

Research article

Volcanic soils alleviate the allelopathic capacity of *Empetrum nigrum* in degraded tundra ecosystems

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Oikos

2025: e11336

doi: [10.1002/oik.11336](https://doi.org/10.1002/oik.11336)

Subject Editor: Julia Kemppinen

Editor-in-Chief:

Paulo R. Guimaraes

Accepted 25 May 2025



Land degradation due to unsustainable land use is of major concern worldwide and recovery is often slow. A potential mechanism behind slow recovery of degraded ecosystems is the retarding impacts of allelopathic plant species on the establishment of species that might facilitate the recovery process. However, the strength of the retarding impact may depend on soil type. In this study, we investigated the potential role of an abundant, evergreen and allelopathic dwarf shrub, *Empetrum nigrum*, in trapping tundra ecosystems in a degraded state in Iceland after centuries of unsustainable land use. We first ran a series of bioassays to assess the potential allelopathic legacy effects of the *Empetrum*-associated volcanic soils (Andosol and Vitrisol) on seed germination and root elongation of the common grass species *Festuca richardsonii* in comparison with *Empetrum*-associated non-volcanic Histosol and Podzol soil types. Then we assessed the *Empetrum* leaf–soil interactions for all soil types using leaves from a degraded site in Iceland. We found no potential allelopathic legacy effects of *Empetrum*-associated volcanic soils, whereas the non-volcanic soils negatively impacted *Festuca* root elongation. *Empetrum* leaves alone affected both seed germination and root elongation. These effects were strongly alleviated by the volcanic soils, but not by the non-volcanic soils. We conclude that abundant allelopathic plant species may significantly contribute to trapping tundra ecosystems in a degraded state, but the strength of this trapping mechanism depends on the soil environment.

Keywords: allelopathy, dwarf shrub heath, *Empetrum*, land degradation, soil interactions, sub-Arctic

Introduction

Land degradation, due to unsustainable land use, is a major issue worldwide (Pravělie 2021) and the recovery to a non-degraded state is often slow after removing the drivers



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of degradation (Bestelmeyer et al. 2003). Slow recovery of degraded land has been related to several constraints, including shifts in plant species dominance towards species with traits that change ecosystem characteristics, thus constraining management efforts for restoration (Suding et al. 2004). One such plant trait is allelopathy, i.e. the chemical interaction among plant species, which can cause negative interference within and between plant species, by e.g. restricting the local distribution of species (Hierro and Callaway 2021). Plant allelopathy can also impact ecosystem processes, resulting in less productive ecosystems (Wardle et al. 1998), and plant–soil feedbacks creating undesirable soil legacy effects (De Long et al. 2023). However, it is not fully understood whether allelopathy can contribute to slow recovery of degraded ecosystems.

Icelandic ecosystems have gone through major changes since the human settlement ~ 1100 years ago. One of the main drivers of change has been heavy livestock grazing, mainly by sheep (Eddudóttir et al. 2020), often causing ecosystem transitions to degraded states (Barrio et al. 2018). Icelandic tundra ecosystems are often persistent in a degraded state and recovery back to less degraded states is extremely slow in response to grazing-cessation (Jónsdóttir et al. 2005, Mörsdorf et al. 2021), particularly if fully collapsed, and would need additional interventions (Barrio et al. 2018). A common and often dominating plant species in degraded tundra ecosystems is the unpalatable and allelopathic evergreen dwarf shrub *Empetrum nigrum* (Jónsdóttir et al. 2005), herein referred to as *Empetrum*. The high abundance of *Empetrum* has very likely been facilitated by heavy sheep grazing, shifting plant community dominance towards unpalatable plant species (Marteinsdóttir et al. 2017). The ability of *Empetrum* to slowly encroach land independently of varying grazing pressures has potentially contributed as well (Tuomi et al. 2024). However, the capacity of *Empetrum* to contribute to trapping tundra ecosystems in degraded states is uncertain.

There is evidence from Scandinavian studies that *Empetrum* may impact ecosystem processes in various ways by, for example, reducing decomposition rates, nutrient availability and aboveground productivity (Tybirk et al. 2000). Because these impacts on ecosystem processes can cause legacy effects in the system, *Empetrum* has also been termed a niche constructor, i.e. an organism that modifies its environment (Bråthen et al. 2018). Previous studies have documented that *Empetrum* can inhibit seedling establishment in natural Fennoscandian ecosystems (Nilsson and Zackrisson 1992, Nilsson 1994, Nilsson et al. 2002, Grau et al. 2010, González et al. 2021). Furthermore, laboratory experiments have documented that both leaves and associated soils from Scandinavian *Empetrum* populations inhibit plant growth and development (Nilsson and Zackrisson 1992, Bråthen et al. 2010, González et al. 2015, Pilsbacher et al. 2021). Preliminary studies of Icelandic *Empetrum* populations indicate similar allelopathic capacities (Valsdóttir 2021). Therefore, it can be expected that one of the trapping mechanisms in degraded ecosystems is allelopathy by retarding species like *Empetrum*.

In *Empetrum*-associated soil, plant residues accumulating in the form of *Empetrum* leaf-litter are most likely a source of allelopathic soil legacy effects (Wallstedt et al. 2000). In addition, *Empetrum* allelochemicals can become reversible, adsorbed into particles of decomposed organic matter and mineral particles in the soil (Wallstedt et al. 2000). Generally, the allelopathic capacity of a plant species is related to the bioavailable concentration of its allelochemicals in the soil solution, which mainly depends on retention, transportation, and chemical degradation in the soil environment and how that is affected by abiotic and biotic factors (Scavo et al. 2019). Physical factors, such as a high water-holding-capacity, and chemical factors, such as a low cation-exchange-capacity and pH, can decrease retention and increase transportation of allelochemicals in soils, and thereby increase the bioavailability (Scavo et al. 2019). Furthermore, alkaline and acidic soil pH can decrease or increase the phytotoxicity of allelochemicals depending on the chemical nature of the compounds (Scavo et al. 2019). A high soil organic matter content typically alleviates phytotoxicity by increasing the buffer power on soil pH thereby avoiding excesses of alkalinity and acidity, and by increasing cation-exchange-capacity, due to its high surface area and negative surface charges (Scavo et al. 2019). Moreover, biotic factors, such as microbial degradation or transformation of chemical compounds, can either reduce or increase the phytotoxicity of allelochemicals (Inderjit et al. 2005). Allelopathic legacy effects from *Empetrum* have been alleviated in the presence of biotic factors, such as animal feces (nitrogen) addition, and by abiotic treatments like burning (Nilsson et al. 2002, Bråthen et al. 2010). The addition of a key *Empetrum* allelochemical (the bibenzyl Batatasin-III) to soil, suggests that this allelochemical is retained by organic matter and is therefore more available in mineral soil compared to organic soil (González et al. 2015). However, soil physical and chemical factors affecting legacy effects have received little attention.

The geological parent material can contribute to varying soil properties, arising from the physical and chemical nature of different soil minerals that can impact e.g. charge characteristics and pH (Wilson 2019). Icelandic soils have developed from volcanic parent material into Andosol arising from amorphous clay minerals, such as allophane, imogolite, and ferrihydrite (Arnalds 2015). Andosols in Iceland are typically characterized by having a relatively high cation-exchange-capacity and high pH, i.e. between 5 and 7 depending on the input of aeolian additions of new volcanic material and the amount of precipitation, which can lower pH through leaching (Arnalds 2015). Therefore, the capacity to alleviate the phytotoxicity of allelochemicals might be relatively high in Icelandic Andosol compared to non-volcanic soils that typically comprise layered clay minerals, such as smectite and kaolinite (Arnalds 2015). Massive soil erosion in Iceland has turned Andosol in some areas into Vitrisol (Vitric Andosol according to the FAO World Reference Base), which is characterized by a very low soil organic matter content, i.e. typically < 1% (Arnalds 2008), and might differ from Andosol

in the ability to alleviate bioavailability and phytotoxicity of allelochemicals.

In this study, we investigated the potential role of Icelandic *Empetrum* populations in retarding the recovery of degraded tundra ecosystems with volcanic soils. Specifically, we asked: Q1) are there allelopathic legacy effects in *Empetrum*-associated Andosol, and how do they differ from *Empetrum*-associated non-volcanic soils? Q2) Do *Empetrum*-associated Andosol and non-volcanic soils modify the allelopathic effects of *Empetrum* leaves differently? In addition, we included Vitrisol in our experiments to compare the effects with volcanic soils in more degraded tundra ecosystems that are not associated with *Empetrum*. We expected that both soil legacy effects and soil–leaf interaction in Andosol are different from non-volcanic soils due to its unique physical and chemical properties. We assessed potential allelopathic soil legacy effects and soil interaction with *Empetrum* allelopathic capacities, in a series of bioassays on seed germination and seedling root growth of the grass species *Festuca richardsonii* (herein referred to as *Festuca*), which represents a common fast-growing palatable plant species in Iceland. Even though there is some variation among plant species in their sensitivity to *Empetrum* allelochemicals, previous studies indicate clear allelopathic effects of *Empetrum* on multiple target species (such as González et al. 2015). Since we are not addressing the variation in sensitivity, we are therefore only using one common target species to address our questions.

Methods

Sites for leaf sampling and soil collection

Leaf sampling and andosol collection site

Empetrum-associated volcanic soils (Andosol soils) were collected in a tundra ecosystem (65°08'N, 19°40'W, 480 m a.s.l.) located in Auðkúluheiði (Fig. 1A), which is a summer grazing common in the northwestern highlands of Iceland. The area is characterized by a sub-Arctic alpine climate with a monthly average (June–August) summer temperature of 8°C and precipitation of 41 mm (2011–2021, Kolka Weather station, 65°13'N, 19°43'W, 476 m a.s.l.; Data Bank of the Meteorological Office of Iceland). The vegetation is dominated by *Betula nana* and *Empetrum* dwarf shrubs along with a high abundance of bryophytes and lichens, especially *Racomitrium lanuginosum* and *Cetraria islandica* (Jónsdóttir et al. 2005). The dwarf shrub heath has a considerable number of erosion spots (2% cover) within the vegetation and is considered partly degraded (Mulloy et al. 2021). The soil is classified as Brown Andosol (Arnalds 2015), and we will refer to this site as the 'Andosol site'. Soil was collected from two sub-sites located approximately 200 m apart within the Andosol site, with one ('Andosol sub-site 1') characterized by having fewer and smaller erosion spots and a higher vascular plant cover than the other ('Andosol sub-site 2'; Fig. 1B).

Empetrum leaves representing the *Empetrum* population were sampled in Auðkúluheiði at the Andosol site (Fig. 1A).

Empetrum is on average 22% of the total vegetation cover but is patchily distributed, ranging from 0 to 60% cover within 50 × 50 cm plots (Jónsdóttir unpubl.; see Mulloy et al. (2021) for experimental design). To establish realistic bioassay treatments in the lab, we assessed the variation in the *Empetrum* leaf biomass at the Andosol site. We estimated *Empetrum* green leaf biomass by inserting a core of 7 cm in diameter (38.5 cm²) in six points placed 2 m apart along two 10 m transects, and seven points placed 2 m apart in a 12 m transect (two samples were lost during transportation, so that N=17). The transects were located approximately 200 m apart. Subsequently, the aboveground *Empetrum* biomass was collected from each core, and later on dried and weighed in the laboratory. The average *Empetrum* green leaf biomass was 41 ± 54 g m⁻² (min=0 g m⁻²; max=134 g m⁻²). *Empetrum* leaf biomass was also estimated, similarly as above, for five core samples (N=5) collected from monospecific *Empetrum* patches (100% cover) located at least 5 m apart. The average *Empetrum* green leaf biomass was 197 ± 15 g m⁻² (min=118 g m⁻²; max=296 g m⁻²), and *Empetrum* senescent leaf biomass (i.e. both litter and on plant withered leaves) was 540 ± 88 g m⁻² (min=270 g m⁻²; max=881 g m⁻²), inside monospecific patches.

Volcanic Vitrisol collection site

To compare *Empetrum*-associated Andosol with soil at severely eroded sites in Iceland that are no longer associated with *Empetrum*, soil was collected from a habitat that is considered a fully degraded (collapsed) dwarf shrub heath in Auðkúluheiði (Fig. 1A; approximately 400 m away from the Andosol site). The vegetation cover there is scarce with no *Empetrum* (Mulloy et al. 2021). The remaining soils are low in organic matter and classified as 'Vitrisol' (Arnalds 2008). This site will herein be referred to as the 'Vitrisol site' (Fig. 1B). The transitioning of this site to a more productive state is extremely unlikely without management interventions, such as grazing exclusion, seeding and fertilizing (Barrio et al. 2018).

Non-volcanic Histosol collection site in the Faroe Islands

For comparison with the volcanic soil types, *Empetrum*-associated non-volcanic soil was collected at one site in the Faroe Islands (Fig. 1A). The Faroese soil was collected on the southern part of Streymoy (61°59'N, 06°50'W, 171 m a.s.l.). The Faroe Islands are characterized by a monthly average (July–August) summer temperature of 10.5°C and precipitation of 58 mm in the lowlands (2014–2022, Tórshavn, DMI report 23-09, DMI - Danish Meteorological institute; Fosaa 2001). The vegetation at the collection site is dominated by the dwarf shrub *Calluna vulgaris* and the moss *Hylocomium splendens*, along with different graminoid species. *Empetrum* grows mainly on well-drained slopes. Furthermore, the Faroese soils have developed from basalt parent material formed during the Paleocene, i.e. ~ 60–50 million years ago (Storey et al. 2007), i.e. much older than in Iceland which is still forming today. The soil at the sampling site was organic soil (Rutherford and Taylor 1981),

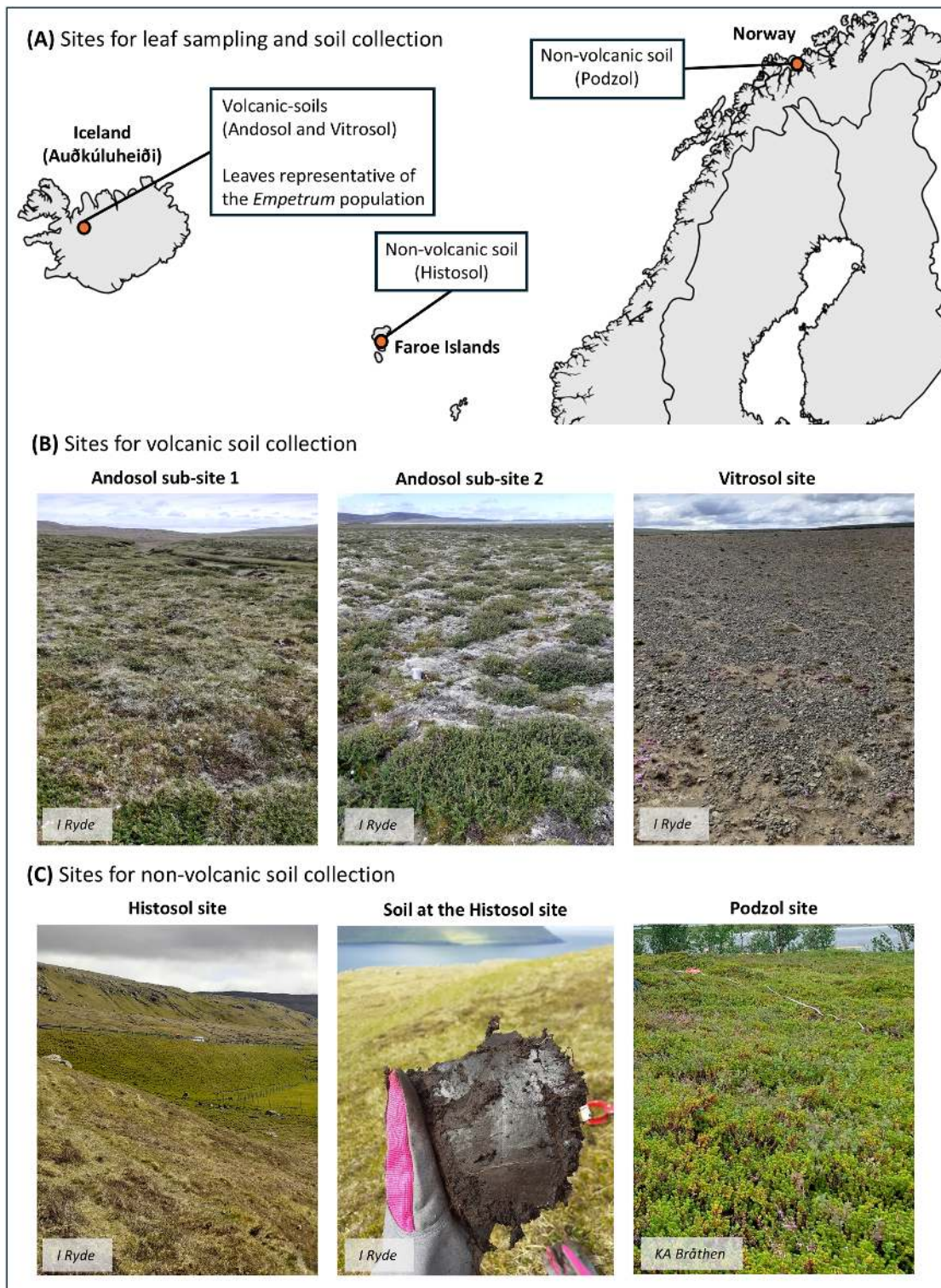


Figure 1. Leaf sampling and soil collection. (A) Map showing the locations for leaf sampling and soil collection. Photographs of the sites from where (B) the volcanic soils were collected in Iceland and (C) from where the non-volcanic soils were collected. Figure generated in part with Biorender.com.

homogeneously dark brown (almost black; Fig. 1C) down to at least 30 cm depth. The soil type may be classified as Histosol according to the world soil reference base system (IUSS Working Group WRB 2022). According to the Soil Atlas of the Northern Circumpolar Region (Joint Research Centre, Institute for Environment and Sustainability 2010), Histosols are common in the sub-Arctic and can be non-peaty and well decomposed, i.e. identification of plant parts in the soil is nearly impossible. This corresponds well with the soil at the sampling site. Therefore, we will herein refer to this soil as 'Histosol' and the sampling site as the 'Histosol site' (Fig. 1C).

Non-volcanic Podzol collection site in northern Norway

Non-volcanic soil was also collected at one site (69°52'N, 21°45'E, 46 m a.s.l.) in Kvænangen, northern Norway (Fig. 1A). The area is characterized by a monthly average (June–August) summer temperature of 12°C and precipitation of 48 mm (2011–2021, Nordstraum i Kvænangen, 69°50'N, 21°53'E, 20 m a.s.l.; Norsk Klimaservicesenter, Meteorologisk Institutt). The vegetation is dominated by *Empetrum* having a 100% cover. Other plant species registered in the area are the dwarf shrub *Vaccinium uliginosum* (vegetation cover < 5%), the forb *Solidago virgaurea*, and the grass *Avenella flexuosa*. According to the Soil Atlas of the Northern Circumpolar Region (Joint Research Centre, Institute for Environment and Sustainability 2010), the soil in this area is classified as podzol. The soils at the collection site have developed from a parent material of quartzite (okologiskegrunnkart.artsdatabanken.no, accessed 11 November 2024) formed during the Precambrian-Palaeozoic age, i.e. > 500 million years ago (Nasuti et al. 2015). Podzols often arise from quartzite parent material, are common in boreal areas with high precipitation and ericaceous vegetation, and often characterized by being nutrient poor and having a pH around 4 in the organic horizon (FAO 2001). This corresponds well with this site and the soil that we collected in Norway. Podzol also has a high hydrophobicity, i.e. soil water repellency (Deurer et al. 2011), which was very obviously the case for the soils we collected. Therefore, we will herein refer to this site as the 'Podzol site' and the soil as 'Podzol' (Fig. 1C).

Sampling and preparation methods

Leaf sampling and preparation

To collect a representative leaf-sample of an *Empetrum* population from a degraded tundra ecosystem in the Icelandic highlands, leaf sampling was done within the two Andosol sub-sites in Auðkúluheiði. At each sub-site, leaves were collected (11–13 July 2023) from a 9-point 6 × 6 m sampling grid. This was done by cutting five to seven branches off the three *Empetrum* individuals closest to each grid point. That means that leaves from 54 different *Empetrum* individuals were collected (i.e. 27 from each Andosol sub-site) to represent the *Empetrum* population in Auðkúluheiði. The branches were immediately put in tea filters (130 × 100 mm, 60/420.21.04, Finum), inside Ziploc-bags containing silica

gel (Granular 0.2–1.0 mm, 10087, Sigma Aldrich), to reduce metabolic conversions (Gericke et al. 2021).

In the laboratory, fully developed green leaves were retrieved from the collected samples, as these contain the highest concentrations of allelochemicals (Wallstedt et al. 1997). Subsequently, the retrieved leaves from both Andosol sub-sites were pooled to create one leaf sample representative for the Auðkúluheiði *Empetrum* population. The pooled leaf sample was stored dry, in Ziploc-bags with silica beads, until further use.

Soil sampling and preparation

At each sampling site, a 6 × 6 m 9-point sampling grid was established. All *Empetrum*-associated soils were collected, i.e. Andosols (11–13 July 2023), Histosol (28 May 2022), and Podzol (5 August 2023), as the upper 5 cm soil below *Empetrum* shrubs at the 9 points within each sampling grid. The Andosols were collected from the same 9-point grids that were used for *Empetrum* leaf sampling. The Vitrisol, which was not associated with *Empetrum*, was collected (11–13 July 2023) as the upper 5 cm soil of non-vegetated ground similarly as above. A total of 1 litre of soil was pooled from each sampling site and kept as cold as possible in the field.

In the laboratory, all pooled soil samples were kept frozen (−20°C) until they were freeze-dried to reduce metabolic conversions. *Empetrum* plant residues present within soils can be a major source of allelopathic legacy effects (Wallstedt et al. 2000). The soils in our study were therefore fractionated to prevent strong allelopathic effects by *Empetrum* plant residues from clouding potential differences between soil types, in potential legacy effects and interactions between soil and fresh *Empetrum* leaves. The soils were fractionated by sieving into 'small' (< 1 mm) and 'large' (< 2 mm; > 1 mm) soil particles. No plant residues were visible among the small soil particles, whereas the large soil particles were mainly plant residues, except for the Vitrisol where they were simply larger sand particles. Furthermore, the soil fractionation ensured comparability of the interaction between *Empetrum* leaves and equal volumes of equal sized particles from the different soil types.

For small and large soil particles from each soil type, the water-holding-capacity (using the funnel-method modified from Govindasamy et al. (2023)) and pH(H₂O) were measured (Table 1). In addition, the carbon (C) and nitrogen (N) contents of the soils were measured in three technical replicates of ~ 100 mg from the small and large particles of each soil type, by an organic elemental analyzer (vario MACRO cube, Elementar Analysensysteme GmbH) with sulfanilamid (200005129, Elementar Analysensysteme GmbH) as standard (Table 1). All sieved and pooled soil samples were stored dry in desiccators with silica until further use.

Bioassays

Basic design

All bioassays (Fig. 2A) in our study were modified from González et al. (2015) and Valsdóttir (2021). They were

Table 1. Soil characteristics. The fraction of small and large soil particles out of the total soil mass was measured for the one composite soil sample collected for each soil sampling site (i.e. $n=1$). Other listed soil characteristics are the mean $\pm$ standard error of the water-holding-capacity (WHC), pH(H₂O), carbon (C) and nitrogen (N) content, and C/N ratio measured for small (size: < 1 mm) and large (size: < 2 mm; > 1 mm) particles from different soil types. Values detected below the limit of quantification are indicated by: $< \text{LOQ}$. NA: Not available.

Particle size	Volcanic	Soil type	Fraction (%)	WHC	pH $n=3$	C (%) $n=3$	N (%) $n=3$	C/N $n=3$
			$n=1$	(ml g ⁻¹) $n=3$				
Large	yes	Andosol 1	9	4.1 $\pm$ 0.1	5.9 $\pm$ 0.0	28.1 $\pm$ 0.2	0.7 $\pm$ 0.0	39.4 $\pm$ 0.2
		Andosol 2	15	4.5 $\pm$ 0.1	5.7 $\pm$ 0.0	27.0 $\pm$ 0.4	0.8 $\pm$ 0.0	35.0 $\pm$ 0.2
		Vitrisol	18	0.4 $\pm$ 0.0	6.8 $\pm$ 0.0	$< \text{LOQ}$	$< \text{LOQ}$	NA
	no	Histosol	13	4.5 $\pm$ 0.2	4.8 $\pm$ 0.0	29.7 $\pm$ 0.2	1.6 $\pm$ 0.0	18.5 $\pm$ 0.1
		Podsol	14	5.0 $\pm$ 0.3	4.1 $\pm$ 0.0	36.6 $\pm$ 0.3	0.7 $\pm$ 0.0	50.4 $\pm$ 0.1
Small	yes	Andosol 1	91	1.3 $\pm$ 0.1	6.0 $\pm$ 0.1	4.2 $\pm$ 0.0	0.2 $\pm$ 0.0	19.4 $\pm$ 0.6
		Andosol 2	85	1.4 $\pm$ 0.0	6.0 $\pm$ 0.0	7.3 $\pm$ 0.1	0.4 $\pm$ 0.0	17.8 $\pm$ 0.2
		Vitrisol	82	0.6 $\pm$ 0.0	6.6 $\pm$ 0.0	0.5 $\pm$ 0.0	$< \text{LOQ}$	NA
	no	Histosol	87	4.6 $\pm$ 0.1	4.7 $\pm$ 0.0	25.1 $\pm$ 0.3	1.2 $\pm$ 0.0	20.6 $\pm$ 0.2
		Podsol	86	4.0 $\pm$ 0.1	4.0 $\pm$ 0.0	26.1 $\pm$ 0.2	0.7 $\pm$ 0.0	38.0 $\pm$ 0.2

constructed so that firstly, a substrate was added to the bottom of Petri dishes (60 mm). The substrate could be either different amounts of whole *Empetrum* leaves (i.e. no further treatment of leaves was done before leaf-addition to Petri dishes), soil from the different soil types, or a mix of whole *Empetrum* leaves and soil. When soil was added, they were always re-wetted by the addition of distilled water corresponding to the water-holding-capacity for the specific soil type and amount of soil added. Secondly, two filter papers (grade 118, Retention 15 μm , 47 mm) were added and wetted by 1.5 ml of distilled water. Finally, *Festuca* seeds (provided by the Icelandic Soil Conservation Service; collected 2021–2022) were added on top.

Allelopathic effects of the substrates were measured as the inhibition of *Festuca* seed germination (defined here as radicle protrusion) or seedling root elongation. In bioassays assessing seed germination, ten seeds were added to each Petri dish and germination estimated as the number of germinated seeds out of ten, i.e. one Petri dish corresponded to one replicate. These bioassays were constructed with one replicate per substrate type in 10 blocks ($n=10$). In bioassays assessing seedling root elongation, five *Festuca* seedlings (pre-germinated seeds with 2 mm of root), each considered as one replicate, were added to one Petri dish per type of substrate in three blocks ($n=15$). Root elongation was estimated as the total root length after end incubation for each seedling.

All Petri dishes, in all bioassays, were sealed with parafilm to prevent water-loss prior to incubation, which was done at constant light and 20°C in a growth chamber. Furthermore, all Petri dishes were moved every other day inside the growth chamber to account for any edge-effects. Because of the generally high germination rate observed (i.e. nearly 10/10), the seeds were not sterilized prior to incubation. However, some of the seedlings in the bioassays assessing root elongation, were impacted by mold during incubation. All seedlings affected by mold were not included in the datasets for statistical analyses. Furthermore, in one bioassay, six seedlings and not five had accidentally been put into one of the Petri dishes. This resulted in the number of replicates of seedlings to vary between $n=9$ and $n=16$.

Variations in potential allelopathic legacy effects between the different soil types (Q1)

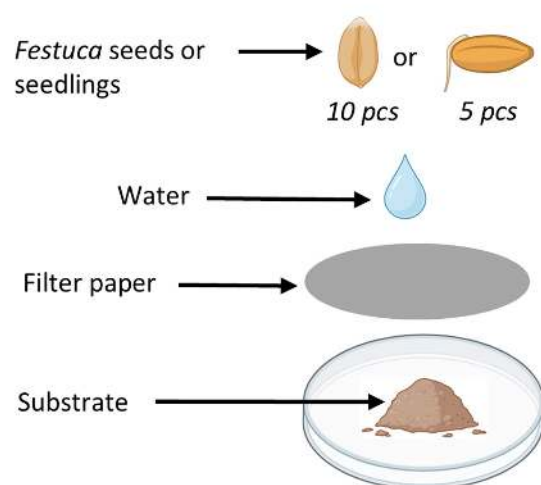
To assess the potential allelopathic legacy effects of Icelandic volcanic soil compared to non-volcanic soil (Fig. 2B), bioassays were run with soil substrates, i.e. 3 ml of freeze-dried soil from the different soil types to the bottom of the Petri dishes. A volume of 3 ml was enough to cover the bottom of the Petri dishes with a thin layer (~ 1.5 mm thickness) of soil. To ensure that potential variations in water content within the Petri dishes were not interfering with effects of different soil types, the effects of different water-additions were assessed. The addition of distilled water above 1 ml (i.e. 1 ml, 1.5 ml and 2 ml) and above 0.5 ml (i.e. 0.5 ml, 1.0 ml, 1.5 ml and 2 ml) to Petri dishes with filter paper, did not affect *Festuca* seed germination and root elongation, respectively (Supporting information).

The bioassays were established in a factorial block design with two factors: ‘Soil type’ (Levels: No soil, Andosol 1, Andosol 2, Vitrisol, Histosol and Podzol) and ‘Particle size’ (Levels: No soil, Small and Large). The soil type level ‘No soil’ confounded with the particle size level ‘No soil’ and contained only 1.5 ml of distilled water, two filter papers and *Festuca* seeds or seedlings. As such, the bioassays included 11 different substrate types (Fig. 2B). Seed germination was assessed in one bioassay ($N=110$) after 14 days and seedling root elongation in another bioassay ($N=165$) after 5 days of incubation.

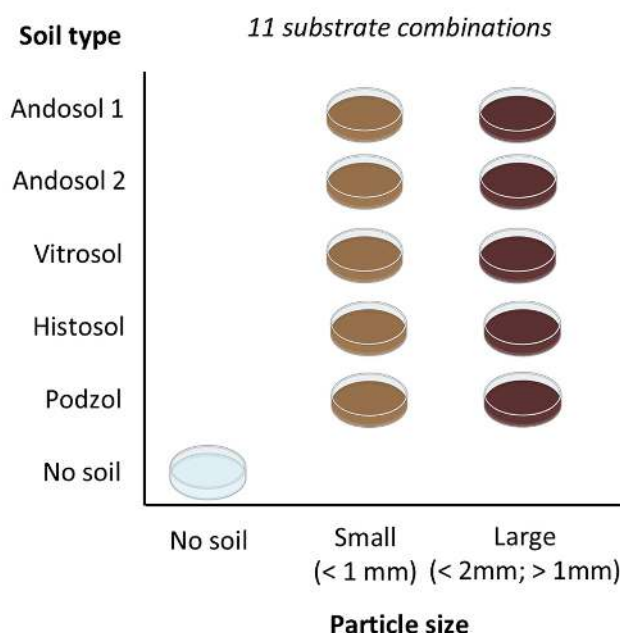
Modification of the allelopathic capacity of *Empetrum* by different soil types (Q2)

To assess how soil particles from Icelandic volcanic soils interact with potential allelochemicals from *Empetrum* leaves compared to soil particles from non-volcanic soils (Fig. 2C), bioassays were run with soil substrates, i.e. 1.5 ml of freeze-dried soil to the bottom of the Petri dishes. For each soil type, Petri dishes were prepared with and without whole *Empetrum* leaves mixed into the soil. For comparison, a ‘No-soil’ treatment was included to assess *Festuca* seed germination and seedling root elongation when not exposed to soil or *Empetrum* leaves, and when exposed to *Empetrum* leaves only

(A) Basic design of bioassays



(B) Allelopathic legacy effects (Q1)



(C) Soil modification of *Empetrum* allelopathic capacities (Q2)

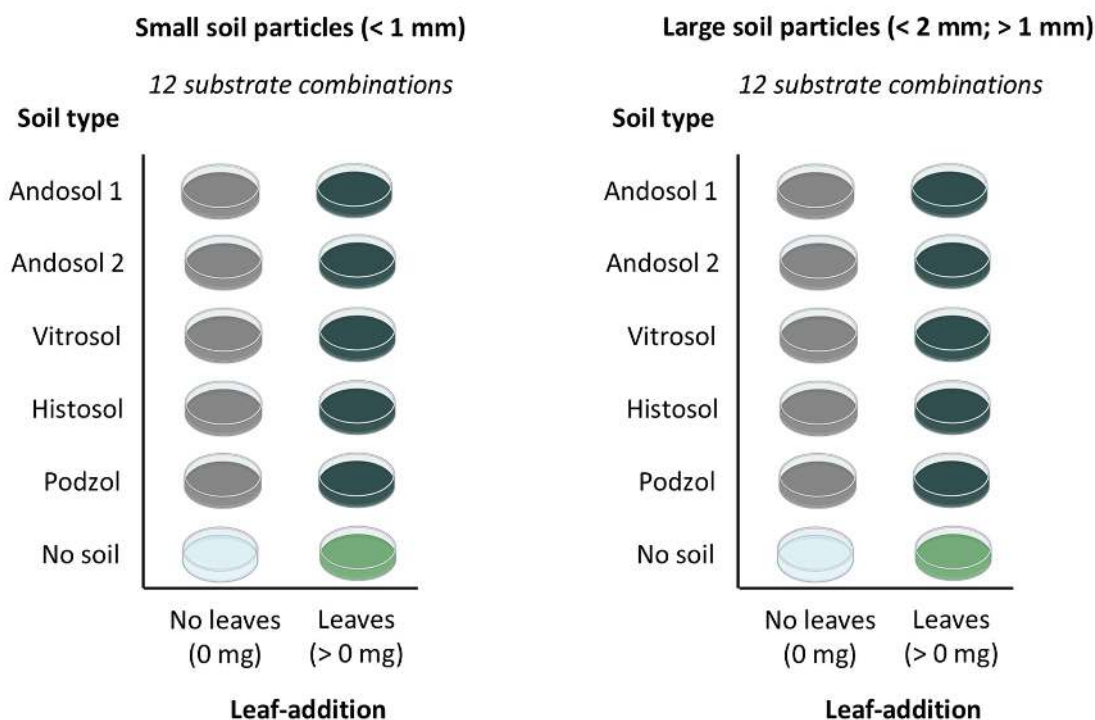


Figure 2. Bioassays. (A) Basic design of bioassays. (B) Experimental design for the assessment of research question 1 (Q1), regarding potential allelopathic legacy effects of *Empetrum*-associated soils. (C) Experimental design for the assessment of research question 2 (Q2), regarding interactions between soil and fresh *Empetrum* leaves. Figure generated in part with Biorender.com.

(Fig. 2C). The bioassays were established separately for the small and large soil particles in a factorial block design with two factors: 'Soil type' and 'Leaf-addition' (Levels: No leaf-addition and Leaf-addition). As such, the bioassays included

12 different substrate types (Fig. 2C). The 'No leaf-addition' always corresponded to the addition of 0 mg of *Empetrum* leaves to the Petri dishes. In the first round of bioassays, the 'Leaf-addition' level corresponded to the addition of 130 mg

of *Empetrum* leaves in combination with 1.5 ml of soil to the Petri dishes. This was done to mimic natural conditions at the two Andosol sub-sites in Auðkúluheiði, i.e. the *Empetrum* green leaf biomass estimated inside monospecific *Empetrum* patches corresponded to approximately 130 mg per 1 g of the upper 2 cm soil collected inside the sample cores, and 1.5 ml of the andosols were approximately 1 g.

Seed germination was assessed in bioassays (N = 120) after 16 and 14 days of incubation with small and large soil particles, respectively. These bioassays were not repeated with leaf-densities lower than 130, because a preliminary experiment showed no allelopathic effects on *Festuca* seed germination by 80–100 mg of *Empetrum* leaves in Andosol 1 (Supporting information).

Root elongation was first assessed in a bioassay (N = 180) with small soil particles and 130 mg of leaf-addition. After 7 days of incubation, root elongation was close to totally inhibited by the 130 mg of *Empetrum* leaves in small Andosol particles (Supporting information). Therefore, the bioassay was subsequently done with a leaf-addition of 20 mg to small and large soil particles, which were assessed after 5 days of incubation. These bioassays were not repeated with lower leaf-densities as we found no clear inhibitory effects of 4–10 mg of *Empetrum* leaves on root elongation in Andosol 1 (Supporting information).

Statistics

Statistical analyses were performed using R ver. 4.3.3 (www.r-project.org). Mixed effects models were established by using the ‘lme4’ package (Bates et al. 2015). All models included either ‘Germination’ or ‘Root elongation’ as response variables. ‘Germination’ was treated as binomial distributed data and analyzed by generalized linear mixed-effects models (*glmer* function) that included the random factor ‘Block’ as intercept, i.e. ‘(1|Block)’. ‘Root elongation’ was treated as normally distributed data and analyzed by linear mixed-effects models (*lmer* function) including the nested random factors ‘Block’ and ‘Petri dish’ as intercepts, i.e. ‘(1|Block/Petri dish)’. Overall statistical effects were analyzed by comparing full and reduced models using the *anova* function. Pairwise comparisons were performed using the *emmeans* function from the ‘emmeans’ package, with a Bonferroni correction for models including ‘Germination’ and a Tukey’s or Sidak correction for models including ‘Root elongation’ (Lenth 2023). All statistical results, including p-values, are available in summary statistics tables in the Supporting information.

Q1: To analyze potential allelopathic legacy effects of the different soil types, models included the factors ‘Soil type’ and ‘Particle size’ as explanatory variables. To fulfill the requirements of normal distribution and homogeneity of variance, ‘Root elongation’ was square root transformed. Pairwise comparisons were made between small and large soil particles for each soil type, and between the ‘No soil’ level and the different soil types for each soil particle size.

Q2: To analyze the modification of the allelopathic effects of *Empetrum* leaves by the different soil types, models included the factors ‘Soil type’ and ‘Leaf-addition’ as

explanatory variables. To fulfill the requirements of normal distribution and homogeneity of variance, ‘Root elongation’ was log-transformed in the model including the higher level of leaf-addition (130 mg), and square root transformed in the model including the lower level of leaf-addition (20 mg). Pairwise comparisons were made between leaf-additions for each soil type and between the different soil types for the two levels of leaf-addition separately.

Results

Variations in potential legacy effects of the different soil types (Q1)

The Icelandic volcanic soils did not possess any potential legacy effects inhibiting *Festuca* seed germination or root elongation (Fig. 3). None of the different soil types, i.e. the volcanic Andosols (*Empetrum*-associated) and Vitrisol (not associated with *Empetrum*) as well as the non-volcanic Histosol and Podzol (*Empetrum*-associated), inhibited *Festuca* seed germination compared to seed germination in no soil (Fig. 3A; $p = 1$). Furthermore, the volcanic Andosol and Vitrisol did not inhibit *Festuca* seedling root elongation (Fig. 3B; $p > 0.59$). Small and large soil particles of the non-volcanic Histosol and Podzol inhibited *Festuca* seedling root elongation by approximately 73% and 82% on average, respectively (Fig. 3B; $p < 0.0001$). Germination and root elongation were not affected differently by small and large particle sizes in either of the soil types (Fig. 3A, B; $p > 0.64$).

Modification of the allelopathic capacity of *Empetrum* by different soil types (Q2)

The allelopathic effects of *Empetrum* leaves collected in Auðkúluheiði on *Festuca* seed germination were similar in volcanic and non-volcanic soils (Fig. 4A, B). *Festuca* seed germination with 130 mg of *Empetrum* leaves alone (i.e. with no soil) was inhibited by approximately 83% on average compared to germination with no soil and no leaf-addition (Fig. 4A, B; $p < 0.001$). Small and large particles of the Andosols and non-volcanic soils (i.e. Faroese Histosol and Norwegian Podzol) with *Empetrum* leaf-addition, inhibited seed germination by approximately 17% and 28%, respectively, compared to the soils with no leaf-addition (Fig. 4A, B; $p < 0.02$). *Empetrum* leaf-addition to both small and large particles of Vitrisol inhibited seed germination more than the leaf-addition to any of the other soil types, i.e. by approximately 28% ($p < 0.001$) and 68% ($p < 0.001$), respectively, compared to Vitrisol with no leaf-addition (Fig. 4A, B). No differences in seed germination were found between soils with no leaf-addition (Fig. 4A, B; $p > 0.98$).

The volcanic soils modified the allelopathic effects of *Empetrum* leaves on *Festuca* seedling root elongation (Fig. 4C, D). *Festuca* root elongation with 20 mg of *Empetrum* leaves alone (i.e. with no soil) was inhibited by approximately 81% on average compared to root elongation with no soil and no leaf-addition (Fig. 4C, D, $p < 0.001$). In contrast, the Andosols with *Empetrum* leaf-addition inhibited seedling

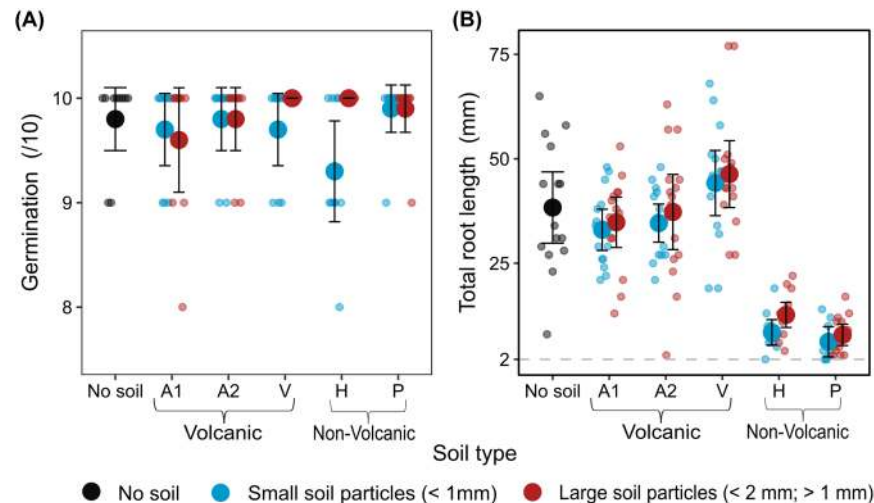


Figure 3. Potential allelopathic legacy effects of the different soil types on *Festuca*. Raw values (small dots) and predicted means (large dots) $\pm$ 95% confidence intervals of *Festuca* (A) seed germination (14 incubation days), and (B) seedling root elongation (5 incubation days), with small and large particles from the soil types: No soil, Andosol 1 (A1), Andosol 2 (A2), Vitrisol (V), Histosol (H), and Podzol (P). Dashed line (B) represents the initial root length of seedlings. (A): $n=10$. (B): $n=15$, except small ($n=11$) and large ($n=14$) particles of Histosol, and small ($n=9$) and large ($n=14$) particles of Podzol.

root elongation by approximately 38% on average compared to Andosols with no leaf-addition (Fig. 4C, D, $p < 0.001$). When comparing root elongation between soils with no leaf-addition, no differences were detected between the Andosols, Vitrisol (large particles) and no soil (Fig. 4C, D, $p > 0.63$). Root elongation with the small particles of Vitrisol and no leaf-addition was higher compared to the no soil with no leaf-addition (Fig. 4C, $p=0.054$). The non-volcanic Histosol and Podzol with no leaf-addition, inhibited root elongation by approximately 61% and 69%, respectively, compared to root elongation with no soil and no leaf-addition (Fig. 4C, D, $p < 0.001$). The addition of 20 mg of leaves to the non-volcanic soils inhibited *Festuca* root elongation by approximately 44% and 55% compared to non-volcanic soils with no leaf-addition (Fig. 4C, D, $p < 0.01$, except from large particles of Vitrisol: $p=0.09$). The inhibition by 20 mg of *Empetrum* leaves alone, did not differ from the inhibition of *Festuca* root elongation by 20 mg of *Empetrum* leaves mixed with small and large soil particles of the non-volcanic soil and Vitrisol (Fig. 4C, D, $p > 0.16$).

Discussion

Here we show that the non-volcanic Histosol and Podzol soil types exhibited a negative effect on *Festuca* performance, indicating allelopathic legacy similar to previous studies (González et al. 2021), while no such legacy effect was evident in the Andosols (Q1). In addition, we observed that allelopathic effects of *Empetrum* leaves were as strong in non-volcanic soils as when mixed with no soil, whereas they were strongly reduced by Andosols (Q2). Accordingly, our results suggest that the allelopathic capacities of *Empetrum* are alleviated in Icelandic tundra ecosystems with Andosol

soils compared to other tundra ecosystems with non-volcanic soils. Furthermore, we observed no differences in the inhibitory effects of *Empetrum* leaves on *Festuca* between soils from the two Andosol sub-sites, indicating that the difference in degree of degradation between Andosol sub-site 1 and 2 are not great enough to change the soils' ability to modify *Empetrum* allelopathic capacities. We also saw that the inhibitory effects of leaves on *Festuca* were reduced by Vitrisol, but much weaker than by Andosols, suggesting that the ability to modify allelopathic capacities of *Empetrum* decreases with a transition to a more degraded ecosystem.

Soil type had a clear effect on *Festuca* root elongation, indicating that Andosols generally have lower potential allelopathic legacy effects relative to non-volcanic soils. Soil type had no effect on *Festuca* seed germination, which might be explained by its insensitivity to low *Empetrum*-leaf densities observed in our study. We observed no potential allelopathic legacy effects on *Festuca* root elongation by the Andosols, whereas the non-volcanic soils did inhibit *Festuca* root elongation. Allelochemicals leaching out of *Empetrum* leaf litter is the main source of *Empetrum*-related allelopathic effects in soil (Wallstedt et al. 2000). Since the *Empetrum*-associated Andosols and non-volcanic soils were all collected from below *Empetrum* shrubs (i.e. from specific locations within each study site having 100% *Empetrum* cover), the load of *Empetrum* leaves and thereby the source of allelochemicals, was assumed to be similar between the compared soils. Therefore, the observed differences in *Festuca* root elongation inhibition between volcanic and non-volcanic soils might be due to different properties of the soils and also their interactions with *Empetrum* allelochemicals. That includes soil microbial communities, that likely vary between soil types and might interact differently with *Empetrum* allelochemicals increasing or decreasing their phytotoxicity (Inderjit et al.

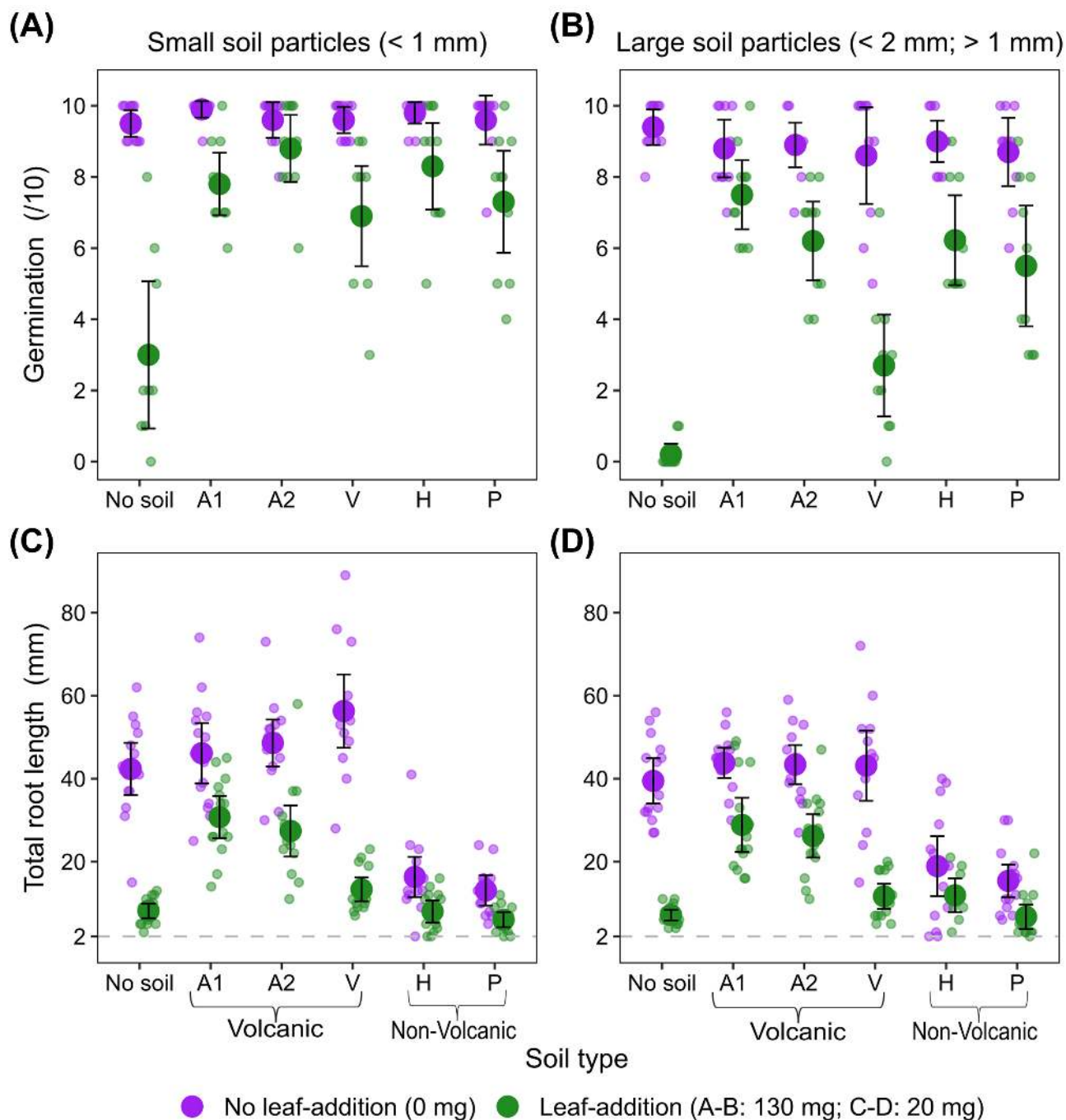


Figure 4. Modification of *Empetrum* allelopathic capacities by different soil types. Raw values (small dots) and predicted means (large dots) $\pm$ 95% confidence intervals of *Festuca* (A–B) seed germination (A: 16 incubation days; B: 14 incubation days) and (C–D) seedling root elongation (5 incubation days), with small (A and C) and large (B and D) particles from the soil types: No soil, Andosol 1 (A1), Andosol 2 (A2), Vitrisol (V), Histosol (H), and Podzol (P), with and without *Empetrum* leaf-addition. Dashed line (C–D) represents the initial root length of seedlings. (A): $n = 10$, except no soil with leaf-addition ($n = 9$). (B): $n = 10$, except H with leaf-addition ($n = 9$). (C): $n = 15$, except V with no leaf-addition ($n = 14$), H with leaf-addition ($n = 14$), P with no leaf-addition ($n = 13$), and P with leaf-addition ($n = 14$). (D): $n = 15$, except V with no leaf-addition ($n = 10$), H with leaf-addition ($n = 10$), and P with no leaf-addition ($n = 16$).

2005). Further studies are needed to disentangle those interactions. Two key *Empetrum* bibenzyl allelochemicals have previously been identified: Batatasin-III (Odén et al. 1992) and the relatively understudied 3,4-dimethoxy-2',5-dihydr

oxybibenzyl (Jarevång et al. 1998). Batatasin-III leaches into soil water and is transported through soil with drainage (Brännäs et al. 2004). In Scandinavian ecosystems, Batatasin-III can be retained and accumulate in soil to some extent

(Gallet et al. 1999, Wallstedt et al. 2005), leaving considerable allelopathic legacy effects within *Empetrum*-associated soils (González et al. 2021). The Batatasin-III concentration in soil solutions was found to be highest in the upper humus layers and decreasing downwards into the mineral layers (Wallstedt et al. 2000). We fractionated the upper 5 cm of *Empetrum*-associated soil into small and large particles, and thereby separated the *Empetrum* leaf-litter (source of *Empetrum* allelopathic effects) and other visible plant residues from the smaller and more decomposed soil organic matter and mineral particles. We found no differences in potential allelopathic legacy effects between the two particle sizes for both volcanic and non-volcanic soils. This might suggest that the *Empetrum* allelochemicals are equally present in the soil water solution of the small and large particles.

A much lower pH of the non-volcanic soils (4.0–4.8) compared to that of the Andosols (5.7–6.0) and Vitrisol (6.6–6.8) might contribute to explaining the observed differences in potential allelopathic legacy effects imposed by the volcanic and non-volcanic soils on *Festuca* root elongation. González et al. (2015) documented no direct effects of pH (4.0–5.6) treatments in interaction with Batatasin-III (0.1–2.0 mM), in Petri dishes with no soil, on seedling root elongation of several plant species. The effects of pH may therefore be indirect, i.e. pH impacts the cation-exchange-capacity of the soils and thereby their ability to retain allelochemicals (Scavo et al. 2019). Andosols have high pH and high cation-exchange-capacity (Arnalds 2015) and might as such retain *Empetrum* allelochemicals more strongly than the acidic non-volcanic soils, although it is also possible that concentrations of BIII and related compounds may decrease via autocatalytic polymerization (Xiao 2022). Furthermore, as phenol oxidase and peroxidase activities generally increase with increasing pH (Sinsabaugh 2010), microbial degradation of *Empetrum* allelochemicals might be higher in volcanic soils than in non-volcanic soils. Batatasin-III has previously been found to be stable in soil (Gallet et al. 1999, Brännäs et al. 2004) and very likely inhibit soil microorganisms (Wallstedt et al. 2000). However, Batatasin-III (and 3,4-dimethoxy-2',5'-dihydroxybibenzyl) are most likely not solely responsible for *Empetrum* allelopathic capacities, and the interaction between different soil characteristics and a broader range of allelochemicals should be studied. Other soil characteristics of the small soil particles, such as a lower soil organic matter content of the Andosols (reflected by a % C content of 4.2–7.3) compared to the non-volcanic soils (i.e. a % C of 25.1–36.6), might suggest a lower retention of allelochemicals by the Andosols than that of the non-volcanic soils (Scavo et al. 2019). Nevertheless, in our study the differences in soil carbon content between the Andosols and non-volcanic soils, are likely less important when explaining legacy differences than the large differences in pH. The same applies to the large soil particles, where the measured soil characteristics other than pH were relatively similar between Andosols and non-volcanic soils.

The substantial reduction of *Empetrum* allelopathic effects on *Festuca* root elongation by Andosols supports that

Andosols have a higher capacity to retain allelochemicals due to the unique properties of volcanic soils. The *Empetrum* allelopathic effects on *Festuca* seed germination were reduced similarly by all soil types, which could be due to *Festuca* seed germination and root elongation being affected by different *Empetrum* allelochemicals that interacts with the soil in different ways (González et al. 2015). The differences between the two non-volcanic soil types, in the ability to reduce the allelopathic capacity of *Empetrum* leaves, might partly be explained by the Faroese Histosol having a higher nitrogen content (1.2–1.6% N) than the Norwegian Podzol (0.7% N). Bråthen et al. (2010) found that organic fertilization considerably alleviated the allelopathic capacity of *Empetrum*-associated soil. This might be related to the direct phytotoxic effects of Batatasin-III inhibiting ion uptake (e.g. nitrogen) by the disruption of membrane integrity and H⁺-ATPase activity (Wallstedt et al. 2001). A higher nutrient concentration in the Histosol (indicated by C/N: 18.5–20.6) compared to the Podzol (C/N: 38.0–50.4), might therefore contribute to its slightly greater alleviation of *Empetrum* allelopathic capacities.

We observed no effects on *Festuca* seed germination or root elongation by Vitrisol, the soil type of the fully collapsed tundra ecosystems and thus not associated with *Empetrum*. Although allochthonous *Empetrum* leaf litter may potentially influence soils not directly associated with *Empetrum* (Pilsbacher et al. 2021), it was probably of minor importance in the extremely degraded and highly wind-exposed tundra ecosystems where the Vitrisol was collected. Furthermore, the Vitrisol decreased the allelopathic capacity of *Empetrum* leaves on *Festuca* seed germination and root elongation less strongly than all other soil types. These results might be explained by this soil being more sandy and having a low soil organic matter content (indicated by < 0.5% C), suggesting a low capacity to retain allelochemicals (Scavo et al. 2019). As such, our results could suggest that the allelopathic capacity of *Empetrum* would be higher in relatively more sandy soils. Interestingly, a study by Grau et al. (2010) showed that *Empetrum* facilitated the establishment of *P. sylvestris* seedlings in a coastal sand dune. They suggested that the facilitating effects of mechanistic sheltering by *Empetrum* protecting the *P. sylvestris* seedlings from abiotic stress in the harsh environment were stronger than the retarding effects of allelochemicals in the sand dunes environment. Therefore, if *Empetrum* plants manage to establish in those fully collapsed Vitrisol ecosystems we might see an initial facilitating effect on the establishment of other species.

We measured significant *Festuca* seed germination and root elongation inhibition by *Empetrum* leaf-density levels (in Petri dishes of 28.3 cm²) of 130 mg and 20 mg, respectively, which corresponds to an *Empetrum* leaf biomass of 45 g m⁻² and 7 g m⁻², respectively. The estimated *Empetrum* green leaf biomass outside (41 ± 54 g m⁻² on average) and inside (197 ± 15 g m⁻² on average) *Empetrum* monospecific patches, in the degraded tundra ecosystem (Andosol site) in Auðkúluheiði, is therefore most likely enough to retard seedling establishment. The concentrations of allelochemicals in senescent *Empetrum*

leaves are lower than in fully developed green leaves but very likely still present in considerable amounts, thus capable of imposing allelopathic effects on neighboring plant species (Wallstedt et al. 1997). The high *Empetrum* senescent leaf biomass ($540 \pm 88 \text{ g m}^{-2}$ on average) estimated inside *Empetrum* monospecific patches therefore most likely add significantly to the allelopathic effects in tundra ecosystems. The variation in *Empetrum* leaf biomass was very high, e.g. outside of the *Empetrum* monospecific patches it was $0\text{--}134 \text{ g m}^{-2}$, reflecting the spatial distribution of clonal patches as well as accumulation of wind spread *Empetrum* leaves in sheltered areas. These areas are as such more exposed to allelopathic effects from allochthonous *Empetrum* litter (Pilsbacher et al. 2021). An average *Empetrum* cover of approximately 22%, as estimated within the degraded tundra ecosystem (Jónsdóttir unpubl.), can therefore most likely retard seedling establishment in certain areas and contribute to the retardation of ecosystem recovery.

In our study, we investigated the allelopathic effects of *Empetrum* leaves on a single plant species, the palatable grass *Festuca*, to simplify the bioassays and allow us to focus on variation between different soil particles sizes and multiple soil types. Previously, several plant species have been assessed for their sensitivity to *Empetrum* foliar tissues and allelochemicals. González et al. (2015) tested the effect of Batatasin-III on 24 different vascular plant species representing forbs, grasses, dwarf shrubs, and trees, and found that they were all impacted negatively in a similar manner. As such, one would expect that most plant species will respond similarly to treatments with *Empetrum* leaves, suggesting that testing a single species suffices. However, we acknowledge that there are some species differences in the sensitivity to *Empetrum* allelochemicals (González et al. 2015), and that more studies on several target species of ecological importance will increase our understanding of the allelopathic capacities of *Empetrum* in Icelandic tundra ecosystems.

Based on our bioassays, we conclude that the interaction between *Empetrum* allelochemicals and soil particles most likely depends on various soil characteristics of different soil types. Thereby, abundant allelopathic plant species may contribute to trapping tundra ecosystems in a degraded state, but the strength of this trapping mechanism depends on the soil environment. Within degraded Icelandic tundra ecosystems, *Empetrum* allelochemicals most likely contribute to their slow recovery by retarding the establishment of other plant species. However, the allelopathic capacity of *Empetrum* may be alleviated by the Andosol in comparison with soils of Scandinavian tundra ecosystems. To further our understanding of the underlying mechanisms of our observations, comprehensive chemical analyses of *Empetrum* tissues and associated soils are needed. Moreover, field studies are essential to relate the findings of the bioassays to natural ecosystems.

Acknowledgements – We would like to thank our collaborators Isabel C. Barrio and Alejandro S. Villegas, and other members of the Tundra Ecology Lab (University of Iceland and Agricultural University of Iceland), and Bjarne W. Strobel and the Plant

Ecophysiology research group (University of Copenhagen), for their interest and feedback on our work.

Funding – This study was funded by The Icelandic Research Fund to ISJ (grant numbers: 217665-051, 217665-052, 217665-053) and to IR (grant number: 2410195-051). EHJN acknowledges the NovoNordisk Foundation (grant number: 0054890) and the Independent Danish Council for Independent Research (grant numbers: 1131-00002B and 1051-00083B).

Author contributions

Ingvild Ryde: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Funding acquisition (supporting); Investigation (lead); Methodology (lead); Project administration (equal); Supervision (supporting); Validation (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Jóhanna F. Kristinsdóttir:** Formal analysis (supporting); Investigation (supporting); Methodology (supporting). **Marika Halmová:** Investigation (supporting); Methodology (supporting). **Augustin Baussey:** Investigation (supporting); Methodology (supporting). **Kari Anne Bråthen:** Conceptualization (equal); Methodology (supporting); Resources (supporting); Supervision (equal); Validation (equal); Writing – review and editing (equal). **Elizabeth H. J. Neilson:** Conceptualization (equal); Funding acquisition (supporting); Methodology (supporting); Resources (supporting); Supervision (equal); Validation (equal); Writing – review and editing (equal). **Ingibjörg S. Jónsdóttir:** Conceptualization (equal); Funding acquisition (lead); Methodology (supporting); Project administration (equal); Resources (lead); Supervision (lead); Validation (equal); Writing – review and editing (equal).

Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.tx95x6b8b> (Ryde et al. 2025).

Supporting information

The Supporting information associated with this article is available with the online version.

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