Fresh tephra deposits from the Tajogaite Volcano boost thermophile proliferation and soil organic matter recovery

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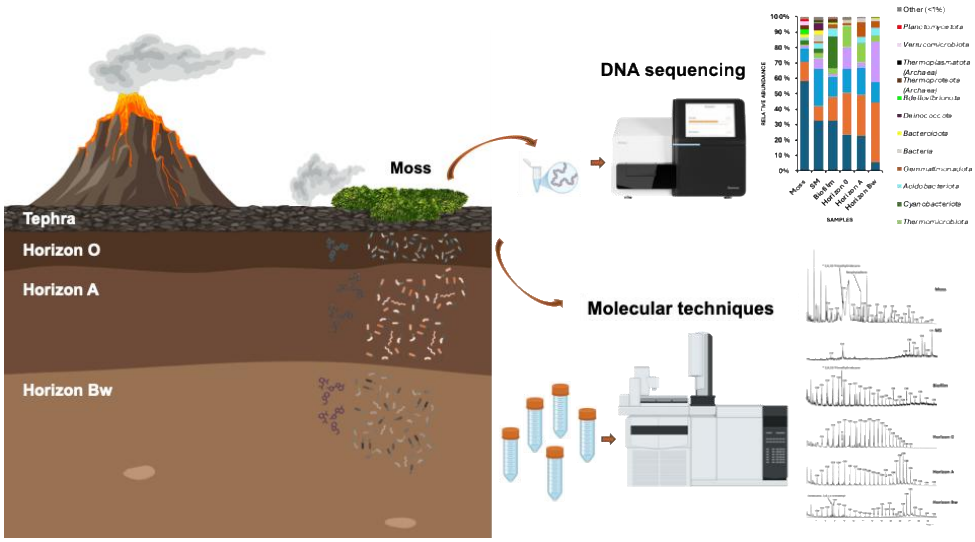
Abstract. Tephra fallout deposition during volcanic eruptions overlays existing soils, profoundly altering their physical, chemical, and biological properties. This study investigates the impact of the newly deposited tephra blanket from the 2021 Tajogaite eruption (La Palma Island) on the molecular composition of soil organic matter and microbial diversity across different soil horizons. A combination of 16S ~~and 18S~~ rRNA gene sequencing, pyrolysis-gas chromatography/mass spectrometry (Py-GC/MS), and elemental and isotope ratio mass spectrometry (EA/IRMS) was employed. Our results demonstrate that tephra deposits significantly modify the organic matter composition of the underlying soils, promoting microbial activity linked to the degradation and transformation of organic carbon and nitrogen compounds. The soil horizon directly beneath the tephra layer (horizon 0~~O~~) displayed a higher abundance of labile organic compounds and a reduced presence of recalcitrant compounds compared to the deeper horizons (A and Bw). This pattern is strongly associated with the predominance of thermophilic bacteria, which contribute actively to the breakdown of complex organic materials such as lignin and hydrocarbons, and drive key biogeochemical processes including nitrogen and carbon cycling. The continuous geothermal influence of nearby fumaroles further supports the persistence and ecological success of thermophilic communities in these volcanic soils. These findings underscore the critical role of volcanic activity not only in reshaping soil structure but also in enhancing soil fertility and resilience through microbial-mediated processes. Understanding these dynamics is essential for

soil management and ecosystem recovery strategies in volcanic regions, providing new insights into the long-term effects of tephra deposition on soil health and the carbon cycle.

Graphical abstract



1. Introduction

The Tajogaite volcanic eruption, which began in September 2021 on La Palma Island (Canary Islands, Spain), was an extraordinary geological event that significantly transformed the local environment (Birnbaum et al., 2023; Troll et al., 2024). Over 85 days, the eruption released over 200 million cubic meters of lava and pyroclasts, burying over 1,200 hectares of land and displacing 7000 residents. The voluminous ashfall, with a complex tephra blanket reaching up to 2.5 m thick, profoundly impacted the ecosystem of La Palma and posed substantial challenges for local agriculture, infrastructure, and human health (Craig et al., 2016; Bonadonna et al., 2022, 2023; Birnbaum et al., 2023; Sánchez-España et al., 2023; Biass et al., 2024). According to these authors, the grain size of the tephra blanket varied during the eruption from lapilli >6 cm to very fine ash (<2 mm) that spread to La Gomera, El Hierro, Tenerife and Gran Canaria islands during the more explosive phases. Ashfall significantly impacted agricultural productivity (Sánchez-España et al., 2023; Taddeucci et al., 2023). The loss of fertile topsoil and the alteration of soil properties created long-term challenges for agricultural recovery and land use (Ustiatik et al., 2023). Volcanic tephra is a fine-grained unconsolidated deposit, highly reactive material that can considerably modify soil structure, chemistry, and biology (Nanzyo et al., 1993; Arnalds, 2013; Wygel et al., 2019). When deposited on existing soil layers, tephra can create a new surface horizon that introduces novel mineral substrates and interacts with soil organic matter (SOM), triggering complex chemical and biological transformations (Hayakawa et al., 2020; Wijesinghe et al., 2020; Peng et al., 2021). These changes can influence soil fertility, stability, and overall health by modifying nutrient availability, pH, and soil aggregation (Peng et al., 2021; De la Rosa et al., 2023). Additionally, the ash can act as a catalyst for the formation of new organic-mineral complexes, altering SOM decomposition pathways and the long-term sequestration of carbon and other essential nutrients (Nierop and Buurman, 2007; Hernández et al., 2012; Iwasaki et al., 2021). Understanding these processes is crucial, particularly in volcanic regions where soil resilience is key to ecosystem recovery.

Soil health is intrinsically linked to the composition and stability of SOM (Arias et al., 2005), which consists of a diverse array of plant-derived, microbial, and fungal compounds (González-Pérez et al., 2004). Fresh tephra deposition in regions affected by volcanic activity can significantly alter the soil capacity to retain nutrients and support plant and microbial communities, ultimately influencing the trajectory of ecosystem recovery (Hernández et al., 2012; Yokobe et al., 2020; Muñoz et al., 2021). Furthermore, the interactions between volcanic ashfall and SOM can lead to the formation of polycyclic aromatic hydrocarbons (PAHs) and other condensed compounds (Nanzyo et al., 1993; Tomašek et al., 2021).

The effects of volcanic ash extend beyond physical and chemical changes; they also shape the microbial communities in soils (Zeglin et al., 2016; Yokobe et al., 2020; Chen et al., 2021). Microorganisms are highly sensitive to changes in soil properties, and ash deposition can create new niches that favour specific microbial taxa adapted to the altered conditions (Chen et al., 2021). This alteration in microbial diversity can have profound implications for soil function, influencing processes such as SOM decomposition, biogeochemical cycle of carbon and nitrogen, nutrient cycling, and the production of secondary metabolites (Campos et al., 2020; Gutierrez-Patricio et al., 2024).

Under the hypothesis that tephra deposits from volcanic eruptions can modify the microbiota and the organic matter composition of the underlying soils, ~~T~~this work aimed to investigate the impact of the Tajogaite volcanic eruption on the molecular and microbial diversity of an existing soil profile ~~that has been~~ covered by tephra deposits and ~~delucidate~~elucidate its influence ~~i~~on soil resiliency and ecosystem recovery capacity. Using advanced molecular and microbiological techniques, including pyrolysis-gas chromatography/mass spectrometry (Py-GC/MS), stable isotope analysis, and 16S ~~and 18S~~ rRNA gene-sequencing, the soil profile~~s under recent ash deposition~~ was ~~were~~ analysed to unravel how volcanic ash alters SOM quality and microbial community structure.

~~The findings provide key insights into the mechanisms driving soil transformation following volcanic events and highlight the critical role of SOM and microbial dynamics in soil resilience and ecosystem recovery.~~

2 Material and Methods

2.1 Study site and sampling

The soil profile studied is located in the *Las Manchas* area of La Palma Island, within the region most affected by the 2021 Tajogaite volcanic eruption. La Palma Island, part of the Canary Islands archipelago and located approximately 400 km west of the African coast, has a total area of 708 km² and is one of the youngest in the archipelago, formed during the last 1.8 million years (Hoernle et al., 2009). La Palma Island shows the most complete record of the evolution of an oceanic volcanic island, starting from the Pliocene submarine basal complex, the metamorphism originated by magmatic intrusion, the building of a Quaternary volcanic edifice, and giant landslides and intense erosion that defines the final morphology of *Caldera de Taburiente*. Volcanism displaced to a N-S elongated polygenetic *Cumbre Nueva* volcanic ridge that has developed over the last c. 125 ka (Carracedo et al., 2001; Sánchez-España et al., 2023) being the most active area of this island (Longpre & Felpeto, 2021).

The 2021 Tajogaite volcanic eruption, which began on September 19 and lasted for 85 days, emitted over 200 million cubic meters of lava and pyroclastic materials, creating extensive lava flows that covered approximately 1,200 hectares and extended into the Atlantic Ocean, forming two new lava deltas (Ferrer et al., 2023). The pyroclastic materials deposited during this eruption ranged in size from fine ash to large lapilli and created a stark contrast with the pre-existing landscape (Bonadonna et al., 2022; Ferrer et al., 2023). The eruption also introduced a tephra blanket, up to 3 m thick in areas close to the volcanic cone, that overlies the native soils (Bonadonna et al., 2023).

The study site is located in the *Las Manchas* area (Los Llanos de Aridane municipality), situated on the western slopes of the Cumbre Nueva Ridge (Fig. 1A). Before the eruption, the soils in this area were classified as Typic Ustivitrands (Soil Survey Staff, 2022). These soils typically exhibit a sandy loam texture, low bulk density, and a high degree of aggregation, particularly in the surface horizons, which are enriched with organic matter (see Table S1).

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Following the eruption, the pre-existing soils in the study area were buried under a 20 cm thick layer of tephra and ash. Two years after the event, mosses colonized the tephra deposit surface, and biofilms developed at the soil-tephra interface (Fig. 1B). Sampling included the collection of moss growing on the fresh tephra (MOSS), the tephra layer directly beneath the moss cover (moss substrate, MS), a dark green biofilm on horizon 0~~O~~ (Biofilm), and three soil horizons: 0–2 cm (Horizon O) ~~(0–2 cm)~~, ~~A (~~2–10 cm~~)~~ (Horizon A) and ~~Bw (~~10–20 cm~~)~~ (Horizon Bw) (Fig. 1B). All samples analyzed in this study were composite samples, generated by collecting five subsamples per sample type across distinct sampling points and/or soil horizons, followed by thorough homogenization and pooling into a single representative mixture. This volcanic ash-derived soil profile was located near steam-emitting fumaroles, in a sector with a high temperature anomaly in the soil. These fumaroles vent water vapour as the main component and other chemical species, such as SO_2, H_2S, HCl, and CO gases up to 20.7, 17.7, >30.0 and 19.5 ppm, respectively, at temperatures higher than the ambient (Campeny et al., 2023; Martínez-Martínez et al., 2023).

This site provides a unique opportunity to study the interactions between fresh tephra deposits and the underlying soil, particularly their effects on soil structure, organic matter composition, and microbial communities.

All samples were collected using sterile tools, such as spatulas or individually wrapped disposable scoops, to avoid contamination, and all samples were immediately placed into sterile Whirl-Pak bags. The samples were kept on ice during transportation to the laboratory for subsequent analysis. Subsamples of each material were used for DNA-based analysis, carbon and nitrogen elemental and isotope analysis, and molecular composition.

The environmental conditions of the sampling area were monitored by installing a temperature and relative humidity sensor (HOBO MX2301A, ONSET ®, Fig. S1A and B) near the fumarole vent to assess the temperature of the water vapour emissions from the fumarole. This sensor took measurements every hour for one year.

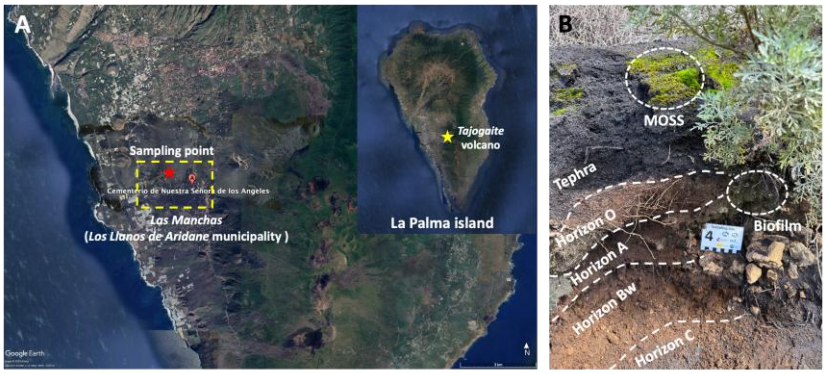

Figure 1: A) Location of the soil profile under tephra blanket in *Las Manchas* (La Palma, Spain), and B) sampling area of the volcanic ash-derived soil profile comprising ~~m~~Moss, moss substrate (MS), B~~b~~iofilm located in the horizon O, and three horizons (O, A and Bw).

2.2 Carbon and nitrogen elemental and isotope analysis

The compositional analysis of organic carbon and nitrogen in both pyroclastic materials and soil samples was carried out using a Flash 2000 HT Elemental Micro-analyzer connected to a Thermal Conductivity Detector (EA/TCD; Thermo Scientific in Bremen, Germany). Samples, ranging in weight from 5 to 10 milligrams, were processed in duplicate (n = 2) following a decarbonization treatment as outlined by Jiménez-Morillo et al., (2016, 2020a). The calibration of carbon and nitrogen content employed certified standards such as acetanilide, nicotinamide, and aspartic acid, provided by Thermo Scientific, Bremen, Germany. The carbon and nitrogen isotope ratios ($^{13}C/^{12}C$ and $^{15}N/^{14}N$) were determined using an Elemental Analyzer connected to a Thermo Fisher Delta V Advantage Isotope Ratio Mass Spectrometer (EA/IRMS), following the method described by (Jiménez-Morillo et al., 2020b). These procedures were conducted at the Stable Isotope Laboratory - MOSS at IRNAS-CSIC (Spain). Isotope values are expressed in delta (δ) notation in parts per thousand (‰) relative to certified standards set by the International Atomic Energy Agency (IAEA), with a standard deviation for bulk $\delta^{13}C$ of ± 0.05 ‰ and $\delta^{15}N$ of ± 0.1 ‰. Duplicate analyses were performed for samples and standards (n = 2).

2.3 Analytical pyrolysis (Py-GC/MS)

The analytical pyrolysis (Py-GC/MS) technique was composed of i) a double-shot pyrolyzer, model 3030D (Frontier Laboratories, Japan), set at 500 °C; ii) an Agilent 6890N gas chromatograph, and iii) an Agilent 5973 MSD (mass selective detector) mass spectrometer, operating at an electron impact energy of 70 eV. The chromatographic separation involved an HP-5MS UI capillary column (30 m length, 0.25 mm internal diameter, 0.25 µm film thickness) with a helium flow rate of 1 mL min^{-1}. The sample injection was conducted in splitless mode at 250 °C, and the temperature program was adopted from protocols described by Jiménez-Morillo et al., (2020a). Ion fragments ranging from 50 to 550 m/z were recorded, and compound identification was conducted by comparison with virtual spectral libraries, such as the NIST20 and Wiley7. The molecular compounds released by Py-GC/MS were categorized into the eight biogenic families proposed by Jiménez-Morillo et al (2016a): unspecific aromatic compounds (ARO), polysaccharides (POL), peptides (PEP), lignin (LIG), lipids (LIP), nitrogen-containing compounds (N-comp), polycyclic aromatic hydrocarbons (PAHs), and steranes (STR). Chromatographic peak area >0.2% of the total chromatographic area was not taken into account. For a detailed study of homologous series of *n*-alkanes and *n*-alken-2-ones, single ion monitoring of specific fragments - specifically ions with m/z 57 and m/z 59, respectively - was adopted.

2.4. DNA extraction and 16S rRNA gene amplicon sequencing

Genomic DNA was extracted from 250 mg of each sample (n = 6) using the DNeasy PowerSoil Pro Kit (Qiagen, Germany) following the manufacturer's instructions. DNA concentration was quantified using a Qubit 4.0 fluorometer (Invitrogen).

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The V3–V4 hypervariable region of the prokaryotic 16S rRNA gene was amplified using the universal primers 341F (5′-CCTACGGGNGGCWGCAG-3′) and 805R (5′-GACTACHVGGGTATCTAATCC-3′) with Illumina overhang adapter sequences, following Klindworth et al. (2013). Amplicon libraries were sequenced on an Illumina MiSeq platform using 2 × 250 bp paired-end chemistry. Library preparation and sequencing were performed by Novogene Sequencing Services (China). Raw sequencing reads were deposited in the NCBI Sequence Read Archive (SRA) under accession PRJNA1192049.

~~**2.5. Bioinformatic processing and diversity analyses**~~

~~Raw paired-end reads were processed in QIIME 2 (v2024.5) (Bolyen et al., 2019). Primer sequences were removed prior to denoising, and reads were quality filtered, denoised, and merged using the q2-dada2 plugin (Callahan et al., 2016) to generate an amplicon sequence variant (ASV) feature table; chimeric sequences were removed using the consensus method implemented in DADA2. Taxonomy was assigned using a Naïve Bayes classifier trained for the V3–V4 region against the SILVA reference database (release 138) (Quast et al., 2013).~~

~~The alpha and beta diversity analyses were calculated using the QIIME 2 version 2024.5 to quantify the microbial diversity within each sample. Alpha diversity metrics were computed to summarize within-sample diversity. Beta diversity was assessed using Bray–Curtis (abundance-based) and Jaccard (presence/absence) dissimilarities, and community patterns were visualized by principal coordinates analysis (PCoA). Given the limited number of samples (n = 6) and the absence of biological replication per sample type, results were interpreted descriptively to highlight patterns rather than to perform formal hypothesis testing among groups.~~

~~2.4 DNA extraction and sequencing~~

~~Genomic DNA was extracted from 250 mg of each of the five samples using the DNeasy PowerSoil Pro Kit (Qiagen, Germany) following the manufacturer's instructions. The DNA was quantified using a Qubit 4.0 fluorometer (Invitrogen).~~

~~The extracted DNA was analyzed through next-generation sequencing (NGS), targeting the V3–V4 hypervariable region of the 16S rRNA gene for prokaryotes. Amplicons were sequenced using the Illumina MiSeq platform to generate 250bp paired-end raw reads, performed by Novogene Sequencing Services (China).~~

~~Raw amplicon sequence data were processed using QIIME 2 version 2024.5 (Bolyen et al., 2019). The table of Amplicon Sequence Variants (ASVs) was generated using DADA2, following its instructions (Callahan et al., 2016). Taxonomic classification was assigned using the SILVA reference database, version 138 (Quast et al., 2013). Alpha diversity analysis was calculated in QIIME2 version 2024.5 (Bolyen et al., 2019) to quantify the microbial diversity within each sample.~~

~~The raw reads were deposited in the NCBI Sequence Read Archive (SRA) database under accession number PRJNA1192049.~~

2.5. Bioinformatic processing

Raw paired-end reads were processed using QIIME 2 (v2024.5) (Bolyen et al., 2019). Primer sequences were removed prior to denoising to prevent primer-derived artifacts and to improve read merging. Reads were then quality filtered and denoised

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using the q2-dada2 plugin (Callahan et al., 2016), which infers exact amplicon sequence variants (ASVs) by modeling sequencing errors and resolving unique biological sequences. Forward and reverse reads were merged to reconstruct the full V3–V4 amplicon, generating an ASV feature table for downstream ecological analyses. Chimeric sequences produced during PCR amplification were identified and removed using the consensus approach implemented in DADA2, reducing spurious diversity. Taxonomy was assigned with a Naïve Bayes classifier trained on the V3–V4 region against the SILVA reference database (release 138) (Quast et al., 2013), ensuring that taxonomic classification was optimized for the targeted amplicon region.

2.6. Diversity and statistical analyses

Alpha diversity analyse was computed in QIIME 2 (v2024.5). Alpha diversity was calculated to summarize within-sample diversity using richness and diversity indices (e.g., observed ASVs, Chao1, Shannon, and Simpson, as appropriate). To aid interpretation of the ordination, we produced a PCoA biplot by projecting (i) geochemical/pyrolytic descriptors (e.g., compound-class abundances from pyrolysis and elemental contents) and (ii) the relative abundances of dominant microbial phyla onto the same ordination space. Vectors (arrows) represent the direction of increasing values for each variable and their strength of association with the ordination axes (longer vectors indicate stronger relationships). This combined representation was used to highlight which chemical pools and microbial groups co-varied across samples and to identify the main gradients driving separation along PCo1 and PCo2.

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3 Results and discussion

3.1 Elemental and isotope composition of carbon and nitrogen

Table 1: Isotope and elemental composition of nitrogen (N) and carbon (C) of Moss, moss substrate (MS), Biofilm and three soil horizons (O, A and Bw). Significant ($p < 0.05$) differences between samples are indicated by different letters ("one-way ANOVA"; means compared to the Tukey test, $p = 0.05$).

Sample	$\delta^{15}N$ (‰, V-Air)	$\delta^{13}C$ (‰, VPDB)	N (%)	C (%)
Moss	-5.1±0.4d	-28.5±0.1b	0.62±0.12b	12.53±1.69c
MS*	5.0±2.9bc	-24.3±1.6ab	3.17±0.80ab	28.71±4.53bc
Biofilm	1.9±0.9c	-28.4±3.5ab	4.37±1.86a	38.59±16.65ab
Horizon O	7.9±0.5b	-29.2±1.6b	4.99±0.78a	55.27±8.09a
Horizon A	6.0±0.4bc	-24.8±1.3ab	1.60±0.51b	17.60±3.39bc
Horizon Bw	16.6±3.1a	-23.5±0.4a	0.95±0.87b	8.65±4.48c

*MS = moss substrate

Table 1 depicts the average values and standard deviations of the elemental and isotope composition of carbon (C) and nitrogen (N) in M~~m~~oss, moss substrate (MS), B~~b~~iofilm, and three soil horizons (Horizon 0~~O~~, A, and Bw). Horizon 0~~O~~ samples exhibited the highest average of C and N content (55.3 ± 8.1 and 5.0 ± 0.8, respectively), which may be associated with a noticeable root layer (Fig. 1). The B~~b~~iofilm also shows notable C and N content (38.59% and 4.37%, respectively) and is located in Horizon O. These values are typical of biofilms, and its ratio C/N close to 9 (8.83 on average) indicates that the biofilm was found in a healthy state. Previous studies have shown that biofilms with C/N ratio close to 9 have higher concentrations of carbohydrates and proteins in the biofilm and a significant upregulation of the Quorum Sensing genes (Ramos et al., 2023).

In contrast, the C and N values in the horizons A (17.6 ± 3.39 and 1.6 ± 0.51, respectively) and Bw (8.65 ± 4.48 and 0.95 ± 0.87, respectively) were consistent with those reported in different soil types, the concentration of both elements in horizon A is three-fold of those found in B (Girona-García et al., 2018; Jiménez-Morillo et al., 2020a). These findings align with previous studies indicating a decline in C and N content with increasing soil depth. For M~~m~~oss and moss substrate (MS), the higher C content in MS compared to M~~m~~oss could be attributed to the presence of numerous small moss roots, which form a three-dimensional network that aggregates and stabilizes lapilli grains. Additionally, the presence of root exudates, rich in C and N compounds, may contribute to this remarkable concentration of organic compounds. This is the first indication of soil re-generation after the volcanic eruption of Tajogaite, which reveals the importance of moss in this process. Previous studies about the colonization of soils affected by volcanic activity highlight the abundance of photosynthetic organisms, including moss, as pioneer colonizers (Smith, 1984; Ingimundardóttir et al., 2014; Vilmundardóttir et al., 2018; Dragone et al., 2023).

Regarding the C isotope composition, all samples exhibited $\delta^{13}C$ values within the typical range for C_3 plants (between -25 ‰ and -35 ‰ (Katsumi et al., 2015; Ghezzi and Jimenez-Morillo et al., 2024). However, significant differences were observed among the samples. Moss, Horizon O, and B~~b~~iofilm displayed the most negative $\delta^{13}C$ values (-28.5 ‰ ± 0.1, -28.4 ‰ ± 3.5, and -29.2 ‰ ± 1.6, respectively), which reflected the presence of fresh organic matter (Jiménez-Morillo et al., 2020b). In contrast, samples from the A and Bw soil horizons and the moss substrate (MS) were enriched in ^{13}C (Table 1). This trend has also been observed by Girona-García et al., (2018) in soil profiles under pine and beech forests, where deeper horizons exhibited higher $\delta^{13}C$ values. Such ^{13}C-enrichment in soil samples is often associated with more humified organic matter (Jiménez-Morillo et al., 2020b). For the MS ($\delta^{13}C$ = -24.3 ‰ ± 1.6), the observed ^{13}C-enrichment may be attributed to i) the heavier isotope signature of root exudates compared to other organic compounds commonly found in soil samples (Girona-García et al., 2018), and ii) microbial activity linked to diverse families of microorganisms (Jiménez-Morillo et al., 2020b; Miller et al., 2022; San-Emeterio et al., 2023). In addition, Horizons A and Bw have similar $\delta^{13}C$ values (-24.8 ± 1.3 and -23.5 ± 0.4, respectively) to the MS, which is mainly composed of tephra. This could be indicative of the volcanic origins of the paleo soil (Horizons A and B) (Carracedo et al., 2022) and the importance of lapilli, among other volcanic materials from previous eruptions, in the carbon cycle during the soil formation (Matus et al., 2014 and references therein).

A key finding is the strong negative correlation observed between $\delta^{13}C$ values and C content across the different soil horizons and the Bbiofilm (Fig. 2). This trend is particularly pronounced in the soil horizon samples ($R^2 = 0.9991$; solid line). However, when the Bbiofilm sample is included, the correlation weakens slightly ($R^2 = 0.9572$; dashed line).

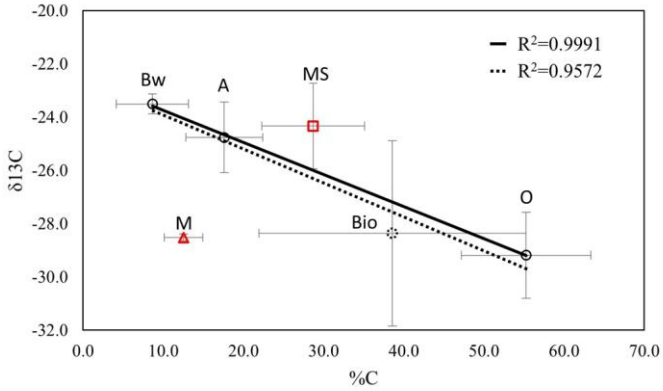


Figure 2: Plot of average (n=3) $\delta^{13}C$ vs %C of Mmoss (red triangle), moss substrate (MS, red square), Bbiofilms (black dashed circle) and soil horizons O, A and Bw (open black circles) with linear regression of horizons (solid line) and including biofilms (dashed line).

This negative correlation between $\delta^{13}C$ and C content has been previously described in soils worldwide. In all cases, this trend has been attributed to either the decomposition of organic matter, the fractionation by microbial activity or the shift of a predominant contribution from plants to microorganisms in the residual organic matter as it progresses through the soil horizons (Ågren et al., 1996; Volk et al., 2018; Ehleringer et al., 2000; Krüger et al., 2024). The microbial activity may process fresh organic matter, leaving behind evolved (humified) material with a heavier isotope. This alteration may also reduce the C content due to microbial respiration. A similar pattern has been observed in the isotope composition of highly humified (evolved) organic matter associated with very fine sand particles in shallow soil layer (Jiménez-Morillo et al., 2020a), which may confirm the influence of microorganisms in the humification process of fresh organic matter. However, the Mmoss and the tephra collected under the moss (MS) did not correlate with the soil. This is probably because the samples were collected shortly after the volcanic eruption that accumulated the tephra over the previous soil (Horizon O). Therefore, the C cycle of this interface was still in an early stage of the andisol formation process, preventing the observation of statistical correlations between the soil samples and the tephra.

Regarding the nitrogen isotope composition ($\delta^{15}N$), the Mmoss sample exhibited the lowest $\delta^{15}N$ value (Table 1), a typical characteristic for mosses (Zechmeister et al., 2008). In contrast, the other samples displayed positive $\delta^{15}N$ values (Table 1). For the MS sample, the ^{15}N-enrichment and their statistical similarity with $\delta^{15}N$ values observed in the soil and biofilm samples suggest that it could be derived from the activity of certain microorganisms, such as cyanobacteria, that utilize nitrogen-derived compounds excreted by the moss roots (Carrell et al., 2022). In addition, the deepest soil sample (Horizon Bw) showed the

highest $\delta^{15}N$ enrichment, which could be associated with denitrification processes (Girona-García et al., 2018). While humification is well known to cause ^{15}N-enrichment, particularly in forest soils (Szpak, 2014), ^{15}N-depletion can occur during the uptake of inorganic N by vegetation (Högberg, 1997). Therefore, the observed trend can be best explained by the alteration of biomass by heterotrophic organisms, which produce ^{15}N-depleted compounds while progressively enriching the remaining biomass with ^{15}N over time (Billings and Richter, 2006; Makarov, 2009; Szpak, 2014; Girona-García et al., 2018).

3.2 Molecular composition of organic fraction

The use of analytical pyrolysis (Py-GC/MS) has revealed remarkable molecular differences between soil, tephra, Bb~~b~~iofilm, and M~~m~~oss samples (Fig. 3). The M~~m~~oss sample is rich in organic compounds, particularly lipids (31.56%) and polysaccharides (29.75%), aligning with findings from previous studies (Klavina et al., 2015; Petkova et al., 2023). Among the lipid compounds identified were essential oils, such as α-Terpinene and Phytol, *n*-alkanes (e.g., heptadecane, heneicosane; Klegin et al., 2023) and *n*-alkanoic acids (e.g., 9,12,15-Octadecatrienoic acid, 13-Eicosenoic acid, 22-Tricosenoic acid; Yucel, 2021; Klegin et al., 2023). Polysaccharides in bryophytes play an important role in the chemical evolution of vegetation and assist as structural components, which are also assumed to contribute to bryophyte stress tolerance (Klavina et al., 2015). In this study, the identified polysaccharides were primarily furans (e.g., 2(5H)-Furanone, 5-methyl-, 2-Furancarboxylic acid, methyl ester, 3-Furaldehyde) and levoglucosan (β-D-Glucopyranose, 1,6-anpah). However, due to dehydration and molecular restructuring during pyrolysis, complete identification of polysaccharides is not feasible (González-Pérez et al., 2016). The molecular analysis also revealed a significant presence of non-specific aromatic compounds (13.60%) and peptide compounds (11.69%). Among the aromatic compounds, phenol derivatives such as Phenol, 2-methyl-, Phenol, 2,3-dimethyl-, 1,2-Benzenediol, and Phenol, 2,3,5-trimethyl were prominent. These phenolic compounds are considered critical in early plant evolution, particularly in moss growth and cuticle permeability, which were key for adaptation to terrestrial environments (Renault et al., 2017). Such phenolic compounds are precursors to lignin, synthesized by the phenylpropanoid pathway, which strengthens cell walls, aids in water transport, and supports upright growth (Fraser and Chapple, 2011). Peptide-derived compounds were also found, with their primary function being the defence of mosses against environmental stressors such as drought and high temperatures (Ren et al., 2024). Additionally, these peptides provide resistance against microbial pathogens (Valeeva et al., 2022). Plants produce a range of bioactive metabolites, peptides, and small molecules that contribute to defence mechanisms and microbial resistance (Valeeva et al., 2022). In addition, peptide compounds are crucial regulators of ecosystem function because they may provide as direct supplies of nutrients for soil microorganisms and plants (Wang et al., 2023).

Only a few organic compounds were identified in the MS samples, mainly high molecular weight alkyl lipids (*n*-alkanes) and sterols, being the second the dominant group (65%). Key sterols detected include Stigmastan-3,5-dien, Campesterol, and γ-Sitosterol, also found in the M~~m~~oss samples (Table S2). The presence of Campesterol and γ-Sitosterol may indicate an input of organic matter from the moss via rhizoid exudates. Sterols are crucial for various plant physiological processes, not only

supporting cell membrane structure and fluidity but also acting as hormone precursors and playing a role in responses to biotic and abiotic stress (Valitova et al., 2016; Cabianca et al., 2021). In addition, the presence of high molecular weight alkyl compounds, originating from epicuticular waxes, supports the hypothesis that there is a direct input of organic material from the moss to the substrate (tephra). The $\delta^{13}C$ value observed in this sample does not align with the molecular composition identified by Py-GC/MS, as the detected compounds usually exhibit a markedly negative isotope signature (Park and Epstein, 1961; San-Emeterio et al., 2023). However, the observed ^{13}C-enrichment in this sample against the moss could be attributed to low-molecular-weight polysaccharide-derived compounds undetected by this analytical technique.

The Bb~~b~~iofilm sample collected from Horizon 0~~O~~ consists mainly of lipids (40.54%), non-specific aromatic compounds (38.36%), polysaccharides in the form of furans (13.08%), and peptides (8.02%). This molecular composition aligns perfectly with the main molecular composition found in Bb~~b~~iofilm samples analyzed in different volcanic regions (Miller et al., 2020; Ghezzi and Jiménez-Morillo et al., 2024; Palma et al., 2024). The lipid composition is mainly dominated by *n*-alkane/alkene pairs with different proportions, which will be discussed in the section 3.3.1.

The Horizon 0~~O~~ sample is dominated by lipid compounds (42.43%), mainly alkyl compounds (*n*-alkane/alkene pairs and *n*-alkanoic acids), followed by aromatic moieties (17.80%) and polysaccharides (12.57%). In addition, this is the only sample with a relatively high concentration of methoxyphenols, i.e., lignin-derived compounds (12.18%). The abundance of alkyl compounds suggests the existence of different organic fractions from distinct origins: i) organic matter from pre-eruption vegetation, also indicated by the $\delta^{13}C$ of the Horizon 0~~O~~ sample (-29.2 ± 1.6) typical of C_3 plants, ii) the degradation of lipid membranes from microorganisms induced by the deposition of tephra during the Tajogaite volcanic eruption, and iii) highly evolved organic matter from post-eruption microbial activity in the soil (Jiménez-Morillo et al., 2017; Bull et al., 2000; Jiménez-Morillo et al., 2016b; Leal and Jimenez-Morillo et al., 2023). In contrast, the presence of lignin- and polysaccharide-derived compounds probably indicates the recent input of herbaceous/shrubby plant material (Fig. 1). It could also stem from root exudates of vegetation present before the ash deposition, supported by the high concentration of roots in the Horizon 0~~O~~ (Fig. 1). Lignin compounds, particularly from the guaiacol and syringol groups, confirm a contribution of tree-derived organic matter (San-Emeterio et al., 2023). However, the greater abundance of guaiacol over syringol suggests ongoing microbial degradation activity, as syringol is more easily degraded by microorganisms (San-Emeterio et al., 2023). Additionally, condensed compounds (PAHs) were found in the shallow horizon. This could be generated by: i) ancient fires with particles trapped in the soil layers (Jiménez-Morillo et al., 2016b), ii) high-temperature vapour emissions, from volcanic fracture, leading to defunctionalization and condensation of polar aromatic compounds (Capaccioni et al., 1995) or, iii) microbial activity. Several pathways have been described for hydrocarbon synthesis by microorganisms (Ladygyna et al., 2006 and references therein). Some of these biogenic PAHs have been detected in forest soil (Kraus et al., 2005) with high degradation of lignin, in peatlands and wetlands (Wakeham et al., 2016), where organic matter accumulates and transforms slowly, and in

lake and marine sediments (Love et al., 2021), where microbial activity and anoxic conditions promote the polymerization of aromatic compounds.

The two deepest Horizons (A and Bw) of the soil profile share a similar molecular composition, dominated by non-specific aromatic compounds, lipid compounds (mainly *n*-alkane/alkene pairs), polysaccharides and peptides, with a complete absence of lignin molecules. This pattern has been observed in forest soils across the Iberian Peninsula (Aznar et al., 2016; Jiménez-Morillo et al., 2016a; De la Rosa et al., 2019), indicating the presence of microbial-derived compounds and linked to high microbial activity (Jiménez-Morillo et al., 2018). The abundance of non-specific aromatic compounds may also result from fungal degradation of plant lignins (Kellner et al., 2014). However, important differences include a higher proportion of condensed compounds (PAH = 15.17%) in the upper Horizon, while the deeper horizon has more sterane compounds (10.76%). In the Horizon A, highly condensed PAHs, such as phenanthrene and pyrene suggest the presence of pyrogenic material, usually associated to organic matter combustion (González-Pérez et al., 2014; Miller et al., 2020, 2022). In contrast, the deeper Horizon only contains branched naphthalene compounds, possibly due to lower-intensity fires or microbial degradation of condensed compounds by thermophiles (Musat et al., 2009; Mohapatra and Phale, 2021). In the sterane family, the deeper Horizon (Bw) contains Stigmastan-3,5,22-triene, Ergosta-4,6,22-trien-3-ol, and Friedelan-3-one. These plant- and fungi-synthesized compounds are well-preserved in deeper layers due to their stability (Kristan and Rižner, 2012), with clear accumulation in the lower horizons, while they are almost absent in the Horizon 0~~O~~ and the B~~biofilm~~ (Fig. 3).

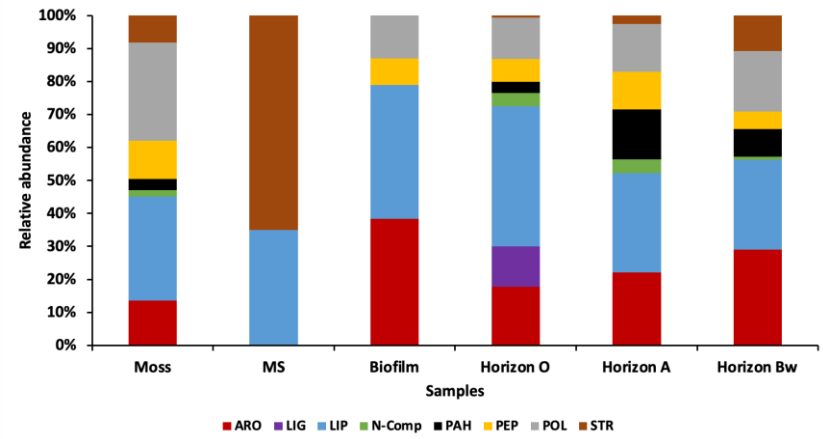


Figure 3: Relative abundance (%) of the main organic families identified by Py/GC/MS from M~~m~~oss, moss substrate (MS), B~~b~~iofilm, and soil horizons (O, A, Bw) samples. The main organic families are: unspecific aromatic compounds (ARO), polysaccharides (POL), peptides (PEP), lignin (LIG), lipids (LIP), nitrogen-containing compounds (N-comp), polycyclic aromatic hydrocarbons (PAHs), and steranes (STR).

3.3. Lipid analysis by Py-GC/MS

3.3.1. *n*-Alkanes

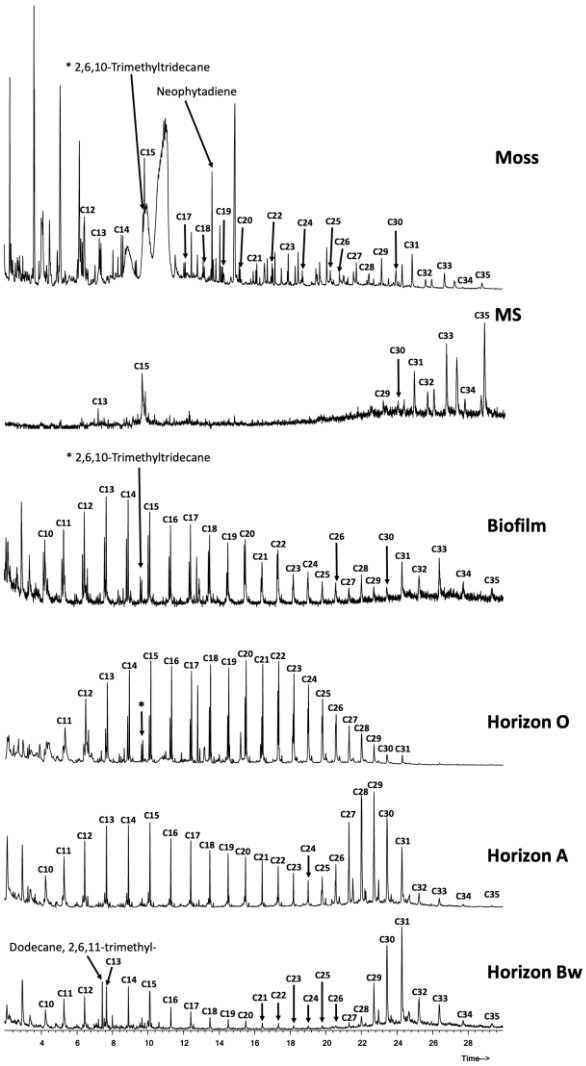


Figure 4: *n*-alkane (m/z 57) distribution obtained by direct pyrolysis (Py-GC/MS) of Mmoss, moss substrate (MS), Bbiofilms and soil horizons (O, A and Bw) samples.

The *n*-alkane series were identified using m/z 57 in the selected-ion-monitoring (SIM) chromatogram (Fig. 4). Chain lengths ranged from C_{10} to C_{35}, reflecting various organic matter sources (Jiménez-Morillo et al., 2017). In the Mmoss sample, a bimodal distribution was observed with peaks at *n*-pentadecane (C_{15}) and *n*-hentriacontane (C_{31}), with odd-chain *n*-alkanes

predominating, especially in longer chains (>C_{25}). This suggests *n*-alkanes from moss epicuticular waxes, with a peak at *n*-hentriacontane (Schwark et al., 2002). The presence of low-molecular-weight (LMW) *n*-alkanes (<C_{20}) may point to associated microorganisms, as LMW *n*-alkanes typically originate from microbial cell walls (Jiménez-Morillo et al., 2017, 2022).

In the MS sample, the dominance of odd-chain high-molecular-weight (HMW) *n*-alkanes supported direct organic matter input from moss. However, the abundance of *n*-tritriacontane (C_{33}) and *n*-pentatriacontane (C_{35}) *n*-alkanes may also indicate C4 vegetation (Vogts et al., 2009; Feakins et al., 2016) or the adaptation of pre-eruption vegetation to water stress caused by volcanic ash.

In Horizon O, a bimodal *n*-alkane distribution with peaks at C_{15} and *n*-docosane (C_{22}) suggested the presence of organic matter from soil microorganisms or the degradation of plant biomass by microorganisms over time (Jiménez-Morillo et al., 2016b, 2017). The gradual decline in HMW *n*-alkanes and the absence of a clear odd-over-even pattern indicates microbial degradation processing of organic matter (De Blas et al., 2013; Jiménez-Morillo et al., 2022; Leal and Jimenéz-Morillo et al., 2023). The higher root density in this layer could also contribute to the observed *n*-alkane pattern.

The Bbiofilm sample was dominated by LMW *n*-alkanes, confirming its microbial origin (Jiménez-Morillo et al., 2017). The presence of branched alkanes like neophytadiene, 2,6,10-trimethyltridecane, and 2,6,11-trimethyldodecane further supports a microbial contribution (Palma et al., 2024).

In deeper horizons (A and Bw), there is a clearer differentiation between LMW and HMW *n*-alkanes, indicating two carbon pools from microorganisms (LMW *n*-alkanes) and plant vegetation biomass (HMW *n*-alkanes). The microbial fraction may stem from lipidic membranes (Miller et al., 2016) or microbial degradation of plant biomass, such as alkyl compounds from lignocellulose breakdown (Rabbi et al., 2014; Jiménez-Morillo et al., 2022; Miller et al., 2022). The nonspecific aromatic compounds previously discussed also suggest the lignin breakdown process. However, the most significant differences among horizons are seen in HMW *n*-alkanes. The Horizon A peaks at *n*-nonacosane (C_{29}), indicating tree or shrub vegetation, while the Horizon Bw peaks at *n*-hentriacontane (C_{31}), suggesting herbaceous vegetation (Bull et al., 2000). Therefore, results indicate a change in vegetation probably due to the alteration of the environmental conditions.

3.3.2. *n*-Alkane-2-ones

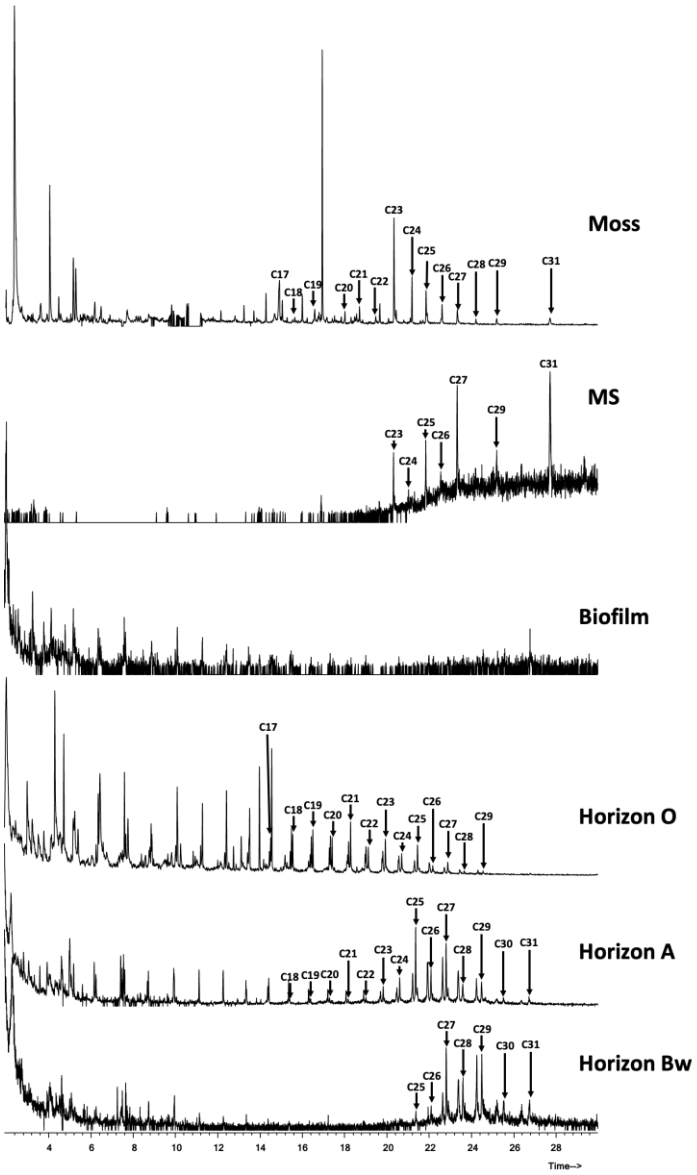


Figure 5: *n*-alkan-2-one (m/z 59) distribution was obtained by direct pyrolysis (Py-GC/MS) of Mmoss, moss substrate (MS), Bbiofilms and soil horizons (O, A and Bw) samples.

The pyrolyzed samples from La Palma, except for the Bbiofilm sample, revealed a series of *n*-alkane-2-ones (m/z 59 ion chromatograms) ranging from C_{17} to C_{31}, with a general odd-over-even chain-length predominance (Fig. 5). However, each sample showed distinct patterns. In the Mmoss sample, the maximum was at *n*-alkane-2-one C_{23}, without a clear parity pattern,

though the odd-over-even trend was evident in LMW *n*-alkane-2-ones. This suggests a mixture of lipids from both the moss and its associated microbiome, as also seen in the *n*-alkanes (Fig. 4).

The MS sample showed a *n*-alkane-2-ones distribution similar to that observed for *n*-alkanes (Fig. 4), being dominated by C_{27} and C_{31} molecules, which supports the idea of a direct contribution of organic matter from the Mmoss.

The soil horizons showed differences in the *n*-alkane-2-one distribution (Fig. 5). In Horizon O, the maximum was at *n*-alkane-2-one C_{21}, while in horizons A and Bw, the maxima were at C_{25} and C_{27}, respectively. The Horizon 0O had a range of *n*-alkane-2-ones from C_{17} to C_{29}, suggesting more degraded organic matter, possibly due to fine ash deposition affecting organic matter or microorganisms. In Horizon A, the *n*-alkane-2-one distribution resembled typical soils, with two carbon pools: i) LMW *n*-alkane-2-ones from microbial activity, and ii) HMW ones from plant-derived organic matter (Jaffé et al., 1996; Kumar et al., 2020). This aligns with the *n*-alkane distribution (Fig. 4) and overall molecular analysis (Fig. 3). In contrast, the Horizon Bw contained only HMW *n*-alkane-2-ones (>C_{25}), considered biomarkers of vegetation (Kumar et al., 2020; Palma et al., 2024). This aligns with the isotope carbon signature observed in the soil (Table 1 and Fig. 2) that indicates the influence of microbial processes at the top layer (Horizon O) and a gradual shift to plant-influenced processes towards the bottom (Horizon Bw). The absence of LMW *n*-alkane-2-ones in Horizon Bw could be due to concentrations below detection limits, as this horizon had low TOC (Fig. 1). Environmental factors such as moisture and nutrient availability may affect *n*-alkane-2-one formation by altering the degradation of *n*-alkanes and *n*-alkanoic acids (Lehtonen and Ketola, 1990; Zhang et al., 2004). Zhang et al. (2004) identified potential sources of *n*-alkane-2-ones, including: (i) epicuticular waxes from plants; (ii) microbial oxidation of *n*-alkanes; (iii) *β*-oxidation and decarboxylation of *n*-alkanoic acids; and (iv) microbial cracking of HMW *n*-alkane-2-ones into LMW ones. The predominance of LMW n-alkane-2-ones in Horizon 0O further supports an active microbial contribution to organic matter transformation.

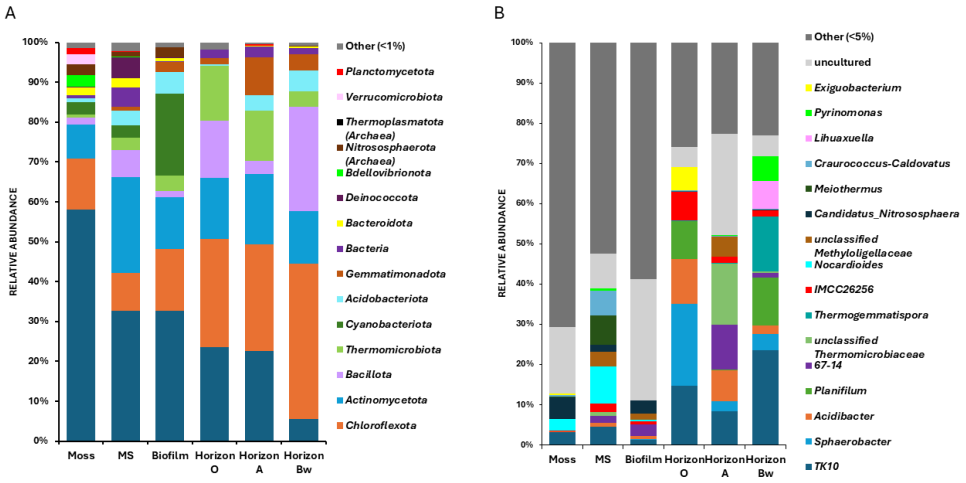
3.4 Bacterial community composition

A total of 198.129 ASVs (amplicon sequence variants) were analysed from 16S rRNA gene sequencing. The richness and evenness of microbial communities were estimated using Chao1, Shannon and Simpson indices (Table 2). The Bbiofilm was the most biodiverse sample, with the highest species richness, and Shannon and Simpson indices of 7.860 and 0.989, respectively, followed by horizons Bw and A and mossMoss. In contrast, Horizon 0O showed a lower diversity, with Shannon and Simpson indices of 4.166 and 0.689, respectively. According to the Chao1 richness estimator, Horizon 0O and the Bbiofilm showed the highest predicted microbial richness, indicating that most of the species present in these samples were successfully detected, with minimal undetected diversity. It is noteworthy that the microbial community in the tephra collected beneath the moss (MS) reached a substantial diversity and richness within just two years following the deposition of the Tajogaite volcanic tephra.

Table 2: Alfpha diversity 16S of Mmoss, moss substrate (MS), Bbiofilms and soil horizons samples.

Sample	Shannon	Simpson	chao1	Observed
Moss	6.359	0.973	426.143	426
MS	5.522	0.950	255.500	254
Biofilm	7.860	0.989	832.783	832
Horizon O	4.166	0.689	833.948	829
Horizon A	6.531	0.972	510.315	473
Horizon Bw	7.321	0.972	814.125	812

Most of the sequences identified belong to the Bacteria kingdom; however, Archaea, was also found, primarily in the mossMoss, biofilm and MS samples, comprising 2.63%, 2.48% and 1.31%, respectively (Fig. 6A). They have been reported as early colonizers in samples from the volcanic island *Hunga Tonga Hunga Ha'apai*, in the Kingdom of Tonga (Fujimura et al., 2016; Dragone et al., 2023). Archaea are known for their ability to inhabit extreme environments and play critical roles in biogeochemical cycles (Offre et al., 2013; Martínez-Espinosa, 2020). The main archaeal class detected in these samples was *Nitrososphaeria,* belonging to the phylum *Nitrososphaerota*, which plays a key role in the nitrogen cycle by transforming ammonia into nitrite, thereby contributing to the nitrogen availability in the soil. This process indirectly supports plant nutrition (Leininger et al., 2006; Lehtovirta-Morley et al., 2024) and influences the distribution of N concentration described in the Bbiofilm and MS samples. The presence of N in these samples infers that the identified genus *Nitrososphaeria* is oxidizing the ammonium to nitrite, which requires the presence of oxygen. This might explain the presence of this archaeathese archaea only in the mMoss, MS and Bbiofilm samples, which are in contact with the atmosphere.



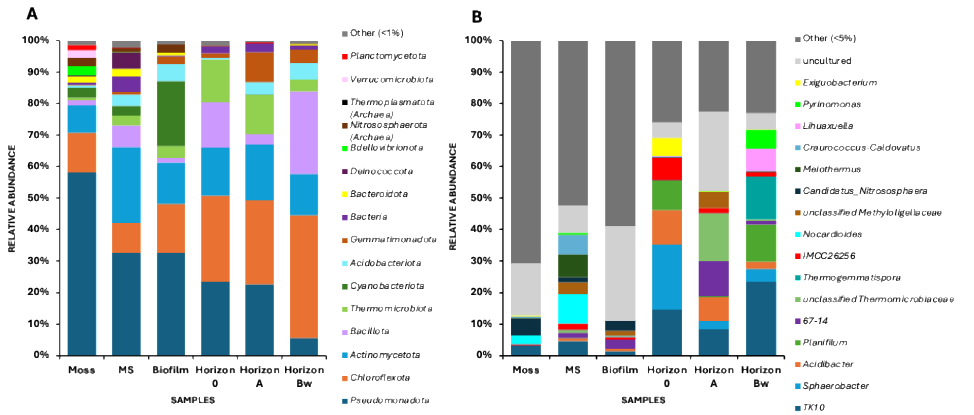


Figure 6: Relative abundances of microbial phyla (A) and genera (B) across different samples collected from ~~moss~~Moss, moss substrate (MS), B~~b~~iofilm, and soil horizons (O, A and Bw) samples.

The bacterial phylum *Pseudomonadota* was found in all samples, with relative abundances decreasing with depth, ranging from 58.1% (~~m~~Moss) to 5.6% (horizon Bw). Members of this phylum included *Acidibacter, the Craurococcus-Caldovatus* bacteria group, and the *Methyloligellaceae* family (Fig. 6B). The acidophilic, ferric iron-reducing, heterotrophic bacterium *Acidibacter,* previously isolated from the Guadiana pit lake, currently has only one described species (Falagán and Johnson, 2014). This bacterium was found in all three horizons, although its abundance decreased with depth, indicating its adaptation to metabolize fresh organic matter, which is more abundant in the Horizon O. The *Caldovatus* genus, a thermophilic bacterium, was found in the MS sample (6.29%). This genus includes only two described species, *C. aquaticus* and *C. sediminis* (Habib et al., 2017; Hu et al., 2022). The *Methyloligellaceae* family is characterised by its ability to use methane as a carbon and energy source, playing a key role in the carbon cycle (Bryukhanov et al., 2024), dominating the Horizon A, MS and B~~b~~iofilm samples.

Other bacterial genera identified greater than 1% of relative abundance were *Aureimonas, Bosea, Hyphomonas, Legionella, Methylorubrum* and *Nordella* in the M~~m~~oss sample; *Candidatus Halysiosphaera, Limnobacter,* and *Chthonobacter* in the MS; *Dongia* in the B~~b~~iofilm; and *Bauldia* in both the B~~b~~iofilm and Horizon A, and *Brevundimonas* in both the ~~m~~Moss and MS samples. Notably, the genus *Bosea*, detected in the ~~m~~Moss sample, is known for its ability to obtain energy through the oxidation of reduced sulfur compounds, a process highly relevant in volcanic environments where sulfur-rich fumaroles, such as those produced during the Tajogaite eruption, have been documented (Martínez-Martínez et al., 2023). Furthermore, this metabolic activity relies on the availability of organic carbon, which was confirmed in all samples through EA/IRMS and Py-GC/MS analyses, highlighting the active coupling between volcanic sulfur emissions and early microbial colonization of the tephra substrate.

The phylum *Chloroflexota* was also present in all samples and was particularly abundant in the O, A and Bw horizons, with relative abundances of 27.23%, 26.77% and 38.92%, respectively. The most abundant members of this phylum were TK10, S085 and KD4-96, present in all samples along with the thermophilic bacteria *Thermogemmatispora* and *Litorilinea*, found predominantly in horizon Bw and the Bbiofilm, respectively. Species of *Thermogemmatispora* are involved in carbon monoxide oxidation in geothermal environments (King and King, 2014). The *Candidatus Chloroploca*, found in the mMoss, is capable of using sulfide oxidation as an electron donor (Gorlenko et al., 2014).

The *Actinomycetota* was the most abundant phylum in the MS sample, with the following genera being particularly prominent: *Nocardioides* (9.33%), IMCC26256 (2.02%), 67-14 (1.64%), *Conexibacter* (1.23%) and *Gaiella* (1.01%). In the Bbiofilm, the *Micronomospora, Actinophytocola,* and 67-14 genera were the most abundant, with a relative abundance of 4.16%, 1.81%, and 2.94%, respectively. In the soil horizons, thermophilic bacteria such as *Thermasporomyces* and *Thermopolyspora* (Horizon O) and *Thermoleophilum* (dominant in the Horizon Bw) were prevalent. Species of the *Thermopolyspora* genus are capable of degrading lignocellulosic compounds (Yang et al., 2022), which aligns with the detection of lignin exclusively in the Horizon O sample by Py-GC/MS. In contrast, members of the genus *Thermoleophilum* can grow exclusively on C_{12}–C_{19} *n*-alkanes, cyclohexane, cycloheptane, C_{12}–C_{18} alcohols and C_{13}–C_{19} ketones (Yakimov et al., 2003), all of which were identified in the soil samples through Py-GC/MS (Table S2).

The *Bacillota* was a dominant phylum in Horizons Bw (26.29%) and 0O (14.28%), as well as in the MS sample (6.90%). The most abundant genera within this phylum in the soil horizon samples were *Brockia, Thermaerobacter, Thermobacillus,* and *Lihuaxuella* (dominant in the Horizon Bw). The *Limnochorda* was found primarily in all three horizons, while *Planifilum*, dominant in Horizons 0O and Bw, plays a key role in the degradation of organic matter and harbors potential antibiotic-resistance genes (Tseng et al., 2024). This genus was also found in the basaltic subsurface of young volcanic islands in Iceland (Bergsten et al., 2022). Non-thermophilic genera of the *Bacillota* phylum, such as *Exiguobacterium* and *Bacillus*, were also identified in all three sample types.

The *Thermomicrobiota* phylum was present in all samples, particularly in horizons 0O (13.63%) and A (12.53%), mainly represented by the *Sphaerobacter* genus, which was found in the three soil horizons, with particularly high dominance in Horizon 0O (20.51%). This bacterium was originally isolated from thermophilically treated sludge, and proteogenomic analysis indicated that it contains numerous aromatic degradation pathways, such as those involved in lignin degradation (D'haeseleer et al., 2013), suggesting its role in the breakdown of complex organic matter. Notably, lignin was detected in the Horizon 0O sample (Fig. 3), while aromatic compounds have been detected in all samples (Fig. 3).

The hyperthermophilic family *Thermomicrobiaceae* was also found, predominantly in horizon A (15.11%), represented by the 67-14 bacterium.

The *Cyanobacteriota* phylum was mainly found in the Bbiofilm (20.64%), MS (3.07%), and mMoss (3.04%) samples. Members of this phylum play a crucial role as nitrogen fixers and contribute significantly to the primary production of organic

compounds (Rippin et al., 2018), as represented by genera such as *Arthronema* and *Nodosilinea*. This is consistent with the detection of nitrogen in the Bbiofilm, MS, and Mmoss samples, and supported by isotope ratios that predicted the presence of photosynthetic microorganisms. *Arthronema* is a filamentous cyanobacterium highly adaptive, typical of extreme desert environments, where it contributes to the nutritional chain and soil formation. Additionally, it exhibits antitumor and antioxidant properties and produces phycobiliproteins (Iliev and Andreeva, 2006; Chaneva et al., 2007; Gardeva et al., 2014; Petrova et al., 2020). Markers of proteins (peptides) were detected by Py-GC/MS in all samples, except MS. Although this technique cannot identify specific proteins, the presence of phycobiliproteins cannot be ruled out.

Other phyla identified in these samples included *Acidobacteriota,* mainly found in the Bbiofilm, MS and the A and Bw horizons; *Gemmatimonadota*, predominantly present in the Bbiofilm and soil horizon samples; and *Deinococcota* and *Bacteroidota,* primarily in the MS sample, represented by *Meiothermus* and *Persicitalea*. The *Deinococcota* phylum is known as one of the most extremophilic phyla of bacteria, due to its resistance to extreme stressors such as oxidation, radiation, desiccation, and high temperature (Vilhelmsson et al., 2023).

In general, the sampling area exhibited a significant presence of thermophilic bacteria, particularly in Horizons O and Bw, and in the Bbiofilm. This abundance is likely related to the proximity of steam-emitting fumaroles near the sampling site. These thermophilic microorganisms, which thrive at elevated temperatures, are highly adapted to the geothermal conditions generated by the fumaroles. Thermophilic genera such as *Thermasporomyces*, *Thermopolyspora*, *Thermobacillus*, *Planifium* and *Pyrinomonas,* were observed in the soil horizons. Notably, the only described species of the genus *Pyrinomonas*, *Pyrinomonas methylaliphatogenes,* was originally isolated from geothermally heated soils associated with fumaroles (Crowe et al., 2014). Members of these genera are recognized for their ability to degrade complex organic materials, such as lignocellulose (Yang et al., 2022), detected in these soil samples, and for their active role in the degradation of organic matter (Tseng et al., 2024). This enzymatic capability is particularly beneficial in volcanic soils, where organic matter turnover is critical for early soil development and nutrient cycling. The dominance of *Thermoleophilum* in the Horizon Bw highlights its ecological role in metabolizing hydrocarbons, such as PAHs, present in all the soil samples analysed. The hyperthermophilic family *Thermomicrobiaceae*, predominantly found in Horizon A, and the genus *Sphaerobacter*, highly abundant in the Horizon O, as well as the thermophilic bacteria *Thermogemmatispora* and *Litorilinea*, predominantly in the deeper soil horizons and the Bbiofilm, further underline the influence of geothermal activity on microbial composition.

The presence of thermophiles across all collected samples, along with their co-occurrence with non-thermophilic genera, suggests an ecological adaptation of the microbial community to thermal disturbances associated with volcanic activity and fumarolic emissions. Furthermore, the relatively lower abundance of thermophiles in horizon A compared to horizons 0O and Bw suggests that thermal events occurred more frequently or with great intensity during the formation of horizons 0O and Bw. The adaptation of thermophiles to high temperatures enables them to dominate during periods of elevated temperatures (e.g., in the presence of fumaroles), while mesophilic counterparts persist and thrive in cooler periods. Temperature and humidity

were continuously monitored at the sampling site using a HOBO sensor over one year. During this period, temperatures generally fluctuated between 20°C and 30°C, with the highest temperature (51.33°C) recorded on August 12 and the lowest (13.76°C) recorded on February 24 (Fig. S1B). The highest temperatures always coincided with the periods of lowest recorded humidity.

3.5 Linkages between biogeochemical data and microbial community composition

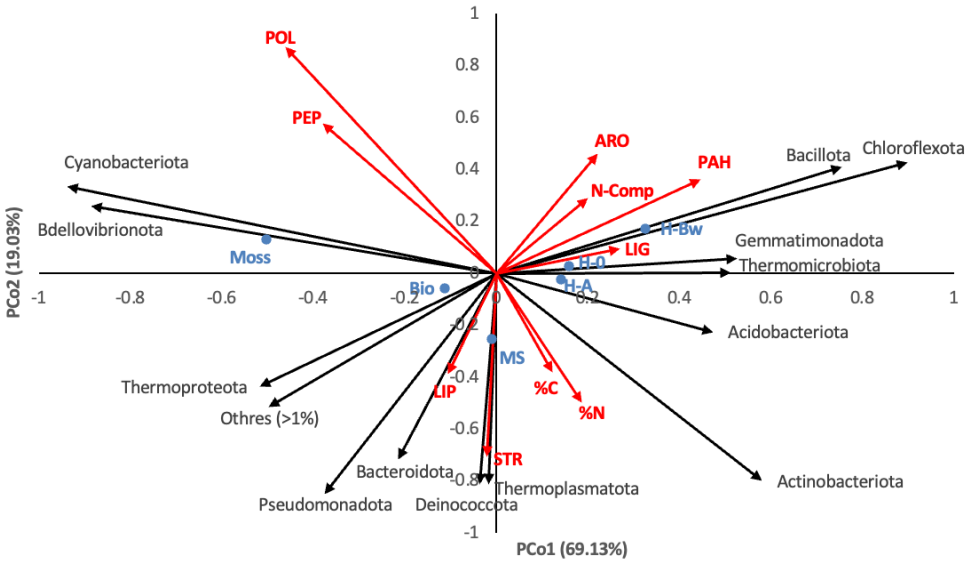


Figure 7. Combined principal coordinates analysis (PCoA) of the samples (blue labels) showing the projected loading weights of geochemical variables (red labels) and the most abundant phyla (black labels).

To synthesize the coupled patterns observed in the molecular (Py-GC/MS), elemental (%C and %N), and 16S rRNA datasets, we explored the ordination space defined by the PCoA biplot (Fig. 7). The first two axes captured over 85% of the multivariate structure (PCo1 = 69.13%; PCo2 = 19.03%), revealing a dominant compositional gradient that separates the surface colonization system (M~~m~~oss–B~~b~~iofilm–moss substrate) from the mineral soil horizons and, within the latter, differentiates the deeper horizon (H-Bw) from the upper layers (H-0 and H-A). PCo1 (69.13%) represents a major change from surface-associated, phototrophy-linked communities and labile biopolymers to soil-horizon assemblages associated with more processed and thermally-influenced organic pools. On the negative side of PCo1, the Moss sample plots together with vectors for *Cyanobacteriota* and *Bdellovibrionota*, consistent with a surface microbiome shaped by primary production and early successional colonizers. *Cyanobacteriota* are most prominent in the B~~b~~iofilm and are also present in Moss and MS, supporting a role for photosynthetic microorganisms as early sources of organic inputs and nitrogen to the developing system (Rippin et

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al., 2018). In the same direction, the biplot loads polysaccharides (POL) and peptides (PEP) toward positive PCo2 but negative/near-zero PCo1, matching the expectation that extracellular polymeric substances and proteinaceous biomarkers contribute strongly to surface/interface organic matter (Palma et al., 2024). This interpretation is aligned with the biofilm chemistry, since the molecular composition of Bb~~b~~iofilm is characterized by abundant lipids and aromatics but also a substantial polysaccharide and peptide fraction (Fig. 3), together with high C and N contents (Table 1). Conversely, the positive side of PCo1 is driven by soil-horizon taxa and organic families that indicate stronger transformation and/or thermal overprinting. The deepest horizon (H-Bw) is displaced toward the vectors of *Chloroflexota* and *Bacillota*, two phyla reported as dominant in the soil horizons (with *Chloroflexota* especially abundant in O, A and Bw, Fig. 6). This association is coherent with the ecological roles, since thermophilic and thermotolerant groups in these horizons are linked to degradation of complex organic substrates and hydrocarbons under geothermal influence near fumarolic activity (King and King, 2014). The same positive-PCo1 space is also aligned with aromatic compounds (ARO), nitrogen-containing compounds (N-Comp) and PAHs, consistent with the Py-GC/MS evidence that condensed aromatics/PAHs are particularly enhanced in the upper mineral horizon (A), reflecting pyrogenic inputs and/or strong thermal processing (Fig. 3). Importantly, several of the taxa discussed in the paper (e.g., *Thermomicrobiota* representatives such as *Sphaerobacter*) are known to encode aromatic degradation pathways, providing a mechanistic link between the enrichment in aromatic/PAH-like pools and the microbial potential for their turnover (D'haeseleer et al., 2013). PCo2 (19.03%) separates biopolymer-rich signatures from lipid/sterane and bulk-elemental signals, helping to distinguish the interface substrates from the more recalcitrant or source-specific pools. Positive PCo2 is dominated by POL and PEP, while negative PCo2 loads toward lipids (LIP) and steranes (STR), together with the elemental %C and %N vectors. In practice, this axis helps explain why Moss (and, to a lesser extent, the biofilm/interface samples) align with carbohydrate/protein-like inputs typical of fresh biomass and extracellular matrices. In contrast, the moss substrate (MS) shifts downward along PCo2, consistent with the strong plant-wax/lipid imprint described for MS (odd-dominated high-molecular-weight *n*-alkanes indicative of direct plant inputs; Fig. 4). Meanwhile, the sterane signal, preferentially preserved/accumulated in deeper horizons due to the stability of plant/fungal sterols and related compounds, supports the interpretation that part of the vertical separation reflects increasing preservation of recalcitrant biomarkers with depth.

The integrated PCoA supports a coherent conceptual model (Fig. 8) for this newly formed tephra–soil system: (i) moss establishment initiates a surface organic subsidy (biopolymers and labile inputs) and introduces/maintains phototrophy-linked taxa; (ii) at the interface, biofilms act as a biochemical and ecological "bridge," concentrating C and N and sustaining a mixed community consistent with rapid microbial assembly, and (iii) in the mineral horizons, particularly under geothermal influence, microbial communities change toward phyla and thermophilic lineages associated with the transformation of lignocellulosic and hydrocarbon pools, matching the observed enrichment in aromatic and PAH-like compounds and the depth-dependent preservation of stable biomarkers.

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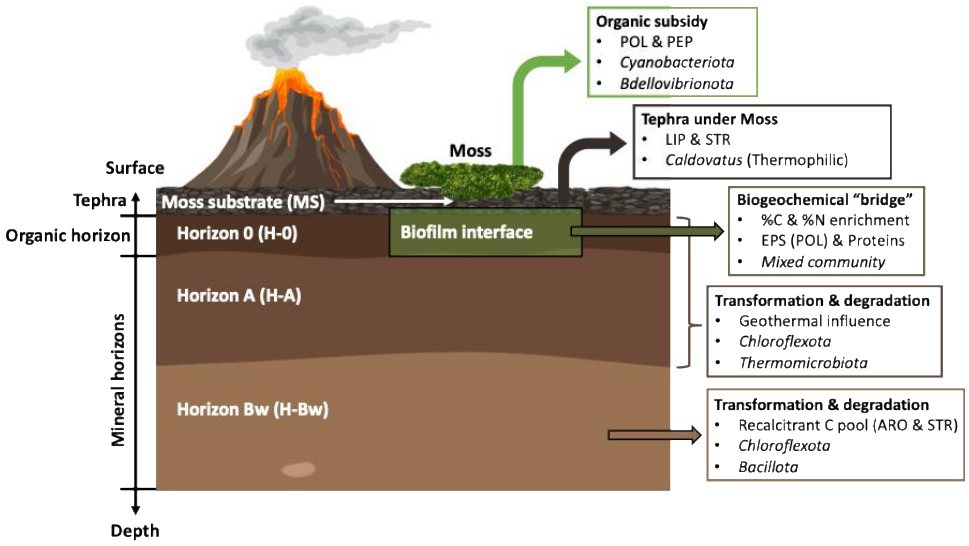

Figure 8. Integrated conceptual model of the tephra–soil system colonized by moss after volcanic deposition.

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4 Conclusions

This study demonstrates that the moss colonizing the upper layer of the tephra deposits releases organic compounds that serve as carbon sources for microorganisms, facilitating rapid microbial colonization of the inert volcanic substrate within two years after the Tajogaite eruption. This eruption produced a complex tephra blanket exceeding 50 cm in thickness, composed of lapilli and fine ash, which accumulated over the pre-existing soil (Horizon O).

Our analyses reveal that Horizon 0~~O~~ exhibits a distinctive hydrocarbon signature, indicative of both high-temperature thermal processes and active microbial transformation of organic matter. In contrast, the deeper soil layers (Horizons A and Bw) display alkane patterns characteristic of plant-derived organic matter inputs. Furthermore, $\delta^{13}C$ isotopic data strongly suggest intense microbial processing of organic carbon in Horizon 0~~O~~, reinforcing the hypothesis that microbial activity significantly contributes to the formation of hydrocarbons in this horizon.

Importantly, microbial sequencing revealed the presence of taxa capable of hydrocarbon metabolism, including the family *Methyloligellaceae*, supporting the hypothesis that some of the detected polycyclic aromatic hydrocarbons (PAHs) could be of biogenic origin.

In addition, our results indicate that the deposition of fresh tephra materials from the Tajogaite Volcano has the potential to alter soil organic matter (SOM) dynamics, favouring the accumulation of labile organic compounds and reducing the abundance of recalcitrant components such as lignin, which are typically more resistant to degradation.

The dominance of thermophilic bacteria, particularly in Horizons 0~~O~~ and Bw, highlights their key ecological role in the breakdown of recalcitrant organic matter, the facilitation of nitrogen and carbon cycling, and the stabilization of the evolving soil structure. Their metabolic versatility, including the ability to degrade lignin-derived compounds and synthesize hydrocarbons, positions thermophiles as critical drivers in the early formation of andisols and the recovery of soils disturbed by volcanic activity.

Finally, the persistent presence of thermophilic microorganisms across the studied profile reflects the influence of volcanic and fumarolic activity in shaping the microbial community structure in the post-eruptive landscape of the Tajogaite Volcano. Given the recurrent volcanic activity on La Palma Island, particularly along the *Cumbre Vieja* Volcanic Ridge, thermophilic communities are likely an enduring and essential component of soil ecosystem dynamics in this region.

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Author contributions

The manuscript was written through the contributions of all authors. All authors have approved the final version of the manuscript. S.G-P: data curation, formal analysis, methodology, visualization, writing−original draft. A.G.A.: data curation, formal analysis, methodology, writing−original draft. P.N-J.: methodology, validation, writing−original draft. J.M.-S.: methodology, validation, writing−review and editing. J.M-M.: methodology, validation, writing−review and editing. B.M-H.: methodology, writing−review and editing. J.V.: methodology, validation, writing−review and editing. N.T.J.-M.: data curation, formal analysis, methodology, visualization, validation, writing−original draft, writing−review and editing. A.Z.M.: data curation, formal analysis, methodology, validation, visualization, supervision, funding acquisition, writing−original draft, writing−review and editing.

Competing interests

The authors declare that they have no conflict of interest.

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