


PRACTICE AND TECHNICAL ARTICLE

A restoration strategy to promote tree establishment in mining-polluted rocky outcrops using bryophytes

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Abstract

Introduction: Mining activities can lead to the formation of degraded, barren, or metal-contaminated ecosystems. Resource-poor ecosystems such as rocky outcrops are more sensitive to mining degradation, and their natural regeneration can be challenging due to soil erosion, lack of resources or seeds, and soil acidification.

Objectives: Our aim was to test the effectiveness of using locally collected bryophyte (*Ceratodon purpureus* [Hedw.] Brid.) mats as a restoration treatment to protect and promote the establishment of tree seedlings in mining-polluted rocky outcrops in Rouyn-Noranda (Canada).

Methods: The bryophyte restoration treatment inspired by natural succession processes was compared to a control, where only local soil was used as substrate, and to a liming treatment that increases soil pH. The three treatments were applied to sixty 1 × 1 m units located on five outcrops at various distances (1.9–26.9 km) from the pollution source. Four tested tree species were each seeded at a density of 100 seeds/m² on all units.

Results: The bryophyte treatment had a positive effect on the establishment success of Jack pine seedlings (*Pinus banksiana* Lamb.) with an establishment rate of 12% compared to 5 and 4% for liming and control treatments, respectively. Wind exposure had a significant negative effect on seedling establishment, potentially masking any negative effects of soil heavy metal concentration, which were not statistically significant.

Conclusions: Our strategy using bryophytes and mimicking natural succession has the potential to effectively regenerate trees in degraded rocky outcrops.

Implications for Practice: Using bryophytes as seedbeds helps restore small forest vegetation patches on mining-polluted rocky outcrops by mimicking natural succession processes. Bryophyte mats should be associated with the selection of seeds from resistant tree species (e.g. Jack pine). Solutions for wind management must be included as seedlings did not establish on wind-exposed sites. Liming may be used to increase soil pH, but does not have a positive short-term effect on seedling establishment. Even if the preliminary results were promising, long-term monitoring is necessary to explicitly assess whether bryophytes effectively mitigate potential effects of heavy metal contamination and facilitate tree establishment past the seedling stage.

Key words: barren restoration, bryophyte restoration, copper contamination, heavy metal contamination, Jack pine establishment, lead contamination, smelter pollution, wind erosion

Introduction

Mining-related pollution negatively impacts terrestrial ecosystems, often leading to loss of vegetation and soil fertility (Gauthier et al. 2023). In particular, smelters emit large amounts of heavy metals that accumulate in nearby water and soil (Dinis et al. 2021). This contamination negatively affects seed germination, growth, photosynthesis, and other plant metabolic processes (Seneviratne et al. 2019). Furthermore, smelters emit sulfur dioxide, which acidifies soil and therefore increases the availability of heavy metals and their toxicity to vegetation (Kicińska et al. 2022). As a consequence, mining pollution can generate barren lands that require active restoration (Winterhalder 1996).

When degradation is severe, interventionist methods such as soil transplantation and massive tree planting may be necessary (Prach et al. 2020). However, the cost of these methods may not be justified when ecosystem resilience is sufficient to ensure rehabilitation (Hodačová & Prach 2003). Passive restoration

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sometimes proves effective by simply protecting natural seedlings from disturbances or sowing seeds on smaller areas to establish plants that produce new seeds (Martins 2017). By relying on a diverse mixture of native species, passive restoration may also restore biodiversity more effectively (Prach & Pyšek 2001; Hodačová & Prach 2003).

Knowledge of natural succession processes can inform the restoration of degraded lands (Prach & Pyšek 2001). The first stage of recolonization in cold climates often involves the establishment of lichen and bryophyte mats (Garibotti et al. 2011). Once established, the bryophyte layer acts as a seed nursery by creating microtopographic and microclimatic conditions that retain moisture and reduce temperature variations (Qian et al. 1998). In a context of heavy metal pollution, some bryophyte species such as *Ceratodon purpureus* ([Hedw.] Brid.) are effective phyto-extractors that resist and accumulate metals (Jules & Shaw 1994). Consequently, bryophytes could initiate the restoration of degraded ecosystems.

In Rouyn-Noranda and Sudbury (Canada), smelters have contributed to soil contamination and caused spatially extensive damage to surrounding vegetation (Gibson et al. 2000). Several restoration methods aiming at grass and shrub establishment have already been tested, such as soil transplantation, fertilizer application, and heavy metal extraction (Winterhalder 1996; Watkinson et al. 2022). Liming is also useful in the context of mining pollution because it raises soil pH (Savard et al. 2004). Despite past efforts, however, cost- and time-effective methods for restoring mining-polluted outcrops near Rouyn-Noranda still lack.

In this study, we test a restoration treatment based on natural succession for rocky outcrops degraded by heavy metal

pollution from mining activities in Rouyn-Noranda. This treatment aims to promote tree germination and establishment by using a bryophyte substrate consisting of acrocarp moss mats (*C. purpureus*) locally collected from uncontaminated areas. We hypothesized that the bryophyte treatment would achieve higher restoration success compared to control (local substrate) and liming treatments, due to bryophyte's ability to shelter and protect germinated seedlings (Garibotti et al. 2011). We also expected that heavy metal contamination would negatively impact seedling establishment regardless of treatment.

Methods

Study Area

Our study sites are located around the city of Rouyn-Noranda, Quebec, Canada (Fig. 1). The study area lies within the Canadian Shield and is characterized by shallow soils and numerous natural rocky outcrops (Shilts et al. 1987). Despite their shallow soil, these outcrops naturally support forest and display holes and cracks that are colonized by roots of tree species resistant to their poor and relatively dry conditions (Asselin et al. 2006). Jack pine (*Pinus banksiana* Lamb.) and Paper birch (*Betula papyrifera* Marshall) are abundant early successional trees (Bergeron & Dubue 1988), while Eastern white cedar (*Thuja occidentalis* L.) is a late successional dominant tree (Bergeron 2000). Green alder (*Alnus viridis* ssp. *crispa* [Aiton] Turill.) also grows on rocky outcrops and may improve soil fertility through nitrogen fixation (Essery 2010).

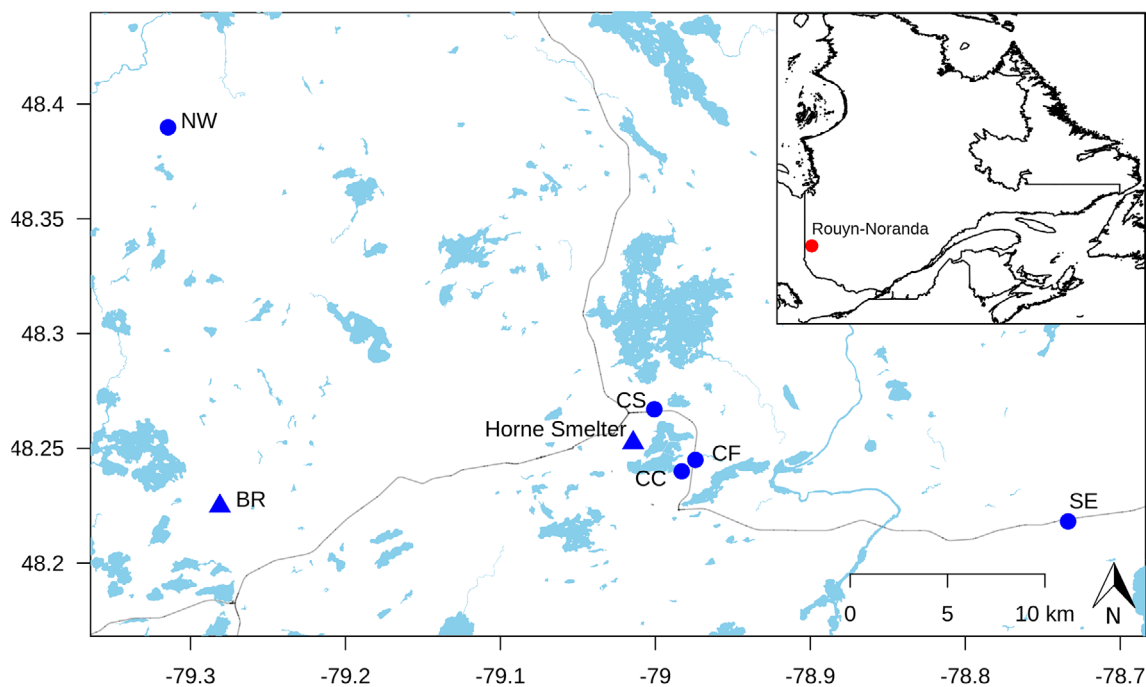


Figure 1. Location of study sites around the Home smelter in Rouyn-Noranda within Quebec, Canada. The CS site is close to the smelter surrounded by mine tailings, the CF site is close to the smelter and surrounded by forest, the CC site is close to the smelter in the city, the NW site is distant and to the northwest, the SE site is distant and to the southeast. BR, bryophyte gathering site.

Table 1. Characteristics of study sites.

Site	Category based on distance from the smelter	Actual distance from the smelter (km)	Nearby ecosystems	Position relative to the smelter
CS	Close	1.9	Mine tailings	North-East
CF	Close	3.1	Jack pine forest	East
CC	Close	2.7	Urban area	South-East
NW	Distant	26.9	Jack pine forest	North-West
SE	Distant	21.1	Jack pine forest	South-East

The Home smelter in Rouyn-Noranda was associated with a nearby copper (Cu) mine operating from 1927 to 1976. The smelter is still active today in processing Cu concentrate from distant mines and recycling Cu and precious metals from electronic components. Pollution associated with the mine and smelter led to forest degradation on rocky outcrops near Rouyn-Noranda and to forest regeneration failure (Leverington & Schindler 2018).

Site Selection and Experimental Design

We selected five basalt or dacite rocky outcrops, three of which are close (≤ 3 km) to the Home smelter and two, which are distant (>20 km; Table 1; Fig. 1). The two distant sites were chosen along a west–east axis to consider the potential effect of pollutant transport by the prevailing westerlies. Sites also differed according to their surrounding environment, with three of them surrounded by forest (Table 1). All sites were accessible by road and had a barren area large enough to install 12 experimental units.

In the summer of 2022, we installed 60 experimental units, with 4 units per site (replicates) for each of three restoration treatments. Each unit consisted of a 1 m² square quadrat built with 105 cm \times 8 cm \times 5 cm wood planks (Fig. 2). The units were placed in flat or concave areas where natural colonization would be more likely to occur. All quadrats were filled with a

3-cm thick sand layer to level substrate irregularities. Treatments were evenly distributed among sites and randomly assigned to the 12 units within each site.

The bryophyte treatment consisted of *Ceratodon purpureus* mats placed on the sand (Fig. 2A). *Ceratodon purpureus* is a cosmopolitan acrocarp moss which forms dense mats and naturally occurs in disturbed and dry habitats. We collected the bryophytes with their own soil substrate, a mixture of organic litter and sand, from a site 18 km southwest of the smelter (Fig. 1). A control treatment consisted of locally sampled soil (organic layer and topsoil, <10 cm) around each outcrop site such that soil conditions were representative of those at the site (Fig. 2B). For this treatment, the collected soil was directly applied to the units to fill a 5 cm layer above the sand layer. A liming treatment (dolomitic limestone, CaMg[CO₃]₂) was also tested in which local soil (same as control treatment) was mixed with 200 g of lime (Fig. 2C).

At the end of July 2022, we sowed seeds of four tree species (Jack pine, Paper birch, Green alder, and Eastern white cedar). We chose these species because they naturally form the dominant ecosystem on undisturbed rocky outcrops in the study area. Seeds were obtained from the National Tree Seed Centre (NTSC, Fredericton, NB, Canada) and their provenance was Quebec or Ontario. The germination rates measured by the NTSC were 76% for Jack pine, 95.5% for Paper birch, 76.5% for Green alder, and 91.5% for Eastern white cedar. We sowed 100 seeds of each species per experimental unit and then lightly stirred the substrate to bury the seeds. We counted germinated seeds during the first week of September 2022 and established seedlings at the beginning of August 2023.

Soil Measurements

Eight soil samples were collected at each site in 2022 from the soil that was used in control and liming treatments to assess soil fertility and contamination. Samples were dried in an oven at 50°C for 24 hours and sieved to 2 mm for chemical analyses.



Figure 2. Examples of the three treatments as of August 2023: (A) bryophyte, (B) control and (C) liming.

Ten grams of each sample were used to measure pH. The pH was measured again at the end of summer 2023, but this time with one soil sample per unit (total of 60 samples). For the 2022 samples, the remaining portion of each sample was mixed equally to form five composite samples (one for each study site), which were analyzed for cation exchange capacity (CEC), carbon/nitrogen ratio (C/N), and metals. The analyzed metals were Cu, lead (Pb), and cadmium (Cd) as these are the main ones emitted by the Horne smelter (Dinis et al. 2021). The substrate of the bryophytes and the sand used in our treatments was also tested and displayed low metal concentrations (0.05–15 mg/kg depending on the element; Table S1). Detailed methodology for soil analyses can be found in Supplement S1.

Foliage Measurements

Foliage samples of vegetation at the study sites were also collected during the summer of 2022 to evaluate pre-existing contamination. Three vegetation layers were sampled: shrubs (*Kalmia angustifolia* and/or *Rhododendron groenlandicum*), herbaceous vascular plants (*Maianthemum canadense* and/or *Poaceae* spp.), and bryophytes (*Polytrichum* spp.). The samples were dried in an oven at 37°C for 24 hours, sieved to 2 mm, and then analyzed for metals following the methods used for soils.

Measurement of Abiotic Site Conditions

Additional wind and solar radiation measurements were taken to further characterize the study sites. These measurements are detailed in Supplement S1.

Statistical Analysis

Out of the four tree species, only Jack pine established sufficiently for statistical analysis. We modeled the number of established Jack pine seedlings per experimental unit in 2023 using a generalized linear mixed model with a log link function and a negative binomial distribution of model residuals. We fitted four models that respectively included (1) Cu concentration in the soil, (2) wind exposure, (3) sunlight exposure, and (4) none of the preceding three variables. The effects of treatment (fixed effect) and site (random effect) were included in all four models. Only one numerical variable was tested per model due to strong correlation between them (Table S2). We chose Cu as a representative heavy metal as Cu was extracted by the Horne Cu mine and is still produced by the smelter today. Cd and Pb concentration were not used to build models due to their very high (>0.98) correlation with Cu concentration (Table S2). Models were fitted using the `glmer.nb` function of the `lme4` R package (Bates et al. 2015) and model selection was done using the `AICcmodavg` R package (Mazerolle 2023). Additionally, differences in pH after 1 year between units and differences in sunlight exposure between sites and units were calculated with analysis of variance (ANOVA) and post hoc Tukey tests. All statistical analyses were conducted using R version 4.4.1

(R Core Team 2024) and the complete dataset is available in Supplement S2.

Results

Heavy Metal Concentration and Abiotic Variables

Metal concentrations in the local soil sampled at two of the sites close to the smelter (CS and CC) were up to 200 times higher (787 and 1394 mg/kg for Cu; 281 and 743 mg/kg for Pb) than those at the other sites (Table 2). Sites CS and CC were also more exposed to wind, likely due to their lack of a nearby forest cover (Table 2).

Heavy metal content in the local vegetation was higher at the close sites, with Pb (up to 1066 mg/kg) and Cu (up to 4549 mg/kg) concentrations 10–200 times higher than distant sites (Table S3). Despite the low soil metal concentrations at site CF (3.1 km from the smelter), metal concentrations in vegetation were high, comparable to other sites close to the smelter (Tables 2 & S3). In general, metals were more concentrated (up to 46 times more) in the bryophyte layer than in the herbaceous and shrub layers (Table S3).

Physicochemical characterization of the soils confirmed that sites surrounded by forest had a higher C/N ratio and sites with high heavy metal content in soil had a higher CEC (Table S4). Experimental units of sites surrounded by forest were also less exposed to sunlight (Fig. S1). All treatments increased soil pH of the units in 2023 relative to 2022, with the liming treatment showing a greater increase (up to 2.5) compared to the control, while the soil in the bryophyte treatment showed intermediate values between control and liming treatments (Fig. S2).

Germination and Establishment of Seedlings

Jack pine established most effectively, with 1655 germinated seeds in 2022 and 431 seedlings established in 2023 across all sites. Conversely, only 14 Paper birch seedlings, 14 Green alder seedlings, and no Eastern white cedar seedlings were counted in 2023. On average, 3.4 and 12.9 Jack pine seedlings established per unit at close and distant sites, respectively (Fig. 3; Table 3).

The bryophyte treatment yielded more germinated Jack pine seeds in 2022 and established seedlings in 2023 than other treatments (Table 4). The 2022–2023 survival rate of pine seedlings

Table 2. Heavy metal concentration in the soils (mg/kg) for copper (Cu), lead (Pb), and cadmium (Cd), and wind exposure (m/s; 95th percentile of the average wind speed) at the study sites. The full distribution of wind speed values is shown in Fig. S3.

Site	Cu (mg/kg)	Pb (mg/kg)	Cd (mg/kg)	Nearby forest cover	Wind exposure (m/s)
CS	787	281	1.16	No	7.1
CF	37	4	0.33	Yes	0.7
CC	1394	743	2.61	No	4.5
NW	14	3	0.10	Yes	1.6
SE	25	7	0.32	Yes	0.7

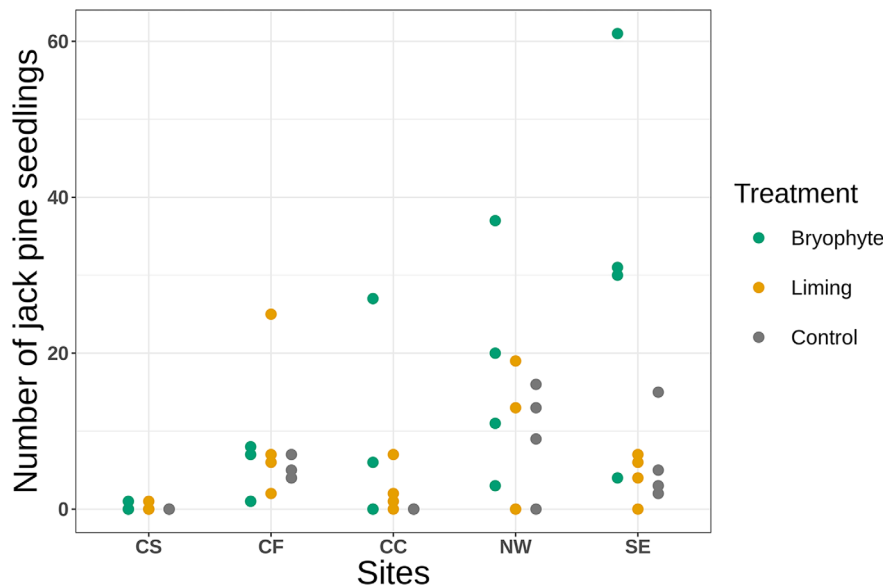


Figure 3. Number of Jack pine seedlings established in 2023 by site and treatment used. Four units per treatment were assessed at each site. See Table 1 for site characteristics.

was also greater under the bryophyte treatment, with a 36.5% survival compared to 19.2 and 18.2% for the other treatments (Table 4). However, the positive effect of the bryophyte treatment was heterogeneous across sites and may therefore vary based on site characteristics (Fig. 3). Over the timespan of our study, we did not observe natural bryophyte colonization in the control or liming plots. However, we did observe a tendency for herbs to colonize liming plots.

To disentangle the effect of abiotic variables on Jack pine establishment, we tested four statistical models. The best model according to AICc was the one including wind exposure (marginal pseudo- $r^2 = 0.59$), while the worst model was the one including Cu concentration (Table S5). For the best model, confidence intervals (95%) around coefficients indicated that the bryophyte treatment had a higher success of seedling establishment compared to liming and control, and that wind exposure reduced seedling establishment (Table S6). Model predictions show the positive effect of the bryophyte treatment but also that wind exposure largely masks this effect at higher (>3 m/s) wind speed (Fig. 4). The expected numbers of established seedlings are, respectively, 38, 15, and 9 under zero wind speed for the

bryophyte, liming, and control treatments in our experimental conditions (Fig. 4).

Discussion

Our results show that the bryophyte treatment had a positive effect on Jack pine establishment 1 year after seeding under low wind speed conditions. Seedlings under bryophyte treatment may have benefitted from the moisture retention granted by bryophytes (Hu et al. 2023), which could have been critical given the high sun exposure at our sites. Moreover, at the end of the winter of 2023, we observed ice needles on several units under control and liming treatment, but not under bryophyte treatment. The protective effect of bryophytes against ice needles has already been documented (Groeneveld & Rochefort 2005) and may have contributed to the establishment success of seedlings. The increase in substrate pH associated with the bryophyte treatment could also have benefitted the seedlings, although this is likely not the only explanation as the liming treatment increased the pH even more. Overall, the bryophyte treatment is a promising option for low-impact and cost-effective restoration inspired by natural succession. This treatment could be used to reintroduce small vegetation patches

Table 3. Number of Jack pine seedlings counted in 2022 and 2023 at each site and their survival ($n_{2023}/n_{2022} \times 100$) and establishment rates ($n_{2023}/1200$ seeds per site $\times 100$). For site characteristics, refer to Table 1.

Site	n germinated seeds 2022	n established seeds 2023	Survival rate 2023/2022 (%)	Establishment rate (%)
CS	63	2	3.2	0.2
CF	358	77	21.5	6.4
CC	78	43	55.1	3.6
NW	733	141	19.2	11.8
SE	423	168	39.7	14.0

Table 4. Total number of Jack pine seedlings counted in 2022 and 2023 for each treatment and their survival ($n_{2023}/n_{2022} \times 100$) and establishment rates ($n_{2023}/2000$ seeds per treatment $\times 100$).

Treatment	n germinated seeds 2022	n established seeds 2023	Survival rate 2023/2022 (%)	Establishment rate (%)
Bryophyte	679	248	36.5	12.4
Liming	520	100	19.2	5.0
Control	456	83	18.2	4.2

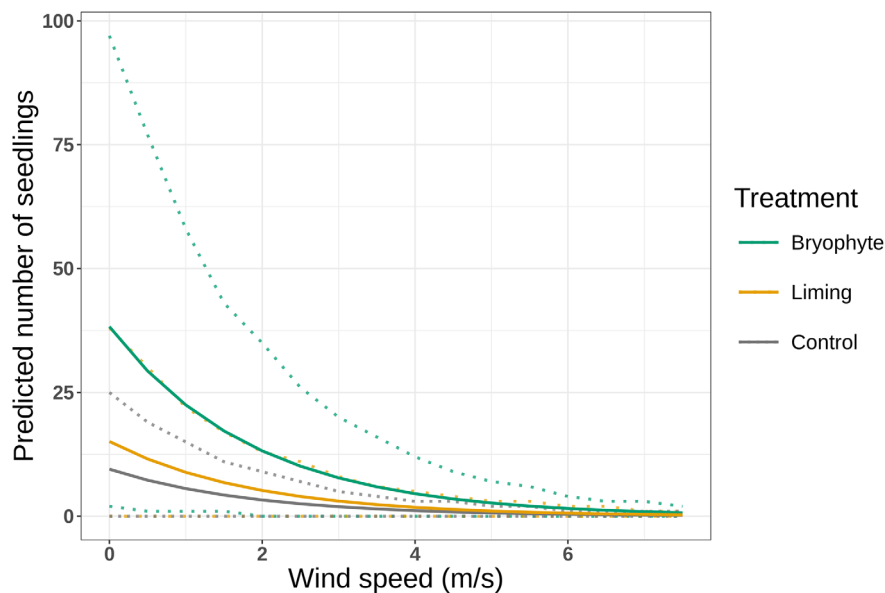


Figure 4. Predicted number of established Jack pine seedlings per 1 m² unit according to a generalized mixed linear model with treatment and wind exposure as fixed effects. Confidence intervals (80%) are shown with dotted lines.

of native, well-adapted tree species in degraded sites, thereby facilitating natural succession, regeneration, and enhancing biodiversity.

Despite the success of the bryophyte treatment, our results show that wind exposure has a negative impact on Jack pine establishment and may cancel out any positive effects. The negative impact of wind on seedling survival could be explained by the damage caused to plants by strong winds. Dust abrasion damages seeds and adult plants, and the hydric stress caused by high wind exposure reduces plant growth and productivity (Duniway et al. 2019). These impacts were likely the main cause of the very limited establishment success observed for the other three planted species. Although Paper birch, Green alder, and Eastern white cedar are commonly found on vegetated rocky outcrops, Jack pine can outperform these species on barren surfaces due to its rapid root development and responsive stomatal behavior (Marchand et al. 2021). It is also possible that some seeds were carried out of the experimental units by the wind. Wind speed measured at the sites appeared to be correlated with the area of the barren surface at the outcrops. The wind protection offered by a nearby forest cover could therefore be relevant in a restoration context (Gardiner et al. 2016).

We could not confirm a negative impact of heavy metal contamination on restoration success in this study, perhaps because wind exposure masked any such effect at this short time scale. While wind exposure has immediate effects on seeds and seedlings, metal exposure is an accumulative process that depends on the availability and quantity of metals over time (Filipović-Trajković et al. 2012). It is likely that the metal concentration at close sites reached toxic levels, even though it is difficult to find exact toxicity thresholds for heavy metals (Ghori et al. 2019). Indeed, the Cu concentrations in the soil of our two most contaminated sites (787 and 1394 mg/kg) were similar to those found in Sudbury, where a negative impact of toxicity

has been demonstrated (Dudka et al. 1996; Adamo et al. 2002). Similarly, effects of Pb on plant roots appear at 10 mg/kg (Sharma & Dubey 2005), far below the values measured at close sites. Pre-existing vegetation at the sites may also play a role in heavy metal availability. For example, site CF (surrounded by forest) displayed heavy metal concentrations that were high in vegetation, but low in soil. Since heavy metals can bioaccumulate in vegetation (Wang et al. 2021), a large portion of the metals may have been transferred from the soil to the vegetation at this site.

Our results are limited to the early tree establishment stage, and it is therefore possible that the bryophyte treatment will not be effective over the longer term. For example, the shallow soils at our sites may not provide enough material for rooting once the trees are past the seedling stage, especially if winds are strong. In a similar study that tested bryophyte turf for seed germination, Delach and Kimmerer (2002) found that the facilitative effect did not persist past the establishment stage. In other ecosystems, competition between bryophytes and tree seedlings has been documented (Harmon & Franklin 1989), indicating that the effects of bryophytes may not be purely facilitative. Despite the potential for bryophytes to accumulate heavy metals (Gezahegn et al. 2025), it remains unclear whether they can significantly reduce their availability and toxicity over the long term in heavily polluted sites. Longer-term studies on the bryophyte treatment tested here are therefore warranted and should focus on the interplay between wind exposure, heavy metal concentration, and contaminant uptake by vegetation.

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Supporting Information

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

Table S1. Heavy metal concentration (in mg/kg) for copper, lead, and cadmium in the soil substrate of the bryophytes and the sand used in our treatments.

Table S2. Correlation between numeric explanatory variables.

Table S3. Heavy metal concentration in local vegetation foliage for copper (Cu), lead (Pb), and cadmium (Cd) at each site.

Table S4. C/N ratio and CEC (cation exchange capacity; in mEq/100 g) in soil for our study sites and bryophyte and sand pick-up sites.

Table S5. Model comparison for seedling establishment.

Table S6. Estimates and 95% confidence intervals of the fixed effects of the best model (treatment and wind exposure).

Figure S1. Exposure to sunlight of units at our study sites (in % of a full light reference measure).

Figure S2. Soil pH difference between the start of the experiment in 2022 and 1 year later in 2023, depending on treatment used.

Figure S3. Distribution of wind speed values at each site averaged over 10-minute moving window intervals from 25 August to 5 September 2023.

Supplement S1. Supplementary methods.

Supplement S2. Dataset.

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