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Ecology of Biological Soil Crusts and Associated Microorganisms

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Abstract

Biological soil crusts (BSCs) develop when surface soil particles are consolidated by microorganisms into stable surface crusts. BSC microorganisms include viruses, non-symbiotic and lichenized fungi, archaea, bacteria, cyanobacteria, terrestrial microalgae, and tiny mosses. Most early research concluded that BSCs were limited to arid areas or deserts, not because of their absence elsewhere, but because they were most visibly conspicuous there. BSC habitats were historically referred to as *glades*, *barrens*, and *balds* in the USA, and as *inselbergs*, *alvars*, and *the Burren* in Europe. Although still most evident in deserts, BSCs have been observed in most ecosystems worldwide. In mesic climes, BSCs occur where physical perturbation, fire, or some other form of disturbance has removed or significantly reduced the vascular plant overstory. Microorganisms that create BSCs are tiny, lightweight, and easily attached to windborne dust particles. They regularly fall to Earth from the upper atmosphere and outer space. In addition to the soil, BSC microorganisms are present on most exposed surfaces, including plants, animals, rocks, buildings, vehicles, gravestones, ice, snow, water, etc. BSC microorganisms have been recorded in aerial, edaphic, and aquatic environments worldwide. When inhaled by humans or other animals, they become components of the respiratory microbiome. BSCs are thought to be negatively affected by global warming, although many studies have revealed their persistence for millions of years through multiple cycles of global warming and cooling. BSC microorganisms protect Earth from the potential negative effects of global warming by sequestering atmospheric carbon dioxide into organic matter.

Keywords

Glades, Barrens, Balds, Alvars, Inselbergs, The Burren, Stone Varnish, Global

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Warming

1. Introduction

There are three primary types of soil surface crusts: physical, chemical, and biological [1]. The crusts limit the passage of air and water between underlying soil layers. Physical soil crusts form when soil particles at the soil surface are sorted and reorganized by wind and/or water into a thin layer that is more compact and less permeable than underlying layers [2]. Chemical soil crusts occur when alkali [3], gypsum [4], salt [5], silica [6], sodium [7], or other chemistries concentrate near the soil surface, reduce permeability and aeration, and create a hardened surface crust. Biological soil crusts occur when living microorganisms near the soil surface bind soil particles into a surface layer or crust. The term biological soil crust was not recognized by scientists and land managers until near the beginning of the current century [8]. The term cryptogamic soil crust was originally used in place of biological soil crust [9]-[11], but although the term continues to be used occasionally, it is incorrect. According to widely accepted dictionaries of etymology (*i.e.*, the study of the origin and use of words), the prefix *crypto-* implies small, hidden, or obscure, and the suffix *-gamic* refers to sexual reproduction by the joining of male and female gametes to form a zygote. As most microorganisms reproduce primarily asexually [12], the term cryptogamic is mostly incorrect. Other adjectives have been added to describe soil crusts of biological origin, including cryptobiotic, microbiotic, microphytic, microbial, and phytochemical, and the terms biocrusts and microcrusts. The prefixes *crypto-* and *micro-* are not always correct because not all BSC microorganisms, particularly when fully grown, are truly cryptic or micro in size. For example, most lichens and mosses are easily observed and identified with the unaided human eye, and do not meet the definition. Furthermore, many of the descriptors fail to include the terms *soil* or *edaphic*, which is what makes BSCs unique. The same microorganisms can also be found on the foliage or phyllosphere of vascular plants worldwide [13], where they perform no functional role in a *soil* crust.

2. BSCs Are Not Limited to Deserts

BSCs were long assumed to be limited to arid areas or deserts, largely because most of the original related research on the subject was conducted there, not because they were absent elsewhere. For example, the area known as the Ozarks or the Ozark Plateau in southwestern Missouri, northwestern Arkansas, and small portions of Kansas and Oklahoma, USA, is neither arid nor semi-arid. Average annual precipitation there exceeds 1300 mm, and it is recognized for the presence of soil microorganisms now known to be components of BSCs [14] [15].

The first author was born in the Ozarks, but has since lived in the extreme north of the hyper-arid Atacama Desert of Chile where annual precipitation averages <

1 mm, and on the north shore of the island of Oahu, Hawai'i where annual precipitation can exceed 23,000 mm. His career, initially associated with the U.S. Army Corps of Engineers took him to severely disturbed military lands throughout the USA and Europe, where he heard the term BSC habitat used synonymously with *ley*, *moor*, *heath*, *veld*, etc. He now resides in Salem, Utah with an average annual precipitation of 457 mm. The second author is from La Serena, Chile at the southern extremity of the Atacama Desert, with an average annual precipitation of about 80 mm. He was instrumental in initiating BSC research in South America. The third author lives in Cottbus, Germany, with an average annual precipitation of 527 mm, and has conducted BSC research in Europe, Asia, and Africa.

Areas associated with bare and/or shallow soil, rock outcrops, and sparse vegetation [16], often surrounded by or interspersed with woodland or savanna [17], widespread occurrence of BSC microorganisms [18] [19], and often maintained by periodic burning [20] [21], were formerly referred to as *glades* [22] [23] in the USA. Over time, descriptive adjectives were added to denote the type of soil, rock outcrop, or relatively shallow bedrock in the glades, such as calcareous [24], chert [25], dolomite [26], granite [27], gravel [28], limestone [29], mafic (igneous) [30], quartzite [31], sandstone [32], shale [33], etc. As cedar or juniper trees, frequently colonize the shallow soil or rock outcrops in BSC habitat, an additional adjective was added, as in *cedar* glades [22]. Glades have now been identified by a large variety of names by various U.S. governmental land management agencies.

Given the exposed rock surfaces, bare soil, and sparse vegetation, BSC habitat and glades are sometimes referred to as merely as rock outcrops [34] [35], balds, or barrens. Balds have been referred to, more specifically, as alder or *Rhododendron* balds [36], grassy balds [37], or heath balds [38] depending on the dominant type of sparse plant overstory. One of the most notable areas referred to as bald is the town of Bald Knob, Arkansas, so-named for a large outcropping of layered stone that was a natural landmark when the town was approached from the east or south [39]. Several mountains throughout the USA have been known as Mount Baldy due to the paucity of plant cover.

Barrens have likewise been divided into separate types, such as in coastal barrens [40], coastal pine barrens [41], pine or jack pine barrens [42] [43], sand barrens [44], serpentine barrens [45], and shale barrens [46]. Glades, balds, and barrens are all names used to describe mostly barren insular ecosystems of southeastern and other regions of the USA [47] [48].

German scientists contributed the term *inselberg* to identify an isolated rocky hill, outcropping, knob, ridge, or small mountain within a generally flat surrounding terrain. Inselbergs vary in size from small to large. Similar to rock outcrops, inselbergs are generally inhabited by BSC microorganisms including viruses, non-symbiotic and lichenized fungi, archaea, bacteria, cyanobacteria, terrestrial algae, and bryophytes [49]-[51].

Swedish scientists contributed the term *alvar,* which means much the same type of partially barren habitat with considerable limestone or dolomite substrate. They have been reported as being present in Canada [52], Estonia [53], Finland [54], Russia [55], and Sweden [56], as well as in the U.S. state of New York [57], and in the Great Lakes region of the upper mid-western USA [58].

In county Clare of south-western Ireland, rocky ecosystems were formerly referred to as *the Burren*, from the Irish or Celtic word *boírean* meaning a rocky place, generally with a limestone karstic substrate [59]-[61]. Average annual precipitation in the Burren ranges from 800 to 1200 mm.

Alpine areas and areas exposed by receding glaciers, with limited woody plant cover and considerable rocky or bare soil, often form BSCs. They have also been referred to as glades [62], further compelling evidence that BSCs are not unique to desert ecosystems. The terms BSC habitat, glade, barren, bald, inselberg, alvar, the Burren, alpine areas, moor, ley, and heath are substantially synonymous, referring to areas with exposed rock outcrops, bedrock, or rock pavement, limited vascular plant cover, few woody plants, and abundant soil microorganisms. The precise composition of microorganisms may vary depending on climate and soil, but their functional roles remain similar. BSCs have now been reported from hyper-arid areas [63] to tropical rain-forests [64] and tropical islands [65] [66], and from the hottest deserts [67] to frigid polar regions [68]. There have even been suggestions that microorganisms involved in BCs on Earth may also occur on and perform similar functions on other planets in our solar system [69] [70].

3. Recovery of BSCs Following Disturbance Is More Rapid than Previously Thought

BSCs can be affected by a variety of disturbance types, including climatic shifts, fire, or chemical or physical perturbation. Unassisted, passive restoration depends on the aerial arrival of viable microorganisms onto substrates that foster growth and reproduction, and favorable climatic conditions [71]. Recovery to pre-disturbance microorganism species composition and ecological function has been estimated to require up to a millennium or longer in arid areas [72] [73]. However, recent studies in arid regions have shown that passive recovery may occur within 20 years or less [74]-[76]. In moister temperate regions, recovery may be even more rapid. Investigations in post-mining sites and former militarily-disturbed areas show recovery in less than 10 years [77] [78] and initial BSCs can be found after only 3 years [79] [80]. Recovery depends on soil characteristics [81], arrival of viable airborne propagules that orbit the Earth in the atmosphere, and on appropriate climatic conditions that facilitate the growth of filaments and production of exopolysaccharide compounds that entangle and/or cement soil particles into a stable and functional BSC.

4. "Desert Varnish": A Scientific Misnomer

Microorganisms form BSCs in all climatic regions. Many of the same microorganisms also participate with windborne dust and silica to form a translucent or opaque coating, covering, patina, lacquer, varnish, rind, glaze, film, or biofilm on the rocky or stoney surfaces [82] [83], including those as small as individual sand grains [84] [85]. Although not BSCs *per se*, because they do not cover the soil, such surficial coverings are often observed in arid habitats, and have frequently been referred to as "*desert varnish*". However, they are not unique to deserts at all. Hence, the term "*stone varnish*" is much more appropriate, and avoids the misnomer of "desert" varnish. The varnish results from the interactions of BSC microorganisms with silica and the oxides of manganese, iron, aluminum, titanium, or other elements in windblown dust. The varnish has been documented in Antarctica [86], Argentina [87], Australia [88], Chile [89], China [90], East Africa [91], Egypt [92], Germany [93], Iceland [94], Iran [95], Israel [96], Italy [97], Kenya [98], Libya [99], Mexico [100], Mongolia [101], Norway [102], Peru [103], Portugal [104], Saudi Arabia [105], Sweden [106], the autonomous region of Xizang, China (formerly known as the Tibetan autonomous region or simply Tibet) [107], Tunisia [108], Venezuela [109], etc. In the USA, the varnish has been recorded in the states of Arizona [110], Arkansas [111], California [112], Colorado [113], Hawai'i [114], Nevada [115], New Mexico [116], New York [117], Tennessee [118], and Texas [119]. In fact, stone varnish is necessary for the creation of petroglyphs which have been recorded in at least 27 additional states and territories [120]. It could be logically concluded that the geographic distribution of petroglyphs corresponds to the presence of stone varnish. Anywhere that a petroglyph is found, is indicative of the presence stone varnish.

Coverings similar to desert varnish occur on rock or stone surfaces deep in lakes and oceans [121], but the dust-sized particle and chemicals may have been carried by water rather than by wind, or the varnish may have been formed long ago when water levels were lower. Alternatively, microorganisms and dust-sized soil particles, the essential building blocks of stone varnish, can be carried by water and deposited in lakes and oceans.

It is important to distinguish between petroglyphs and petrographs. The prefix *petro-* is derived from the Greek word *petra* which translates as rock or stone. The suffix -*glyph* means to abrade, carve, chip, etch, incise, scratch, or scrape. Hence, petroglyphs are usually found where stone varnish is found and has been removed by chipping, scraping, etc. The suffix -*graph* means to draw or write on. Hence, petrographs are created by painting or drawing directly on a stone or surface, while petroglyphs are created by chipping or scraping away a varnish from a stone or rock surface [122]. Petroglyphs can also be found on the rock walls inside of caves that have been darkened by years of soot formation from campfires or cooking fires, and subsequently scraped to create drawings [123]. The terms petroglyph and petrograph are sometimes used interchangeably, but they are not the same.

Given the wide range of locations where stone varnish has been found, from frigid to hot deserts, and to tropical rainforests, the term "desert" varnish is an obvious misnomer. The term "stone varnish" does not limit the occurrence of the phenomenon to a single climatic region. BSCs, a related phenomenon created by many of the same microorganisms, has been reported in almost all ecozones, ranging from the Arctic [124] [125] and Antarctic [126] [127] in cold polar regions, to mesic temperate climates [128] [129], to semi-arid areas [130] [131], to hot, arid areas worldwide [8] [132]. They would likely occur more often in tropical rainforests, if there were expanses of bare soil or rock that remained available for colonization by microorganisms for long periods of time. Most microorganisms are deposited there instead on plant surfaces, tree bark, or detritus that covers the soil, thus establishing microorganism communities there rather than on the soil [133].

5. BSC Microorganisms Are More Diverse than Previously Believed

For years, the only microorganisms recognized as constituents of BSCs were fungi (non-symbiotic and lichenized), bacteria, cyanobacteria, terrestrial microalgae, and bryophytes [8] [134]. To that list, we can now add archaea [135] and viruses [136], being cautious to recall that the mere presence of a microorganism does not necessarily imply participation in the ecological functioning of a BSC. Archaea are primitive unicellular prokaryotes similar to bacteria, but with distinct molecular characteristics that place them in their own domain: *Archaea*.

Viruses are likely the smallest microorganisms involved in BSCs [137] [138]. Scientific literature often refers to viruses as phages, a term used to describe viruses that infect, live, and replicate within a living host. A mycophage [139] or mycovirus [140] infects and lives within a fungus. A bacteriophage or bacterial virus infects and replicates within bacterial cells [141]. Viruses infecting archaea are known as archaeophages or archaeal viruses [142], and those infecting cyanobacteria have been referred to as cyanophages [143] or cyanobacterial viruses [144]. Some phages are filamentous [145] or infect filamentous microorganisms, and are, thus, potentially capable of assisting in the binding of dust and other small soil particles. Some viruses in BSCs may also fix atmospheric carbon dioxide [146] [147] and atmospheric nitrogen [148] [149], thus participating in nutrient cycling. The general roles of viruses in soils have been poorly studied historically, primarily due to the historic focus on epidemiology [150]. The modified focus may facilitate additional discoveries more closely related to the functions of BSCs and associated microorganisms.

6. Most BSC Microorganisms Are Tiny, Ubiquitous, and Aerially-Dispersed

Most microorganisms reproduce asexually [151], although some are capable of sexual reproduction as well [12]. Microorganisms are ubiquitous and abundant in the atmosphere and in terrestrial and marine environments [152] [153]. Most are tiny and their propagules are even smaller, often measured in microns or millionths of a meter [154]. Their weight is correspondingly miniscule, and they are easily suspended and carried into the atmosphere by wind or air currents [155] [156]. Due to their tiny size and weight, many microorganisms are easily attached to and accompany airborne dust particles [157] [158]. Many microorganisms can survive in the upper layers of the atmosphere and in outer space [159] [160], including viruses [161], non-symbiotic fungi [162], lichenized fungi [163], archaea [164], bacteria [165], cyanobacteria [166], terrestrial microalgae [167], and bryophytes [168]. While in the Earth's atmosphere, they are easily dispersed via a so-called "*microbial conveyor belt*" [169] or "*dispersal loop*" [170]. Much of the dispersal also takes place via jet streams, which are fast-moving winds that occur in the tropopause [171]. However, it is reasonable to ask if and how they are carried even higher, as it has been suggested that microorganisms can escape Earth's atmosphere and reach outer space [172]-[174]. An additional mechanism by which microorganisms are carried in an upward direction toward outer space is via the polar vortices [175] [176] that have now been documented to extend at least as high as the mesosphere [177]. Many terrestrial microorganisms have landed on the surface of the International Space Station which orbits the Earth in the thermosphere [178]. All planets have polar vortices [179]-[181]. Hence, interplanetary space-travel by microorganisms seems plausible [169] [170].

Straddling the Earth's equator between approximately 30˚ north and 30˚ south latitudes, global prevailing near-surface winds tend to blow primarily from east to west, forming what are known as the *tropical easterlies* or *trade winds* [182]. Between about 30˚ and 60˚ latitudes, either north or south of the equator, near-surface winds reverse direction due to the *coriolis effect* of the rotating planet [183], blow from west to east, and are known as the *westerlies*. The surface winds reverse again between 60˚ north and south latitudes and the respective poles, again blow primarily from east to west, and are known as the *polar easterlies*. Based on those patterns, BSC microorganisms first arriving in the western United States, including the Mojave and Great Basin deserts and the Great Plains, generally originate with dust storms in China and Mongolia [184]. Dust and accompanying microorganisms originating in the Sahara and Sahel Deserts of Africa generally arrive via easterly winds to the Caribbean, northern Mexico, and the southeastern USA [185].

7. What Goes up Must Also Come Down

Microorganisms and their propagules are frequently lifted into the atmosphere, but do not likely stay there forever. While some may remain airborne for multiple generations [186], they eventually fall back to Earth or may be lifted into outer space [187]. Microorganisms returning to Earth by its gravitational pull may be deposited without differentiation onto any relatively flat surface. Those landing on bare soil resulting from aridity and/or physical disturbance from heavy grazing [188] [189], military training [189]-[191], strip or open-pit mining [189] [192] [193] are often incorporated into BSCs. BSC microorganisms may land on well-mixed soil or on sand, including coastal beaches or shorelines, and inland sand dunes, all of which develop BSCs [194] [195]. However, many other surfaces are also available. Where there is minimal bare soil, they likely become integrated into the phyllosphere microbiome associated with the surface of living plants [13], thus becoming critical for carbon [196] and nitrogen [197] fixation, or the litter or duff layer that lies on the soil surface below the living plant overstory [198]-[200]. Microorganisms deposited onto plants become *epiphytic* residents of the phyllosphere, one of the most prevalent and diverse microbial habitats on Earth, important for plant decomposition [199] [200], and a critical link between atmospheric gases and mineral fixation [201] [202]. Microorganisms have been documented as being present on needle-leaved coniferous trees and shrubs, broad-leaved trees and shrubs, fruit trees, nut trees, grasses and grains, ferns, forbs, cacti, and on all other plants exposed to the atmosphere [13].

Microorganisms and their propagules fall from the upper atmosphere and outer space, and can land on any available surface. Those that land on plants become part of the phyllosphere microbiome where they perform the essential functions of carbon and nitrogen fixation as previously discussed, and combat host plant diseases, pathogens, and pests [203]-[205]. Microorganisms not landing on bare soil or plant surfaces may land on rocks and stones [206] [207], lava [208] [209], animals [210] [211], buildings of any age [212]-[214], gravestones or tombstones [215] [216], statues and sculptures [217] [218], wooden fences [219], abandoned vehicles [220], mine tailings [221] [222], glaciers [223], snow [224], fresh water [225], salt water [226], etc.

Several edible species of vagrant crustose lichens have been identified as the probable *manna* that fell from the upper atmosphere or heaven and saved the prophet Moses and the Israelites from starvation as they wandered for 40 years in the Egyptian desert after escaping the Egyptian pharaoh, as discussed in the biblical Old Testament [227].

Given that microorganisms and their propagules are distributed aerially, they are likely dispersed onto most surfaces globally [228]. The first author first discovered the universality of microorganisms associated with biological soil crusts years ago while studying the crusts south of Tooele, Utah. He was surprised to document the presence of cyanobacteria on the foliage or phyllosphere of big sagebrush (*Artemisia tridentata*) and Utah juniper (*Juniperus osteosperma*). While there has been a rush to report their presence of microorganisms on the foliage or phyllosphere of all plants [229], it seems reasonable to ask if there are any surfaces that cannot host them. Almost all surfaces are habitable, with the rare exceptions of metallic copper [230], silver nitrate [231], and those treated with anti-microbial coatings [232] [233].

Because microorganisms are tiny and lightweight, and carried by wind, air currents, and precipitation, they have the potential to be dispersed to and land on any surface that is exposed to the atmosphere or water. That includes deep within caves [234] [235] and mineshafts [236] [237]. As it turns out, at least some cyanobacteria are capable of photosynthesis by utilizing far-red light wavelengths light in the absence of visible light wavelengths [238] [239]. At least some archaea and bacteria can fix carbon via chemosynthesis, *i.e.*, the oxidation of inorganic carbon compounds such as carbon dioxide or methane to produce glucose or other complex carbon-rich carbohydrates, in the absence of sunlight and photosynthesis

[240] [241]. Microorganisms involved in chemosynthesis in subterranean and deep-sea environments [242] [243] may account for more than half of ecosystem carbon fixation under those conditions [244]. Chemosynthetic microorganisms have also been identified in sunlit environments as well, such as in the atmosphere throughout cold deserts [245], and in hypersaline microbial mats [246].

7.1. Humans and Other Animals Inhale Airborne Microorganisms

Dust-associated microorganisms are extremely common and ubiquitous in planetary atmospheres [247] [248]. Humans and other animals each inhale as many as half a million or more microorganisms daily [249] [250]. Many of the microorganisms become lodged in the upper respiratory tract, thus becoming components of the respiratory microbiome [251]. Not all microorganisms cause humans to become ill, because many come into contact with mucus or other natural antimicrobial substances [252]. The same is true for human skin [253], eyes [254], and the alimentary tract [255].

7.2. Microorganisms and Climate Warming

Much of recent speculation regarding the potential impacts of global climate change is alarmist, predicts irreversible climate warming [256], and the possible extinction or significant reduction to humanity, resulting from increased levels of greenhouse gases, primarily carbon dioxide in the atmosphere. Multiple studies seem to indicate that climate warming trends over the past century may be due to human activities. Political organizations worldwide have issued public statements endorsing that position. Regrettably, most of such studies are severely limited in timescale. Large, abrupt, aberrant, and widespread climate change has occurred repeatedly in at least the past 65 million years, often with significant ecological and environmental impacts [257] [258]. Perhaps the best-studied example of climate change on Earth occurred between about 12,900 and 11,700 years ago, a period near the end of the last ice age known as the Younger Dryas that was marked by abrupt and rapid warming and cooling [259]-[261]. The climate change we have witnessed over the last 150 years, including that documented by the so-called "hockey stick" graph that shows recent sudden and rapid climate warming [262], is not at all unusual. Regardless of the hype from popular media, it is not likely to forebode the end of humanity. Of importance is the fact that while atmospheric CO_2 concentrations in recent times seem to precede global warming, on a much longer or paleoclimate time scale, the trend seems to reverse [263] or becomes statistically indiscernible [264].

The prognosis of significant reductions in precipitation and biodiversity, and increased temperatures in arid and semi-arid zones, may indeed alter the effect and the speed of recovery and functioning of BSCs in those environments in the short-term. For example, in arid and semi-arid ecosystems, climate change may provoke further desertification [265]. Many studies that have measured responses to short-term actual or simulated climate change or increased ultraviolet-B radiation have demonstrated reductions in the cover and diversity of BSCs and the microorganisms that create them [266], increased respiration [267], reduced photosynthesis and growth [268], or reduced nitrogen fixation and/or abundance of nitrogen fixing microorganisms [269] [270]. It has been suggested that climate change may cause mass extinctions over the next 100 years [271] [272]. However, a thorough review of the scientific literature reveals only a single species, the Bramble Cay (*Melomys rubicola*), that may have become extinct due to climate change [273]. It is a diminutive rat found on a single tiny island near Australia whose habitat was presumably inundated as the result of climate change, and to which there was no adjacent or otherwise suitable habitat reasonably close for immigration.

Greenhouse gases include water vapor, carbon dioxide, methane, nitrous oxide, fluorinated gases, etc. [274]. Although there have been notable exceptions, there seems to be widespread belief among a small but vocal sector of contemporary scientists that carbon dioxide is the primary culprit that has driven climate change for the last 500 million years [275]. It has been suggested that the Earth's climate may continue to warm until at least the end of the current century and may reach that of the Pliocene by 2050 [276], thus reversing millions of years of long-term cooling [277]. It is encouraging that carbon sequestration (the capture of atmospheric CO_2 and its storage in carbon sinks such as living organisms, carbonaceous soil, coal, BSCs, etc.) [278], mitigates the supposed detrimental effects of carbon dioxide and global warming.

Microorganisms are everywhere and perform many essential roles, including combating soil erosion by moving water [279] and wind [280]. They also perform a variety of ecological functions related to combating climate change. Microorganism in the phyllosphere [281], in the soil [282], and in freshwater [283] and marine environments [284] perform of carbon sequestration. Of importance are the many microorganisms inhabiting the Earth, its oceans, the atmosphere above Earth, and outer space. Bacteria and archaea are the most abundant and diverse microorganisms on Earth [285]. They are capable of fixing (converting or sequestering) atmospheric carbon dioxide into organic carbon through traditional photosynthesis, photosynthesis utilizing alternative light wavelengths, chemosynthesis, and multiple other pathways [286] [287], thus protecting Earth from the perceived problems associated with global warming.

In addition to increases human-induced carbon dioxide, there are numerous natural causes of climate change including changes in Earth's axis of rotation and orbit which caused long periods of cooler temperatures known as the ice ages and shorter warm periods known as interglacial periods, variable solar activity, volcanic activity, changes in the Earth's reflectivity, and natural changes to the occurrence of carbon dioxide in the atmosphere [288]. It is impossible to rationally define any single factor that predominates.

8. Conclusions

Biological soil crusts, created by microorganisms at the soil surface, are a natural and abundant phenomenon on Earth. Once thought to be limited to deserts, they have since been observed in most ecosystems worldwide. They and a related phenomenon, desert varnish, are apparently ubiquitous. Biological soil crust habitat has been known by multiple synonyms, including glades, barrens, and balds in the USA, and inselbergs, alvars, and the Burren in Europe. Alpine areas, moors, leys, heaths, and land left behind by receding glaciers can be substantially similar habitat, although the species composition of dominant vascular plants and associated microorganisms may vary greatly. Biological soil crusts can be negatively affected by fire, physical perturbation, or climatic shifts. Depending on the nature and scope of perturbation, post-disturbance recovery was once thought to require millennia, but has since been shown to happen passively within a few years to a few decades as microorganisms and microorganism-carrying dust in the atmosphere settle back to Earth. Microorganisms that participate in biological soil crusts were once thought to include only fungi, bacteria, cyanobacteria, terrestrial microalgae, and bryophytes. To that list, we can now add archaea and viruses. The microorganisms that participate in biological soil crusts are tiny and ubiquitous. They are so numerous in the air that humans and other animals are known to inhale up to half a million each on a daily basis. The microorganisms are extremely plentiful and are known to participate in carbon fixation (conversion of carbon dioxide into organic matter), thus protecting our planet from the negative effects of carbon dioxide as a greenhouse gas.

A question worthy of further future research includes whether the three known types of soil crusts are truly separate, or if biological soil crusts can grow anywhere chemical and/or physical soil crusts already exist. Given the apparent ubiquity of microorganisms and the fact that they fall from the upper atmosphere and outer space, it seems reasonable to ask if there are any types of soil where BSCs are absent. Plentiful published data seem to cast doubt on that assumption. Certainly, some locations may lack unique chemistries to facilitate chemical soil crusts with associated microorganisms. However, we have personally witnessed chemical soil crusts with an abundance of microorganisms, but we have never seen the opposite. Biological soil crusts also occur on sand, silt, and clay, but again, we have never witnessed any soil completely devoid of microorganisms.

Another area of productive research includes the possibility of stone or rock varnish deep under water. Did this phenomenon arise at some point before the stone was submerged? Or, since dust-sized soil particles and microorganisms are abundant in bodies of water, is it possible for stone varnish to form in the absence of airborne or windborne particles? Logic would suggest that it is likely, unless exposure to the atmosphere is necessary. There are numerous examples of natural and man-made stonework that have been submerged for hundreds of years. It could be enlightening to examine them for the possibility of desert varnish that appeared subsequent to submergence.

Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

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