

1 **Interfering with neighbouring communities: Allelopathy astray in the tundra delays seedling development**

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11 **Key Words:**

12 *Empetrum*, germination, allochthonous leaves, recipient systems, plant growth, snowbed, bioassays, niche

13 construction

14

15 **Authors' contributions**

16 AKP and KAB conceived the ideas and designed methodology; AKP, KAB, BL and RR collected the data; AKP,

17 KAB and BL analysed the data; KAB led the writing of the manuscript. All authors contributed critically to the

18 drafts and gave final approval for publication.

19

20 **Data availability**

21 Data is accessible at UiT Open Research Data (<https://opendata.uit.no>, <https://doi.org/10.18710/PGDJFB>).

22

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27

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29 **Abstract**

- 30 1. Altered species composition caused by environmental and climatic change can affect the transfer of plant
31 residues among communities. Whereas transferred residues are typically considered a resource in recipient
32 systems, residues of allelopathic species may instead cause interference.
- 33 2. Evergreen dwarf shrubs, specifically the allelopathic species *Empetrum nigrum* are increasing in abundance
34 in response to a warming climate. *Empetrum* has small, evergreen leaves that can be transferred to other
35 communities when withered and lost from the plant.
- 36 3. We hypothesize that *Empetrum* can have allelopathic effects in the recipient communities of the withered
37 leaves. We call this allochthonous allelopathy as opposed to autochthonous allelopathy, which is well
38 documented in communities where it grows.
- 39 4. We measured influx of allochthonous *Empetrum* leaves onto snow-covered snowbeds, where they are easily
40 identified within the debris. Next, we compared the bioactivity of allochthonous withered leaves with that of
41 green *Empetrum* leaves. Finally, we conducted an experiment testing the germination and seedling growth of
42 ten tundra species in snowbed soil supplemented with no (control) and three densities of allochthonous
43 *Empetrum* leaves.
- 44 5. We found *Empetrum* leaves to be common on the snow cover of snowbeds. We found *Empetrum* leaves
45 collected on snowbeds to be as bioactive as green leaves. Finally, we found forb species to have reduced
46 germination and all ten species to have delayed seedling development when growing in snowbed soil
47 supplemented with withered *Empetrum* leaves. Seedlings under the control treatment were 2.3 times longer
48 and had 3.2 times more leaves in comparison to seedlings grown under the strongest allochthonous leaf
49 treatment.
- 50 6. Results from our study imply that *Empetrum* is allelopathic in recipient systems of its allochthonous leaves.
51 The abundant nature of *Empetrum* in the tundra, suggests that allochthonous allelopathy is a common
52 phenomenon, causing biotic stress in snowbeds and potentially other parts of the tundra. Exemplifying the
53 ability of a plant to interfere in neighbouring communities, our study demonstrates a plant trait that may
54 provide insight to other study systems.

55 Introduction

56 Movement of plant detritus is ubiquitous and can strongly influence ecosystem dynamics in neighbouring systems
57 (Polis, Anderson & Holt 1997). Altered species composition caused by environmental and climatic change can
58 therefore have consequences beyond their particular systems. The movement of terrestrial detritus into riparian
59 systems, typically termed allochthonous input, can represent important nutrient resources subsidizing both
60 freshwater food webs and neighbouring plant communities (Xiong & Nilsson 1997). Likewise, plant detritus
61 boosts the nutrient and energy availability in terrestrial recipient systems, such as aeolian ecosystems where
62 plant detritus is an essential resource (Polis, Anderson & Holt 1997). However, there is considerable variation in
63 both the quality of plant residues (Cornwell *et al.* 2008), and in the fate of plant residues in any given recipient
64 system (Freschet, Aerts & Cornelissen 2012). The effect of allochthonous plant detritus, or “away-field” detritus
65 (*sensu* Ayres *et al.* 2009), is therefore highly context dependent. Identifying the quality and quantity of plant
66 residues moving between systems can provide a better understanding of ecosystem dynamics and modification
67 under environmental and climatic change.

68 The capacity to be a source of allochthonous plant detritus varies between species causing recipient systems to
69 receive a selection of the leaf litter produced in source systems. Species whose withered parts possess traits
70 facilitating the movement with physical forces such as wind and water (Polis, Anderson & Holt 1997) are likely to
71 be more common in the plant detritus. The source species and plant parts of allochthonous detritus are therefore
72 not random, but rather dominated by plants with adapted traits.

73 After deposition, the traits contained in the detritus can affect the recipient system. Allochthonous as opposed to
74 autochthonous litter may have a lower content of nutrients and secondary metabolites depending on the extent to
75 which the litter is disintegrated during movement. In addition, decomposition rates, and hence the release of
76 nutrients and secondary metabolites, can be lower in the recipient system due to the soil biota not being adapted
77 to the litter (Veen *et al.* 2015). This suggests allochthonous plant detritus is in general of low nutrient quality in
78 recipient systems. However, secondary metabolites can still be active in leaves after they have withered
79 (Hättenschwiler, Tiunov & Scheu 2005). Secondary metabolites in allochthonous plant litter may thus modify the
80 environment of the recipient system through processes of ecosystem engineering or niche construction (Odling-

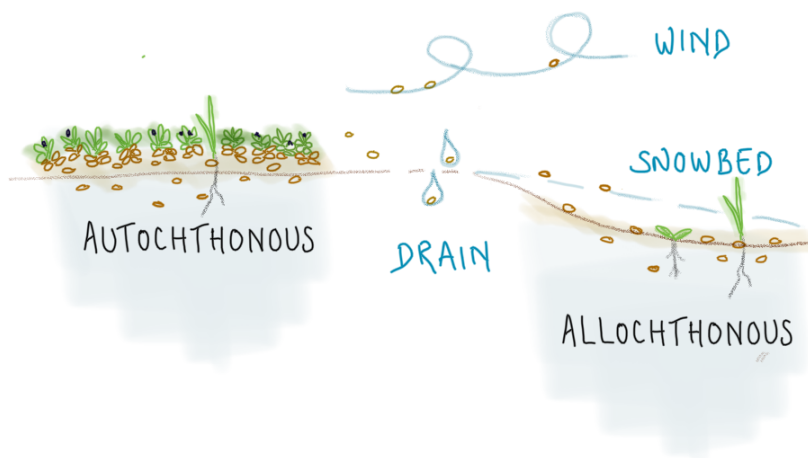
81 Smee *et al.* 2013). Depending on whether the resulting niche construction is of benefit to the source species, by
82 creating a suitable, future habitat, allochthonous detritus with secondary metabolites may even be selected for
83 (Matthews *et al.* 2014). In summary, plant species that produce allochthonous plant detritus may affect
84 communities in which they do not grow mostly through their secondary metabolites. We term this allochthonous
85 niche construction.

86 Here we address *Empetrum nigrum* as a candidate for allochthonous niche construction by means of
87 environmental modification through allelopathy (Figure 1). *Empetrum* is a dwarf shrub common in heaths of
88 circumboreal-polar areas (<http://nhm2.uio.no/paf/>) and is allelopathic in its home-soil (Nilsson & Zackrisson 1992;
89 Bråthen, Fodstad & Gallet 2010). The allelopathic capacity of *Empetrum* leaves is attributed to the production of
90 secondary metabolites, most notably the dihydrostilbene Batatasin-III (Odén *et al.* 1992; Wallstedt *et al.* 1997;
91 Nilsson, Gallet & Wallstedt 1998) in the glands of its small, evergreen leaves (Muravnik & Shavarda 2012, Figure
92 S1 in Supporting Information). Batatasin-III is temporally stable, resistant to microbial degradation (Wallstedt *et al.*
93 1997; Wallstedt, Gallet & Nilsson 2005) and resists change in response to altered environmental conditions
94 (González *et al.* 2015). The withered leaves of *Empetrum* decompose slowly (Tybirk *et al.* 2000; Parker *et al.*
95 2018) and retain allelopathic secondary metabolites, although at lower concentrations than in green leaves
96 (Gallet, Nilsson & Zackrisson 1999). Copious amounts of *Empetrum* litter can accumulate as reported from a
97 boreal forest site where the average litter abundance was 425 ± 60 g/m² (Wallstedt *et al.* 2000). With an average
98 leaf weight of 0.53 mg (± 0.11 mg) (Appendix 1 in Supplementary Information) the leaves are comparable to
99 intermediate sized tundra seeds (González *et al.* 2010). It thus can be inferred that the leaves are able to
100 disperse with both fluvial and aeolian processes (Figure 1) and accumulate on snowbeds like seeds (Larsson &
101 Molau 2001) (Figure S2). In summary, *Empetrum* might have capacity for allochthonous niche construction when
102 its leaves are transported to other communities (Figure 1).

103 The tundra is changing in response to a warming climate, particularly through shrub encroachment (Olofsson *et al.*
104 2009; Bråthen *et al.* 2017; Vowles & Björk 2019). Studies on ongoing and predicted changes often focus on
105 responses to abiotic (warming, changing snow conditions, nutrients) and biotic factors (herbivory) (Björkman *et al.*
106 2020). However, in the tundra, species composition and richness can be more strongly linked to dominant plant
107 species than to changes in abiotic factors and herbivory (le Roux *et al.* 2013). Furthermore, these dominant

108 species are often favoured by climate warming (Wookey *et al.* 2009). *Empetrum* is one of these dominant
109 species, responds positively to warming, and its presence is a predictor of species presence and/or species
110 richness in the tundra (Pellissier *et al.* 2010; Ravolainen *et al.* 2010; le Roux *et al.* 2014; Bråthen, González &
111 Yoccoz 2018). By addressing allochthonous niche construction, this study explores the potential for *Empetrum* to
112 also be a predictor in neighbouring communities. We focus on snowbeds, because they are affected by climate
113 change (Björk & Molau 2007). With an ongoing decline in the duration of snow cover by 30% (Box *et al.* 2019),
114 changes in vegetation composition are already considerable (Wipf & Rixen 2010). Here we ask whether snowbed
115 communities can be affected by *Empetrum* through allochthonous allelopathy.

116 We performed our study in three parts. We quantified allochthonous *Empetrum* leaves on snowbeds, we
117 assessed bioactivity in allochthonous *Empetrum* leaves collected on the snow-cover of snowbeds and compared
118 it to the bioactivity of green leaves. Finally, we conducted an experiment testing germination and seedling growth
119 of ten tundra species in snowbed soil treated with allochthonous *Empetrum* leaves. We predicted that; I)
120 Allochthonous *Empetrum* leaves exist in snowbed environments. II) The bioactivity of allochthonous *Empetrum*
121 leaves is similar to that of green leaves. III) Germination and plant growth of tundra species will decrease with
122 increasing concentration of allochthonous *Empetrum* leaves added to their soil, independent of their growth form
123 and habitat affinity.



124

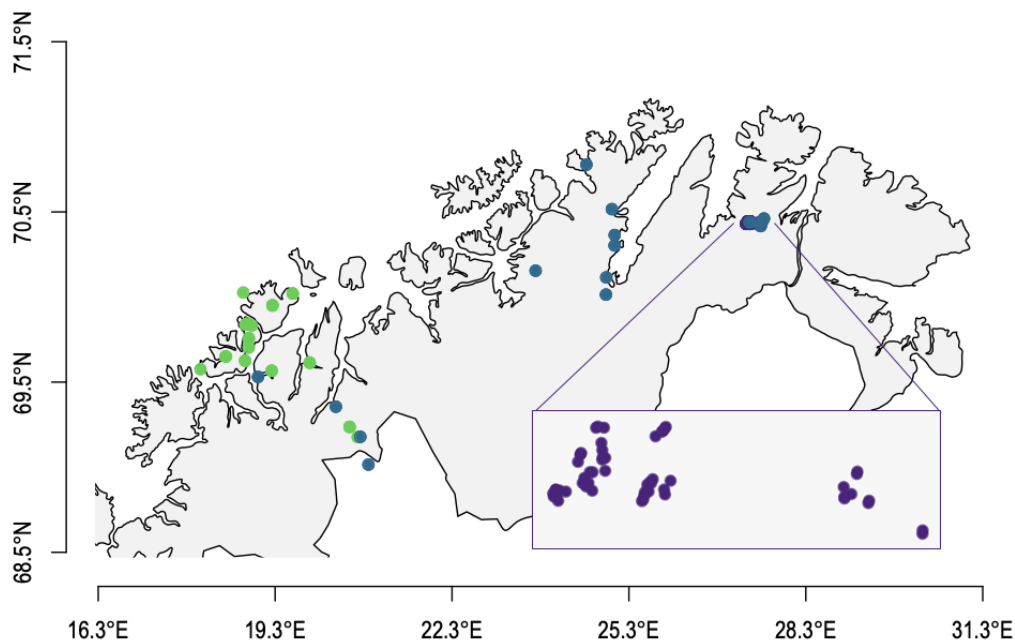
125 **Figure 1.** A conceptual presentation of the allelopathic effect of *Empetrum* in recipient snowbed communities.
126 Soil beneath *Empetrum* is allelopathic (Nilsson & Zackrisson 1992; Bråthen, Fodstad & Gallet 2010). The
127 secondary metabolites in *Empetrum* leaves are released as leachates from both fresh senescing and withered
128 leaves (brown leaves, autochthonous litter) during snowmelt and rain events (Brännäs *et al.* 2004) (shaded area).
129 The withered leaves have not lost their allelopathic capacity (Gallet, Nilsson & Zackrisson 1999). If the withered
130 leaves are transported to neighbouring habitats through wind, snowdrift, or meltwater streams (Körner 2003), we
131 hypothesize they can cause *allochthonous* allelopathy in recipient systems.

132

133 **Material and Methods**

134 **Study sites**

135 The study sites were located across Northern Fennoscandia, with particular sampling efforts above the treeline at
136 the mountain pass of Ifjord (Ifjordfjellet), Finnmark county (250 – 450 m asl) for the snowbed study, and in tundra
137 sites in northern Troms county (50 - 600 m asl) for the sampling of soil, leaves and seeds (Figure 2). Bioactivity
138 tests, chemical analyses and the phytotron experiment were conducted at UiT- The Arctic University of Norway.



139

140 **Figure 2.** Map of sampling locations. Locations of the snow bed study were at Ifjordfjellet (purple dots in inset).

141 Sampling locations of leaves for the bioactivity assessment were distributed over several sites across Northern

142 Fennoscandia (bluegreen dots). Sampling locations for seeds, soil and dead leaves for the phytotron experiment,

143 were situated in Troms (light green dots). Leaves for the bioactivity assessment were also sampled at Ifjordfjellet

144 (no specific locations marked).

145 **Snowbed study**

146 The study of allochthonous *Empetrum* leaves on snowbeds was conducted within an area of 20 km² of Ifjordfjellet
147 during five days in late June 2013 (Figure 2). Typical habitats of this tundra area are dwarf shrub heaths
148 dominated by *Empetrum nigrum*, *Vaccinium myrtillus* and *Betula nana* and snowbeds dominated by acrocarp
149 bryophytes such as *Dicranum* spp., vascular plants such as the prostrate shrub *Salix herbacea*, small forbs such
150 as *Sibbaldia procumbens* and *Omalotheca supina* and graminoids such as *Anthoxanthum nipponicum*.

151 All accessible snowbeds in the area were included in the study as long as they had a snow cover larger than 20
152 m² (size set to avoid sampling only small snowbeds). Detritus accumulates in non-uniform patterns on snowbeds
153 (Figure S2). Therefore, we chose a subjective placement of 40 cm × 40 cm plots within each snowbed on the
154 patches with the highest detritus concentration. In each plot, the presence and abundance of *Empetrum* leaves in
155 the accumulated detritus was recorded as one of five categories (0, 1-10, 10-20, 20-30, and more than 30
156 leaves). On average 8 plots per snowbed (with a minimum of four and a maximum of ten plots) were examined
157 for a total of 408 plots on 45 snow-covered snowbeds.

158 To assess whether the influx of leaves was dependent on the distance to the nearest *Empetrum* source, we
159 measured the distance between the snowbed's edge to the closest area of *Empetrum* dominance. The distances
160 measured were exact to the meter up to 20 meters, after which distances were measured to the closest 10 m.

161 For an assessment of the importance of snowbed slope for the accumulation of leaves, the snowbeds' slope was
162 measured in the centre of their snow cover.

163 **Bioactivity and chemical content of allochthonous leaves**

164 We conducted bioassays on *Empetrum* leaves collected from two snow-covered snowbeds at Ifjordfjellet in 2009
165 to ascertain whether allochthonous *Empetrum* leaves retain bioactivity. In addition, we analysed their Batatasin-III
166 and total phenolics content. For a comparison of allochthonous leaves and green leaves, we ran bioassays and
167 chemical analyses of green *Empetrum* leaves collected at Ifjordfjellet (n=8) (Figure 2). Finally, to assess whether
168 our findings from Ifjordfjellet are representative for the larger region, we collected and tested green leaves across
169 Northern Fennoscandia (n=12).

170 The bioassays and the Batatasin-III analysis were conducted using methodology described in González *et al.*
171 (2015). For each collection site, approx. 25 mg of leaves were placed in each of two Ø 4.5 cm Petri dishes under
172 two pieces of Whatman No 1 filter paper. The filter papers were moistened with 1.5 ml distilled water and 10
173 germinated lettuce (*Lactuca sativa*) seedlings were transferred onto them. Then the lid was attached with
174 parafilm. Three Petri dishes without *Empetrum* leaves served as controls. After five days, average root length per
175 Petri dish was calculated.

176 Batatasin-III was extracted from 25 mg of dried leaves with ethyl acetate. Extracts were evaporated to dryness
177 with Speedvac concentrator and Rotary evaporator. Dried residue was dissolved in 1 ml acetonitril:water 1:1
178 (V:V), acidified with 0.5% acetic acid and filtered with a 0.45 µm Millipore filter. Separation and quantification of
179 Batatasin-III was performed with gradient high-performance liquid chromatography (HPLC) and DAD detection
180 using a 996 Photodiode array (PDA) detector. Batatasin-III was separated on Waters x-bridge C18-5 µm particle
181 size column (4.6 x 150 mm) (part no. 186003116) at 30°C, with injection volume of 20 µl, flow rate of 1ml min⁻¹,
182 and retention time of 20.8 min. Batatasin-III was confirmed using an internal standard and quantified using an
183 appropriate calibration curve produced by the Waters Alliance chromatographic system. The wavelength
184 measured was 273.2 nm. Batatasin-III was determined using a gradient of mobile phases with milliQ water and
185 acetonitrile, both acidified with 0.5% acetic acid.

186 The phenolic analysis was based on the same extract as the Batatasin-III analysis. We measured total phenolics
187 by the Folin-Ciocalteu colorimetry method. We followed the basic protocol 1 in Current Protocols in Food

188 Analytical Chemistry (Waterhouse 2002), with Gallic acid as standard and reading absorbance at 750 nm using a
189 Spectra MAX 250.

190 ***Abundance of Empetrum***

191 Using published survey data (Bråthen & Lortie 2016a), we compared the abundance of *Empetrum* at Ifjordfjellet,
192 to that of other regions in Fennoscandia to assess whether the density of allochthonous leaves found in the
193 snowbed study could be representative to that of other tundra regions. In the survey, *Empetrum* abundance was
194 measured as point intercepts and converted to biomass. Because these measures of *Empetrum* abundance are a
195 minor part of this particular study, we refer to previously published papers for an explanation of the study design
196 (e.g. Bråthen & Lortie 2016b).

197 ***Collection of Empetrum leaves, seeds and soil for phytotron experiment***

198 *Empetrum* leaves, soil and seeds for the phytotron experiment were sampled at various sites in Troms county,
199 Norway, in between July and early October 2012 (Figure 2). Withered leaf samples were collected in areas where
200 *Empetrum* was a dominant species. Soil and seeds were collected from sites with 500 m minimum distance to
201 *Empetrum* dominated areas.

202 Because of the focus on dispersed *Empetrum* leaf litter, all leaves for the phytotron experiment were collected
203 from branches already detached from the mother plant or branches showing clear signs of withering. Leaf
204 samples were stored dry and at room temperature. A pre-experiment assessment of the withered leaves
205 demonstrated that they were clearly bioactive (Appendix 2).

206 Plant species representing different growth forms (forbs, woody plants or graminoids) and habitat affinities
207 (snowbed or more generalist), had to be present in at least three sites to justify seed collection. Consequently,
208 the seeds of the forbs *Bistorta vivipara*, *Omalotheca supina*, *Pedicularis lapponica*, *Sibbaldia procumbens* and
209 *Solidago virgaurea*, the grasses *Anthoxanthum nipponicum*, *Avenella flexuosa* and *Nardus stricta*, and the woody
210 species *Chamaepericlymenum suecicum*, *Dryas octopetala*, *Empetrum nigrum*, *Salix herbacea* and *Vaccinium*
211 *myrtillus* were gathered. We refer to Pan Arctic Flora database (<http://nhm2.uio.no/paf/>) for nomenclature and Lid
212 and Lid (2005) for categorization of species according to habitat. We collected approximately 50 seeds or 25
213 inflorescences for each species present at a given site. The range of seed collection sites ensured that seeds

214 represent different populations and environmental contexts. Seeds were stored at room temperature until cleaned
215 and thereafter frozen at -10°C.

216 We tested the baseline germination rate using 100 seeds per species (Appendix 3). The low germination rates of
217 *Pedicularis*, *Chamaepericlymenum*, and *Empetrum* excluded them from further experiments.

218 Soil was collected from snowbeds in the vicinity of five seed collection sites (Figure 2). This geographic range
219 ensured variation in environmental contexts. Preference was given to snowbeds with deeper organic layers and
220 sparse vegetation covers. This ensured collecting a sufficient amount of soil organic matter and avoided soil with
221 high root density. First, a soil core (Ø 5 cm, 10 cm deep) was taken. If the soil profile showed at least 6 cm of
222 non-sandy topsoil, 200-250 grams of topsoil was collected at each of 10 subsites and the litter and moss layer
223 discarded. The collected soil was dried at room temperature and sieved with a 4 mm sieve to remove non-organic
224 matter and roots. Soil from all subsites within a site was pooled and stored at -10°C. Soil analysis (Appendix 4),
225 showed that the sites were comparable in soil quality (Table 1).

226 **Table 1.** Description of the snowbed soils included in the greenhouse experiment in terms of soil pH and soil
227 element concentration (average \pm SD of soils from five collection sites).

pH	P	K	N	C - org	C - inorg	Water
	(%)	(%)	(%)	(%)	(%)	(%)
4.52 \pm 0.17	0.0013 \pm 0.0001	0.0102 \pm 0.0013	0.96 \pm 0.08	43.6 \pm 3.3	13.6 \pm 1.6	42.8 \pm 1.7

228

229 ***Estimation of abundance of Empetrum leaves in soil from snowbeds***

230 We measured the abundance of *Empetrum* leaves in two soil cores (\varnothing 5.5 cm, 10 cm deep) at the snow cover
231 edge of each of the five snowbeds sampled for soil, to ascertain the concentrations of *Empetrum* leaves in
232 snowbed soils.

233 The soil cores were weighed, dried at 95°C for 12 hours and sieved. All *Empetrum* leaves found during sieving
234 were counted. Importantly the leaves occurred throughout the soil core, indicating that leaves become
235 incorporated over time. Using the approximation of 1 leaf = 1 mg, leaf abundance within 1 kg of soil was
236 calculated. Leaf abundance in soil varied from 10 g to 43 g kg⁻¹ soil, with 6 out of 10 samples having 25 - 35 g kg⁻¹
237 soil. From this, we established a treatment gradient with four levels at 0, 15, 30 and 45 g *Empetrum* leaves kg⁻¹
238 soil at field capacity.

239 ***Phytotron experiment***

240 The experiment was conducted in autumn 2012 in the phytotron at UiT- The Arctic University of Norway.

241 First, the frozen soil was thawed in a dark room at 4°C for three days and mixed with sand at a 1:5 ratio as
242 suggested by Medina-Roldán, Paz-Ferreiro and Bardgett (2012) to remove site-specific differences. The soil was
243 placed in a dark room for 48 hours at 0.5°C and then quartered. One part was kept as control (0 g leaves kg⁻¹
244 soil), while the remaining parts were mixed with dry, withered *Empetrum* leaves in the previously established
245 treatment concentrations. The soil was then transferred into standard cylindrical planting pots (\varnothing 9 cm, 7.5 cm
246 deep) for a total of 20 pots per treatment.

247 Seeds were thawed and planted for a total of ten seeds in each of two pots per species and treatment. The soil
248 was covered with fine grade Perlite© to avoid water loss. In order to break seed dormancy, the seeds were
249 stratified in a darkened room at 0.5°C for 7 days. Seeds were left to germinate under 24 hours artificial light at
250 8°C (simulating the low-alpine light and temperature of Northern Fennoscandia).

251 The seeds were visited every three days for watering and germination assessment. After the first seed
252 germinated in a pot, seed germination was registered for a period of 25 days and summed for a maximum of 10
253 per pot.

254 All germinated seedlings above the first five were removed from pots to avoid seedling competition. The
255 remaining five seedlings were allowed to grow for 25 days after which their height and number of secondary
256 leaves was recorded. The pot-specific germination of the ≥ 5 first seedlings was synchronized within the tree day
257 interval between visits. Thus, no measures to control for varying seedling ages within pots was conducted.

258 **Data Analysis**

259 We analysed the data using linear mixed effects models (Pinheiro & Bates 2000) in the R environment version
260 3.4.4 (<http://www.r-project.org>). We used the lme package for statistical analysis and the ggplot2 package for
261 the graphic representation of data. Whenever data did not conform to normal distribution, they were transformed
262 for the analysis and back-transformed for the presentation of model predictions.

263 The average density distribution of *Empetrum* leaves within snowbeds was displayed according to the five leaf
264 density categories. The density of *Empetrum* leaves on snowbeds in response to distance from *Empetrum* heath
265 and snowbed slope was modelled with the leaf density as a fixed factor and the identity of snowbeds as random
266 factor. The leaf density categories were treated as a continuous variable from 0 to 4. The interaction between
267 distance and slope did not improve the model and was excluded from the final model.

268 The test of bioactivity and chemical content dependence on leaf source (allochthonous or green *Empetrum*
269 leaves), used leaf source as fixed factor and sampling locations as random factor. Testing bioactivity and
270 chemical content dependence on region (Ifjord vs other sampling regions within Northern Fennoscandia), we
271 used region (Ifjord vs other Fennoscandian) as a fixed factor and the location of all regions as random factor.

272 For the analysis of *Empetrum* abundance in Ifjord vs other regions within Northern Fennoscandia, we used region
273 (Ifjord vs other Fennoscandian) as fixed factor and the hierarchical sampling levels of the study design in
274 Bråthen and Lortie (2016b) as random factors.

275 Both the germination test and the seedling growth test were modelled with treatment as a continuous predictor.
276 When testing whether the treatment effect was dependent on growth form (forbs, grasses and woody) and/or
277 habitat affinity (heath, snowbed, general), we used treatment in interaction with growth form and habitat affinity as
278 fixed factors. For each model Pot ID nested in species identity was applied as random factor. Growth form or
279 habitat affinity were not retained in models where they did not explain variation in treatment effects.

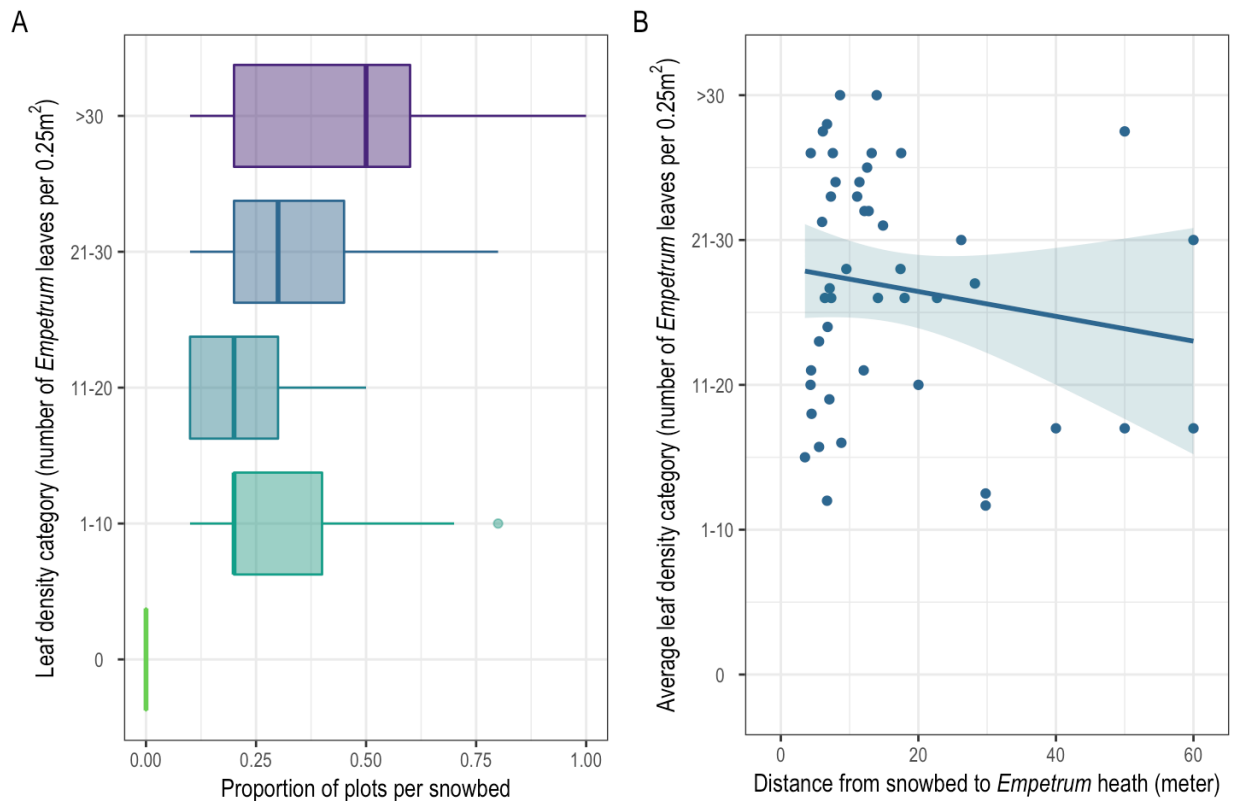
280 To display the effect of treatment on the species level, we used the ggplot2 package with linear model fit.

281

282 **Results**

283 ***Snowbed study***

284 *Empetrum* leaves were found on the snow cover of all 45 surveyed snowbeds, in the majority of plots per
285 snowbed and, for most plots, in medium to high abundance (Figure 3). Leaf density on snowbeds was
286 independent of snowbed slope (effect size - 0.009 ± 0.016 CI) and distance from *Empetrum* heath (effect size -
287 0.007 ± 0.008 CI) (Figure 3).

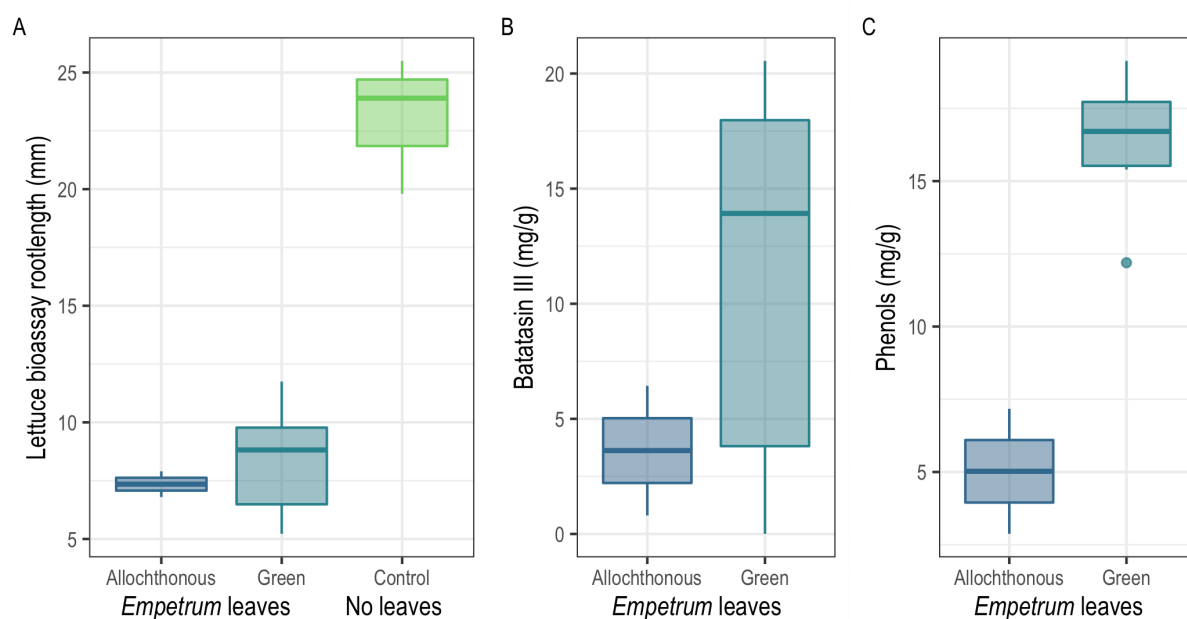


288

289 **Figure 3.** Density of *Empetrum* leaves on the snow cover of 45 snowbeds at Ifjordfjellet (A). Boxplots display
 290 outliers more than 1.5 times the interquartile range. Average density of *Empetrum* leaves on the snow-covered
 291 snowbeds in response to distance from the snowbed edge to the nearest *Empetrum*-dominated vegetation (B).

292 **Bioactivity and chemical content of allochthonous leaves**

293 We found similar bioactivity in green and allochthonous leaves in terms of how they affected lettuce root length
 294 (effect size 0.128 ± 0.430 C.I.), and that the lettuce roots in the controls (no leaves) was considerably longer than
 295 that of lettuce affected by the allochthonous leaves (effect size 1.874 ± 0.700 C.I.) (Figure 4). However, the leaf
 296 content of phenols was clearly highest in green leaves (effect size 11.142 ± 3.716 C.I.) and although not
 297 significant, the leaf content of Batatasin-III was also higher (effect size 7.536 ± 13.643 C.I.) (Figure 4).



299

300 **Figure 4.** Comparison of the bioactivity and chemical content of *Empetrum* leaves of allochthonous (on
 301 snowbeds) and autochthonous (green leaves on plants) source. The bioactivity assay (A) includes a control
 302 treatment (no leaves). Chemical content of Batatasin-III (B) and total Phenols (C) in allochthonous and green
 303 leaves. Boxplots display outliers more than 1.5 times the interquartile range.

304 **Comparison of green leaves between Ifjord and other regions in Fennoscandia.**

305 In order to evaluate whether results from Ifjordfjellet (the site of the snowbed study and of the collection of leaves
 306 for comparison between green and allochthonous leaves) were representative, we compared *Empetrum*
 307 abundance, bioactivity and chemical content of green, fresh leaves in Ifjord to that of other regions in Northern
 308 Fennoscandia.

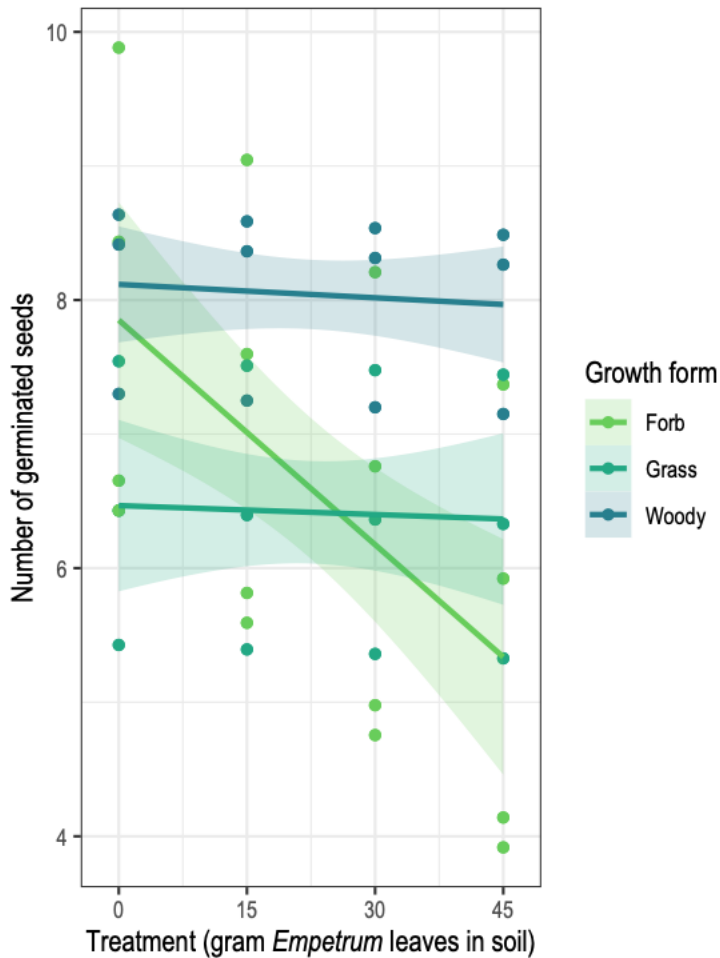
309 *Empetrum* was present in 87 % of plant communities in Ifjord and 85 % of plant communities in other regions,
 310 suggesting that *Empetrum* is extraordinarily common in the low alpine areas of Ifjord and other regions of
 311 Fennoscandia (Bråthen et al 2017). The abundance of *Empetrum* in terms of biomass was similar between the
 312 regions (effect size 2.771 ± 10.164 C.I.) (Figure S3).

313 Green leaves from Ifjord were more effective in limiting lettuce root length than green leaves from other regions in
 314 Northern Fennoscandia (effect size 3.911 ± 1.667 C.I.) (Figure S3). The leaf content of Batatasin-III, however,

315 was comparatively lower in *Empetrum* leaves from Ifjord (effect size - 13.771 ± 6.664 C.I.). There also was a
316 tendency for lower phenol content at Ifjord (effect size - 16.795 ± 24.575 C.I.) (Figure S3). Thus, results of
317 bioactivity and chemical content were inconsistent in indicating the direction of difference in the allelopathic effect
318 by *Empetrum* leaves from Ifjord in comparison to other regions in Fennoscandia, indicating there are potentially
319 other compounds having effect that were not studied here. Overall the results indicate that *Empetrum* leaves are
320 bioactive and contain both Batatasin-III and phenols across Northern Fennoscandia.

321 **Greenhouse experiment**

322 Seed germination was reduced by the allochthonous leaf treatment, but only among forb species (Table 2, Figure
323 5). Among forbs, the treatment effect corresponded to the sum of germinated seeds being reduced from 7.9
324 seeds under control conditions, to 7, 6.2 and 5.3 germinated seeds under the 15 g, 30 g and 45 g allochthonous
325 leaf treatment respectively. This reduction corresponds to a 1.5-fold, or 33% decrease between the control and
326 the strongest allochthonous leaf treatment. There was no modification of treatment effect by habitat affinity (effect
327 size 0.026 ± 0.042 C.I.).

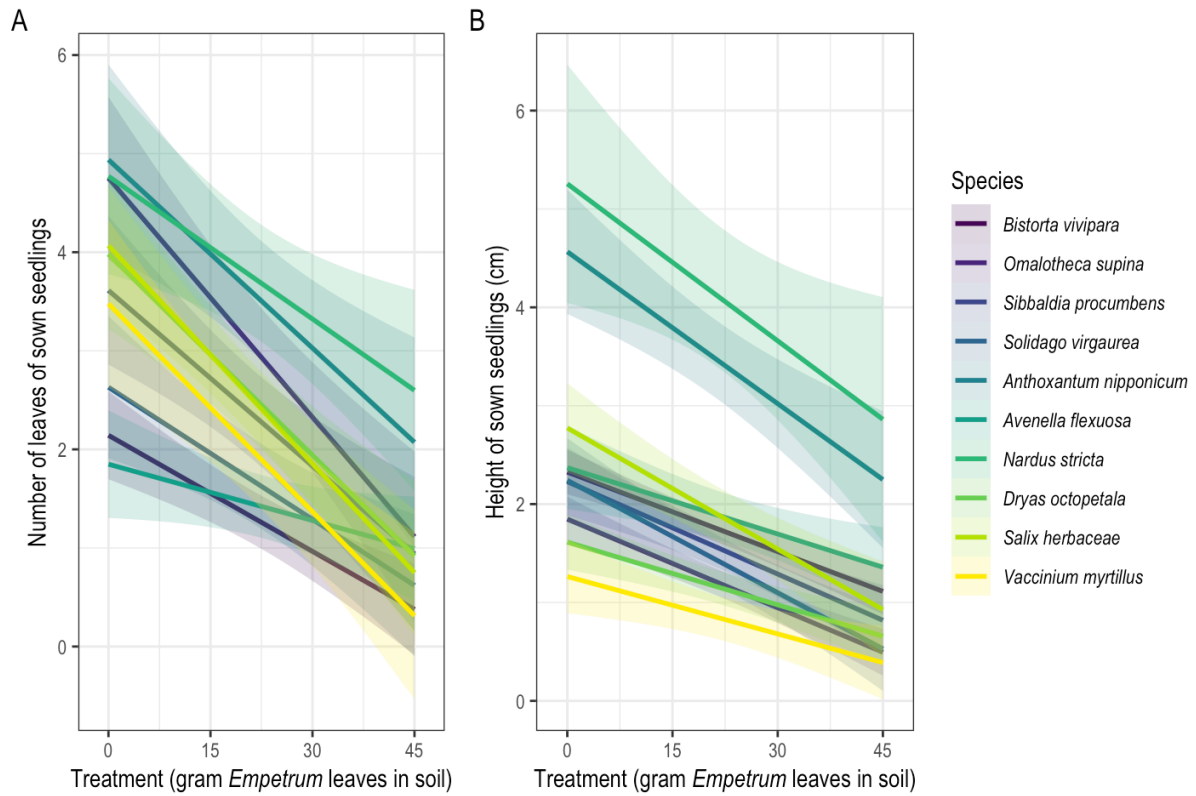


328

329 **Figure 5.** Sum of germinated seeds per pot per growth form in response to treatment with *Empetrum* leaves in
 330 soil.

331 Seedling growth was reduced by the allochthonous leaf treatments in terms of the number of secondary leaves
 332 and leaf height (Table 2, Figure 6). The seedlings had an average of 3.9, 2.5, 1.8 and 1.2 leaves and an average
 333 of 2.8, 1.9, 1.6 and 1.2 cm height under the control (0 g), 15 g, 30 g and 45 g allochthonous leaf treatment
 334 respectively. In total, seedlings under the control treatment were 2.3 times longer and had 3.2 times more leaves
 335 in comparison to seedlings grown in the strongest allochthonous leaf treatment.

336 Leaf number was clearly affected by treatment independent of growth form (effect size of grass 0.008 ± 0.029
 337 C.I. and woody -0.029 ± 0.032 C.I. vs that of forbs) or habitat affinity (effect size of snowbed -0.029 ± 0.029 C.I. vs
 338 generalist species). Similarly, growth expressed as leaf height was clearly affected by treatment independent of
 339 growth form (effect size of grass -0.012 ± 0.024 C.I. and woody 0.002 ± 0.026 C.I. vs that of forbs) or habitat
 340 affinity (effect size of snowbed -0.004 ± 0.024 C.I. vs that of generalists).



341

342 **Figure 6.** Growth response of seedlings of a range of species to treatment with *Empetrum* leaves added to their
 343 soil. Growth responses are presented in terms of number of secondary leaves (A) and height (B).

344 **Table 2.** Effect size ($\pm 95\%$ C.I.) of treatment effects of allochthonous leaves on the sum of germinated seeds and
 345 seedling growth. Growth was measured as the number of secondary leaves and leaf height. Estimates from
 346 mixed models with species and Pot ID as random factors.

Response	Interacting factor	Effect size ($\pm 95\%$ C.I.)
GERMINATION	Forbs	-0.056 (-0.084, -0.028)
	Grasses	-0.002 (-0.035, 0.030)
	Shrubs	-0.003 (-0.036, 0.029)
GROWTH		
	Number of leaves	-0.057 (-0.069, -0.044)
	Height	-0.034 (-0.043, -0.024)

347

348 **Discussion**

349 In this study we find evidence of allochthonous allelopathy using the model species *Empetrum nigrum*. First, a
350 high concentration of *Empetrum* leaves was found in the debris on snow beds distanced 3 to 50 meters away
351 from *Empetrum* heath, establishing *Empetrum* as a source of allochthonous detritus into snowbed environments.
352 Second, allochthonous leaves were as bioactive as green leaves in reducing the growth of lettuce seedlings.
353 Although at lower concentrations than green leaves, the allochthonous leaves contained secondary metabolites
354 associated to the allelopathic capacity of *Empetrum* (Gallet, Nilsson & Zackrisson 1999, this study). Third, both
355 seed germination and seedling growth of a range of tundra plant species negatively responded to allochthonous
356 *Empetrum* leaves in soil at concentrations likely to occur in snowbed soils. Surprisingly, germination was
357 negatively affected only in forb species. Our findings suggest that *Empetrum* can reduce primary productivity at
358 vital life stages of vascular plant species in tundra snowbeds through allochthonous allelopathy.

359 Delaying the development of plant species in recipient systems of allochthonous *Empetrum* leaf litter, may be at
360 *Empetrum*'s benefit and even selected for. If the recipient system represents a potential habitat, modifying the
361 environment to the disadvantage of other species result in benefits to the niche constructor (Matthews *et al.*
362 2014). *Empetrum* establishment in snowbeds is likely. *Empetrum* berries are dispersed by zoochory of migratory
363 animals such as reindeer (Bråthen *et al.* 2007a), providing opportunities for establishment in new habitats. In
364 snowbeds, reduced competition for light and other resources by the extant flora in response to the allochthonous
365 allelopathy, could facilitate the establishment of slow growing species such as *Empetrum*. Because it is dispersed
366 by endozoochory, resources in the faeces could further boost *Empetrum* growth and reduce the allelopathic
367 impact of the allochthonous *Empetrum* leaves present (Bråthen, Fodstad & Gallet 2010). The latter process also
368 facilitates the establishment of other species dispersed with zoochory. In contrast, in areas unsuitable as new
369 habitats, for instance late snowbeds with insufficient growth season length for *Empetrum*, the allochthonous
370 allelopathy could contribute to the appearance of barren snowbeds with low productivity.

371 Batatasin-III "becomes physically trapped by organic matter" (Wallstedt, Gallet & Nilsson 2005) which neutralises
372 its allelopathic effect (González *et al.* 2015). For this reason, snowbed soil rich in organic matter content might
373 absorb and neutralize the allelopathic effect of Batatasin-III. However, if Batatasin-III is retained in low degradable

374 leaves, prevented from being trapped by the organic soil (Parker *et al.* 2018) and released in leachate pulses
375 whenever water drains the soil, it may take substantial organic material such as mammalian faeces or even fire,
376 to neutralize its bioactivity (Bråthen, Fodstad & Gallet 2010). Wallstedt *et al.* (2000) found indications that
377 Batatasin-III can disturb membrane integrity and, consequently, disrupt fundamental processes such as ion
378 uptake from roots. Perhaps for this reason, signs of reduced growth were observed for all species only after
379 seedlings had started growing and their roots came in contact with the Batatasin-III reservoir.

380 This study found delayed development at the seedling stage in common species from three growth forms when
381 growing in snowbed soil with withered leaves of *Empetrum*. The finding corresponds a study on the effect of
382 Batatasin-III, where reduced germination and seedling growth for a range of tundra growth forms was observed
383 (González *et al.* 2015). It is noteworthy that the deciduous shrub *Betula nana* and the evergreen dwarf shrub
384 *Vaccinium vitis-idea*—species encroaching into snowbed environments in response to climate warming along
385 with *Empetrum* (Vowles *et al.* 2017) — also experienced reduced germination and seedling growth in response
386 to Batatasin-III (González *et al.* 2015). *Empetrum* might, therefore, delay seedling establishment of other shrub
387 species and their encroachment through allochthonous allelopathy. It remains unknown, whether *Empetrum*
388 gains enough competitive advantage through allochthonous allelopathy to outcompete other expanding shrubs or
389 whether *Empetrum* simultaneously delays its own establishment, thereby negating any competitive advantage.

390 Snowbeds are among the habitats most affected by climate change (Björk & Molau 2007). The decline in the
391 duration of snow cover is likely to cause a reduction in forbs that, in contrast to species of other growth forms,
392 benefit from late snowmelt and are hence most vulnerable to earlier snowmelt (Wipf & Rixen 2010). In addition,
393 results from this study indicate that forbs are most vulnerable to allochthonous allelopathy by *Empetrum*,
394 exhibiting reduced germination rates in addition to reduced seedling growth. Yet, importantly, all growth forms
395 were equally affected by allochthonous allelopathy by *Empetrum* at their seedling stage, which suggests overall
396 reduced growth. Plants in snowbeds represent an important resource to many tundra herbivores (review in Björk
397 & Molau 2007). Changes in vegetation composition and productivity will therefore also have consequences to
398 trophic aboveground interactions. In particular, lemmings, depending on snowbeds for their winter-habitat, might
399 be affected. Yet, lemming activity could also cause disturbances that promote seedling density richness in
400 snowbeds (Nystuen *et al.* 2014) and counteract the allelopathic effects by *Empetrum* with their faeces. Such

401 disturbance may, in turn, benefit forbs, that are found to be the most disturbance resistant growth form (Evju,
402 Hagen & Hofgaard 2012). In summary, snowbeds are affected by a multitude of factors. Here, we identify
403 allochthonous allelopathy as an additional factor to be considered when predicting snowbed change.

404 Our results suggest that allochthonous allelopathy in snowbeds is a phenomenon to be expected over large
405 spatial scales in Northern Fennoscandia and other regions where *Empetrum* is common. The extent of
406 allochthonous allelopathy is likely to increase as *Empetrum* is advancing in response to climate change (Bråthen,
407 González & Yoccoz 2018; Vowles & Björk 2019) and resistant to climatic variability (González *et al.* 2019).
408 Furthermore, although *Empetrum* is vulnerable to trampling (Tybirk *et al.* 2000), it is not decreasing in response
409 to higher animal densities (Bråthen *et al.* 2007b), and can even increase in the presence of mammalian
410 herbivores (Vowles *et al.* 2017). Our study focused on snowbeds as recipient system. It is likely that *Empetrum*
411 can be a source for allochthonous detritus to other habitat types, albeit with lower influx rate of leaves and a
412 weaker allochthonous allelopathic effect. Large-scale, observational studies suggest that the contribution of
413 *autochthonous* allelopathy by *Empetrum* is substantial (Ravolainen *et al.* 2010; Bråthen & Ravolainen 2015; Mod
414 *et al.* 2016), lowering the species richness and abundance of herbaceous vascular plants (Bråthen, González &
415 Yoccoz 2018). However, *Empetrum* also explains biodiversity patterns at spatial scales at the landscape level
416 (Ravolainen *et al.* 2010), suggesting *allochthonous* allelopathy is also of considerable importance.

417

418 **Conclusion**

419 Changes in the tundra are ongoing. These changes are varied and not always as predicted (Björkman *et al.*
420 2020). This indicates there are several contributing factors and processes that still need to be established. We
421 suggest that one such factor is *allochthonous allelopathy*, which, along with niche construction by dominant
422 plants in their home communities, can represent a confounding factor to the consequences of environmental and
423 climatic change. Allochthonous allelopathy can be a common and increasing phenomenon, as indicated by the
424 abundance of *Empetrum*, causing biotic stress in snowbeds and other parts of the tundra. Furthermore,
425 *allochthonous allelopathy* may modify the capacity of existing and novel species in the tundra to encroach further.

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556

557 SUPPORTING INFORMATION

558 Additional supporting information may be found in the online version of this article.

559 Figure S1. Small glands on the *Empetrum nigrum* leaves and molecular formula of Batatasin III

560 Figure S2. Photocollage depicting the process of transport and accumulation of allochthonous *Empetrum nigrum*
561 leaves

562 Figure S3 Comparison between Ifjord and other regions within Northern Fennoscandia

563 Figure S4. Root length of lettuce seedlings in response to exposure to different amounts of *Empetrum nigrum*
564 leaves

565 Table S1. Soil content description for each of the five sites included in the greenhouse experiment.

566 Appendix 1. Leaf traits enabling dispersal

567 Appendix 2. Pre-experiment assessment of bioactivity of leaves

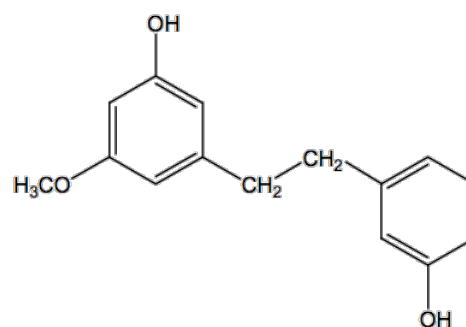
568 Appendix 3. Baseline germination rate

569 Appendix 4. Soil analysis

570

571 SUPPORTING INFORMATION

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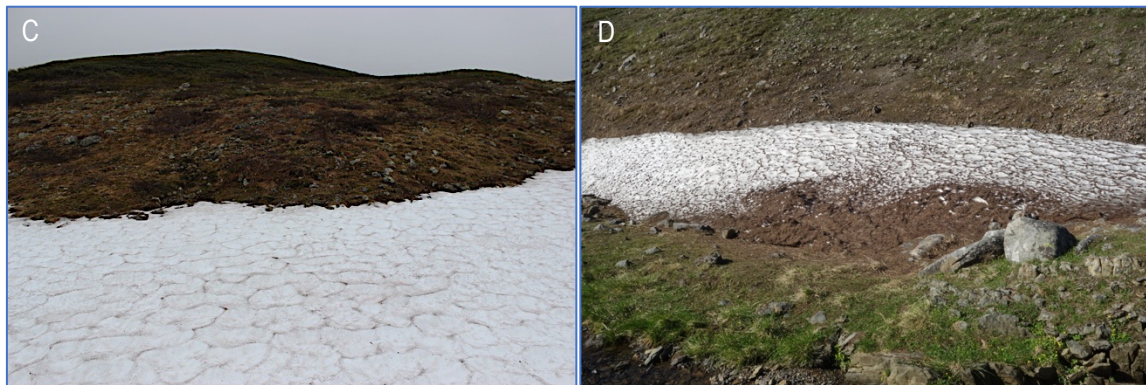
573

574 **Figure S1. Small glands on the *Empetrum nigrum* leaves and molecular formula of Batatasin III.** A
575 photograph depicting the white-looking small glands on the *Empetrum nigrum* leaves where Batatasin-III can be
576 found, and the formula of the dihydrostilbene Batatasin-III. Photograph taken by last author.

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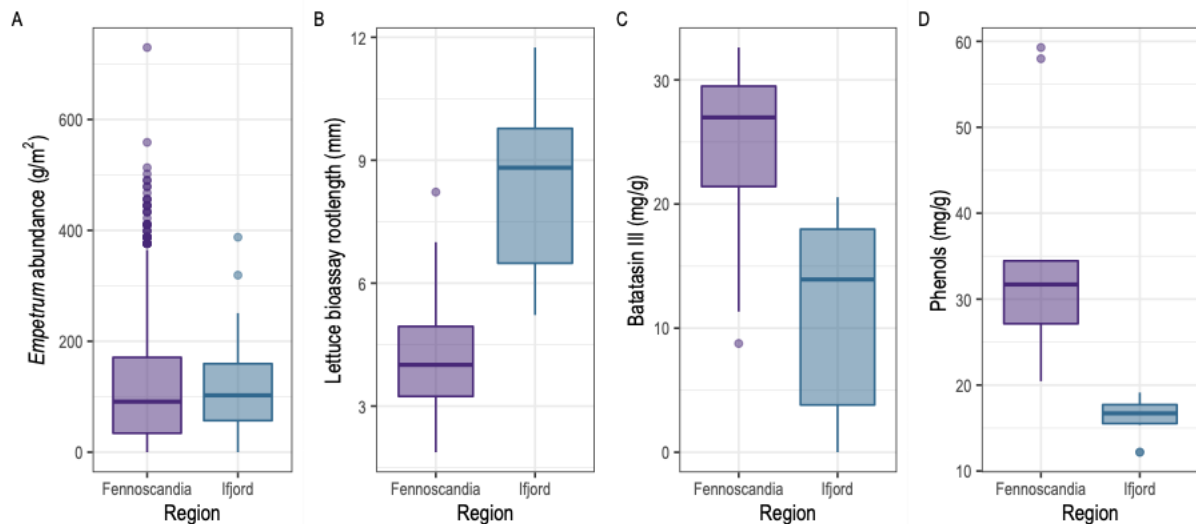


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581

582 **Figure S2. Photocollage depicting the process of transport and accumulation of allochthonous *Empetrum***
 583 ***nigrum* leaves. A. *Empetrum* can cover vast areas and dominate in the vegetation. B. Autochthonous withered**
 584 **leaves of *Empetrum* can be attached to the plant but are easily detached when touched or when exposed to**
 585 **strong winds. C. Detritus on snowbed surfaces contain withered leaves of *Empetrum*. D. When the snow cover of**
 586 **snowbeds melts out, vast amounts of accumulated detritus may be exposed. E. The abundance of detritus can**
 587 **be so high it almost completely covers the ground, also causing shade. F. A closer look reveals at the detritus**
 588 **reveals that withered *Empetrum* leaves are common. Photographs were taken in the Varanger Peninsula**
 589 **National Park in July 2015 by last author.**

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591

592 **Figure S3 Comparison between Ifjord and other regions within Northern Fennoscandia.** Comparison of
 593 *Empetrum* abundance (A), green leaf bioactivity (B), chemical content of Batatasin-III (C) and total Phenols (D)
 594 from Ifjord, where the snowbed study was conducted, compared to that of other regions within Northern
 595 Fennoscandia. Boxplots display outliers when more than 1.5 times the interquartile range.

596

597

598 Appendix 1. Leaf traits enabling dispersal

599 *Empetrum nigrum* has small leaves (Lid & Lid 2005). Small size is a leaf trait that is likely to facilitate dispersal. In
 600 order to compare leaf traits of *Empetrum* to that of seed traits with known dispersal range, we measured 50
 601 *Empetrum nigrum* fresh leaves. The leaves had an average leaf weight of 0.53 mg (+/- 0.11 mg), with an average
 602 length between 4.5 to 5 mm and a width of 1mm at the broadest point. Comparing these values to that of the
 603 terminal velocity of wind dispersed seeds of similar proportions (Kattge *et al.* 2011), suggests *Empetrum* leaves
 604 have aerodynamic properties that facilitate wind dispersal. In addition, these leaf trait values suggest *Empetrum*
 605 leaves are easily transported with meltwater streams (Körner 2003).

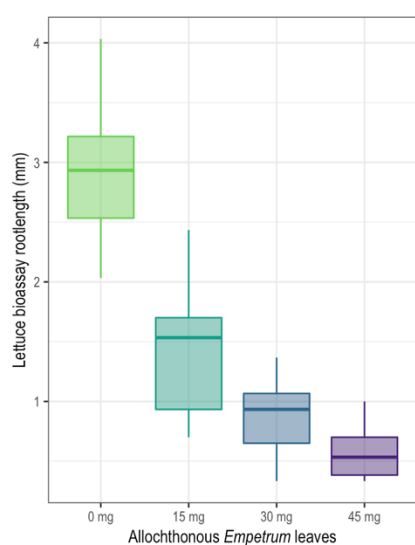
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607 Appendix 2. Pre-experiment assessment of bioactivity of leaves

608 The bioactivity of the collected withered leaves was assessed in a pre-experiment bioassay using lettuce
 609 (*Lactuca sativa*) seedlings. The bioassays were conducted using methodology as described in González *et al.*
 610 (2015). For each treatment 0 mg, 15 mg, 30 mg or 45 mg of withered leaves were placed into each of 15 Ø 4.5

611 cm Petri dishes with two pieces of Whatman No 1 filterpapers on top. The filterpapers were moistened with 1.5 ml
612 distilled water before a set of 3 germinated lettuce seedlings were carefully transferred on top of the filterpaper
613 and the lid attached with parafilm. The assay lasted for three days after which the rootlength of each seedling
614 was measured and the average rootlength per petridish was calculated.

615 The withered *Empetrum* leaves collected for the allochthonous leaf treatment showed clear bioactivity at all
616 treatment levels. The root lengths of the lettuce seedlings were reduced from an average of 2.933 cm of controls
617 (no leaves) with -1.510, -2.071 and -2.373 cm (all \pm 0.286 C.I.), at treatments with 15, 30 and 45 mg withered
618 leaves per Petri dish respectively.



619

620 **Figure S4.** Root length of lettuce seedlings in response to a three-day treatment with allochthonous (withered)
621 leaves at concentrations of 0, 15, 30 and 45 mg leaves per Petri dish.

622 Using the molecular weight of Batatasin-III of 244.28 g/mol (molecular formula of Batatasin-III in SI I) and
623 anticipating a leaf concentration of 5 mg Batatasin-III g⁻¹ allochthonous leaves (Figure 5 this study), the 0, 15, 30
624 and 45 mg leaf treatments in the experiment correspond to a Batatasin-III treatment effect of 0, 0.3, 0.6 and 0.9
625 μ Mol respectively. This allochthonous treatment effect is a magnitude lower than the 0.1 - 4 mM applied in
626 bioassays finding clear effects of Batatasin-III (González *et al.* 2015). The leaf treatments are however more
627 similar to the concentration of 1.3 μ M Batatasin-III, as calculated from a concentration of 0.32 μ g Batatasin-III g⁻¹
628 humus collected at *Empetrum* sites (Bråthen, Fodstad & Gallet 2010). This latter concentration was also related
629 to a very clear autochthonous allelopathic effect, significantly reducing the growth of the grass *Avenella flexuosa*
630 and the forb *Soildago virgaurea*, two of the species also tested here, during a nine-week long experiment
631 (Bråthen *et al.* 2010). Importantly therefore, it may not be Batatasin-III alone that cause reduced growth as
632 *Empetrum* leaves of low or no Batatasin-III content still have high bioactivity (González *et al.* 2015).

633

634 **Appendix 3. Baseline germination rate**

635 In order to obtain a baseline germination rate, 100 seeds of each species were placed in a 4.5 cm diameter petri
 636 dish equipped with Whatmann filterpaper (Nr. 1), moistened with 1.5 ml distilled water and germinated at room
 637 temperature. Germination rates differed markedly between the species: *Bistorta vivipara* (94.67 %), *Omalotheca*
 638 *supina* (57.12 %), *Pedicularis lapponica* (0 %), *Sibbaldia procumbens* (52.34 %), *Solidago virgaurea* (78.11 %),
 639 *Anthoxantum nipponicum* (73.98 %), *Avenella flexuosa* (60.34 %), *Nardus stricta* (63 %), *Chamaepericlymenum*
 640 *suecicum* (0 %), *Dryas octopetala* (89.47%), *Empetrum nigrum* (2.47 %), *Salix herbacea* (89.79%), and
 641 *Vaccinium myrtillus* (76.80 %).

642

643 **Appendix 4. Soil analysis**

644 In order to compare the make-up of soils from the five sampling locations, soil analyses were conducted. A total
 645 of three samples of 25 gram soil from each of the five soil sampling sites were taken for chemical analysis of pH
 646 and content of P, K and N, whereas a total of ten samples of 5 gram soil were taken for a combustion analysis of
 647 water and C content. Chemical analysis was conducted at the Institute for Sustainable Plant Production (NPP) of
 648 the Austrian Agency for Health and Food Safety (AGES). The combustion analysis was conducted at UiT. Each 5
 649 gram sample of soil was placed in a pre-weighed crucible. The samples were then dried at 95 degrees Celsius for
 650 12 hours and allowed to cool before weighing. Thereafter, the samples were incinerated at 450°C for 4 hours,
 651 allowed to cool and then weighed again before the soil organic, ash and water content were calculated. Water
 652 was calculated as the weight of the dried sample subtracted from the weight of the fresh sample, the organic
 653 Carbon content as the weight of burnt sample subtracted from the weight of the dried sample, and the inorganic
 654 Carbon content (ash) as the weight of the burnt sample.

655

656 **Table S1.** Soil content description for each of the five sites included in the greenhouse experiment.

657

Site number	pH	P (%)	K (%)	N (%)	C - organic (%)	C - inorganic (ash) (%)	Water (%)
1	4.8	0.0014	0.0096	0.97	42	15	43
2	4.5	0.0013	0.0101	0.86	46	12	42
3	4.3	0.0013	0.0101	1.01	45	13	42
4	4.6	0.0015	0.0126	1.08	38	16	46
5	4.4	0.0011	0.0086	0.87	47	12	41

Average	4.52	0.0013	0.0102	0.96	43.6	13.6	42.8
SD	0.17	0.0001	0.0013	0.08	3.3	1.6	1.7

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