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RESEARCH ARTICLE

Assisted dispersal and retention of lichen-dominated biocrust material for arctic restoration

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Arctic biocrust loss due to industrial activity can have long-lasting ecological impacts, highlighting the importance of restoring disturbed tundra environments. This research focused on biocrust establishment on substrates of by-product materials from diamond mining (crushed rock, lake sediment, processed kimberlite), inoculant dispersal (dry placement, slurry), habitat amelioration (erosion control blanket, tundra soil, woody debris), and containment (jute mat), over three field seasons at Diavik Diamond Mine, Inc., Northwest Territories. Three years after inoculation, lichens were detected on 100% of inoculated plots and 70% of uninoculated plots (likely blown in from inoculated plots). Uninoculated plots had significantly lower species richness and vegetation cover than inoculated plots. Biocrust retention was highest on plots with erosion control blanket, containment, woody debris, and crushed rock; larger scale application of these treatments should be assessed in future. Plots with processed kimberlite, no habitat amelioration or tundra soil, and no containment had the lowest cover, species richness, and individual species abundance in year 3. This research suggests that active restoration techniques using lichen biocrust inoculation and habitat amelioration is required for successful biocrust revegetation outcomes on substrates of mining by-products in the arctic.

Key words: arctic, biocrust, lichen, restoration, revegetation, tundra

Implications for Practice

- Arctic macrolichens and bryophytes in biocrusts survived for three field seasons on three diamond mining by-products; biocrust survival was greater on crushed rock and lake sediment than on processed kimberlite. Thus unamended processed kimberlite is not recommended for restoration.
- Biocrust application is necessary to ensure sufficient species composition and abundance on mining by-products in arctic environments.
- Habitat amelioration and containment techniques that increased microtopographic variability, including erosion control blanket, jute mat, and woody debris had more consistent and predictable responses for retaining biocrust material on small field plots; larger scale field application of these techniques should be investigated to accelerate biocrust restoration of disturbed arctic environments.

Introduction

Resource extraction by mining and oil and gas companies has large environmental footprints, and continues to expand in Canada's Arctic. Diamond mining creates vast piles of crushed rock and processed kimberlite, leaving previously vegetated areas exposed to wind and water erosion and unable to support the unique tundra species (Rausch & Kershaw 2007). To restore ecological function to these environments, either natural or assisted revegetation is needed for dominant communities including shrub-heath species (Ficko & Naeth 2021) and biological soil crusts (biocrusts). Biocrusts are complex communities of poikilohydric organisms, such as algae, bacteria, cyanobacteria, fungi, lichens, liverworts, and mosses, that form a thin horizontal layer in association with the top few centimeters of the soil surface (Eldridge & Greene 1994; Belnap & Lange 2003; Belnap et al. 2016). Biocrusts may be pioneer communities in primary and secondary succession pathways or components of mature arid and semi-arid ecosystems, including polar environments, where they often have higher species diversity than vascular plants (Bowker 2007; Rosentreter et al. 2016; Wietrzyk-Pełka et al. 2021). Biocrusts reduce soil erosion and increase soil stability, modify infiltration and soil water retention, create habitat for soil invertebrates, alter seedling establishment and plant productivity, and increase soil fertility and nutrient cycling (West 1990; Eldridge & Greene 1994; Belnap & Lange 2003; Weber et al. 2016). In boreal and

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tundra environments, biocrusts can form mats of fruticose lichens, contributing a significant portion of the winter diet of caribou which are hunted or farmed by many inhabitants of arctic regions including Indigenous and First Nations communities (Ahti 1977; Thomas & Hervieux 1986; Kumpula 2001).

Biocrusts are sensitive to trampling, grazing, mining, pipeline construction, climate change, invasive species, and fire (Eldridge & Greene 1994; Harper & Kershaw 1996; Ferrenberg et al. 2015; Weber et al. 2016). Biocrust disturbances can affect terrestrial biogeochemical cycling, which can cause long-term changes in local (potentially global) ecosystems (Jandt et al. 2008; Ferrenberg et al. 2015; Ferrenberg et al. 2017). Despite their importance, research focusing on biocrust restoration has mostly only occurred in the last few decades, perhaps because biocrust rehabilitation was perceived as being unrealistic due to "their slow unassisted recovery from disturbance" (Bowker 2007). However, linear extrapolations of short-term studies show recovery times from as little as 6 years to millennia in the harshest environments (Weber et al. 2016). Kidron et al. (2020) suggested that most types of crusts can recover within 20 years following disturbance, unless abiotic factors such as soil recovery are also necessary following disturbance, in which case recovery may take thousands of years. Assessment of biocrust growth and survival in the arctic and on mining by-products is an important area for future research.

Potential factors affecting succession and recovery of biocrusts include type and extent of disturbance, likelihood of further disturbances or threats to establishment, proximity to inoculating material, reproductive strategies of component species, environmental conditions, and habitat and substrate including soil type, soil stability, and soil texture (Eldridge & Greene 1994; Belnap & Eldridge 2001; Smith 2014). While lichens, bryophytes, and algae can reproduce by sexual diaspores, asexual reproduction by fragmentation and vegetative diaspores is more common for many species (Bowler & Rundel 1975; Vitt et al. 1988; Brodo et al. 2001; Root & Dodson 2016). Assisted recovery must address propagule scarcity (inoculation), resource limitations (resource augmentation), and actively eroding soils (artificial soil stabilization; Bowker 2007), with the latter two interventions recently referred to as habitat ameliorations (Antoninka et al. 2020; Bowker et al. 2020). In particular, several studies using *Cladonia* species showed that increasing microtopography appeared to increase inoculant retention and survival (Maestre 2003; Roturier et al. 2007). For large disturbances such as mine sites, substrate composition, limited resources for revegetation, propagule scarcity, especially for internal areas far from undisturbed vegetation sources, and high transportation costs are key restoration barriers.

Interest in assisted biocrust establishment using single or multiple biocrust species has recently increased, often to restore ecological benefits (Pointing & Belnap 2012; Bu et al. 2013; Zhao et al. 2016; Antoninka et al. 2018). No known research addresses propagation and dispersal of lichen biocrusts for restoration in arctic tundra, although studies assessed assisted dispersal of biocrusts in alpine environments (Letendre et al. 2019), and lichens in other ecosystems (reviewed in Smith 2014) including reindeer husbandry (Roturier et al. 2007; Roturier & Bergsten 2009), endangered species conservation (Lidén et al. 2004), lichen biodiversity maintenance in managed forests (Sillett & McCune 1998; Hazell & Gustafsson 1999; Hilmo 2002), and restoration (Duncan 2011; Gypser et al. 2015; Ballesteros et al. 2017; Lorite et al. 2020). Inoculation techniques commonly assessed in the growth chamber and field have included transplantation of whole crust pieces, sieving crust material to simulate natural vegetative fragmentation, dry or wet (in a slurry) dispersal, and spreading of individual species (Belnap 1993; Scarlett 1994; Roturier & Bergsten 2009; Stewart & Siciliano 2015). Inoculation with field collected, mixed species biocrust material in a slurry or by dry placement accelerated recovery on disturbed soils, with higher species coverage and diversity, chlorophyll content, and improved soil properties (Belnap 1993; Scarlett 1994; Bowler 1999; Maestre et al. 2006; Xiao et al. 2008; Chiquoine et al. 2016; Antoninka et al. 2018; Bowker et al. 2020). Given the increase in arctic resource exploration and extraction, further evaluation of inoculation techniques and methods to assess recovery and restore crusts to severely disturbed areas in remote field locations are needed.

In this study we begin to redress that knowledge gap, using biocrust material collected in a tundra ecosystem at Diavik Diamond Mine, Inc., Northwest Territories, Canada. Our aim was to investigate the effectiveness of a variety of restoration techniques in enhancing arctic, lichen-dominated biocrust restoration. We used macrolichens as indicators of the entire biocrust community because they are the dominant life form in the arctic biocrust at our research site and they are easy to identify nondestructively. Given the remoteness of the site, we investigated the effects of readily available substrates, and addition of biocrust inoculant, habitat amelioration, and containment techniques on the reestablishment of the lichen-dominated biocrust. Of the available mining by-product substrates (crushed rock, lake sediment, and processed kimberlite), we hypothesized the microtopography created by crushed rock would promote biocrust retention. To test the hypothesis that hydrated inoculant would have higher retention and regrowth, we used dry and wet (slurry) inoculant dispersal to introduce propagules. Of the three amelioration techniques investigated, (erosion control blanket, tundra soil, and woody debris) we hypothesized that locally harvested tundra soil would be most similar and thus most effective at promoting biocrust propagule retention and recovery. Finally, we tested whether the addition of containment (jute mat) would also promote biocrust retention given the open, windy nature of the site. To test these hypotheses, we assessed biocrust cover, species richness, and species composition changes 3 years after biocrust inoculation.

Methods

Research Site Description

Diavik Diamond Mine is located on an island in Lac-de-Gras, 320 km northeast of Yellowknife, Northwest Territories (64°30′41″N, 110°17′23″W), approximately 100 km north of the treeline (the local latitude north of which no trees grow). Lac-de-Gras is in the Southern Arctic Ecozone, and the Point Upland Arctic Ecoregion (Ecosystem Classification Group 2012), with mean annual precipitation 285 mm (over half snow) and mean annual temperature −9°C, from 2011 to 2016. In upland areas, turbic and static cryosolic soils dominate (Drozdowski et al. 2012), with dwarf heath shrubs, including *Arctous rubra* (Rehder & Wilson) Fernald (red bearberry), *Betula glandulosa* Michx. (bog birch), *Empetrum nigrum* L. (crowberry), *Kalmia procumbens* (L.) Gift & Kron (alpine azalea), *Rhododendron tomentosum* Harmaja (marsh Labrador tea), *Salix* sp. (willow), *Vaccinium uliginosum* L. (bog bilberry) and *Vaccinium vitis-idaea* L. (bog cranberry), and lichen-dominated biocrust communities.

Arctic biocrust species diversity often exceeds vascular plant diversity. Approximately 360 lichen species are documented for Northwest Territories (Goward & Björk 2012), with over 50 macrolichen species identified at Diavik (Ficko unpublished; Fig. S1). Dominant lichens included *Alectoria ochroleuca* (Hoffm.) A. Massal., *Bryocaulon divergens* (Ach.) Kärnefelt, *Bryoria nitidula* (Th. Fr.) Brodo & D. Hawksw., *Cetraria* Ach. sp., *Cladonia* P. Browne sp. (cupped species, reindeer lichens), *Dactylina arctica* (Hooker f.) Nyl., *Flavocetraria cucullata* (Bellardi) Kärnefelt & A. Thell, *Flavocetraria nivalis* (L.) Kärnefelt & A. Thell, *Gowardia nigricans* (Ach.) P. Halonen, L. Myllys, S. Velmala, & H. Hyvärinen, *Masonhalea richardsonii* (Hooker) Kärnefelt, *Melanelia* stygia (L.) Essl., *Parmelia* Ach. sp., *Sphaerophorus globosus* (Hudson) Vainio, *Stereocaulon* Hoffm. sp., *Thamnolia vermicularis* (Sw.) Ach. ex Schaerer. Taxonomy follows Esslinger (2019). Eighteen species of mosses (Lamarre 2016) and three liverworts were present at Diavik.

Experimental Design and Treatments

A split-split-plot experimental design embodied four crossed factors. There were three substrates (crushed rock, lake sediment, and processed kimberlite) × three inoculation treatments (dry, slurry, and none) × four habitat amelioration treatments (erosion control blanket, tundra soil, woody debris, and none)- × two containment treatments (jute mat and none; Fig. 1).

Three blocks on raised gravel beds of crushed granite waste rock (0.13, 0.31, and 0.34 ha in area) had been established in 2008 on natural eskers and were remixed with an excavator to loosen compact soil and remove any vegetation prior to our research. Each block was divided into three equal sized main plots, which randomly received one of three mine waste materials as substrate; crushed rock (no substrate over gravel bed), 50-cm lake sediment (from mining pits after diking and water pumping), or 50-cm fine processed kimberlite (released as slurry then dried). Substrate properties influence nutrients and water retention which affect biocrust growth and recovery. Crushed rock contained the largest portion of coarse fragments (particle size <1 mm to <50 cm; loamy sand texture; pH 7.8), followed by lake sediment (particle size <1 mm to <30 cm; sandy loam texture; pH 7.1), then processed kimberlite (particle size <1 mm; sand-loamy sand texture; pH 8.7) (Miller & Naeth 2017). Processed kimberlite had highest sand content; lake sediment had highest silt and clay (Miller et al. 2021).

Fifteen 24-m^2 sub-plots were established in main plots in available space around other research programs (five replicates per substrate). These sub-plots were divided into 1 × 1 m sub-sub-plots to accommodate 24 combinations of inoculation, habitat amelioration, and containment treatments, which were randomly allocated and applied to a 50 × 50 cm quadrat in the center of each sub-sub-plot. Thus there were 360 sub-sub-plots (24 treatment combinations × 3 substrates × 5 replicates; Fig. S2).

Habitat amelioration and containment treatments were to assess common techniques for vascular plant revegetation. Jute mat is often used to prevent erosion, retain moisture, and suppress weeds. Jute mat was considered a containment treatment as it was placed on top of other treatments. Coconut fiber erosion control blankets and jute mat were obtained from Cascade Geotechnical, Inc., and cut into 60 × 60 cm squares. Erosion control blankets and jute mat were anchored by a border of rocks; this rock border was placed around all plots for consistency.

Tundra soil (sandy loam texture; pH 4.5) was collected from an unmined area at Diavik. A mix of mineral soil and humus soil was collected to a depth of 10–15 cm. Soil was mixed on a tarp using shovels to increase homogeneity. Large clods were broken into smaller pieces. Each soil treatment received approximately 3 L of soil evenly spread to a depth of 1 cm.

Woody debris was collected from tundra surrounding the plots. Cuttings were collected from *B. glandulosa*, *E. nigrum*, and *R. tomentosum*, 5–45 cm long. A mix of all three species was spread on each plot. Small handfuls of substrate material were placed on top of cuttings to help prevent litter movement. Approximately 75% cover was initially achieved using cuttings as leaves were present.

Biocrust samples were collected with a trowel from the same area as tundra soil by removing 1–2 cm deep patches with visible macrolichens where the crust naturally split when disturbed. Material was air dried and sieved (1-cm grid; Fig. S1) to increase propagule number from donor thalli using the natural fragmentation capacity of lichens. Sieved material (28.2 kg) was hand mixed in large bins to create a homogenous mixture of species which was placed in paper bags and stored at 4°C prior to dispersal on 1 and 2 July. Baseline inoculation species richness was determined by examining the contents of 10% of the standardized by weight inoculation bags, and identifying the fragments within to species.

Inoculation treatments mimicked natural vegetative fragment dispersal (Jónsdóttir et al. 1999) and common revegetation techniques for spreading seed or propagules. Dry placement material was dispersed by evenly scattering 100 g of sieved lichen in a thin layer across the surface of each sub-sub-plot. Slurries were prepared by mixing 100 g of sieved biocrust material with 1 L of untreated lake water. After 5 minutes, the slurry was poured as evenly as possible across the sub-sub-plot. Material in large clumps was gently spread with a hand rake evenly across the surface. Biocrust material was spread on top of erosion control blanket, tundra soil, woody debris, and sub-sub-plots with no habitat amelioration. Jute mat was placed on top of each applicable sub-sub-plot.

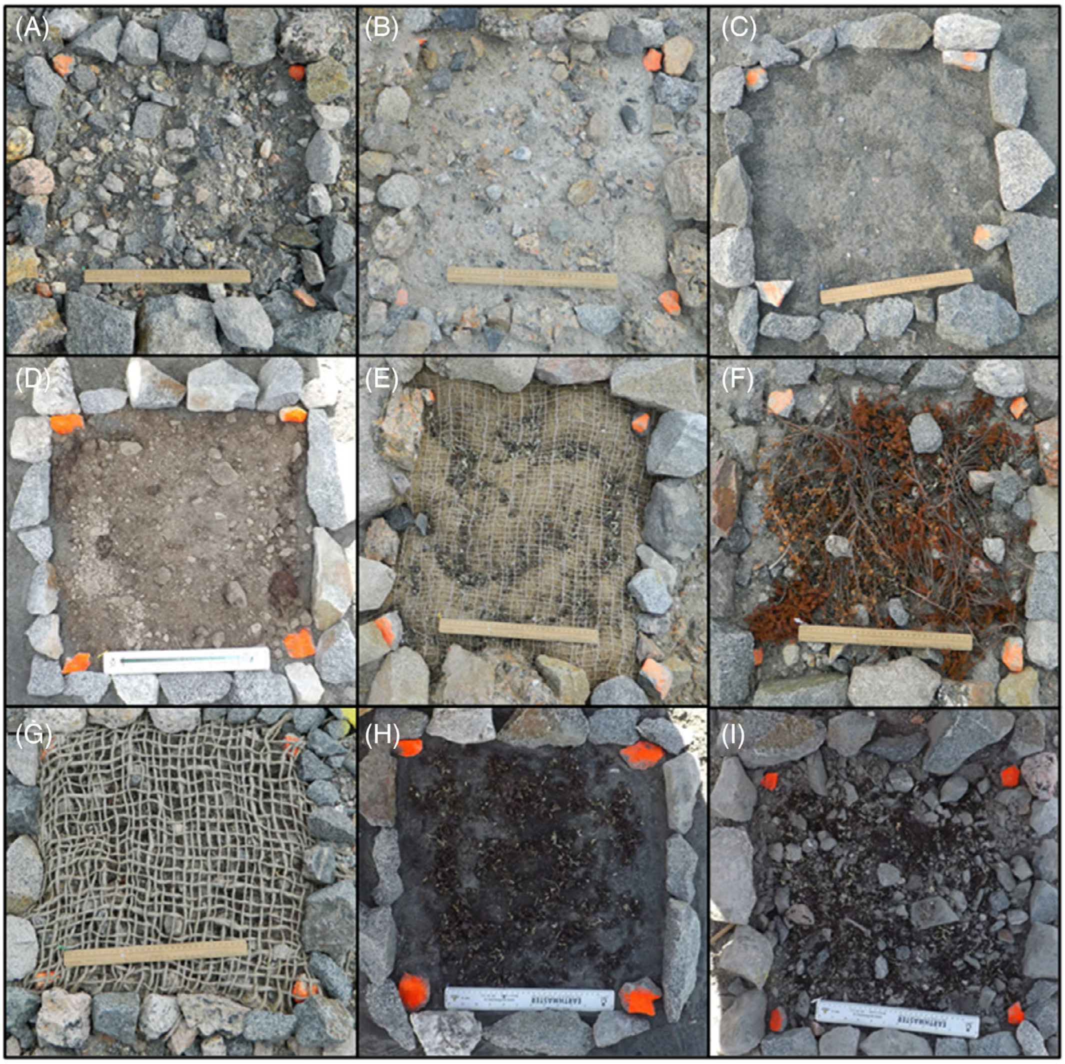

Figure 1. Images of four biocrust treatments: substrate—(A) crushed rock, (B) lake sediment, (C) processed kimberlite; habitat amelioration—(D) tundra soil, (E) erosion control blanket, (F) woody debris; containment—(G) jute; and inoculation—(H) slurry, (I) dry placement. A 30-cm ruler is shown for scale. All pictures were taken at the first assessment period except (H) and (I) which are from immediately after dispersal.

Biocrust Assessment

Nondestructive assessment of macrolichen allowed for multi-year monitoring of sub-sub-plots. While cyanobacteria and algae are frequently early colonizers of disturbed plots and have frequently been used in biocrust assessment, we investigated whether macrolichens can be used in restoration, as they are dominant, visible species in mature tundra communities.

Sub-sub-plots were visually assessed during the third week of August in years 1 (1 month after setup), 2, and 3 (2014–2016). Each sub-sub-plot was monitored for presence or absence of bryophytes and 14 species, genus, and/or morphology of lichens (hereafter lichens) including *Cetraria*, cupped *Cladonia*, reindeer *Cladonia* (previously genus *Cladina*), wand *Cladonia*, *Dactylina*, *F. cucullata*, *F. nivalis*, foliose lichens, brown hair lichens, yellow hair lichens, *M. richardsonii*, *Sphaerophorus*, *Stereocaulon*, and *T. vermicularis* to determine species richness. Nadir pictures (images taken looking directly downward, in this case with the plane of the lens parallel to the ground because of the lack of slope) were taken of each sub-sub-plot at 100 cm height with a manual focus digital camera. A colored toothpick marked the north facing corner of each plot, and a 30-cm ruler lined up with the toothpick each year to show scale. In year 3, total cover was assessed for each sub-sub-plot, and lichens were further quantified into four categories: none, tiny (1–4 fragments), some (5–19 fragments), or lots (greater than 20 fragments).

Statistical Analyses

Responses to treatment effects for year 3 data for species richness and cover were analyzed using mixed effect models (Proc Mixed) in SAS 9.4 (SAS Institute, Inc. 2013). Data for no lichen inoculation treatments were removed prior to modeling as they had a mean cover of less than 1, and residuals were markedly smaller than those of any other treatment. Optimization of models was assessed using the Akaike Information Criterion with correction for small sample size. Substrate, lichen dispersal technique, habitat amelioration, containment treatments, and all two way, three way, and four way interactions among them were designated fixed effects in the models. Substrates were randomly applied to plots on three blocks, and then subdivided into sub-plots prior to application of treatments. For species richness, heterogenous residuals for substrate and habitat amelioration were included in the final model used to determine *p*-values for fixed effects, along with block and block × substrate as random effects. For cover, heterogenous residuals for substrate and habitat amelioration were included in the final model with block, block × substrate, and sub-plot included as random effects. Preplanned orthogonal contrasts were conducted for significant main effects ($p \leq 0.05$) and adjusted for interactions by comparing relevant pairs of experimental variables for species richness and cover, respectively. Measurements are presented as means ±1 standard error.

Year 3 biocrust community composition was visualized using nonmetric multidimensional scaling ordinations with Bray–Curtis dissimilarity indices using the metaMDS function in the vegan package in R (Oksanen et al. 2020). After removing no lichen inoculation treatments, we combined dry and slurry treatments as they were not statistically different in univariate analyses. A two-dimension solution was consistently indicated as having lowest stress so we solved for the best solution. Points (sub-sub-plots) and vectors (percent cover, species richness) were made using ggplot2 package in R (Wickham 2016). Ellipses were made using stat_ellipse function in ggplot2, and represent 70% of the data. To determine differences between treatment groups, we used the adonis function in the vegan package to calculate permuational analysis of variance (PerMANOVA, 9,999 permutations) with Bray–Curtis distance matrix, permuted within block. Pair-wise comparisons with a holm adjustment for multiple comparisons were conducted using pairwise.perm.manova function in the RVAideMemoire package in R (Hervé 2021). As PerMANOVA cannot distinguish between differences in centroid location or dispersion, we tested differences in beta-diversity between treatment groups using Betadisper function in the vegan package by examining homogeneity of group dispersions with spatial medians as the group centroid for different treatments. Pair-wise comparisons within each treatment were conducted with a Tukey post hoc

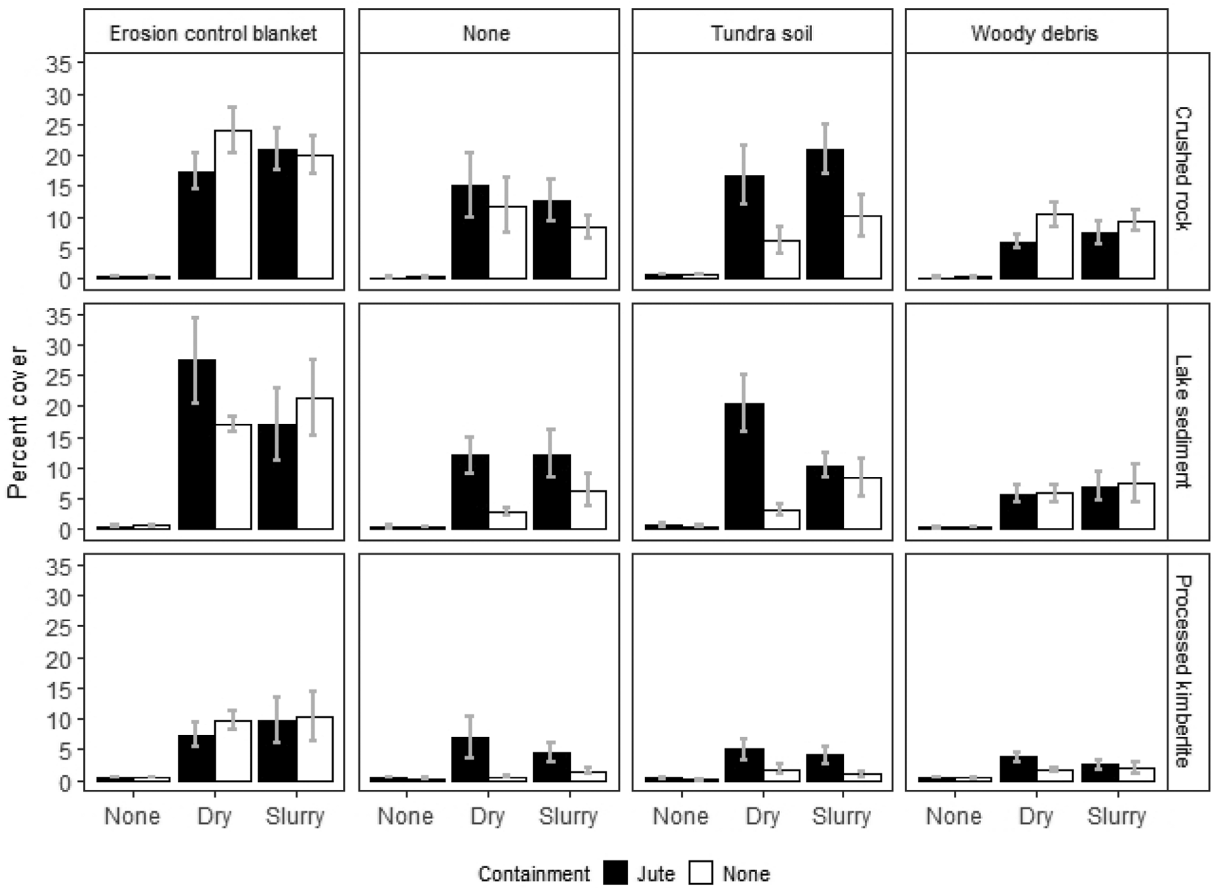

Figure 2. Year 3 cover by inoculation (*x*-axis), substrate (horizontal panels), habitat amelioration (vertical panels), and containment treatments. Each bar represents the mean, error bars are ± SE, $n = 5$. See Tables S1 and S2 for significantly different treatments.

test, adjusted for multiple comparisons. Negative eigenvalues in Betadisper were corrected by the Lingoes method (Legendre & Anderson 1999).

Change in individual species presence was calculated by subtracting probability of presence in year 2 from year 3, and was presented graphically using ggplot2. For photographic analysis, photos were cropped and edited to enhance color contrast and minimize shadows. A 15 × 15 grid (225 points) in SamplePoint (Booth et al. 2006) was overlaid on top of each picture to manually identify lichen species, litter, or substrate at each point.

Results

Assessment Technique

Due to the amelioration and containment treatments, photographs taken at the distance of 1 m above the sub-sub-plots, did not provide sufficient focus to clearly identify biocrust material to species or from nonbiocrust material for analysis of cover, and could not be compared to field measurements. Subsequently, all data presented from hereon in are from visual assessments by paired observers in the field.

Inoculation

In year 3, lichens were detected on 100% of inoculated plots and 70% of uninoculated plots. Species richness in inoculated plots ($n = 240$) was 13.4 ± 0.1 with a maximum of 15 species, 7.1 times greater than 1.9 ± 0.2 with a maximum of 9 for uninoculated plots ($n = 120$), and only 1.1 times less than initial species richness of 14.8 ± 0.1 (calculated from 10% of material in inoculant sample bags). Cover for inoculated plots was 9.9 ± 0.6 across all treatments, and <1 (maximum 2) on uninoculated plots. Because the differences in cover and species richness between uninoculated controls and inoculated plots were so great, statistics were neither necessary nor informative (because of different residual structure and data distributions). Subsequently, we restricted our statistical analyses to comparisons of different treatment combinations of inoculated plots.

Lichen dispersal (dry vs. wet slurry) did not significantly impact species richness ($p = 0.337$) or cover ($p = 0.898$) after uninoculated plots were removed from year 3 data analysis (Table S1; Figs. 2 & 3). A significant three way interaction ($p = 0.03$) indicated greater cover with dry inoculant than with slurry on lake sediment with containment; slurry inoculant on lake sediment without containment had greater cover than dry inoculant (Table S2). Change in individual species presence

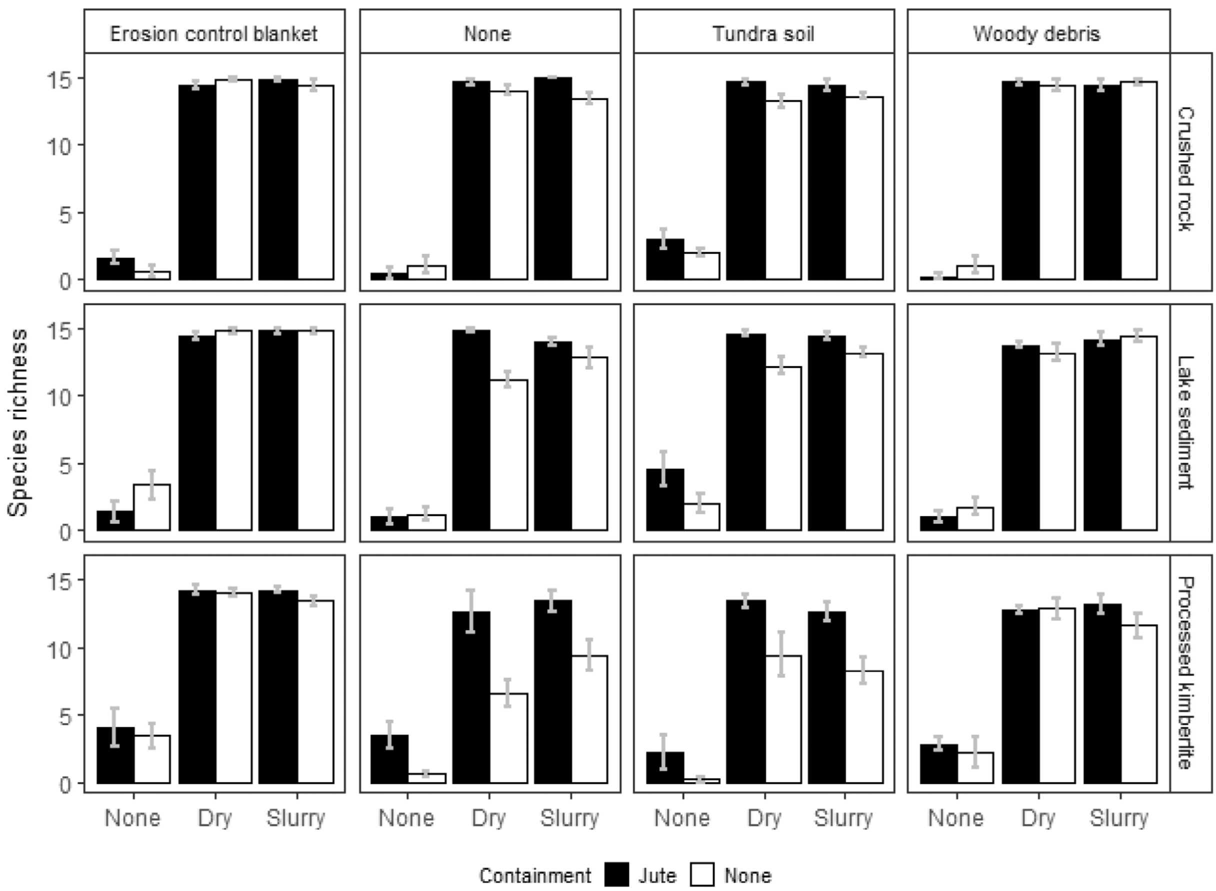

Figure 3. Year 3 species richness by inoculation (x-axis), substrate (horizontal panels), habitat amelioration (vertical panels), and containment treatments. Each bar represents the mean, error bars are ± SE, $n = 5$. See Tables S1 and S3 for significantly different treatments.

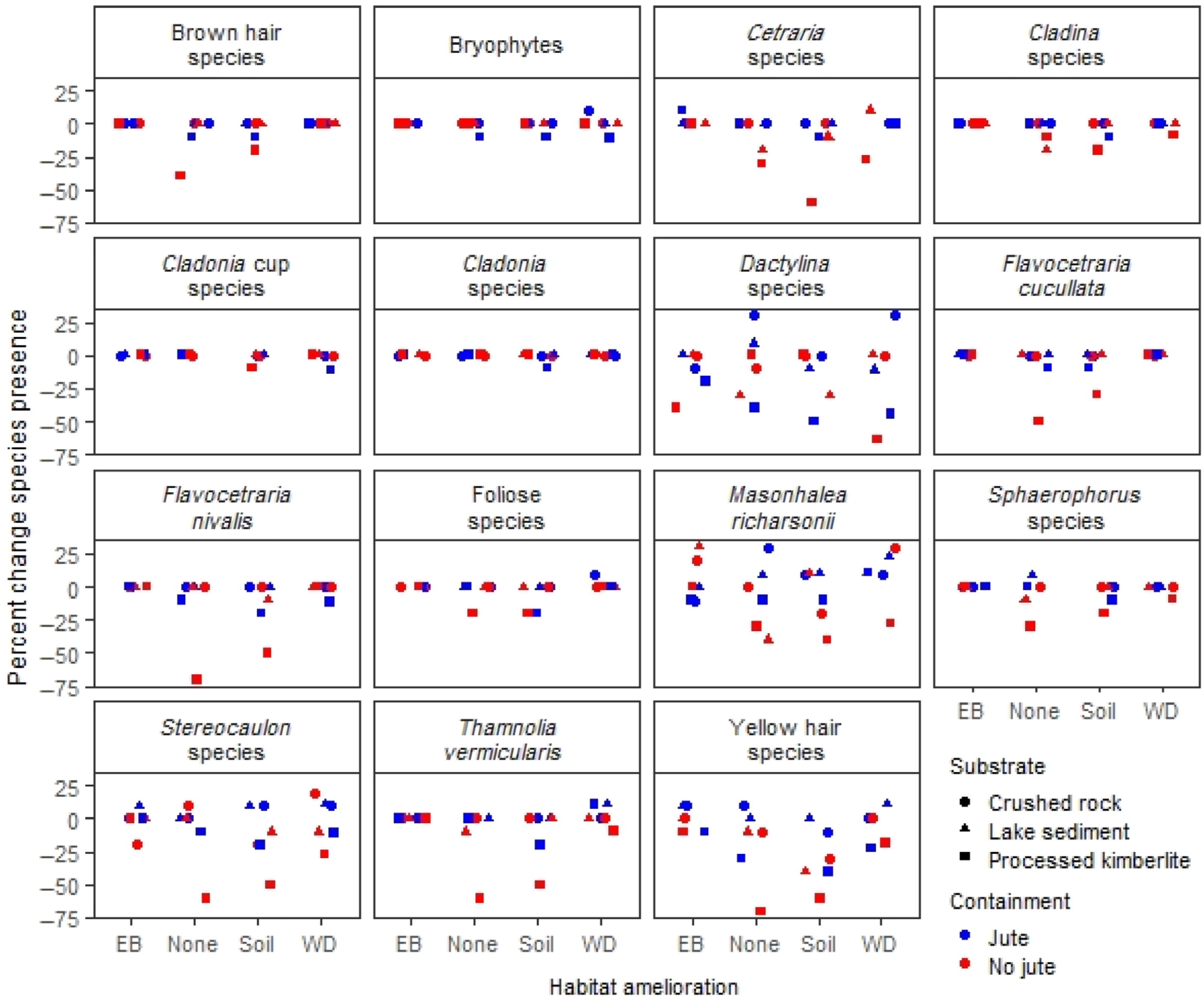

Figure 4. Percent change in individual species presence between years 2 and 3 for habitat amelioration (x-axis; EB = erosion control blanket, none = no habitat amelioration, soil = tundra soil, WD = woody debris), substrate (shape), and containment (color) treatment. Each shape in the jitter plot had a random value (between 0 and ±0.1) added to the value on the x-axis to visually separate shapes. Each shape represents the mean, n = 10.

between years 2 and 3 showed greatest declines (up to 70%) on processed kimberlite without containment and no habitat amelioration or tundra soil (Fig. 4). *Cetraria*, *Dactylina*, *F. cucullata*, *F. nivalis*, *Stereocaulon*, *T. vermicularis*, and yellow hair species declined 50 to 70% for some treatments; wand and cup *Cladonia* and bryophytes declined the least (maximum 11%).

Substrate

Cover on crushed rock (mean 9.2 ± 0.9, maximum 35) and lake sediment (mean 7.9 ± 0.9, maximum 45) was 3 and 2.5 times greater, respectively, than on processed kimberlite (mean 3.1 ± 0.4, maximum 20; Tables S1 & S2) by year 3. Similarly, species richness was 1.2 times greater on crushed rock (14.3 ± 0.1) and on lake sediment (13.9 ± 0.1) than on processed kimberlite (12.0 ± 0.3; Table S3).

A significant three way interaction occurred between substrate, habitat amelioration, and containment for cover (p = 0.15) and species richness (p = 0.037), and between substrate, inoculation technique, and containment for cover (p = 0.03; Table S1; Figs. 2 & 3). All plots on crushed rock had greater cover than on processed kimberlite regardless of inoculation, containment, or habitat amelioration treatments, while species richness on crushed rock was generally greater than processed kimberlite regardless of habitat amelioration or containment treatments, except with erosion control blanket and containment (Tables S2 & S3). Cover and species richness on lake sediment were either similar to crushed rock or an intermediary between crushed rock and processed kimberlite across habitat amelioration and containment treatments (except species richness for plots with no habitat amelioration and no containment was in between crushed rock and processed kimberlite and significantly different from both), and across inoculation and containment treatments for cover.

Community composition and dispersion (beta-diversity, variance in multivariate space) were significantly different among substrates in year 3, except crushed rock and lake sediment only differed in community composition (Table S4; Fig. 5). Crushed rock had the least variance of the three substrates, and was more strongly associated with greater cover, while processed kimberlite had the highest dispersion.

Habitat Amelioration

Erosion control blanket was the most successful habitat amelioration treatment rather than tundra soil, the natural habitat for biocrusts, with greatest species richness (14.4 ± 0.1) and cover (16.9 ± 1.3) in year 3 (Fig. 2). Erosion control blanket and woody debris had similar trends for species richness; however, woody debris had similar cover (5.7 ± 0.6) to no habitat amelioration (8.0 ± 1.0), as it was more difficult to detect lichen species under woody debris. No habitat amelioration and tundra soil had similar trends, with lower species richness and cover than erosion control blanket.

Three way interactions for substrate, habitat amelioration, and containment treatments were noted for species richness and cover (Table S1; Figs. 2 & 3). Species richness did not differ with habitat amelioration treatments on each substrate with containment (Table S3). Cover for sub-sub-plots with containment was more variable depending on substrate and habitat amelioration treatment (Table S2). Erosion control blanket and containment always had greater cover than woody debris, while cover for no habitat amelioration and tundra soil varied with substrate. Without containment, erosion control blanket treatments generally had greater species richness and cover than other habitat amelioration treatments on all substrates. Lichens were frequently observed clustered in dips on erosion control blanket with no containment. Erosion control blanket and woody debris had greater species richness than no habitat amelioration and tundra soil on crushed rock with no containment, while erosion control blanket > woody debris > tundra soil > no habitat amelioration on lake sediment or processed kimberlite with no containment.

Community composition was significantly different among habitat amendment treatments, except between no habitat amelioration and tundra soil (Table S4; Fig. 5). Erosion control blanket had the least variance, and was more highly associated with cover. No habitat amelioration and tundra soil had most dispersion, and were not significantly different from each other. Erosion control blanket versus woody debris, and woody debris versus tundra soil, differed in community composition abundance but not dispersion, while all other treatments differed in dispersion.

Containment

Containment often had more evenly distributed lichens, and had 1.4 and 1.1 times greater cover (11.5 ± 0.9) and species richness (14.1 ± 0.1), respectively, than no containment. Without containment there was more variability in species richness. A three way interaction between substrate, habitat amelioration, and containment was significant for species richness and cover, and between substrate, inoculation technique, and containment for cover (Table S1; Figs. 2 & 3). Containment on lake sediment with dry inoculant had greater cover than no containment (Table S2). However, with both containment and woody debris, it was often visually challenging to detect lichens.

Community composition and dispersion were significantly different with and without containment in year 3 (Table S4; Fig. 5). Containment had less variance than no containment, and was more highly associated with greater species richness.

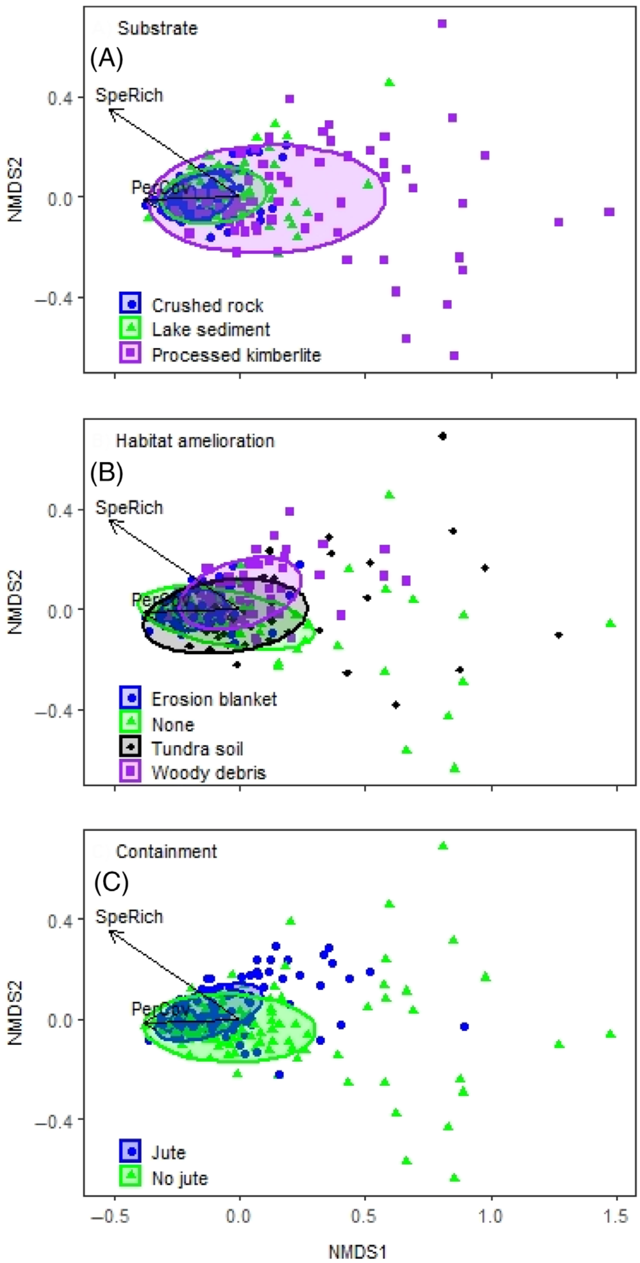

Figure 5. Nonmetric multidimensional scaling (NMDS) two-dimensional visualization of community composition for (A) substrate, (B) habitat amelioration, and (C) containment treatments. Arrows are scaled (0.65) and represent relative length and direction for cover (PerCov) and species richness (SpeRich). Ellipses represent 70% of the data. Stress = 0.10252.

Discussion

Inoculation to Optimize Biocrust Establishment

Our study is the first to demonstrate effective biocrust inoculation on mining by-products at a disturbed site in the arctic over three field seasons. The persistence of lichens on all substrates, and decreased presence of some species by year 3 is similar to results from other locations and disturbances. In a more southern location, Chiquoine et al. (2016) found inoculation with biocrust material was the only treatment to restore moss and lichen species to abandoned road surfaces in the Mojave Desert in Nevada after 18 months. Similarly, Zhao et al. (2019) found biocrusts developed from natural crust fragments collected in the Tengger Desert in northern China were more developed after 12 months compared to cultivated cyanobacteria inoculant, and had higher cover than uninoculated plots. Belnap (1993) found inoculated plots had significantly greater species richness and cover than uninoculated plots at four sites in Utah after 2–5 years, although values were significantly lower than undisturbed control sites. Antoninka et al. (2018) found greater initial cover with inoculation than without in two field experiments in Utah, with convergence after 12 or 26 months indicating natural recovery could occur. However, inoculated plots had greater cover of late successional species and species richness after 6 months, and higher soil aggregate stability, indicating the value of inoculation to accelerate restoration of ecosystem functions by biocrusts.

Proximity to undisturbed crusts has been considered important for natural recovery of disturbed areas (Belnap 1993; Bowker 2007; Weber et al. 2016; Antoninka et al. 2018). Our results show that inoculation significantly increased species richness and cover relative to uninoculated plots, indicating the importance of assisted restoration to accelerate biocrust establishment in the arctic. Lichens on uninoculated sub-sub-plots likely blew in from adjacent sub-sub-plots rather than from the tundra surrounding the experimental areas, as lichen fragments similar to sieved pieces were observed blowing between sub-sub-plots in the field, and spray painted lichen fragments were observed up to 10 m away from plots in the predominant wind direction after 24 hours (Ficko unpublished).

We expected slurry dispersal would have the best response, as lichens would have been heavier, softer, and more likely to settle into habitat ameliorants, attaching to the substrate as they changed shape with drying. Being wet during dispersal may have had a priming effect, as lichens are only metabolically active when wet (Lange 2001; Lange et al. 2001; Rajeev et al. 2013). Given the lack of differences between inoculation treatments, it is possible our hypothesis was incorrect and there was no difference in attachment. Alternatively, saturation with water may have had a counter-productive negative effect, hindering photosynthesis initially as thallus saturation slows absorption and movement of O_2 and CO_2 (Cowan et al. 1992; Lange et al. 2001). Saturation would have had a greater impact on species in our study, as most lichens were green algal dominants, which have a low threshold for water and can often start photosynthesizing from dew or high ambient humidity (Lange et al. 1994; reviewed in Nash 1996). Similarly, Antoninka et al. (2020) found watering biocrust inoculant during application did not significantly increase establishment, but noted above average rain and snow throughout their experiment. Maestre et al. (2006) found microcosms inoculated with biocrust slurry and composted sewage sludge, and watered 5 days per week, had highest nitrogen fixation and chlorophyll a content relative to no inoculation, dry inoculation, no sewage sludge, or watering twice a week after 6 months in a growth chamber. Microcosms inoculated with a slurry and watered five times a week had increased net CO_2 exchange rate. Differences in results for inoculation type relative to our study may be due to how slurries were prepared (sieving to 1 cm and mixing with water in our study versus grinding biocrust material with water in a mortar and pestle), which variables were assessed, and field versus growth chamber conditions.

While high watering frequency improved biocrust growth in the growth chamber, likely by initiating frequent photosynthesis, it would be significantly more challenging to facilitate repeated watering on a large scale at a remote arctic site with low rainfall. For large disturbances such as mine sites, particularly in the arctic, inoculation will be necessary to ensure biocrust establishment due to changes in substrates from the surrounding environment, lack of proximity to natural biocrust material, and harsh environmental conditions with a short growing season. As we found no difference in main effects between dispersal of dry biocrust inoculant or slurry, either a wet, hydroseeding-type mechanism or a dry, broadcast-type mechanism for dispersing biocrust fragments could be explored for large scale application in the arctic.

Substrate, Habitat Amelioration, and Containment Influences on Biocrust Growth and Functions

Stable soils with little disturbance are necessary for lichen-dominated biocrust establishment due to slow growth. At our site, crushed rock and lake sediment were more stable substrates than sandy textured processed kimberlite, and generally had more microtopographic variability. Decreased richness and cover, and presence of individual species on processed kimberlite in year 3 are likely due to loss of lichens by burial or wind (Ficko observations). Similarly, Zhao et al. (2021*b*) found that unamended sandy soils were more prone to wind erosion and had the lowest biocrust coverage after 12 months in the Tengger Desert. Large photosynthetic organisms in biocrusts such as lichens and bryophytes can die if buried too deeply or for too long (Jia et al. 2008). Processed kimberlite, the main by-product of diamond mining, is unlikely a suitable long-term substrate for biocrusts by itself as it has highest pH and sand content of the three substrates (Miller et al. 2021).

Much research has been conducted on ecological benefits of biocrusts for soils, but relatively little on how environmental and substrate properties such as temperature, humidity, slope, aspect, microtopography, salinity, and nutrients affect biocrust growth and succession (Zhao et al. 2016). Soil texture and pH influence species composition and distribution (Robinson et al. 1989; Belnap & Eldridge 2001), indicating decreases in presence of individual species in our study may have been due to substrate properties. For example, there was a higher frequency of various lichen and liverwort species on loamy than sandy soils at undisturbed sites in Australia (Eldridge & Greene 1994). Two studies on disturbed sites in Utah found better crust development on substrates with higher silt content (Anderson et al. 1982), or on fine textured clay loam soil than coarse textured sandy loam soil (Antoninka et al. 2020), with fine textured soil benefiting more from surface roughening to increase microtopography than coarse textured soil. Zhao et al. (2021b) found that covering sandy soils with fine textured substrates (silt, clay, very fine sand) stabilized soils and increased biocrust coverage 12 months after inoculation. Gould and Walker (1999) and Robinson et al. (1989) found decreases in lichen species richness as pH increased from 4 to 9 in different environments in the Northwest Territories. Löbel et al. (2006) found a linear increase in lichen species richness as pH increased from 3 to 8 in dry grasslands in Sweden. Zraik et al. (2018) found species specific associations with soil pH, sand shape (angular, round), and percent sand for lichens in Manitoba, indicating the importance of substrate properties to improve biocrust restoration. Crushed rock and lake sediment are also by-products of mining in the arctic, and have potential as substrates for biocrusts when combined with habitat amelioration such as erosion control blanket.

Our results determined that habitat amelioration techniques can increase biocrust species diversity, abundance, and cover on disturbed sites. While tundra soil is the natural habitat of lichen biocrusts, erosion control blanket and woody debris increased microtopography and were more successful in retaining lichens than no habitat amelioration or tundra soil, which were more exposed and susceptible to wind and weathering over time. Arctic environments naturally have diverse microtopography that supports a variety of vascular and nonvascular species (Peterson & Billings 1980; Sohlberg & Bliss 1984). Adding microtopography to post mining surface substrates creates heterogeneous microsites which have improved vegetation establishment and growth in North America and Australia (Melnik et al. 2018; Cross et al. 2021; Miller et al. 2021). Similarly for nonvascular species, Roturier et al. (2007) found differences in fragment movement and reestablishment of *Cladonia arbuscula* ssp. *mitis* on habitat amelioration treatments, with less movement of fragments placed on moss, twigs, or bark, than on bare soil. Jute mat on the soil surface prior to inoculation increased total biocrust cover for lichens and mosses after 6 and 18 months, but slightly decreased late successional cover (Bowker et al. 2020). Jute mat likely provides benefits other than containment, such as increasing microtopography, attachment sites for lichens, and/or water retention. Condon and Pyke (2016) found greater cover with jute mat for two moss species from biocrusts in Idaho and Oregon.

These results suggest habitat amelioration practices that increase microtopography such as erosion control blanket, or containment treatments such as jute mat, can also increase soil stability on some surfaces such as processed kimberlite, addressing two barriers for biocrust reestablishment as outlined by Bowker (2007). Although our results indicate application of erosion control blanket provided the most consistent and predictable response, followed by containment, then woody debris, further research is required to determine if larger scale application of these treatments has the same effect on biocrust survival as our small 0.5 × 0.5–m plots. Future studies could also assess if combinations of different habitat amelioration techniques are beneficial to biocrust reestablishment.

In this research we focused on assessing macrolichens from field collected biocrusts over time, since appropriate species richness and cover, and sufficient quantities of various species are necessary for restoration of important ecological functions provided by biocrusts. While only a few lichens had bleached by year 3, habitat amelioration and containment treatments made it too challenging to quantify specific growth patterns by photographic analyses. Similarly, habitat amelioration techniques such as woody debris combined with containment made even visual assessments of species richness and cover challenging. We attempted to improve accuracy and consistency of results by having two people do assessments in years 2 and 3, including a lichen expert. We recommend addition of other methods to quantify how ecological functions are changing as a result of biocrust development, such as quantifying chlorophyll a (common proxy for biocrust biomass; Castle et al. 2011), chlorophyll fluorescence (index for biocrust health and recovery; Maxwell & Johnson 2000), soil aggregate stability, and/or available nitrogen. Longer term monitoring is necessary as mature biocrusts can take many decades to fully establish.

Biocrust Application in the Arctic

Very few techniques to scale up dispersal of biocrust inoculant for large scale disturbances such as mine sites have been tested, especially for lichen dominant biocrusts. Restoration techniques have generally focused on seeding vascular plants to accelerate recovery of disturbed sites by drill, broadcast, aerial, or hydro seeding, although implementation in the arctic still faces many challenges (Matheus & Omtzigt 2011). As collection of natural biocrust material for restoration creates new disturbances, methods to rapidly mass cultivate cyanobacteria from biocrusts have been developed to increase the number of propagules, and can be applied in powdered or slurry form in the field (reviewed in Zhao et al. 2016; Giraldo-Silva et al. 2019). However, methods to mass most lichens have not been developed, and suitable species compositions for different environments are largely unknown. For planned disturbances such as mine sites like Diavik, salvaging biocrust material prior to disturbances could ensure appropriate material for use during mine closure, although research on appropriate storage and dispersal techniques is needed (reviewed in Tucker et al. 2020). Doherty et al. (2020) recently determined that manually broadcasting moss fragments on imprinted soil had small but significant increases in cover after 2 years at a disturbed site in Montana, but drill seeding moss fragments was unsuccessful, possibly due to burial.

Of our three substrates, processed kimberlite was least effective, alone or in combination with habitat amelioration or containment treatments. Given the extent of planned and current disturbances in the arctic, development of anthroposols from mining by-products mixed with organic or inorganic amendments (e.g. Reid & Naeth 2005*a*, 2005*b*; Larney & Angers 2012; Miller & Naeth 2017) may improve tundra restoration by creating suitable substrates for biocrusts from by-products currently stored on site. Other techniques to investigate to decrease stress and potentially improve biocrust recovery include use of shade to decrease direct UV exposure, season of dispersal to maximize preferred environmental factors such as times with higher moisture and cooler temperatures, regular watering of crusts following dispersal, creation of microtopography using furrows or imprinting, and dispersing larger fragments or even mats of biocrust material (Lamarre 2016; Zhao et al. 2016; Antoninka et al. 2020; Zhao et al. 2021a). Creation of suitable substrates and habitats are necessary to support establishment and recovery of vascular plants and biocrusts following disturbances in the arctic. Given the logistical challenges and costs with transporting anything to the arctic, integration of management and revegetation strategies will be necessary to ensure successful restoration of disturbed ecological functions.

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Supporting Information

The following information may be found in the online version of this article:

Figure S1. Representative images of the macrolichen dominated biocrust present at Diavik.
Figure S2. Google map showing location of three blocks at Diavik, and schematics showing plots and sub-plots on each block.
Table S1. Mixed model results for cover and species richness.
Table S2. Mixed model pair wise comparisons by orthogonal contrasts for cover.
Table S3. Mixed model pair wise comparisons by orthogonal contrasts for species richness.
Table S4. Changes in multivariate community composition abundance for containment, habitat amelioration, and substrate treatments in year 3.

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