

Fire Chronology Drives Understorey Diversity but Not Regeneration Dynamics in Himalayan Chir Pine Forests

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Abstract

Fire is reshaping forest composition across the Himalayan region, yet post-fire regeneration mechanisms remain poorly understood in the global South. Chir pine (*Pinus roxburghii*) forests account for 95.56% of Bhutan's recent fire-burned area, making them a critical test case for fire-adapted regeneration in resource-limited mountain ecosystems. This study identified a fundamental decoupling between soil recovery and vegetation succession across contrasting fire chronologies. We surveyed 60 nested plots across two sites in Wangdue Phodrang: one burned in 2019 (five-year recovery), and one burned in 2025 (recent burn). Non-metric multidimensional scaling revealed significant compositional differences between sites (PERMANOVA: shrubs $F = 3.78$, $p = 0.001$; herbs $F = 5.94$, $p = 0.001$), with the older burn site exhibiting greater herb diversity ($H' = 2.04$ vs 1.74). Recently burned areas showed significantly elevated pH (6.13 vs 5.84), electrical conductivity (0.07 vs 0.05 dS/m), and available potassium (248.21 vs 9.29 mg/kg), reflecting ash deposition. Critically, Spearman correlation analysis revealed weak, non-significant relationships between regeneration density and all soil properties at both sites ($p > 0.05$). *Pinus roxburghii* seedling and sapling densities were statistically equivalent across sites ($p > 0.05$), demonstrating remarkable regenerative resilience regardless of soil nutrient variation. This study provides the first integrated assessment of post-fire regeneration mechanisms in Bhutanese forests and reveals that natural regeneration operates independently of soil chemistry. These findings fundamentally challenge the global assumption that soil remediation is a prerequisite for forest recovery. In resource-limited mountain regions facing climate-driven fire intensification, this evidence that early regeneration success depends on microsite conditions and seed availability rather than edaphic restoration has transformative implications: managers must abandon costly, disruptive soil rehabilitation programs and instead protect the non-edaphic drivers of recovery, microhabitat complexity, natural seed dispersal, and minimal soil disturbance. By privileging nature-based recovery over engineered intervention, mountain forest management across the Himalayan region can achieve better ecological outcomes with far fewer resources, offering a scalable recovery pathway for the millions of hectares of fire-impacted forests facing unprecedented climate pressure globally.

Introduction

A forest fire is defined as any uncontrolled fire in combustible vegetation occurring in countryside or wilderness areas (Binjola et al., 2022). Although fires can result from natural phenomena such as lightning, the majority are human induced, particularly in the Himalayan region (Bhattarai et al., 2022). Fire plays a dual ecological role: low- to moderate-intensity fires can enrich soil nutrients and promote species diversity, facilitating ecological succession, whereas high-intensity fires may cause severe land degradation and biodiversity loss (McLauchlan et al., 2020). The global fire season of 2024 and 2025 burned approximately 3.7 million km² and emitted 2.2 Pg C, ranking among the most destructive on record (Kelley et al., 2025). Bhutan, with 69.71% of its 38,394 km² under forest cover, recorded 261 forest fire incidents between 2020 and 2024, burning approximately 70,696 acres of forested land (Department of Forest and Park Services [DoFPS], 2024). The chir pine (*Pinus roxburghii*) forest, constituting 2.93% of

the national forest estate, was the most fire-prone type in 2024, accounting for 95.56% of the total burned area (DoFPS, 2024). Despite this, site-specific post-fire studies in Bhutanese chir pine forests remain scarce, with most existing research geographically biased towards the Western Himalayan sites in India (Tenzin et al., 2024). *Pinus roxburghii* forests are distributed across the dry valleys of Bhutan at altitudes of 700 to 2,000 m asl, receiving 1,000 to 1,500 mm of annual precipitation (Mukhia et al., 2011). The species' highly flammable needle litter and resin-rich tissues make it inherently vulnerable to fire (Dobhal et al., 2025; Fulé et al., 2021). Wangdue Phodrang Dzongkhag, despite harbouring the largest forest cover of 258,969 ha, recorded the highest tree-cover loss of 35 ha per year from 2001 to 2024 (DoFPS, 2024). Understanding how fire shapes vegetation recovery and soil dynamics across different fire chronologies is thus critical for informing forest management and climate adaptation strategies in Bhutan.

This study addresses existing knowledge gaps by providing an integrated analysis of post-fire vegetation diversity and variability in soil properties across contrasting fire histories in the chir pine forests of Thedtsho Gewog, Wangdue Phodrang. Specifically, the study aimed to: (1) quantify and compare the vegetation composition across two sites with contrasting fire histories; (2) evaluate and compare soil properties between the two sites; and (3) analyse the relationship between regeneration density and soil properties in the post-fire environment.

Materials and Methods

Study area

The study was conducted in Thedtsho Gewog (27°29'20" N, 89°52'49" E), Wangdue Phodrang. The Dzongkhag, covering 4,029 km², has altitudes ranging from 800 to 5,800 m asl. and recorded an average temperature of 18.8°C with 574.9 mm annual rainfall in 2024 (National Statistics Bureau [NSB], 2025). Two study sites were selected based on fire records obtained from the Wangdue Division Office: Site 1 burned in 2019 (five-year post-fire) and Site 2 burned in 2025 (recent burn). Both sites experienced surface fires in the same forest type, making them suitable for a chronosequence comparison.

Study design and vegetation sampling

A systematic random sampling design was applied, with plots laid out at 100 m intervals using QGIS 3.44.5, Google Earth Pro, and Sentinel Hub fire perimeter data (Shacha et al., 2021). A total of 30 plots per site (60 plots combined; total plot area: 58.98 ha) were established, consistent with the central limit theorem, which is widely applied in ecological studies (Fox, 2025). Nested quadrats were used for vegetation assessment: 20 m × 20 m for trees (DBH ≥ 10 cm), 5 m × 5 m for shrubs and saplings (DBH 5–9 cm), and 1 m × 1 m for herbs and seedlings (DBH < 5

cm, height > 30 cm). Diameter at breast height (DBH) was measured at 1.37 m. Plant identification was supported by PlantNet, the Bhutan Biodiversity Portal, the Flora Archive of Bhutan, and expert consultation.

Soil sampling and laboratory analysis

Soil samples were collected from a depth of 0–15 cm using a 10 cm × 10 cm sampling frame within each herb plot ($n = 30$ per site). After air drying for two weeks, samples were sieved through a 2 mm mesh and finely ground. Soil pH and EC were measured using respective meters. Soil organic carbon (SOC) and nitrogen (N) were determined by the loss-on-ignition method; available phosphorus (P) by the Bray-Kurtz method; and exchangeable potassium (K) by the ammonium acetate method (Moktan, 2024).

Data analysis

Species diversity was assessed using the Shannon-Wiener Index (H'), Pielou's Evenness Index (J'), and Margalef Richness Index (DMg). Species dominance was determined through the Importance Value Index (IVI): for trees, $IVI = \text{Relative Density (RD)} + \text{Relative Frequency (RF)}$

+ Relative Basal Area (RBA); for shrubs and herbs, $IVI = \text{RD} + \text{RF} + \text{Relative Abundance (RA)}$. Community composition was assessed using the Bray-Curtis dissimilarity matrix and visualised through Non-metric Multidimensional Scaling (NMDS) ordination. Permutational Multivariate Analysis of Variance (PERMANOVA) and homogeneity of multivariate dispersions (PERMDISP) tests were conducted with 999 permutations.

Soil data normality was tested using the Shapiro-Wilk test. Soil pH, being normally distributed, was compared using an independent-samples t-test; all other soil parameters were compared using the nonparametric Mann-Whitney U test. Regeneration density (seedlings and saplings) between sites was compared using the Wilcoxon rank-sum test. Spearman's rank-order correlation was used to assess relationships between regeneration density and soil properties, given the non-normality of the data. All statistical analyses were performed in R version 4.5.3, and data management was conducted in Microsoft Excel

.

Results

Vegetation composition

Pinus roxburghii was the sole tree species at both sites, producing a Shannon diversity index (H') of 0 for the tree layer. Both sites recorded low to moderate shrub diversity as depicted in Tables 1 and 2. Site 1 showed greater species richness (DMg = 2.15) compared to Site 2 (DMg =

1.52), while Site 2 exhibited slightly higher evenness ($J' = 0.66$ vs 0.60) (Table 1). Herb diversity was higher at Site 1 ($H' = 2.04$) than at Site 2 ($H' = 1.74$), with greater evenness ($J' = 0.85$ vs 0.70) (Table 2).

Table 1
Species diversity indices for the shrub layer at the two study sites

Sites	H'	J'	DMg
Site 1	1.66	0.60	2.15
Site 2	1.65	0.66	1.52
Note: H' = Shannon diversity index; J' = Pielou's evenness index; DMg = Margalef species richness index.			

Table 2
Species diversity indices for the herb layer at the two study sites

Sites	H'	J'	DMg
Site 1	2.04	0.85	1.83
Site 2	1.74	0.70	2.10
Note: H' = Shannon diversity index; J' = Pielou's evenness index; DMg = Margalef species richness index.			

Species dominance

Pinus roxburghii was dominant in the tree layer at both sites ($IVI = 300$). At Site 1, *Lespedeza cuneata* was the most dominant shrub ($IVI = 85.54$), followed by *Duhaldea cappa* ($IVI = 61.62$), *Indigofera heterantha*, *Berberis asiatica*, and *Artemisia myriantha*. At Site 2, *Duhaldea cappa* was dominant ($IVI = 62.02$), followed by *Lespedeza cuneata*, *Indigofera heterantha*, *Cajanus scarabaeoides*, and *Barleria cristata*. *Cymbopogon* spp. dominated the herb layer at both sites ($IVI = 76.02$ at Site 1; 63.23 at Site 2).

Table 3
Dominant shrub species in 2019 Burned area

Species	Individuals	RD	RF	RA	IVI
<i>Lespedeza cuneata</i>	469	43.95	16	25.59	85.54
<i>Duhaldea cappa</i>	303	28.39	20	13.23	61.62
<i>Indigofera heterantha</i>	90	8.43	11	7.14	26.57
<i>Berberis asiatica</i>	45	4.22	17	2.31	23.53
<i>Artemisia myriantha</i>	42	3.94	14	2.62	20.56

Table 4
Dominant Shrub Species in 2025 Burned Area

Species	Individuals	RD	RF	RA	IVI
<i>Duhaldea cappa</i>	506	18.15	30.43	13.44	62.02
<i>Lespedeza cuneata</i>	340	12.20	17.39	15.80	45.39
<i>Indigofera heterantha</i>	304	10.9	17.39	14.13	42.42
<i>Cajanus scarabaeoides</i>	32	1.15	1.09	23.79	26.03
<i>Barleria cristata</i>	79	2.83	7.61	8.39	18.83

Community composition

NMDS ordination based on Bray-Curtis dissimilarity revealed a significant difference in shrub community composition between the two sites (*PERMANOVA*: $F(1,58) = 3.78$, $R^2 = 0.06$, $p = 0.001$), as well as in the herb layer $F(1,58) = 5.94$, $R^2 = 0.09$, $p = 0.001$). Beta-dispersion tests (*PERMDISP*) confirmed significant heterogeneity in both layers (shrub: $F = 6.47$, $p = 0.005$; herb: $F = 6.82$, $p = 0.01$), with Site 1 exhibiting greater compositional variability than Site 2. Stress values below 0.20 in both ordinations confirmed an acceptable fit for ecological interpretation (Clarke, 1993). Results are summarised in Table 5.

Table 5
PERMANOVA and *PERMDISP* results for shrub and herb understorey vegetation

Layer / Test	Source	df	R^2	F	p
Shrub <i>PERMANOVA</i>	Sites	1, 58	0.061	3.78	0.001**
Shrub <i>PERMDISP</i>	Groups	1, 58	—	6.47	0.005*
Herb <i>PERMANOVA</i>	Sites	1, 58	0.093	5.94	0.001***
Herb <i>PERMDISP</i>	Groups	1, 58	—	6.82	0.010*
Note: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. <i>PERMANOVA</i> run with 999 permutations using Bray-Curtis dissimilarity.					

Soil properties

Soil pH was significantly higher at Site 2 (6.13 ± 0.13) than at Site 1 (5.84 ± 0.18) ($p < 0.05$). EC was also significantly higher at Site 2 (0.07 ± 0.01 dS/m) than at Site 1 (0.05 ± 0.02 dS/m) ($p < 0.05$). Available K was elevated at Site 2 (248.21 ± 160.55 mg/kg) compared to Site 1 (9.29 ± 2.96 mg/kg) ($p < 0.05$). Available P was significantly ($p < .05$) higher at Site 1 (0.64 ± 0.83 ppm) than at Site 2 (0.30 ± 0.33 ppm) ($p < 0.05$). In contrast, SOC (Site 1: $10.54 \pm 2.29\%$;

Site 2: $8.20 \pm 15.56\%$) and N (Site 1: $0.53 \pm 0.11\%$; Site 2: $0.41 \pm 0.78\%$) did not differ significantly between sites ($p > 0.05$). Full descriptive statistics are presented in Table 6.

Table 6
Descriptive statistics (mean $\pm$ SD) for soil physicochemical properties across the two study sites

Parameter	Site 1 Max	Site 1 Min	Site 1 Mean $\pm$ SD	Site 2 Mean $\pm$ SD
pH	6.23	5.51	5.84 ± 0.18	$6.13 \pm 0.13^*$
EC (dS/m)	0.10	0.01	0.05 ± 0.02	$0.07 \pm 0.01^*$
N (%)	0.78	0.38	0.53 ± 0.11	0.41 ± 0.78 ns
SOC (%)	15.52	7.59	10.54 ± 2.29	8.20 ± 15.56 ns
P (ppm)	3.39	0.03	0.64 ± 0.83	$0.30 \pm 0.33^*$
K (mg/kg)	13.80	2.80	9.29 ± 2.96	$248.21 \pm 160.55^*$
Note: <i>*Significantly different from Site 1 ($p < 0.05$); ns = non-significant.</i>				

Regeneration status and soil regeneration correlations

Both sites exhibited a positive regeneration trend (seedlings > saplings > trees), classified as 'good' regeneration status (Anbes et al., 2025). No significant difference was found in seedling density (Site 1: $5,333 \pm 5,074 \text{ ha}^{-1}$; Site 2: $3,667 \pm 4,901 \text{ ha}^{-1}$) or sapling density (Site 1: $1,040$

$\pm 818 \text{ ha}^{-1}$; Site 2: $747 \pm 619 \text{ ha}^{-1}$) between sites ($p > 0.05$).

Spearman's correlation analysis revealed weak, non-significant relationships ($p > 0.05$) between regeneration density and all soil properties at both sites. At Site 1, seedlings showed weak negative correlations with P ($\rho = -0.26$) and K ($\rho = -0.24$). At Site 2, seedlings exhibited weak positive correlations with K ($\rho = 0.21$) and P ($\rho = 0.08$). A strong positive correlation between SOC and N was significant at both sites ($p < 0.05$).

Discussion

Vegetation composition and species dominance

The monospecific *Pinus roxburghii* tree layer at both sites reflects fire-driven overstorey simplification, consistent with reports that high-frequency fire progressively eliminates fire-intolerant broadleaved species while favouring this resilient conifer (Bargali et al., 2022; Weeks et al., 2023). The low-to-moderate shrub diversity at both sites indicates early to mid-successional stages; however, the greater species richness at the five-year burn site suggests that ecological diversity accumulates progressively with time since fire (Bashirzadeh et al., 2023; Davies et al., 2021). The dominance of leguminous shrubs

Lespedeza cuneata, *Indigo-fera heterantha*, and *Cajanus scarabaeoides* at both sites aligns with the post-fire advantage of nitrogen-fixing species in nutrient-limited soils following combustion (Reverchon et al., 2012). The prevalence of *Cymbopogon* spp. as the dominant herb at both sites reflects the open-canopy, high-insolation conditions created by fire, which favour this light-demanding grass (Darabant, 2017).

Community composition

The significant PERMANOVA results for both shrub and herb layers indicate that fire chronology drives compositional divergence between sites. However, the low R^2 values (< 0.09) indicate that site identity explains less than 10% of the total compositional variation, with the remainder attributable to within-site heterogeneity, including microhabitat conditions, fire-severity patchiness, and microclimate (Paudel et al., 2023). The greater compositional variability at Site 1, evidenced by the *PERMDISP* results and broader NMDS scatter, reflects the diversification of ecological niches over five years of recovery, consistent with post-fire successional heterogenization (Dinage, 2009; Gallagher, 2021). The tight clustering of Site 2 plots represents the biotic homogenization characteristic of recently disturbed communities dominated by pioneer species (Kumar and Pandey, 2022; Sharma et al., 2023).

Soil properties

The significantly elevated soil pH and EC at the recently burned site are consistent with the release of base cations and inorganic ions through ash deposition (Dhungana et al., 2024; Nan-dakumar et al., 2023; Sharma et al., 2023). These changes are typically transient, returning to pre-fire levels as base cations are progressively leached (Graham et al., 2016; Xue et al., 2014). The dramatic increase in available K at Site 2 reflects freshly deposited ash; its high water-solubility leads to rapid loss through leaching over time, explaining the markedly lower K at

Site 1 (Swindle et al., 2021). The significantly higher available P at the older burn site corroborates findings that initial post-fire increases in P are short-lived, declining below older-burn levels within approximately 1 year (Deng et al., 2024). The non-significant differences in SOC and N between sites suggest that five years of litter input, microbial stabilization, and vegetation recovery have partially restored these pools to pre-fire conditions (Guleria et al., 2017; Vishvamitera et al., 2022).

Regeneration and soil–regeneration relationships

The good regeneration status at both sites reflects the inherent fire-adaptedness of *P. rox-burghii*, which possesses morphological traits, such as thick bark, deep tap root, and serotinous cones, enabling rapid re-establishment even under nutrient-limited soil conditions (Srivastava and Bahar, 2007). The absence of significant differences in seedling and sapling densities among sites suggests that regeneration resilience is maintained over short- to medium-term post-fire timescales. The weak, non-significant soil–regeneration correlations indicate that edaphic factors alone do not govern post-fire regeneration. Non-edaphic factors, including microsite conditions, light availability, precipitation, seed availability, and fire severity, are likely more decisive (Ruggirello et al., 2023; Stewart et al., 2021). These findings align with Seaman et al. (2015), who showed that regenerating conifers develop nutrient conservation strategies

that decouple establishment success from absolute soil nutrient concentrations. The strong positive SOC–N correlation confirms their co-accumulation driven by shared ecological processes (Wi-bowo and Kasno, 2021).

Conclusion

This study provides the first integrated assessment of post-fire vegetation dynamics and soil properties across contrasting fire chronologies in chir pine forests of Bhutan. The results demonstrate that fire chronology significantly shapes understory vegetation structure and key soil parameters, with recently burned sites characterized by elevated pH, EC, and K, and older burn sites showing greater species diversity, higher SOC, N, and P. The monospecific dominance of *Pinus roxburghii* at both sites reflects fire-driven overstorey simplification. Importantly, the weak soil–regeneration correlations at both sites indicate that non-edaphic factors govern post-fire regeneration, and that *P. roxburghii* exhibits considerable regenerative resilience irrespective of soil nutrient status.

These findings provide essential baseline information for fire ecology research in Bhutanese forests. From a management perspective, early-stage post-fire interventions should prioritize minimizing soil disturbance and supporting natural regeneration rather than extensive soil remediation. Future research should incorporate multiple fire history sites, long-term monitoring plots, functional trait analyses, and environmental covariates such as slope, aspect, and soil moisture to better isolate fire effects from other landscape drivers.

Limitations and Recommendations

This study has certain limitations that should be considered when interpreting the results. First, the comparison was based on only two fire-history sites, which limits the ability to generalize findings across broader landscapes. Secondly, the study design captures a single time snapshot rather than long-term monitoring, which restricts understanding of temporal successional trajectories. Additionally, data collection during the winter season posed constraints on plant identification, and since most plants are absent during the winter, this might result in different findings if a similar study is carried out at different times within the same forest type.

Despite these limitations, the study provides useful baseline information on post-fire vegetation and soil dynamics in chir pine forests. It is recommended that future research include a larger number of sites spanning multiple fire histories and environmental gradients to strengthen inference. Long-term monitoring plots should be established to track successional changes over time.

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Figures

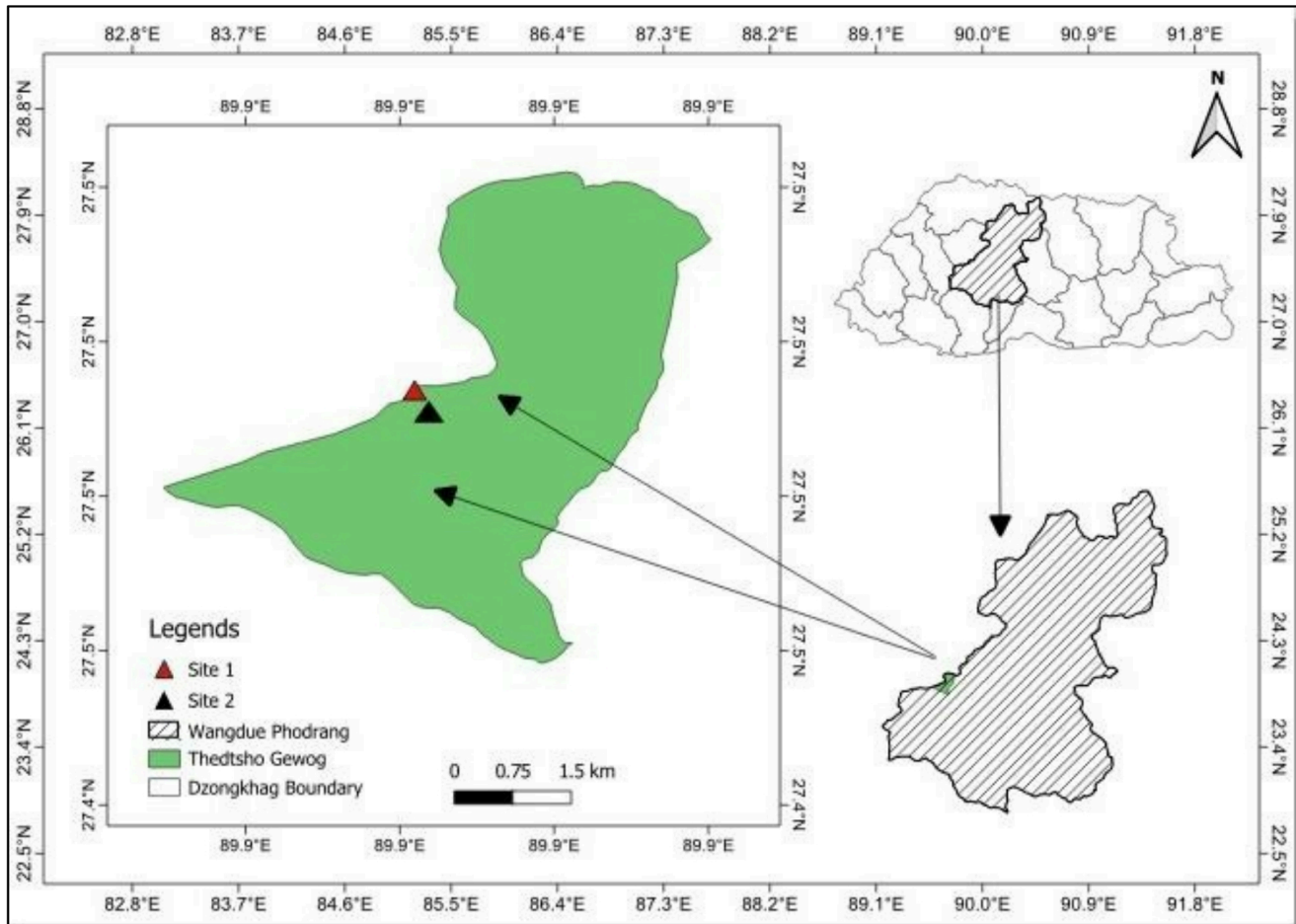


Figure 1

Study Area

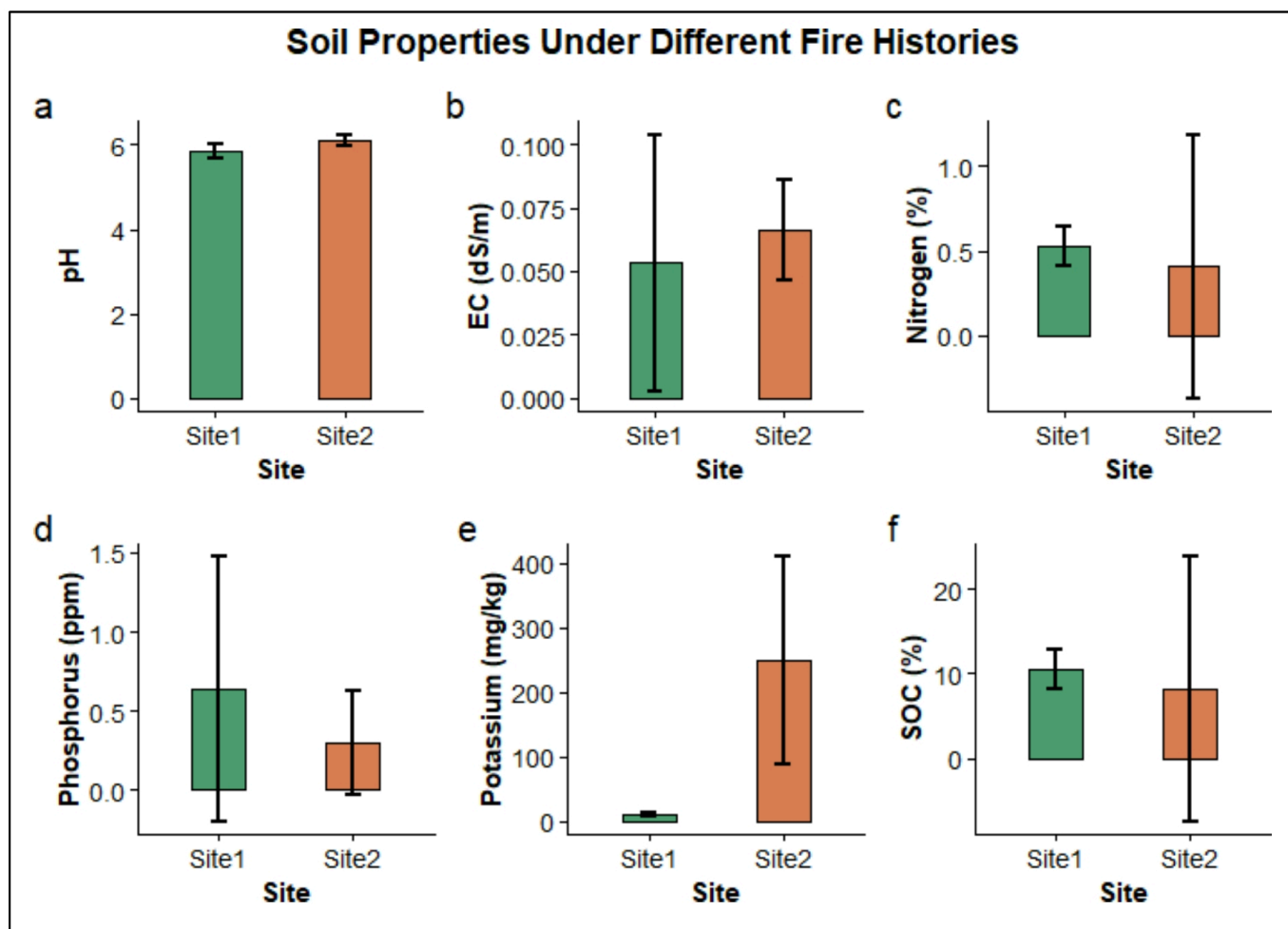


Figure 2

Soil properties variability across the sites

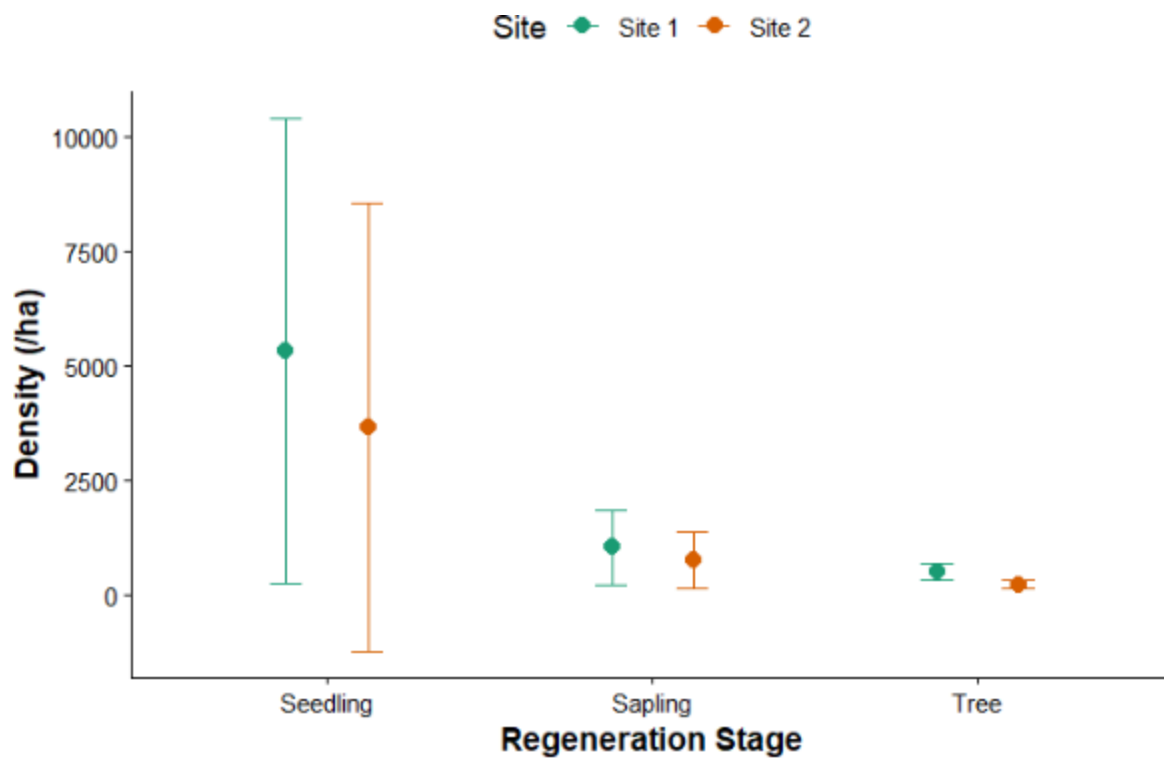


Figure 3

Regeneration Status across the sites

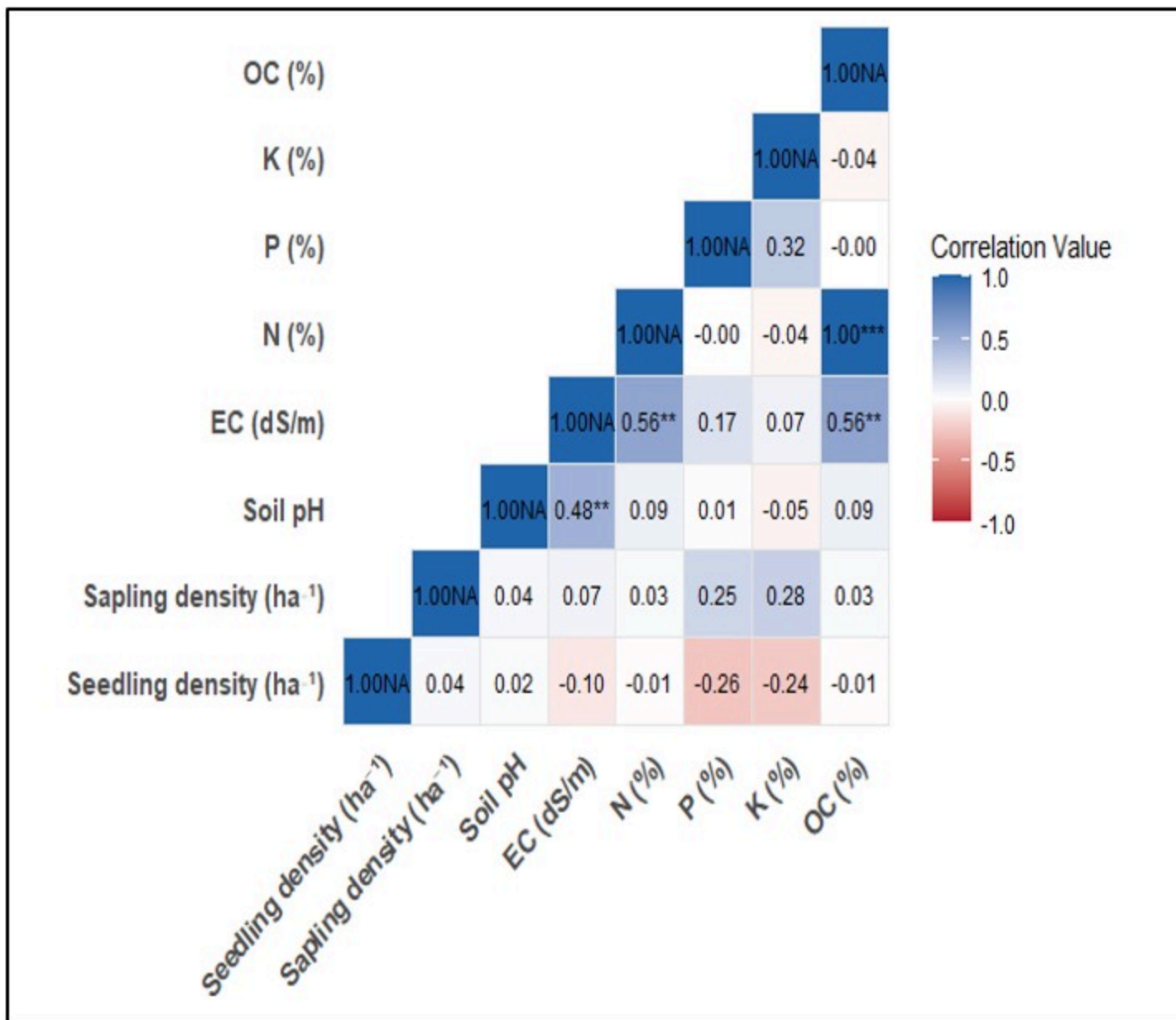


Figure 4

Spearman correlation between re-generations and soil properties across Site 1 (2019 Burned Area)

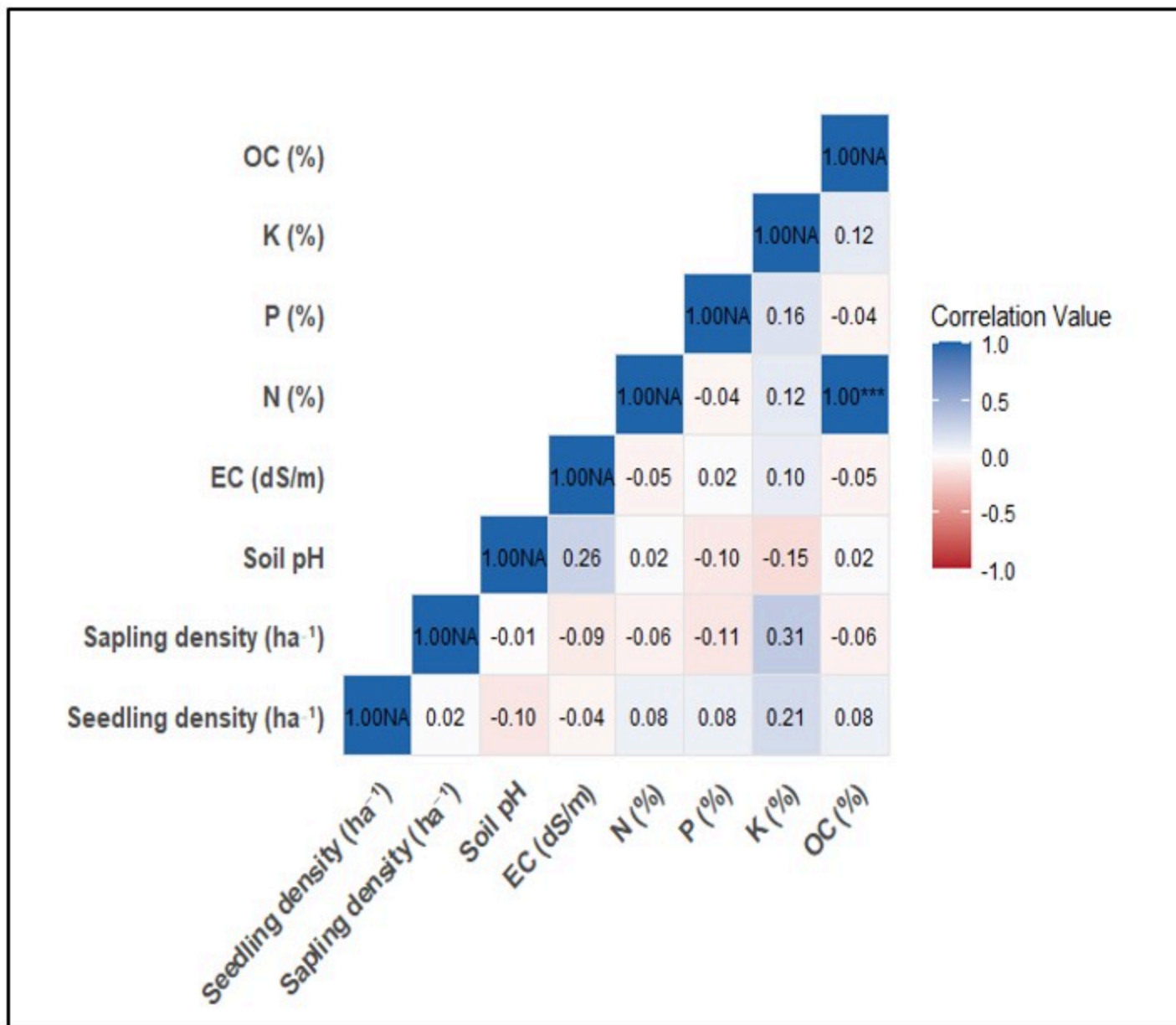


Figure 5

Spearman correlation between re-generations and soil properties across Site 1 (2025 Burned Area)