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RESEARCH ARTICLE

Microsite selection improves post-fire restoration of singleleaf pinyon pine on Washoe Tribal lands in the Pine Nut Mountains, NV, USA

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Abstract

Introduction: Singleleaf pinyon pine (*Pinus monophylla*) holds both ecological and cultural significance for Indigenous Tribes of the Great Basin, such as the Washoe Tribe of Nevada and California. Recent wildfires on Washoe Tribal lands have resulted in the loss of important pinyon pine groves, prompting collaborative efforts to develop post-fire restoration guidelines.
Objectives: This study evaluates the influence of microsite conditions on singleleaf pinyon pine post-fire restoration across gradients of elevation and topography through a collaborative planting experiment on Washoe Tribal lands.
Methods: One-year-old seedlings were outplanted in seven restoration islands, into four microsite types: under shrubs, woody debris, perennial grasses/forbs, and in open interspaces. Seedlings were surveyed 1 year following planting, and their survival was modeled as a function of local microsite conditions, topography, and elevation.
Results: Of all seedlings, 28% survived the first year after planting, and we found that microsite, topographic position, and elevation strongly impacted seedling survival. Survival probability increased with elevation. Seedlings planted under shrubs and grasses/forbs had much higher survival (35% and 40%, respectively) than those planted in open interspaces (10%). We identified an important interaction between canopy cover and topographic position, where the benefits of shade were most pronounced on ridgelines but diminished in valleys.
Conclusions: Shaded microsites were important for pinyon pine seedling survival, but this effect varied along topographic gradients, consistent with the stress gradient hypothesis. Reduced survival at lower elevations aligns with potential climate change responses, as rising temperatures are expected to limit tree regeneration at lower elevation range limits.
Implications for Practice: Our results highlight the need for strategic site selection to maximize post-fire restoration success, where microsite favorability for dryland tree regeneration is considered in the context of a bioclimatic setting. Although we found relative differences in survival among shaded microsite types, our findings suggest that restoration outcomes can be improved by opportunistically using natural features (e.g., woody debris) and local vegetation. Our collaborative restoration effort is embedded within a community-based adaptive management project, which facilitates long-term monitoring and provides a culturally meaningful path for ecological stewardship in the face of increasing fire risks and invasive species.

Key words: community-based restoration, microsite selection, pinyon pine, post-fire restoration, restoration islands

Introduction

Fire regimes in western North America are shifting due to a combination of climate change, invasive species, and human-driven landscape alterations (Balch et al. 2013; Abatzoglou & Williams 2016; Hessburg et al. 2021). These changes are amplifying the frequency and intensity of wildfires in the Great Basin region (Miller et al. 2009; Balch et al. 2013; Board et al. 2018), while also limiting the recovery of native plant communities (Shriver et al. 2018). Shifting fire regimes pose significant challenges for both ecological integrity and the cultural ecosystem services critical to Indigenous peoples, whose traditional practices and livelihoods are deeply tied to these landscapes (Fatorić & Seekamp 2017). Conventional restoration practices often prioritize short-term stabilization and economic criteria, overlooking culturally significant species (Weir et al. 2024). As Great Basin ecosystems face threats from climate change, invasive species, and other disturbances (Redmond et al. 2023), the

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long-term implications for Tribal communities and lands are significant. Integrating Indigenous priorities is essential to foster more holistic ecosystem restoration, ensuring biodiversity recovery and protecting the cultural values embedded in the landscape (Jones et al. 2025).

Among these culturally significant species is singleleaf pinyon pine (*Pinus monophylla* Torr. & Frém.; hereafter "pinyon pine"), a dominant component of the Great Basin pinyon-juniper woodlands that span 19 million ha and support a diverse range of plant, animal, and soil communities (Paulin et al. 1999; Floyd et al. 2004; Weisberg & Ko 2012). Pinyon pine holds immense importance for many Indigenous peoples of the Great Basin (Fogg 1966), such as the Washoe Tribe of Nevada and California (Wá·šiw), for whom pinyon seeds (pine nuts; ťágɨm) are a long-standing food source central to cultural identity and creation stories. For the Washoe people, an annual pine nut harvest each fall traditionally started with the ceremonial pine nut dance, and communities would spend weeks each fall in family groves, harvesting and processing pine nuts while tending the groves of trees (Rhiana Jones, personal communication). Traditional stewardship of pine nut groves varies but includes pruning lower branches, cleaning duff from under trees, and collecting dead wood and other surface fuels for cooking fires (Anderson 2005).

While pinyon pine remains regionally abundant, it is threatened by increasingly frequent wildfires and the associated spread of invasive annual grasses (Balch et al. 2013; Board et al. 2018). Burned pinyon-juniper woodlands are vulnerable to conversion into grasslands dominated by invasive annual grasses such as cheatgrass (*Bromus tectorum* L.; Brooks et al. 2004; Urza et al. 2024), which are known to inhibit the post-fire recovery of native vegetation and increase the risk of subsequent fire (Balch et al. 2013; Yelenik & D'Antonio 2013). Following fire, pinyon pine recovery is constrained by limited seed dispersal, slow growth rates, and dependence on protected microsites for successful regeneration (Chambers et al. 1999). Pinyon pine establishment is thus often limited for several decades after fire (Phillips et al. 2024), typically following the recovery of shrubs, which ameliorate harsh environmental conditions and facilitate seedling survival (Chambers 2001; Urza et al. 2019). In addition to nurse shrubs, post-fire survival of dryland tree seedlings has been shown to be improved by early successional species, non-living objects that create shaded microsites (e.g., downed logs, snags, or rocks), or by the presence of organic litter (Ouzts et al. 2015; Crockett & Hurteau 2022; Swanson et al. 2023). Climate and topographic gradients also influence post-fire regeneration processes, and restoration planting has been shown to be more successful in cool, wet sites, north-facing aspects, and topographic depressions (Marshall et al. 2023; Rodman et al. 2024). Importantly, the effect of microsite conditions on seedling survival can be mediated by abiotic conditions. For example, a previous study found that natural pinyon pine seedlings were more likely to occur under big sagebrush (*Artemisia tridentata* Nutt.) shrubs in drier and warmer sites (Ziffer-Berger et al. 2014); this finding is consistent with the stress gradient hypothesis, which predicts that the importance of positive (i.e., facilitative) plant–plant interactions increases along gradients of increasing abiotic stress (Bertness & Callaway 1994; Pugnaire & Luque 2001).

A striking example of fire-related impacts occurs in the Pine Nut Mountains of western Nevada, the location of most of the Washoe Tribe's Trust and Allotment lands. Oral histories and early ethnographic accounts describe how Washoe people would travel to the Pine Nut Mountains each fall to gather pine nuts (Rhiana Jones, personal communication; Washoe THPO 2025; Price 1962), and archaeological records of pine nut caches and home sites provide physical evidence of a long and sustained history of stewardship (Hagerty 1970). The Pine Nut Mountains were deforested during the mid-1800s to support the booming mining industry in northern Nevada (Angel 1881). Tribal Allotment lands in the Pine Nut Mountains were authorized under the 1887 Dawes Act (Washoe THPO 2025), and over the next 100 years pinyon-juniper woodlands recovered across much of the area (U.S. Forest Service 1939). Since 2010, 36% of Washoe Tribal Trust and Allotment lands (10,896 ha) have burned at least once (Monitoring Trends in Burn Severity [MTBS] 2024), mostly in the Pine Nut Mountains (Fig. 1), and post-fire increases in cheatgrass cover have caused some areas to burn up to three times over the past 15 years. The loss of local pinyon pine groves has limited access for pine nut harvest and cultural practices, causing profound impacts to Washoe communities (Rhiana Jones, personal communication). Given the progressive loss of pinyon pine woodlands, efforts to accelerate its recovery have gained urgency for the Washoe Tribe, spurring collaborative restoration efforts between Tribes and restoration ecology researchers. These efforts include the development of propagation protocols for singleleaf pinyon pine (Urza et al. 2025), the construction of a Tribal nursery and resilience garden, field-based experiments, and community engagement. In 2024, the Washoe Tribe declared a State of Emergency for pinyon pine, affirming "the need to take immediate and concerted effort towards pinyon pine conservation on Washoe Tribal lands, and in the surrounding ancestral territory" (Washoe Tribe of Nevada and California 2024).

This study focuses on a post-fire pinyon pine restoration planting effort on Washoe Tribal Allotment land. We asked: (1) How does planted pinyon pine seedling survival differ between microsite types? We expected survival to be lowest in open interspaces, highest under non-living shade objects, and intermediate under living nurse plants, which can simultaneously facilitate and compete with seedlings growing under their canopy. (2) How do topographic gradients interact with microsite conditions to affect the survival of planted seedlings? We expected that seedling survival would be highest in higher elevation, concave, and valley-bottom planting sites, where abiotic stress is lower. We also expected that the effect of shaded microsites on seedling survival would be greatest in more stressful locations, where shade helps with conserving soil moisture and protecting seedlings from excessive heat, an expectation supported both by local traditional ecological knowledge (Rhiana Jones, personal communication) and by ecological theory (Bertness & Callaway 1994). Given the collaborative nature of the project, we also reflected on our process, asking: (3) What opportunities exist for collaboration between ecologists and Tribal land managers to support the recovery of this culturally significant species? By answering these questions, we aim to inform future restoration efforts, build capacity for community-

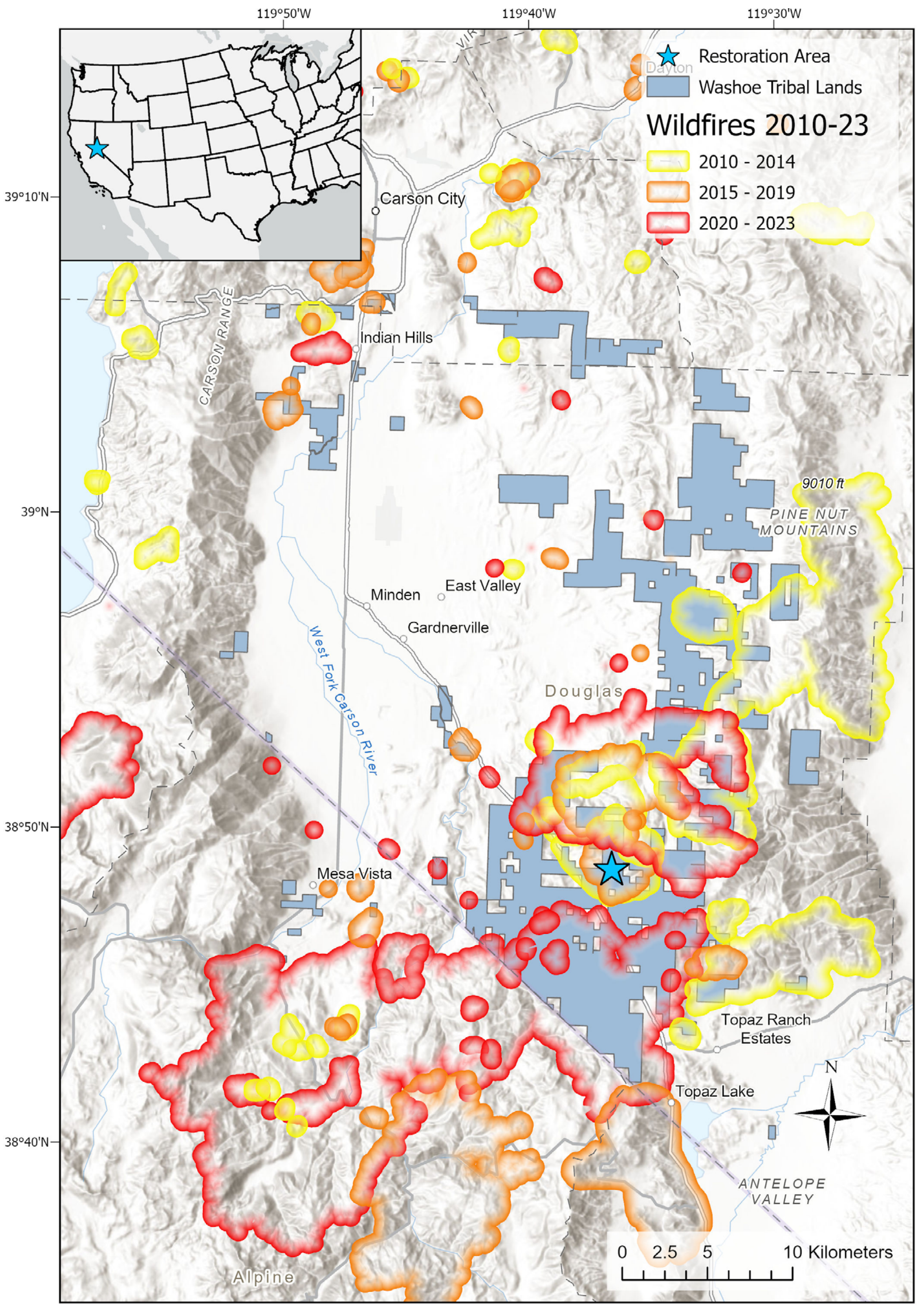

Figure 1. Map of recent fires (warm-colored polygons) in relation to Washoe Tribal Trust and Allotment lands (light blue polygons). Fire perimeters are from Monitoring Trends in Burn Severity (2024), which only includes fires larger than 404 ha. The turquoise star indicates the location of the restoration area.

based restoration, and contribute to the long-term recovery of pinyon pine woodlands.

Methods

Research Partnership

The partnership that led to this project originated in 2019, 2 years before the initiation of the research study. The Washoe Tribe was planning restoration activities following a series of large wildfires that burned on Tribal lands (Fig. 1), and while they hoped to include pinyon pine in their restoration, they were unable to find commercially available seedlings. Meanwhile, researchers with the U.S. Forest Service and the University of Nevada, Reno were starting a series of experiments on pinyon pine regeneration. Nearly 2 years of field visits and conversations occurred before starting work together, and the partnership was grounded in "CARE principles for Indigenous data governance": collective benefit, authority to control, responsibility, and ethics (Carroll et al. 2020). The restoration areas were selected by the Washoe Environmental Protection Department, and the study design was developed collaboratively, using seedlings grown by the researchers. Importantly, the partners developed a Data Sovereignty Agreement, which clarified the purpose of data collection, specified confidential information, and provided guidance on data sharing.

Study Area

This study occurred within the Pine Nut Mountains of northwestern Nevada, which extend 64 km north-to-south from the Virginia Range to the Sierra Nevada near Topaz Lake (Fig. 1). Bounded by the Carson Valley to the west and Mason Valley to the east, the Pine Nut Mountains derive their name from the abundance of pinyon pine, which occurs at elevations ranging from approximately 1,600 to 2,400 m. In unburned areas, pinyon pine commonly coexists with Utah juniper (P'a·l; *Juniperus osteosperma* [Torr.] Little) to form pinyon-juniper woodlands at higher elevations, while big sagebrush (*Artemisia tridentata* Nutt.) often co-dominates the lower slopes with perennial bunchgrass species such as Indian ricegrass (*Achnatherum hymenoides* [Roem. & Schult.] Barkworth), Sandberg bluegrass (*Poa secunda* J. Presl), Thurber's needlegrass (*Achnatherum thurberianum* [Piper] Barkworth), and bottlebrush squirreltail (*Elymus elymoides* [Raf.] Swezey). In recently burned areas, plant communities are frequently dominated by the highly invasive, non-native annual grass cheatgrass (*Bromus tectorum*) and several exotic annual forbs (e.g., *Salsola tragus* L., *Sisymbrium altissimum* L.).

In 2021, the Washoe Environmental Protection Department established seven restoration planting sites (Table S1) on recently burned Washoe Tribal Allotment land in the Pine Nut Mountains, encompassing a total of 250 ha of former pinyon pine woodlands (Fig. 2). Sites were located on north-facing slopes and near roads and were arrayed along an elevational gradient (1,889–2,072 m) with mean annual precipitation for the 1991–2020 period ranging from 363 mm at low-elevation sites to 608 mm at high-elevation sites (PRISM Climate Group 2024).

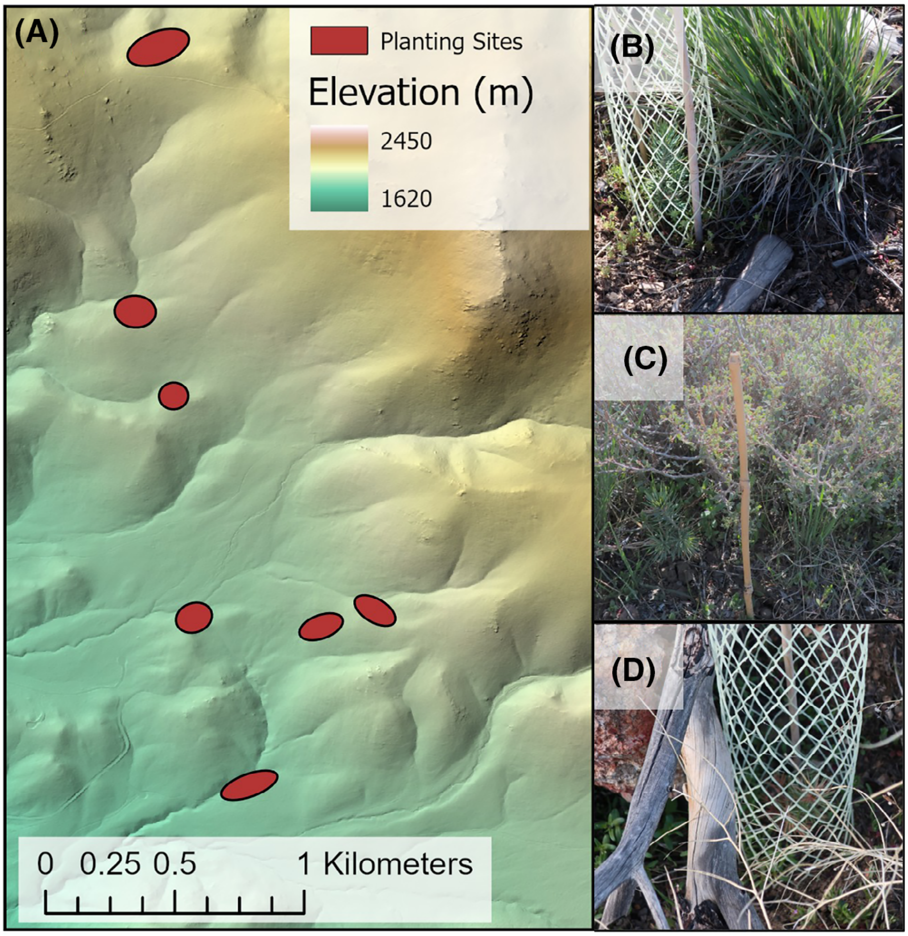

Figure 2. (A) Map of the restoration planting sites for pinyon pine seedlings in the Pine Nut Mountains, located on Washoe Tribal Allotment lands by the Washoe Environmental Protection Department. The planting sites are shown as dark red polygons, and the background color ramp illustrates the elevation gradient. Exact coordinates are not given for reasons of confidentiality. Photos: pinyon pine seedlings planted (B) next to a perennial bunchgrass (*Elymus elymoides*), (C) next to a shrub (*Purshia tridentata*; seedling tube removed for visibility), and (D) next to woody debris. Photos by P. Weisberg.

All of the restoration sites are mapped within the Duco-Vetagrande-Pinenut soil association (Natural Resources Conservation Service 2025). This association is characterized by shallow, well drained, non-saline soils with low to very low available water supply, with parent material of colluvium derived from volcanic rock. The restoration sites had burned at least twice between 2012 and 2020 (MTBS 2024). All sites had burned in the Carter Springs fire of 2012 (1,400 ha) and in the Cutter, Preacher, and Holiday fire complex of 2017 (2,900 ha); the highest-elevation site (Site P) burned a third time in the Numbers fire of 2020 (7,435 ha).

Study Design

In 2019, pinyon pine cones were collected from multiple locations in Nevada and California (see Vasey et al. 2023 for details on seed source locations). Seeds were extracted from the cones, subjected to cold-wet stratification to facilitate germination, and subsequently cultivated in a greenhouse in 2020 using the propagation protocols described in Urza et al. (2025). Although pinyon pine seedling functional traits are known to vary among seed sources (Vasey et al. 2023), tracking the seedlings by their seed source was not feasible in our project. Seedlings were mixed prior to planting such that seed sources were roughly evenly distributed among the restoration sites and microsite types.

In May and June of 2021, 1-year-old pinyon pine seedlings were planted in the seven restoration sites. The timing of planting (early summer instead of spring) was constrained by logistical and access challenges, despite the hot summer months being less favorable for establishment compared to the fall or spring seasons. Coordinated by the Washoe Environmental Protection Department, Tribal members, volunteers, and contract crews planted approximately 1,000 containerized seedlings across the sites. There are no standard recommendations for transplanting pinyon pine seedlings, but our decision to plant after 1 year of greenhouse propagation was based on observations of slowed aboveground growth and the extension of seedling taproots to the bottom of our 14″-deep containers. Planters were instructed to preferentially plant seedlings on the north side of an object that could provide shade (beneath shrub canopies, adjacent to a perennial grass or forb, or in the shade of woody debris), with remaining seedlings planted into open interspaces (Table 1). Woody debris included downed logs and large wood pieces from pinyon and juniper trees present before burning. The allocation of seedlings to different microsite types was based on the availability of each type at the site, and microsite types were thus not evenly represented (Table S1). Mesh tubes were installed around each seedling to protect from herbivory.

Field Data Collection

In August and September of 2022, we relocated and surveyed 372 of the planted seedlings to explore how microsite conditions interact with various abiotic indicators of site productivity to influence seedling survival (Table 2). Each seedling's location was recorded using a handheld global positioning system (typical accuracy of 3–6 m), and live seedlings were uniquely tagged for identification. Seedling survival was recorded as a binary variable, with "1" for alive and "0" for deceased. We recorded qualitative observations of disturbance for each seedling, including signs of herbivory, trampling, uprooted seedlings, or soil disturbance. We used microsite categories (Table 1) to understand the potentially facilitative role of neighboring plants and objects. Organic litter presence was assessed because of its potential impact on insulation of near-surface soils from temperature extremes, water retention, and nutrient availability in dryland ecosystems (Boeken & Orenstein 2001). Litter surrounding each seedling was classified as either "present" (1) or "absent" (0). Litter was commonly present in all microsite types, even those without living nurse objects (Table S2).

To assess the effect of shade levels on seedling survival, we measured percent canopy cover with hemispherical photographs taken at midday in each seedling location (Olympus Tough

Table 1. List of plant species and aggregated microsite types used in the restoration experiment for pinyon pine seedlings. The table includes the common and scientific names of the species, along with the quantity (*n*) of surveyed seedlings under each. Washoe plant names were provided by the Washoe Tribe of Nevada and California (2021; Herman Fillmore, personal communication), and their further use requires consultation with the Tribe.

Microsite Type	*Common Name*	*Washoe Name*	*Scientific Name*	n
Grass/forb	Bottlebrush squirrel tail		*Elymus elymoides*	13
	Great Basin wild rye	wášuʔ	*Leymus cinereus*	1
	Silvery lupine	délem damʔlá·ḱɨm	*Lupinus argenteus*	1
Shrub	Antelope bitterbrush	Balŋaʔćaŋ	*Purshia tridentata*	96
	Big sagebrush	Da·bal	*Artemisia tridentata*	4
	Blue elderberry	Ba·duʔ	*Sambucus nigra* ssp. *caerulea*	2
	Desert gooseberry	Sewɨt yogɨl	*Ribes velutinum*	8
	Desert peach	ćipápa	*Prunus andersonii*	1
	Green ephedra	Me·gal	*Ephedra viridis*	6
	Mountain snowberry	ʔú·ćo or ʔú·ću	*Symphoricarpos oreophilus*	3
	Rubber rabbitbrush	Bo·ṕo	*Ericameria nauseosa*	35
	Spineless horsebrush		*Tetradymia canescens*	3
Interspace				48
Woody debris				151
Total				372

Table 2. Description of predictor variables included in the statistical analysis, including the units of measurement, and the hypothesized effects of each variable on seedling survival.

Predictor Variable	*Units*	*Measurement Type*	*Hypothesized Effect*
Microsite type	Categorical	Microsite	Regulates microclimate (temperature, humidity), modifies light intensity, and influences soil nutrient and water availability
Organic litter presence	Binary	Microsite	Enhances soil moisture retention, provides organic matter, and protects against temperature extremes and erosion
Canopy cover	Proportion	Microsite	Shading alters light availability and microclimate (temperature, humidity), impacting photosynthesis and water loss
Curvature	Index value	Topography	Affects water runoff and retention, influencing local soil moisture and nutrient distribution
Topographic Position Index (TPI)	Index value	Topography	Influences water drainage, sunlight exposure, and wind patterns
Heat Load Index	Index value	Topography	Influences solar radiation and thus temperature and soil water dynamics
Elevation	Meters	Topography	Determines temperature and moisture gradients

TG-6 digital camera equipped with an FCON-T01 Fisheye Converter). We used a unified calculation approach, involving manual adjustments to blue contrast and image thresholding, following the procedures outlined in ter Steege's (2018) Hemiphot.R. Canopy cover included any objects that provided shade by obscuring the sky, including live and dead foliage, dead wood, rocks, and microtopographic features.

Topographic Predictor Variables

We used a half-meter digital elevation model derived from light detection and ranging data (U.S. Geological Survey 2023), which we resampled at a 10-m resolution to quantify topographic conditions at a scale appropriate for the location accuracy of seedlings. For all variables, values were extracted for each seedling location. Profile curvature, which we calculated using a 30 m $\times$ 30 m neighborhood size, is related to water flow, nutrient distribution, microclimate variations, and wind exposure, influencing the distribution of plants (Chase et al. 2012). Positive curvature values indicate convex surfaces, promoting water runoff and reducing soil retention, while negative values indicate concave surfaces that retain both water and soil.

We used elevation as a proxy for temperature and precipitation gradients and hydrological variations across the site (Daly et al. 2008). The Topographic Position Index (TPI) was calculated using the method described by Weiss (2001), which compares the elevation of each point to the average elevation within a defined neighborhood. Positive TPI values signify that a point is higher than its surroundings, while negative values indicate lower positions. The choice of neighborhood radius (R) affects the scale of features captured: larger R-values highlight broad landscape units, whereas smaller R-values detect finer details like minor valleys and ridges. We used a radius of 333 m, with the aim of identifying key features such as ridge lines, lateral drainages within major valleys, and canyon bottoms (Fig. S1). Importantly, TPI values capture a range of landforms at all elevations. While elevation represents the dominant environmental gradient across the study area, TPI reflects the variability of landform positions within that gradient.

We also calculated Heat Load Index following Eq. 1 from McCune and Keon (2002), which integrates slope steepness, latitude, and aspect to quantify site-specific thermal conditions. It differentiates between more southwest-facing slopes, which receive more solar radiation (higher heat load), and more northeast-facing slopes, which are cooler (lower heat load). The inclusion of slope steepness captures variations in solar intensity due to topographic inclination, while latitude accounts for geographic differences in solar incidence and day length. The restoration sites were all on generally north-facing slopes, but variation in the specific aspect and slope steepness resulted in variation in heat load both within and among sites.

Statistical Analysis

All analyses were conducted using R statistical software (R Core Team 2024). To quantify the influence of microsite conditions and topography on seedling survival, we employed generalized linear mixed-effects models with a binomial distribution and logit link function, using the "lme4" package (Bates et al. 2015). The response variable was individual seedling survival (0/1), observed 1 year after planting. All predictor variables listed in Table 2 were included as additive effects in all candidate models. To explore potential microsite-by-topography interactions, we fitted a series of models, each incorporating an interaction term between one microsite variable and one topographic variable (Table 2). Planting site was included as a random intercept in all models to account for spatial clustering of the planted seedlings and differences among conditions in each site. Model selection was based on the Akaike Information Criterion (AIC), with the lowest AIC indicating the most supported model that best balanced fit and complexity. Model effects and interactions were visualized using the "effects" package (Fox & Weisberg 2019).

Results

Microsite conditions differed among microsite types (Table S2). Shrubs provided, on average, the tallest shade structure to adjacent seedlings (median height 59 cm), with the highest canopy cover (mean 0.73). Woody debris and grasses/forbs provided intermediate levels of shade (median height 30 and 31 cm and mean canopy cover 0.39 and 0.32, respectively). Open interspaces had very low canopy cover (mean 0.09). All microsite types were likely to have organic litter covering the soil surface and had low observed disturbance. Topographic conditions varied widely among restoration sites (Table S1) and among individual seedling locations (Table S3).

Despite harsh post-fire climate conditions that were exacerbated by planting during the hot summer months, 28% of seedlings survived the first year. Logistic regression modeling of seedling survival identified several important predictors, and the most supported model included an interaction between TPI and canopy cover with all other variables as additive effects (Table 3; Table S4). Microsite type had a substantial impact on seedling survival ($\chi^2 = 7.3$, df = 3), with seedlings under shrubs and grasses/forbs showing much higher survival odds compared to those in interspaces (Fig. 3A). Compared to 10% seedling survival in interspaces, seedling survival was 35% under shrubs (odds ratio [OR] = 4.66, 90% CI: 1.54–14.09), 40% under grasses/forbs (OR = 7.84, 90% CI: 1.93–31.82), and 25% under woody debris (OR = 3.20, 90% CI: 1.18–8.68; Table 4).

Elevation was a strong predictor of seedling survival (Fig. 3B; $\chi^2 = 17.6$, df = 1). With every 63-m (one standard deviation) increase in elevation, the odds of seedling establishment increased by approximately 2.5 times (OR = 2.47, 90% CI: 1.73–3.52). The relationship between organic litter and survival was variable (Fig. 3C; $\chi^2 = 3.4$, df = 1), but on average, seedlings with litter cover were nearly three times more likely to survive than those without (OR = 2.88, 90% CI: 1.12–7.39). We found weak effects of heat load index (Fig. 3D; $\chi^2 = 0.07$, df = 1) and curvature (Fig. 3E; $\chi^2 = 0.37$, df = 1) on seedling survival.

Table 3. Results for the most supported model predicting pinyon pine seedling survival 1 year following planting. The model included an interaction between Topographic Position Index (TPI) and canopy cover and all other variables as fixed effects. Continuous variables were scaled prior to analysis, such that odds ratios are associated with a one-standard deviation change in the predictor. Differences among microsite types are shown in Table 4.

Variable	*Odds Ratio*	*90% Confidence Interval*	*Z-value*
(Intercept)	0.04	0.01–0.14	−4.11
Organic litter	2.88	1.12–7.39	1.84
Canopy cover	0.99	0.74–1.33	−0.04
TPI	0.79	0.58–1.08	−1.26
Curvature	0.89	0.65–1.22	−0.61
Elevation	2.47	1.73–3.52	4.19
Heat Load Index	0.96	0.77–1.21	−0.26
Canopy cover: TPI	1.35	1.07–1.70	2.10
Marginal R^2	0.26		
Conditional R^2	0.27		

The interaction between TPI and canopy cover ($\chi^2 = 4.4$, df = 1) greatly influenced seedling survival. The effect of canopy cover on survival depended on topographic position, where seedlings planted in sites with higher TPI values (indicating ridge-like positions) were more likely to survive in microsites with greater canopy cover, and seedlings planted in sites with lower TPI values (valley positions) were more likely to survive in microsites with lower canopy cover (Fig. 4).

The random intercept of site showed weak differences in estimated seedling survival among restoration sites (Fig. S2). The differences in estimated intercepts among sites did not correspond to differences among sites in topographic conditions or distribution of seedlings among microsite types (Table S1).

The model selection process found a similar level of support for the model that included an interaction between canopy cover and curvature (in place of the interaction between canopy cover and TPI; Table S4). Curvature and TPI were moderately positively correlated ($r = 0.64$), and their interactions with canopy cover showed similar patterns. Seedlings planted in convex sites (higher curvature values) were more likely to survive in microsites with greater canopy cover, and seedlings planted in concave sites with lower curvature values were more likely to survive in microsites with lower canopy cover (Fig. S3).

Discussion

Post-Fire Reforestation Requires Identifying Suitable Microsites within the Context of Broad-Scale Environmental Gradients

As for many dryland tree species, the restoration success of pinyon pine following fire strongly depends on microsite conditions. Our research underscores the importance of microsite conditions for early seedling survival, as nurse shrubs or other shade structures buffer seedlings from extreme environmental conditions (Redmond et al. 2018; Urza et al. 2019; Crockett & Hurteau 2022). Although restoration success is notoriously challenging to predict (Brudvig et al. 2017), prioritizing microsites with favorable conditions, such as shade from nurse plants or the presence of litter, can improve restoration outcomes (Holl & Aide 2011; Stevens et al. 2021). In our study, we found that pinyon pine seedlings planted in shaded microsites, such as under shrubs and adjacent to perennial grasses, forbs, and woody debris, had more than three times greater survival than those in unshaded interspaces. These results were consistent with previous studies from the U.S. Southwest, which have found that nurse shrubs increased planted conifer seedling survival by 46% (Marsh et al. 2023), and that non-living shade objects such as woody debris increased survival by 20% or more (Marshall et al. 2023; Swanson et al. 2023). We also found a positive effect of organic litter on seedling survival, consistent with previous research finding that litter mitigates moisture and temperature stress (Aber et al. 1991; Brooker 2006; Maestre et al. 2009). In a range-wide analysis of pinyon pine seedlings, Ziffer-Berger et al. (2014) found a weaker shrub-seedling association in areas with greater litter cover, suggesting that organic litter in interspaces may promote seedling establishment or survival.

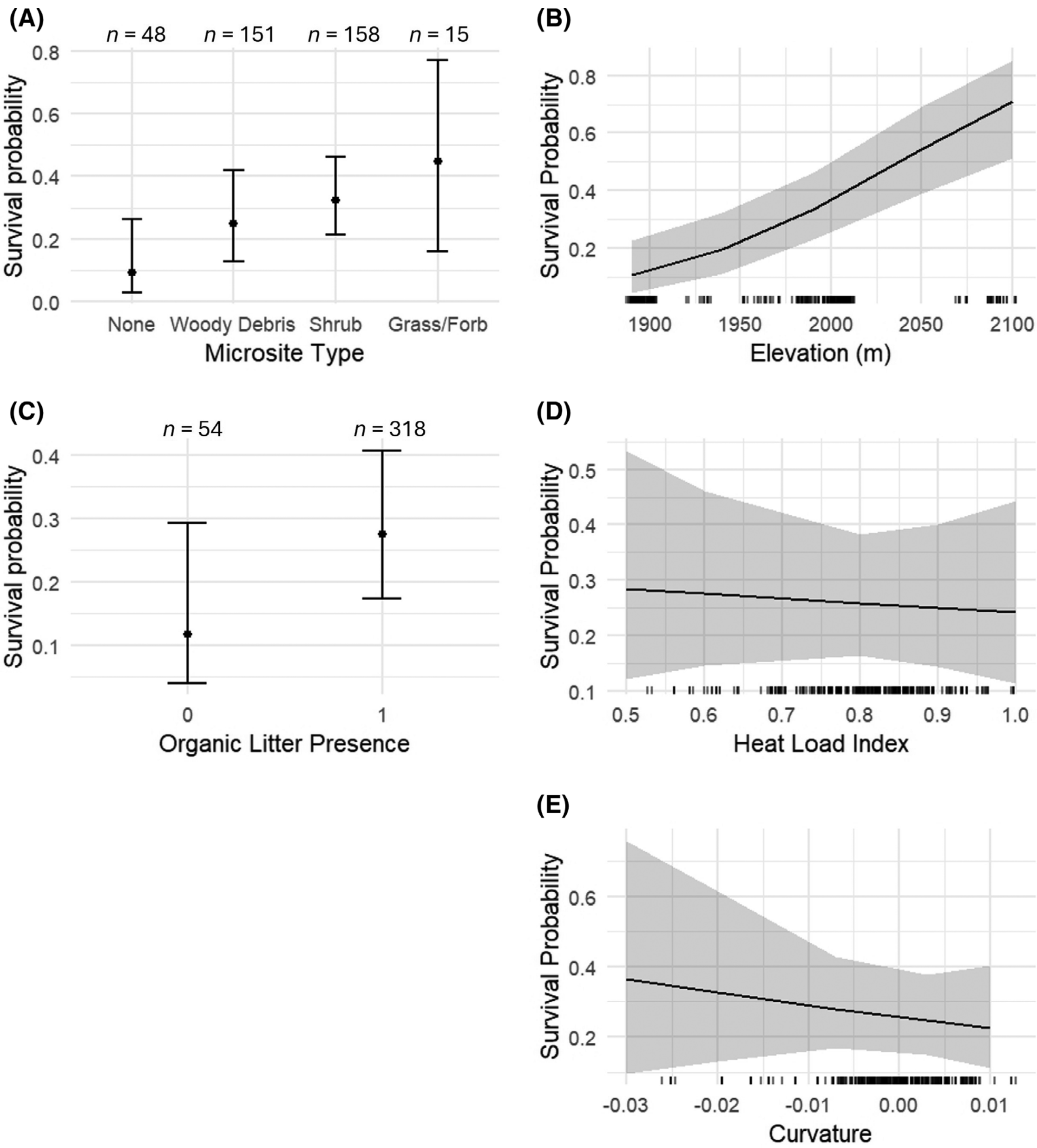

Figure 3. Partial effects plots showing predictor variable effects on pinyon pine seedling survival (mean predictions ± 95% CI). (A) Pinyon pine seedlings planted with a nurse plant or object (woody debris, shrubs, grasses/forbs) showed higher survival probabilities compared to those in interspaces. (B) The probability of seedling survival increased with elevation. (C) Seedlings in microsites with litter had higher survival compared to areas without litter. We found weak effects of (D) heat load index and (E) curvature on seedling survival. In (B), (D), and (E), black rug marks along the x-axis indicate the positions of individual data points.

Our study suggests that pinyon pine seedlings can establish successfully in association with various nurse plant species, including resprouting shrub, forb, and grass species commonly found in post-fire landscapes (Urza et al. 2017), in contrast to previous observations that pinyon pine seedlings are predominantly found under sagebrush canopies (Drivas & Everett 1988; Chambers 2001). Mutualist seed dispersers, such as pinyon jays, may preferentially cache seeds near sagebrush (Boone et al. 2021), which could contribute to the frequent association between pinyon pine seedlings and sagebrush. Although it is possible that pinyon pine seedlings survive best under sagebrush over longer time scales, our study lacked the experimental design or sample size to test that for our study area. Instead, our findings suggest that restoration outcomes can be improved by opportunistically using natural features (e.g., downed logs or woody debris) and local vegetation (Crockett & Hurteau 2022).

Our results further suggest that effective restoration requires understanding broad-scale environmental contexts to identify appropriate microsites for establishment. This is particularly important in dryland ecosystems, where facilitative plant–plant

Table 4. Observed survival percentages, odds ratios, and 90% confidence intervals for the effect of microsite type on pinyon pine seedling survival. Interspace condition was the reference category, and odds ratios for other microsite types were calculated relative to the interspace type.

Microsite Type	*Observed Survival (%)*	*Odds Ratio*	*90% Confidence Interval*
Interspace	10	—	—
Woody debris	25	3.20	1.18–8.68
Shrub	35	4.66	1.54–14.09
Grass/forb	40	7.84	1.93–31.82

interactions that help to buffer environmental stress are often key to seedling survival (Brooker et al. 2008). In our study, we found that TPI mediated the effect of canopy cover on seedling survival, and the facilitative effect of shade cover was greatest in areas with high abiotic stress—a finding consistent with predictions from the stress gradient hypothesis (Bertness & Callaway 1994; Pugnaire & Luque 2001). Seedling survival increased with higher canopy cover on ridge tops (high TPI) with convex surfaces, suggesting that cover was important for buffering against abiotic extremes in exposed locations (Rose et al. 2020; Swanson et al. 2023). In contrast, canopy cover had a negative effect on seedling survival in valley bottoms (low TPI) with concave surfaces, suggesting that cover plays a less critical role in locations where abiotic stress is low (Suggitt et al. 2011). TPI, an intermediate-scale metric of abiotic conditions, operates independently of elevation, and our results illustrate the importance of considering local topographic variability within restoration sites.

Elevation, a proxy for local gradients of temperature and precipitation, was found to be strongly positively related to seedling survival. This finding aligns with a regional study of post-fire tree planting outcomes, which found that seedling survival was highest in locations with cooler, wetter environmental conditions (Rodman et al. 2024). As climate change—including reduced snowpack and rising temperatures—is expected to limit tree regeneration at lower elevation range limits (Gray et al. 2006; Conlisk et al. 2017; Davis et al. 2023), restoration practitioners might consider focusing primarily in areas expected to be favorable to seedling survival in projected future climate conditions (Harris et al. 2006; Stevens et al. 2021). Restoration efforts can also incorporate other strategies for promoting climate adaptation, such as using nursery practices that enhance drought tolerance (Pinto et al. 2023) or selecting seedlings from more drought-adapted populations (Young et al. 2020; Marshall et al. 2024; Moran et al. 2024). We used seedlings grown from multiple seed sources in our study, and seed source climate is known to predict pinyon pine seedling traits (Vasey et al. 2023), but we were unable to track differences among seed sources due to logistical constraints. Because the seed sources were mixed such that they were roughly evenly distributed among planting sites and microsite locations, variation among seed sources likely introduced variation, rather than directional bias, into observed seedling outcomes. Nonetheless, future restoration studies should explicitly test the effect of seed source climate on planted seedling survival to inform pinyon pine restoration efforts.

Challenges and Opportunities for Collaborative Community-Based Restoration

Restoring pinyon pine is challenging on Washoe Tribal lands, where ongoing environmental changes from climate change,

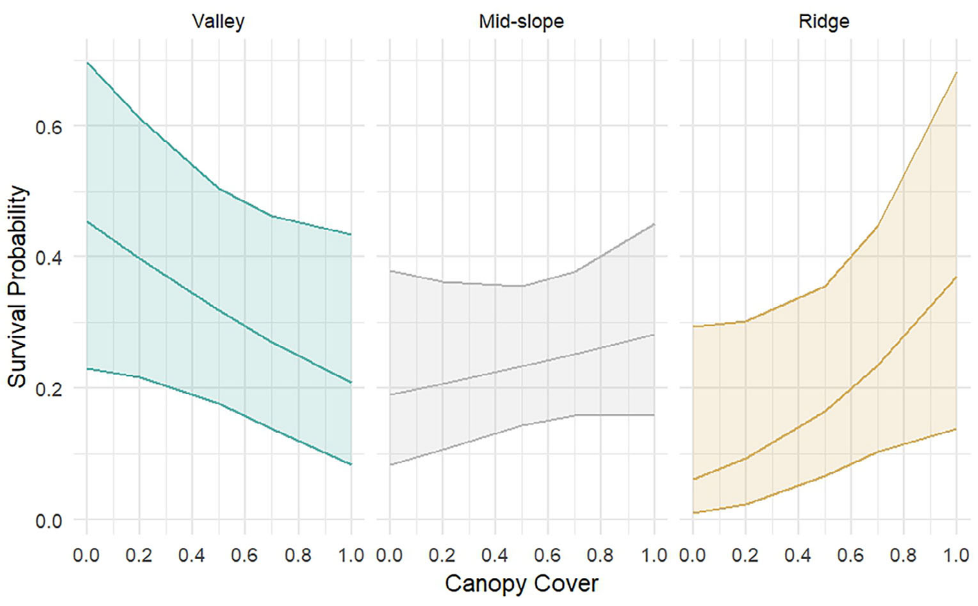

Figure 4. Probability of pinyon pine seedling survival as a function of canopy cover across varying Topographic Position Index (TPI) values. Panels show survival probabilities for TPI values ranging from −5 (valley bottoms; left panel), 0 (flat or mid-slope areas; center panel), and 5 (ridgetops; right panel). Shown are mean predictions ± 95% CI.

altered fire regimes, and invasive annual grasses confound restoration efforts (Washoe Tribe of Nevada and California 2024). The Washoe Tribe, deeply connected to the forest ecosystems that provide cultural and subsistence resources, faces heightened vulnerability to these changes (Parrotta & Agnoletti 2012; Farrell et al. 2021). Addressing the challenge of rapid environmental change requires innovative approaches that integrate ecological and cultural perspectives, transcending boundaries between social and ecological systems (Berkes 2004). Collaborations between the Washoe Tribe and restoration ecology researchers offer an opportunity to address these issues by blending technical expertise with traditional ecological knowledge and linking restoration efforts to the Tribe's values and practices (Donoghue et al. 2010; Jones et al. 2025).

In this study, the collaboration between the Washoe Tribe of Nevada and California and research co-authors was built on a foundation of trusting relationships that developed over several years. The Washoe Tribe's declaration of a state of emergency for pinyon pine (Washoe Tribe of Nevada and California 2024) underscores the urgency of their collaboration with researchers to bring greater attention to this issue. Joint field visits to burned landscapes on Washoe Tribal lands facilitated discussions about the drivers of ecosystem change. When an opportunity arose to adapt an ongoing study to address knowledge gaps in post-fire restoration, the partnership readily seized it. Researchers contributed study design and data analysis capabilities, while the Washoe Tribe provided in-depth knowledge of the landscape and implemented the planting effort. Seedlings were strategically planted in high-potential restoration islands (Hulvey et al. 2017) identified through shared planning, optimizing resources for sustainable restoration. Our approach mirrors efforts such as the East Jemez Landscape Futures working group, a group of land managers, scientists, Native American Tribal members, and NGOs which are working to restore culturally important species in the Jemez Mountains of New Mexico (Stevens et al. 2021). This integrated approach reflects global trends toward participatory restoration, which emphasizes ethical knowledge exchange and the leadership of local communities in ecological restoration (Derak et al. 2018; Silva et al. 2023; Weir et al. 2024).

Community-based restoration, as demonstrated in this collaboration, is critical for the Washoe Tribe to achieve long-term ecological stewardship of their lands. The Washoe Tribe's community-based approach to restoration fosters adaptability, blending traditional ecological knowledge with scientific methods to respond to dynamic environmental conditions. Centering Tribal community needs through collaborative workshops and open, respectful communication fosters ownership and creates lasting partnerships, ensuring the sustainability of restoration efforts (Weir et al. 2024). In the case of pinyon pine restoration on Washoe Tribal lands, the results of this study are being used to update restoration protocols and are being integrated into broader strategies to build resilience to future wildfires in linked social and ecological communities. Tribal-led stewardship also helps to ensure the project's longevity beyond the academic research cycle.

Community-based restoration nurtures a cross-cultural conservation ethic, embedding participants in a personal and collective relationship with the landscape (Berkes 2004). This often aligns with Indigenous worldviews, where stewardship is interwoven with cultural and spiritual values and where humans are considered part of the ecosystem (Leigh 2005). While conventional ecosystem science may focus on organism–environment interactions, Indigenous perspectives see landscapes as spaces where cultural meaning and ecological health are inseparable (Berkes 2004; Kealiikanakaoleohaililani & Giardina 2016). Through place-based restoration, communities not only restore ecosystems but also reaffirm the cultural narratives and spiritual connections tied to the land. As a result, community-based restoration can become an act of cultural reconnection, healing both the land and the community (Brace et al. 2006).

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Mean topographic conditions at each of the seven restoration planting sites and distribution of seedlings within each microsite type.
Table S2. Distribution of microsite conditions within each microsite type.
Table S3. Distribution of observed values for each continuous predictor variable.
Table S4. Model comparisons based on Akaike Information Criterion (AIC) values, with each row representing a different model.
Table S5. Results for the second-most supported model (ΔAIC $= 0.4$) predicting pinyon pine seedling survival 1 year following planting.
Figure S1. Topographic Position Index (TPI) map showing the distribution of TPI values within the study area, where TPI is calculated at a neighborhood size of 333 m.
Figure S2. Caterpillar plot showing the estimated random effects for each restoration site (mean estimate ±95% confidence intervals).
Figure S3. Probability of pinyon pine seedling survival as a function of canopy cover across varying curvature values, as estimated from the second-most supported model (Table S5).

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