



## Lichens and soil: A living interface shaping terrestrial ecosystems

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**Abstract.** This review explores the critical role of lichens at the intersection of rock, air, and soil, highlighting their active participation in soil formation, nutrient cycling, and microbial diversity across various ecosystems. Lichens are identified as pioneering colonizers of newly exposed substrates, driving bioweathering and aiding in soil genesis. We discuss the importance of biological soil crusts (biocrusts), emphasizing their contributions to soil stability, nutrient retention, and interactions with vascular plants. Additionally, we examine recent findings related to nutrient cycling, microbial diversity, and the implications for climate change and ecological restoration.

**Key Words:** biological soil crusts, climate change, ecological restoration, lichens, microbial diversity, nutrient cycling, soil formation.

**Purpose of the Study.** The primary aim of this paper is to synthesize contemporary research that details the multifaceted roles of lichens in terrestrial ecosystems. By addressing their contributions to soil formation and nutrient dynamics, the study seeks to enhance understanding of their ecological significance and inform conservation strategies.

**Lichens and Soil. A Living Interface Shaping Terrestrial Ecosystems.** Lichens occupy a unique position at the boundary between rock, air and soil, and contemporary research increasingly shows that this interface is anything but passive. From polar deserts and tropical dry forests to agricultural fields and cities, lichens and lichen rich biological soil crusts (biocrusts) are emerging as key engineers of soil formation, nutrient cycling, and microbial diversity across the planet (Weber et al 2016; Bowker et al 2018).

**Lichens as Architects of the Youngest Soils.** On newly exposed rock or glacial deposits, lichens are among the first colonizers. Their hyphae and photobionts penetrate microfractures, secrete organic acids, and trap dust, initiating bioweathering and the first stages of true soil formation. A palaeogenomic reconstruction of postglacial landscapes over the last 23000 years shows that lichens and other early colonizers dominated bioweathering in late glacial stages, especially on basaltic substrates, before giving way to mycorrhizal fungi and more complex nitrogen cycling in the Holocene. This work links lichen facilitated weathering directly to long term trajectories of soil development and podzolization, including acidification and iron mobilization associated with forest

expansion. Such findings are important for current discussions about enhanced rock weathering as a carbon capture strategy, because they show that cryptogamic communities, and lichens in particular, have already been driving mineral dissolution and nutrient release on geological timescales.

In gypsum ecosystems (harsh, ion rich substrates often considered marginal) lichens are not exceptions but dominant soil surface organisms. A recent global dataset compiled more than 6000 records of gypsum associated lichens, representing 336 species across 26 countries, and confirmed that lichens are central components of the biological soil crusts in these soils. Families such as Teloschistaceae, Verrucariaceae and Cladoniaceae are especially well represented, with species like *Psora decipiens* and *Squamarina lentigera* occurring widely. These communities contribute to water retention, nutrient cycling and protection against erosion on substrates that would otherwise be extremely unstable (Delgado-Baquerizo et al 2015).

**Biocrusts. The “Living Skin” Connecting Lichens and Soil.** Many of the most consequential interactions between lichens and soil occur within biocrusts, thin but highly structured communities that can cover ~12% of the Earth’s land surface, especially in water and cold limited environments (Bowker et al 2018). Biocrusts, composed of cyanobacteria, algae, lichens, bryophytes and associated microbes, form a cohesive matrix at the soil surface. This “living skin” stabilizes loose particles, reduces erosion, and alters hydrology and energy balance by changing infiltration, albedo and surface roughness (Weber et al 2016; Chamizo et al 2017; Bowker et al 2018).

Nutrient cycling is one of their defining functions. Reviews and experimental studies show that biocrusts build or modify soil nutrient stocks through nitrogen fixation, dust trapping, organic matter inputs and enzyme mediated mineralization (Liu et al 2017; Bowker et al 2018; Torres-Cruz et al 2018; Moreira-Grez et al 2019; Duan et al 2024). In the Arctic drylands of West Greenland, lichen rich biocrusts dominated by the nitrogen fixing lichen *Stereocaulon* gradually accumulate carbon and nitrogen in their underlying soils over ~180 years, even though soil nutrient levels remain lower than in adjacent vegetated tundra. Here, biocrusts both stabilize erodible surfaces and act as persistent, patch forming features that maintain spatial heterogeneity of soil nutrients and vegetation.

A meta perspective from Chinese drylands synthesizes how biocrusts regulate soil nitrogen, phosphorus and organic matter, with implications for regional and global carbon cycles. Biocrust lichens contribute fixed nitrogen (directly or via associated cyanobacteria), increase soil organic carbon, and promote the formation of finely aggregated, carbon rich surface layers that interact strongly with dust and atmospheric inputs (Duan et al 2024). These functions are now being explicitly considered in efforts to quantify the carbon sequestration potential of cryptogamic covers at large scales (Weber et al 2016; Bowker et al 2018).

**Nutrient Cycling. From Phosphorus and Nitrogen to Multifunctionality.** Beyond broad conceptual roles, more recent experiments allow a mechanistic view of how lichen rich crusts modulate specific nutrients. A multi-year microcosm experiment in Mediterranean drylands examined six biocrust forming lichen species under simulated warming and rainfall reduction. Soils beneath lichen thalli had higher inorganic and total available phosphorus and greater acid phosphatase activity than bare soils, although the magnitude of these effects varied strongly among lichen species. Climate manipulation increased available organic P independently of lichen identity, but the lichens clearly amplified the pool of readily accessible P, indicating that they can buffer or modify climate impacts on P cycling at the soil surface. This species specific control implies that changes in lichen community composition under climate change, not just total crust cover, will alter soil fertility trajectories (Concostrina-Zubiri et al 2020, 2022).

Nutrient release does not only occur in living thalli. A microcosm decomposition study compared litter of a common biocrust lichen, *Cladonia foliacea*, with that of a moss, *Syntrichia caninervis*, and showed that both contributed substantially to soil organic carbon, dissolved organic nitrogen, ammonium and phosphatase activity during

decomposition. *Cladonia* decomposed steadily over almost a year, whereas *Syntrichia* lost most of its mass within two months and then stabilized, leading to different temporal patterns of nutrient input. Overall, biocrust litter increased soil C and N pools and enzymatic activity, confirming that the decay of crust components is a crucial, previously under appreciated pathway linking lichens to soil nutrient cycling in drylands (Weber et al 2016; Bowker et al 2018).

At a broader functional level, a metagenomic study of biocrust succession in the Mu Us Desert (northern China) compared algal, lichen and moss dominated crusts and their underlying soils. Soil multifunctionality, an integrated index of ten C, N and P cycling attributes, was highest under moss crusts, intermediate under lichen crusts and lowest under algal crusts. Intriguingly, lichen crusts showed the greatest taxonomic diversity and network complexity, but soil multifunctionality correlated more strongly with the diversity of functional genes, especially those related to nitrogen cycling and carbon degradation, and with microbial network density than with pure taxonomic richness. These findings highlight that lichens influence soil processes not just by their presence or species number, but by shaping the structure and functional potential of microbial consortia within and beneath the crust (Liu et al 2017; Duan et al 2024; Jiang et al 2025).

**Soil Microbial Diversity. Lichens as Micro Islands and Reservoirs.** Modern sequencing approaches reveal that lichens themselves act as micro ecosystems hosting distinct and often highly specialized bacterial and fungal communities. A landscape scale study of four *Peltigera* cyanolichens across Patagonia sampled the lichen thalli, their substrates, and surrounding soils across multiple bioclimatic zones. Bacterial communities within thalli were less diverse but more phylogenetically convergent and deterministically assembled than those in soil or substrate, with host phylogeny, especially of the cyanobacterial partner, and climate acting as strong ecological filters. In contrast, nearby soils harbored more diverse and less tightly filtered bacterial communities. The authors argue that *Peltigera* thalli function as island like habitats that foster specialized, locally adapted bacteria, thereby increasing landscape level (gamma) diversity (Schwob et al 2024).

A global survey of topsoils from 235 ecosystems identified 880 phylotypes of lichenized fungi in soil communities, with their diversity and relative abundance peaking in shrublands and dry grasslands. Environmental filters such as aridity, plant cover and soil pH were the main drivers of the distribution of these lichenized soil fungi, and dominant genera like *Endocarpon* and *Verrucaria* showed similar environmental preferences. These data demonstrate that the influence of lichens on soil biota is not restricted to the visible thalli: their mycobionts, propagules and fragments contribute a phylogenetically and functionally distinct fungal component to soil communities worldwide, particularly in drylands (Bowker et al 2018).

Similar habitat filtering is observed in extreme environments. In the High Arctic, high throughput sequencing across nine habitat types, including soil, lichens, moss, vascular plants, waters, sediments and dung revealed strong habitat specificity in fungal assemblages. Lichenized fungi formed a distinct guild whose composition differed markedly from that in bulk soil and other substrates, underlining the role of lichen–soil interfaces in structuring polar mycobiomes (Stoppiello et al 2025).

Even at the scale of individual monuments, lichens influence soil like microbial matrices. On the Leshan Giant Buddha, an iconic stone statue in China, soils accumulating on rock surfaces covered by successional stages from lichens to bryophytes and vascular plants showed increasing total organic carbon, nitrogen and phosphorus, with marked shifts in bacterial and fungal community composition. Lichen covered rock had significantly lower C, N and P than sites covered by ferns, grasses or shrubs, and cyanobacteria were relatively more abundant under lichens than under later successional covers. This system illustrates at fine scale how lichens initiate biogenic soil development on bare rock and set trajectories for later plant–microbe interactions (Moreira-Grez et al 2019).

**Lichens, Soil and Plants: Recruitment, Filters and Restoration.** By modifying surface roughness, porosity, moisture and nutrient distribution, lichen rich biocrusts also influence plant establishment, acting as both facilitators and filters for vascular plant recruitment, with important implications for dryland restoration and management (Bowker et al 2018; Antoninka et al 2020; Corbin & Thiet 2020; Gufwan et al 2025; Le et al 2025; Ramsey et al 2025).

**Conclusions.** Lichens serve as pivotal agents in shaping terrestrial ecosystems through their influence on soil formation and stability. Their unique functionalities as components of biocrusts facilitate nutrient cycling and support microbial diversity. As climate pressures escalate, understanding the role of lichens becomes increasingly essential, particularly regarding their potential in carbon sequestration and ecological restoration efforts. Continued research will be crucial to fully elucidate their contributions and to leverage their ecological functions for sustainable land management practices. This review underscores the need for a holistic approach to studying lichens, as their intricate interactions within ecosystems are foundational to maintaining biodiversity and ecosystem resilience.

**Conflict of Interest.** The authors declare that there is no conflict of interest.

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