# ARTICLE

# Disturbing to restore? Effects of mounding on understory communities on seismic lines in treed peatlands

Laureen F.I. Echiverri, S. Ellen Macdonald, and Scott E. Nielsen

**Abstract:** In peatlands, microtopography strongly affects understory plant communities. Disturbance can result in a loss of microtopographic variation, primarily through the loss of hummocks. To address this, mounding treatments can be used to restore microtopography. We examined the effects of mounding on the understory vegetation on seismic lines in wooded fens. Seismic lines are deforested linear corridors (~3 to 8 m wide) created for oil and gas exploration. Our objectives were to compare the recovery of understory communities on unmounded and mounded seismic lines and determine how recovery varies with microtopographic position. Recovery was evident in the unmounded seismic lines, with higher shrub and total understory cover at the "tops" of the small, natural hummocks than at lower microtopographic positions — much like the trends in adjacent treed fens. In contrast, mounding treatments that artificially created hummocks on seismic lines significantly changed understory communities. Mounded seismic lines had higher forb cover, much lower bryophyte cover, less variation along the microtopographic gradient, and community composition less similar to that of the reference sites than unmounded seismic lines due to higher abundance of marsh-associated species. Our results suggest that mounding narrow seismic lines can be detrimental to the recovery of the understory communities in treed peatlands.

*Key words:* moderate-rich fens, linear disturbances, mounding, restoration, understory vegetation.

**Résumé :** Dans les tourbières, la microtopographie influence fortement les communautés végétales de sous-étage. Une perturbation peut entraîner une baisse de variation de la microtopographie, surtout par la perte de monticules. Pour résoudre ce problème, la création de monticules peut être utilisée pour restaurer la microtopographie. Nous avons étudié les effets de la création de monticules sur la végétation de sous-étage dans des lignes sismiques traversant des tourbières boisées. Les lignes sismiques sont des couloirs linéaires déboisés (environ 3 à 8 m de large), créés pour l'exploration pétrolière et gazière. Nos objectifs étaient de comparer le rétablissement des communautés de sous-étage dans des lignes sismiques avec et sans création de monticules, et de déterminer comment le rétablissement varie en fonction de la position microtopographique. Le rétablissement était manifeste dans les lignes sismiques sans création de monticules, où le recouvrement d'arbustes et de végétation totale sur le dessus de petits monticules naturels était plus grand qu'aux positions microtopographiques inférieures, ce qui tendait aussi à être le cas dans les tourbières boisées adjacentes. En revanche, la création artificielle de monticules dans les lignes sismiques a considérablement changé les communautés de plantes de sous-étage. Les lignes sismiques avec des monticules artificiels avaient un recouvrement de plantes herbacées plus élevé, un recouvrement de bryophytes beaucoup plus faible, moins de variation le long du gradient microtopographique, et une composition de la végétation moins semblable à celle des stations de référence que celle des lignes sismiques non traitées, en raison d'une plus grande abondance d'espèces associées aux marais. Nos résultats indiquent que la création de monticules dans les lignes sismiques étroites peut nuire au rétablissement des communautés de plantes de sous-étage dans les tourbières boisées. [Traduit par la Rédaction]

*Mots-clés :* tourbières modérément riches, perturbations linéaires, création de monticules, restauration, végétation de sous-étage.

## Introduction

Forests across the world are experiencing increases in the levels of human disturbance that are influencing their ecological function and biodiversity (Haddad et al. 2015). In regions with oil and gas reserves, seismic lines, which are linear corridors of cleared forests used to locate fossil fuel reserves, represent a major source of human-caused disturbance(Dabros et al. 2018). There are two types of seismic lines: two-dimensional (2D) or conventional seismic lines (approximately 4–12 m wide) and three-dimensional (3D) or low-impact seismic lines (approximately 3 m wide). Conventional seismic lines are increasingly being replaced with low-impact seismic lines to mitigate the environmental impacts of oil

exploration in the boreal ecosystems. Low-impact seismic lines are created using lighter equipment and thus minimize the disturbance of the understory vegetation and underlying soil (Dabros et al. 2018). Although seismic lines are relatively narrow, they can extend for kilometres (Pattison et al. 2016) and can be locally dense (up to 40 km·km$^{-2}$). In addition, vegetation on seismic lines can be slow to recover (Lee and Boutin 2006; van Rensen et al. 2015), leaving a lasting imprint. Seismic lines affect understory vegetation composition, both within the seismic line itself and into the adjacent forest due to edge effects (MacFarlane 2003; Dabros et al. 2017). Lastly, seismic lines also act as travel corridors for predators such as wolves by improving accessibility to previously difficult terrain (Dickie et al. 2017; DeMars and Boutin 2018).

**L.F.I. Echiverri, S.E. Macdonald,\* and S.E. Nielsen.** Department of Renewable Resources, University of Alberta, 751 General Services Building, Edmonton, AB T6G 2H1, Canada.

**Corresponding author:** Laureen Echiverri (email: echiverr@ualberta.ca).

Due to the increased habitat fragmentation and predation risk to threatened species such as caribou (COSEWIC 2002), restoration of seismic lines, as measured by tree establishment and the limitation of predator movement, has become a priority. One restoration tool being used is "mounding" — the excavation and piling of soil to create "mounds" (Sutton 1993; Pyper et al. 2014). The purpose of mounding is to create suitable microhabitats for successful tree establishment and to hinder human and predator use of legacy seismic lines (Government of Alberta 2017). In this study, we focus on measuring the effectiveness of mounding to restore ground vegetation in wooded moderate-rich fens, where recovery of seismic lines has been shown to be particularly slow (Lee and Boutin 2006; van Rensen et al. 2015). While mounding has been shown to have promising effects on tree establishment in peatlands (Lieffers et al. 2017; Filicetti et al. 2019), the effects on other ecological aspects of peatlands — notably understory plant communities — requires further study. Because low-impact seismic lines have extensive coverage in areas of active exploration for oil sands resources, we will be focusing on the impact of mounding in low-impact seismic lines on the understory vegetation.

Peatlands are known for their hummock–hollow topography, which creates a diversity of microhabitats for peatland flora and fauna. Hummocks are mounds of elevated peatland vegetation, about 20–50 cm above the lowest surface level, while hollows are depressions or the lowest surface level. Understory communities are stratified along the hummock–hollow gradient based on their ability to tolerate anoxic conditions or, in the case of bryophytes, desiccation (Rydin and Jeglum 2006; Vitt and Wieder 2008). Some forbs and graminoids are adapted to survive the flooded conditions of hollows and lower microtopographic positions (i.e., having aerenchyma), while woody plants are inhibited by saturated conditions (Pouliot et al. 2012). In contrast, distance from the water table limits bryophyte distribution based on their ability to avoid desiccation in the relatively drier hummock tops (Rydin and Jeglum 2006). In turn, development of hummock–hollow microtopography is largely a reflection of differences in net primary production and decomposition rates among bryophyte species and the role of vascular plants, especially shrubs, in providing structural support for upward growth of bryophytes (Malmer et al. 1994; Vitt 2000; Rydin et al. 2006; Pouliot et al. 2011; Turetsky et al. 2012).

Compaction of peat caused by machine traffic along seismic lines in peatlands results in them being depressed in elevation relative to the surrounding areas and exhibiting reduced microtopographic complexity (Stevenson et al. 2019). The reduced elevation leads to wetter conditions on the seismic line than in the reference adjacent forest (Dabros et al. 2017), which can hinder establishment of woody vegetation. Mounding treatments result in an elevated microhabitat, which increases habitat heterogeneity and allows vegetation to escape the saturated conditions common to compacted peatlands (Lieffers et al. 2017; Caners et al. 2019). For example, in wooded moderate-rich fens, Caners et al. (2019) found higher richness and cover of woody vegetation on mounded portions of abandoned, flooded well pads. It is, however, a delicate balance as conditions that are too dry or too far removed from the water table can inhibit bryophyte establishment. For example, Price et al. (1998) found that in drier, postharvested peatlands (bog and poor fen complex), elevated microtopographic positions had reduced *Sphagnum* colonization due to a drier and warmer microclimate. Thus, mounding may benefit vascular plants but could also result in reduced bryophyte cover at the tops of artificial hummocks. This may benefit vascular plants as they would otherwise compete with bryophytes for nutrients and space (Malmer et al. 1994; Rydin and Jeglum 2006).

Here our objective was to compare the recovery of understory plant communities on mounded and unmounded seismic lines in wooded moderate-rich fens. We defined recovery as similarity to the adjacent reference wooded fen (hereafter referred to as reference sites). As understory communities stratify along the hummock–hollow gradient, we compared the effects of mounding at three microtopographic positions: top of hummock, slope or side of the hummock, and the level ground adjacent to mounds. In the reference sites, we expected shrub cover and total vascular cover to be highest at the tops of the hummocks, as the anoxic conditions at lower microtopographic positions will limit the establishment of vascular plants. Because some forb and graminoid species are adapted to anoxic conditions, we did not expect to see a strong influence of microtopographic position on forb and graminoid cover. Hummocks are naturally created by bryophyte growth; thus, we expected higher bryophyte cover at the tops of the hummocks. In the mounding treatments, we expected the restoration of the aerated rooting zone to lead to higher total vascular plant cover and shrub cover at the top of the mounds, much as in the reference sites; however, we expected the drier conditions at the top of the mounds to limit bryophyte establishment and reduce bryophyte cover. Because unmounded seismic lines have limited microtopography, we expected no difference in vascular plant and shrub cover between positions. In addition, we expected that the wetter conditions of seismic lines would result in higher bryophyte cover and reduced shrub cover.

## Methods

This study was conducted in treed moderate-rich fens near Kirby Lake, Alberta, approximately 45 km south of Conklin, Alberta, Canada (55°21′57.51″N, 111°09′46.10″W). Sites were considered moderate-rich fens based on groundwater pH values that ranged from 5.69 to 7.12 ($\mu$ = 6.46) and a moderate electrical conductivity ($\mu$ = 102.84 $\mu$s·cm$^{-1}$). Reference wooded fens were dominated by black spruce (*Picea mariana* (Mill.) B.S.P.) or tamarack (*Larix laricina* (Du Roi) K. Koch) (Appendix A, Table A1) and *Rhododendron groenlandicum* (Oeder) Kron and Judd, *Maianthemum trifolium* (L.) Sloboda, and *Sphagnum* spp. in the understory layer. Average daily temperature in the region is 2.1 °C, with an average annual precipitation of 421 mm (from nearby meteorological station Cold Lake A; Environment and Climate Change Canada 2019).

Seismic lines in the area were created in 1998–2001 during exploration for bitumen (oil sands) reserves as part of a 3D seismic program, which involves creation of narrow (~3 m width) lines in an intensive (50 to 100 m spacing) grid. These seismic lines were created in the winter, with lightweight equipment to minimize disturbance of soil and the understory. Travel by machinery on these lines has been limited since their creation. A sample of representative seismic lines was mounded in 2015 and sampling occurred three years later (late June to mid July 2018). Mounding was done using a construction excavator with a bucket attachment, which excavated and placed the inverted substrate adjacent to the newly created pit. Mounds were created to be 0.75 m wide, 1 m long, and 0.80 m tall and were placed every 6 m along the seismic lines. For additional details on mounding specifications, see Filicetti et al. (2019).

We sampled seismic lines with mounding treatments ($n = 8$) and unmounded seismic lines ($n = 9$) (Supplementary Fig. S1[1]). For each of these, we also sampled the adjacent wooded fen to represent the reference condition. Sampling for the reference wooded fen took place 25 to 50 m from the center of the seismic line, with the ecosite type kept consistent between the seismic line and the reference wooded fen. Average mound height (± standard error) was 40.1 ± 4.0 cm on the mounded seismic lines, 32.1 ± 1.4 cm on

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[1]Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfr-2020-0092.

**Table 1.** Results of the mixed-effects models for vascular species richness, Shannon's diversity, Simpson's diversity, total vascular plant cover, shrub cover, forb cover, graminoid cover, and bryophyte cover as affected by mounding treatment, microtopographic position, and their interaction.

| Response variable | Treatment | | | Position | | | Treatment × position | | |
|---|---|---|---|---|---|---|---|---|---|
| | *F* | df | *P* | *F* | df | *P* | *F* | df | *P* |
| **Diversity** | | | | | | | | | |
| Vascular plant richness | **82.31** | **2** | **<0.001** | 0.32 | 2 | 0.727 | 0.41 | 4 | 0.801 |
| Vascular Shannon's diversity | **76.29** | **2** | **<0.001** | 0.54 | 2 | 0.583 | 0.78 | 4 | 0.541 |
| Vascular Simpson's diversity | **54.98** | **2** | **<0.001** | 0.65 | 2 | 0.524 | 0.766 | 4 | 0.548 |
| **Abundance (cover)** | | | | | | | | | |
| Total vascular plant cover | 0.47 | 2 | 0.625 | **4.01** | **2** | **0.019** | **2.70** | **4** | **0.031** |
| Shrub cover | **3.54** | **2** | **0.030** | **9.28** | **2** | **<0.001** | 1.81 | 4 | 0.127 |
| Forb cover | **5.75** | **2** | **0.004** | 0.65 | 2 | 0.521 | 0.62 | 4 | 0.652 |
| Graminoid cover | **78.78** | **2** | **<0.001** | 0.32 | 2 | 0.725 | 1.57 | 4 | 0.183 |
| Bryophyte cover | **57.98** | **2** | **<0.001** | 0.72 | 2 | 0.488 | **11.30** | **4** | **<0.001** |

**Note:** df, numerator degrees of freedom. Values in bold type indicate significance ($\alpha$ = 0.05). Total vascular plant cover, shrub cover, forb cover, and graminoid cover were log-transformed for analysis.

the unmounded seismic lines, and 30.7 ± 2.2 cm in the reference sites (*n* = 5) (C.M.A. Franklin, unpublished data).

At each seismic line and paired reference wooded fen, we established a 20 m transect along the center of the seismic line and a parallel one in the adjacent reference wooded fen. Three mounds, those closest to the 5 m, 15 m, and 20 m distances, were chosen and sampled along each transect. For each selected mound, we used a 20 cm × 20 cm (400 cm$^2$) quadrat to assess vegetation at each of three microtopographic positions: the top of the mound, the south-facing slope, and on the adjacent level ground (Supplementary Fig. S2[1]). To maintain consistency across the different positions sampled, we only sampled one quadrat for each slope position. To ensure that the effect of aspect was consistent across treatments, we standardized our sampling to the south-facing slope as we expected this aspect to have the strongest effect. Because hollows in our sites were predominantly pools of water with little to no vegetation, we excluded this microtopographic position from the analysis, but note that the mounding treatment overall led to saturated hollows that had limited plant cover. In each quadrat, we visually estimated the cover of each understory vascular species and total bryophyte cover (we are exploring community-level responses of the bryophyte community in a separate paper). For unmounded seismic lines with no clear mounds present, quadrats were randomly placed with the same microtopographic positions being maintained relative to each other, i.e., the level ground position was still placed at the lowest position, followed by slope, and top at the highest position.

Groundwater samples were collected from shallow, excavated wells at the 10 m midpoint transect distance using 500 mL Nalgene bottles. Samples were stored in 4 °C for 48 h prior to analysis by the Biogeochemical Analytical Service Laboratory (BASL) at the University of Alberta. Samples were analyzed for pH, electrical conductivity, alkalinity (mg·L$^{-1}$ CaCO$_3$), and base cation content (mg·L$^{-1}$).

### Statistical analysis

Response variables for vascular plants were species richness, Shannon's diversity, Simpson's diversity, total cover, and shrub, forb, graminoid, and bryophyte cover. To examine the effects of mounding treatment, microtopographic position, and their interaction, we used linear mixed-effects models with mounding treatment (mounded seismic line, unmounded seismic line, and reference sites), microtopographic position, and their interactions as fixed effects, and seismic line as a random effect (the three mounds on a transect at a given sampling location were treated as subsamples). For the model comparisons, the reference treatment and the level position were used as reference categories. Vascular plant diversity indices and bryophyte cover used a Gaussian distribution, while total vascular plant cover, shrub cover, forb cover, and graminoid cover were log-transformed and then analyzed with a Gaussian distribution. All analyses were done with

the lme4 package (Bates et al. 2015) in the R statistics programming environment (version 3.5.2; R Core Team 2018). Residuals were examined to ensure normality and homogeneity of variance. When the predictor variables were significant, post hoc analyses were completed using the emmeans package, with *P* values adjusted using the Tukey HSD method (Lenth 2019). When the interaction term was significant, we tested for differences between all microtopographic positions within each treatment and between treatments for each microtopographic position.

Finally, the effects of treatment, microtopographic position, and their interaction on vascular community composition were visualized using nonmetric multidimensional scaling (NMDS) and tested using permutational multivariate analysis of variance (ANOVA) (PERMANOVA), with 1000 permutations for tests of significance. A separate NMDS showed that the reference sites for unmounded seismic lines did not differ from the reference sites for mounded seismic lines (available from authors). NMDS and PERMANOVA were done with the vegan package (Oksanen et al. 2018). Indicator species for each treatment and microtopographic position were identified using the indicspecies package (De Caceres and Legendre 2009). For the indicator species analysis, rare species (species found in less than 5% of the sampled sites) were not included.

## Results

### Vascular plant diversity and cover

For vascular plant species richness, Shannon's diversity, Simpson's diversity, forb cover, and graminoid cover, only the treatment effect of mounding was significant (Table 1). The reference sites had significantly lower (~35%) vascular plant richness, diversity (Shannon's and Simpson's), and graminoid cover (from an average of 1% in reference sites to ~5% in both seismic lines) than mounded or unmounded seismic lines, which did not differ from one another (Figs. 1 and 2B). Graminoid cover in unmounded sites was composed primarily of *Carex* spp. Forb cover was slightly significantly higher on the mounded seismic lines than on unmounded seismic lines and in the reference sites, which did not differ from one another (Fig. 2A).

Shrub cover was significantly affected by both mounding treatment and position, but not their interaction (Table 1; Fig. 3). For all treatments, the top position had significantly higher shrub cover (~60%) than the slope or the level position; the latter two microtopographic positions did not differ (Fig. 3A). Reference sites had significantly higher shrub cover than unmounded seismic lines, while mounded seismic lines were intermediate and did not differ from either (Fig. 3B).

For total vascular plant cover, the interaction between treatment and position was significant (Table 1; Fig. 4). In the reference sites, the top microtopographic position had significantly higher vascular cover (~50%) than the slope position (Fig. 4); values for

**Fig. 1.** Boxplots (in Tukey style) of (A) vascular plant richness (no. per 0.04 m²), (B) Shannon's diversity, and (C) Simpson's diversity by treatment (reference sites, mounded seismic line, and unmounded seismic line). Different letters indicate significant ($P < 0.05$) differences between treatments, based on pairwise comparison of estimated marginal means. There were no significant effects of microtopographic position or interaction of position and mounding treatment (see Table 1). The thick horizontal line within the boxplot represents the median; the lower and upper hinges represent the 25th and 75th percentiles, respectively; the whiskers represent the smallest and largest values within 1.5 times the interquartile range (IQR); and the outliers (values greater than or less than 1.5 × IQR) are represented as dots outside the box and whiskers.
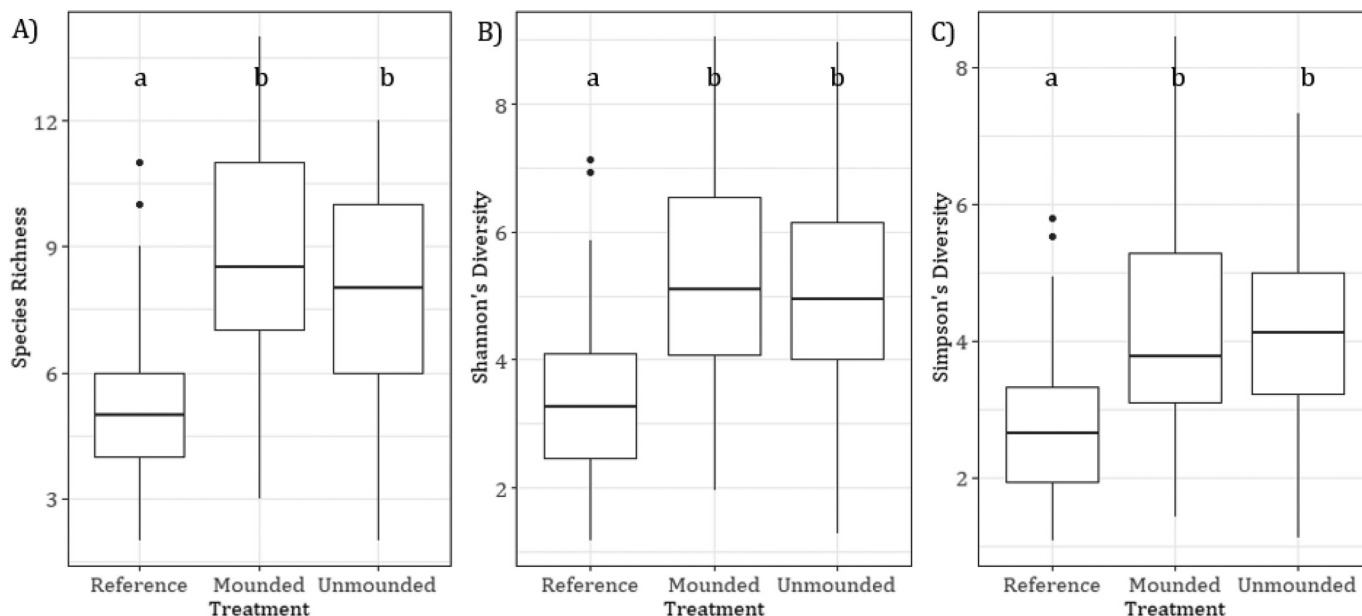


**Fig. 2.** Boxplots (in Tukey style) of (A) total forb and (B) graminoid cover by treatment (reference sites, mounded seismic line, and unmounded seismic line). Different letters indicate significant ($P < 0.05$) differences between treatments, based on pairwise comparisons of estimated marginal means. There were no significant effects of microtopographic position or interaction of position and mounding treatment (see Table 1). For the statistics used to create the boxplot, see Fig. 1.
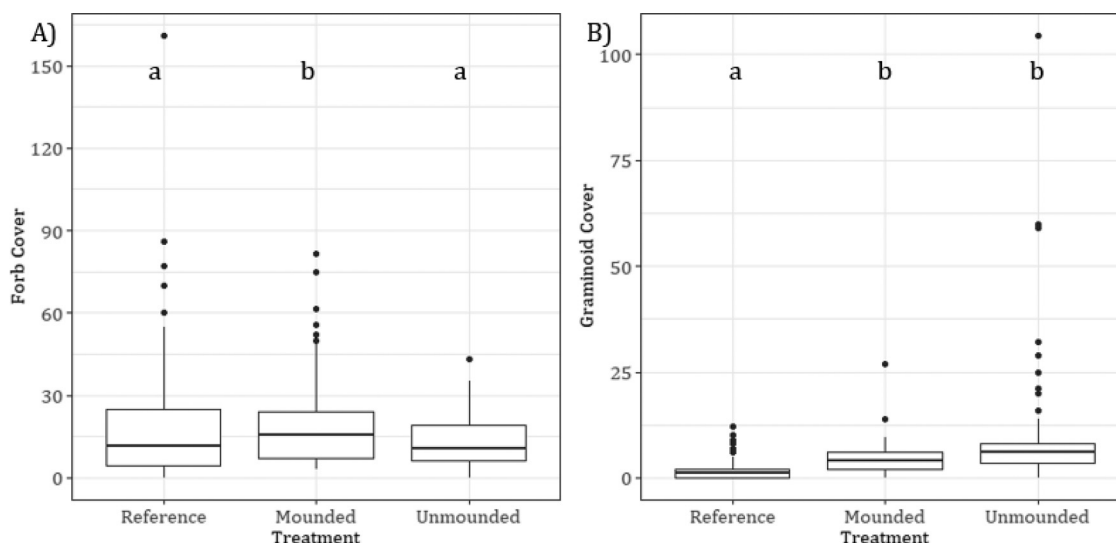


the level position were intermediate and did not differ from either (Fig. 4). On the mounded seismic lines, there were no significant differences in vascular cover between the different microtopographic positions (Fig. 4). On the unmounded seismic lines, the top position had significantly higher vascular cover (~60%) than the level position (Fig. 4); vascular cover on the slope position was intermediate and did not differ from either (Fig. 4). There were no significant differences in vascular cover between the treatments for any of the microtopographic positions.

All three treatments were dominated by *Rhododendron groenlandicum*, *Maianthemum trifolium*, and *Betula pumila* L. *Maianthemum trifolium* was

most abundant at the level position for all three treatments (Appendix A, Table A2). For both unmounded seismic lines and reference sites, *Rhododendron groenlandicum* was most abundant at the top position, while in mounded sites, *R. groenlandicum* cover did not differ between positions. Both mounded seismic lines and reference sites were also dominated by *Rubus chamaemorus* L. and *Menyanthes trifoliata* L., with *M. trifoliata* having the highest cover at the level position. *Equisetum fluviatile* L. was also a dominant species on mounded seismic lines. *Salix planifolia* Pursh and *Carex aquatilis* Wahlenb. also dominated on unmounded seismic lines, with *S. planifolia* being most abundant at the top position.

**Fig. 3.** Boxplots (in Tukey style) of total shrub cover by (A) position and (B) treatment. Different letters indicate significant ($P < 0.05$) differences between treatments or microtopographic positions, based on pairwise comparisons of estimated marginal means of log-transformed shrub cover. For the statistics used to create the boxplot, see Fig. 1.
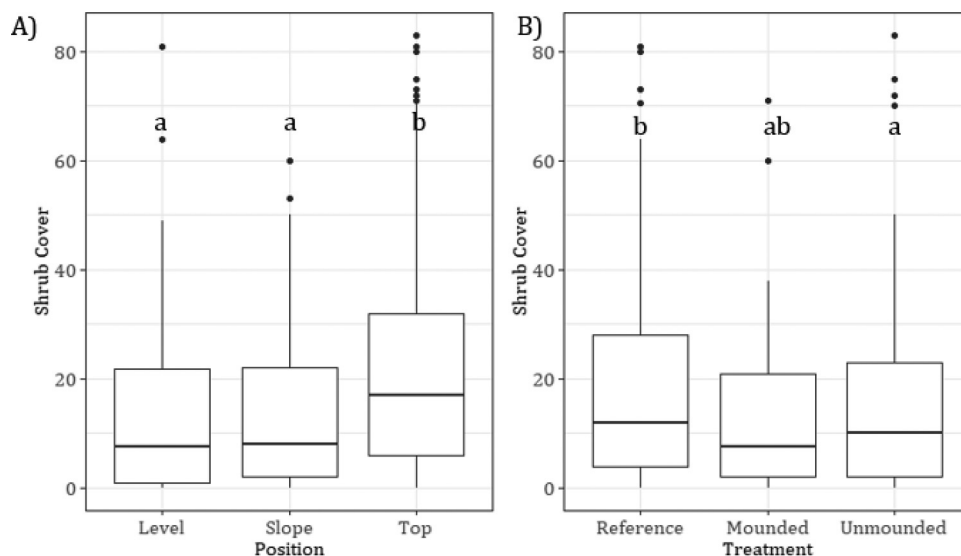


**Fig. 4.** Boxplots (in Tukey style) of total vascular plant cover by treatment (reference sites, mounded seismic line, and unmounded seismic line) and microtopographic position. Different letters indicate significant ($P < 0.05$) differences between microtopographic positions within each treatment, based on pairwise comparisons of estimated marginal means. For the statistics used to create the boxplot, see Fig. 1.
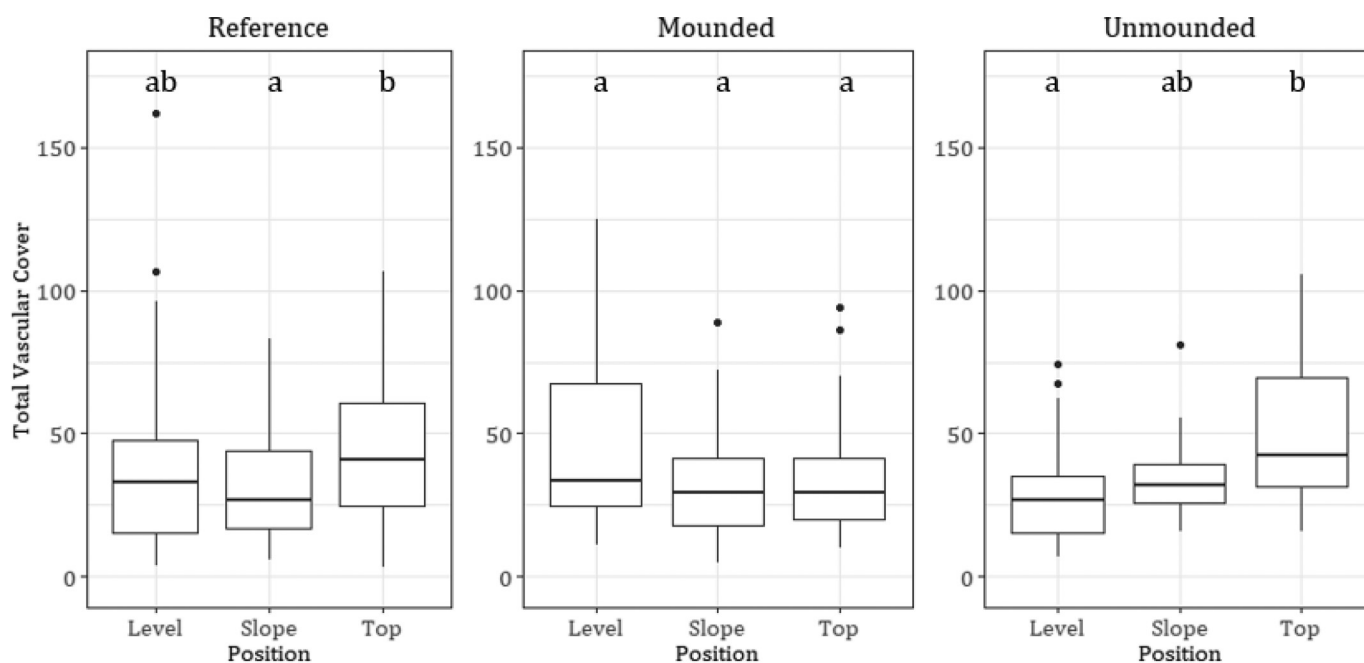


## Bryophyte cover

For bryophyte cover, the interaction between treatment and position was significant (Table 1; Fig. 5). In the reference site, the level position had significantly less (~30%) bryophyte cover than both the slope and top positions, which did not differ from one another (Fig. 5). In contrast, on mounded seismic lines, the top position had significantly lower bryophyte cover (~70%) than both the level and slope positions, which did not differ from one another (Fig. 5). On unmounded seismic lines, there were no significant differences in bryophyte cover between the positions (Fig. 5).

Looking at bryophyte cover between treatments for each microtopographic position separately, there were significant differences between all three treatments for the slope and top positions. In both cases, the reference site had significantly higher (~30%) bryo-

phyte cover than unmounded treatments, which had significantly higher cover (~50%) than mounded seismic lines (Fig. 5). For the level position, there were no significant differences in bryophyte cover between treatments (Fig. 5). For both unmounded and reference sites, *Sphagnum* spp. were the dominant bryophytes at the slope and top positions.

## Vascular community composition

Treatment, microtopographic position, and their interaction were significant for vascular plant community composition (Table 2). In the reference sites, composition at the level position was significantly different from that at both the slope and top positions, which did not differ from one another (Table 3). In both mounded and unmounded seismic lines, composition at the level position

**Fig. 5.** Boxplots in (Tukey style) of bryophyte cover by position in the reference sites, mounded seismic lines, and unmounded seismic lines. Different letters indicate significant ($P < 0.05$) differences between treatments within each position (lowercase letters) or between positions within each treatment (uppercase letters), based on pairwise comparisons of estimated marginal means. For the statistics used to create the boxplot, see Fig. 1.
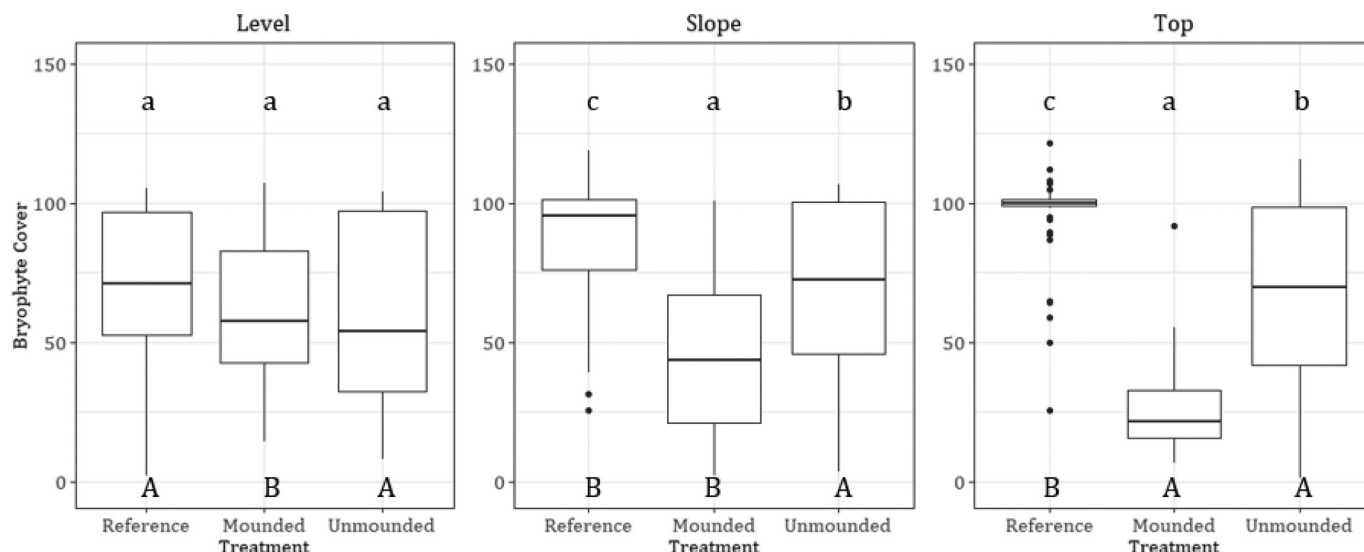


**Table 2.** Results of PERMANOVA for vascular plant community composition as affected by mounding treatment, microtopographic position, and their interaction.

|  | Treatment | | | Position | | | Treatment × position | | |
|---|---|---|---|---|---|---|---|---|---|
|  | F | df | P | F | df | P | F | df | P |
| Community composition | **10.984** | **2** | **0.001** | **3.147** | **2** | **0.001** | 1.547 | 4 | **0.008** |

**Note:** df, numerator degrees of freedom. Values in bold type indicate significance ($\alpha = 0.05$).

**Table 3.** PERMANOVA results showing the effect of microtopographic position on vascular plant community composition within each treatment, and vice versa, and the pairwise tests within each treatment and microtopographic position.

|  | Treatment | | | Position | | | Pairwise comparison (P values) | | |
|---|---|---|---|---|---|---|---|---|---|
| Treatment | F | df | P | F | df | P | Level vs. slope | Level vs. top | Slope vs.top |
| Reference |  |  |  | 3.518 | 2 | 0.001 | **0.020** | **0.003** | 0.051 |
| Mounded |  |  |  | 1.619 | 2 | 0.001 | 0.154 | **0.003** | 0.325 |
| Unmounded |  |  |  | 1.394 | 2 | 0.001 | 0.987 | **0.012** | 0.987 |
| Position |  |  |  |  |  |  | Mounded vs. reference | Reference vs. unmounded | Unmounded vs. mounded |
| Level | 2.592 | 2 | 0.001 |  |  |  | **0.012** | **0.003** | 0.055 |
| Slope | 4.915 | 2 | 0.001 |  |  |  | **0.003** | **0.003** | **0.003** |
| Top | 6.418 | 2 | 0.001 |  |  |  | **0.003** | **0.003** | **0.003** |

**Note:** df, numerator degrees of freedom. Values in bold type indicate significance ($\alpha = 0.05$).

significantly differed from that at the top position; the slope position did not differ from either the top or the level position (Table 3). There were significant differences between all three treatments for the slope and top positions for vascular plant composition (Table 3). At the level position, the reference sites had significantly different composition from both mounded and unmounded seismic lines, which did not differ from each other (Table 3).

The NMDS ordination (based on three dimensions with a final stress of 0.178) showed that the vascular plant community composition of the three microtopographic positions were nested within each other in order of microtopographic position: the top position was nested within the slope position, which was nested within the level position (Fig. 6A). *Caltha palustris* L., *Comarum palustre* L., and *Maianthemum trifolium* were associated with the level position, while *Drosera rotundifolia* L., *Vaccinium microcarpum* (Turcz. ex Rupr.) Schmalh., *Salix* spp., *Populus tremuloides* seedlings, and *Betula pumila* were associated with the top position. The NMDS also

showed some separation between the three treatments, with unmounded sites found in between the clusters of the reference sites and mounded sites (Fig. 6B). In addition, unmounded sites strongly overlapped with the reference sites cluster (Fig. 6B). *Populus tremuloides* Michx. seedlings, *Chamerion angustifolium* (L.) Holub, *Calamagrostis* spp., *Caltha palustris*, *Equisetum* spp., and *Petasites frigidus* (L.) Fr. were associated with mounded seismic lines, while woody plants were associated with the reference wooded fens.

Based on the indicator analysis, *Rubus chamaemorus* and woody species such as *Rhododendron groenlandicum*, *Vaccinium vitis-idaea* L., and *Picea mariana* were indicator species for the reference sites (Table 4). *Equisetum* spp. and *Stellaria* spp. were indicators for the mounded sites (Table 4). Finally, peatland-associated species such as *Vaccinium microcarpum*, *Carex magellanica* Lam., *Carex chordorrhiza* Ehrh. ex L. f., and *Andromeda polifolia* L. were indicators for the unmounded seismic lines (Table 4). There were no indicator species for the microtopographic positions.

**Fig. 6.** Results of a nonmetric multidimensional scaling (NMDS), an unconstrained ordination, of understory vascular community composition in (A) three microtopographic positions (level, slope, and top) and (B) three treatments (reference sites, mounded, and unmounded seismic lines). Points represent sampled sites, with color and shape representing treatment or position. Ellipses represent the 95% confidence intervals for each microtopographic position or treatment centroid, with color and line type representing treatment or position. The most abundant species are represented by six letter codes (first three letters of genus and species epithet; see Appendix A, Table A2). The optimal solution was three-dimensional and had a final stress of 0.178.
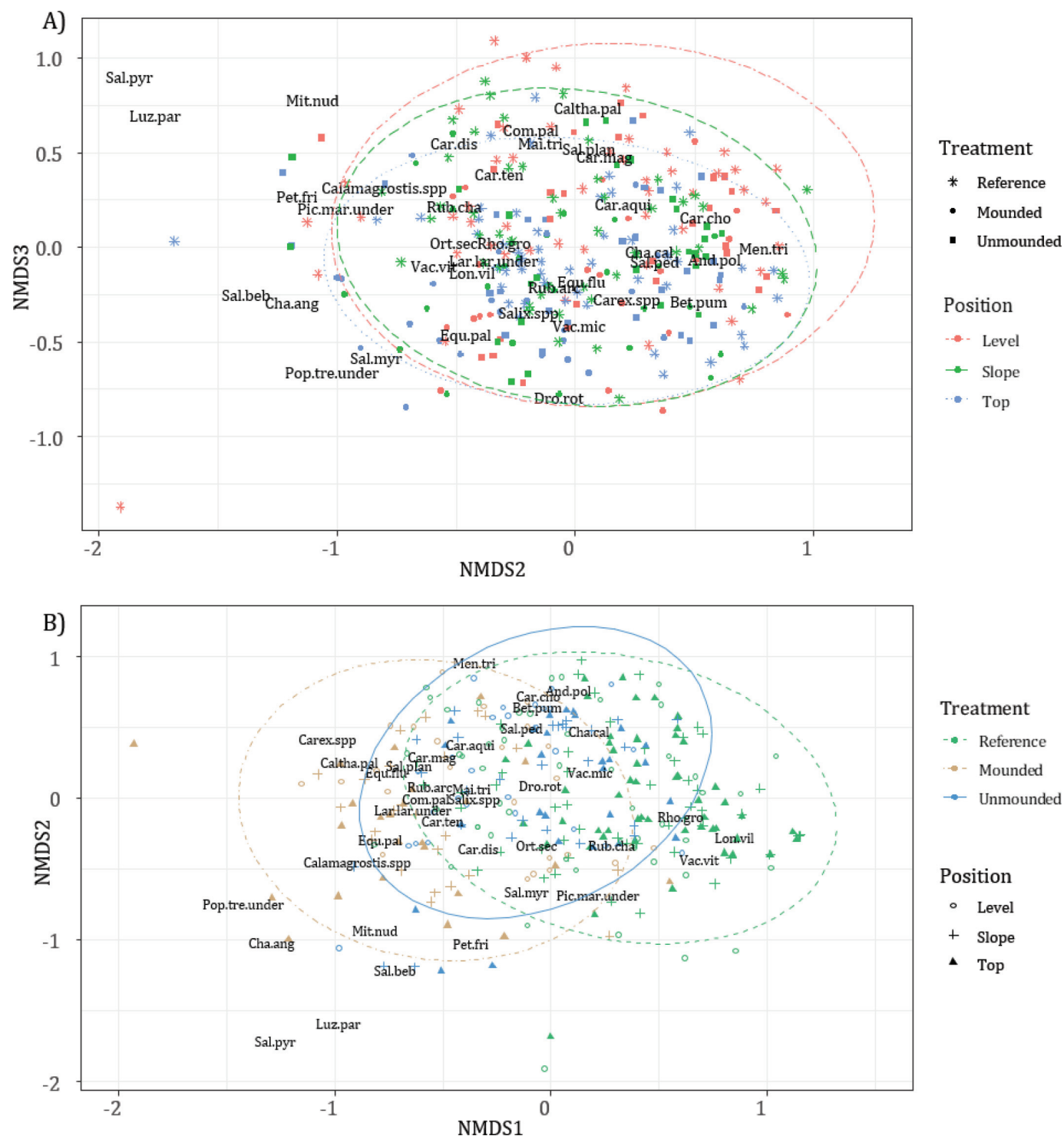
## Discussion

Mounding of seismic lines changes the abundance (cover) of both vascular plants and bryophytes, with the effects varying by microtopographic position. As expected, shrub cover was lower on the unmounded seismic lines than in the reference sites. In addition, shrub cover was higher at the top position for both the mounded seismic lines and reference sites. However, contrary to our expectations, this gradient in shrub cover along the micro-

**Table 4.** Results of indicator species analysis for understory vascular plant communities in reference sites, mounded seismic lines, and unmounded seismic lines.

| Treatment | Species | Component A | Component B | Indicator value | $P$ |
|---|---|---|---|---|---|
| Reference | *Rhododendron groenlandicum* | 0.640 | 0.628 | 0.634 | 0.001 |
| | *Vaccinium vitis-idaea* | 0.544 | 0.392 | 0.462 | 0.002 |
| | *Rubus chamaemorus* | 0.577 | 0.366 | 0.459 | 0.004 |
| | *Picea mariana* | 0.847 | 0.137 | 0.341 | 0.028 |
| Mounded | *Equisetum fluviatile* | 0.766 | 0.764 | 0.765 | 0.001 |
| | *Stellaria* spp. | 0.905 | 0.292 | 0.514 | 0.001 |
| | *Equisetum palustre* | 0.638 | 0.389 | 0.498 | 0.001 |
| | *Carex* spp. | 0.829 | 0.236 | 0.442 | 0.001 |
| | *Salix* spp. | 0.762 | 0.181 | 0.371 | 0.001 |
| | *Equisetum arvense* | 0.803 | 0.167 | 0.366 | 0.001 |
| | *Equisetum scirpoides* | 0.628 | 0.153 | 0.310 | 0.022 |
| Unmounded | *Carex aquatilis* | 0.596 | 0.753 | 0.670 | 0.001 |
| | *Vaccinium microcarpum* | 0.589 | 0.556 | 0.572 | 0.001 |
| | *Calamagrostis* spp. | 0.576 | 0.469 | 0.520 | 0.004 |
| | *Carex disperma* | 0.740 | 0.333 | 0.497 | 0.001 |
| | *Carex magellanica* | 0.838 | 0.284 | 0.488 | 0.001 |
| | *Carex chordorrhiza* | 0.504 | 0.444 | 0.473 | 0.002 |
| | *Andromeda polifolia* | 0.546 | 0.309 | 0.410 | 0.013 |
| | *Salix planifolia* | 0.749 | 0.136 | 0.319 | 0.003 |
| | *Carex gynocrates* | 0.652 | 0.111 | 0.269 | 0.026 |

**Note:** Component A represents the probability of a site belonging to a treatment based on the presence of the indicator species; component B represents the probability of encountering the indicator species in sites belonging to a treatment; indicator value is the product of component A and component B (see De Caceres and Legendre 2009). The $P$ value represents the significance of the association between the indicator species and its corresponding treatment, based on a permutation test of 1000 runs.

topographic positions also occurred in unmounded seismic lines, where we expected microtopography to be limited. In reference sites, we found that total vascular cover was higher at the top of hummocks. Unexpectedly, unmounded seismic lines also had higher vascular cover at the top of the mounds, while total vascular cover did not differ with position in mounded seismic lines. In line with our hypotheses, the top of hummocks had higher bryophyte cover than lower microtopographic positions in the reference sites, while within mounded seismic lines, bryophyte cover was lower at the top of the hummocks compared with lower microtopographic positions. Lastly, as expected, forb and graminoid cover did not differ between microtopographic positions.

Unmounded seismic lines reflected a recovering community. Though we expected limited microtopographic variation on unmounded lines, we found that total vascular plant cover and shrub cover followed similar trends across microtopographic positions as in the reference treed fen. Although shrub cover was lower on the unmounded seismic lines than in the reference sites, it is interesting to note that the natural hummock development on unmounded seismic lines had reached a height that supports significantly higher shrub cover than the lower microtopographic positions. This reflects the presence of an aerated rooting zone on hummocks, which is required for shrub growth and is one objective of the mounding treatments (Rydin and Jeglum 2006). The indicator species analysis further illustrates shrub recovery, with two shrub species (*Andromeda polifolia* and *Salix planifolia*) identified as indicators of unmounded seismic lines. A developing shrub layer will help with continued hummock formation as shrubs provide structural support to the upward growth of bryophytes (Pouliot et al. 2012). Changes in total vascular plant cover and the NMDS ordination further illustrates the recovery of the vascular community composition on unmounded seismic lines as both show the similarity of unmounded seismic lines to reference sites. Lastly, the indicator species associated with unmounded sites were predominantly species common in peatlands such as *Carex magellanica* and *Andromeda polifolia*, thus indicating a trajectory of continued peatland development rather than a shift towards a different ecosite. As Graf (2009) suggests, recovery on legacy seismic lines may not be as nonexistent as the lack of tree regeneration might be taken to indicate.

Understory recovery on the unmounded seismic lines was also reflected in the changes of bryophyte cover, with unmounded seismic lines having significantly higher bryophyte cover than mounded seismic lines. The recovery of bryophyte cover on unmounded seismic lines reflects their tolerance for the flooded conditions of seismic lines and their faster growth in wet conditions, as mound height in unmounded seismic lines was comparable with those in the reference sites. In their submergence experiments, Borkenhagen and Cooper (2018) found that after submergence, bryophytes species tolerant to flooding compensated in growth for the loss of bryophytes that were more sensitive to flooding; thus, total bryophyte cover was resilient to flooding. Experimental studies also show that growth of some *Sphagnum* spp. such as *S. angustifolium* is not hindered by shallow flooding and that optimal bryophyte growth occurs when the water level is close to the surface (Rochefort et al. 2002; Graf and Rochefort 2010).

In contrast to our reference treed fen sites, bryophyte cover on mounded seismic lines was significantly reduced on the tops of the artificial hummocks. This is likely a result of unsuitable microclimatic conditions in the top position of the artificial hummocks, as bryophytes, especially *Sphagnum* spp., can have limited tolerance of extended periods of desiccation (Price et al. 1998; Turetsky et al. 2012). In peatlands, natural hummocks develop by the upward growth of bryophytes. As hummock height increases, bryophytes at the top of hummocks rely on capillary action to maintain access to the water table and avoid desiccation (Rydin and Jeglum 2006; Vitt and Wieder 2008). However, with mounding treatments, this connection to the water table is lost and could explain the limited bryophyte establishment on the tops of the mounds with a drier microclimate. In postharvested peatlands, Price et al. (1998) found increased soil temperatures and reduced soil moisture on raised microtopographic positions, which proved to be unsuitable for colonization of *Sphagnum*. The presence of vascular plants or early-successional bryophytes on the hummocks could ameliorate the microclimatic conditions (Groeneveld et al.

2007; Graf and Rochefort 2010), allowing for bryophyte abundance to increase with time. On the other hand, high levels of vascular plant cover could also be detrimental to bryophyte growth, as vascular plants can limit light available to bryophytes (Malmer et al. 1994; Graf and Rochefort 2010).

Thus, while mounding has been shown to improve tree establishment (Lieffers et al. 2017; Filicetti et al. 2019), we found that it resulted in a loss of bryophyte cover. Bryophyte cover, however, is only one aspect of the bryophyte community. For example, Caners et al. (2019) found that unmounded portions of a well pad had higher cover, but lower richness, of true mosses (class Bryopsida) than mounded portions. In general, the loss in bryophyte cover on mounded sites is concerning as bryophytes are primarily responsible for peat accumulation and play an important role in ecosystem functioning (Turetsky et al. 2012).

In addition to the loss of bryophyte cover, mounding seems to cause a shift in vascular community composition. In the NMDS ordination, mounded seismic lines are further away from the reference sites than the unmounded seismic lines (Fig. 6), with higher abundance of marsh-associated species such as *Equisetum fluviatile*, *Caltha palustris*, and *Petasites frigidus* and disturbance-adapted species such as *Chamerion angustifolium* and *Populus tremuloides*. This is further reflected in the indicator species analysis, where disturbance-adapted species such as *Equisetum arvense* L. and *Stellaria* spp. are indicators of mounded seismic lines (Table 4). The shift in vascular community composition could be temporary, as we sampled only a few years after the application of mounding treatments; however, if bryophyte dominance and peat development are not re-established, mounded seismic lines could potentially develop into a different ecosite type.

Caners et al. (2019) studied the effects of mounding that occurred immediately after decommissioning of well pads in treed peatlands and found that mounding improves recovery of the understory communities. However, in our study, we found not only that recovery was well underway in unmounded seismic lines, but also that mounding could be detrimental to understory recovery. The difference between our findings could be due to the difference in disturbance severity between well pads and seismic lines. Well pads not only undergo repeated peat compression due to traffic from heavy machinery, but also are intentionally compressed and additional water is introduced to some pads to improve frost penetration (Caners et al. 2019). In contrast, compression of peat on seismic lines is a by-product of machine traffic, and as part of best management practices, compression is minimized through the use of lightweight equipment (Dabros et al. 2018). The saturated conditions on seismic lines are due to this compression, with no additional water introduced to the system. Thus, we can expect the peat compression and subsequent flooding in seismic lines to be relatively mild compared with the disturbance experienced on well pads; thus, recovery of these seismic lines may require minimal intervention. Another important difference between the Caners et al. (2019) study and ours is that in Caners et al. (2019), mounding was applied directly after the well pads were disabled, whereas in ours, mounding was applied to the site approximately 15 years after seismic line creation. Restoration of older legacy seismic lines will always be delayed for several years after seismic line creation (Dabros et al. 2018). These results highlight the need for development of restoration treatments that are specific to different disturbance types.

More work is needed to examine bryophyte diversity and composition between the three treatments, as well as continued monitoring to determine whether (*i*) bryophyte cover on the tops of the artificial hummocks will recover, (*ii*) tree growth is faster on these artificial hummocks, and (*iii*) the artificial hummocks will cause shifts in understory composition over time. Studies also need to explore differences in recovery along the bog–fen gradient (but see Filicetti et al. 2019). Lastly, further research should investigate the effects of mounding on other ecological measures,

especially the effects on carbon cycling and hydrological flow, as peatlands play an important role in regulating these (Rydin and Jeglum 2006; Strack et al. 2019).

We found signs of recovery in the understory communities of unmounded low-impact seismic lines. This indicates that recovery may be slow but not entirely lacking on narrow, linear disturbances in treed peatlands (Graf 2009). However, our study only examined low-impact seismic lines, which undergo minimal understory and soil disturbance. In addition, their narrow width allows for proximity to diaspores from the adjacent reference treed fen, which can facilitate regeneration. Further research should examine the recovery of the understory in larger, conventional seismic lines as responses may differ from those reported here on low-impact seismic lines.

In addition, our study shows that re-disturbing these linear footprints to apply a restoration treatment could have detrimental effects on the understory. This is primarily shown through a significant reduction of bryophyte cover in mounded seismic lines. The loss in bryophyte cover may assist with tree regeneration, as bryophytes can limit tree growth through competition for nutrients and burial of seedlings (i.e., vascular plants must keep up with the growth of *Sphagnum*) (Malmer et al. 1994; Rydin and Jeglum 2006). However, bryophytes are also the drivers of peat accumulation and play an important role in overall functioning of the peatland ecosystem (Graf and Rochefort 2010). In fact, restoration efforts in harvested peatlands in eastern Canada often have the short-term objective of restoring *Sphagnum* or brown moss cover and the long-term objective of re-establishing "a functional peat-accumulating ecosystem" (Rochefort 2000; Rochefort et al. 2003). In Alberta, the current restoration objective for seismic lines in treed peatlands is primarily the recovery of caribou, rather than a return of peatland function, with restoration success defined by the presence and density of trees (Graf 2009; Government of Alberta 2017). However, if the treatments used to encourage tree establishment lead to a loss in bryophyte cover, the organisms responsible for peat accumulation and peatland functioning, we will need to explore less disruptive restoration options or re-assess our restoration objectives.

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## Appendix A

**Table A1.** Mean and standard error (in parentheses) tree density, basal area, and tree height by species, and water chemistry variables for the unmounded and mounded reference habitats.

| Variables | Unmounded reference | Mounded reference |
|---|---|---|
| **Total tree density** | 8527.78 (579.52) | 7500.00 (1187.73) |
| *Larix laricina* | 888.89 (356.27) | 625.00 (340.69) |
| *Picea mariana* | 7638.89 (709.69) | 6875.00 (1327.93) |
| Total basal area | 550.81 (44.88) | 486.84 (70.59) |
| *Larix laricina* | 108.79 (38.40) | 80.07 (46.17) |
| *Picea mariana* | 442.02 (56.73) | 406.77 (84.93) |
| **Mean tree height** | 5.20 (0.53) | 6.25 (0.72) |
| *Larix laricina**  | 1.02 (0.67) | 3.4 (1.32) |
| *Picea mariana* | 5.24 (0.53) | 6.07 (0.76) |
| **Water chemistry** | | |
| pH | 6.36 (0.14) | 6.65 (0.14) |
| Conductivity | 73.91 (15.26) | 126.24 (25.96) |
| Alkalinity | 31.18 (8.37) | 59.48 (13.23) |
| Seismic line width | 4.11 (0.07) | 4.25 (0.09) |

**Note:** Variables did not significantly differ between the two reference types ($P > 0.05$) according to $t$ tests.

*Due to limited samples, we were unable to test the statistical differences in *L. laricina* height between the two reference types.

**Table A2.** Mean percent cover and standard error (in parentheses) and the species code (see Fig. 6) for vascular plants found in each treatment (unmounded, mounded, and reference) and microtopographic position (top, slope, and level).

| Latin binomial (species code) | Unmounded | | | Mounded | | | Reference | | |
|---|---|---|---|---|---|---|---|---|---|
| | Top | Slope | Level | Top | Slope | Level | Top | Slope | Level |
| *Agrostis scabra* (Agr.sca) | — | — | — | 0.04 (0.04) | — | — | — | — | — |
| *Andromeda polifolia* (And.pol) | 2.15 (0.60) | 1.44 (0.55) | 0.93 (0.35) | 0.08 (0.08) | 1.00 (0.66) | 0.42 (0.17) | 0.98 (0.31) | 0.93 (0.59) | 0.35 (0.17) |
| *Betula papyrifera* (Bet.pap) | — | — | — | 0.13 (0.09) | — | 1.46 (1.46) | — | — | — |
| *Betula pumila* (Bet.pum) | 5.44 (2.88) | 1.56 (0.65) | 2.52 (1.25) | 1.33 (0.93) | 2.54 (2.50) | 1.88 (1.04) | 2.88 (1.43) | 1.03 (0.61) | 3.05 (1.28) |
| *Calamagrostis* spp. | 3.13 (2.20) | 1.11 (0.56) | 1.02 (0.32) | 1.52 (0.63) | 1.13 (0.31) | 0.65 (0.21) | 0.17 (0.06) | 0.24 (0.12) | 0.18 (0.07) |
| *Caltha palustris* (Cal.pal) | | | 0.74 (0.74) | 0.08 (0.08) | — | 1.50 (0.97) | 0.29 (0.29) | 0.08 (0.08) | 2.26 (1.65) |
| *Carex aquatilis* (Car.aqu) | 2.56 (0.73) | 2.85 (0.53) | 2.11 (0.39) | 0.69 (0.23) | 1.33 (0.35) | 1.79 (0.39) | 0.54 (0.17) | 0.35 (0.12) | 0.38 (0.13) |
| *Carex canescens* (Car.can) | — | 0.07 (0.05) | 0.11 (0.82) | 0.08 (0.08) | — | 0.04 (0.04) | — | — | — |
| *Carex capillaris* (Car.cap) | — | — | — | 0.13 (0.13) | — | — | — | — | — |
| *Carex chordorrhiza* (Car.cho) | 0.96 (0.26) | 0.61 (0.14) | 0.57 (0.14) | 0.17 (0.10) | 0.15 (0.07) | 0.27 (0.11) | 0.62 (0.21) | 0.47 (0.15) | 0.44 (0.10) |
| *Carex diandra* (Car.dia) | — | — | — | 0.19 (0.13) | 0.13 (0.13) | 0.21 (0.15) | — | — | — |
| *Carex disperma* (Car.dis) | 0.57 (0.22) | 0.81 (0.32) | 1.22 (0.92) | 0.13 (0.09) | 0.29 (0.17) | 0.17 (0.10) | 0.04 (0.02) | 0.08 (0.04) | 0.22 (0.16) |
| *Carex gynocrates* (Car.gyn) | 0.15 (0.11) | 0.19 (0.11) | 0.17 (0.12) | — | — | 0.04 (0.04) | 0.03 (0.02) | 0.06 (0.04) | 0.14 (0.07) |
| *Carex interior* (Car.int) | — | — | — | — | 0.04 (0.03) | — | — | — | — |
| *Carex leptalea* (Car.lep) | — | — | — | 0.04 (0.03) | 0.13 (0.13) | 0.04 (0.04) | — | — | — |
| *Carex limosa* (Car.lim) | 0.04 (0.04) | — | 0.04 (0.04) | — | — | — | — | — | — |
| *Carex magellanica* (Car.mag) | 1.52 (0.78) | 2.37 (1.09) | 1.63 (0.95) | — | 0.06 (0.05) | 0.46 (0.24) | 0.01 (0.01) | 0.12 (0.05) | 0.42 (0.22) |
| *Carex tenuiflora* (Car.ten) | 0.15 (0.07) | 0.09 (0.05) | 0.13 (0.08) | 0.35 (0.19) | 0.21 (0.09) | 0.08 (0.08) | 0.05 (0.04) | 0.11 (0.05) | 0.31 (0.20) |
| *Carex vaginata* (Car.vag) | 0.15 (0.09) | 0.37 (0.37) | 0.19 (0.13) | 0.08 (0.08) | — | 0.04 (0.04) | 0.01 (0.01) | — | 0.29 (0.022) |
| *Carex* spp. | 0.07 (0.07) | — | 0.09 (0.07) | 0.54 (0.44) | 0.27 (0.15) | 0.75 (0.24) | 0.04 (0.04) | 0.10 (0.08) | 0.02 (0.01) |
| *Chaemenerion angustifolium* (Cha.ang) | — | 0.19 (0.19) | — | 1.63 (0.70) | 0.17 (0.13) | 0.13 (0.13) | — | — | — |
| *Chamaedaphne calyculata* (Cha.cal) | 0.56 (0.29) | 0.89 (0.40) | 0.96 (0.35) | — | 0.17 (0.17) | 0.17 (0.13) | 1.38 (0.50) | 0.72 (0.35) | 1.32 (0.43) |
| *Chrysosplenium* spp. | — | — | — | 1.46 (1.25) | 0.08 (0.08) | 0.04 (0.04) | — | — | — |
| *Comarum palustre* (Com.pal) | 0.93 (0.75) | 1.15 (0.51) | 1.04 (0.40) | 0.21 (0.15) | 1.88 (1.11) | 1.54 (0.77) | 0.06 (0.06) | 1.06 (0.43) | 0.43 (0.26) |
| *Coptidium lapponicum* (Cop.lap) | — | — | 0.02 (0.02) | — | — | — | — | 0.08 (0.08) | — |
| *Cornus canadensis* (Cor.can) | — | — | — | 0.08 (0.08) | — | — | — | — | — |
| *Corallorhiza trifida* (Cor.tri) | — | — | — | — | — | — | — | — | 0.01 (0.01) |
| *Drosera rotundifolia* (Dro.rot) | 0.31 (0.13) | 0.19 (0.09) | 0.20 (0.09) | 0.19 (0.09) | 0.04 (0.03) | 0.35 (0.18) | 0.15 (0.07) | 0.33 (0.15) | 0.01 (0.01) |
| *Epilobium ciliatum* (Epi.cil) | — | — | — | 0.19 (0.12) | 0.35 (0.26) | 0.88 (0.66) | — | — | — |
| *Epilobium palustre* (Epi.pal) | — | 0.04 (0.04) | 0.07 (0.07) | 0.04 (0.04) | 0.08 (0.06) | 0.13 (0.13) | — | — | — |
| *Epilobium* spp. | 0.04 (0.04) | — | — | 0.06 (0.03) | 0.06 (0.05) | 0.04 (0.04) | — | — | — |
| *Equisetum arvense* (Equ.arv) | 0.04 (0.04) | 0.07 (0.07) | — | 0.63 (0.42) | 0.38 (0.19) | 0.25 (0.14) | 0.03 (0.02) | 0.01 (0.01) | 0.16 (0.09) |
| *Equisetum fluviatile* (Equ.flu) | 0.28 (0.10) | 0.44 (0.12) | 0.31 (0.09) | 1.90 (0.40) | 2.71 (0.81) | 2.25 (0.67) | 0.17 (0.06) | 0.40 (0.12) | 0.49 (0.18) |
| *Equisetum palustre* (Equ.pal) | 0.48 (0.23) | 0.22 (0.11) | 0.11 (0.06) | 0.63 (0.21) | 0.75 (0.25) | 0.44 (0.19) | 0.10 (0.04) | 0.06 (0.03) | 0.06 (0.03) |
| *Equisetum scirpoides* (Equ.sci) | 0.13 (0.05) | 0.04 (0.03) | 0.07 (0.03) | 0.17 (0.13) | 0.27 (0.17) | 0.17 (0.07) | — | 0.04 (0.02) | 0.08 (0.05) |
| *Equisetum sylvaticum* (Equ.syl) | 0.22 (0.16) | 0.28 (0.20) | 0.04 (0.04) | 0.30 (0.19) | 0.38 (0.20) | 0.17 (0.10) | 0.01 (0.01) | 0.06 (0.04) | 0.20 (0.08) |
| *Eriophorum gracile* (Eri.gra) | — | — | — | — | — | 0.04 (0.04) | — | — | — |
| Forb spp. | — | 0.02 (0.02) | — | 0.08 (0.05) | 0.17 (0.07) | 0.02 (0.02) | — | 0.04 (0.04) | — |
| *Fragaria virginiana* (Fra.vir) | — | 0.22 (0.22) | — | — | — | — | — | — | — |
| *Galium* spp. | — | — | — | — | 0.08 (0.05) | 0.10 (0.09) | 0.01 (0.01) | 0.01 (0.01) | 0.03 (0.02) |
| Graminoid spp. | — | — | — | 0.17 (0.17) | 0.13 (0.09) | — | — | — | 0.01 (0.01) |
| *Larix laricina* (Lar.lar) | — | 1.11 (0.82) | 0.15 (0.15) | 0.42 (0.24) | 0.19 (0.07) | 0.04 (0.04) | 0.04 (0.04) | 0.03 (0.02) | 0.16 (0.16) |
| *Lonicera villosa* (Lon.vil) | — | — | — | — | — | 0.80 (0.80) | 0.59 (0.59) | 0.31 (0.31) | — |
| *Luzula parviflora* (Luz.par) | 3.70 (3.70) | — | 0.07 (0.07) | 0.08 (0.08) | — | — | — | — | — |
| *Lysimachia thyrsiflora* (Lys.thy) | — | — | — | 0.42 (0.42) | — | — | — | — | — |
| *Maianthemum trifolium* (Mai.tri) | 2.91 (0.90) | 3.85 (0.82) | 4.48 (0.77) | 3.75 (1.00) | 5.79 (1.49) | 8.08 (3.29) | 2.92 (0.96) | 5.00 (1.35) | 9.43 (1.89) |
| *Melampyrum lineare* (Mel.lin) | — | — | — | 0.08 (0.08) | — | — | — | — | — |
| *Menyanthes trifoliata* (Men.tri) | 0.56 (0.39) | 0.41 (0.27) | 0.44 (0.23) | 0.71 (0.63) | 0.54 (0.43) | 4.63 (2.80) | 0.73 (0.54) | 1.10 (0.81) | 4.31 (1.53) |
| *Mitella nuda* (Mit.nud) | 0.04 (0.04) | 0.63 (0.56) | 0.41 (0.24) | 0.13 (0.09) | 0.21 (0.21) | 0.42 (0.42) | — | 0.04 (0.04) | 0.14 (0.14) |
| Orchid spp. | — | 0.30 (0.21) | — | — | — | — | — | — | — |
| *Orthilia secunda* (Ort.sec) | 0.07 (0.05) | 0.17 (0.12) | 0.02 (0.02) | 0.67 (0.50) | 0.10 (0.09) | 0.13 (0.09) | 0.47 (0.31) | 0.06 (0.03) | 0.10 (0.10) |
| *Pedicularis* spp. | 0.07 (0.07) | 0.004 (0.004) | — | — | 0.08 (0.08) | 0.04 (0.04) | — | — | — |
| *Petasites frigidus* (Pet.fri) | 0.43 (0.30) | 0.50 (0.44) | 0.78 (0.56) | 2.08 (2.08) | 0.04 (0.04) | 1.38 (0.96) | 0.39 (0.39) | 0.73 (0.42) | 1.25 (1.00) |
| *Picea mariana* (Pic.mar) | 0.04 (0.04) | 0.07 (0.07) | — | 0.69 (0.32) | 0.15 (0.09) | — | 2.24 (0.96) | 1.18 (0.58) | 1.81 (1.57) |
| *Populus balsamifera* (Pop.bal) | — | — | — | 1.33 (0.88) | 0.04 (0.04) | — | — | — | — |
| *Populus* spp. | — | — | — | 0.92 (0.55) | 0.13 (0.09) | — | — | — | — |
| *Populus tremuloides* (Pop.tre) | — | — | — | 2.00 (0.78) | 0.44 (0.22) | — | — | — | — |
| *Rhododendron groenlandicum* (Rho.gro) | 5.35 (1.43) | 2.19 (0.81) | 1.30 (0.49) | 1.50 (1.26) | 1.08 (0.75) | 2.83 (1.35) | 11.24 (1.66) | 8.73 (1.46) | 5.38 (1.42) |

**Table A2** (*concluded*).

| Latin binomial (species code) | Unmounded | | | Mounded | | | Reference | | |
|---|---|---|---|---|---|---|---|---|---|
| | Top | Slope | Level | Top | Slope | Level | Top | Slope | Level |
| *Ribes oxyacanthoides* (Rib.oxy) | — | — | 0.74 (0.74) | — | — | — | — | — | — |
| *Rubus arcticus* (Rub.arc) | 0.48 (0.26) | 0.26 (0.16) | 0.19 (0.13) | 0.63 (0.51) | 0.21 (0.21) | 0.27 (0.25) | 0.12 (0.12) | 0.09 (0.09) | — |
| *Rubus chamaemorus* (Rub.cha) | 2.89 (1.23) | 2.41 (1.13) | 0.89 (0.65) | 0.54 (0.39) | 3.46 (2.24) | 1.04 (0.61) | 7.80 (1.96) | 4.53 (1.17) | 2.96 (1.02) |
| *Rubus idaeus* (Rub.ida) | — | — | — | — | 0.63 (0.63) | — | — | — | — |
| *Salix bebbiana* (Sal.beb) | — | — | 0.11 (0.11) | 1.04 (1.04) | 0.17 (0.13) | — | 0.49 (0.49) | — | — |
| *Salix myrtillifolia* (Sal.myr) | 0.93 (0.93) | 0.22 (0.22) | 0.74 (0.51) | 0.54 (0.46) | 0.04 (0.04) | 0.88 (0.62) | — | — | — |
| *Salix pedicellaris* (Sal.ped) | 1.48 (0.86) | 0.44 (0.31) | 1.02 (0.40) | 0.50 (0.35) | 1.79 (1.03) | 2.17 (0.92) | 3.12 (1.46) | 0.63 (0.31) | 0.96 (0.36) |
| *Salix planifolia* (Sal.pla) | 6.85 (3.89) | 1.19 (0.94) | 2.44 (1.32) | 0.33 (0.33) | — | 2.54 (1.39) | 0.59 (0.59) | — | 0.06 (0.06) |
| *Salix pseudomyrsinites* | — | — | — | — | — | 0.75 (0.75) | — | — | — |
| *Salix pyrifolia* (Sal.pyr) | — | 1.85 (1.85) | — | — | — | — | — | — | — |
| *Salix* spp. | 0.26 (0.26) | — | 0.15 (0.12) | 0.63 (0.34) | 1.38 (0.79) | 0.06 (0.05) | 0.14 (0.14) | 0.04 (0.04) | 0.06 (0.06) |
| *Stellaria* spp. | 0.04 (0.03) | 0.04 (0.04) | 0.04 (0.04) | 0.833 (0.26) | 0.46 (0.15) | 0.15 (0.07) | — | 0.04 (0.03) | — |
| *Vaccinium microcarpum* (Vac.mic) | 3.89 (0.70) | 2.50 (0.68) | 1.04 (0.38) | 0.27 (0.17) | 0.31 (0.15) | 1.19 (0.56) | 2.16 (0.35) | 0.85 (0.27) | 0.39 (0.16) |
| *Vaccinium vitis-idaea* (Vac.vit) | 1.30 (0.72) | 0.59 (0.41) | 0.19 (0.13) | 1.58 (1.26) | 0.10 (0.09) | 0.75 (0.48) | 3.19 (0.72) | 1.32 (0.36) | 0.86 (0.26) |
| *Viburnum edule* (Vib.edu) | 0.04 (0.04) | — | — | — | — | — | — | — | — |

**Note:** Nomenclature follows VASCAN (Brouillet et al. 2010).