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Volcanic eruption and wildfires as compounding drivers of first-year seedling establishment in Canary pine

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ABSTRACT

On the island of La Palma, located in the Canary Islands, Spain, the Canary pine forest is largely unmanaged and depends on natural regeneration for sustainable population dynamics. Canary pine (*Pinus canariensis* C.Sm. ex DC.) has been continuously exposed to volcanic eruptions over evolutionary time scales. The species exhibits many adaptations to wildfires, but the current fire regime is likely not natural. While both volcanic eruptions and wildfires can devastate existing vegetation and unbalance ecosystems, they can also facilitate plant growth through mechanisms like nutrient release and increased light availability. Occasional successful regeneration events, driven by high first-year seedling establishment following a disturbance, could be essential to maintaining population structures. We investigated the interactions of volcanic eruption and past wildfires on first-year seedling establishment in the Canary pine forest after the 2021 Cumbre Vieja volcanic eruption. We combined in-situ seedling abundance data from 117 plots (5 m radius) with remote sensing to test the hypotheses that (1) the favorable conditions created by the eruption triggered a localized pulse in first-year seedling establishment of Canary pine and (2) seedling establishment was diminished in areas affected previously by wildfires (2012 and 2016). Using a two-part approach, consisting of univariate analysis of individual factors and multivariate analysis with generalized additive models, we find evidence consistent with our hypotheses. Plots located closer to the volcano and more heavily impacted by the eruption were significantly associated with higher seedling abundance (> 50 per plot). Furthermore, plots that had experienced prior burning in addition to volcanic impact showed lower seedling densities compared to plots impacted solely by the volcano. This suggests that fire history negatively influenced first-year seedling establishment following the eruption. We discuss the role of both wildfires and volcanic eruptions in the evolutionary history of Canary pine and highlight the task of disentangling the legacies of these two disturbances. Serotiny, traditionally considered to be a fire-specific adaptation, appears to also function after and increase the resilience of Canary pine to volcanic eruptions at the stand-level. Lastly, we raise the question of whether recurrent disturbances exceeding natural system dynamics could endanger the future demography of Canary pine by limiting infrequent but necessary forest regeneration events.

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1. Introduction

1.1. Background

Forest ecosystems are subject to various biotic and abiotic disturbances, which influence long-term successional dynamics and shape community composition. For many conifer species, disturbances are critical drivers of functional regeneration, directly stimulating seed release as well creating opportunities for the establishment and recruitment of juveniles. Disturbances that are climate-sensitive will experience shifts in frequency, severity, and duration amid climate change (Lindner et al., 2010)—an effect that is expected to be especially pronounced for coniferous forests (Seidl et al., 2017). There is mounting evidence to suggest that both climate change and disturbance regime shifts are leading to a decline in forest resilience (Forzieri et al., 2022) as well as regeneration failure in coniferous forests (Hansen et al., 2018; Stevens-Rumann et al., 2022). This emerging problem could be exacerbated on oceanic islands, where endemic species, unique ecosystems, and volcanic eruptions combine to create additional challenges for biodiversity conservation and forest management.

The Canary Islands are an oceanic archipelago characterized by large areas of laurel and pine forest as well as other natural and semi-natural ecosystems (Castanho et al., 2021). Of these, the Canary pine forest is the most extensive and is dominated by a single endemic conifer, Canary pine (*Pinus canariensis* C.Sm. ex DC.; Fig. 1a). On La Palma, the northwestern-most island of the archipelago, forest exploitation and management have historically been of less importance. Currently, most of the island is under protected status, resulting in forests that rely almost entirely on natural regeneration to maintain population structures. The Canary pine forest is prone to frequent disturbances such as wildfires and volcanic eruptions. Understanding how these disturbances, both individually and as compounding events, affect functional regeneration processes like first-year seedling establishment is crucial to the effective preservation and management of this ecosystem.

1.2. Volcanic Eruptions

Volcanic eruptions have occurred repeatedly on La Palma in recent history (e.g., 1949, 1971, and 2021; Longpré and Felpeto, 2021). In late 2021, the Tajogaite Volcano on La Palma erupted over three months (19 September 2021 – 13 December 2021), causing economic losses exceeding 400 million euros and forcing the evacuation of 6400 residents from numerous towns and villages, many of which remain irrecoverable under ash and lava to this day (for detailed description of the eruption, see Longpré, 2021 and Weiser et al., 2023). Through extensive lava flows (covering an area of over 1200 ha), the emission of toxic sulfuric gases, as well as the ejection of airborne pyroclastic deposits (tephra), the eruption also had a strong and partly disastrous impact on the Canary pine forest. The direct effects on local terrestrial biodiversity as well as forest health were devastating and have been well-documented (Medina et al., 2021; Nogales et al., 2022, Weiser et al., 2022, 2023), along with a first study on forest recovery (Shatto et al., 2024b). However, the impact of the eruption on fundamental forest processes such as seedling establishment has not yet been examined.

Volcanic eruptions are known to be one of the most catastrophic disturbances on Earth. At the same time, eruptions also release resources (Jentsch and White, 2019) and initiate primary succession (Walker and del Moral, 2003). On continents, eruptions are often spatially limited in their ecological effects, impacting only a small portion of species populations, ecosystems, and biomes. However, on oceanic islands, eruptions affect an isolated landmass, triggering selection for significant fractions of an island's biota (Beierkuhnlein et al., 2023). In extreme cases, eruptions can even sterilize entire islands, as was the case on Krakatoa in 1883 (Tagawa et al., 1985; Whittaker et al., 1989, 2000; Thornton, 1996; Whittaker and Riswan, 1995) and Gran Canaria

(Pérez-Torrado et al., 1995; Emerson, 2003). Furthermore, volcanism is directly linked to oceanic island genesis and continues to influence the development of biota and ecosystems during the volcanically active phase of an island's existence (Steinbauer et al., 2013; Chiarucci et al., 2021; Beierkuhnlein et al., 2023).

Until recently, research into the effects of volcanic eruptions on vegetation dynamics has been limited mainly to continental settings (e. g. Rees, 1979; Tsuyuzaki, 1989; Arnalds, 2013; Korablev and Neshataeva, 2016). The most well-known case is the eruption of Mount St. Helens in 1980 (e.g., Wood and Morris, 1990; del Moral and Grishin, 1999; del Moral and Rozzell, 2005; Dale et al., 2005; Ibekwe et al., 2007; Halvorson and Smith, 2008; Zobel and Antos, 2018). Aside from research concerning primary successional trajectories on ancient lava flows (Elias and Dias, 2004; Irl et al., 2019; Rodríguez et al., 2022), ecosystem responses and species-specific adaptations to volcanism on oceanic islands as well as vegetation establishment and development on young tephra layers remain understudied (Saputra et al., 2022; Beierkuhnlein et al., 2023). The role of volcanic eruptions in the life history of Canary pine has not been clarified. Eruptions can be numerous over the lifetime of individual trees, but their frequency and severity will vary by island and island age. Large temporal gaps of volcanic activity may also occur. The recent eruption in late 2021 provided a rare opportunity to investigate ecosystem responses to volcanism as well as species-specific adaptations *in flagranti*.

1.3. Wildfires

Alongside volcanic eruptions, wildfires have been the most frequent major disturbance to the Canary pine forest, with the most recent one occurring in July 2023 (Höllermann, 2000; Molina-Terrén et al., 2016). Due to its capacity to resist and survive wildfires, Canary pine has garnered a reputation as one of the most fire-resilient species in the world (Arévalo et al., 2001; Climent et al., 2004; Fernandes et al., 2008). These characteristics include thick bark, serotinous cones, self-pruning, deep rooting, high longevity, and the ability to resprout after total defoliation and even crown combustion from all surviving organs, such as the roots, trunk, and branches (Fig. 1b).

After a fire, epicormic shoots develop on mature trees with bluish-green primary needles, which are gradually replaced by secondary needles during further development, enabling trees to easily survive complete loss of foliage (Pausas and Keeley, 2017). This reinforces the impression of a highly resilient monodominant forest in the wake of major disturbances. However, the long-term persistence of a forest ecosystem depends also on the completion of life cycles, reproduction, seedling establishment, and the recruitment of juveniles. Canary pine exhibits serotinous traits, though the occurrence of these traits was found to be highly plastic at the stand-level (from between 3 % and 35 % of trees; Climent et al., 2004). There is significant evidence for delayed release of seeds from the canopy seedbank when stimulated by fire (Climent et al., 2004; Tapias et al., 2004; Otto et al., 2010). Following a wildfire, very high densities of seedlings have been reported (Höllermann, 2000; Otto et al., 2010; Méndez, 2010; Méndez et al., 2015).

Weiser et al. (2021) showed that the Canary pine forest undergoes a post-fire nutrient pulse and short-term development of a luxuriant herb layer when precipitation makes released nutrients available to plants. Legumes such as the endemic *Lotus campylocladus* Webb & Berthel. subsp. *hillebrandii* (Christ) Sandral & D.D.Sokoloff are especially favored under post-fire conditions and can suppress the establishment of pine seedlings (Fig. 1c). High densities of seedlings and saplings of Canary pine have also been reported for stands that did not recently burn, suggesting that fires are not a prerequisite for regeneration (Barbour et al., 2012). This is further supported by the fact that before human settlement, wildfires appear seldom in palaeoecological records, with lightning strikes and volcanic eruptions as the only known triggers (de Nascimento et al., 2009; Nogué et al., 2013; Ravazzi et al., 2021).
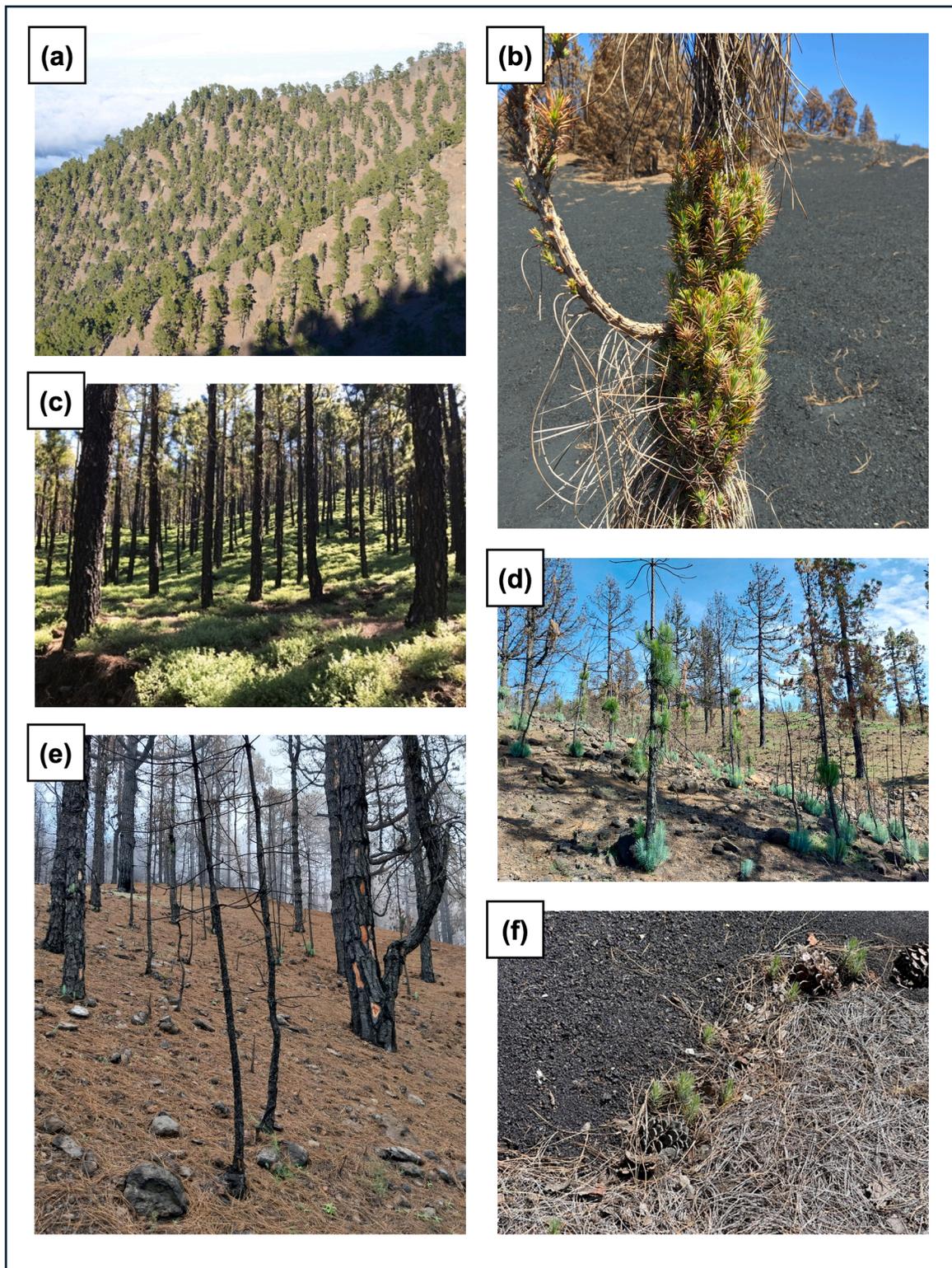
Fig. 1. (a) Even-aged Canary pine stand on the steep slopes of northern La Palma at ca. 1500 m a.s.l (March 2013). Neither extensive understory vegetation nor natural regeneration is developed in these fire-prone forests. (b) Epicormic resprouting of the trunk and branches on a Canary pine tree near the Tajogaite Volcano, taken in April 2022. (c) Herbaceous vegetation develops after fires open the canopy and precipitation events increase nutrient availability. Legumes, such as *Lotus campylocladus* subsp. *hillebrandii,* dominate until a period of drought or until mineralized nutrients from the ashes have been leached. (d) Epicormic resprouting of Canary pine trees and juveniles at a moderately-affected fire site in northwestern La Palma, taken eight months after the 2023 wildfire. (e) Charred Canary pine juveniles with no visible epicormic resprouting at a severely affected fire-site in northwestern La Palma, taken eight months after the 2023 wildfire. (f) A group of young Canary pine seedlings on top of the fresh tephra layer next to opened serotinous cones and needle litter. Authors of the photos: C. Beierkuhnlein (a, c, f); F. Weiser (b); V. Wilkens (d, e).

In contrast to mature pine trees, seedlings are highly susceptible to wildfires. It can take two to six years after establishment before heteroblastic transition to a main shoot occurs and many years after that until thick bark develops (Climent et al., 2006). The thresholds for post-fire survival of juveniles have not yet been clarified, though it is plausible that site-specific conditions, forest structure, fire severity, and individual characteristics (e.g. stem diameter and height) could all influence outcomes. Juveniles can demonstrate the ability to resprout from the root collar and stem following a fire event (Fig. 1d). However, many young individuals do not appear to survive, but it cannot be excluded that they will also begin resprouting given additional precipitation (Fig. 1e).

During the last 20 years, about 46 % of the Canary pine forest area on La Palma has burned at least once (EFFIS Burned Area Data; San-Miguel-Ayanz et al., 2012). There are likely few stands remaining that have not experienced repeated wildfires under the current fire regime, which has been ongoing since the latter half of the 20th century (Höllermann, 2000; Molina-Terrén et al., 2016). In conjunction with the vulnerability of Canary pine in its early life stages, the current human-driven fire regime could pose a risk to the long-term perspective of this important ecosystem by inhibiting functional regeneration.

1.4. Research aim

Inspired by relatively high abundance of one-year-old Canary pine seedlings observed on fresh tephra in the forest east of the Tajogaite Volcano (Fig. 1f), we set out to assess first-year seedling establishment of Canary pine across the island of La Palma in April 2023, 14 months after the end of the latest eruption. We focused particularly on the forest surrounding the volcano, which was partly affected by previous wildfires in 2012 and 2016. We aimed to understand the compounding effects of volcanic eruption and wildfires on first-year seedling establishment. Accordingly, we formulated the following hypotheses:

1. The recent volcanic eruption led to favorable conditions that stimulated a localized pulse of first-year Canary pine seedling establishment. Favorable conditions attributable to volcanic eruption include increased light availability due to canopy dynamics, a nutrient pulse, resetting of the soil seedbank, and decreased interspecific competition.
2. Wildfires in 2012 and 2016, to the north and south of the crater respectively, diminished potential first-year seedling establishment driven by the eruption in these areas, as the reproductive capacity of the forest was likely already exhausted without sufficient recovery time.

We tested these hypotheses using in-situ data of seedling abundance in conjunction with Earth observation products (i.e. NDVI), which enabled us to quantify the local impact of both the recent eruption and past wildfires.

2. Methods & materials

2.1. Study area

La Palma is the northwestern-most island of the Canary Islands (Fig. 2). With a geological age of 1.7 Ma (van den Bogaard, 2013), it is the second youngest island in the archipelago. Volcanic activity is ongoing, as evidenced by seven eruptions occurring within the last 500 years (Longpré and Felpeto, 2021), including the most recent one in late 2021 (Longpré, 2021).

The island exhibits pronounced topography, culminating at the summit of Roque de los Muchachos (2426 m a.s.l.). The resulting elevational and climatic gradients support a multiplex of distinct ecosystems. The Canary pine forest is the most extensive ecosystem on the island, covering approximately 35 % of the area and is driven mainly by natural dynamics (del Arco Aguilar et al., 2010). Under more humid
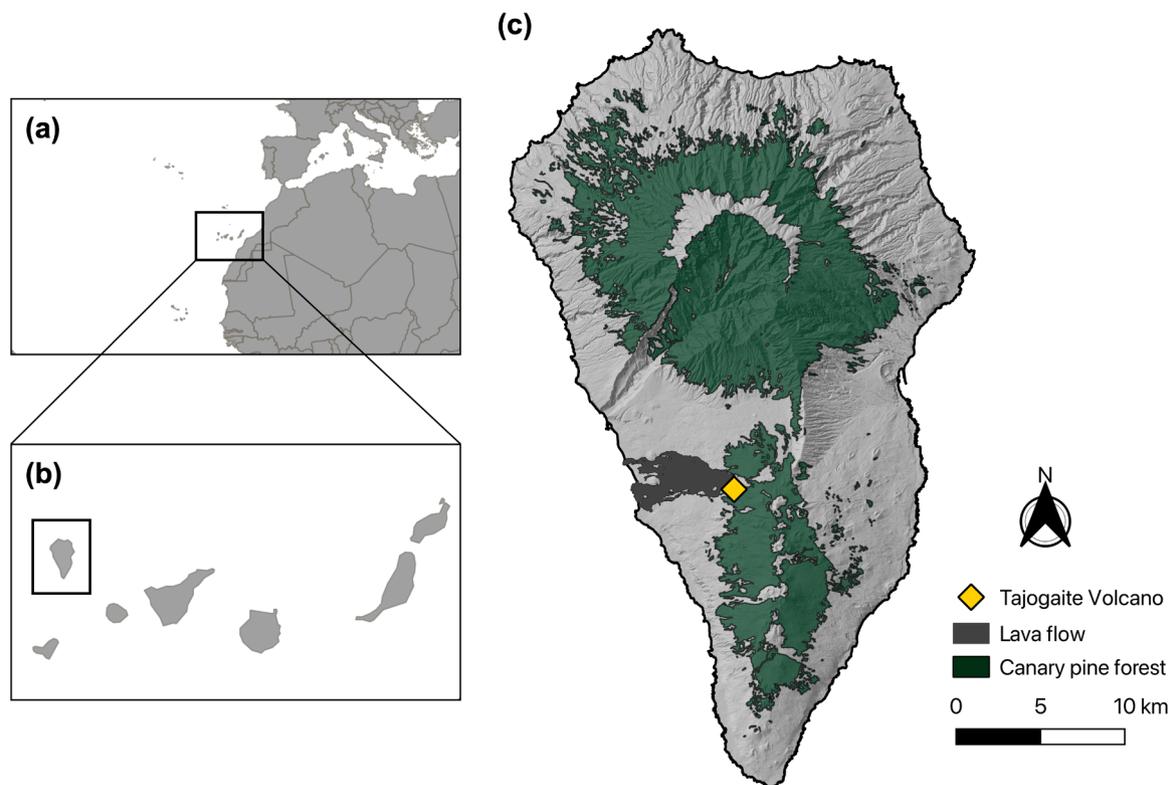

Fig. 2. Study area. (a) Location of the Canary archipelago, about 100 km off the coast of North Africa; (b) location of the island of La Palma within the archipelago; (c) hillshade map of La Palma, produced using 2 m DEM (digital elevation model) of the island (Centro Nacional de Información Geográfica CNIG, 2022), showing the location of the eruption crater and lava flow of the Tajogaite Volcano, as well as the extent of the Canary pine forest.

conditions, like on the northeastern slopes exposed to the trade winds, the Canary pine forest transitions downwards into a mixed forest-type called Fayal-Brezal, consisting primarily of *Erica canariensis* Rivas Mart., Martin Osorio & Wildpret and *Myrica faya* Aiton. Further down, particularly in the ravines, there are old-growth laurel forest formations. Near the coastal cliffs, where conditions are much more arid, succulent scrub takes over, but there are hints that even here, pine forests had a much broader distribution in the past (López de Heredia et al., 2014). Above the treeline, located at approximately 2000 m a.s.l., the Canary pine forest graduates into alpine scrubland dominated by endemic species (Irl et al., 2015; Wieser et al., 2016; Steinbauer et al., 2017).

2.2. Target species

Canary pine forms monospecific canopies and governs the endemic Canary pine forest ecosystem. Mature trees tend to reach up to 30 – 40 m in height. The species has a wide-ranging distribution, from close to sea level and up to the treeline (Weigel et al., 2018). Canary pine exhibits high phenotypic plasticity, allowing it to cope with a broad spectrum of environmental conditions (López et al., 2010). Population genetics studies have shown differences between sites and adaptations to aridity at lower elevations, although the species builds large coherent forests with high levels of gene flow (López de Heredia et al., 2014). Considering its phylogenetic age of ca. 20 Ma (Eckert and Hall, 2006; Jin et al., 2021), it may be surprising that no further diversification of this key species occurred within the archipelago. However, despite geographic isolation, populations of Canary pine appear to remain connected across the archipelago through wind dispersal and birds (Nogales et al., 1999).

2.3. Data collection

We collected seedling abundance data in 117 plots of 5 m radius (ca. 78.5 m^2) to assess first-year seedling establishment of the Canary pine forest on La Palma in April 2023. Seedling abundance in all plots was classified based on the following scale: zero seedlings, < 10 seedlings, 10 – 50 seedlings, and > 50 seedlings. These values correspond to seedling densities of 0 ind. / m^2, < 0.13 ind. / m^2, 0.13 – 0.64 ind. / m^2, and > 0.64 ind. / m^2, respectively. We only counted one-year-old seedlings and excluded any epicormic shoots originating from the trunk or roots of mature trees. Furthermore, we also recorded seedling densities for five randomly placed 1 m^2 quadrats within each plot. Since much of the Canary pine forest extends across steep ridges and down into inaccessible ravines, we randomly chose the location of all plots in-situ, using management roads and hiking paths to access sampling sites to ensure reachability (all plots were set at least 50 m into the forest). We maintained a minimum distance between plots of roughly 200 m. We focused our sampling on the southern pine forest, aiming to get representative coverage of the volcanic eruption as well as adjacent areas that had previously burned in 2012 and 2016. Elsewhere on the island, we aimed to sample forest areas, which had been undisturbed by fires for at least 10 – 15 years, in three major climatic zones: the humid northeast, arid northwest, and mild southeast.

2.4. Remote sensing

We quantified the impact of the volcanic eruption and previous wildfires in 2012 and 2016 using remote sensing data (Table 1; see Figure S1 for visualization of predictors). Plot-level seedling abundance data was then combined with remote sensing data to test our hypotheses.

The depth of the new tephra layer was obtained from an interpolation by Shatto et al. (2024a). Euclidean distance was calculated from each plot to the volcanic crater at (28°36′46″ N, 17°51′58″ W). We used NDVI (normalized difference vegetation index), a popular metric for assessing changes in vegetation health, to quantify vegetation damage caused by the eruption ($\Delta NDVI_e$), the recovery afterwards ($\Delta NDVI_r$),

Table 1
Description of all predictor variables that were investigated in this study.

Predictors [units]	Explanation	Data Basis	Reference
Distance [m]	The effects of the volcanic eruption and the favorable conditions for seedling establishment are expected to wane as distance from the crater increases.	The Euclidean distance between each plot and the eruption crater at (28°36′46″ N, 17°51′58″ W) was calculated.	-
Tephra depth [cm]	Depth of the fresh tephra layer accumulated during the recent eruption. Existing vegetation cover was buried, creating a potentially nutrient-rich germination bed for Canary pine seedlings.	Inverse Distance Weighting interpolation of a combined dataset compiled from in-situ and drone-based tephra measurements.	Shatto et al., (2024a)
$\Delta NDVI_e$	Percent difference in NDVI before and after the eruption. High reductions in NDVI are likely associated with loss of needles and opening of the canopy, increasing the sunlight that reaches the forest floor.	Cloud-free Sentinel−2 Level 2 A imagery; 3 January 2022 – 30 November 2019	Weiser et al., (2022)
$\Delta NDVI_r$	Percent difference in NDVI between the period directly following the eruption and one year later. Proxy for the recovery of the Canary pine ecosystem.	Cloud-free Sentinel−2 Level 2 A imagery; 28 April 2023 – 28 April 2022	Copernicus
$\Delta NDVI_{2012}$	Percent difference in NDVI before and after the July – August 2012 wildfire. Proxy for wildfire severity.	MOD13Q1.061 Terra Vegetation Indices 16-Day Global 250 m ("MODIS/061/MOD13Q1")	Google Earth Engine Data Catalog
$\Delta NDVI_{2016}$	Percent difference in NDVI before and after the August 2016 wildfire. Proxy for wildfire severity.	MOD13Q1.061 Terra Vegetation Indices 16-Day Global 250 m ("MODIS/061/MOD13Q1")	Google Earth Engine Data Catalog

and as a proxy for the impact of the 2012 and 2016 wildfires ($\Delta NDVI_{2012}$ and $\Delta NDVI_{2016}$, respectively). We adopted $\Delta NDVI_e$, which was calculated between 30 November 2019 and 3 January 2022, from Weiser et al. (2022). We calculated $\Delta NDVI_r$ using two cloud-free Sentinel-2 Level-2A images from 28 April 2023 and 28 April 2022. $\Delta NDVI_{2012}$ and $\Delta NDVI_{2016}$ were calculated using MODIS Terra 16-Day 250 m NDVI composites with Google Earth Engine (Gorelick et al., 2017; see Methods in Supplementary Material for explanation of sensor choice).

2.5. Data Analysis

We partitioned our analysis into a separate univariate and multivariate approach to explore the data thoroughly from different perspectives. All data preparation and analyses were carried out in R version 4.4 (R Core Team, 2024) and QGIS version 3.28 (QGIS.org, 2024).

In the univariate approach, we examined the relationship between seedling abundance classes and each individual predictor (Table 1). We also checked for possible relationships with topographic variables, including slope, elevation, and aspect (see Figure S4). Furthermore, we categorized our plots into three groups: those impacted by both wildfires and the volcanic eruption, those affected exclusively by the volcanic

eruption, and recently undisturbed plots. We then assessed whether mean seedling densities (ind./m²) differed significantly between these categories. Kruskal-Wallis test was applied to test for significant differences between seedling classes or plot categories. Afterwards, pairwise post-hoc Dunn's tests were performed, and significance thresholds were adjusted using the Benjamini-Hochberg approach to correct for multiple comparisons (Benjamini and Hochberg, 1995).

Next, in our multivariate approach, we fitted generalized additive models (GAM) from the binomial family using a binary logistic response variable of the > 50 seedlings class (1) against all other lesser abundance classes (0). GAMs are a flexible extension of generalized linear models that use smooth functions to allow for non-linear relationships between each predictor and the response variable (Wood, 2011; 2017). We aimed to use the > 50 seedlings class as a proxy for modelling, predicting, and mapping the presence of suitable conditions that lead to unusually high seedling establishment post-eruption. We checked for multicollinearity by performing a pairwise Pearson correlation analysis and calculated the variance inflation factor (VIF) for all predictors. Pearson correlation analysis was carried out using the *corrplot* package (Wei and Simko, 2021) and VIF was calculated using the *usdm* package (Naimi et al., 2014).

We fitted GAMs using the *mgcv* package (Wood and Wood, 2015) and specified smooth terms with cubic splines for all predictors to account for possible non-linear effects of our predictor variables on the likelihood of finding > 50 seedlings. We used backwards AIC selection (Akaike information criterion) from the full model containing all predictors to select the most parsimonious model. Model goodness-of-fit was evaluated using deviance explained. To validate model fit, we performed leave-one-out cross validation and calculated the mean Brier score over all folds. Brier score is a simple metric for testing the accuracy of class predictions, defined as the mean squared difference between predicted probabilities and the true outcome (Brier, 1950). We used the *DHARMa* package (Hartig, 2022) to perform model diagnostics, including testing for spatial autocorrelation and uniformity of residuals. Lastly, we tested whether the inclusion of any topographical variables (elevation, slope, or aspect) would lead to a more parsimonious model by accounting for potential confounding effects (see Table S2).

We used adjusted prediction plots to visualize the fitted relationship between individual predictors and the likelihood of finding > 50 seedlings. In these plots, all predictors except for the focal one are marginalized over and held constant at fixed values (at their median values, in our case), enabling the fitted relationship between the focal predictor
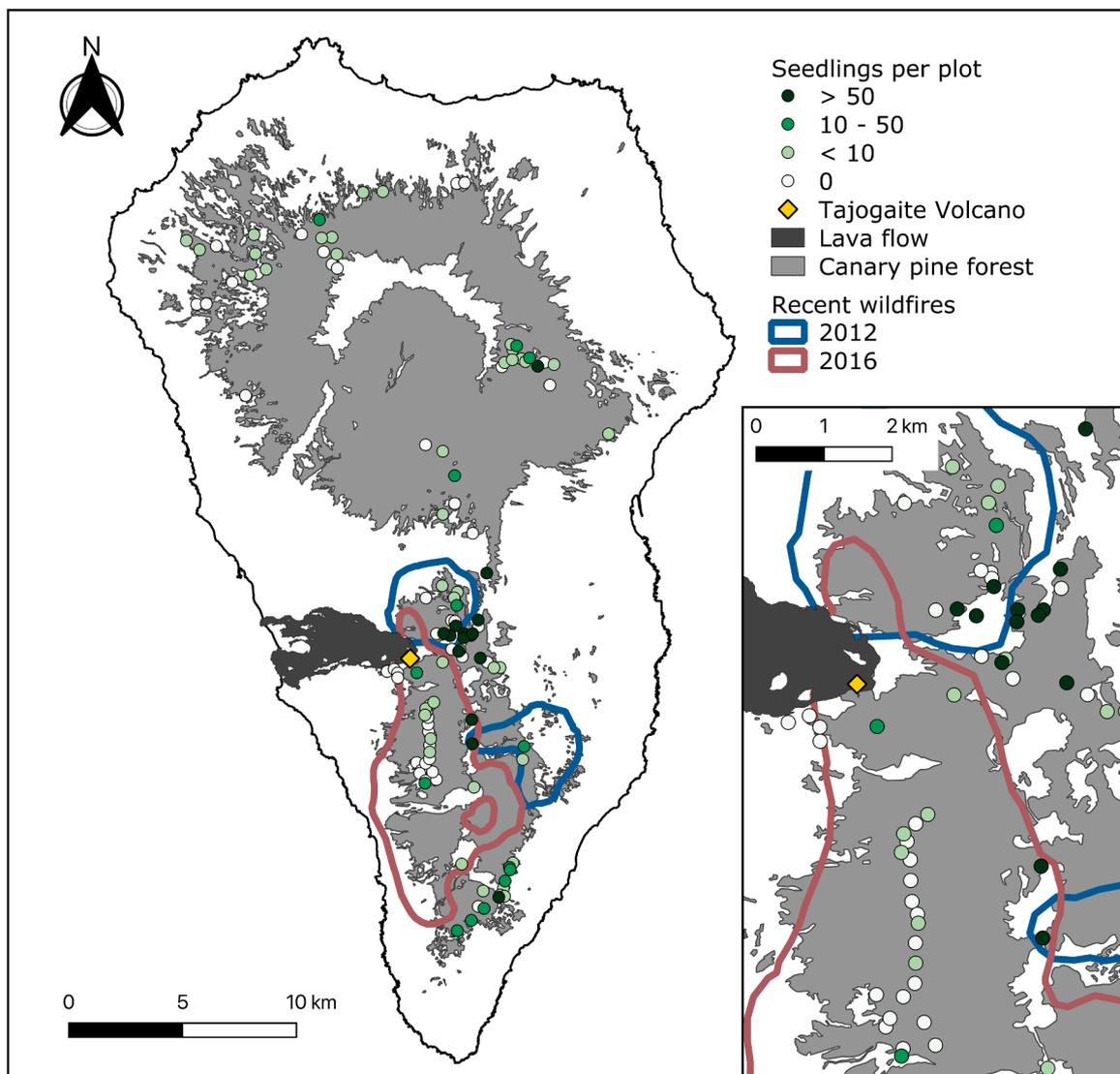

Fig. 3. Results of field data collection of Canary pine seedling abundance at 117 plots (5 m radius) across the island of La Palma. The approximate areas burned during recent wildfires in 2012 and 2016, obtained from EFFIS Emergency Services Management, have been overlayed. The extent of the lava flow and the location of the eruption crater of the Tajogaite Volcano are shown.

and the response to be observed. Lastly, we used our fitted model to produce a spatial prediction for the presence of > 50 seedlings across the southern Canary pine forest.

3. Results

Mapping seedling abundance data revealed an unusual clustering of most plots containing > 50 seedlings in the forest east of the Tajogaite Volcano (Fig. 3). The area impacted by 2012 and 2016 wildfires showed relatively lower seedling abundance, with most plots containing either zero or < 10 seedlings. Seedling densities, obtained through sampling of five randomly placed 1 m^2 quadrats within each plot, generally showed similar spatial patterns (Figure S1). Of the 117 plots surveyed, we found 47 to contain zero seedlings, 41 to contain < 10 seedlings, 14 to contain $10 - 50$ seedlings, and 15 to contain > 50 seedlings.

Plots containing > 50 seedlings tended to be closer to the crater (lower distance), to have a higher tephra depth, to have experienced more damage during the eruption (negative $\Delta NDVI_e$), and to have a higher recovery afterwards (positive $\Delta NDVI_r$) (Fig. 4). These differences were found to be significant when compared with lower abundance classes, but not always when compared with plots containing zero seedlings. In the case of tephra depth, differences may also have been skewed by several zero seedling plots located on an extremely deep tephra layer ($2 - 3$ m) close to crater. While $\Delta NDVI_{2012}$ showed no significant differences between abundance classes, $\Delta NDVI_{2016}$ was significantly greater for the > 50 seedlings class compared to the zero seedlings class. Supplemental analysis with topographic variables, including elevation, slope, and aspect showed no notable significant differences between seedling abundance classes (Figure S4).

Mean seedling densities (ind./m^2) were compared across three disturbance categories—plots affected by both wildfires and the eruption, undisturbed plots, and plots affected only by the eruption—separately for all plots (Fig. 5a) and plots containing at least one seedling (Fig. 5b). When all plots were considered, plots impacted by the volcano were found to have significantly higher mean seedling densities than plots affected by both wildfires and the eruption. Differences with undisturbed plots were not found to be significant. However, when only plots containing at least one seedling are considered, plots impacted by the volcano showed significantly higher mean seedling densities than both previously burned plots and undisturbed plots.

Pearson correlation analysis of all predictor variables (Figure S3) revealed the strongest correlation, with a coefficient of -0.72, occurring between tephra depth and $\Delta NDVI_e$. However, this was below the threshold of $|r| < 0.8$, following the criteria of Shrestha (2020), for considering predictor variable removal. Furthermore, VIF was found to be well below 5 for all predictors (Table S1 in Supplementary Material; Marcoulides and Raykov, 2019). Therefore, we proceeded to fitting our GAM with all predictor variables as previously outlined in Table 1.

We performed backwards AIC selection from our full model to the most parsimonious model. During this process, $\Delta NDVI_{2012}$ was removed from our model. Our final fitted model had a deviance explained of 40.5 % and a mean Brier score of 0.06, indicating both goodness-of-fit and stability during cross validation (Table 2). We conducted model diagnostics and found no significant spatial autocorrelation, while also confirming the uniformity of the residuals (see Supplementary Materials for details). Robustness tests with topographic variables revealed no grounds for their inclusion in the final model (Table S2 in Supplementary Material).

Distance to the eruption crater ($\chi^2 = 3.656$, p-value $= 0.023$), $\Delta NDVI_e$ ($\chi^2 = 1.646$, p-value $= 0.043$), $\Delta NDVI_r$ ($\chi^2 = 3.417$, p-value $= 0.046$), and $\Delta NDVI_{2016}$ ($\chi^2 = 8.864$, p-value $= 0.002$) were found to be significantly associated with the probability of finding > 50 seedlings in a plot. The effect of tephra depth was not found to be significant, although it approached significance ($\chi^2 = 3.660$, p-value $= 0.057$).

We plotted adjusted prediction curves for all predictors remaining in the final model (Fig. 6a). Our final fitted model revealed that as the

distance to the eruption crater decreased, the probability of finding > 50 seedlings increased. As tephra depth decreased, a plateau in the likelihood of finding > 50 seedlings was reached between 0 and 10 cm, though this predictor was not found to be significant. Areas that were heavily impacted by the eruption ($\Delta NDVI_e$) as well as areas that experienced high recovery afterwards ($\Delta NDVI_e$) showed a notable increase in the likelihood of finding > 50 seedlings. Lastly, the probability of finding > 50 seedlings rapidly approached zero for sites that were moderately to severely affected by the 2016 wildfire ($\Delta NDVI_{2016} < -25$ %). We used the fitted model to make a spatial prediction for the expected distribution of the > 50 seedlings class across the southern Canary pine forest (Fig. 6b).

4. Discussion

4.1. Ecological implications

We found evidence that first-year seedling establishment of Canary pine was locally enhanced by the recent eruption. Both univariate and multivariate analyses concurred that volcanic predictors like distance to the crater, $\Delta NDVI_e$, and $\Delta NDVI_r$ were significantly associated with high seedling abundance (> 50 per 5 m radius plot). When controlling for variability in seed availability by considering only plots containing at least one seedling, we found mean seedling densities to be significantly higher in plots impacted by the volcano than plots that were either undisturbed or had also been previously burned. Furthermore, we observed peak seedling densities east of the volcano similar to densities that have been reported in studies of post-fire seedling establishment (Höllermann, 2000; Otto et al., 2010; Méndez et al., 2015). Quadrats containing $10 - 12$ seedlings / m^2 were found within several plots near Refugio El Pilar (Figure S2). For reference, Otto et al. (2010) detected peaks of $14 - 16$ seedlings / m^2 at moderate to high-severity fire sites after the 2007 wildfire on Tenerife. Of the 15 plots found to contain > 50 seedlings, 13 were located within the 7 km impact radius of the volcanic eruption, as identified by Weiser et al. (2022). We did not observe a comparable abundance of one-year-old seedlings in other parts of the island, implying that this was a one-off event tied to the volcanic eruption. However, this finding did not hold for forests near the volcano that had previously burned. Mean seedling densities were found to be significantly higher in plots impacted exclusively by the volcano than in plots affected by both the volcano and past wildfires. This discrepancy was especially pronounced to the south, as $\Delta NDVI_{2016}$ remained a significant predictor in our model.

These results were consistent with our hypotheses. The observed spatial pattern of seedling abundance is unlikely to be attributable to the anisotropic impact of the eruption. Although both Weiser et al. (2022) and Shatto et al. (2024b) found anisotropic patterns in vegetation damage and recovery rate, these effects were likely already accounted for in our model by $\Delta NDVI_e$ and $\Delta NDVI_r$. Microclimate and fine-scale topographic heterogeneity has been previously found to influence post-fire regeneration in *Pinus contorta* Douglas ex Loudon and *Pseudotsuga menziesii* var. *latifolia* (Mirb.) Franco forests (Hoecker et al., 2020) as well as in mixed-conifer forests in the Bitterroot Range of the Rocky Mountains (Clark-Wolf et al., 2022). We ruled out the possibility of topographical variables like elevation, slope, and aspect having a confounding influence in our model, finding also no significant differences in univariate analysis between plots containing > 50 seedlings and other abundance classes. Due to the lack of a reliable network of meteorological stations before late 2022, real-time precipitation data was unavailable for most of the period following the eruption. However, available precipitation data from October 2022 up to field data collection in April 2023 is indicative of a dry winter (Cabildo de La Palma). Nevertheless, we cannot completely rule out the influence of precipitation. There are also many unresolved questions about water availability and water-holding capacity of young tephra layers.

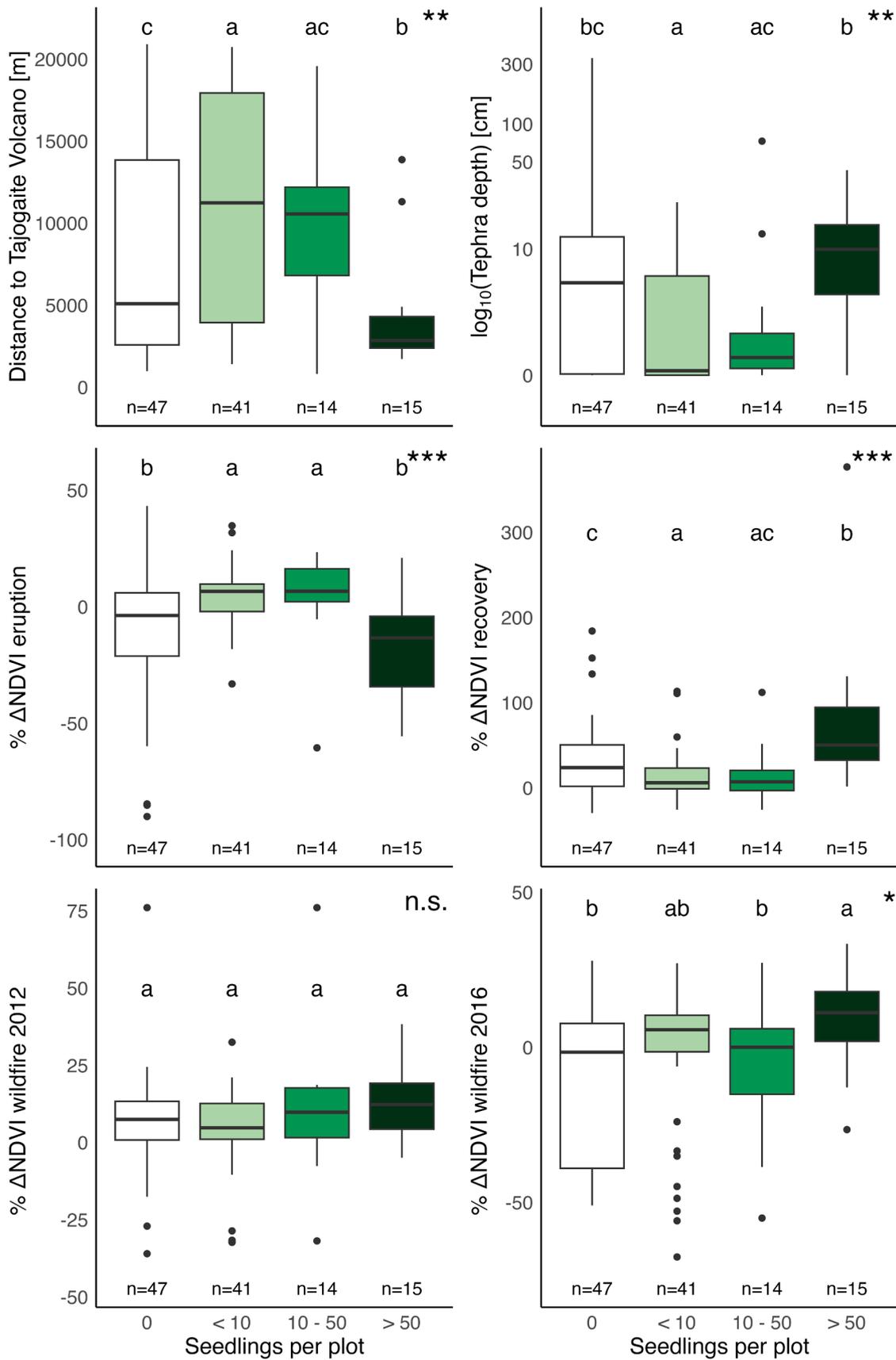Conifers exhibit complex and time-consuming pollination,

Fig. 4. Boxplots displaying how predictors varied across seedling abundance classes. Significance levels in the top-right of each boxplot indicate the results of the Kruskal-Wallis test (n.s. not significant, * p < 0.05, ** p < 0.01, *** p < 0.001). Compact letter display was calculated using post-hoc pairwise Dunn's tests and the significance threshold was adjusted accordingly with a Benjamini–Hochberg correction for multiple comparisons. Colors correspond to seedling abundance classes shown in Fig. 3.
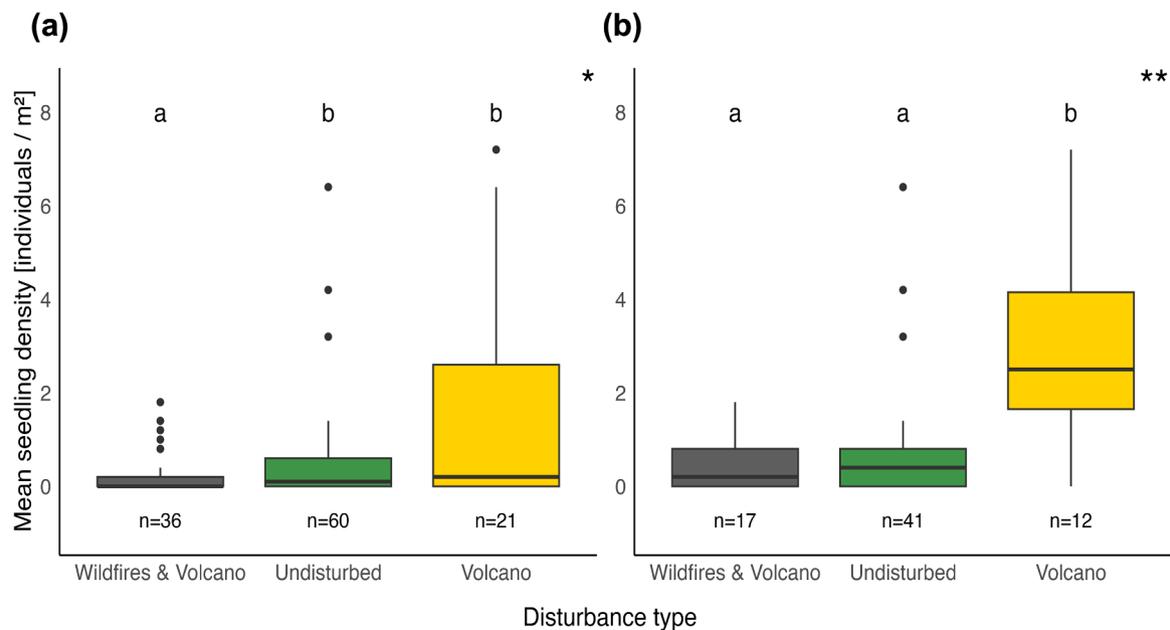
Fig. 5. Boxplots displaying differences in mean Canary pine seedling density, depending on whether a plot was affected by both wildfires and volcanic eruption, by the eruption exclusively, or was undisturbed. **(a)** includes all 117 plots; **(b)** includes only plots that contained at least one seedling individual. Significance levels in the top-right of each boxplot indicate the results of the Kruskal-Wallis test (n.s. not significant, * p < 0.05, ** p < 0.01, *** p < 0.001). Compact letter display was calculated using post-hoc pairwise Dunn's tests and the significance threshold was adjusted accordingly with a Benjamini–Hochberg correction for multiple comparisons.

Table 2

Model summary statistics for the final generalized additive model fitted to the data after backwards AIC selection. Estimated degrees of freedom (EDF) and results of the Chi-squared tests (χ^2) for each predictor are shown. The statistical significance of each smooth term is indicated by p-values. Goodness-of-fit was evaluated with deviance explained and model fit was validated using the mean Brier score, calculated across all folds during leave-one-out cross validation. The AIC score of the final model is shown.

Predictors	EDF	χ^2	p-value
Distance	0.971	3.656	**0.023**
Tephra depth	1.391	3.660	0.057
$\Delta NDVI_e$	0.470	1.646	**0.044**
$\Delta NDVI_r$	1.189	3.417	**0.046**
$\Delta NDVI_{2016}$	1.384	8.864	**0.002**
Deviance explained: 40.5 %	Brier score (LOOCV): 0.06	AIC: 69.62	

fertilization, and maturation of seeds (Tomlinson and Takaso, 2002; Williams, 2009). In *Pinus*, the reproductive cycle generally lasts 3 – 4 years, but can be even longer for some sub-tropical and tropical species (Fernando, 2014). Severe disturbances such as crown-fires could further delay this process, as adult individuals will likely invest resources into the recovery of photosynthetic and structural organs before reproductive ones (Méndez, 2010; "fight or flight?", Lauder et al., 2019). We speculate that the wildfire in 2016 depleted reserves of serotinous cones on mature trees. In consequence, the canopy seed bank was still recovering by the time of the 2021 eruption ("immaturity risk", Keeley et al., 1999). Additionally, the soil seed bank was buried under a layer of tephra ranging from a few centimeters to several meters in depth (Medina et al., in prep.; Shatto et al., 2024a). To the east of the crater, near Refugio El Pilar, there are old growth stands that have not burned in decades. The canopy seed bank in these stands would have been well-developed, resulting in a huge abundance of first-year seedlings when seed release was stimulated. The mechanism by which the eruption or post-eruption conditions could have triggered seed release is not entirely clear. Serotinous cones of Canary pine are known to open after reaching certain temperature thresholds during a fire, but xeric

conditions can also soften the resin that keeps the scales glued together (Escudero et al., 1999; Climent et al., 2004; Fernando, 2014).

A localized pulse in the establishment of first-year seedlings will not necessarily translate into functional regeneration unless seedlings develop into juveniles and juvenile recruitment is successful. The juvenile phase is known to be particularly sensitive (Jackson et al., 2009). In Canary pine, mortality of first-year seedlings has been found to be very high, particularly when germinating under post-disturbance conditions (Méndez, 2010). However, mortality rates of established seedlings on young tephra layers post-volcanic eruption are not known. Further investigation and long-term monitoring are required to draw conclusions about the effects of volcanic eruptions on functional regeneration of the Canary pine forest.

4.2. Volcanic eruption and wildfire

Severe and abrupt disturbances can cause complete upheavals of existing ecosystems. However, if they are recurrent, surviving individuals are selected towards adaptation and recovery, even if the severity of these disturbance pulses and the responses of species, communities, and ecosystems to them vary (Jones and Schmitz, 2009; Jentsch and White, 2019; Hillebrand and Kunze, 2020). Strombolian-type volcanic eruptions are characteristic for oceanic islands, including the recurrent deposition of pyroclastic ashes, forming thick tephra layers as a new substrate (Beierkuhnlein et al., 2023). Considering its phylogenetic age (ca. 20 Ma), it is plausible that Canary pine has been exposed to such impacts over evolutionary timescales (Eckert and Hall, 2006; Navascués et al., 2006; Jin et al., 2021).

Although there is good evidence for the existence of a natural fire regime in the Canary Islands, current data does not extend back further than the Late Pleistocene, with most records dating to the Holocene. Natural wildfires have been detected through palaeoecological studies on Tenerife from 4700 – 2000 yr BP (de Nascimento et al., 2009), on La Gomera since at least 7000 yr BP (Nogué et al., 2013), and in the Gran Canaria highlands between 4800 and 2000 yr BP (possibly linked to volcanic activity; Ravazzi et al., 2021). The earliest evidence of fires in the archipelago was found in sediments from Gran Canaria, dated to 27,
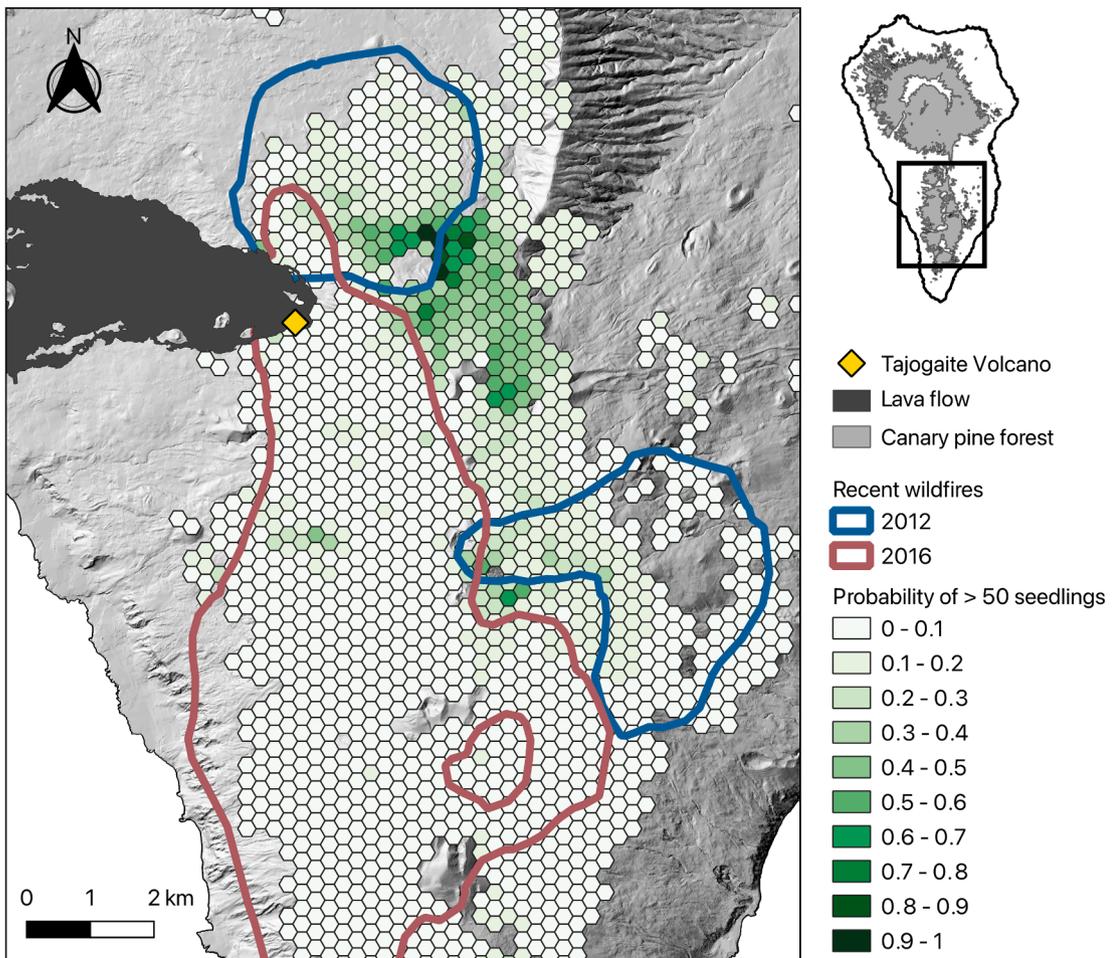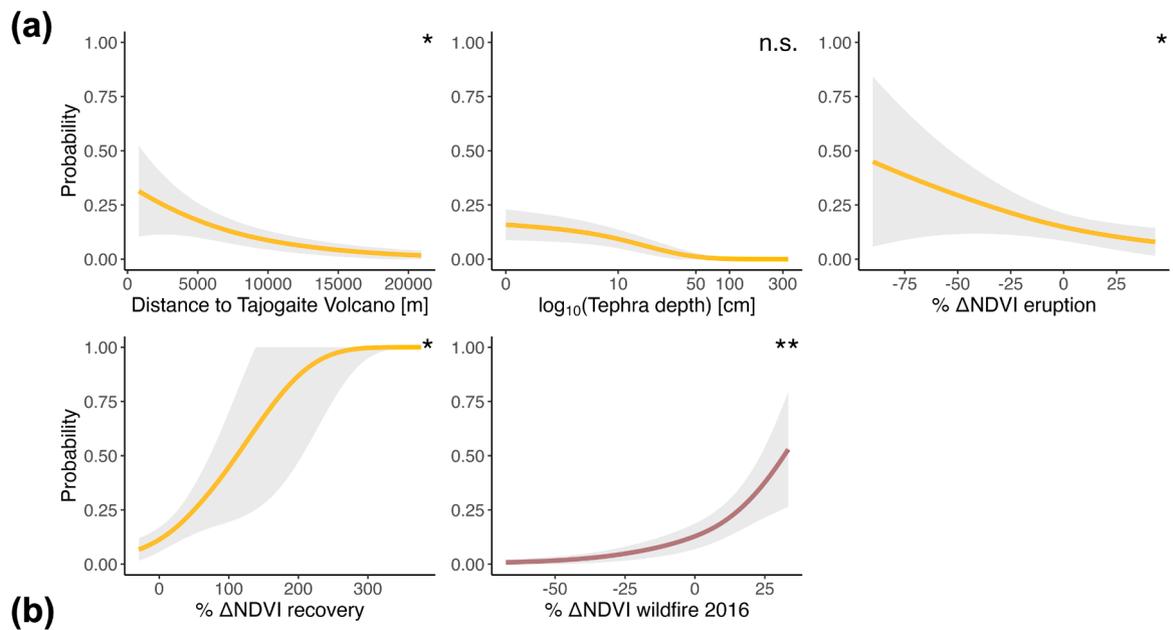
Fig. 6. (a) Adjusted predictions for the final model, showing the relationship between all predictors and the response (probability of finding > 50 seedlings), when all other predictors except for the focal predictor are fixed at their median values. Solid lines show fitted curves, with colors corresponding to the colors in Fig. 6b, whereas shaded areas denote 95 % confidence intervals. Significance levels in the top-right of each plot indicate the results of the Chi-squared test for each predictor (n.s. not significant, * p < 0.05, ** p < 0.01, *** p < 0.001). (b) Model prediction of the probability of finding > 50 seedlings for the southern Canary pine forest, projected onto a 250 m hexagon grid. The approximate areas burned during recent wildfires in 2012 and 2016, obtained from EFFIS Emergency Services Management, have been overlayed. The extent of the lava flow and the location of the eruption crater of the Tajogaite Volcano are shown.

000 – 26,000 yr BP (Martín, 2023). It has been estimated that only between 0.4 – 0.5 % of known fires in the Canary Islands were ignited by lightning, suggesting that natural fire return intervals must be quite long, in the range of multiple decades or centuries (Höllermann, 2000; Climent et al., 2004).

Generally, though, evidence of natural fires is irregular and microcharcoal remnants first become very prominent in sediments only around 3000 – 2000 yr BP, coinciding with the arrival and settlement of humans in the archipelago (Mitchell, 2023; Serrano et al., 2023). The archipelago's first inhabitants, the Guanches, likely utilized fire regularly to maintain open landscapes for pastureland and agriculture (de Nascimento et al., 2009). Following settlement by the Spanish in the late 15th century, deliberate forest fires were outlawed (Molina-Terrén et al., 2016). Dendrochronological analyses have estimated composite fire return intervals on La Palma since 1850, finding that mean return intervals were quite short during periods of intensive land use in the 19th century (1.4 years), before increasing to 2.7 – 9.2 years under modern fire management (Molina-Terrén et al., 2016). The emergence of the current anthropogenic fire regime could also be influenced by the aridification of climatic conditions in North Africa, which is considered a driver of wildfire abundance (Nogué et al., 2013).

Given that wildfires appear irregularly in the palaeoecological record of the Canary Islands prior to human habitation and that we have limited understanding of the natural fire regime prior to the Late Pleistocene, it is worth questioning whether apparent adaptations of Canary pine to fire represent evolved traits specific to fire survival and resilience, or if those traits are a coincidental byproduct of selection due to volcanic activity. The most recent volcanic eruption surprisingly demonstrated that agents other than wildfire can trigger both epicormic resprouting as well as seed release from serotinous cones, leading to high first-year seedling establishment. However, epicormic resprouting and serotiny are characteristic for many tree species typically natie to fire-prone ecosystems with sub-tropical or Mediterranean climates, most of which are not prone to volcanism (Pausas et al., 2017; Pausas and Keeley, 2017). For these reasons, the reverse scenario must also be considered: traits in Canary pine that support resilience to volcanic eruptions could be coincidental byproducts of fire-specific adaptations, perhaps even inherited from ancestral species on the continent (Navascués, 2005).

Most likely, both fires and volcanic eruptions have significantly shaped the evolutionary history of Canary pine and of the Canary pine forest ecosystem. Disentangling the legacies of these disturbances should be a priority for further research.

4.3. Management implications

The Canary pine forest ecosystem provides essential ecosystem services for the human society of the Canary Islands. The water balance of the western Canary Islands heavily depends on moisture from trade wind clouds that first condenses on the long needles of trees before infiltrating into the ground as fog drip (Aboal et al., 2000; Marzol-Jaén et al., 2010). Within these monodominant forests, Canary pine cannot be replaced by other native species. Therefore, investigating the potential extent of forest regeneration pulses and the mechanisms that facilitate seedling establishment are critical to forest management and conserving this vital ecosystem.

For many tree species, functional regeneration is closely linked to disturbance dynamics through the creation of environmental heterogeneity and resource abundance. As a heliophile species, canopy closure and thick accumulation of needle litter can inhibit functional regeneration of Canary pine, especially in closed humid forest stands. Therefore, disturbances of any kind, including wildfires and volcanic eruptions, as well as landslides, storms, and other gap dynamics, create opportunities for regeneration. Forest management activities, such as thinning or the creation of artificial gaps, seem to have strong positive effects on juvenile recruitment in Canary pine plantations (Arévalo and

Fernández-Palacios, 2008; Arévalo et al., 2011; Otto et al., 2012). Chlorotic damage caused by exposure of Canary pine trees to sulfuric gases led to widespread crown defoliation upwards of 7 km away from the eruption (Weiser et al., 2022). The resulting sunlight abundance combined with a fresh nutrient-rich tephra layer likely facilitated the perfect germination conditions for Canary pine seedlings.

However, if return intervals are shortened or disturbance severity exceeds natural system dynamics, critical life-cycle processes could be inhibited. Today, wildfires in the Canary Islands are mostly ignited through human activity. Their high frequency, high severity, and large spatial extent no doubt exceed the natural fire cycles and could even threaten reproduction of other endemic species (Garzón-Machado et al., 2012). Global fire-regimes are undergoing significant changes as more frequent favorable conditions, such as drought years, coincide with an increased likelihood of ignition due to human activities (Pausas and Keeley, 2021). Current projections for wildfire risk in the Canary Islands under various climate change scenarios anticipate drastic increases in the length of the fire season and the number of extreme risk days (Carrillo et al., 2022).

We found that to the south of the volcano, first-year seedling establishment of Canary pine was likely constrained due to an insufficient recovery time between compounding disturbances. Comparable findings have been reported for *Pinus halepensis* Mill. (Màrcia et al., 2006; Espelta et al., 2008), *Pinus contorta* (Braziunas et al., 2023), and eucalypt (Fairman et al., 2015; 2019) stands affected by recurrent wildfires, which may also limit long-term regeneration in those forests. Our results demonstrate that recurrent disturbances with shortened return intervals can even adversely affect seedling establishment in Canary pine, a species considered to be highly resilient to disturbances as well as dependent upon them for regeneration.

While infrequent disturbances of intermediate severity are crucial for ecosystem functioning, disturbances of unnatural return interval and severity—to which the species is not adapted—could threaten the future population demography of Canary pine stands, especially if processes like seedling establishment are inhibited. The high frequency and large extent of recent wildfires on the island of La Palma evokes the issue of wildfire management. Although both passive (fire breaks) and active measures (deployment of firefighters to extinguish fires) are employed, fire management on La Palma is limited by availability of personnel and accessibility of terrain. Generally, the safety of human lives and structures are prioritized, allowing fires to spread freely away from inhabited areas. Currently, 83 % of the Canary pine forest on La Palma falls within protected areas (Weiser et al., 2022), a designation that comes with restrictions to both management and land-use. If natural dynamics are threatened, the Canary pine forest may require additional human intervention in the long term, such as more sophisticated active fire control or assisted regeneration, to ensure the stability of this unique ecosystem. Further research should prioritize identifying the minimum fire return interval as well as quantifying the level of natural regeneration required to maintain existing population structures over long timescales.

5. Conclusion

In this study, we investigated how first-year seedling establishment in Canary pine responded to a volcanic eruption, and if recent wildfires had modified this response. We found evidence that the 2021 Cumbre Vieja volcanic eruption facilitated a pulse of first-year seedling establishment to the east of the crater near Refugio El Pilar. However, particularly in the south, stands affected by recent wildfires showed a comparatively lower abundance and even absence of one-year-old seedlings. We believe that a shortened return interval between disturbances did not allow enough time for the canopy seed bank to recover before the eruption, while the soil seed bank was subsequently buried under fresh tephra deposits. It is not clear whether wildfires or volcanic eruptions are the major drivers for the dominance patterns of Canary

pine, as both disturbances likely played significant roles in shaping the evolutionary history of the species and the ecosystem supported under its canopy. Lastly, given our results, we raise the question of whether recurrent disturbances of an unnatural severity and shortened return interval could pose a systemic threat to the future population stability of Canary pine. Individual mature trees seem to exhibit excellent resilience to wildfire and volcanic eruption, but this cannot translate into sustained population dynamics if sensitive life stages such as seedling establishment fail.

CRediT authorship contribution statement

Manuel Nogales: Writing – review & editing. **Anke Jentsch:** Writing – review & editing. **María Guerrero-Campos:** Writing – review & editing. **Patricia Marrero:** Writing – review & editing. **Félix M. Medina:** Writing – review & editing. **Anna Walentowitz:** Writing – review & editing, Methodology. **Christopher Shatto:** Writing – review & editing, Methodology. **Rüdiger Otto:** Writing – review & editing. **Frank Weiser:** Writing – review & editing, Methodology. **Carl Beier-kuhnlein:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Conceptualization. **Vincent Wilkens:** Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Data curation. **Ole R. Vetaas:** Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2024.122468.

Data availability

Data will be made available on request.

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