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Fine-scale topographic filtering and seed limitation shape post-fire regeneration patterns in Mediterranean pine forests

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1 Abstract

Post-fire regeneration in Mediterranean pine forests is increasingly constrained by recurrent high-severity fires and changing climate conditions, while post-disturbance interventions such as salvage logging may further hinder natural recovery at the local scale. We assessed the drivers of early natural regeneration in a coastal *Pinus halepensis* Mill. forest in Spotorno (NW Italy) affected by two subsequent high-severity wildfires (September 2006 and July 2015) followed by salvage logging. Pine seedlings were mapped in spring 2025 with an RTK GNSS antenna, while high-resolution UAV images and LiDAR products were used to derive terrain- and forest structure-based predictors. Topographically mediated constraints on regeneration were quantified using the Topographic Wetness Index (TWI) and the Heat Load Index (HLI), which capture spatial variation in soil moisture accumulation and heat exposure. Seed availability was represented by the distance to remnant adult pines, identified from the canopy height model using a local-maximum filtering approach. Spatial point pattern analysis was used to test whether empirically evident regeneration clusters reflected plant–plant interactions, or environmentally-driven density variation. Drivers of regeneration were modelled using GLMs, GAMs and Random Forests (RF), and two pseudo-absence strategies in the RF were explicitly compared by training models with (i) ecologically informed, spatially homogeneous pseudo-absences and (ii) randomly sampled pseudo-absences. The informed pseudo-absence Random Forest achieved substantially higher discrimination (AUC = 0.895; ACC = 0.821; SEN = 0.785; SPE = 0.864) than the random-absence model (AUC = 0.653; ACC = 0.607; SEN = 0.648; SPE = 0.571). The best model was applied to generate a 5 x 5 m ecological suitability map identifying regeneration “hotspots”, i.e., near seed sources, in warm, well-drained microsite conditions, and persistent “coldspots” in convergent terrain and seed-limited areas. This workflow provides an operational, transferable basis for precision-oriented post-fire restoration planning in Mediterranean landscapes where passive recovery is uncertain.

2 Introduction

Over the last decades, natural disturbances have intensified globally, reshaping forests structure, composition and recovery trajectories. Across Europe, disturbance impacts have increased significantly since the mid-20th century, with strong increasing trends in both frequency and severity (Patacca et al., 2022)). These shifts are tightly linked to climate warming and growing drought stress, which amplify fire season, promote large windthrow events and favour insect outbreaks (Seidl et al., 2017; Stevens-Rumann et al., 2018). As a result, many low-elevation conifer forests are increasingly pushed toward regeneration thresholds where post-fire recovery is no longer guaranteed (Davis et al., 2019). Research indicates that recruitment failures are becoming more common after large fires coupled with droughts (Harvey et al., 2016), raising concerns over long-term ecosystem resilience. At the same time, early-successional ecosystems created by natural disturbances present high biodiversity, structural complexity and fundamental biological legacies (Franklin et al., 2000; Swanson et al., 2011). These legacies, i.e., deadwood, surviving trees, residual understory vegetation, support ecological processes essential for ecosystem recovery.

The Mediterranean Basin is one of the regions where these dynamics are most prominent. Coastal pine forests are exposed to strong summer drought, shallow soils, high solar radiation and recurrent high-severity wildfires, all of which constrain early post-fire forest regeneration. Seedling establishment depends largely on seed availability, particularly distance to surviving seed trees (Leverkus et al., 2014), but is also strongly

modulated by microsite conditions. Soil moisture and soil temperature exert a major control on recruitment success (Wooten et al., 2022), and biological legacies such as logs, stumps and coarse woody debris create favourable regeneration niches by buffering extreme temperatures, reducing evaporative losses and providing shade that improves near-ground microclimatic conditions (Marzano et al., 2013). In addition to nurse effects from shrubs and woody legacies, short-range aggregation among juvenile conspecifics may also arise under stressful conditions, potentially reflecting positive interactions or shared safe-site dynamics (Muhammed, 2020).

In Mediterranean ecosystems, shrub vegetation can further enhance regeneration by acting as nurse structures, mitigating thermal and hydric stress and facilitating seedling establishment under harsh post-fire conditions (Castro et al., 2011; Gómez-Aparicio et al., 2004; Padilla and Pugnaire, 2006). Deadwood may also protect seedlings from browsing in systems characterised by high ungulate pressure (Marangon et al., 2022). Conversely, salvage logging (SL), the removal of dead or damaged trees after fire, windthrow or insect outbreaks, can disrupt these facilitative mechanisms by removing woody legacies and shrub cover, leading to higher soil temperatures, reduced soil moisture and lower regeneration density (Marcolin et al., 2019).

Such complexity has led researchers to advocate for precision-based restoration strategies. Precision Forest Restoration (PFR; Castro et al., 2021) integrates fine-resolution environmental information, biological legacies and species-specific regeneration requirements to guide targeted interventions where natural recovery is unlikely. A PFR implementation relies on ecological niche modelling to evaluate the environmental conditions suitable for planting or sowing target species, making necessary the use of remotely derived, high-resolution indicators of ecosystem suitability. Variables such as slope, aspect, topographic driven soil moisture such as the Topographic Wetness Index (TWI; Beven and Kirby, 1979; Kopecký et al., 2021) and solar heat exposure (e.g., Heat Load index, HLI; McCune and Keon, 2002) are some of the environmental predictors that can be used to identify areas of high or low regeneration suitability (Cerioni et al., 2024). Identifying where establishment is hindered enables managers to prioritize active restoration through planting or microsite manipulation in critical zones, while allowing passive recovery elsewhere. This paradigm provides a robust ecological foundation for adapting management in regions where climate-driven disturbance regimes are intensifying (Müller et al., 2019).

Remote sensing and predictive modelling increasingly enable this shift from coarse post-fire assessments and homogeneous restoration to operationally actionable, fine-scale planning. UAV and LiDAR products can capture post-fire terrain controls, canopy structure and residual biological legacies at spatial grains relevant to seedling establishment, providing key inputs for spatial modelling and decision support (Martín-Alcón and Coll, 2016). Moreover, the integration of LiDAR-derived structure with modelling frameworks has also been proposed to strengthen disturbance-oriented assessments (e.g., fuel-related metrics supporting fire-behaviour applications), reinforcing the broader potential of close-range remote sensing for pre- and post-fire forest management (Mauri et al., 2025). When coupled with robust statistical or modelling approaches, these data can be translated into spatial predictions of regeneration suitability, supporting evidence-based decisions on where natural regeneration can be relied upon and where active restoration measures are required (Castro et al., 2021).

In parallel, post-disturbance interventions such as salvage logging remain widely implemented, often motivated by economic recovery, hazard mitigation or perceived fuel reduction. However, SL can act as a secondary disturbance and disrupt key ecological processes and structural legacies (Lindenmayer and Noss, 2006), with documented drawbacks on regeneration, microsite diversity and biodiversity in many contexts (Donato et al., 2006; Thorn et al., 2018). Evidence syntheses further indicate that SL rarely mitigates subsequent disturbances (Thompson et al., 2007) and may increase risks such as erosion and microclimatic stress under certain conditions (Leverkus et al., 2020), although outcomes are context-dependent and can vary with disturbance magnitude, operational intensity and stand history (Royo et al., 2016; Taerwe et al.,

2019). This strengthens the need for spatially explicit tools that help identify where natural recovery is likely to proceed alone and where targeted interventions are most justified.

In this study, we apply a precision-based framework to a coastal Mediterranean pine forest in Spotorno (Liguria, NW Italy) to investigate the environmental drivers of early post-fire forest regeneration and to support spatially explicit restoration planning. The site has been repeatedly affected by high-severity wildfires and subsequent salvage logging, providing a valuable natural laboratory to test regeneration controls and mapping approaches under compound disturbance conditions. Using airborne-derived environmental predictors and spatially explicit field observations, our objectives were to:

1. identify the main environmental drivers shaping early post-fire regeneration in a Mediterranean pine forest under repeated fire and post-fire management;
2. quantify their relative contribution using a machine-learning approach combined with ecologically informed pseudo-absences;
3. produce a high-resolution ecological suitability map to guide evidence-based restoration prioritisation.

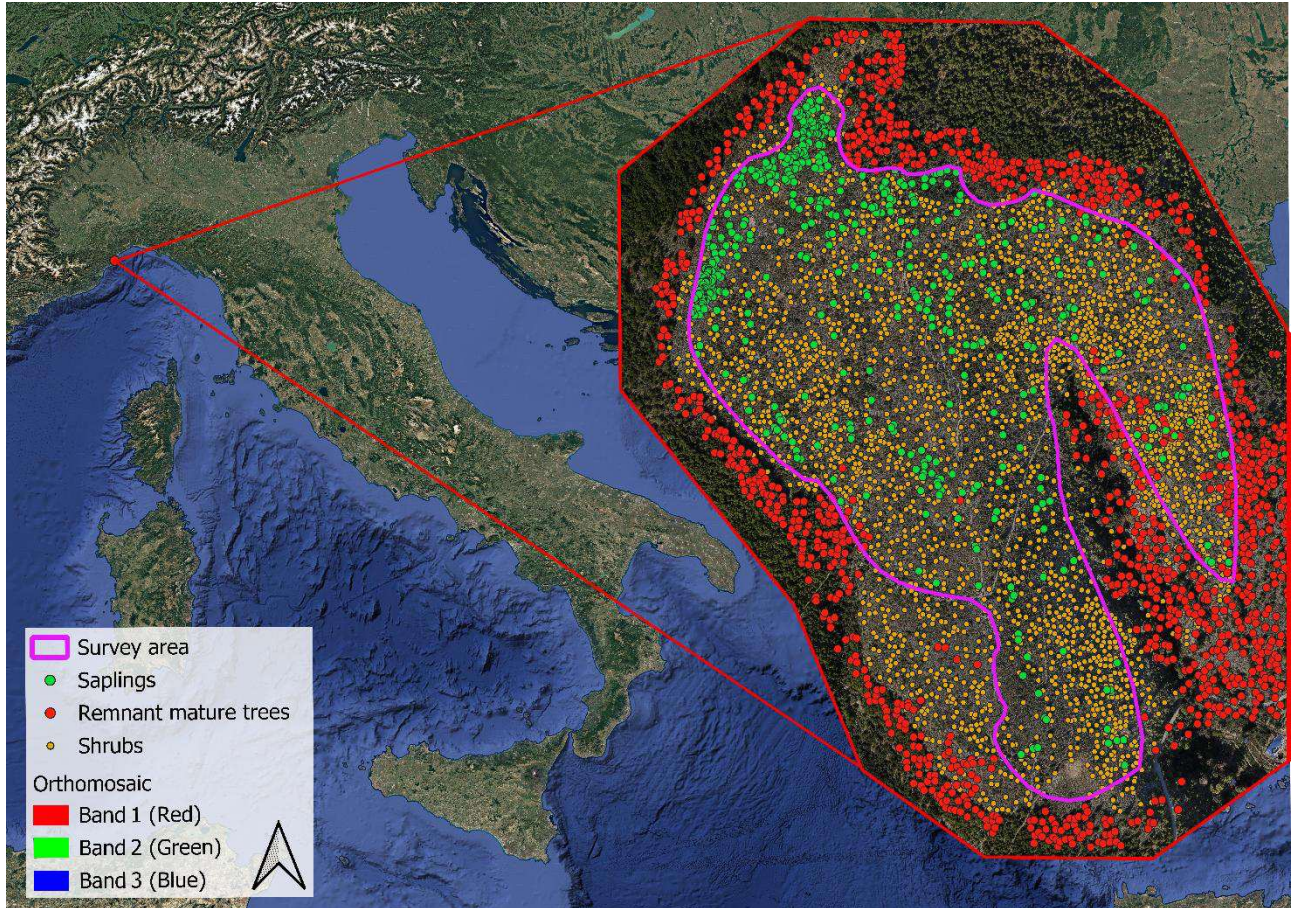
3 Materials and Methods

The study was carried out in a coastal Mediterranean pine forest located in Spotorno (Liguria, NW Italy) (Figure 1); the forest in the area was dominated by *Pinus halepensis* Mill. with scattered *Quercus ilex* L. individuals, and a diverse shrubs layer including *Pistacia lentiscus* L., *P. terebinthus* L., *Cotinus coggygria* Scop., *Cistus salviifolius* L., *Ulex parviflorus* Pourr. and *Juniperus communis* L. In the last twenty years the site experienced two high-severity wildfires (September 2006 and July 2015), and the subsequent post-fire salvage logging to reducing fuel loads. The study area (~12 ha) encompassed the entire burned slope except for a small southwestern sector and a 5–10 m buffer along the forest margin. These zones were excluded from sampling because they largely fell within the canopy projection area of remnant edge trees, where seed availability is structurally confounded with canopy cover: including them would have inflated regeneration estimates in a way that could not be disentangled from the distance-to-seed-source effect modelled across the rest of the slope. The combination of steep terrain, shallow soils, and recurrent dry seasons produced a heterogeneous post-fire environment where regeneration patterns vary sharply across short spatial scales.

3.1 Field data sampling and remote sensing acquisition

All naturally regenerating Aleppo pine (*Pinus halepensis* Mill.) seedlings in the study area were mapped in spring 2025 using an Emlid RX3 GNSS receiver operating in RTK mode, achieving sub-decimeter positional accuracy (Figure 1). Given the 2015 fire, saplings could be at most 10 years old at the time of sampling (spring 2025). However, comparing the height of the saplings with age estimations obtained by counting the internodes, most individuals appeared to have been established within the last 5 years. To characterize the post-fire structure of the stand, we acquired two UAV datasets: high-resolution RGB imagery to create a 2 cm orthomosaic; a LiDAR survey processed in TerraScan (Terrasolid Ltd., Finland) to derive a 2 cm Digital Surface Model (DSM) and a 2 cm Digital Terrain Model (DTM). The DTM was subsequently resampled to 5 m to ensure numerical stability in hydrological modelling. A 2 cm Canopy Height Model (CHM) was computed subtracting DSM and DTM. Remnant adult Aleppo pine trees were detected automatically from the CHM using a revised local maximum filtering method, following Xu et al.(2021). Trees exceeding 4 m in crown diameter and 4.5 m in height (modal values in the studied forest) were retained as seed-source individuals, and their position was used to compute Euclidean distances from seedling in QGIS and R (QGIS Development Team, 2023; R Core Team, 2024). The same crown-detection process was applied to map the shrubs (Figure 1). Shrubs were mapped using the same CHM-based local-maximum detection workflow (Figure 1). First, CHM pixels ≥ 4 m were masked out to exclude tree canopies and restrict the analysis to low-stature vegetation. Shrub canopies were then identified using given height thresholds (min = 0.5 m, max = 2.5 m)

136 and a minimum crown diameter of 0.5 m; non-vegetated surfaces and rock outcrops were excluded by
 137 restricting detection to vegetation-classified pixels in TerraScan. These objects were segmented from the
 138 CHM and converted to centroids, allowing the computation of Euclidean distance-to-shrubs. To avoid double
 139 counting and ensure consistency with field observations, any CHM-derived tree or shrub centroid
 140 overlapping with a field-mapped individual was graphically verified through the high-resolution UAV
 141 orthomosaic, confirming that the local CHM maximum corresponded to a tree or shrub canopy rather than a
 142 seedling establishing beneath it.



143
 144 *Figure 1: Location of the Spotorno study site (Liguria, NW Italy) and sampling extent. The background shows the UAV-derived RGB*
 145 *orthomosaic (2 cm), clipped to the study boundary (excluding the small southwestern sector and a 5–10 m buffer along the forest*
 146 *margin). Points indicate field-mapped *Pinus halepensis* Mill seedlings (spring 2025) and CHM-detected remnant adult pines and*
 147 *shrubs used to derive distance-to-seed-source and distance-to-shrub predictors.*

144 Environmental predictors relevant to post-fire regeneration were derived from the UAV products and
 145 subsequent terrain modelling. Topographic descriptors included slope and aspect, flow accumulation
 146 computed using a Multi-Flow Direction algorithm (Quinn et al., 1991), and the Topographic Wetness Index
 147 (TWI) calculated as suggested by Kopecký et al. (2021):
 148
 149

150
$$TWI = \ln \frac{\text{flow accumulation}}{\tan(\text{slope})}$$

151 Solar radiation exposure was represented by the Heat Load Index (HLI) computed according to McCune and
 152 Keon (2002), which integrates slope, aspect and latitude into a biologically relevant measure of potential
 153 heat load.

154
$$HLI = \exp(HLI_{\ln})$$

155 Were:

$$HLL_n = -1.46 + 1.582 \cdot \cos(lat) \cdot \cos(slope) - \cos(folded\ aspect) \cdot \sin(slope) \cdot \sin(lat) - 0.262 \\ \cdot \sin(lat) \cdot \sin(slope) + 0.607 \cdot \sin(folded\ aspect) \cdot \sin(slope)$$

And:

$$folded_aspect = |\pi - |aspect - 5\pi/4||$$

Distances to remnant living mature trees, nearest shrubs and to unburnt forest edge were computed for every raster cell. All predictor rasters were aligned to a common grid, reprojected, and clipped to the study area boundary. Seedlings presence was rasterized at the resolution of the environmental predictor stack (5 x 5 m), generating a binary presence layer and a count layer reporting the number of seedlings falling within each cell. This count layer was used to assign sampling weights in the regression models: cells containing more seedlings received proportionally higher weights, ensuring that presences with multiple individuals contributed more strongly to model estimation than isolated ones. Raster processing and spatial operations were performed in R using the “terra” and “sf” packages (Hijmans, 2023; Pebesma, 2018).

3.2 Spatial point pattern analysis

Spatial point pattern analyses were conducted in R using the “spatstat” package (Baddeley et al., 2015), to evaluate whether natural regeneration exhibited patterns of aggregation, randomness, or inhibition, and if this varied across spatial scales. We first computed Ripley’s inhomogeneous K function, $K_{inhom}(r)$ (Ripley, 1976), to assess cumulative departures from complete spatial randomness while accounting for spatial variation in intensity (i.e., the underlying spatial variation in expected sapling density driven by environmental heterogeneity). Secondly, to identify the specific distances at which clustering or inhibition occurred, we used the inhomogeneous pair correlation function, also known as the O-ring statistic, $g_{inhom}(r)$ (Wiegand and A. Moloney, 2004). While Ripley’s K integrates spatial dependence cumulatively for all distances up to a given radius r , the O-ring function isolates interactions at an exact distance r , evaluating point density within a thin annulus, allowing the detection of clustering or inhibition at specific spatial scales rather than cumulatively. All analyses were conducted using an inhomogeneous Poisson process as the null model, to account for environmental heterogeneity across the burned landscape.

3.3 Multivariate exploration of environmental gradients

To reduce redundancy among predictors and identify major underlying gradients, we performed a Principal Component Analysis (PCA) and a hierarchical clustering based on angular distance. Maximal Information Coefficients (MIC) and distance correlation (dCor) were also computed to evaluate nonlinear associations and confirm variable groupings. These analyses were used to guide predictor selection and avoid collinearity in subsequent modelling. Based on these results and on ecological reasoning, we selected four candidate predictors: HLI, TWI, distance to seed trees, and distance to shrubs. All multivariate analyses were conducted in R (R Core Team, 2024), relying on base functions and on the packages “minerva” (Reshef et al., 2011) and “energy” (Székely and Rizzo, 2017).

3.4 Regression modelling

Generalized Linear Models (GLMs; quasibinomial family) and Generalized Additive Models (GAMs; binomial with REML smoothing) were fitted using the selected predictors: Topographic Wetness Index (TWI), Heat Load Index (HLI), distance to adult pines, and distance to shrubs. GLMs were used to estimate parametric effects (direction and significance), whereas GAMs allowed the exploration of potential non-linear responses through cubic regression splines (Wood, 2017). All models were trained on the presence and random pseudo-absence dataset (see §3.5), using presence weights derived from seedling counts. Predictor variables were standardised, and a suite of diagnostic metrics was used to verify model adequacy and rule out multicollinearity (Variance Inflation Factors, VIF), assess smoother complexity in GAMs (k-index), and evaluate global model performance (AIC, deviance explained). Residual behaviour was inspected using

200 simulated residual diagnostics implemented in the “DHARMA” package (Hartig, 2022) while multicollinearity
201 diagnostics were computed using the “car” package (Fox & Weisberg, 2019).

202 **3.5 Pseudo-absence generation and Random Forest modelling**

203 Because true absences are difficult to define in early post-fire settings, pseudo-absences were generated
204 using both a random strategy and an ecologically informed, spatially balanced strategy. For the informed
205 approach, all non-presence raster cells (5 x 5 m) were assigned an unfavorability score based on GLM/GAM
206 results, i.e., increasing with high TWI, low HLI and large distance from adult pines. Each component was
207 rescaled and combined into a single score. To enforce spatial balance, candidate non-presence cells were
208 stratified into 25 spatial blocks (5 x 5) based on x–y rank bins, ensuring similar sampling effort across the
209 study extent. Within each block, pseudo-absences were preferentially sampled from the upper tail of the
210 local unfavorability distribution until reaching the target sample size (starting from the 80th percentile and
211 progressively relaxing to the 60th percentile if needed). This approach ensured spatial homogeneity while
212 prioritising ecologically plausible absence locations. The final training dataset was balanced by sampling the
213 same number of pseudo-absences as presences (n = 329). Random Forest classifiers were then fitted using
214 the “randomForest” package in R (Breiman, 2001; Liaw & Wiener, 2002) to model regeneration probability
215 as a function of the predictors retained after preliminary screening (TWI, HLI and distance to remnant adult
216 pines; shrub distance was excluded). Two RF training datasets were built by pairing presences with either (i)
217 ecologically informed pseudo-absences (as above) or (ii) randomly sampled pseudo-absences. Model
218 performance was evaluated using a 70–30% train–test split, repeated 100 times to obtain stable estimates
219 of discrimination and classification metrics (AUC, accuracy, sensitivity and specificity). To obtain a clearer
220 model interpretation, we complemented permutation-based variable importance (MeanDecreaseAccuracy)
221 with SHAP (SHapley Additive exPlanations) analyses. SHAP values were computed for the best-performing RF
222 model using the “fastshap” package (nsim = 100) with class-1 predicted probability as the prediction function,
223 and visualised as SHAP dependence plots for each predictor. The best-performing RF model was then applied
224 to the full set of predictor rasters to produce a 5 x 5 m ecological suitability map for post-fire regeneration
225 across the study area.

226 **4 Results**

227 **4.1 Spatial pattern of regeneration**

228 Seedling occurrence was highly heterogeneous across the burned area (Figure 2). Kernel-smoothed intensity
229 surfaces showed regeneration hotspots concentrated mainly along the north-western sector and in a few
230 interior ridges, whereas large central depressions and drainage lines remained almost completely devoid of
231 pine recruits. Overlay with adult trees revealed that most seedlings established in the proximity of surviving
232 Aleppo pines individuals, especially where these coincided with warm, moderately sloping microsites.

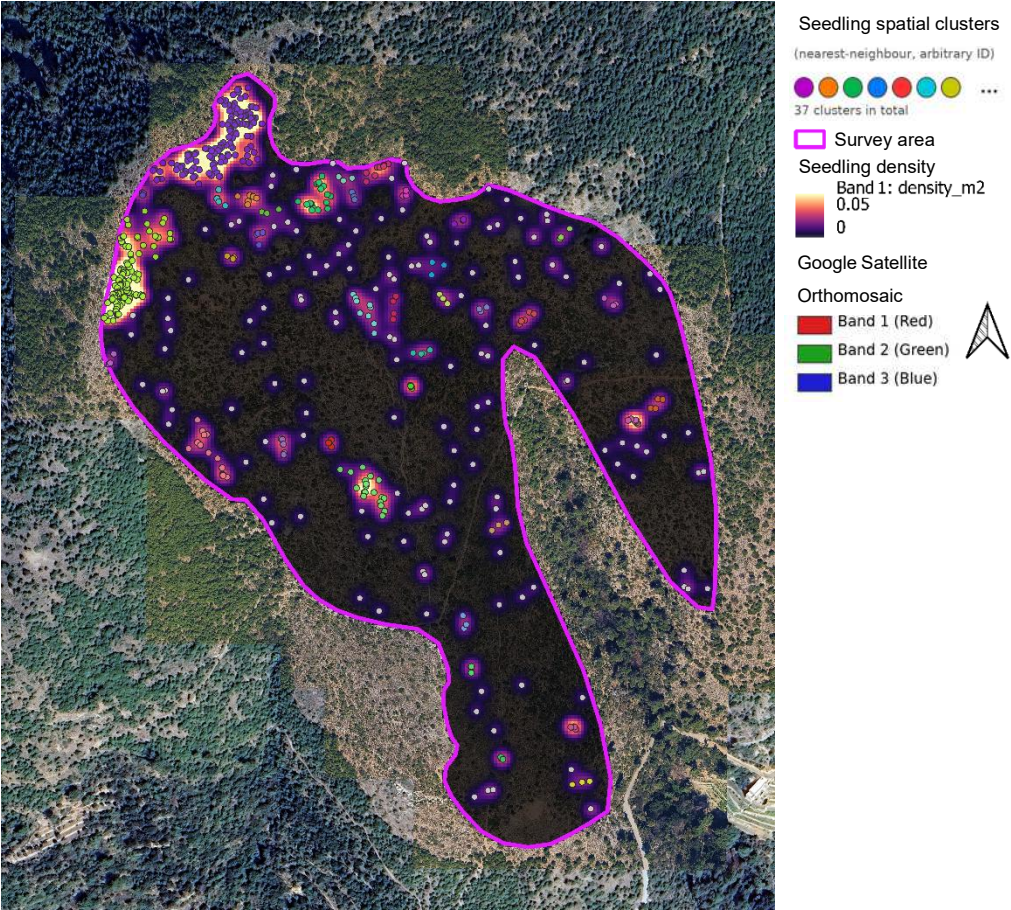


Figure 2: Distribution of *Pinus halepensis* seedlings across the burned slope. A kernel-smoothed intensity surface highlights regeneration “hotspots” and “coldspots”, showing strong spatial heterogeneity.

233 Spatial point pattern analysis confirmed that these regeneration clusters did not arise from direct biotic
234 interactions among seedlings. Both Ripley’s K function, $K_{inhom}(r)$, and the pair correlation, $g_{inhom}(r)$, remained
235 entirely within the simulation envelopes of the inhomogeneous Poisson null model across all examined
236 distances (Figure 3). No significant aggregation or inhibition was detected at either fine (1–10 m) or broader
237 (10–80 m) spatial scales. This indicates that regeneration hotspots primarily reflect the convergence of
238 locally favourable environmental conditions, rather than facilitative or competitive interactions among
239 conspecific individuals.

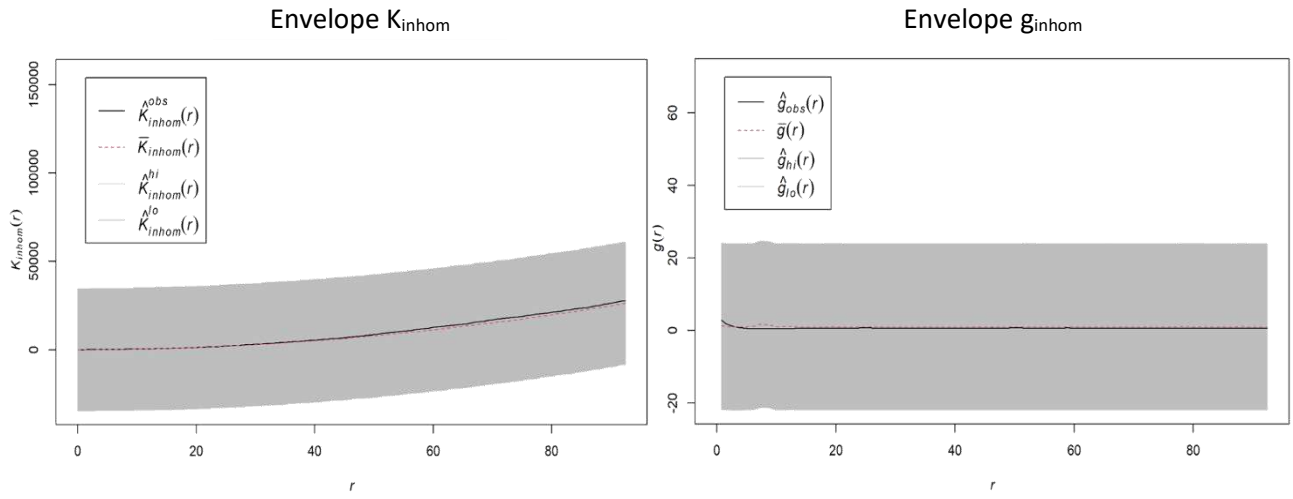


Figure 3: Inhomogeneous Ripley's K function ($K_{inhom}(r)$) and inhomogeneous O -ring function ($g_{inhom}(r)$) for the seedling point pattern, compared against Monte Carlo simulation envelopes from an inhomogeneous Poisson null model. Observed functions remaining within the envelopes indicate no detectable aggregation or inhibition beyond environmentally driven intensity variation.

241 **4.2 Multivariate identification of dominant environmental axes**

242 The multivariate analysis revealed clear ecological structuring within the environmental dataset. PCA
243 ordination and angular-distance clustering consistently grouped predictors into three coherent ecological
244 axes (Figure 4):

- 245
- Related to radiation (HLI, aspect components)
 - 246 • morphometric moisture group (TWI, flow accumulation, slope)
 - 247 • Proximity to remnant vegetation related group (distance to seed trees, distance to perimeter).

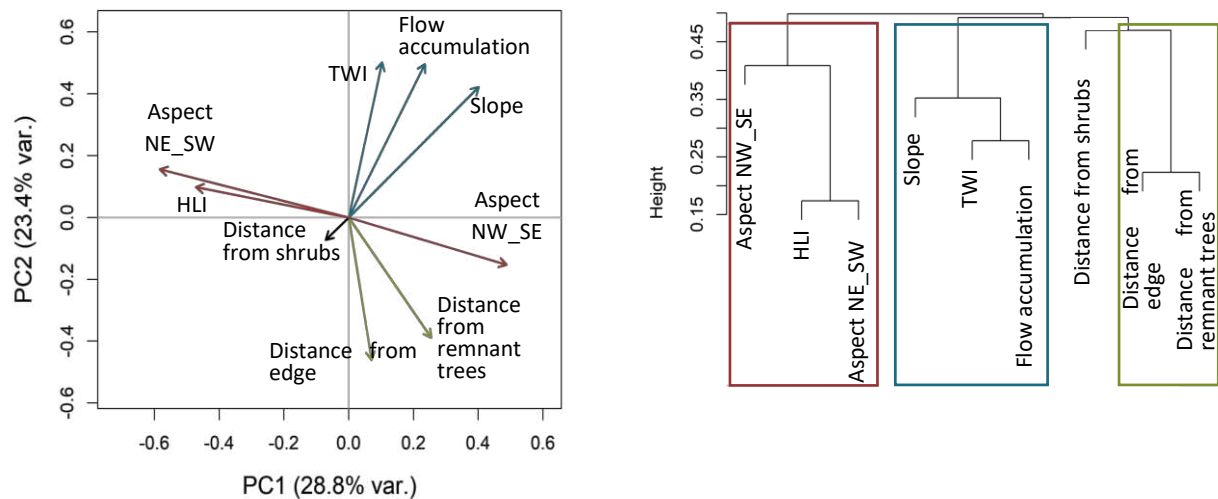


Figure 4: Principal Component Analysis (PCA) ordination and angular-distance hierarchical clustering of terrain, radiation, and proximity variables. The analyses identify the dominant ecological axes structuring the predictor space (radiation/heat-load, moisture-morphometry, and proximity to remnant vegetation).

248 These groupings were independently confirmed by Maximal Information Coefficients (MIC) and distance
249 correlation (dCor) (Figure 5), which highlighted strong nonlinear associations within each axis and weaker
250 cross-axis correlations.

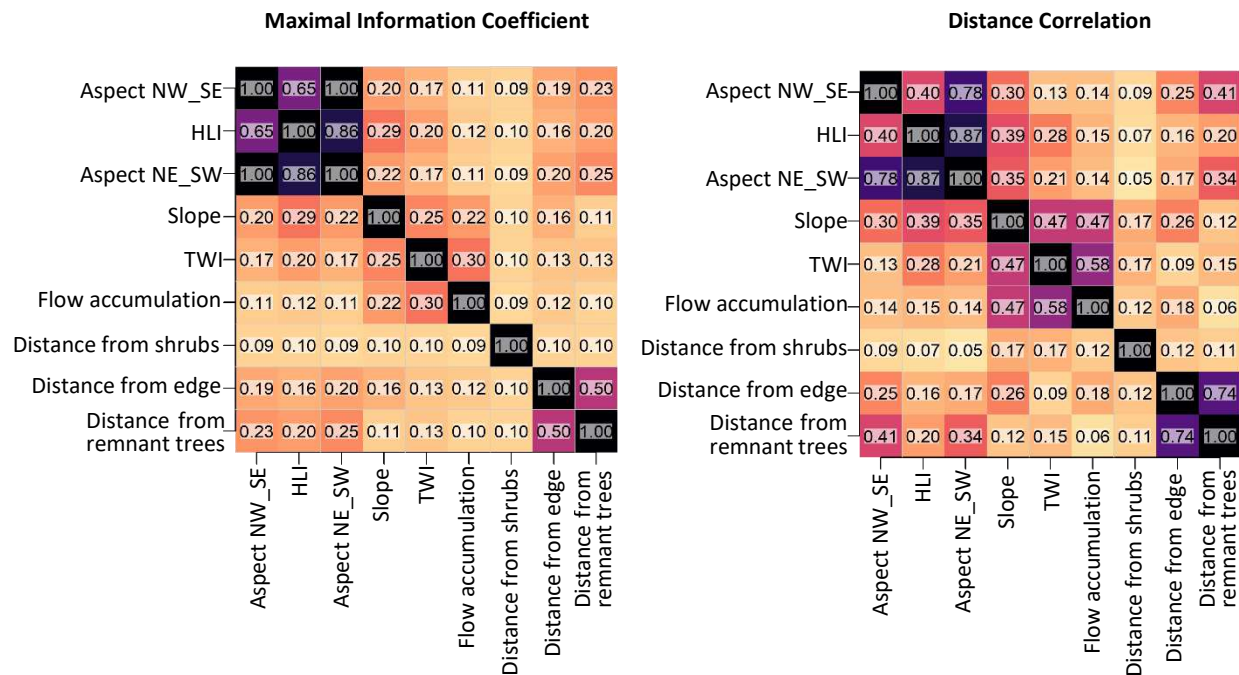


Figure 5: Maximal Information Coefficient (MIC) and distance-correlation (dCor) matrices summarising linear and non-linear relationships among predictors.

251 **4.3 Regression models**

252 GLMs and GAMs fitted with these predictors converged on consistent ecological relationships. In GLMs, TWI
253 showed a strong and significant negative effect on seedling presence, whereas HLI exerted a positive effect,
254 indicating higher establishment in warm, well-drained microsites. GAM smooth functions confirmed these
255 patterns, with regeneration probability remaining high at intermediate TWI values and declining sharply
256 toward strongly convergent, moisture-accumulating topographic positions. Distance to adult pines also
257 exerted a clear and statistically significant negative effect in both GLMs and GAMs, indicating that
258 establishment probability decreases progressively with increasing distance from surviving seed-dispersal
259 trees. Conversely, distance to shrubs was non-significant in all model formulations: indicating no detectable
260 effect of shrub proximity.

261 **4.4 Random Forest performance and variable importance**

262 Random Forest models trained with the three selected predictors (TWI, HLI, distance to adult pines) showed
263 marked differences in performance depending on the pseudo-absence strategy. The classifier using
264 ecologically informed pseudo-absences achieved high predictive ability (AUC = 0.895, ACC = 0.821, SEN =
265 0.785, SPE = 0.864), whereas the equivalent model with random pseudo-absences performed substantially
266 worse (AUC = 0.653, ACC = 0.607, SEN = 0.648, SPE = 0.571).

267 Permutation-based importance and effect-direction metrics (.) consistently ranked TWI as the most
268 influential predictor, with a strong negative correlation with predicted probability. HLI emerged as the second
269 most important variable with a positive correlation, while distance to adult pines showed a moderate
270 negative correlation, indicating decreasing suitability with increasing distance from seed sources.

- 271
- 272 • **HLI:** regeneration probability increased with heat load, becoming positive above ~0.84 HLI and rising
273 more sharply from ~0.86 to 0.90 (Figure 7).
 - 274 • **TWI:** probability remained relatively high at low–intermediate wetness (TWI ≈ 3.8–4.7), then
275 dropped steeply beyond a threshold of ~4.8–4.9, and stayed consistently low at the wettest, most
276 convergent positions (TWI ≥ 6.0, up to ~7.5; (Figure 7).
 - 277 • **Distance to adult pines:** Distance to adult pines: probability was highest close to seed trees (~0–30
278 m), approached the average effect around ~35–40 m, and declined steadily beyond ~40 m, with
increasingly negative contributions past ~60 m (Figure 7).

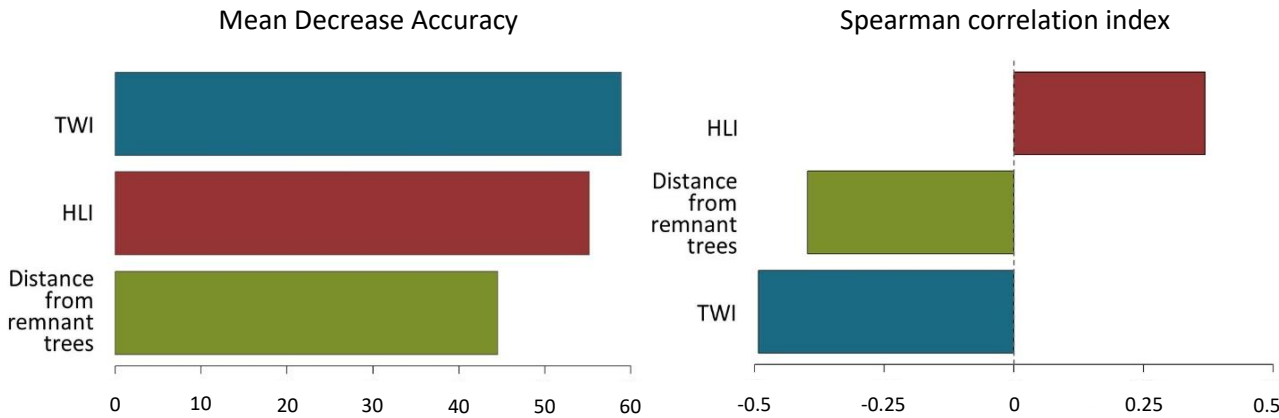


Figure 6: Permutation-based importance (left) is expressed as Mean Decrease Accuracy, i.e., the reduction in classification accuracy when a predictor is randomly permuted; higher values indicate greater contribution to model performance. Effect direction (right) is summarised by the Spearman rank correlation between each predictor and the predicted presence probability, providing a monotonic indication of whether regeneration suitability tends to increase (positive) or decrease (negative) along the predictor gradient. Results refer to the best-performing Random Forest trained with ecologically informed pseudo-absences using the three predictors (TWI, HLI, and distance to remnant adult pines).

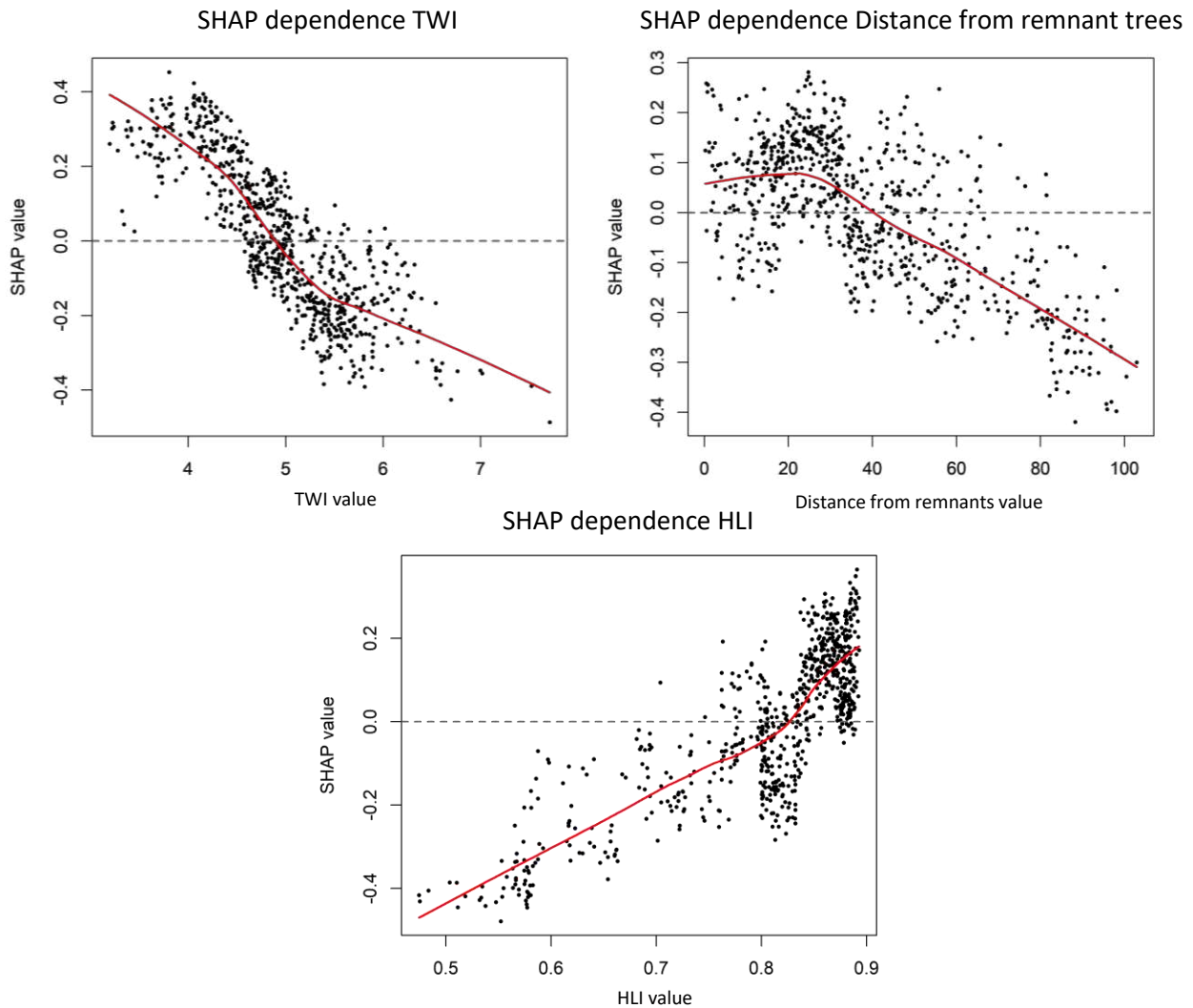


Figure 7: SHAP dependence plots. The x-axis represents the observed values of each environmental variable, while the y-axis shows SHAP values expressed in units of predicted presence probability, quantifying the additive contribution of each variable to model predictions relative to the average probability. Each point represents a raster cell, and the smoothed curve summarizes the average marginal effect along the observed gradient.

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The Random Forest model trained with ecologically informed pseudo-absences was then applied to the full set of predictor's rasters (TWI, HLI and distance from remnant adult pines) to produce a high-resolution ecological suitability map for post-fire pine regeneration (Figure 8), highlighting highest suitability along warm, moderately inclined slopes close to adult pines. While, strongly convergent hollows, channels and shaded interior slopes displayed very low predicted suitability, particularly where also distant from seed sources; overall, the map delineates a clear mosaic of regeneration "hotspots" and persistent "coldspots" at 5 m resolution.

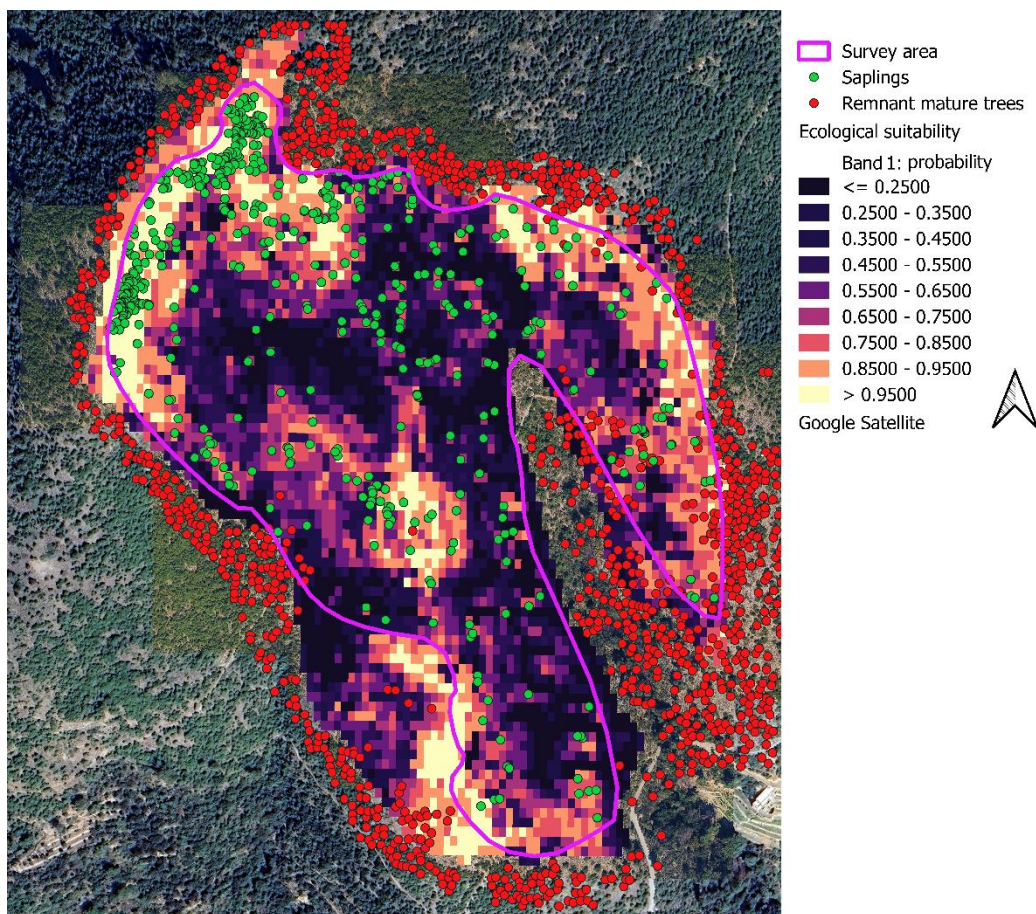


Figure 8: Suitability map for post-fire regeneration of *Pinus halepensis* in the study area (5 × 5 m resolution). Values represent the predicted probability of presence from the best-performing Random Forest model, trained with ecologically informed pseudo-absences and the selected predictors (TWI, HLI, and distance to remnant adult trees). The map highlights regeneration "hotspots" near seed trees and in warm, well-drained microsites, and persistent "coldspots" in convergent positions with high topographic moisture and/or far from seed sources. (Optional symbols/overlays: mapped seedlings and remnant trees as shown in the legend).

289 5 Discussion

290 This study emphasizes the central role of environmental drivers in shaping early post-fire regeneration
291 patterns in Mediterranean pine forests. Rather than being uniformly distributed across the burned area,
292 regeneration was spatially structured along fine-scale environmental gradients, reflecting strong microsite
293 filtering processes. Overall, the regression results indicate that regeneration is favoured in warm, relatively
294 dry, well-drained microsites, whereas concave, runoff-converging positions are consistently unsuitable. The
295 establishment probability drops sharply in erosion-prone hollows and drainage lines characterised by high
296 TWI, where hydrological concentration and soil loss can hinder recruitment. Furthermore, regeneration is
297 strongly seed-limited, with suitability declining with increasing distance from surviving adult pines.

298 Microsite moisture conditions and solar heat exposure emerged as primary constraints on establishment, in
299 line with evidence that early recruitment in drought-prone systems is highly sensitive to soil-atmosphere
300 interactions (Davis et al., 2019; Wooten et al., 2022). Hydrologically convergent positions, identified by high
301 TWI values, were consistently associated with low regeneration suitability. Beyond “wetness” per se, runoff-
302 convergent terrain in Mediterranean post-fire landscapes often coincides with enhanced overland flow,
303 rilling and sediment redistribution, especially after vegetation removal and soil surface alteration, which can
304 destabilise the seedbed and reduce establishment success (Lucas-Borja et al., 2019; Shakesby, 2011).

305 Conversely, moderately dry, well-drained microsites exposed to higher heat loads promoted pine
306 regeneration, likely by favouring rapid early growth during short favourable windows and limiting soil surface
307 disturbance and erosion in the runoff gullies (Marcolin et al., 2019; Marzano et al., 2013). Notably, the fact
308 that most individuals measured in the field were likely <5 years old (despite a maximum potential age of 10
309 years since the 2015 fire) suggesting that recruitment may have been episodic and concentrated in a subset
310 of climatically favourable years, consistent with the pulsed recruitment dynamics reported for
311 Mediterranean Aleppo pine populations under strong interannual climatic variability (Nathan and Ne’eman,
312 2004).

313 Alongside microsite conditions, proximity to surviving adult pines emerged as a critical determinant of
314 regeneration patterns, highlighting the importance of seed supply for post-fire recovery. As widely reported
315 in the literature, pine seedling establishment probability is inversely related to distance from seed trees,
316 especially after high-severity disturbances that reduce local seed sources (Leverkus et al., 2014; Mantero et
317 al., 2023). Consistent declines in regeneration density after 30–60 metres from living seed trees have been
318 documented across contrasting systems, including Mediterranean and Alpine settings (Beghin et al., 2010;
319 Mantero et al., 2024) and fire-prone pine landscapes more broadly (Haire and McGarigal, 2010). In
320 Mediterranean Aleppo pine specifically, empirical studies have shown a pronounced spatial decrease in seed
321 dispersal with distance from adult trees, reinforcing that distance from seed trees is a stronger driver of the
322 spatial distribution of post-fire regeneration than microsite suitability alone (Nathan et al., 2000).

323 In this context, the observed spatial heterogeneity is the outcome of the interaction between dispersal
324 constraints and fine-scale environmental suitability, rather than spatial clustering driven by facilitative
325 intraspecific interactions among seedlings; nevertheless, such biotic processes cannot be excluded a priori
326 and may become relevant under different ecological contexts or at other stages of post-fire succession.
327 Contrary to expectations, given the documented potential for Mediterranean shrubs to facilitate tree
328 saplings by ameliorating stressful microclimatic conditions and/or reducing biotic pressure (Gómez-Aparicio,
329 2009), distance to shrubs did not exert a detectable influence on seedling establishment once topography
330 and seed-source distance were accounted for. This is notable because facilitation is generally predicted to
331 become more important as abiotic stress increases (Bertness and Callaway, 1994), and several studies in
332 Mediterranean regions show that nurse shrubs can measurably enhance woody recruitment and are often
333 useful in restoration applications (Gómez-Aparicio et al., 2004).

334 The absence of a detectable shrub signal here likely reflects the structurally homogeneous distribution of
335 garigue vegetation across the burned area, which limits the formation of distinct shrub-driven microhabitat
336 gradients at the scale of analysis. In addition, distance-to-centroid metrics may not fully capture the relevant
337 neighbourhood processes (e.g., canopy shape complexity, shading footprint, or fine-scale soil amelioration),
338 potentially reducing sensitivity to shrub effects where shrub cover is homogeneously widespread and spatial
339 contrasts are weak. While shrubs are known to act both as competitors and nurse plants in Mediterranean
340 systems (Castro et al., 2011), their effects are often strongly context-dependent and may be most detectable
341 when shrub cover is patchy enough to create sharp microhabitat contrasts, or during successional stages
342 characterised by different ecological niches that shift the competition/facilitation balance. Shrub-mediated
343 interactions may become relevant at later successional stages as vegetation structure and competitive
344 dynamics evolve (Gómez-Aparicio, 2009). The absence of a detectable shrub effect in this study therefore
345 does not exclude biotic interactions a priori, but rather suggests that, during the phase examined here (10 y
346 after fire), abiotic filtering and seed availability override shrub-mediated processes.

347 By integrating ecologically informed pseudo-absences with machine learning models, this study
348 demonstrates the potential of precision-based approaches to support post-fire restoration planning. The
349 marked performance difference between models trained with random versus ecologically reasoned pseudo-
350 absences highlights the importance of embedding ecological knowledge into predictive modelling
351 approaches, particularly when true absence data are unavailable (Breiman, 2001; Cerioni et al., 2024).
352 Methodological evidence on species distribution modelling similarly shows that pseudo-absence design can
353 strongly affect discrimination and inference, and that constraining pseudo-absences to environmentally and
354 spatially plausible regions can improve model reliability (Barbet-Massin et al., 2012). The resulting suitability
355 map delineates a mosaic of regeneration “hotspots” and “coldspots” at fine spatial resolution, providing a
356 practical framework to guide targeted interventions. Consistent with the Precision Forest Restoration
357 concept (Castro et al., 2021), such maps can help managers prioritize active restoration measures (e.g.,
358 planting, sowing, or microsite creation) in areas where natural recovery is unlikely, while allowing passive
359 restoration to proceed elsewhere, thereby improving the efficiency of restoration under limited resources.

360 This study provides valuable findings on post-fire restoration drivers in Mediterranean area, but some
361 limitations should be acknowledged. The study area covers only 12 hectares, and although environmental
362 heterogeneity was substantial, extending the proposed methodology to larger spatial extents, additional
363 burned slopes, and multiple fire events would strengthen the generality of the conclusions. In addition,
364 regeneration dynamics were assessed at a single time snapshot; longer-term monitoring would be required
365 to evaluate whether the relative importance of environmental drivers and dispersal constraints persists or
366 shifts as stand structure develops and biotic interactions potentially intensify. Finally, while UAV and LiDAR
367 products offer clear advantages for high-resolution modelling, uncertainties in feature detection (e.g.,
368 remnant tree identification thresholds, shrub segmentation, and their translation into distance predictors)
369 can propagate into predictive mapping and should be explored in further sensitivity analyses where possible.

370 Despite these limitations, the strong agreement between model outcomes and well-established ecological
371 evidence supports the robustness of the proposed framework. The pronounced effect of distance from
372 surviving adult pines is consistent with numerous studies documenting seed limitation as a key constraint on
373 post-fire regeneration in both Mediterranean and Alpine forests (Beghin et al., 2010; Castro et al., 2011;
374 Marzano et al., 2013). Likewise, the dominant role of topographically driven moisture accumulation and heat
375 exposure reflects widely observed controls of microclimate, soil water availability and post-fire surface
376 processes on early seedling establishment in drought-prone, fire-affected landscapes (Lucas-Borja et al.,
377 2019; Marañón-Jiménez et al., 2013; Wooten et al., 2022). Overall, the integration of spatially explicit
378 environmental predictors with ecologically informed pseudo-absence selection and machine-learning
379 models provides a transferable and scalable framework, offering a robust basis for identifying regeneration

380 bottlenecks and guiding adaptive restoration strategies across fire-prone landscapes, increasingly affected
381 by climate extremes and the consequent change in disturbance regime.

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