling banks”, and chances of survival (see Baskin and Baskin 2001 and references therein). The wind also favours the dispersion of pine seeds from cones opened by the effect of the extreme heat caused by the eruption. This is consistent with other studies showing that tree seedling emergence and establishment were higher in tephra deposits than in pre-eruption forest substrates (Tsuyuzaki et al. 1997; Tsuyuzaki and Hase 2005; Tsuyuzaki 2009; Ghermandi et al. 2015; Zobel and Antos 2017; Hintz et al. 2021). Comparisons of the nutrient content of tephra with the pre-eruption soil indicate that tephra should be satisfactory for plant growth, at least for major nutrients (Antos 1984).

Regarding the presence of *L. campylocladus*, one year after the eruption, the increasing seed production in this legume was related to a decreasing ash deposition with decreasing distance from the crater (A. Jentsch, pers. obs.), probably because thin volcanic ashfall thickness enriches soils with nutrients (see Appendix S3). This increase in seed production explains the significant increase in *L. campylocladus* seedlings during the second year after the eruption (Table 3, Figure 6).

It is noteworthy that the low representation of *Ch. proliferus* and the complete absence of *C. symphytifolius* in these plots, even though both species are among the most abundant in the mature pine forest of La Palma (del Arco et al. 1999). Given that



FIGURE 6 | Abundant mats of *L. campylocladus* appearing one year after the Tajogaite volcano eruption within the area of moderate to low ashfall (1–2 cm depth) after a moist winter season. Photo by Anke Jentsch.

the primary method for the recovery of the understory in pine forests involves the re-establishment of seedlings from the seed bank (Otto et al. 2010; Méndez et al. 2015; Weiser et al. 2021), this absence could be related to the physical dormancy of these species (Baskin and Baskin 2001), as well as to the mechanical scarification and thermal treatment used to improve their germination rates (Pérez-García et al. 2008). Since seedlings of these species are unable to emerge at ash depths > 5 cm, these would be the most plausible reasons for areas where plants survived and were able to disperse their seeds on the volcanic ash beyond the 5 km distance from the crater (Nogales et al. 2022; Beierkuhnlein et al. 2023).

4.3 | Concluding Remarks

This novel experiment has yielded a remarkable pattern of seedling emergence, depending on the tephra layer deposition. It showed that the seed bank became ineffective when buried underneath more than 5 cm of volcanic tephra. This applies to all sites within a distance of 5 km from the crater, representing a considerable area of the island of La Palma. Generally, this pattern coincides with observations in the field (see also Grishin et al. 1996). Although many plant species have the ability to survive burial for up to three to eight years (Zobel and Antos 1997; Antos and Zobel 2005), and their survival increases with decreasing tephra depth due to erosion (Antos and Zobel 1985; Kent et al. 2001), few individuals of most species survive the deepest tephra accumulations (Antos and Zobel 1985; Kent et al. 2001). This volcanic legacy, therefore, strongly influences the seedlings and the number of plant species present (del Moral and Grishin 1999; Tsuyuzaki and Hase 2005).

A comparable impact of pyroclastic deposits on seed banks has probably occurred during other volcanic eruptions. On small volcanic islands, even a shallow tephra deposit can severely impede the regeneration of plant species from the seed bank over a short-term temporal frame. This impact is particularly important for short-lived plant species with high turnover in their life cycles. However, the fine-grained ash could be easily washed away by the very heavy rainfall that hit the island, and the vegetation can recover well, except in areas where meters of ash have accumulated, as was observed during the long eruption of the Soufriere Hills volcano on the small island of Montserrat in the Caribbean (see Druitt and Kokelaar 2002). Indeed, even a long-lived seed bank can become useless, and species populations can decline or even become extinct. Oceanic islands are those of volcanic origin located on the oceanic crust and thus completely separated from continental land masses, exhibiting a high percentage of endemic plants. In island ecosystems, patterns of endemism are mainly explained by spatial isolation and low species richness, resulting in unoccupied niches and potential evolutionary options.

The recent eruption on the island of La Palma has provided a valuable opportunity to study a natural impact disturbance of significance on an evolutionary time scale that is representative of oceanic islands in general. Our findings indicate that the extinction risk of island plant species is higher for short-life-cycle plant species that rely on the seed bank and increases with the intensity of volcanic eruptions and ash deposition.

Author Contributions

Félix Manuel Medina, María Guerrero-Campos, and Manuel Nogales designed and performed the experiment, analyzed the data, and wrote the manuscript. Guillermo Hernández Martín collected seeds and monitored seedling emergence. Thomas Boulesteix made chemical and physical analyses. Frank Weiser and Anna Walentowitz provided field data about ash depth distribution and prepared Figure 1. Anke Jentsch revised all disturbance ecology concerns. Carl Beierkuhnlein revised ideas on plant communities and study design. Patricia Marrero and Christopher Shato contributed to the writing and edited the manuscript. Víctor Chano designed the experiment, providing essential information. All authors actively contributed to writing and editing the article and approved the submitted version.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All data are included in this manuscript.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.