

Review

Mofettes as Models for Basic Research on Soil and Rhizosphere Microbial Communities and Possible Applications of These Extreme Ecosystems

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Abstract: Mofettes or natural CO₂ springs release large amounts of geogenic CO₂ at ambient temperature, leading to long-term soil hypoxia in these extreme ecosystems. Thus, they can serve as natural long-term experiments in ecology and evolution and other environmental studies, providing stable long-term changes in abiotic factors that are most pronounced in mofette soils. This paper reviews basic research on rhizosphere processes, soil microbial communities, and microbial diversity in mofettes, focusing on reports describing the effects of altered soil gas regimes on root respiration and the diversity and community structure of archaea, bacteria, and fungi in soil. Furthermore, an insight into possible applications of mofette ecosystems is given. For more than 20 years, mofettes have provided new insights into the importance of long-term changes in abiotic environmental factors in regulating soil biodiversity, serving as a model for extreme ecosystems. Mofettes provide an innovative approach to the study of many ecological processes that occur slowly and, therefore, require extensive and lengthy observations and experiments, acting as a space-for-time substitution. Previous studies in mofettes around the world have determined plant responses to elevated CO₂ concentrations over multiple generations, described new species of collembolans and yeasts, and identified stable patterns in microbial communities describing specific acidophilic and methanogenic consortia of soil archaea and bacteria, as well as stable communities of plant symbiotic arbuscular mycorrhizal fungi. As the development of high-throughput molecular techniques has accelerated rapidly in the last decade, mofettes now serve more than ever as a natural long-term experimental system to study soil and rhizosphere ecology and contribute to further research on long-term ecological and evolutionary processes that are crucial for understanding past evolutionary events, managing future ecosystems, and predicting ecological responses to global change. Some recent developments target the specific geological and biological characteristics of these extreme ecosystems, including in terms of applications related to environmental impact assessment of carbon capture and storage systems, as well as conservation status, tourism, culture and education, i.e., broader ecosystem services of mofettes, which are addressed in this review together with basic research on soil biodiversity.

Keywords: soil biodiversity; microorganisms; arbuscular mycorrhizal fungi; extreme environments; yeasts; roots; education; nature conservation; ecosystem services; carbon capture and storage



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1. Introduction—Mofette Ecosystems

Natural CO₂ springs or mofettes are extreme ecosystems in which geological CO₂ at ambient temperature reaches the surface, leading to a strong change in soil gas concen-

trations (Figure 1). Terrestrial mofettes are places where CO₂, originating mainly from the deep mantle (>99%), escapes diffusely at ambient temperature, together with traces of other gases such as methane (CH₄), nitrogen (N₂), hydrogen sulfide (H₂S), and noble gases. Geogenic CO₂ displaces O₂ in the pore spaces of the soil, often leading to soil hypoxia or even anoxia. This increasing CO₂ concentration displaces the air in the soil and leads to increased CO₂ concentrations in the overlying atmosphere, which can sometimes reach dangerously high, even lethal, concentrations due to specific topographic features or meteorological conditions that hinder air mixing. Since CO₂ from mofettes is denser than air, it can accumulate in low-lying areas, potentially forming gas lakes with concentrations ranging from 5% to nearly 100%. Mofettes are found in areas of tectonic activity all over the world [1,2]. Natural CO₂ release has been observed in numerous volcanic-hydrothermal systems and rift zones worldwide. Mofettes are often associated with seismic activity and occur in both pre- and post-volcanic regions. In Europe, they are found in Slovenia (Radenci region), Italy (Tuscany and volcanic areas), Germany (Eifel, Rhön, Teutoburger Forest and Northwest Franconia), Czechia (Cheb Basin), Iceland, Romania (Hargitha Mountains), Hungary, and France (Massif Central). Global examples include the caldera of the Yellowstone volcano, the Inyo crater chain, geothermal fields in New Zealand, Japan, Kamchatka, and Indonesia (Djeng Plateau) [2].



Figure 1. Mofette area (natural CO₂ springs)—degassing of CO₂ in groundwater of the Cheb Basin, Czechia. Photo by I. Maček.

First scientific reports about mofette areas appeared in the 1990s. The majority of the mofette publications (over 60% according to the Web of Science—May 2025 survey) are in the field of geosciences, including geophysics and geochemistry, as well as environmental sciences. However, this is followed by papers from the fields of soil science (9% of publications), microbiology (8%), geology, plant sciences, and ecology (each accounting for around 5% of publications). Other fields are represented with a smaller number of papers.

One of the most investigated mofette areas is in Slovenia, where they are found in the north-eastern part of the country, with several mofettes forming the Stavešinci mofette system [3,4]. This is one of the best described mofette areas based on their soil microbiological characteristics. In addition to the well-described gas regime, other soil parameters (e.g., soil chemistry, soil pH) [3,4] and the ecophysiological responses of plants

(e.g., root respiration, photosynthesis) have also been well described in Slovenian and other mofettes (e.g., [1,2,5–9]). As these natural experiments provide valuable information on exposure to certain factors over multiple generations [10], mofettes may serve as models for scenarios with high atmospheric CO₂ levels. This would complement more controlled experimental designs such as free air CO₂ enrichment (FACE) studies [10–12]. Mofette systems also offer new insights into the responses and adaptations of plant roots and microorganisms to long-term changes in the soil abiotic environment, as mofette soils are the most exposed to geogenic gases [8,13–15]. This is now an important research direction driven by the rapid development of new molecular tools that are increasingly being used in microbial soil ecology research, including amplicon sequencing of phylogenetic and functional genetic markers, biotechnological research, and genomics [15,16].

In this review, we provide an overview of the mofette research focusing on soil and rhizosphere ecology over the last 20 years, concentrating in the early years on studies investigating the effects of the altered gas regime in the soil on plant underground responses (e.g., root morphology and root respiration) [8,17] and later on soil microorganisms, their communities, and diversity in Slovenian (e.g., [13–15,18,19]) and other European mofettes (e.g., [20–28]). The final part of this paper also describes the application-oriented use of mofettes, including their potential use in environmental impact assessments (EIAs) for potential carbon capture and storage (CCS) sites [20,25,29] (see Section 4.2), and the recent development of their conservation status and use for local tourism, cultural, and educational activities in Slovenia and Austria, both in line with the targeted conservation of mofette features (e.g., development of local trails and information points, exhibitions, and training of local guides and teachers) (Figure 2).

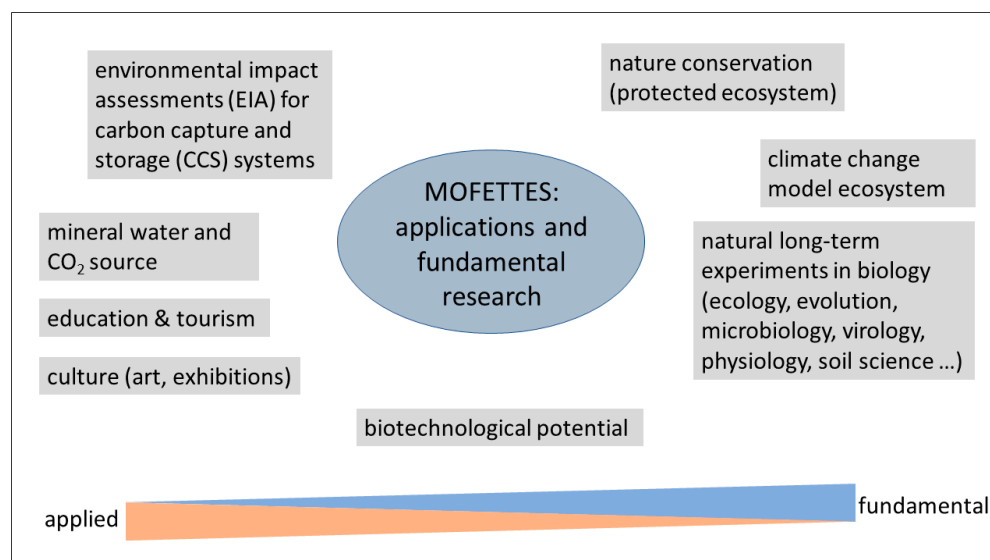


Figure 2. A scale illustrating the potential for basic (fundamental) research (maximum on the right side of the figure) and application (maximum on the left side of the figure) in mofettes.

2. Methods

The paper provides a review of mofette scientific papers on rhizosphere and microbial ecology indexed in the Web of Science and SCOPUS databases. The literature search focused on studies that addressed relevant topics for the review, i.e., the keywords “mofette* AND microb*” and “mofette* AND root*”, with the last search in relevant databases conducted in early May 2025. The PRISMA guidelines were followed when selecting the mofette papers, as shown in Figure 3. After removing 11 records that were not relevant to the topic, with three records being excluded because they did not provide original data on

plant roots (rhizosphere) or microbial ecology, 22 records remained to be included in the review. The included papers date from 2004 to 2024. The 22 included papers formed the set of publications proposed for this review, with some additional references included in the review based on the author's personal choice, directly or indirectly related to the topic of the review and contributing to the explanations of the topic, especially in the introduction, application, and final conclusions and perspectives.

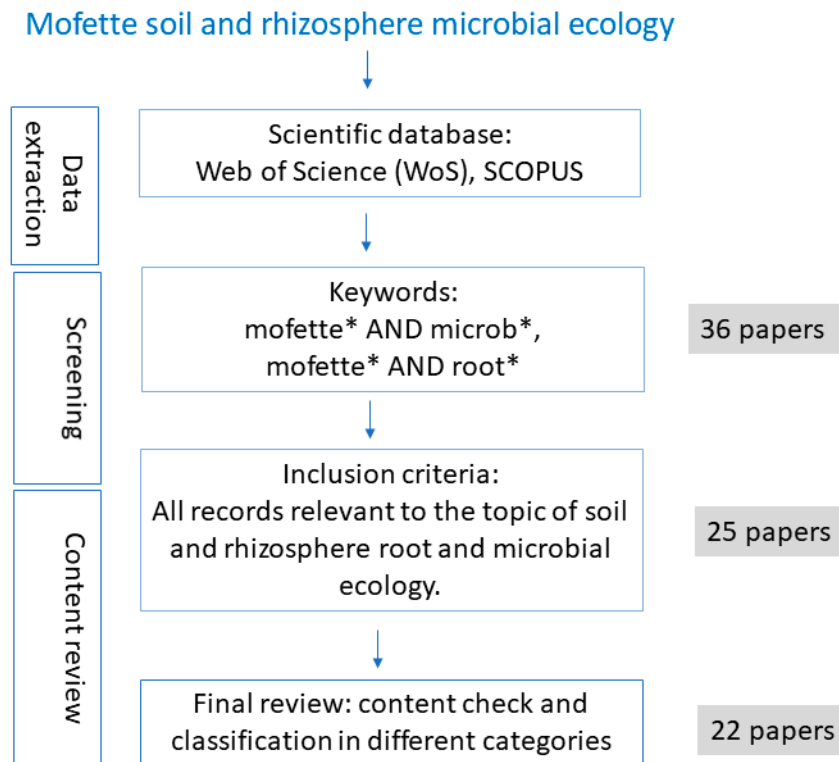


Figure 3. PRISMA flow figure of the literature selection and review process. The literature search focused on studies that addressed relevant topics for the review, i.e., the keywords “mofette* AND microb*” and “mofette* AND root*”.

3. Results—Soil Ecology Studies in Mofettes

Soil biodiversity is essential for the maintenance of soil health and the regulation of soil functions [30,31]. Within the totality of soil organisms, microbes represent the most diverse group, and understanding the mechanisms that control soil microbial community development is critical for predicting the ecological impacts of environmental change [12,15]. Over 60% of the mofette publications (May 2025 records) in the Web of Science are in the field of geosciences, including geophysics and geochemistry, as well as environmental sciences, which makes sense based on their specific geological character. This is followed by papers on soil science (9% of publications), microbiology (8%), geology, plant sciences, and ecology (each accounting for around 5% of the mofette publications), which were included in this review based on the PRISMA principle (Figure 3). Fields such as meteorology, water resources, agronomy, and environmental engineering, each account for less than 3% of the mofette publications, and even fewer in a variety of other fields. In summary, life sciences, including biology, cover around 20% of all mofette records in the Web of Sciences and SCOPUS, including the 22 papers in this review on roots and rhizosphere processes and microbial ecology and diversity.

Mofettes are characterized by a modified gas composition and by hypoxic conditions in the soil, which also results in variations of other abiotic factors in the soil (Figure 4). One notable aspect of this is the altered pH of the soil, which is impacted by the dissolution of

CO₂ in water. Research consistently demonstrates a strong correlation between soil pH and the concentration of CO₂ in the soil [2]. Furthermore, the consistent spatial distribution of pH across seasons and years suggests that mofette soil CO₂ levels are relatively stable [2–4]. In mofettes, the availability of mineral nutrients in soils is influenced by several processes. The absence of eukaryotic organisms and lower microbial activity contribute to a reduction in the decomposition and mineralization of organic matter [2,24,32]. The chemistry of mineral nutrients is also affected by soil pH, hypoxia, and low redox potential, which influence the availability of essential nutrients [32,33]. These factors are abiotic in nature and can be critical and site-dependent, so they must be carefully considered if mofettes are to be used as sites for long-term studies in biology and life sciences [2,14].



Figure 4. Grassland mofettes near Stavešinci, Slovenia. In the middle of the picture, a decrease in plant growth due to high CO₂ content in the soil and hypoxia can be seen. Photo by I. Maček.

3.1. Rhizosphere and Plant Root Function in Mofette Soils

The root system of plants is the main organ affected by geogenic carbon dioxide (CO₂) concentrations, mainly through mechanisms such as soil hypoxia, changes in the availability of mineral nutrients, and changes in pH [2,8]. Therefore, the mofette research in the field of soil biological processes initially focused on plant roots [8,19]. The phenomenon of increased root density in near-surface soil layers observed in mofettes is attributed to the retraction of roots from deeper, hypoxic soil horizons, which is accompanied by increased root growth near the soil surface. Consequently, species with a shallow root system and species with an increased ability to form secondary roots are likely to be more competitive in these systems than their deep-rooted conspecifics.

Aerenchyma is considered a characteristic adaptive trait of plants inhabiting wetland ecosystems; however, it may also develop as a physiological response to environmental stresses such as prolonged flooding, soil hypoxia, or nutrient deficiency. The development of aerenchyma in plant tissues facilitates the maintenance of an elevated partial pressure of rhizosphere molecular oxygen, thus supporting the aerobic respiration processes of root

systems in the presence of elevated concentrations of carbon dioxide (CO₂) in the soil. It is known that the presence of aerenchyma significantly reduces the internal diffusion resistance not only for O₂ and nitrogen gas (N₂), but also for various gases generated by metabolic processes, including CO₂ and ethylene, between the root structures and the aerial parts of the plant. In particular, extensive aerenchyma development has been documented in *Zea mays* grown in the Slovenian Stavešinci mofettes [17]. In addition, changes in the rhizosphere mediated by plants—including vertical O₂ transport and diffusion from root structures—may exert an influence on biotic communities living in hypoxic environments, including soil-associated microbes and endophytic organisms [2,13].

In pronounced hypoxia, root respiration is also subject to modulation. Measurements on several plant species have shown that respiration in roots only decreases significantly when exposed to CO₂ levels that limit the availability of oxygen (O₂) in the rhizosphere, with CO₂ concentrations above 50% causing O₂ saturation in aqueous solutions to fall below 10% [8]. Hypoxia in the soil can further hinder ion absorption by the roots, as aerobic metabolic capacity is limited and there is increased reliance on comparatively less efficient anaerobic metabolic pathways [33]. In plants that are not adapted to such hypoxic conditions, the lack of O₂ can trigger fermentation processes within the root cells, leading to the accumulation of by-products such as lactic acid and ethanol. In contrast to the aerial parts of the plant, which have a cuticle with low gas permeability and regulate gas exchange mainly via the stomata, young roots lack such a protective cuticle. Therefore, elevated CO₂ has a direct effect on root metabolism by causing a decrease in intracellular pH [34]. Both gaseous and dissolved CO₂ can freely move through the rhizodermal layer and apoplastic regions—areas outside the plasma membrane primarily made up of cell walls and intercellular air spaces—facilitating direct uptake into the root cells and tissues. As a result, root cells are acutely affected by elevated soil CO₂ concentrations, such as those prevalent in mofette areas, which can lead to acidification of the cytoplasm. If the CO₂ concentrations reach threshold values at which the pH decrease can no longer be buffered by intracellular homeostatic mechanisms, the metabolic processes in the roots can be impaired [35]. Analogous physiological reactions to high CO₂ concentrations can also be expected in the soil meso- and microfauna (see the reviews in [2,16]) as well as in the soil microbial communities (see the following sections).

Furthermore, mineral nutrient uptake into plant roots may also be limited by additional factors prevalent in environments with elevated CO₂ concentrations, such as reduced stomatal conductance, decreased transpiration rates, and a reduction in xylem sap flow rates, all of which can negatively impact ion transport to the aerial parts of the plant [33,36]. In plants exposed to geological CO₂, the concentration of mineral nutrients is consistently reduced, as shown by the reduction in nitrogen (N), sulphur (S), phosphorus (P), potassium (K), and zinc (Zn) content in the leaves of *Phleum pratense* from the Stavešinci mofette [9] (Figure 4).

In summary, although elevated CO₂ does probably not exert a direct selection pressure that induces an evolutionary response in plant species, plants that thrive in mofette environments must acclimate to hypoxic conditions through a number of morphological and structural traits that facilitate their growth and survival under these extreme gas conditions. Those are traits that promote aerobic respiration in root tissues, mitigate problems related to the availability of mineral nutrients, and prevent the occurrence of anoxic conditions and cytoplasmic acidification.

3.2. Microbial Diversity in Mofette Soils

The concentration of oxygen in soil and its pH levels are critical factors influencing the composition of microbial communities [14]. Soils with elevated levels of carbon dioxide

typically host anaerobic and acidophilic microbes, notably exhibiting a significant rise in strictly anaerobic methanogenic archaea [14,24] (Figure 5). This phenomenon has significant consequences for the production of biogenic methane, carbon dioxide fixation, and the overall functioning of ecosystems [14,19]. Research indicates that geological CO₂ serves as a vital microbial carbon source in mofette regions. High levels of geological CO₂ have been found to enhance the fixation of carbon dioxide in the absence of light by prokaryotic organisms that utilize it, which also play a role in the unique decomposition of soil organic matter in mofette environments.



Figure 5. Schematic representation of the effects of CO₂ degassing in mofettes on selected abiotic and biotic factors. The gradients of the different factors are indicated by the thickness of the shapes. A thicker shape indicates a higher value of the specific parameter near the center of the mofette (e.g., CO₂ concentration), while a thinner shape indicates the opposite (e.g., O₂ concentration).

Mofette ecosystems serve as good models for studying the principles of microbial community ecology and provide a framework for investigating open questions regarding soil microbial community responses to prolonged disturbance, community stability, and community composition [2,16]. Moreover, investigating the fluctuations of various microbial groups, ranging from prokaryotic organisms to fungi, as they react to ongoing disturbances and stresses is essential for understanding the consequences of human-induced factors such as climate change, nutrient enrichment, land use alterations, and pollution. Cutting-edge molecular techniques, combined with artificial intelligence, enhance the analysis of microbial communities and their spatial and temporal dynamics, allowing scientists to tackle open queries regarding environmental influences and microbial reactions to global change factors [2,16].

In terms of application, sites naturally exposed to extremely high CO₂ concentrations could represent an untapped source of microorganisms with unique abilities to catalytically convert CO₂ into valuable organic chemicals and fuels [24]. Therefore, mofettes have biotechnological potential that makes them a potential site for bioprospecting organisms of importance to biotechnology and even the energy sector and medicine [2,16,24], originating from a range of different phylogenetic groups.

3.2.1. Archaea and Bacteria

The soil diversity of prokaryotes (archaea and bacteria) is high, but their responses to environmental factors that regulate their community assembly are still largely enigmatic.

The results of several studies in Slovenian (e.g., [13–15,18,19]) and other European mofettes (e.g., [20–24,27–29]) have shown that there are diverse mofette microbial communities in soils, with soil pH and oxygen content being the most important factors causing changes in the structure of mofette microbial communities as well as reductions in their species richness [14]. Soils exposed to elevated CO₂ concentrations are typically enriched with anaerobes and acidophiles, characterized by an increase in methanogenic archaea in soils exposed to high CO₂ concentrations [14,24] (Figure 5). These results have important implications for enhanced microbial methane production, carbon dioxide fixation, and overall functionality of this specific ecosystem [14,19,24]. The observation of mofette prokaryotes offers the potential for predictive modeling of the assembly of characteristic microbial mofette communities over different time periods, suggesting temporal stability that could extend to other organisms and other extreme habitats, including eukaryotes such as fungi [13,15] and extreme human-influenced environments.

3.2.2. Fungi

Most studies on fungal communities in mofettes have focused on the symbiotic arbuscular mycorrhizal (AM) fungi [13,15], which belong to the Glomeromycota group [37,38]. Even in extreme habitats such as the Stavešinci mofettes in Slovenia, AM fungi are consistently found in the roots of various plant species [13,15]. These fungi are key and widespread soil organisms that form arbuscular mycorrhizal symbiosis with over two-thirds of all vascular plant species, including agriculturally important crops and trees [39] (Figure 6). The benefits resulting from this symbiotic relationship, such as improved nutrient and water uptake and defense against pathogens, depend on the specific interactions between AM fungi and their host plants [40–43]. AM fungi are obligate biotrophs that feed exclusively on carbon assimilated by plants. Changes in the relative abundance of AM fungal taxa can significantly influence the dynamics of plant communities and thus the composition of plant species in an ecosystem [44]. A numerical dominance of certain AM fungal taxa has been observed in hypoxic mofette substrates, emphasizing the significant influence of environmental parameters on the composition and stability of AM fungal communities [13,15]. A consistent response of AM fungal communities to persistent stress conditions was demonstrated, suggesting that these communities exhibit reduced diversity and variability over time in environments with high geological CO₂ exposure compared to control environments. Furthermore, for the first time, a collection of AM fungal taxa has been identified that are consistently observed across wide geographical distances in several European mofette ecosystems, with some of them also occurring in ecosystems that are significantly impacted by anthropogenic activities [15]. However, how AM fungi adapt to the low-oxygen conditions in mofette regions and whether these symbiotic relationships provide benefits to host plants in hypoxic environments remains to be elucidated [15]. This knowledge gap is partly due to the unsuccessful attempts to isolate AM fungi from mofettes using culture techniques.

Another diverse group of fungi studied in Slovenian mofettes is yeasts. Yeasts are widespread and can colonize both terrestrial and aquatic ecosystems. Their ecological importance is particularly pronounced in soils, where they are crucial in the mineralization of soil organic matter (SOM), the assimilation of carbohydrates from plants, and general nutrient cycling [45,46]. A comprehensive study of yeast diversity associated with natural CO₂ springs in northeastern Slovenia was conducted by Šibanc et al. in 2018 [18]. The inventory of cultivable yeasts inhabiting terrestrial soils and aquatic environments, especially aquatic mofettes, revealed a total of 142 isolated and identified strains originating from habitats strongly influenced by geological CO₂ exposure, including a meadow, stream water, and a forest pond. These strains were categorized into six genera within the Basid-

iomycetes with six species and eleven genera within the Ascomycetes with a total of 18 species [18]. In Slovenian mofettes, the highest observed species richness of ascomycete yeasts (15 species) was found in the aqueous environment of forest mofettes (especially in a pond with visible CO₂ bubble formation) [18]. Of the yeasts isolated, all Ascomycetes representatives showed the ability to grow and ferment glucose under conditions of high CO₂ concentrations. The only exception was *Debaryomyces hansenii*. Interestingly, four strains categorized as unidentified basidiomycete species were successfully isolated by high dilution smears of soil samples from Stavešinci mofettes and subsequently described as a new species *Occultifur mephitis* f.a., sp. nov. [18]. The new yeast species was given the name *Mephitis*, derived from the Latin term (*me.phiētis*. L. fem. gen. n. *mephitis*), which refers to a Roman goddess associated with gases emitted from the soil.

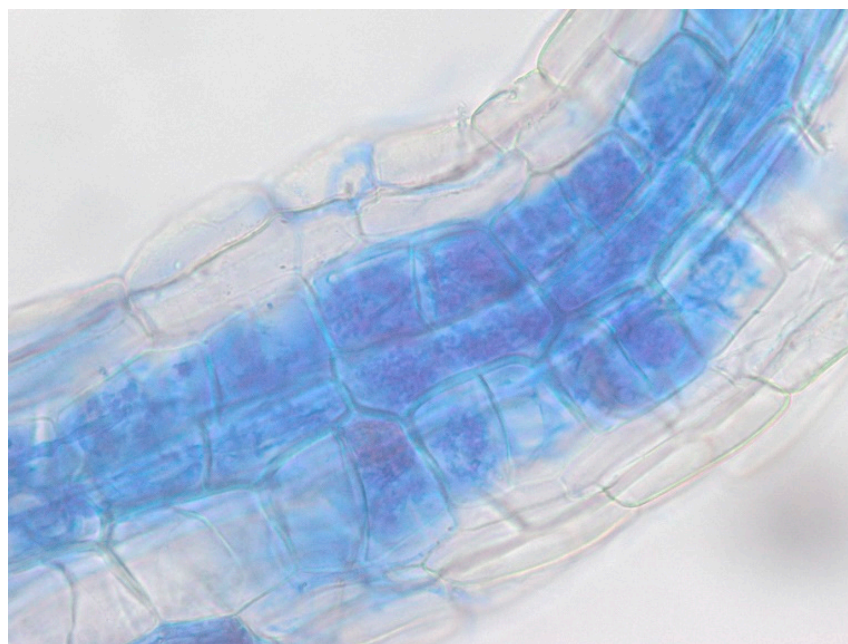


Figure 6. Symbiotic arbuscular mycorrhizal (AM) fungi in trypan blue-stained roots of *Plantago lanceolata* L. The blue structures indicate fungal hyphae and arbuscules in the cells of the root cortex, which serve the nutrient exchange between AM fungi and the plant (magnification 400×). Photo by I. Maček.

3.2.3. Microalgae

The microalgae primary production in terrestrial soil ecosystems remains poorly characterized; however, it is noteworthy that microalgae are recognized as common eukaryotic organisms in mofettes [47]. Due to their considerable population sizes and rapid generation times, microalgae serve as exemplary models for the study of adaptive mechanisms and evolutionary processes in photosynthetic organisms. Microbial autotrophs, which include microalgae, likely benefit from the elevated CO₂ concentrations typically found in mofettes, which presumably enable increased photosynthetic activity and accelerated growth rates. Analogous to the responses observed in land plants, microalgae are likely to undergo acclimatization and adaptation processes in response to these high CO₂ concentrations. Nevertheless, current evidence suggests that microalgal populations in mofettes do not exhibit specific adaptations to high CO₂ conditions, although there are certain strains that show suboptimal growth performance at normal CO₂ levels [48]. This lack of apparent adaptation could be due to overwhelming gene flow from the environment that may overshadow localized adaptive mechanisms. Furthermore, the prospect of evolutionary adaptation among microalgae in response to elevated CO₂ concentrations seems unlikely,

influenced by factors such as heterogeneity in space and time and the possible absence of evolutionary costs associated with the genetic ability to thrive under low CO₂ conditions when simultaneously exposed to high CO₂ levels [49].

3.2.4. Viruses

The recent emergence of pandemics has drawn attention to another form of life, even in environments previously considered unexplored, such as mofettes. In wetland ecosystems, which are also characterized by mofette-like hypoxic conditions, more than one billion viruses per gram could be present in the soil [50]. As of now, viruses constitute a largely uncharted category within mofettes and necessitate additional investigation by the scientific community.

4. Potential Applications

Mofettes have been used as a research environment for the study of a variety of organisms. These studies include microorganisms such as archaea and bacteria (e.g., [14,20–22,24–28]), fungi such as arbuscular mycorrhizal fungi [13,15], yeasts [18], microalgae [47–49] and larger organisms, plants [1,8–10,51], and animals such as spring-tails, nematodes [52,53], and spiders [54]. The different groups show different responses to the diverse abiotic influences in mofette ecosystems [2,16].

Despite significant advances in the ecology of mofettes, further studies are needed to investigate the research hypotheses that the mofette research can address as natural, long-term experimental platforms to study natural phenomena [2,16]. These investigations include the ecological vertical and horizontal interactions (networks) within these ecosystems, including the dynamics that determine taxa abundance within communities, vertical interactions (food webs) (Figure 5), and additional non-trophic interactions between different organisms (ecological networks). However, mofettes also have important potential for more applied research areas such as biotechnology, model systems for CO₂ enrichment, environmental impact assessment (EIAs), conservation, education, and culture (Figure 2).

4.1. Mofette Biotechnological Potential and CO₂ Enrichment Model Systems

Extreme environments can also serve as an unexplored reservoir of microbes with biotechnological significance that have unique abilities to catalyze the conversion of carbon dioxide into organic compounds and fuels of high value and can also be used for other biotechnological applications, e.g., for medicines [2,18,24]. The possibilities presented by native species that have adapted to the unique conditions of mofettes remain mostly uninvestigated, along with the influence of transgenerational plasticity and adaptation in the multigenerational reactions of diverse groups of organisms.

Future studies should also address marginal mofette regions where soil CO₂ levels are not primarily responsible for changes in biological processes, but atmospheric CO₂ levels remain higher than ambient conditions [16]. In such scenarios, mofettes could potentially fulfil their original role as models for scenarios of elevated CO₂ over several generations if sited wisely, complementing FACE (Free Air CO₂ Enrichment) experiments [2,10,16]. This investigation might include both current situations of high atmospheric CO₂ levels and past eras when increased atmospheric CO₂ acted as a driving force for evolutionary changes that influence today's biological diversity.

4.2. Mofettes as Model Ecosystems for Carbon Capture and Storage Assessments

In practical terms, contemporary studies of mofettes have predominantly turned their attention to the development of carbon capture and storage (CCS) technologies [20,25,26]. Mofette sites offer valuable natural ecosystems that can be utilized for environmental impact assessments (EIAs) concerning gas emissions from subterranean carbon storage (see

Figures 1, 2 and 4). CCS involves the process of capturing carbon dioxide (CO₂) emitted from major industrial sources and sequestering it in underground geological formations. This approach is considered one of several possible strategies to limit the increase of CO₂ concentration in the atmosphere worldwide and thus contribute to the mitigation of anthropogenic climate change. Mofettes and other naturally occurring CO₂ reservoirs offer valuable opportunities to study the behavior of CO₂ during and after the storage process. They also facilitate the development and calibration of monitoring techniques to detect leakage phenomena [55–57]. A major benefit of these natural analogues of carbon capture and storage is the extended time frame—often extending to geological time scales—over which CO₂ accumulation and release take place at these locations. The factors monitored at these sites include soil CO₂ levels, rates of soil CO₂ emissions, and a range of physical and chemical soil characteristics influenced by increased CO₂ concentrations, such as pH levels and redox potential. Biological assessment methods include plant community surveys, bacterial community assessments, and molecular techniques based on DNA/RNA analyses, which have previously been employed to describe microbial communities and functional characteristics that may be altered due to CO₂ leaks [28]. Developments in research into the potential environmental impacts of leakage from geological storage of CO₂ since the publication of the IPCC Special Report on Carbon Dioxide Capture and Storage in 2005 have already been reviewed before, including the use of natural systems such as mofettes for this purpose [55,56], as well as controlled CO₂ leakage experiments [57]. As most of the biological studies in mofettes were conducted after the IPCC report on the potential use of mofettes to inform CCS schemes, these studies include conclusions reported in earlier sections of this review (see Section 4). Each of the research mofette sites (e.g., Latera in Italy (e.g., [23]), Larcher See in Germany (e.g., [20–22]), or Stavešinci mofette in Slovenia (e.g., [6–8,13–15])) has provided considerable information on the effects of elevated CO₂ soil gas concentrations and CO₂ surface flux rates on a range of parameters, including botany and soil microbiology, under different European climate conditions [56].

4.3. Nature Conservation, Tourism, Culture and Education

Recently, a trans-regional initiative has developed that involves mofettes and places with mineral water springs in Slovenia and Austria in a joint project that combines different roles from nature conservation, tourism, culture, and education, with the main aim of reducing damage to this valuable ecosystem by accidental visitors. As part of this project, local hiking trails with information points are planned, as well as the training of local guides and teachers to acquire skills for this purpose. The result is an interdisciplinary concept that combines basic and applied knowledge of these interesting and valuable ecosystems in their potential for cultural ecosystem services.

5. Conclusions and Prospects

In recent years, only a few original studies have focused on the biological characteristics of mofettes. However, recent reports have focused on topics that indicate the direction in which mofette-related research is moving in the life sciences. For example, the physiology of fungi under altered atmosphere (the effects of CO₂ stress) was studied in detail with the description of new yeast species in [58], using our earlier work on mofette yeasts with the description of new yeast species from Slovenian mofettes as a source of information. In addition, our recent report on the characteristics of arbuscular mycorrhizal (AM) fungal communities and diversity revealed stable mofette AM fungal communities with specific stress-tolerant AM fungal genotypes consistently present at Slovenian and other European mofette sites [15]. The mofette AM fungal communities are less diverse and dominated by stress-tolerant taxa (Figure 5). These taxa are rare at control sites and in

other environments worldwide but show a stable temporal pattern at the extreme mofette sites and consistently dominate their communities. Extremophilic fungi have also been studied in other environments, including those that survive at high temperatures (thermophilic fungi) [59], in coastal sand dunes [60], and in other extreme environments [61–64], indicating common characteristics of these fungal communities with those from Slovenian and other European mofette sites. This confirms our results and suggests that the response of soil microbial communities to long-term stress is relatively predictable, which may also reflect the response of communities to other anthropogenic stressors (e.g., heavy metal pollution or land use change). In several studies on soil and rhizosphere hypoxia due to waterlogging together with other stressors, the mofette research has been used as a model for hypoxic systems, also with regard to their effects on AM fungal communities [61–64]. In addition, specific mofette communities and potential new taxa have been studied and characterized, not only for microorganisms (see Section 3.2), but also for soil macroorganisms such as soil arthropods, with the aim of identifying resistant taxa that can serve as bioindicators to assess soil ecotoxicity [65]. The study showed that the composition and diversity of arthropod communities in highly acidic mofette soils (Mefite Geological Site in Italy) are effective soil bioindicators reflecting soil ecotoxicity. All these studies show that biological research in mofettes can serve as a stimulus and data source for studies in other environments with a wide range of long-term disturbances and stresses. Key potential areas for future basic and applied mofette research include the exploration of past and future climate change scenarios (a comparison of experiments with elevated CO₂ in mofettes and FACE was reviewed in [10]), soil virology, the exploration of mofette-specific taxa and their traits, from micro- to macroorganisms, including their biotechnological potential, community ecology, and vertical and horizontal ecological interactions in mofette-specific food webs and ecological networks.

Much has been done in the last 20 years of intensive research and other activities in the mofette areas, but there is still room for more, including the application and development of new technologies in biotechnology, molecular ecology, and data analysis, as well as machine learning and artificial intelligence (e.g., research on ecological networks of mofettes is still awaiting attention from the scientific community). Not to forget that mofettes have been proposed as a source of information on the long-term effects of carbon capture and storage systems in the case of leakage of CO₂ into the soil. Field experiments on CO₂ release have also been conducted for this purpose, but they do not provide long-term impact assessments that natural extreme experiments such as mofettes can offer.

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