



Temperate biocrusts: mesic counterparts to their better-known dryland cousins

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Biological soil crusts (biocrusts) are known to serve crucial functions in many arid and semiarid habitats, but less is understood about biocrusts in temperate biomes, where they are often widespread and can play important roles in aboveground and belowground processes. Because the distinctive conditions that support biocrusts in temperate biomes – sandy, acidic, and/or nutrient-poor soils or exposed bedrock – frequently also support rare plant and animal communities, such sites can have considerable conservation value. We detail the distribution of biocrusts in temperate habitats, including many in the northeastern US, where they have not previously been described. Besides adding another layer of biodiversity to the sites in which they occur, biocrusts may also play a critical role in site-level ecology and functioning. As such, integrating temperate biocrust composition, distribution, and functions into ecosystem management may contribute to the stability and resilience of the ecosystems in which they are found in the face of global climate change and other disturbances.

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Biological soil crusts, or biocrusts, are major contributors to the biodiversity and ecosystem functions of deserts, semi-deserts, woodlands, and grasslands worldwide (Belnap 2003; Weber *et al.* 2016). Biocrust communities contain a diverse assemblage of cyanobacteria, algae, lichens, and bryophytes, as well as bacteria, archaea, fungi, and other associated soil organisms. Collectively, biocrust organisms influence erosion rates, water infiltration, nutrient cycling, carbon (C) storage, and vascular plant composition, among other ecological attributes (Weber *et al.* 2016). Increasing recognition of the pivotal role that biocrusts play in dryland ecosystems has spurred calls for greater appreciation, protection, and restoration of these communities (Belnap 2003; Bowker 2007; Ferrenberg *et al.* 2017).

In a nutshell:

- Biological soil crusts (biocrusts) are communities of organisms at the intersection of soil and air that are recognized for their profound influence on dryland ecosystems
- Biocrusts are also found in temperate regions where characteristic soils and disturbance regimes create conditions that support crust-forming organisms in addition to supporting many rare or threatened plant and animal species
- Although the ecology of temperate biocrusts is not well understood, successful management and restoration of the rare ecosystems in which biocrusts occur may be more likely when the composition, distribution, and function of biocrusts are considered

Although attention and research have overwhelmingly focused on biocrusts in arid and semiarid climates, biocrusts frequently occur in more humid regions as well (eg Eldridge 1999; Thiet *et al.* 2014; Schulz *et al.* 2016). In wetter climates, the open canopy and sparse litter that biocrust communities require are usually restricted to areas where vascular plant primary productivity is low (Eldridge *et al.* 2000; Büdel *et al.* 2014). The particular habitats that support biocrusts also often support a broader diversity of distinctive plants and animals absent from the more typical habitats of their region (eg forests; Eldridge 1999; Eldridge *et al.* 2000; Büdel *et al.* 2014), and biocrusts can therefore be thought of as “islands” in a sea of surrounding landscape. Such biocrust islands include barrens, sand plains, alvar communities, sparse grasslands, and sand dunes (Table 1) that are often appreciated and managed for their conservation value at regional and global scales. The presence of biocrusts in these ecosystems makes them even more biodiverse than is commonly recognized.

Diverse biocrusts dominated by algae, cyanobacteria, bryophytes, and lichens have been documented in the US Midwest (eg Iowa [Schulten 1985], northwestern Ohio [Neher *et al.* 2003], northern Indiana [Thiet *et al.* 2005], and Wisconsin [WDNR 2015]), the US Northeast (eg Cape Cod [Smith *et al.* 2004; Thiet *et al.* 2014], New Jersey's Pinelands [Sedia and Ehrenfeld 2005], and New York [Gilman 1995; Stergas and Adams 1989]), Florida (Hawkes and Flechtner 2002), and temperate regions of Europe (eg Sparrius 2011; Büdel *et al.* 2014; Schulz *et al.* 2016) as well as temperate Australia (Eldridge 1999; Eldridge *et al.* 2000; O'Bryan *et al.* 2009). We suspect that a lack of recognition of the status of temperate biocrusts as a discrete community with ecological importance has resulted in numerous additional sites worldwide going unnoticed.

Here, we review what is known about biocrusts in temperate regions where they have been studied (primarily North America, Europe, and Australia), with a focus on the unique

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Table 1. Description of temperate ecosystems known to support biocrusts

Habitat type	Description
Sand dunes and barrier islands	Active and stabilized sand dunes alongside inland seas and large lakes (eg Baltic Sea or North American Great Lakes; Thiet <i>et al.</i> 2005; Schulz <i>et al.</i> 2016) and marine coasts such as Cape Cod, MA (Smith <i>et al.</i> 2004; Thiet <i>et al.</i> 2014) and Long Island, NY. They experience frequent disturbances from migrating sand and, in saline systems, salt spray.
Sand plains and pine barrens	Deep, sandy soils derived from glacial lacustrine dunes, till, and outwash plains. Communities can range from grassland/savanna to woodland to forest with canopy gaps (eg regularly logged forests or forests with relatively low canopy continuity). They are often fire-maintained or selectively logged. Examples include Long Island Pinelands, New Jersey Pinelands, Florida's Lake Wales Ridge, interior pine barrens and sand plains of the US Northeast, and grasslands and shrublands in the "aeolian sand belt" of Europe's northern lowlands (Figure 2; WebTable 1; Hawkes and Flechtner 2002; Sedia and Ehrenfeld 2003; Sparrius 2011).
Alvars or pavement barrens	Shallow soil due to flat sandstone, limestone, or dolomite rock at surface. Vegetation is sparse with extensive exposed bedrock. They are found in northern Europe and in the Great Lakes Basin of North America (eg Gilman 1995; Büdel <i>et al.</i> 2014).
Extreme soils	Exceptionally alkaline or acidic soils. Examples include volcanic plains in western Australia (Morgan 2006).
Human-dominated systems	Ecosystems where human activities have stripped surface soil or deposited coarse, infertile sediments. Examples include mine reclamation (Gypser <i>et al.</i> 2016) and spoil (Lukešová 2001) sites, areas repeatedly cleared of vegetation and subject to erosion (Eldridge <i>et al.</i> 2000; Langhans <i>et al.</i> 2009) and even the fortifications of medieval castles (Büdel <i>et al.</i> 2014).

habitats in which they are found and the current state of knowledge about their ecological role in the ecosystems they populate. In particular, we highlight biocrusts in the temperate northeastern US, where they are much more widespread than previously described. We argue that biocrusts likely play important roles in plant community dynamics (eg establishment and succession), resource dynamics (eg nutrient cycling and water availability), and ecosystem functioning where they occur. Improving our understanding of biocrust composition, distribution, and functions would therefore aid in the management and restoration of these rare ecosystems.

■ Conditions that give rise to biocrusts in temperate biomes

Because the organisms that make up biocrusts are sensitive to shade and are generally poor competitors as compared to vascular plants (Belnap *et al.* 2001), biocrust development requires, at least initially, an open canopy and sparse litter. In arid and semiarid climates, drought limits primary productivity enough for crust organisms to thrive; in arctic and alpine habitats, cold temperatures and short growing seasons serve the same purpose. In contrast, plant growth in temperate biomes is typically high enough that ground-layer organisms are quickly overtopped unless soil conditions limit vascular plant productivity. Edaphic (soil-related) conditions, such as excessive drainage, acidity, or low nutrient levels, and usually all three, are therefore required to support temperate biocrust formation (Table 1; Eldridge *et al.* 2000; Büdel *et al.* 2014). Shallow soil and exposed bedrock in alvars and rocky ridge communities may severely limit plant root growth, while sandy, excessively drained, or nutrient-poor parent material in dunes, sand plains, and pine barrens can induce water and nutrient stress. In such cases, considerable extents of exposed mineral soil occur among sparse plant and litter cover, while insolation (light availability)

at the soil surface is sufficient to support biocrust establishment and persistence (Figure 1). Even in regions where precipitation exceeds 75 cm per year, biocrusts in open barrens and dune systems can colonize bare soils between plants. Büdel *et al.* (2014) described these ecosystems as "arid-microclimate adapted communities" within temperate and maritime climates, and they can be found in a variety of relatively mesic biomes.

Even where appropriate soil conditions exist, most biocrusts in temperate climates likely require periodic disturbances to the vascular plant community (eg fire, mechanical removal, or heavy grazing) to maintain exposed mineral soil and an open canopy. Without disturbances, vascular plants will overtop biocrust organisms, casting shade and depositing litter, thereby destroying biocrust communities. In coastal dune systems, for example, biota experience stress and frequent disturbances in the form of sand saltation, slumping, wind, coastal storms, and salt spray. In inland sand plain and pine barren habitats, periodic fire (Sedia and Ehrenfeld 2005; O'Bryan *et al.* 2009), fossorial mammal activities (ie digging; Eldridge *et al.* 2000), and various activities by Indigenous, Euro-American, and Euro-Australian peoples (eg land clearance for agriculture, grazing, and tree harvest; Motzkin and Foster 2002; Büdel *et al.* 2014) likely performed this role historically. Today, prescribed fire (Little 1998; Sedia and Ehrenfeld 2005; Bried *et al.* 2015), grazing (Langhans *et al.* 2009; Büdel *et al.* 2014), vehicular (eg all-terrain vehicles) and foot traffic, use as gravel borrow pits, and other forms of mechanical scouring are modern disturbances that may maintain suitable conditions for biocrust establishment.

■ Adding another layer to ecosystems of global conservation interest

Although the areal extent of biocrust communities is relatively small, the distinctive soils and habitat conditions

that support temperate biocrusts also support a variety of species of conservation interest. In the northeastern US, these include plants such as wild pink (*Silene caroliniana* ssp. *pennsylvanica*), upright bindweed (*Calystegia spithamea*), and New England blazing star (*Liatris scariosa* var. *novae-angliae*); insects such as the frosted elfin butterfly (*Callophrys irus*) and the endangered Karner blue butterfly (*Lycaeides melissa samuelis*); amphibians such as the eastern spadefoot toad (*Scaphiopus holbrookii*); and birds such as the whip-poor-will (*Caprimulgus vociferous*), common nighthawk (*Chordeiles minor*), and grasshopper sparrow (*Ammodramus savannarum*). In Australia, box woodlands that host biocrusts form a canopy of various *Eucalyptus* species and a tussock grass understory, which provide important seasonal nectar sources for threatened bats like the gray-headed flying fox (*Pteropus poliocephalus*) and little red flying fox (*Pteropus scapulatus*). In Europe, inland sand dunes of glacial origin host nutrient-poor grasslands and heathlands that support a diverse assemblage of arid-adapted plants and animals (Koster 2005; Sparrius 2011).

A variety of natural and anthropogenic factors have greatly reduced the historical extent of the distinctive ecosystems associated with biocrusts. For example, North America's open barren and sandplain ecosystems now occupy a mere fraction of their historical area, as fire suppression, succession to closed-canopy forest, human development, and other land-use changes are ongoing threats to their continued persistence (Noss *et al.* 1995; Motzkin and Foster 2002). Similarly, Australia's box woodlands once occupied millions of hectares in southeastern Australia, but widespread land conversion has left only small and highly fragmented remnants (Prober *et al.* 2001), and grasslands and heathlands in Europe's "sand belt" have been greatly reduced due to land-use changes, nitrogen (N) deposition, and succession to forests (Koster 2009). Presently, many of these systems are considered of high conservation value and are therefore protected by conservation organizations (eg The Nature Conservancy); parks and natural resource agencies at the municipal, state, and federal levels; the UN Educational, Scientific, and Cultural Organization (UNESCO); and other entities (WebTable 1; Koster 2005; Prober *et al.* 2001; Büdel *et al.* 2014). Despite that human activities have created extensive areas where growing conditions cannot support forests yet can host biocrust taxa (eg Table 1, human-dominated systems), such sites typically do not provide the full range of biodiversity or ecosystem services associated with remnant open habitats.

■ Representative taxa of temperate biocrusts

Biocrusts of coastal sand dunes that experience frequent disturbances from blowing and slumping sand are often dominated by algae in the genera *Geminella*, *Klebsormidium*,

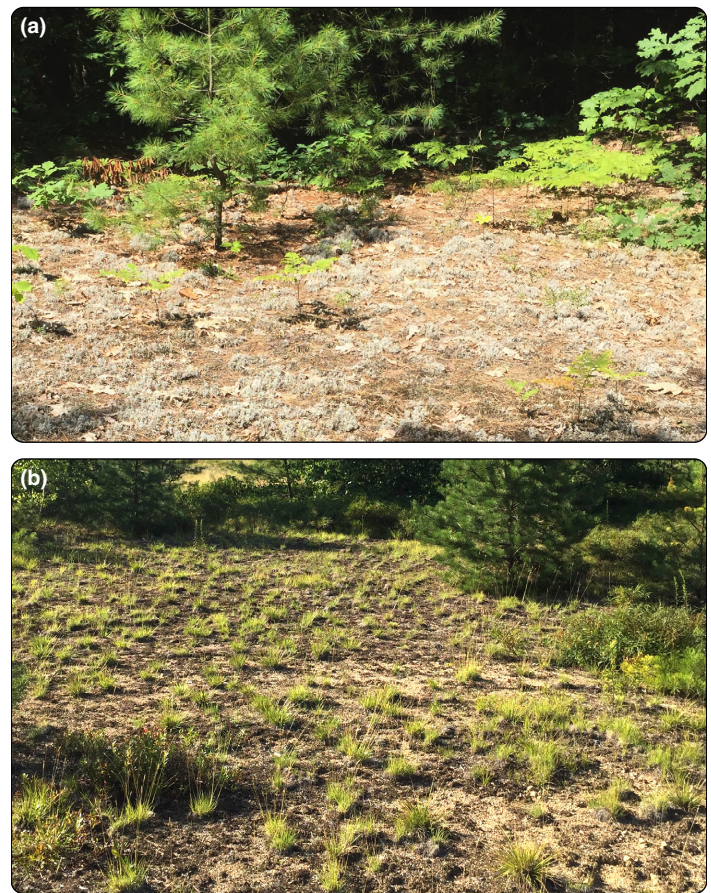


Figure 1. Examples of biological soil crusts (biocrusts) in (a) Rome Sand Plains, New York; and (b) Ossipee Pine Barrens, New Hampshire.

and *Lobochlamys*, and by cyanobacteria – several types of which are N-fixing – including the genera *Hydrocoryne*, *Leptolyngbya*, *Microcoleus*, and *Nostoc* (Smith *et al.* 2004; Thiet *et al.* 2005; Schulz *et al.* 2016). Such genera are also commonly observed in dryland biocrusts (Bowker *et al.* 2016). Thick bryophyte- and lichen-affiliated biocrusts dominated by *Ceratodon purpureus*, *Polytrichum* spp, and *Cladonia* spp establish in relatively stable, wind-scoured swales in temperate sand dunes, where they persist until vascular plants establish (Smith *et al.* 2008; Thiet *et al.* 2014). In newly disturbed and early successional sites, algae and cyanobacteria typically initiate the binding of soil particles and the accumulation of organic matter (Eldridge *et al.* 2006; Fischer *et al.* 2010).

At sites where disturbances are less frequent, such as sand plains, pine barrens, and areas of shallow soil, bryophytes and lichens typically arrive at later stages and replace the algae and cyanobacteria as dominant species (Fischer *et al.* 2014; Gypser *et al.* 2015). Bryophytes especially appear to be a greater component of mature temperate biocrusts than in dryland system biocrusts, although lichen-dominated temperate biocrusts are also common (eg Gilman 1995; Sedia and Ehrenfeld 2003; Büdel *et al.* 2014). Species in temperate North America and Europe include mosses such as *C. purpureus* and *Polytrichum piliferum*; terricolous lichens of the genera *Cladonia* and

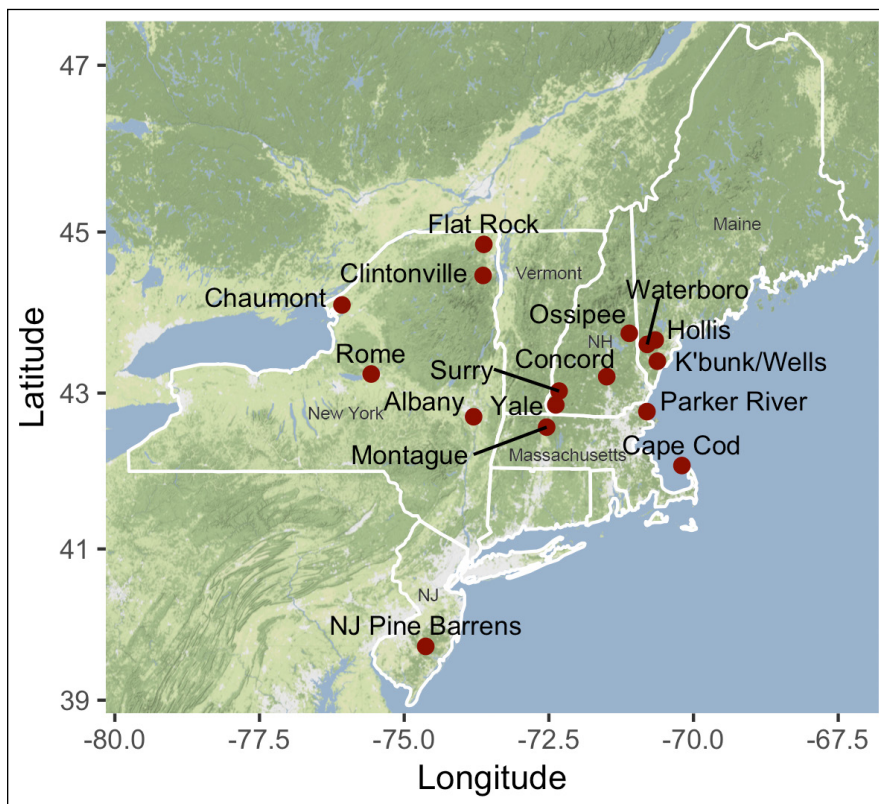


Figure 2. Map of the locations of protected pine barren, sand plain, alvar barren, and coastal dune systems in the northeastern US where we observed biocrusts; numerous other sites in the region also support biocrusts that have not yet been documented and characterized. Kennebunk Plains and Wells Barrens were combined on the map due to their geographic proximity. See WebTable 1 for descriptions of each location. Location points are not to scale.

Placynthiella; species of green algae within the genera *Chlorella*, *Desmococcus*, *Klebsormidium*, *Stichococcus*, *Ulothrix*, and *Zygogonium* (Büdel 2001; Sparrius 2011; Howe 2016); and various genera of cyanobacteria, such as *Leptolyngbya*, *Microcoleus*, and *Nostoc* (Thiet *et al.* 2005). Temperate grassland biocrusts in Australia are dominated by mosses in the genera *Barbula*, *Bryum*, and *Triquetrella*, and lichens in the genera *Cladonia* and *Endocarpon* (Eldridge 1999; Eldridge *et al.* 2000; Rogers 2006).

■ Case study: biocrusts of the temperate US

Although biocrusts have been described in some temperate and subtropical US sites, they are much more widely distributed than is generally recognized. The coastal sand plains and barrier island beaches that support pine barren and coastal dune ecosystems in Cape Cod, Long Island, and New Jersey are the product of glacial retreat at the end of the Wisconsin glacial retreat, which occurred ~10,000–13,000 years before present. Interior glacial relicts and alluvial deposits in former glacial lakebeds that also support pine barrens and sand plains are widely scattered throughout New York, Massachusetts, Vermont, New Hampshire, and Maine. In addition, exposed limestone terraces that support

alvar communities are found throughout the Great Lakes region.

In 2018, we surveyed biocrusts in 12 open ecosystems in New York and New England (Figure 2; WebTable 1) and identified 17 species of bryophytes, 19 species of lichens, nine genera of green algae, five genera of diatoms, and six genera of cyanobacteria (WebTable 2). Biocrust species composition both within and between sites was highly variable. For example, crusts on the Province Lands sand dunes of Cape Cod National Seashore, Massachusetts (Figure 3a), were composed of a mosaic of green algal crusts on dune slopes, and bryophytic and lichen crusts dominated by *C. purpureus*, *Polytrichum commune*, *Cladonia cristatella*, *Cladonia rangiferina*, and *Cladonia gracilis* in dune swales. Biocrusts at inland pine barrens and sand plains, such as Albany Pine Bush Preserve (New York), Ossipec Pine Barrens (New Hampshire), and Rome Sand Plains (New York), ranged from algae and cyanobacteria in recently disturbed sites (Figure 4) to consolidated crusts dominated by the mosses *C. purpureus* and *P. commune*, along with the lichens *C. rangiferina* and *C. cristatella* (Figure 1; Figure 3b). The white pine and red pine (*Pinus strobus* and *Pinus resinosa*, respectively) forests of Yale Tuomey Forest (New Hampshire) and Clintonville Pine Barrens

(New York) were primarily dominated by mosses, such as *Pleurozium schreberi* and *P. piliferum* (Figure 3c), except for small areas where water scouring and mechanical disturbances have exposed bare sand. All of these species are common in the region, and many (eg *C. purpureus*, *Ditrichum lineare*, *P. piliferum*) have been associated with disturbed soils in temperate North America (Crum and Anderson 1981) and with European biocrusts (Büdel 2001; Sparrius 2011; Gypser *et al.* 2015). Algae, diatoms, and cyanobacteria in our samples included green algae in the genera *Chlorococcum*, *Klebsormidium*, and *Chlorella*; diatoms in the genus *Surirella*; and N-fixing cyanobacteria in the genus *Anabaena*.

■ A proposed research agenda for temperate biocrusts

Biocrusts are known to play key roles in dryland ecosystems, having been termed by Belnap *et al.* (2016) “an organizing principle” and the “critical zone” of dryland ecosystems. What is known about temperate biocrusts suggests that they may also play a profound role in the ecosystems they populate. Understanding the functions of temperate biocrusts is especially important given the conservation value of and ongoing threats to the unique pine barren, sand plain, alvar, sparse grassland, heathland, and



Figure 3. (a) Lichen and moss biocrusts in parabolic dunes at the Province Lands, Cape Cod National Seashore (Massachusetts); (b) bryophyte- and lichen-dominated biocrust communities including *Polytrichum piliferum* and *Cladonia rangiferina* at Albany Pine Bush Preserve, New York; (c) moss-dominated biocrusts in the white pine (*Pinus strobus*)-dominated ecosystem at Yale Tuomey Forest, New Hampshire; (d) a white pine “island” within a moss–lichen biocrust at Surry Sand Plain, New Hampshire. Shade and leaf litter from vascular plants can damage or destroy biocrusts and facilitate further vascular plant germination and establishment.

sand dune ecosystems in which they occur. We speculate that biocrusts are integral components of the healthy functioning of these ecosystems. A more holistic understanding of the interactions among biocrusts, vascular plants, and ecosystem dynamics could lead to novel management strategies for conserving and restoring these ecosystems – a necessity in the face of habitat destruction, invasion by non-native species, climate change, and other disturbances that threaten to reduce biodiversity. On the basis of our observations and prior studies, we propose the following questions about temperate biocrusts as a useful framework for further empirical research.

(1) How do temperate biocrusts influence vascular plant establishment, community composition, and succession, and vice versa?

Like drylands biocrusts, temperate biocrusts play important roles in seed germination, seedling establishment, and plant productivity (Havrilla *et al.* 2019). In sand plains and pine barrens, intact biocrusts can be limiting, neutral, or facultative with respect to seedling establishment (Sedia and Ehrenfeld 2003; Langhans *et al.* 2009; Gilbert and Corbin 2019). In sand dunes, biocrusts can enhance seed germination and seedling establishment but reduce plant productivity



Figure 4. Cyanobacteria and algae can (a) rapidly colonize newly exposed mineral soil along roads and trails and also (b) coexist with other biocrust taxa.

(Thiet *et al.* 2014). Once established, vascular plants can limit biocrusts and influence their species composition by shading and smothering biocrusts with leaf and needle litter (Figure 3d; Sedia and Ehrenfeld 2003).

Clearly, the nature of interactions between biocrusts and vascular plants varies in space and time. We hypothesize that the heterogeneous nature of these interactions, with distinct outcomes across spatial and temporal extents, results in a dynamic mosaic of biocrust- and plant-dominated patches (Panel 1). Because biocrusts can both facilitate and inhibit vascular plant establishment and growth (WebFigure 1), both patch types can occur as long as occasional disturbances reset conditions and initiate biocrust succession. Such a mosaic can explain the distinct patches dominated by biocrusts versus vascular plants that often occur within a single site or across

successional seres or stages. This mosaic of crust-dominated and vascular plant-dominated patches, driven by biocrust-plant interactions, likely has important implications for habitat provisioning and ecosystem processes in areas where biocrusts are found. Long-term empirical research at multiple study sites, along with spatial modeling, would improve our understanding of these interactions.

(2) How do temperate biocrusts influence soil nutrient cycling and other soil ecological processes?

Biocrusts may be integral to building and preserving healthy soils, and therefore may be essential for ensuring the long-term stability of the habitats they populate. We know that temperate biocrusts can greatly influence soil C, nutrient inputs, and moisture (eg Smith *et al.* 2004; Sedia and Ehrenfeld 2005; Baumann *et al.* 2017), as they do in dryland ecosystems (Belnap 2003). For example, N-fixing cyanobacteria were widespread in our samples collected from sites in the northeastern US (Figure 4), although their role in N cycling and availability remains largely unexplored. Fundamental questions about the nature of temperate biocrust-soil interactions, their mechanisms, and the scales at which they are relevant remain unanswered.

(3) Does the persistence of rare, open barren and dune ecosystems in temperate climates depend upon functioning interactions among biocrusts, soils, plants, and periodic disturbances?

Studies have shown that dryland ecosystem functioning is dependent on the interactions among biocrusts, soils, and vascular plant cover and composition (eg Weber *et al.* 2016). Such emergent properties, in which ecosystem conditions are a product of the collective system rather than the individual components, may also occur in temperate biocrust ecosystems. The nature of the interactions among biocrusts, soils, and plants in temperate ecosystems may influence key ecological processes, such as primary productivity, plant community composition and succession, and resource distribution (Panel 1), as well as the resilience of these ecosystems to habitat disturbance and climate change. Currently, our understanding of the collective interactions among biocrusts, soils, vascular plants, and ecosystem dynamics in temperate ecosystems is limited.

(4) Can biocrusts be managed to improve the long-term stability and resilience of barren and dune ecosystems in the northeastern US?

Pine barrens, sand plains, coastal dunes, and other temperate ecosystems in which biocrusts occur are a priority for conservation because of their provision of biodiversity and habitat heterogeneity at a landscape scale, and because their historical extents have declined precipitously. Considerable effort and resources are expended annually to manage these

Panel 1. Hypothesized outcomes of biocrust–vascular plant interactions

The outcomes of interactions between temperate biocrusts and vascular plants may be dynamic in space and over time. For example, biocrusts that develop on newly disturbed sites can either inhibit (WebFigure 1, purple arrows) or facilitate (WebFigure 1, blue arrows) vascular plant establishment. In the inhibitory pathway, biocrusts may limit the root penetration of vascular plant seedlings or reduce resource availability for seedlings via competition. The inhibitory effect of biocrusts could be stable over a multiyear timescale and may be responsible for the extensive biocrust cover found in many temperate ecosystems. Alternatively, biocrusts may facilitate seed germination by trapping seeds, providing moist microsites for germination, protecting

seeds from seedivores, and supplying organic matter and soil nutrients in these moisture- and nutrient-limited ecosystems. By this path, vascular plants may progressively shrink the extent of biocrusts via negative feedbacks from plants onto biocrust cover (Figure 3d) until new disturbances to the plant community re-expose the mineral soil and re-open the canopy. The two hypothesized pathways could result in a dynamic mosaic of crust-dominated and vascular plant-dominated patches within a single site as long as periodic disturbances reset the successional trajectory. Either or both of these pathways may be operating at any site, and specifics (eg biocrust species, plant species, timescale) will vary.

systems as open, early-successional ecosystems, including the use of prescribed fire (Little 1998; Bried *et al.* 2015), invasive species management (Malcolm *et al.* 2008), and restoration of degraded sites (Koster 2009; Pfitsch and Williams 2009; Büdel *et al.* 2014). Nonetheless, future challenges associated with human development and climate change loom. Research on dryland crusts suggests that healthy biocrusts could confer stability and resilience to high-stress ecosystems in the face of climate change, and that biocrusts may even facilitate recovery of degraded landscapes (Bowker 2007; Young *et al.* 2016). However, to the best of our knowledge, biocrusts are not integrated into the management plans and activities of any site in the temperate US.

Little is known about the optimal disturbance regime that would best achieve management goals related to biocrusts (Howe 2016; Williams *et al.* 2018). Before we can establish management goals for biocrusts, we must understand their basic structure, composition, and ecology, including their effects on vascular plant productivity, soil properties, and wildlife diversity. Treatment strategies and schedules to maintain biocrust communities could be consistent with – or may differ entirely from – existing protocols designed for animals and vascular plants (eg fire management, tree thinning).

Conclusion

Recognition of the existence and ecological importance of temperate biocrusts offers exciting opportunities to develop a more holistic view of and research agenda for the distinctive, biodiverse, and globally rare ecosystems where they occur. Biocrusts are much more widespread beyond the arid and semiarid systems in which they are better appreciated. We urge plant and soil ecologists working in temperate regions to consider the potentially critical functions of the biocrusts that may populate their study sites. Students, in particular, take note: these areas of biocrust research are wide open. Just as Belnap (2003) raised awareness of “the world at [our] feet” in deserts, we hope that a wider recognition of biocrusts in

temperate ecosystems will lead to the discovery of new and important aspects of these systems.

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