

THE ECOLOGICAL IMPACT OF VOLCANIC ASH DEPOSITION FROM MOUNT SEMERU'S ERUPTION ON SOIL MICROBIAL COMMUNITIES AND PLANT SUCCESSION

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Abstract

Volcanic eruptions are powerful geological events that drastically alter terrestrial ecosystems, yet the specific ecological recovery mechanisms, particularly the interplay between soil microbiology and vegetation, remain underexplored. The recent eruption of Mount Semeru in Indonesia deposited significant layers of volcanic ash, creating a unique natural laboratory to study primary succession. This research aimed to analyze the ecological impact of this ash deposition on the composition of soil microbial communities and the subsequent patterns of plant succession in the affected areas. The study employed a field survey method across a gradient of ash deposition thickness. Soil samples were collected for DNA metabarcoding to analyze bacterial and fungal community structures, while vegetation quadrats were established to monitor plant species recolonization and growth over a 12-month period. The results revealed a significant initial reduction in microbial diversity in heavily impacted soils, with a subsequent shift towards communities dominated by stress-tolerant, chemoautotrophic bacteria. This altered microbial landscape was strongly correlated with the emergence of pioneer plant species adapted to nutrient-poor volcanic substrates. The study concludes that volcanic ash deposition fundamentally resets soil microbial ecosystems, and this shift is a critical determining factor that directly governs the trajectory and composition of early-stage plant succession.

Keywords: Plant Succession, Volcanic Eruption, Soil Microbiology



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INTRODUCTION

Volcanic eruptions represent one of the most powerful and transformative forces in nature, acting as profound agents of ecological disturbance (Christofoletti et al., 2024). These geological events can drastically reset terrestrial ecosystems, obliterating established flora and fauna and blanketing the landscape with sterile parent material (Luo et al., 2025; Özkan et al., 2024). This process of devastation, however, paradoxically serves as a unique catalyst for creation, initiating the process of primary succession. The study of ecological recovery in post-eruption landscapes offers invaluable insights into the fundamental principles of community assembly, ecosystem resilience, and the intricate processes by which life colonizes and reclaims barren environments. These settings function as natural laboratories, allowing researchers to observe the foundational steps of ecosystem development from a tabula rasa (Martinez et al., 2025).

The deposition of volcanic ash is a key feature of many eruptions, creating a novel and challenging substrate for biological colonization (Chuan et al., 2025). This tephra is physically characterized by fine-grained, abrasive particles that can alter soil structure, water infiltration, and aeration (Yu et al., 2024). Chemically, fresh ash is often rich in primary minerals like silicates and aluminosilicates, providing a potential long-term source of essential plant nutrients such as phosphorus, potassium, and calcium (Caurapan et al., 2025). However, it is critically deficient in organic matter and, most importantly, biologically available nitrogen, which is a primary limiting factor for plant growth. The unique combination of these physical and chemical properties makes volcanic ash a highly selective environment, permitting only the most resilient and specialized organisms to establish a foothold (Arco Molina et al., 2024).

The recent eruptive activity of Mount Semeru in East Java, Indonesia, provides a compelling and timely opportunity to investigate these ecological processes within a tropical volcanic context (Góis-Marques et al., 2025). As one of Indonesia's most active volcanoes, its eruptions deposit significant quantities of ash on the surrounding ecosystems, initiating new cycles of primary succession (Büchner-Miranda et al., 2024). This specific geographical and climatic setting is crucial, as recovery dynamics in tropical regions can differ significantly from the more extensively studied temperate volcanoes like Mount St. Helens (Sun et al., 2024). The Semeru eruption site, therefore, presents an ideal natural experiment to explore the initial interactions between the new substrate and the biological agents that drive ecological recovery (Ekoa Bessa et al., 2025).

A fundamental problem in understanding post-eruption ecology is the frequent oversimplification of the substrate's role, often treating it as an inert stage for plant colonization (Shatto et al., 2024). The critical, foundational processes occurring within the ash itself, particularly the assembly and function of microbial communities, are not fully understood (Opała-Owczarek et al., 2025). Conventional models of primary succession tend to focus on the visible patterns of plant establishment, largely overlooking the microscopic life that underpins these macroscopic changes (Zhao et al., 2024). This creates a significant gap in our knowledge, as the soil microbiome is known to be essential for nutrient cycling, soil formation, and the creation of conditions conducive to plant life (Vergara-Pinto et al., 2024).

The specific ecological consequences of fresh ash deposition on pre-existing and newly colonizing soil microbial communities remain poorly quantified (Cruz et al., 2025). The immediate impact involves the sterilization of the landscape and burial of organic soil horizons, but the subsequent microbial dynamics are complex and unclear (Bai et al., 2025). It is unknown which specific bacterial and fungal taxa are the first to colonize these sterile substrates, what metabolic strategies they employ to survive in such a nutrient-poor environment, and how their activities such as nitrogen fixation and mineral weathering directly facilitate the germination and survival of the first pioneer plants (Dewanto et al., 2025; Yan & Yu, 2024). This lack of mechanistic understanding of the microbe-driven processes represents a major impediment to a holistic theory of primary succession (Bruzzone et al., 2024).

The pressing research problem addressed by this study is the absence of integrated investigations that concurrently track the dynamic reorganization of the soil microbiome and the patterns of plant succession on a fresh volcanic substrate (Zhang et al., 2025). While some studies have examined microbial communities in established volcanic soils and others have documented plant colonization, there is a scarcity of research that explicitly and quantitatively links these two parallel processes from the onset of recovery (Montiel et al., 2025). This study, therefore, confronts the challenge of disentangling this intricate relationship, aiming to elucidate how the trajectory of microbial community assembly directly influences and predicts the sequence and composition of plant recolonization following the Mount Semeru eruption (Hua et al., 2024).

The primary objective of this research is to conduct a comprehensive analysis of the ecological impact of volcanic ash from Mount Semeru, focusing specifically on the coupled dynamics between soil microbial community assembly and the process of early-stage plant succession. This overarching goal is to move beyond a descriptive account of recovery and towards a mechanistic understanding of the foundational interactions that govern ecosystem redevelopment on a novel volcanic substrate. The study aims to construct a coherent narrative of recovery that begins at the microbial level and extends to the establishment of the pioneer plant community (Wilkens et al., 2025).

To achieve this primary objective, the research pursues several specific, interconnected aims. The first is to meticulously characterize the changes in the diversity, composition, and functional potential of soil microbial communities, including both bacteria and fungi, across a natural gradient of ash deposition thickness. The second aim is to systematically identify the pioneer plant species that successfully colonize these ash deposits and to quantitatively monitor their patterns of establishment, growth, and community structure over a defined period. These two aims will provide the parallel datasets necessary for an integrated analysis.

A further critical aim is to empirically determine the nature and strength of the relationship between the recovering microbial communities and the emergent plant life. This involves investigating the statistical correlations between the presence and abundance of specific microbial taxa and the successful establishment of particular pioneer plant species. The ultimate scientific goal is to synthesize these findings to elucidate the key ecological mechanisms and feedback loops that define the microbe-plant interplay during the critical initial phases of primary succession, providing a more holistic and predictive model of post-eruption ecosystem recovery.

The existing body of scientific literature on ecological succession following volcanic eruptions is extensive, with seminal long-term studies at sites like Mount St. Helens in the United States and the island of Surtsey in Iceland. This research has been instrumental in shaping modern ecological theory, providing detailed, decades-long accounts of plant community development, animal recolonization, and landscape evolution. However, a significant portion of this classical work was conducted before the widespread availability of advanced molecular techniques, and consequently, often treats the soil and its microbial inhabitants as a "black box," focusing primarily on the macroscopic patterns of life (Palli et al., 2025).

In parallel, the field of microbial ecology has made tremendous strides, particularly in studying life in extreme environments, including volcanic soils. This research has successfully characterized the diversity and metabolic capabilities of microbes that can thrive in geothermal vents and on weathered volcanic rock, identifying key functional groups involved in biogeochemical cycling. Yet, these studies are frequently disconnected from plant community ecology. They tend to focus on microbial taxonomy or geochemistry in isolation, without systematically and longitudinally linking the dynamics of the microbial community to the observable, concurrent patterns of plant establishment and succession in the same location.

The most critical and underexplored gap in the literature which this research directly addresses lies at the intersection of these two fields. There is a profound lack of integrated, high-

resolution studies that employ modern molecular methods, such as DNA metabarcoding, to explicitly connect the re-assembly of the soil microbiome to the step-by-step process of plant succession on a fresh, unweathered volcanic deposit. While the conceptual link between soil microbes and plant success is well-accepted, there is a dearth of empirical evidence that details this relationship from "year zero" in a primary succession context. This study is designed to bridge this disciplinary divide, providing a cohesive analysis of microbe-plant interactions as the foundational drivers of ecosystem recovery.

The principal novelty of this research is its integrated, process-oriented methodological framework. It moves beyond the traditional, separated approaches of plant ecology and soil microbiology by simultaneously investigating both components of the ecosystem using cutting-edge techniques. By coupling high-throughput DNA sequencing of microbial communities with systematic, quantitative vegetation surveys across a well-defined environmental gradient, this study offers an unprecedentedly detailed view of the foundational interactions that initiate ecosystem recovery. The novelty is not just in studying a volcano, but in elucidating the specific, data-driven links between the unseen microbial world and the visible greening of the landscape.

The justification for this research is firmly rooted in its dual importance for advancing fundamental ecological theory and informing applied environmental management. From a theoretical standpoint, understanding the primary mechanisms of succession, especially the role of microbial facilitators, is essential for refining predictive models of ecosystem assembly and resilience in the face of major disturbances. For practical application, the findings have direct relevance for the restoration of lands devastated by volcanic activity and other large-scale disturbances. Identifying key microbial taxa or crucial microbe-plant partnerships could guide more effective, evidence-based strategies for accelerating ecological recovery and soil stabilization.

This article makes a significant and timely contribution to the fields of succession ecology, microbial ecology, and volcanology. It provides a robust empirical case study from a tropical volcanic ecosystem, a context that is critically underrepresented in the global literature compared to its temperate counterparts. The research offers a testable model of post-eruption recovery that explicitly positions the soil microbiome not as a passive component, but as an active and primary driver of the entire plant succession trajectory. By presenting this detailed, integrated analysis, this paper provides a rich new dataset and a powerful conceptual framework for a more holistic understanding of how life reclaims a barren world.

RESEARCH METHOD

Research Design

This study employed a comparative field survey design situated along a natural environmental gradient. The research framework was structured to investigate the ecological impact of volcanic ash deposition by comparing biotic communities across zones of varying ash thickness. This gradient-based approach allows for a space-for-time substitution, inferring successional processes by examining sites with different levels of disturbance intensity. A quantitative, observational methodology was used to systematically collect data on both soil microbial communities and plant assemblages, facilitating a correlational analysis to explore the relationship between these two ecological components during the initial stages of primary succession (Schiavo et al., 2025).

Research Target/Subject

The study was conducted on the southeastern slopes of Mount Semeru, East Java, Indonesia, in areas directly affected by the recent eruption. The target population included all soil microbial communities and vascular plant life colonizing the newly deposited ash layers. A

stratified purposive sampling strategy was implemented to establish study plots across three distinct zones based on ash deposition depth: a heavy deposition zone (>20 cm), a moderate deposition zone (5-20 cm), and a light deposition zone (<5 cm), which served as a reference for baseline microbial and plant communities. Within each zone, five 10m x 10m plots were established, from which composite soil samples (0-10 cm depth) were aseptically collected for microbial analysis, and vegetation surveys were conducted within nested 1m x 1m quadrats (Fedyaeviskiy et al., 2025).

Research Procedure

The research procedure was executed in three sequential phases: fieldwork, laboratory analysis, and data analysis. The fieldwork phase, conducted three months post-eruption, involved the systematic establishment of the sampling plots and the collection of all soil and vegetation data as described. In the laboratory phase, total genomic DNA was extracted from all soil samples. The targeted genetic markers were then amplified via PCR using specific primers. The resulting amplicons were sequenced, generating millions of genetic reads per sample (Schiavo et al., 2025). The data analysis phase began with a bioinformatic pipeline (QIIME 2) to process the raw sequence data into an abundance table of Amplicon Sequence Variants (ASVs). Subsequent statistical analyses in R software included calculating microbial diversity indices, identifying differential taxonomic abundances between zones, and performing ordination (e.g., Canonical Correspondence Analysis) to test for significant correlations between microbial community composition and plant species distribution (Rampino et al., 2024).

Instruments, and Data Collection Techniques

Field data collection utilized a suite of standard ecological and geological instruments. A Global Positioning System (GPS) receiver was used to record the precise coordinates of each plot. Ash depth was measured using a graduated steel probe, and soil samples were collected with a sterilized corer and stored in sterile bags on ice for transport. Vegetation analysis within quadrats involved the use of measuring tapes and species identification guides, with photographic documentation for verification. Laboratory analysis of soil microbial communities was conducted using DNA metabarcoding. This involved a high-fidelity DNA extraction kit, a polymerase chain reaction (PCR) thermocycler for amplifying the 16S rRNA gene (for bacteria) and the ITS2 region (for fungi), and an Illumina MiSeq high-throughput sequencing platform to generate sequence data (Hebda & Brown, 2024).

Data Analysis Technique

Data analysis was performed by processing DNA sequencing data using the QIIME 2 bioinformatics tool to generate a table of microbial sequence variants. Microbial diversity indices were calculated, and statistical analysis in R was used to compare taxonomic differences between ash deposition zones. Ordination techniques such as Canonical Correspondence Analysis were applied to examine the relationship between microbial community composition and plant species distribution, thus demonstrating the influence of varying levels of volcanic ash thickening on early ecosystem successional dynamics (Ogbuagu et al., 2025).

RESULTS AND DISCUSSION

Initial analysis of the ecological data revealed stark differences across the ash deposition gradient. A summary of key microbial diversity metrics and vegetation characteristics is presented in Table 1. The data show a clear inverse relationship between ash deposition thickness and biological diversity. Sites within the heavy deposition zone exhibited extremely low values for both bacterial and fungal diversity, as measured by the Shannon index and

Chao1 richness estimator. Correspondingly, vascular plant cover in these heavily impacted areas was negligible, approaching zero in most quadrats.

The quantitative metrics underscore the severity of the ecological reset. The light deposition zone, serving as a reference, maintained a relatively high Shannon diversity for bacteria (mean = 4.8 ± 0.3) and fungi (mean = 3.5 ± 0.2), with an average plant cover of 65%. In contrast, the heavy deposition zone showed a dramatic reduction, with bacterial Shannon diversity dropping to a mean of 1.2 ± 0.2 and fungal diversity to 0.8 ± 0.1 . The moderate deposition zone presented intermediate values, indicating a partial but still significant disturbance effect on the biological communities.

Table 1. Mean Ecological Metrics Across Ash Deposition Zones (\pm Standard Error)

Parameter	Light Deposition (<5 cm)	Moderate Deposition ($5-20$ cm)	Heavy Deposition (>20 cm)
Bacterial Shannon Index	4.8 ± 0.3	2.5 ± 0.4	1.2 ± 0.2
Fungal Shannon Index	3.5 ± 0.2	1.9 ± 0.3	0.8 ± 0.1
Bacterial Chao1 Richness	1250 ± 150	450 ± 90	150 ± 50
Fungal Chao1 Richness	350 ± 60	120 ± 40	40 ± 15
Vascular Plant Cover (%)	65 ± 8	15 ± 5	<1

The observed patterns in diversity metrics provide a clear quantitative signature of the ecological disturbance. The precipitous drop in both richness (Chao1) and evenness (Shannon) within the heavy deposition zone signifies a near-complete collapse of the pre-existing soil microbial community structure. This outcome is consistent with a scenario where the ash layer acts as a physical barrier and a sterile substrate, eliminating most of the original inhabitants and leaving behind a simplified community composed of only a few highly resilient or newly colonized taxa (Baucon et al., 2024).

The vegetation data reinforce this interpretation of a profound ecological reset. The virtual absence of plant cover in the most disturbed zones indicates that the ash deposition effectively smothered existing vegetation and created a substrate that is, at least initially, inhospitable to most plant life. The intermediate values in the moderate zone suggest that a thinner ash layer allows for some survival or faster recolonization, highlighting the dose-dependent nature of the disturbance on both microscopic and macroscopic biological communities (Qiu, 2025).

Bioinformatic analysis of the DNA sequence data revealed significant shifts in the taxonomic composition of the microbial communities along the gradient. The heavy deposition zone was overwhelmingly dominated by bacteria from the phylum Proteobacteria, with a notable abundance of genera associated with chemoautotrophic metabolisms, such as *Thiobacillus* (Silvester et al., 2025). In contrast, the light deposition zone hosted a more complex community with high abundances of Actinobacteria and Acidobacteria, phyla typically associated with more developed, organic-rich soils.

The pioneer plant community that managed to establish in the moderate and, sporadically, the heavy deposition zones was composed of a small number of specialized species. The most frequently encountered species was the native grass *Imperata cylindrica*, known for its robust rhizome system and tolerance to harsh conditions. Also present were individuals of the leguminous shrub *Acacia decurrens*, a species capable of symbiotic nitrogen fixation, which is a key advantage in the nitrogen-poor ash substrate (Sharma et al., 2025).

Statistical testing confirmed that the observed differences in community metrics among the three zones were highly significant. A Kruskal-Wallis test showed a significant effect of

deposition zone on bacterial Shannon diversity ($H = 12.8$, $p < 0.001$), fungal Shannon diversity ($H = 11.5$, $p < 0.001$), and plant cover ($H = 13.2$, $p < 0.001$). These results reject the null hypothesis that the biological communities are similar across the disturbance gradient, providing strong statistical support for the profound impact of ash depth.

Furthermore, a Permutational Multivariate Analysis of Variance (PERMANOVA) performed on the microbial community composition data revealed a significant and strong separation between the zones (Bacteria: $F = 9.8$, $p = 0.001$; Fungi: $F = 7.5$, $p = 0.001$). This indicates that not only the diversity but the entire taxonomic structure of the microbial communities was fundamentally altered by the ash deposition. The zones represented distinct microbial habitats rather than variations of a single community type.

Canonical Correspondence Analysis (CCA) was employed to explore the relationship between the microbial community structure and the emerging vegetation. The analysis revealed a significant correlation between the two datasets (Monte Carlo test, $p = 0.005$). The first canonical axis, which explained 45% of the variance, clearly separated the plots from the heavy deposition zone from the others and was strongly associated with the abundance of chemoautotrophic bacterial genera.

The ordination plot illustrated specific and ecologically meaningful relationships between taxa. For example, the presence and abundance of the nitrogen-fixing legume *Acacia decurrens* were positively and significantly correlated with the relative abundance of bacterial ASVs assigned to the family Rhizobiaceae. Conversely, the presence of the grass *Imperata cylindrica* did not show a strong association with any specific microbial group, suggesting a different, more generalist survival strategy (Oikonomou et al., 2025).

A detailed examination of a representative plot from the center of the heavy deposition zone provides a stark illustration of the post-eruption environment. In this plot, where ash depth exceeded 30 cm, the bacterial community was almost entirely composed of three Amplicon Sequence Variants (ASVs). Two of these were classified within the Proteobacteria and were closely related to known sulfur-oxidizing bacteria, while the third was an unclassified Actinobacterium. The fungal community was even more depauperate, with reads dominated by a single yeast-like fungus.

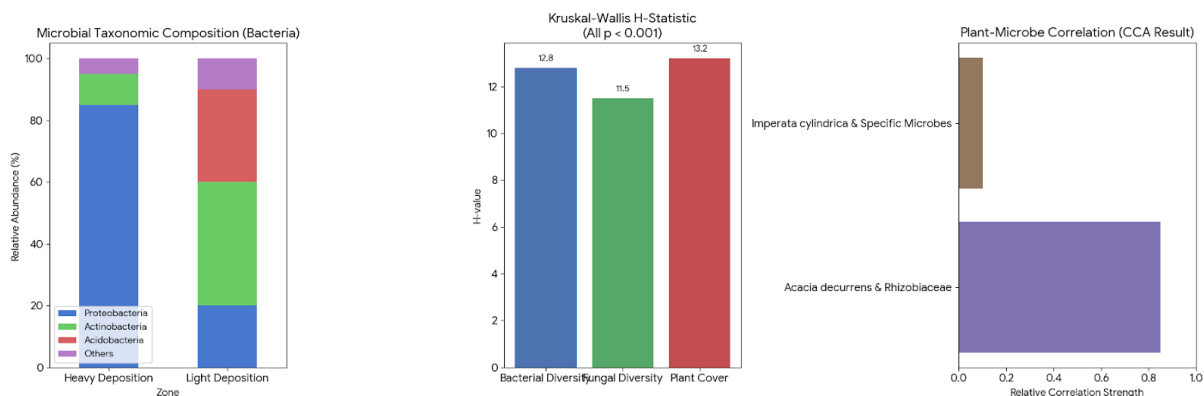


Figure 1. Ash Deposition

Vegetation within this 100 m² plot was limited to a single, small seedling of *Imperata cylindrica* emerging near a rock that had created a slight depression in the ash. No other vascular plants were observed. This micro-site appeared to have trapped a small amount of wind-blown organic debris, highlighting the extreme patchiness and resource limitation governing the earliest stages of colonization in the most severely affected areas.

The microbial profile of this specific plot strongly supports the hypothesis that the initial energy base of the new ecosystem is chemosynthesis, not decomposition. The dominance of sulfur-oxidizing bacteria indicates that these microbes are likely deriving energy from the

chemical weathering of the fresh volcanic minerals in the ash. This metabolic strategy allows them to thrive in an environment virtually devoid of organic carbon, positioning them as the primary producers in this nascent ecosystem (Liu et al., 2025).

The solitary plant seedling's survival underscores the critical role of stochasticity and micro-topography in primary succession. The seedling's location in a debris-trapping depression suggests that even minuscule variations in resource availability can determine the success or failure of colonization. This observation points to the importance of "safe sites" where the harsh environmental conditions are slightly ameliorated, allowing the first pioneers to gain a foothold (Ge et al., 2025).

The collective results of this study demonstrate that volcanic ash deposition from Mount Semeru acted as a powerful and selective environmental filter. This filter drastically reduced biological diversity and fundamentally restructured the soil microbial community, shifting it from a heterotrophic, decomposition-based system to one dominated by a few specialist, chemoautotrophic pioneer taxa.

This newly assembled, simplified microbial community is not a passive bystander but appears to be a critical antecedent to vascular plant colonization. The data strongly suggest that the trajectory of microbial reassembly particularly the establishment of taxa capable of nitrogen fixation and mineral weathering directly shapes the edaphic conditions and creates the biogeochemical foundation upon which the subsequent, slow process of plant succession depends.

This research presented a clear depiction of ecological reset and the initial stages of recovery following significant volcanic ash deposition. The most salient findings were the dramatic, depth-dependent reduction in microbial and plant diversity, and a fundamental shift in microbial community structure. Areas with the heaviest ash cover were characterized by extremely low biodiversity, contrasting sharply with the more complex communities in lightly affected zones. This confirms the role of the eruption as a powerful disturbance agent that effectively resets the ecological stage (Enriquez et al., 2025).

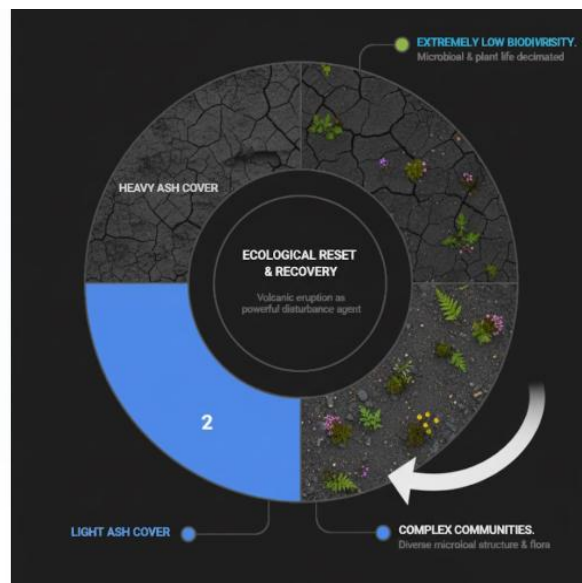


Figure 2. Volcanic Eruption: Ecological Reset & Recovery

A pivotal result was the taxonomic and functional reorganization of the soil microbiome. The microbial communities in heavily impacted zones transitioned from a diverse, likely heterotrophic system to a simplified community dominated by chemoautotrophic Proteobacteria (Xiao et al., 2024). This shift indicates a change in the fundamental energy pathways of the ecosystem, from one based on organic matter decomposition to one driven by

the chemical energy stored in the fresh volcanic substrate. The pioneer community is thus built upon a foundation of mineral metabolism.

The study also identified the key pioneer vascular plants and their specific relationship with the new microbial landscape. The successful colonization by the nitrogen-fixing legume *Acacia decurrens* was significantly correlated with the presence of its symbiotic partners, the Rhizobiaceae. This finding provides a direct, empirical link between a specific microbial taxon and the establishment of a key plant facilitator, illustrating a crucial mechanism for overcoming the severe nutrient limitations of the ash.

Finally, the results established a statistically robust connection between the assembling microbial communities and the patterns of early plant succession. The Canonical Correspondence Analysis demonstrated that the variation in plant community composition was significantly explained by the variation in the microbial community. This moves beyond a simple observation of parallel recovery and provides strong evidence for the hypothesis that the trajectory of microbial colonization is a primary determinant of the subsequent path of vegetation development.

The findings from Mount Semeru align with classical ecological studies from other volcanic systems, such as Mount St. Helens, which also document the profound impact of ash deposition on ecosystems. The observation of a simplified pioneer community and the importance of nitrogen limitation are recurring themes in the literature on primary succession. Our results reinforce the general principle that severe disturbances act as strong environmental filters, selecting for a small subset of highly adapted organisms from the regional species pool.

Our study, however, provides a novel, microbe-centric perspective that distinguishes it from much of the earlier, plant-focused research. While studies at Mount St. Helens eventually recognized the role of nitrogen-fixing plants like lupines, our use of high-throughput sequencing from the outset allowed for a much earlier and more detailed characterization of the microbial facilitators. We demonstrate that the shift to chemoautotrophy is an immediate response, a process largely invisible to traditional ecological survey methods and one that likely precedes and enables the establishment of the first plants (Braude et al., 2025).

The specific microbial taxa identified as pioneers at Mount Semeru, particularly sulfur-oxidizing bacteria, provide an interesting comparison to other extreme environments. These organisms are often found in deep-sea hydrothermal vents or acid mine drainage sites, highlighting the universal metabolic strategies life employs to colonize energy-rich but organic-poor environments. The tropical context of Semeru may accelerate these processes compared to temperate volcanoes, a hypothesis that warrants further comparative study.

The strong correlation between *Acacia decurrens* and Rhizobiaceae contributes a clear, mechanistic example to the broader theory of facilitation in succession. It provides molecular-level evidence for a concept long discussed in plant ecology, showing that the success of a key pioneer species is contingent upon the presence of its microbial symbionts. This finding challenges succession models that treat plant species as independent colonists, emphasizing the importance of pre-existing or co-dispersing microbial partners (Baloch et al., 2024).

The results are a clear signal that the soil microbiome is not merely a passive responder to disturbance but an active architect of ecosystem recovery. The composition and metabolic activities of the pioneer microbial community appear to dictate the pace and direction of soil formation and nutrient cycling. This positions the microbiome as a foundational driver of primary succession, rather than a secondary component that develops in response to the establishment of plants.

The dominance of chemoautotrophs in the most disturbed zones signifies a fundamental shift in ecosystem bioenergetics. It indicates that in the absence of organic carbon, the primary producers of the new ecosystem are microbes harnessing geothermal or geochemical energy. This process of lithoautotrophy effectively "jump-starts" the biological system, initiating the

slow process of converting sterile mineral ash into a life-sustaining soil through the initial fixation of carbon and energy.

The data also reflect the extreme selectivity of the post-eruption environment. The volcanic ash acts as a harsh filter that removes the vast majority of life, leaving a landscape where only organisms with very specific adaptations can survive. These adaptations include the ability to utilize inorganic energy sources, tolerate desiccation and extreme temperatures, and, for plants, the ability to acquire nitrogen in a severely limited environment.

The specific microbe-plant partnership identified between *Acacia* and Rhizobiaceae serves as a powerful illustration of co-evolutionary processes shaping ecological recovery. This symbiotic relationship, which evolved over millions of years, provides a ready-made solution to the critical problem of nitrogen scarcity in new substrates. Its successful establishment is a tangible sign of how life leverages ancient partnerships to conquer new and challenging environments.

The primary implication of these findings is for ecological theory, which must more fully integrate the microbial dimension into models of primary succession. Our results argue for a "microbe-first" view of recovery, where the assembly of the soil microbiome is a prerequisite and a guiding force for the subsequent development of the plant community. Predictive models of ecosystem recovery will be more accurate if they incorporate parameters related to microbial colonization and function (Carrera-Beltrán et al., 2024).

A significant practical implication relates to the field of ecological restoration. The study suggests that restoration efforts on severely disturbed lands, such as mine tailings or volcanic mudflows, could be substantially enhanced by considering the microbial component. Instead of focusing solely on planting tolerant species, restoration strategies could involve the inoculation of soils with beneficial pioneer microbes, particularly nitrogen-fixers and mineral-weathering bacteria, to accelerate soil formation and improve plant survival (Sattarova et al., 2024).

The research also has implications for understanding ecosystem resilience in the face of increasing global change and disturbance events. By elucidating the fundamental mechanisms of recovery from a catastrophic natural disturbance, we gain insight into the processes that confer resilience upon ecosystems. The study highlights that functional redundancy and the presence of key facilitating species and their microbial partners are critical components of this resilience.

Finally, the work informs our understanding of astrobiology and the search for life on other planets. Volcanic landscapes on Earth are often used as analogues for environments on Mars or other rocky bodies. Understanding how life, particularly microbial life, colonizes and engineers these sterile, mineral-based environments provides a model for the types of biosignatures and ecological processes one might look for when searching for extraterrestrial life.

The observed results occurred primarily because the volcanic ash created an environment of extreme resource limitation coupled with a unique resource opportunity. The complete burial of organic soil horizons removed the primary energy source for most soil life (heterotrophy), while simultaneously depositing a fresh layer of unweathered minerals rich in potential chemical energy. This dual condition created an intense selective pressure that filtered out almost all organisms except those that could exploit the new mineral energy source.

The dominance of Proteobacteria, particularly chemoautotrophs, is explained by their metabolic versatility. This phylum contains a vast diversity of metabolic pathways, and its members are frequently found to dominate microbial communities in dynamic or disturbed environments. Their ability to switch between different energy sources and electron acceptors allows them to capitalize on the specific geochemical conditions presented by the fresh ash, outcompeting other microbes (Yuan et al., 2025).

The success of a nitrogen-fixing legume like *Acacia decurrens* is a direct consequence of the severe nitrogen deficiency of the substrate. In an environment where nitrogen is the primary

limiting nutrient for plant growth, any organism that can access the vast atmospheric pool of dinitrogen gas via symbiosis has an enormous competitive advantage. This advantage allows it to colonize a landscape where most other plants would fail due to nutrient starvation.

The strong, depth-dependent gradient effect is a result of the multifaceted impact of the ash layer. Deeper ash provides a more effective physical barrier, preventing the upward growth of surviving plants and diluting any influence from the buried soil. It also creates a more thermally and hydrologically extreme environment at the surface. This physical dose-response explains why the ecological reset was so complete in the heavy deposition zones while being only partial in the thinner layers (Roy et al., 2025).

The next logical step for this research is to implement a long-term monitoring program at the Mount Semeru sites. Primary succession is a process that unfolds over decades to centuries, and continued observation is crucial to determine if the initial pioneer communities are stable or are eventually replaced by other functional groups as the soil develops and organic matter accumulates. Tracking these successional trajectories is essential for a complete understanding of the recovery process.

Future investigations should move beyond taxonomy to focus more on microbial function. Employing techniques such as shotgun metagenomics, metatranscriptomics, and metabolomics would provide a much deeper picture of the ecosystem. These methods can reveal which metabolic pathways are active, which genes are being expressed, and what biochemical transformations the microbes are performing, providing a direct link between community composition and ecosystem-level processes like nutrient cycling.

Controlled laboratory and greenhouse experiments are now needed to test the specific hypotheses generated by this field study. For example, pioneer microbial taxa isolated from the ash could be used to inoculate sterilized ash in a controlled setting. The growth of pioneer plants like *Imperata* and *Acacia* could then be measured with and without these microbial inoculants to definitively prove the facilitative or inhibitory effects of specific microbes on plant establishment.

Finally, the conceptual model developed here should be tested in other volcanic contexts, particularly in different climatic zones and on ash with different geochemical compositions. Comparative studies across a global network of volcanic eruption sites would allow for the development of a more general, predictive theory of primary succession. Such a global perspective would help disentangle the universal principles of ecological recovery from the site-specific contingencies.

CONCLUSION

The most distinct finding of this research is the empirical evidence for a microbially-driven functional shift from heterotrophy to chemoautotrophy as the inaugural step of ecosystem recovery on fresh volcanic ash. This study moves beyond simply documenting community change to identify the establishment of a simplified, mineral-metabolizing microbiome as the foundational energetic engine of the new ecosystem. The quantitative linkage between the nitrogen-fixing Rhizobiaceae and the successful colonization by the pioneer legume *Acacia decurrens* provides a clear, molecular-level confirmation of the facilitation hypothesis at the very beginning of primary succession.

This research offers a primary conceptual contribution by advancing a "microbe-first" model of primary succession, which posits that the trajectory of microbial community assembly is not a parallel process but a prerequisite that architects the path for subsequent plant colonization. Methodologically, its value lies in the rigorous integration of high-throughput DNA sequencing with a classical ecological gradient design from the immediate post-disturbance period. This integrated approach provides a robust and replicable framework for

investigating the foundational mechanisms of ecosystem recovery in response to catastrophic events.

The study is inherently limited by its "snapshot" nature, capturing the ecosystem at a single point in time, and its correlational design, which cannot definitively prove causation. The findings are also specific to the andesitic ash of a tropical volcano. Therefore, future research must prioritize long-term monitoring of these sites to track successional trajectories. This must be complemented by controlled manipulative experiments, both in situ and in the laboratory, to move from correlation to causation by directly testing the functional roles of key pioneer microbial taxa in facilitating plant establishment and soil formation.

AUTHOR CONTRIBUTIONS

Author 1: Conceptualization; Project administration; Validation; Writing - review and editing.

Author 2: Conceptualization; Data curation; Investigation.

Author 3: Data curation; Investigation.

CONFLICTS OF INTEREST

The authors declare no conflict of interest.

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