A Moss-Based Approach for Assessing the Potential for Ecological Restoration in Vegetation-Degraded Volcanic Landscapes: A Case Study of Doneori Oreum in Jeju Island

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Abstract

Aims

This study aims to assess the potential for ecological restoration in vegetation-degraded volcanic landscapes by examining the effects of moss on soil functionality. The goal is to identify the ecological contributions of pioneer moss species to the rehabilitation of these landscapes, focusing on Jeju Island’s Doneori Oreum.

Methods

Soils were collected from vegetation-degraded and vegetation-rich areas within Doneori Oreum, a parasitic volcanic cone on Jeju Island. After characterizing soil physicochemical properties, three native moss species—*Rhacomitrium canescens*, *Hypnum plumaeforme*, and *Ceratodon purpureus*—were applied to the degraded soil under controlled indoor conditions. Changes in soil properties such as pH, organic matter (OM), cation exchange capacity (CEC), total nitrogen (T-N), and available phosphorus (AP) were analyzed.

Results

Degraded soils showed significantly lower OM, CEC, and exchangeable cations compared to vegetation-rich soils, despite higher levels of T-N and AP. This contrast suggests that the absence of vegetation may have limited nutrient uptake and cycling, resulting in the accumulation of unutilized nutrients in degraded soils. Moss application significantly improved all measured soil properties. Each moss species enhanced pH, OM, CEC, AP, T-N, and exchangeable cations (Ca^{2+}, Mg^{2+}, K^{+}), with variation in magnitude, indicating species-specific effects.

Conclusions

Mosses contribute to early-stage soil restoration by stabilizing surface soils, increasing organic matter, and potentially supporting microbial colonization. These findings highlight mosses as promising agents in ecological restoration. However, field-based and long-term studies are necessary to validate their practical effectiveness and to develop optimized restoration strategies.

Introduction

Tourism has long played a significant role in global economic activity, and many countries have fostered it as a key industry. According to the United Nations World Tourism Organization (UNWTO), the number of international tourists increased from 675 million in 2000 to 940 million in 2010, and the tourism sector now accounts for approximately 9% of global GDP. However, despite being referred to as a “smokeless industry,” tourism has often lacked sufficient awareness of its environmental impacts (Barrow, 2006; Hsieh and Kung, 2013).

The expansion of tourism activities has contributed to various environmental problems, including air, water, and soil pollution (Zeng et al., 2021; Xiong et al., 2022), loss of biodiversity (Habibullah et al., 2016), and degradation of ecosystem functions (Pueyo-Ros, 2018). More recently, the phenomenon of overtourism has triggered social conflicts such as reduced quality of life for residents, damage to cultural heritage, and growing anti-tourism sentiments, posing a threat to sustainable tourism (Seraphin et al., 2018; Koens et al., 2018; Benner, 2019).

Within this global trend, Jeju Island—South Korea's representative island tourist destination—serves as a crucial case study. According to Bae and Nam (2019), the total number of tourists visiting Jeju Island in 2015 approached 200 million. As of March, 2015, domestic tourists accounted for 161,003,341, and international tourists totaled 38,007,890. This represented an 18.1% increase in domestic visitors and a 53.8% increase in international visitors compared to the same period in 2014. Jeju Island became particularly popular among Chinese tourists, especially after the Korean government implemented a 30-day visa waiver program for them in May 2013. In addition, the expansion of low-cost carriers (LCCs) has encouraged a broader range of tourist groups to visit Jeju. In 2013, approximately 5,400 Thai tourists visited the island, and this number increased sharply in 2014. Moreover, the spread of the Korean Wave (Hallyu) has led to a growing number of visitors from Thailand and other Southeast Asian countries.

However, the rapid increase in tourism has led to mounting environmental pressures such as resource consumption, waste generation, carbon emissions, and ecosystem degradation. These impacts are especially severe in Jeju, where volcanic landforms and unique ecosystems coexist. Although Jeju has been designated as a UNESCO Biosphere Reserve (2002), World Natural Heritage Site (2007), and Global Geopark (2010), achieving a balance between conservation and tourism remains a critical challenge. Tourism-centered development continues to damage the natural environment and threatens long-term sustainability (Kim et al., 2017).

Among Jeju's natural assets, the parasitic volcanic cones known as "Oreum" possess significant geological, ecological, scenic, and cultural value. Oreum are distributed throughout the mid-mountain and coastal regions and are closely linked to Jeju's local life, cultural heritage, and endemic ecosystems. However, unregulated tourism, quarrying, golf course construction, and road development have caused rapid degradation, and some areas are now beyond recovery (Ko, 2007).

Given the accelerating deterioration of oreum ecosystems, it is urgent to assess ecosystem resistance and resilience and explore feasible restoration strategies. In recent years, restoration ecology has increasingly utilized soil functionality and quality as key diagnostic indicators, with integrative evaluations of biological, chemical, and physical properties gaining traction (Andrews et al., 2004; Doran, 1996; Weil, 2004).

Oreum soils are classified as Andisols, formed by the deposition of volcanic pyroclasts. In the early stages, these soils are typically deficient in organic matter, exhibit strong phosphorus fixation, and suffer from aluminum toxicity, making vegetation establishment difficult (Shoji and Takahashi, 2002). Delayed formation of biotic communities can further hinder the colonization of higher plants and constrain plant–microbe interactions. Nevertheless, these soils have the potential to develop into highly productive systems over time as organic matter accumulates and cation exchange capacity improves. Therefore, strategic intervention in the early stages of restoration is critical.

Despite this, empirical studies evaluating functional changes and restoration potential in such volcanic soils—especially regarding the role of pioneering species such as mosses—remain limited. Mosses, with around 1,200 species distributed worldwide (Crandall-Stotler et al., 2007), are crucial for ecosystem restoration due to their high desiccation tolerance, organic matter accumulation, water retention, and ability to stimulate microbial activity (La Farge et al., 2013; DeFalco et al., 2001; Bowker et al., 2008). Their capacity to form surface mats stabilizes the soil and prevents erosion, making them effective agents for restoring exposed volcanic landscapes.

This study recognizes the initial constraints of volcanic ash soils and experimentally investigates the effects of moss inoculation on soil functionality and ecological transition potential. By diagnosing ecosystem resistance and resilience in disturbed environments, this research aims to provide practical indicators for restoration, address the limitations of species richness-focused evaluations, and propose a novel approach to ecosystem restoration. Ultimately, it seeks to contribute foundational data for sustainable restoration strategies in Jeju's oreum and to present a proactive restoration framework that goes beyond mere conservation.

Methods

Study area

The study site is Doneori Oreum, located across Geumak-ri, Hallim-eup, Jeju-si and Donggwang-ri, Andeok-myeon, Seogwipo-si, Jeju Island (33°19'32.51"N, 126°19'18.70"E). The site has an elevation of 439.6 meters and covers an area of 306,369 m² (Fig. 1A). The temporal scope of the study is defined by the acquisition of a multispectral drone dataset captured on August 10, 2022. Soil samples for assessing soil fertility were collected on August 24, 2022.

The selection of the study site was based on three primary criteria: (1) the presence of scoria-based soils as the parent material of the oreum, (2) restricted human access for over 10 years due to a designated natural resting period, and (3) clear contrasts in vegetation richness, enabling the comparison of land cover types.

To evaluate the potential for vegetation restoration, two distinct subregions were designated within the study site: (a) a vegetation-degraded area, characterized by sparse vegetation cover and exposed soil surface, and (b) a vegetation-rich area, with dense plant cover and high biodiversity (Fig. 1B, C).

This classification allowed for a well-defined experimental design, in which soils from the vegetation-degraded area (a) were used as control plots, while soils from the vegetation-rich area (b) served as comparison plots.

The long-term exclusion of human activity provided favorable conditions for observing natural recovery processes, making the site particularly suitable for conducting ecological restoration research. Based on these conditions, Doneori Oreum was selected as the final study site for this research.

In this study, low-altitude LiDAR imaging was conducted using a DJI Phantom 4 RTK Multispectral unmanned aerial vehicle (UAV) equipped with a multispectral camera comprising six specialized lenses. The lenses included Red Edge (RE), Near-Infrared (NIR), Green (G), Red (R), Blue (B), and visible spectrum (RGB). During each image capture, all six lenses operated simultaneously, enabling the acquisition of images across multiple spectral bands.

The UAV flight was conducted at an altitude approximately 80 meters above the summit of the study area (approximately 440 meters above sea level). The UAV captured images twice, in both vertical and horizontal directions, flying back and forth at an oblique angle of 45 degrees from the horizon. The camera resolution was 1600 × 1300 pixels (aspect ratio 4:3.25). Following image acquisition, aerial triangulation was performed to align and correct the data. Subsequently, orthomosaic images were generated for the Red, Green, Blue, and Near-Infrared (NIR) bands to produce a two-dimensional multi-spectral map. Based on this mapping, two vegetation indices—NDVI (Normalized Difference Vegetation Index) and GNDVI (Green Normalized Difference Vegetation Index)—were calculated. Among these, NDVI was used as the primary indicator in this study, as it provides a quantitative measure of vegetation vitality. Originally proposed by Rouse et al. (1973), NDVI values range from − 1 to 1, with values closer to 1 indicating higher vegetation vigor

Soil sample

A total of 26 surface soil samples (each 1 kg) were collected at a depth of 10 cm during four field surveys conducted between August and October 2022 and two additional surveys between March and April 2023.

Samples were taken using a Edelman soil auger, 10 cm diameter (Eijkelkamp Soil & Water, Netherlands) from 3 to 4 points along diagonal lines across slopes and their symmetrical directions within the target Oreum. The samples from each plot were composited before analysis.

The collected soils were air-dried and passed through a 2 mm sieve prior to analysis. Soil properties were analyzed in accordance with the Standard Methods of Soil and Plant Analysis I and II by the National Institute of Forest Science (NIFoS, 2014a, b).

Moss treatment

Due to the complex interaction of coastal currents, topography, and other climatic factors, Jeju Island experiences distinct seasonal variations. In summer, the influence of the North Pacific air mass results in high rainfall and heavy downpours, while droughts tend to intensify when the Okhotsk air mass strengthens. During winter, the northwesterly monsoon winds cause sharp temperature fluctuations. Generally, the region is characterized by strong winds throughout the year.

Based on these climatic conditions, moss species suitable for restoration of Doneori Oreum were selected according to the following criteria: (1) the ability to survive in dry and cold extreme environments, (2) the capacity to grow on sandy soils or rocks in semi-shaded to full-sun areas, and (3) the presence of native populations within Doneori Oreum.

As a result, three moss species that naturally grow in the study area were identified and selected as experimental materials: *Hypnum plumaeforme* Wilson, *Ceratodon purpureus*, and *Rhacomitrium canescens*.

Surface soil samples collected from the experimental plots of Doneori Oreum were transported to the laboratory. The three moss species were air-dried under natural light for seven days, then ground in a blender for 30 seconds. A 2 g portion of the moss material was evenly applied to each 800 ml plastic container filled with the soil samples. All samples were incubated in a plant growth chamber HS-PGC-768 (HANSOL TECH, Republic of Korea) under controlled conditions—25 ± 3°C temperature, 60 ± 10% humidity, and 2,218 Lux light intensity with a 16h/8h light/dark cycle—for four weeks without exposure to external environmental factors.

Physicochemical analysis of soil properties

To determine soil organic matter (SOM) content, samples were subjected to loss-on-ignition (LOI) by heating at 500°C for 2 hours. The resulting %LOI was converted to %OM (organic matter), and subsequently to soil organic carbon (SOC) using the Van Bemmelen factor of 1.724 (Cambardella et al., 2001; Nunes et al., 2020).

Soil pH was measured after mixing soil and distilled water at a 1:5 (v/v) ratio and shaking the mixture for 30 minutes (5 cycles) using a microwave shaker (CEM Corporation, USA). Measurements were performed using a pH meter (Thermo Fisher Scientific, USA).

Cation exchange capacity (CEC) was determined using the 1N ammonium acetate (NH_4OAc, pH 7.0) extraction method (Sumner and Miller, 1996). Prior to analysis, soil samples were passed through a 2 mm sieve and prepared in a dry state. Then, 10 g of soil was mixed with 50 mL of 1N NH_4OAc solution and shaken at room temperature for 1 hour to exchange the cations with NH_4^+. Excess NH_4OAc solution was removed, and the samples were repeatedly washed with deionized water and 95% ethanol to eliminate residual NH_4^+. Subsequently, 1N KCl solution was added to displace the adsorbed NH_4^+, and the extracted solution was filtered for analysis. The concentration of NH_4^+ in the filtrate was measured using an inductively coupled plasma optical emission spectrometer (ICP-OES, Analytik Jena, Germany), and the CEC value was calculated based on a standard calibration curve.

Available phosphorus was analyzed using the Lancaster method, a standard analytical procedure in Korea (Cox, 2001; Song et al., 2008; Kim et al., 2013). Briefly, 5 g of soil was mixed with 20 mL of phosphorus extraction solution and shaken using a microwave shaker (CEM) for 10 minutes (1 cycle). The mixture was filtered, and 3 mL of the extract was combined with 6 mL of color-developing reagent and 0.4 mL of 1-amino-2-naphthol-4-sulfonic acid. The mixture was incubated at 30°C for 30 minutes, and absorbance was measured at 720 nm using a spectrophotometer (Analytik Jena, Germany) based on a standard calibration curve.

Total nitrogen content was determined using a nitrogen analyzer (OPSIS), based on the Kjeldahl digestion method (Saez-Plaza et al., 2013a; 2013b). In brief, 0.25–2.0 g of soil was mixed with 2 mL of distilled water and stirred, followed by the addition of 1 mL of potassium permanganate and additional mixing. Then, 2 mL of 1:1 diluted sulfuric acid was added and the mixture was left to stand for 5 minutes to decompose organic nitrogen. One drop of N-octyl alcohol and 0.5 g of reduced iron (Fe) were added, and the mixture was heated at 100°C for 1 hour. The sample was then distilled under alkaline conditions and titrated to quantify total nitrogen.

Particle size distribution was analyzed using sieve analysis with six mesh sizes: 53 μm, 105 μm, 250 μm, 500 μm, 1 mm, and 2 mm, to classify coarse and fine fractions (Afrazi and Yazdani, 2021). The procedure followed ASTM D6913 standards. Soil samples were oven-dried at 105°C for 24 hours prior to sieving. The dried samples were passed through the stacked sieves using a mechanical shaker for 10 minutes to fully separate the particles. The mass retained on each sieve was recorded, and the percentage of each size fraction was calculated. Soil texture was classified using the Soil Texture Triangle provided by the United States Department of Agriculture (USDA).

All soil property analyses were outsourced and conducted by AT Analysis Center (Incheon, Republic of Korea). Statistical analysis was performed using GraphPad Prism 5 (Version 5.01, GraphPad Software, INC., 2007), and unpaired t-tests were used to determine significance. Statistical differences were considered significant at $p < 0.0001$.

Results

Particle size distribution (PSD) of soils from vegetation-degraded and vegetation-rich areas

Table 1
Particle size distribution and bulk density of soil samples collected from the vegetation-degraded area (a) and the vegetation-rich area (b). The particle size fractions are expressed as the percentage (%) of the total soil mass retained within each sieve size range

Sample	d ≤ 53 μm	53 μm < d ≤ 105 μm	105 μm < d ≤ 250 μm	250 μm < d ≤ 500 μm
(a)	0.23	1.12	8.83	8.99
(b)	0.09	0.48	4.79	6.37
Sample	**500 μm < d ≤ 1.00 mm**	**1.00 mm < d ≤ 2.00 mm**	**2.00 mm < d**	**Bulk density (g/cm^3)**
(a)	34.95	21.63	24.25	0.86
(b)	29.59	24.2	34.48	0.96

Soil not only provides a habitat for plants and animals but also functions as a reservoir for water and essential nutrients (Jency et al., 2023). As a natural body composed of minerals and organic matter, soil performs key functions for plant growth, and its quality is closely related to vegetation health. Soil quality is typically assessed by nutrient content, and its physicochemical properties are considered indicators of soil fertility (Jency et al., 2023).

During soil formation, physical weathering generates mineral particles of various sizes, which form the foundation of soil structure and pore systems. The resulting particle size distribution (PSD) has long served as a critical criterion for classifying and managing soils in agriculture, road construction, and building development. Since particle size directly affects the soil's specific surface area and pore structure, understanding PSD is essential for interpreting the physical and chemical characteristics of soil (Petersen et al., 1995; Hwang and Powers, 2003).

The particle size analysis results for soils from the vegetation-degraded area (a) and vegetation-rich area (b) are shown in Table 1. In the vegetation-degraded area, the soil consisted of gravel (d > 2.00 mm) at 24.25%, sand (500 μm < d ≤ 2.00 mm) at 56.58%, silt (53 μm < d ≤ 500 μm) at 18.94%, and clay at 0.23%, classifying it as sandy loam based on the soil texture triangle. Similarly, the vegetation-rich area showed 34.48% gravel, 53.79% sand, 11.64% silt, and 0.09% clay, also classifying it as sandy loam (Fig. 2A). The particle-size distribution curves are presented in Fig. 2B.

As shown in Fig. 2B, both regions exhibit similar curve patterns, indicating a coarse-textured soil dominated by gravel and sand with low proportions of fine particles (silt and clay). However, the vegetation-degraded area showed a lower effective particle diameter (D10) and a higher coefficient of uniformity (Cu), suggesting a more heterogeneous mix of particle sizes. Additionally, the bulk density in the vegetation-rich area is approximately 0.1 g/cm^3 higher.

Table 2
Comparison of soil physicochemical properties between the (a) vegetation-degraded area and the (b) vegetation-rich area. Values are expressed as means ± standard error (SE) based on three replicates. Different uppercase letters within each row indicate statistically significant differences between the two sample groups as determined by a non-parametric t-test ($P < 0.001$).

Sample	pH [1:5]	OM (%)	CEC (cmol/kg)	AP (mg/kg)	T-N (%)	Ex. Cat. (cmol/kg)		
						Ca^{2+}	Mg^{2+}	K^{+}
(a)	5.80 ± 0.022A	1.82 ± 0.019B	1.73 ± 0.008B	146.17 ± 0.196A	0.22 ± 0.005A	0.63 ± 0.005B	0.24 ± 0.011B	0.06 ± 0.003B
(b)	5.70 ± 0.097A	13.10 ± 0.075A	17.93 ± 0.061A	33.80 ± 0.244B	0.11 ± 0.004B	12.55 ± 0.041A	3.77 ± 0.046A	0.65 ± 0.009A

Physicochemical properties of soil in vegetation-degraded and vegetation-rich areas

Plant growth is closely associated with the physical and chemical properties of soil, which directly influence the functional structure and productivity of ecosystems. These characteristics serve as key indicators for assessing ecosystem stability and resilience (Shen et al., 2024; Wang et al., 2024). Physical and chemical properties of soil—such as bulk density, texture, porosity, and organic matter content—are crucial because they reflect infiltration capacity, aeration, solute mobility, and water retention capacity. Therefore, when analyzing changes in soil bulk density, it is essential to also investigate physicochemical properties, including porosity, particle size distribution (PSD), organic matter content, and soil nutrient composition (Li et al., 2013; Wang et al., 2024).

The results of physicochemical analysis for soils from the degraded (a) and well-vegetated (b) areas are presented in Table 2. Soil pH is a key variable that regulates a wide range of biological, chemical, and physical properties and processes, ultimately influencing plant growth and biomass productivity (Minasny et al., 2016; Neina, 2019). It plays a particularly important role in nutrient availability, microbial activity, enzymatic reactions, and nitrogen cycling. In this study, the soil pH in the vegetation-degraded area was slightly higher than that in the vegetation-rich area; however, the difference was not statistically significant.

Soil organic matter (OM) and cation exchange capacity (CEC), which closely related indicators of soil fertility, were notably greater in the vegetation-rich area. OM plays a vital role in enhancing CEC and water retention in light-textured soils by releasing essential nutrients such as nitrogen, phosphorus, sulfur, and trace elements during decomposition (Johnston, 1986a), and contributes to soil structure stability by maintaining pore systems (Johnston, 1986b). The vegetation-rich soils exhibited substantially higher levels of organic matter (OM) and cation exchange capacity (CEC), with mean values of 13.10% and 17.93 cmol(+)/kg, respectively. In contrast, the vegetation-degraded soils showed markedly lower values, averaging 1.82% for OM and 1.73 cmol(+)/kg for CEC. In addition, the concentrations of exchangeable cations (Ca^{2+}, Mg^{2+}, K^{+}) were all higher in the vegetation-rich area.

The concentrations of available phosphorus (AP, 146.3 mg/kg) and total nitrogen (T-N, 0.21%) in the vegetation-degraded soil were higher than those in the vegetation-rich soil (33.5 mg/kg and 0.11%, respectively). This suggests that the absolute concentration of nutrients may not necessarily correlate with vegetation development.

Physicochemical analysis of vegetation-degraded soils following moss treatment

Table 3

Comparison of soil physicochemical properties between the vegetation-degraded area (a; control) and moss-treated soils: Hypnum plumaeforme, Campylopus purpureus, and Racomitrium lanuginosum. Values are expressed as mean ± standard error (SE), based on five replicates per group. Statistical analysis was performed using ordinary one-way ANOVA to evaluate differences among groups. Asterisks indicate statistically significant differences from the control group: P < 0.001 (***).

Treatment	pH [1:5]	OM (%)	CEC (cmol/kg)	AP (mg/kg)	T-N (%)	Ex. Cat. (cmol/kg)		
						Ca^{2+}	Mg^{2+}	K^{+}
(a)	6.83 ± 0.005	0.62 ± 0.005	2.16 ± 0.022	8.28 ± 0.005	0.03 ± 0.001	0.42 ± 0.007	0.28 ± 0.004	0.07 ± 0.001
H. plumaeforme	6.54 ± 0.011***	1.37 ± 0.046***	4.20 ± 0.028***	14.86 ± 0.191***	0.08 ± 0.001***	1.22 ± 0.006***	0.66 ± 0.006***	0.19 ± 0.006***
C. purpureus	6.41 ± 0.006***	1.34 ± 0.027***	4.74 ± 0.036***	21.20 ± 0.610***	0.07 ± 0.001***	1.42 ± 0.009***	0.56 ± 0.005***	0.10 ± 0.001***
R. lanuginosum	6.47 ± 0.007***	1.33 ± 0.032***	3.16 ± 0.036***	26.77 ± 0.909***	0.06 ± 0.001***	0.74 ± 0.006***	0.38 ± 0.005***	0.23 ± 0.015***

Previous analyses of soil physicochemical properties did not clearly identify the direct causes of vegetation absence, suggesting instead that the absence of vegetation may result from complex ecological constraints rather than a single limiting factor. This perspective aligns with the findings of Shoji and Takahashi (2002), who reported that in volcanic ash soils, thick ash deposits can hinder the formation of soil structure and biological activity, thereby significantly delaying natural vegetation recovery. They emphasized the ecological importance of pioneer species such as mosses in establishing initial biological foundations. Additionally, Carmel and Kadmon (1999) demonstrated that factors such as initial vegetation cover, topography, slope aspect, and grazing pressure exert significant long-term influences on vegetation development. Building upon these previous studies, the present study focuses on the ecological functions of mosses as a means of establishing early biological foundations and experimentally evaluates their potential to improve soil function and facilitate vegetation restoration.

Following the cultivation of three moss species in vegetation-degraded soils, changes in soil indicators were observed, as shown in Table 3. Although all samples were collected from the same degraded area, even the control group displayed differences from the original field analysis results presented in Table 2. These discrepancies are interpreted as newly expressed biochemical reactivity in response to altered laboratory conditions. Therefore, this study focused on evaluating the ecological effects of moss introduction based on relative changes under consistent conditions, rather than on absolute degrees of restoration. In other words, the experiment was designed to assess restoration potential rather than the restored state itself.

Moss-treated soils exhibited significant overall changes in physicochemical properties. Soil pH decreased in all treatment groups, reaching values closer to the optimal pH of 6.0 for plant growth. The greatest decrease was observed in the *C. purpureus* treatment group, with a reduction of approximately 0.42. Organic matter (OM) content more than doubled in all treatment groups compared to the control. Cation exchange capacity (CEC) increased across all groups, with the *C. purpureus* treatment group showing more than a twofold increase. Available phosphorus (AP) also increased in all treatments, with the *R. lanuginosum* group exhibiting a more than threefold increase. Total nitrogen (T-N) showed a general upward trend in all groups, with the *H. plumaeforme* treatment displaying the highest increase. In addition, concentrations of exchangeable cations (Ca^{2+}, Mg^{2+}, K^{+}) increased overall: Ca^{2+} was highest in the *C. purpureus* group, Mg^{2+} in the *H. plumaeforme* group, and K^{+} in the *R. lanuginosum* group.

Discussions

Soil particle size distribution is not a major determinant of vegetation development in Oreum

Although the particle size composition of the vegetation-degraded and vegetation-rich areas differed slightly—with the degraded area exhibiting lower D10 and higher Cu values—these differences were not pronounced enough to distinctly separate the two sites in terms of soil texture classification. Both soils were classified as sandy loam and shared similar overall particle-size distribution patterns, as shown in Fig. 2B. This observation suggests that physical soil properties alone may not fully explain the marked disparity in vegetation cover between the two areas. Despite comparable textures and bulk density values, the vegetation-degraded soil failed to support substantial plant growth, implying that other factors may play a more dominant role in vegetation maintenance and recovery. Specifically, the absence of vegetation in areas with similar physical conditions highlights the potential importance of biochemical and biological soil factors. Variables such as organic matter content, microbial community structure, and soil moisture retention capacity may be more critical in determining vegetation health and resilience in these volcanic landscapes. The results underscore the need for a more holistic understanding of soil quality that incorporates not only texture and structure, but also biological activity and nutrient cycling in assessing restoration potential.

Functional disconnection between soil nutrient status and vegetation cover

Although soil pH plays a critical role in regulating nutrient availability, microbial activity, enzymatic reactions, and nitrogen cycling (Minasny et al., 2016; Neina, 2019), the minor difference in pH observed between the degraded and well-vegetated areas is unlikely to be a primary factor driving the variation in vegetation cover. Optimal nutrient availability generally occurs around pH 6.0, while more acidic or alkaline conditions can limit the accessibility of key macro- and micronutrients (Fernández and Hoeft, 2009). Yet in this study, both areas showed pH values within a range that would not drastically inhibit biological activity.

Soil organic matter (OM) and cation exchange capacity (CEC), which are closely interrelated indicators of soil fertility, were markedly higher in the vegetation-rich area. OM enhances both CEC and water-holding capacity in light-textured soils by contributing essential nutrients and promoting structural stability (Johnston, 1986a, b).

Higher OM and CEC levels also coincide with increased concentrations of exchangeable cations (Ca^{2+}, Mg^{2+}, K^+), suggesting that these factors work synergistically to support nutrient retention and plant-available nutrient pools.

However, the interpretation of these differences must be contextualized. Johnston (1986b) showed that soil organic matter equilibria are primarily shaped by organic inputs and soil texture over time. In this study, both sites had not been subject to anthropogenic disturbances for more than a decade and were classified as sandy loam based on particle size distribution, indicating comparable physical properties. Therefore, the higher OM and CEC levels in the vegetation-rich soils are more plausibly consequences of vegetation development rather than its cause. Established vegetation can create a positive feedback loop: promoting greater organic input, which in turn enhances soil fertility and further supports plant growth.

Interestingly, available phosphorus (AP) and total nitrogen (T-N) were higher in the degraded soils than in the well-vegetated soils. This counters the conventional assumption that high nutrient concentrations directly support plant productivity. In vegetation-degraded environments where nutrient uptake and microbial activity are limited, nutrients may accumulate without being effectively utilized or cycled (Stevenson & Cole, 1999). By contrast, the lower residual nutrient levels in the vegetation-rich soils likely reflect active uptake, translocation, and recycling within a functioning plant-microbe system (Huang et al., 2005).

Additionally, soil moisture, salinity, and electrical conductivity (EC) were all elevated in the well-vegetated area (Supplementary Table S1). These conditions are typical of soils with higher OM content and better aggregation, which promote water retention and reduce evaporation (Bronick and Lal, 2005). Vegetation not only buffers the soil surface but also redistributes moisture through transpiration. Moreover, root activity and organic acid secretion alter local ionic balances and may lead to rhizospheric salt accumulation via transpiration-driven capillary rise (Qadir et al., 2005; Rengasamy, 2006). Thus, elevated EC values in the vegetation-rich soil likely indicate an active nutrient–water cycling system rather than simple salt buildup.

In summary, our findings underscore a functional disconnect between absolute nutrient levels and vegetation presence. Rather than nutrient quantity alone, it is the bioavailability, retention dynamics, and cycling efficiency that appear to underpin successful vegetation development and persistence.

Moss enhances key soil functional indicators, demonstrating its potential as a tool for vegetation restoration

Although the soil physicochemical analysis conducted in this study did not clearly identify the direct causes of vegetation absence, prior research allows for the inference of potential limiting factors that may hinder vegetation development in volcanic ash-derived soils, such as those found in the Oreum region of Jeju Island.

First, scoria from the southwestern part of Jeju is a high-Fe and high-Al volcanic rock that releases large amounts of aluminum oxide (Al_2O_3) into the soil during weathering. Under acidic conditions, this results in the solubilization and accumulation of toxic Al^{3+} ions (Choi and Ko, 2008). This form of aluminum inhibits root elongation and cellular development, functioning as a chemical barrier that may prevent the initial establishment of higher plants.

Second, thick volcanic ash layers may delay vegetation recovery by impeding the formation of soil structure and biological activity. Shoji and Takahashi (2002) emphasized the ecological importance of pioneer species such as mosses, lichens, and nitrogen-fixing plants under such conditions.

Third, differences in solar exposure due to slope aspect may also influence vegetation patterns. Carmel and Kadmon (1999) reported that topographic factors, such as slope and aspect, significantly affect long-term vegetation dynamics. In this study, the vegetation-degraded site (a) was located on a northwest-facing slope, which receives intense sunlight in the afternoon, leading to increased soil surface temperatures and moisture loss. In contrast, the vegetation-rich site (b) faced east and received morning sunlight at a lower solar angle, resulting in more stable soil moisture conditions.

These findings suggest that instead of simply improving soil quality, it is necessary to establish an initial biological foundation, particularly through the introduction of pioneer species such as mosses. Recently, the ecological functions of biological soil crusts (biocrusts)—comprising algae, fungi, lichens, and mosses—have drawn increasing attention. Mosses are known to contribute to early ecosystem structuring by stabilizing the soil surface, accumulating organic matter, and facilitating microbial colonization (Antoninka et al., 2020; Jech et al., 2025; Rodriguez-Caballero et al., 2022; Wang et al., 2025; Benavent-González et al., 2018; Swenson et al., 2018; Su et al., 2009).

Based on this ecological strategy, this study aimed to improve key soil functional indicators (e.g., OM, CEC) through the introduction of mosses and thereby facilitate the natural establishment of higher plants (Dalling, 2008). Experimental results showed that all three moss-treated groups demonstrated improved soil fertility, including decreases in pH and increases in OM, CEC, AP, T-N, and exchangeable cations (Ca^{2+}, Mg^{2+}, K^{+}). The magnitude of these changes varied by moss species.

These improvements may be attributed to the mosses’ high surface area and elevated CEC, which enhance their ability to trap airborne particles, moisture, and nutrients, as suggested by Cheng et al. (2020). Although microbial communities were not directly analyzed in this study, the observed improvements in soil conditions imply a possible positive influence on soil microbial ecology, warranting further quantitative investigation.

In conclusion, mosses play more than a surface-covering role in the ecological restoration of degraded volcanic soils. They act as key organisms in improving soil quality and establishing foundational structures for ecosystem recovery. Strategic selection of moss species tailored to site-specific ecological conditions is likely to enhance restoration effectiveness.

Conclusion

This study aimed to experimentally examine the effects of introducing pioneer moss species on the restoration of soil functionality and the facilitation of ecological transition in vegetation-degraded volcanic ash soils of Jeju Island’s oreum (parasitic cones). To this end, soils were collected from vegetation-degraded area and treated with three moss species—*Rhacomitrium canescens*, *Hypnum plumaeforme*, and *Ceratodon purpureus*—followed by analysis of changes in key physicochemical indicators.

As a result, all moss-treated groups showed statistically significant increases in major soil indicators such as pH, organic matter (OM), cation exchange capacity (CEC), total nitrogen (T-N), and available phosphorus (AP), compared to the control. In particular, the increase in OM, along with associated enhancements in SOC and CEC, suggests a potential improvement in soil fertility and functionality. Furthermore, the increased concentrations of exchangeable cations (Ca^{2+}, Mg^{2+}, K^{+}) indicate recovery of cation retention capacity, which could serve as a long-term foundation for the natural establishment of higher plants. While all moss species contributed positively to improving soil functional indicators, the degree of effect varied by parameter. This implies that a strategic and selective introduction of moss species can be tailored according to the specific soil characteristics and ecological needs of the restoration area.

These improvements are interpreted not as the result of simple material input, but as ecological effects driven by the physiological and ecological properties of the mosses. Mosses stabilize the soil surface, promote organic matter accumulation and moisture retention, and serve as microhabitats for soil microorganisms—thus playing a key role in establishing the foundational structure for biological activity. Therefore, moss introduction can serve not merely as surface cover, but as a strategic means to initiate ecological transition in the early stages of restoration.

However, since this study was conducted under controlled indoor conditions, further long-term and field-based research is required to assess real-world applicability. In particular, quantitative analyses are needed on changes in microbial communities, long-term moisture retention, and the spontaneous establishment of higher plants following moss colonization. Additionally, experimental evaluation of moss introduction methods (e.g., fragmentation, inoculation, transplanting), application rates, and co-cultivation strategies will be critical for developing effective restoration protocols.

In conclusion, this study provides empirical evidence that moss introduction can lead to meaningful improvements in soil functionality in barren volcanic terrains. These findings offer a valuable ecological foundation for formulating restoration strategies in fragile landscapes such as the oreum regions of Jeju Island.

Declarations

Availability of data and materials

The datasets used and/or analyzed in the current study are available from the corresponding author upon reasonable request.

Competing interests

The authors declare that they have no competing interests.

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Figures

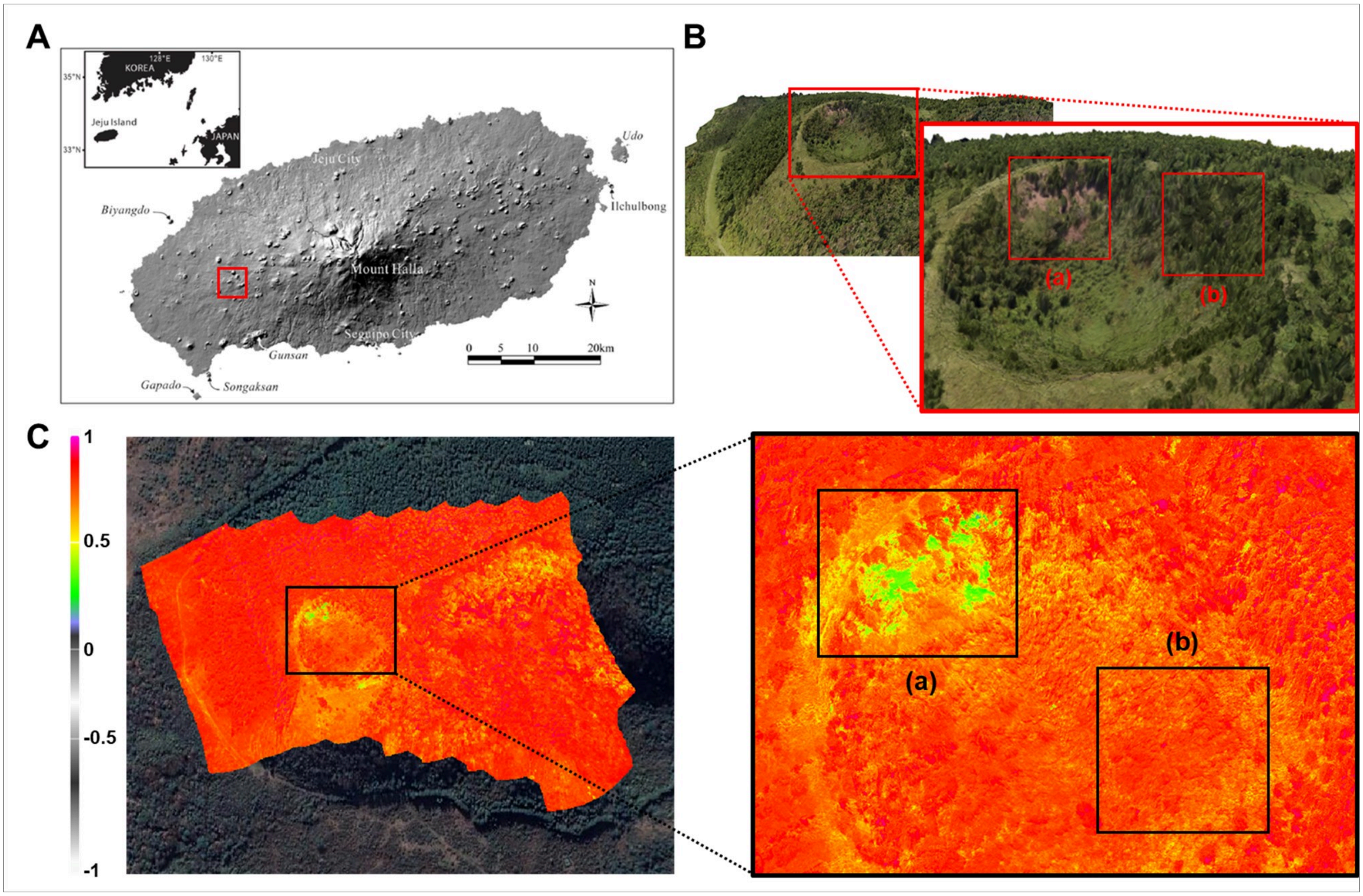

Figure 1

(A) 3-D topographic map of Jeju Island, showing the location of several volcanoes (italicized), of which recent eruptions are assumed to be recorded in historical documents (Source: Ahn US, 2016). (B) UAV-captured aerial view of Doneori Oreum, with marked locations of (a) a vegetation-degraded area and (b) a vegetation-rich area. (C) NDVI mapping of the entire Doneori Oreum, also indicating the locations of (a) and (b) for vegetation comparison.

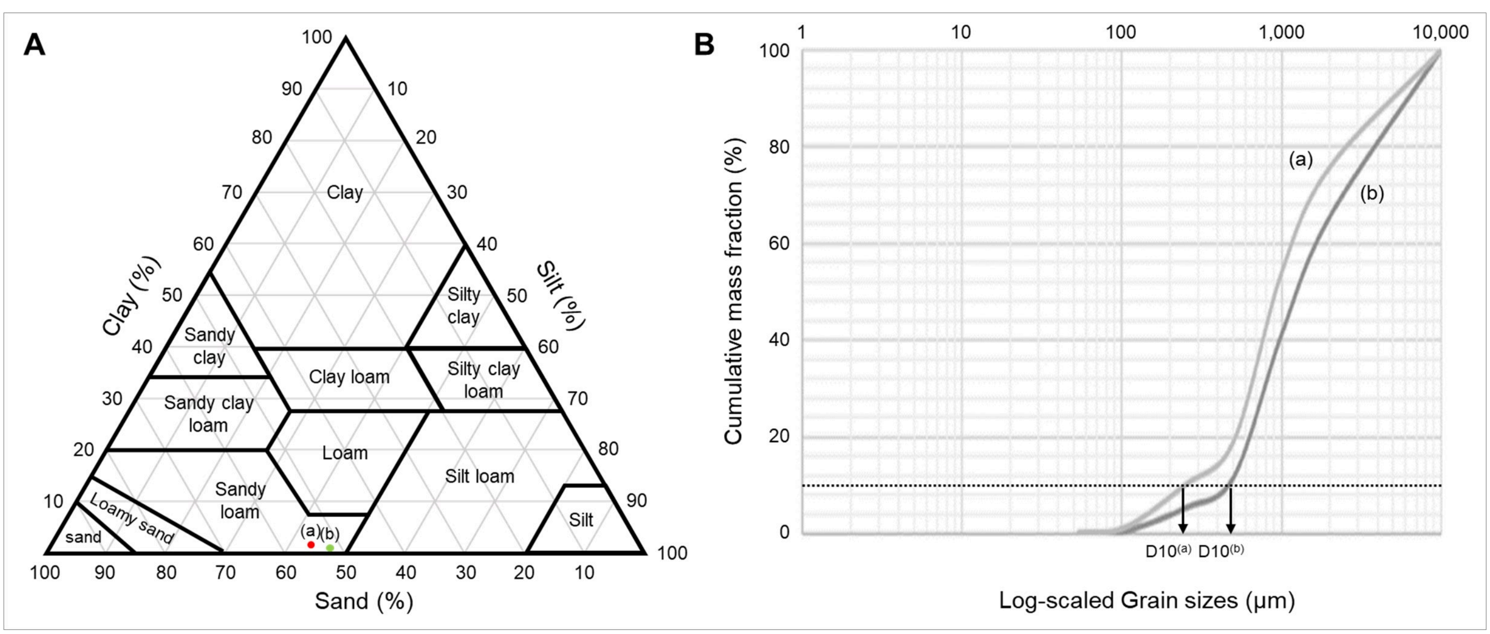

Figure 2

(A) Soil classification of the study areas based on the Soil Texture Triangle provided by the United States Department of Agriculture (USDA). Red dot indicates vegetation-degraded areas, while green dot represents vegetation-rich areas. (B) Particle size distribution curves of soil samples from Doneori Oreum. The gray curve represents the (a) vegetation-degraded area, and the black curve represents the (b) vegetation-rich area. The x-axis indicates particle diameter (μm) on a logarithmic scale, and the y-axis shows the cumulative percentage of particles passing through the sieve. Vertical arrows indicate the D_{10} values for each curve—that is, the particle diameter at which 10% of the sample has passed—for (a) and (b), respectively. D_{10} is commonly used as an indicator of soil permeability.

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