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Of mosses and men: Plant succession, soil development and soil carbon accretion in the sub-Arctic volcanic landscape of Hekla, Iceland

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Abstract

Lava flows pose a hazard in volcanic environments and reset ecosystem development. A succession of dated lava flows provides the possibility to estimate the direction and rates of ecosystem development and can be used to predict future development. We examine plant succession, soil development and soil carbon (C) accretion on the historical (<874 AD) lava flows formed by the Hekla volcano in south Iceland. Vegetation and soil measurements were conducted all around the volcano reflecting the diverse vegetation communities on the lavas, climatic conditions around Hekla mountain and various intensities in deposition of loose material. Multivariate analysis was used to identify groups with similar vegetation composition and patterns in the vegetation. The association of vegetation and soil parameters with lava age, mean annual temperature, mean annual precipitation and soil accumulation rate (SAR) was analysed. Soil carbon concentration increased with increasing lava age becoming comparable to concentrations found on the prehistoric lavas. The combination of a sub-Arctic climate, gradual soil thickening due to input of loose material and the specific properties of volcanic soils allow for continuing accumulation of soil carbon in the soil profile. Four successional stages were identified: initial colonization and cover coalescence (ICC) of *Racomitrium lanuginosum* and *Stereocaulon* spp. (lavas <70 yrs of age); secondary colonization (SC)–*R. lanuginosum* dominance (170−700 yrs); vascular plant dominance (VPD) (>600 yrs); and highland conditions/retrogression (H/R) by tephra deposition (70−860 yrs). The long time span of the SC stage indicates arrested development by the thick *R.lanuginosum* moss mat. The progression from SC into VPD was linked to age of the lava flows and soil depth, which was significantly deeper within the VPD stage. Birch was growing on lavas over 600 yrs old indicating the development towards birch woodland, the climax ecosystem in Iceland.

Keywords

Lava-chronosequence, moss thickening rate, *Racomitrium lanuginosum*, soil accumulation rate, soil depth, tephra deposition

I Introduction

Volcanic activity influences the world´s ecosystems in various ways depending on its nature and intensity. Volcanic areas are distributed all around the planet and are therefore associated with many vegetation and soil types, climate conditions or biotic interactions (Del Moral and Grishin, 1999). Therefore, global patterns of ecosystem response to volcanism are not easily recognized, which increases the importance of regional studies. Lava flows and pyroclastic flows are types of volcanism that erase previous ecosystems, restarting both plant succession and soil formation with recovery time counted in 100s and 1000s of years (Arnalds, 2013). Where the age of the surfaces is well constrained these sites can be used as chronosequences, a space-for-time substitution, to study temporal changes in plant communities and soil development over longer time spans (Matthews, 1992; Walker et al., 2010). The classical studies of primary succession include dune fields in Denmark and along Lake Michigan, glacier fore-fields in Alaska and New Zealand, and volcanic deposits in Hawaii and Krakatau (Walker and Del Moral, 2003). The use of chronosequences has been criticized as it requires all factors influencing ecosystem development, except for time, to remain unchanged. In reality those conditions are rarely met. However, where age-constraints are good, the influence of time as well as other impact factors can be addressed to identify long-term changes in plant succession and soil development (Walker et al., 2010).

Numerous studies have addressed ecosystem development on loose explosive volcanic deposits (Crisafulli et al., 2005; Grishin et al., 1996; Hansen, 1942; Taylor, 1957; Crisafulli and Dale, 2017; Tsuyuzaki and Hase, 2005; Korablev et al., 2018) but fewer have focused on the development on lava flows (Korablev and Neshataeva, 2016; Kurina and Vitousek, 1999; Marchese and Grillo, 2000; Raich et al., 1997; Drake, 1992; Bjarnason, 1991; Cutler et al., 2008b; Magnússon et al., 2009). Plant succession on lava flows is controlled by many different factors, both autogenic and allogenic and their relative importance is variable. These factors include climate (and microclimate) (Marchese and Grillo, 2000; Chadwick et al., 2003), type of lava flow, surface structure of lavas, tephra deposition, rate of accumulation and surface stability (Korablev and Neshataeva, 2016; Deligne et al., 2013), input of loose soil material influencing soil depth, moisture and nutrients (Walker and Del Moral, 2003), and biological factors such as seed dispersal, germination, growth, reproduction success (Marchese and Grillo, 2000; Clarkson, 1998; Korablev and Neshataeva, 2016).

Lava flows create a new hard and highly porous surface inhospitable to life, which for obvious reasons can make soil studies a hardy task. However, additions of loose sediments to the lava surfaces have been shown to improve conditions for colonization of vascular plants (Del Moral and Grishin, 1999). Studies on soil development on lavas are primarily from tropical climates and have focused on weathering rates and soil nutrients. A few have estimated carbon (C) contents of the developing soils (Kamijo et al., 2002; Kitayama et al., 1997; Raich et al., 1997). The realization of soils being the largest terrestrial C pool and an important C sink to mitigate climate change has led to increased interest in assessing how soil forming processes lead to accumulation of C (Lal, 2008). There is a notable lack of studies on soil formation and C accretion on lava flows at high latitudes, although the topic has been widely studied in glaciated regions reporting soil development and carbon accretion in glacier fore-fields (Crocker and Major, 1955; Dümig et al., 2011; Egli et al., 2010; He and Tang, 2008; Matthews, 1992; Kabala and Zapart, 2012; Vilmundardóttir et al., 2014; Vilmundardóttir et al., 2015a).

In Iceland volcanic events are frequent and impacts from lava flows common. The Hekla volcanic system is one of the most active volcanoes in Iceland producing both tephra and lava flows. The region of Hekla borders the southern lowlands, the largest and most productive farmlands in Iceland. It includes the location of the episcopacy, which was important for contemporary documentation of the historical eruptions. In his monumental work, the geographer Sigurður Þórarinsson, assigned timing of formation to the lava fields by combining tephra stratigraphy and historical accounts (Thorarinsson, 1967). The lavas have previously been used as a chronosequence to study colonization and development of plant communities (Bjarnason, 1991; Cutler et al., 2008b) but soil development has received less attention. Tephra fall, a usual concomitant in Hekla eruptions, has been suggested to be an important driver in ecosystem development in volcanic regions, as it provides loose sediments more suitable as a rooting medium for plants (Del Moral and Grishin, 1999; Deligne et al., 2013). This is also a major factor for ecosystem development in Iceland (Arnalds, 2013; Bjarnason, 1991; Eddudóttir et al., 2017).

The onset of human settlement in the region of Hekla began by the time of the Settlement of Iceland in approx. 874 AD (Thorarinsson, 1967) and follows the same trajectory as for other parts of the country (Dugmore et al., 2009). People immediately began changing the ecosystem by clearing woodlands for hayfields, coal making and livestock pasture, practicing their ways of North Atlantic livestock farming for their subsistence (Sigurmundsson et al., 2014; Ross et al., 2016). The settlers were unaware of the vulnerability of the ecosystem with soils highly susceptible to erosion by wind and water and extensive sheep grazing hindering regeneration of willow shrubs and birch woodlands (Dugmore et al., 2009; Aradóttir et al., 1992; Gísladóttir, 2001). In 1104, Hekla erupted for the first time since settlement, spreading tephra over a large part of the country and devastating the settlements north and northwest of the volcano (Dugmore et al., 2007; Thorarinsson, 1967). With the onset of the Little Ice Age (LIA) in the late 12th century (Sicre et al., 2008; Grove, 2001), the climate turned cooler, tephra was deposited from multiple eruptions at Hekla and other nearby volcanoes and conditions for farming deteriorated. Cold, strong north-easterly winds from the highlands during winter and spring imposed an erosive force that redistributed the volcanic tephra onto the vegetated land, creating large sand fronts propagating downwind over the lowlands (Arnalds, 1988; Árnason, 1958). Farmers battled against the sand, however between 1650 and 1800 many farmsteads in the vicinity of Hekla were abandoned or relocated (Sveinsson, 1953; Hreiðarsdóttir et al., 2015). This culminated at the end of the LIA in the late 18th century. The realization of the environmental catastrophe brought on the establishment of the Soil Conservation Service of Iceland (SCSI) in 1907 (Arnalds, 2005).

Volcanogenic soils feature specific physical properties that enable high C sequestration capacities (Dahlgren et al., 2004). In conjunction with sub-arctic conditions and frequent events of tephra deposition, soils in Iceland store high amounts of carbon both in wetlands and in well-drained areas. However, soil erosion is a widespread problem in Iceland; it has depleted the C pool dramatically and reduced the capacity of the soil to function successfully (Arnalds, 2004; Arnalds, 2008; Óskarsson et al., 2004). With all the dynamic processes active in the Hekla region, the natural revegetation and soil development occurring on the lava flows of Hekla provides an important insight into how ecosystems develop within sub-Arctic regions. The SCSI and other researchers have conducted numerous studies on vegetation restoration in the vicinity of Hekla but restoration on eroded surfaces requires human inputs, land-use change and a very long time (Aradóttir et al., 2000; Aradóttir et al., 2013; Arnalds et al., 2013a).

In this study we want to contribute to the still remaining scientific gap that plant succession and soil development within sub-Arctic volcanic landscapes proposes. We revisit the work done by Bjarnason (1991) and investigate ecosystem development on the historical Hekla lava flows spanning 860 years. Since Bjarnason's extensive work, more lava flows have formed and the age constraints have been improved. The objectives of the research were to examine soil development and soil carbon accumulation, tie it with plant succession on the lava flows of historical ages and compare with young prehistoric Hekla lavas found nearby. Sampling sites reflect the various land cover types found on the lava flows, a range in climatic conditions around Hekla mountain and different intensity in tephra deposition. Thus, we investigate the impact of time, climate and accumulation of loose material on plant succession and soil development on the Hekla lavas.

II Material and methods

1. Study setting

The Hekla volcanic system is a ridge-shaped volcano with an associated fissure swarm. It is located at the intersection between the South Icelandic Seismic zone and the Eastern Volcanic Zone, which features the four volcanic systems that have produced 77% of all magma output in Iceland during historical times (Thordarson and Larsen, 2007). Of the 23 historical eruptions in Hekla, 18 occurred in the central volcano and 5 occurred on fissures. Eruptions along the main ridge frequently produce mixed eruptions, creating both tephra and lava of an intermediate composition. The study area around Hekla lies on the margin of the southern lowlands and stretches into the southern part of the central highland plateau (N63°50′−64°5′, W20°0′−19°20′). Frequent low-pressure systems travelling from the North Atlantic Ocean reach the southern lowlands where the moist air masses meet the mountains on the highland margin. The south and southwest parts of the area in turn receive ample precipitation and have a temperate high-precipitation climate with cool and short summers. Within the highlands the precipitation declines, temperatures decrease and snowy conditions prevail (Einarsson, 1984). This difference is reflected in a mean annual temperature (MAT) of ~4.5°C in the lowlands compared with 3.0°C within the highland margin (Table 1). The mean annual precipitation (MAP) within the highland margin is estimated to be close to 1000 mm.

Table 1. Mean annual temperature and precipitation measured by the weather stations at Hella (H) and Mörk í Landi (M) on the southern lowlands and Búrfell (B) on the highland margin. The approximate locations of these weather stations are shown on the inset map in Figure. 1.

Weather station	**Hella**	**Mörk í Landi**	**Búrfell**
Height above sea level	20 m	125 m	249 m
Location	63°49.541'N 20°21.923'W	64°01.755'N 20°01.136'W	64°07.010'N 19°44.691'W
Distance from Mt. Hekla	40 km	17 km	14 km
Mean annual temperature*	4.8°C	4.3°C	3.0°C
- January	0.3°C	-0.5°C	-2.3°C
- July	12.2°C	11.9°C	11.0°C
Mean annual precipitation*	NA	NA	945 mm

* Based on unpublished data from the Icelandic Meteorological Office (IMO, www.vedur.is). MAT values are from the weather stations at Hella (2006–2016), Mörk í Landi (2009–2016) and Búrfell (1994–2016). MAP values are from Búrfell (1997–2016).

2. Field setup

The study area covers roughly 400 km^2 and is characterized by young lava flows from the Hekla volcanic system, tephra deposits and hyaloclastite ridges. Field sampling took place in the summers of 2015 and 2016 and was a part of the interdisciplinary research project '*Environmental Mapping and Monitoring of Iceland by Remote Sensing (EMMIRS)'* at the University of Iceland. The main goal of EMMIRS was creating a remote sensing repository for the Hekla region, collecting hyperspectral and lidar data during the summer of 2015 (Pedersen et al., in prep.-b). Other primary aims were to classify land cover types within the area and to re-estimate the association of lava fields with individual Hekla eruptions (Pedersen et al., in prep.-a). To assess the ecosystem development on the lava flows, all the known historical lava flows around Hekla mountain were visited, spanning an elevation range of 100−800 m a.s.l (Table A1). The lava flows originated from eruptions estimated to have occurred in 1158, 1206, 1300, 1389, 1554, 1693, 1725, 1766, 1845, 1878, 1913, 1947, 1970, 1980, 1991 and 2000 (Figure 1). Twenty-eight sampling sites were located on historical lavas of known age, spanning 860 yrs. Four additional sites were located on lavas whose ages are not accurately known but are constrained by stratigraphic position or known tephra layers. One was located on a lava flow inundated by the 1725 lava flow, therefore slightly older, yet historic. Three transects were located on lavas inundated by the 1300, 1389 and 1554 lava fields. They represent surface ages somewhat older than the Settlement or >1140 yrs, according to tephra stratigraphy by Thorarinsson (1967) (Figure 1).

To capture the diversity in vegetation composition within the study area, digital vegetation maps from the Icelandic Institute of Natural History (IINH) for the Hekla region (IINH, 2005) and the Central Highlands (IINH, 2014) at the 1:25,000 scale, were used as an overlay on the lava fields when choosing transect locations.

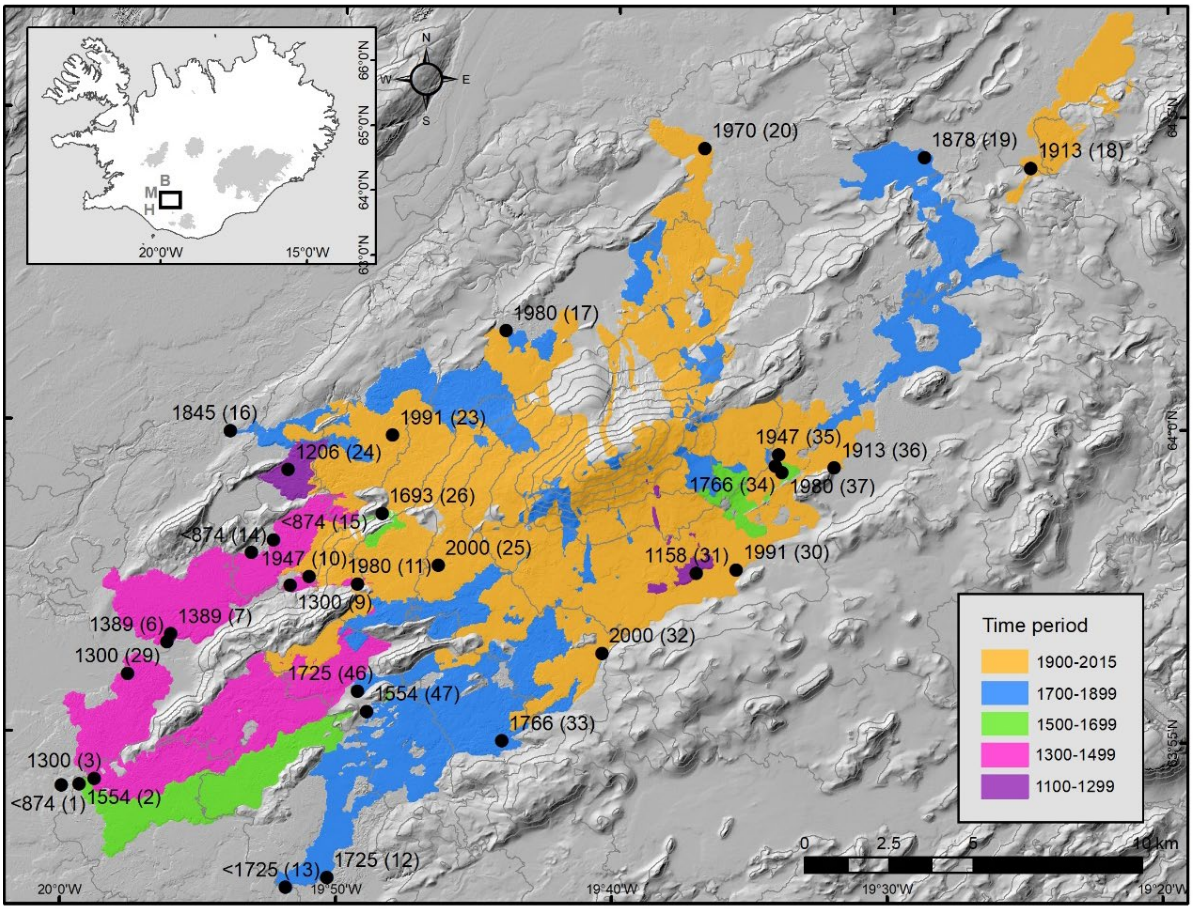

Figure 1. The known historical lava flows of Hekla volcano and location of sampling sites. Colours in the legend refer to the time periods during which the lavas were formed. Dots indicate the location of sampling transects and are labelled with the eruption year and the transect field-number in parenthesis (See Table AI). The extent of the lava fields is from Pedersen et al. (in prep.-a). The background is a hillshade from a lidar digital elevation model (DEM) that was collected and created by the EMMIRS research project (Pedersen et al., in prep.-b) and gaps have been filled with the TDX DEM (Rizzoli et al., 2017). Elevation contours are at 100 m intervals. Capital letters on the inset map indicate the location of the weather stations at Hella (H), Mörk í Landi (M) and Búrfell (B) (Table 1).

3. Field measurements and soil sampling

On the lava fields, 30 m long transects were placed at a minimum distance of 20 m from the margin of the lava field perpendicular to the flow direction. Transects were located within a specific plant community and the surroundings were described and photographed. All vascular plant species found within a 2-m distance of both sides of the transect baseline were recorded and used to generate a list for each transect. Field measurements followed the methods described in the Natura Ísland project (Magnússon et al., 2016) and are listed in Table 2. The cover percentage of species and plant groups was estimated using the Braun-Blanquet cover scale (Goldsmith and Harrison, 1976) within a 33x100-cm frame at 0, 10, 20 and 30-m along the transect. The three species with the highest cover percentage were estimated separately. The height of the tallest vascular plants (excluding birch) found within frames was measured with three replicates per frame. The height of birch individuals was estimated separately for each frame. The same was done to estimate moss thickness. Soil depth was estimated down to 1 m using a steel rod. Plant nomenclature followed Kristinsson (2008) for vascular plants and Jóhannsson (2003) for mosses.

Soils were sampled down to 30 cm depth within each frame at 0–5, 5–15 and 15–30 cm depths using a soil core or a spade as the soil depth allowed. The samples were air dried and stored pending analysis. Bulk density samples were collected for each depth using a soil core of known volume (19.5 cm^3) that was applied perpendicular to the soil profile in duplicates. Tephra layers were recorded in the soil profile and their depth, thickness, colour and grain size documented down to 30 cm depth if possible. Where possible, tephra layers were assigned to specific eruptions based on the properties of the tephra and compared to the profile descriptions made by Thorarinsson (1967). Soil accumulation rates (SAR, mm yr^{-1}) were calculated by dividing the average soil depth (including all soil material, tephra layers etc.) by the age of the relevant lava field. Where soil depth was >1 m, the depth down to the 1510 tephra layer was used to estimate SAR for the past 5 centuries. SAR was not estimated at a few sites where tephra deposits were extremely thick.

Table 2. Plant and soil parameters measured in the field.

Measured parameters	
Vegetated	
Non-vegetated	
Litter	
Anthelia spp. (snow-moss and biological crust)	
Lichens (total cover)	
- *Cetraria/Cladonia* spp.	
- *Peltigera* spp.	
- *Stereocaulon* spp.	
Mosses (total cover)	Thickness (cm)
- *Hylocomium splendens* (Hedw.) Schimp.	
- *Racomitrium ericoides* (Brid.) Brid.	
- *Racomitrium lanuginosum* (Hedw.) Brid	
Vascular plants (total cover)	Height (cm)
- Grasses	
- Sedges & rushes	
- Equisetum	
- Herbs	
- Dwarf shrubs	
- Shrubs & trees	
- *Betula pubescens* Ehrh.	Height (cm)
- *Salix lanata* L.	
- *Salix phylicifolia* L.	
- *Salix arctica* Pall.	
Soil	Thickness (max. 100 cm) Tephra layers
Rock cover	>25 cm^2

4. Soil sample preparation and analysis

Soil samples were analysed at the University of Iceland and the Forest Research Laboratory, Farnham, Surrey, UK. Soil bulk density samples were dried at 105°C and passed through a 2-mm sieve. The volume of coarse fragments (>2-mm) was estimated by water displacement. The bulk density of the fine earth fraction (< 2-mm) was calculated after subtracting the weight and volume of the coarse fraction from the weight and volume of the total bulk density sample. Bulk samples were air dried and passed through a 2-mm sieve prior to analysis. Soil pH (H_2O) was determined in a soil-water suspension (1:5) after stirring for 2 h. Concentrations of total carbon (C) and nitrogen (N) were determined by dry combustion on a Flash 1112 Elementar Analyzer (Thermo-Scientific, Italy) by using ball-milled soil passed through a 150-µm sieve and dried at 50°C.

The C stock was estimated by:

$$\text{C stock (kg C m}^{-2}\text{)} = \text{BD} \times \text{T} \times \text{C\%} \times (100-\text{S}/100) \times 10^{-2}, \qquad (1)$$

where BD is the bulk density (kg m^{-3}), C is the carbon concentration (%), T is the thickness (m) and S is the content of coarse fragments (>2-mm) of the soil layer (vol.%). Concentration of coarse fragments (S) was estimated by:

$$\text{S(\%)} = [\text{coarse fragments >2-mm (m}^3\text{) / total volume (m}^3\text{)}] \times 100. \qquad (2)$$

Total C and N stocks were subsequently determined by combining the stocks of 0–5, 5–15 and 15–30 cm depth intervals, depending on soil depth present for each sampling site.

5. Statistical analysis

The vegetation and soil parameters were averaged for each transect prior to analysis. An extra sample point representing the point of initiation (a new and unvegetated lava field) was added to the dataset prior to analysis. Correlations of vegetation and soil parameters with lava age, MAT, MAP and SAR were analysed using Spearman's non-parametric correlation test. MAT and MAP values for sampling sites were obtained from the modelling results of Bjornsson et al. (2007) and Crochet et al. (2007). The vegetation composition within transects was analysed using DECORANA ordination (Detrended Correspondence Analysis - DCA) to identify patterns in the vegetation succession (ter Braak and Šmilauer, 2012). The relationship of plant, soil and environmental parameters with the ordination pattern was examined from a corresponding second matrix. For the ordination, parameters were log(1+x) transformed where needed. To identify groups with similar vegetation composition, a TWINSPAN classification was used (Hill and Šmilauer, 2005). The analyses were performed in the PC-ORD software vs. 6 (McCune and Mefford, 2011). The ordination and classification were based on presence/absence data and included the top three species with the highest average cover percentage. The species with the highest, second-highest and third-highest average cover were given the values 4, 3, and 2, respectively. All other species present were given the value 1. After identifying groups of different successional stages (SS) their relationship with vegetation, soil and environmental parameters were analysed pairwise for each SS using the nonparametric Wilcoxon method. Statistical analysis, except for the ordination and classification, were performed in the JMP software version 13 (SAS Institute, 2013).

III Results

1. Changes in vegetation and soil over time

Distinct changes in vegetation cover composition and soil properties were observed along the lava sequence. Time was the strongest factor influencing ecological development, MAT similarly showed a strong relationship with vegetation and soil parameters. MAP yielded inverted and less significant relationship compared to MAT. SAR featured a weaker relationship with only a few parameters being significantly related. Vegetation cover, cover of vascular plant groups, vascular plant height and species richness all increased significantly with time since lava emplacement (Table 3). *Stereocaulon* spp., rock cover and MTR showed a negative relationship with time and *Anthelia*, *R.lanuginosum* and moss thickness had no apparent association with lava age. The moss *R.lanuginosum* and *Stereocaulon* spp. lichens were the dominant species colonizing the youngest lava fields, already fully covering a lava in 24 years as seen on the 1991 lava field. *R.lanuginosum* not only covered the lavas rapidly but also thickened quickly, yielding thickening rates of 1.6−1.7 mm yr^{-1} where conditions were favourable southwest of Hekla on lava fields from 1947 and 1991. With increasing surface age, vegetation composition changed as soil depth increased and vascular plants colonized the lavas. Dwarf shrubs, willows and birch and to a lesser degree grasses and herbs increased their cover proportion, accompanied by increasing height of vascular plants. The cover of *Peltigera* spp. lichens and *H.splendens* moss increased on the older lava fields representing the development of heathland and woodland.

The relationship of MAT with vegetation parameters showed similar results as those with time, although with some exceptions. Most vegetation parameters increased with increasing MAT, except for *Stereocaulon* spp., whose cover decreased (Table 3). No effects of MAT were apparent for *Anthelia* spp., *R.lanuginosum*, herbs or MTR. The uneven geochronological distribution of the lava fields may affect the results of this analysis, since the oldest lavas are mostly located in the west and south-west part of the research area and the youngest ones are restricted to higher elevation. MAP values for sampling sites ranged from 1600 to 3000 mm (Table A1). Interestingly, *R.lanuginosum* cover and MTR did not show an apparent relationship with MAP.

SAR showed a significant positive relationship with *Anthelia* spp., vascular plant and herb cover. It is noteworthy that a negative relationship was observed with the cover of *R.lanuginosum* and SAR (Table 3).

Table 3. Relationship between vegetation and soil parameters with lava age, mean annual temperature (MAT), mean annual precipitation (MAP) and soil accumulation rate (SAR).

	Lava age		MAT		MAP		SAR			Lava age		MAT		MAP		SAR	
	r_s	p value	r_s	p value	r_s	p value	r_s	p value		r_s	p value	r_s	p value	r_s	p value	r_s	p value
Vegetation cover	0.612	0.001 ***	0.683	0.001 ***	-0.414	0.019 *	-0.117	0.524	Moss thickness	0.256	0.157	0.454	0.009 **	-0.370	0.037 *	-0.075	0.683
Anthelia spp.	0.130	0.478	-0.317	0.077	0.074	0.688	0.552	0.001 ***	MTR	-0.774	0.001 ***	-0.116	0.527	0.100	0.586	-0.504	0.003 **
Peltigera spp.	0.534	0.002 **	0.399	0.024 **	-0.519	0.002 **	0.238	0.190	Vascular plant height	0.835	0.001 ***	0.669	0.001 ***	-0.640	0.001 ***	0.217	0.233
Stereocaulon spp.	-0.656	0.001 ***	-0.719	0.001 ***	0.300	0.095	0.069	0.709	Birch height	0.532	0.002 **	0.420	0.017 **	-0.328	0.067	0.068	0.714
R. lanuginosum	-0.285	0.113	0.211	0.246	-0.016	0.931	-0.477	0.006 **									
H.splendens	0.563	0.001 ***	0.492	0.004 **	-0.368	0.038 *	0.163	0.373	Species richness	0.646	0.001 ***	0.591	0.001 ***	-0.698	0.001 ***	0.295	0.102
Vascular plants	0.853	0.001 ***	0.553	0.001 ***	-0.434	0.013 *	0.400	0.023 *									
Grasses	0.652	0.001 ***	0.468	0.007 **	-0.559	0.001 ***	0.298	0.098	Soil depth	0.884	0.001 ***	0.386	0.029 *	-0.317	0.078	0.579	0.001 ***
Sedges and rushes	0.694	0.001 ***	0.607	0.001 ***	-0.499	0.004 **	0.249	0.170	SAR	0.321	0.073	-0.076	0.678	-0.192	0.292		
Herbs	0.558	0.001 ***	0.254	0.161	-0.344	0.054	0.387	0.029 *	pH	-0.424	0.049 *	0.072	0.749	-0.096	0.673	-0.133	0.556
Dwarf shrubs	0.798	0.001 ***	0.539	0.002 **	-0.386	0.029 *	0.284	0.115	Bulk density	0.011	0.960	0.056	0.799	-0.083	0.706	0.251	0.247
Shrubs and trees	0.556	0.001 ***	0.419	0.017 *	-0.466	0.007 **	0.188	0.302	TC	0.819	0.001 ***	0.729	0.001 ***	-0.678	0.001 ***	0.241	0.183
Rock cover	-0.791	0.001 ***	-0.704	0.001 ***	0.539	0.002 **	-0.262	0.147	TN	0.823	0.001 ***	0.687	0.001 ***	-0.697	0.001 ***	0.284	0.115

*Signif. codes: 0.001 '***'; 0.01 '**'; 0.05 '*'.*

The soils developing on the lava fields were dark coloured and tephra rich. B_w horizons were rarely observed and only within the oldest lava fields at ~30 cm depth. Increasing soil depth with time reflected both past events of tephra deposition and soil forming processes but SAR rates did not show an apparent relationship with lava age (Table 3). SAR values were highest in areas of heavy tephra deposition while the lowest values occurred in more stable environmental conditions. The lowest SAR rates of 0.2−0.3 mm yr^{-1} were estimated in the south-west part of the study area, within the moss-covered 1300 and 1554 lava fields (Table 4). The highest rates occurred in the northern part in the highlands where SAR values were as high as 4 mm yr^{-1}. The pH values in the topsoil showed a negative relationship with time ranging from 5.7–6.6 with slightly higher values at lower depths. Neither MAT nor SAR had apparent relationships with pH values. Bulk density ranged between 0.5−0.9 g cm^{-3} showing no relationship with lava age, MAT or SAR (Tables 3 and 4). It was generally lower where soils were tephra-rich. TC and TN concentrations increased significantly with increasing lava age and MAT but again, this apparent relationship may be affected by the uneven regional distribution of the lava flows. SAR rates did not have an apparent relationship with TC and TN. TC and TN concentrations were highest for the 0−5 cm depth, with TC ranging between 0.4−11.5% and N 0.02−0.5%. C stocks were highest within the south-west part of the region and mostly ranged between 0.9−1.8 kg C m^{-2} for the top 5 cm within the oldest historical lava fields while N stocks were mostly well below 0.1 kg N m^{-2} within same lava fields. Total C and N stocks for the 0−30 cm depth were highest within the 1206 and 1389 lava fields, 3.5−5.2 kg C m^{-2} and 0.2−0.3 kg N m^{-2}, respectively.

Table 4. Soil properties within sampling sites: soil depth, SAR (soil accumulation rate), pH (H_2O), total carbon and nitrogen concentrations, bulk density and calculated carbon and nitrogen stocks (kg m^{-2}).

Year of eruption	**Transect** no.	**Lava age** years	**Soil depth** (cm)	**SAR** mm yr^{-1}	**pH H_2O**			**TC** (%)			**TN** (%)			**Bulk density** (g cm^{-3})			**kg C m^{-2}**				**kg N m^{-2}**			
Depth (cm)					0-5	5-15	15-30	0-5	5-15	15-30	0-5	5-15	15-30	0-5	5-15	15-30	0-5	5-15	15-30	Total	0-5	5-15	15-30	Total
2000	25	15	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2000	32	16	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1991	23	24	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1991	30	25	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1980	11	35	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1980	17	36	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1980	37	36	2.1	0.8	na	-	-	na	-	-	na	-	-	na	-	-	na	-	-	-	na	-	-	-
1970	20	45	20	4.2	6.4	na	-	0.57	na	-	0.016	na	-	0.63	na	-	0.16	na	-	0.16	0.004	na	-	0.004
1947	10	68	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.00	-	-	-	0.000
1947	35	69	1.1	0.7	na	-	-	na	-	-	na	-	-	na	-	-	na	-	-	0.00	na	-	-	0.000
1913	18	102	33	3.0	6.1	6.3	-	1.89	0.29	-	0.092	0.015	-	0.81	0.61	-	0.71	0.16	-	0.87	0.035	0.008	-	0.043
1913	36	103	4.9	0.6	6.1	-	-	0.89	-	-	0.042	-	-	0.75	-	-	0.31	-	-	0.31	0.015	-	-	0.015
1878	19	137	11	0.4	6.2	-	-	1.89	-	-	0.092	-	-	0.59	-	-	0.54	-	-	0.54	0.026	-	-	0.026
1845	16	170	10	0.4	6.4	-	-	2.15	-	-	0.088	-	-	0.68	-	-	0.73	-	-	0.73	0.030	-	-	0.030
1766	33	250	40	1.6	6.0	6.1	6.4	0.48	0.04	0.02	0.020	0.000	0.000	0.28	1.26	0.13	0.05	0.05	0.00	0.10	0.002	0.000	0.000	0.002
1766	34	250	15.5	0.8	6.2	6.3	-	0.80	0.57	-	0.032	0.021	-	0.26	0.79	-	0.09	0.40	-	0.49	0.003	0.015	-	0.018
1725	12	290	21	0.4	6.6	6.8	-	2.08	1.90	-	0.060	0.051	-	0.78	0.61	-	0.81	1.12	-	1.93	0.023	0.030	-	0.053
1725	46	291	12	0.3	6.0	6.6	-	3.07	2.49	-	0.057	0.116	-	0.46	0.68	-	0.69	1.69	-	2.38	0.013	0.079	-	0.092
<1725	13	290	28	1.1	6.4	6.8	6.9	1.65	1.20	0.68	0.047	0.051	0.037	0.82	0.56	0.55	0.67	0.67	0.49	1.83	0.019	0.028	0.027	0.074
1693	26	322	21	0.4	6.2	6.5	-	1.09	1.11	-	0.037	0.053	-	0.69	0.78	-	0.37	0.86	-	1.24	0.013	0.041	-	0.054
1554	2	461	8	0.2	6.5	-	-	4.65	-	-	0.109	-	-	0.48	-	-	1.12	-	-	1.12	0.026	-	-	0.026
1554	47	462	100	na	6.1	6.5	6.6	0.49	na	0.16	0.021	na	0.007	0.51	0.55	0.36	0.11	na	0.08	0.18	0.005	na	0.003	0.008
1389	6	626	52	0.8	6.1	6.6	7.0	5.71	2.71	1.80	0.332	0.165	0.110	0.63	0.57	0.69	1.80	1.53	1.86	5.19	0.104	0.093	0.114	0.312
1389	7	626	37	0.6	6.3	6.4	6.8	3.44	1.45	1.31	0.145	0.073	0.061	0.75	0.79	0.58	1.28	1.13	1.09	3.50	0.054	0.057	0.051	0.162
1300	3	715	21	0.3	6.6	6.9	-	3.13	1.78	-	0.118	0.090	-	0.60	0.69	-	0.94	1.23	-	2.16	0.035	0.062	-	0.097
1300	9	715	49	0.7	6.7	6.7	6.8	2.17	0.98	0.31	0.074	0.055	0.017	0.83	0.85	0.70	0.90	0.82	0.28	2.00	0.031	0.046	0.016	0.092
1300	29	715	37	0.4	5.9	6.7	7.0	4.55	2.09	0.91	0.195	0.116	0.039	0.62	0.72	na	1.41	1.51	na	2.92	0.060	0.084	na	0.144
1206	24	809	61	0.9	5.7	6.3	6.7	3.10	1.33	1.12	0.118	0.072	0.061	0.72	0.81	0.80	1.10	1.08	1.34	3.51	0.042	0.058	0.073	0.173
1158	31	858	100	na	6.1	6.2	6.3	0.44	0.12	0.19	0.018	0.002	0.007	0.75	na	0.51	0.15	na	0.11	0.26	0.006	na	0.004	0.010
<874	14	1141	72	na	6.0	6.6	6.7	3.74	2.15	2.07	0.149	0.118	0.125	0.76	0.64	0.78	1.41	1.38	2.43	5.21	0.056	0.075	0.147	0.278
<874	15	1141	87	0.4	5.8	6.3	6.7	4.54	2.07	1.58	0.198	0.110	0.093	0.61	0.68	0.51	1.36	1.40	1.16	3.92	0.059	0.074	0.068	0.202
<874	1	1141	93	0.5	5.7	6.4	6.7	11.48	4.74	1.00	0.481	0.290	0.073	0.36	0.63	0.43	2.06	2.98	0.61	5.64	0.086	0.182	0.044	0.313

-: no soil present; na: data not available

2. Identifying successional stages on the Hekla lavas

Results of the DCA ordination showed that axes 1 and 2 explained 81% of the variability (eigenvalues: axis 1=0.57, axis 2=0.24) extracted by the first four axes. Age of the lava fields, soil depth and MAT were the environmental parameters that most strongly influenced the vegetation composition (Figure 2) increasing to the right along axis 1. Axis 2 represented the influence of loose material (tephra fall, soil formation) accumulating on the lava flows and is indicated by the correlation with soil depth and SAR. The youngest lava fields dominated by *R.lanuginosum* had very little soil material and vascular plants were rare. Species richness (vascular plants), soil depth and SAR correlated most strongly with axis 2, while conversely, MTR, rock cover and *R.lanuginosum* cover showed a relatively strong correlation with the youngest lavas, grouped in the lower part of the plot.

Results from TWINSPAN classification indicated three successional stages (SS) on the lavas and an alternate stage representing areas of higher environmental stress induced by increased elevation and/or tephra deposition. The suggested successional stages are indicated with circles on the DCA plot (Figure 2) and are further described below:

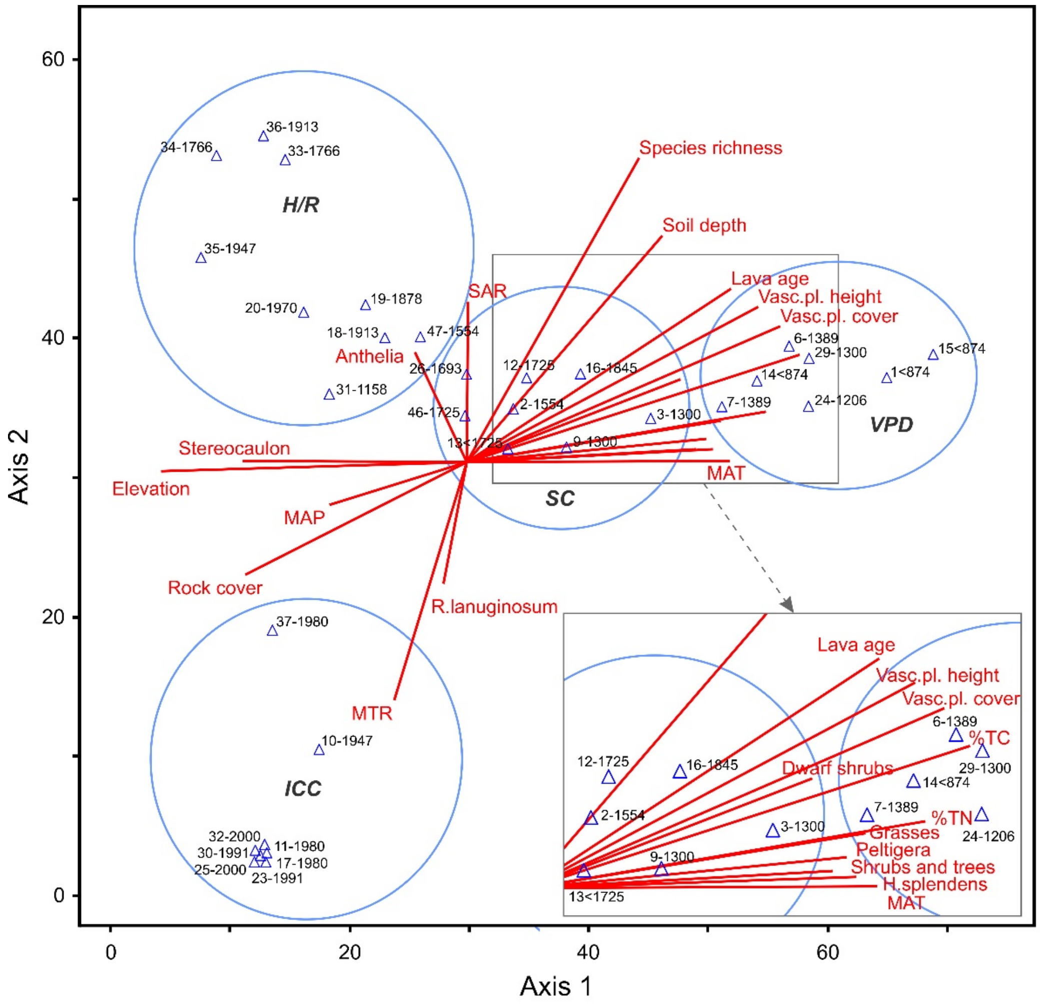

Figure 2. DCA ordination results for 32 transects on Hekla lava fields. Lines indicate direction of main change for each variable and their lengths indicate the strength of the correlation with the vegetation pattern. Circles indicate groups determined by TWINSPAN classification and represent four successional stages: Initial colonization and cover coalescence (ICC); Secondary colonization - R.lanuginosum dominance (SC); Vascular plant dominance (VPD); Highland conditions/Retrogression (H/R).

<u>Initial colonization and cover coalescence (ICC)</u> represents the youngest lavas vegetated with mosses and lichens while vascular plants are almost absent and soil material negligent. *R.lanuginosum* and *Stereocaulon* spp. were the dominant species (Figure 3a). This is the initial succession found on lavas from 2000, 1991, 1980 and 1947. MTR and MAP were significantly highest within this stage (Table 5, Figure 2).

Secondary colonization − *R.lanuginosum* dominance (SC) represents vegetation of an intermediate succession stage (Figure 2). It is characterized by thick moss cover where *R.lanuginosum* is dominant and vascular plants, especially dwarf shrubs (*Empetrum nigrum* and *Salix herbacea*) compose a small part of the cover (Table 5, Figure 3b). Moss was significantly thicker in this stage than the other three (Table 5). Despite the dominance of *R.lanuginosum*, the species richness was not significantly different from Stage 3. Moss thickness and soil pH were significantly higher within with this stage (Tables 5 and 6, Figure 2). This stage was found on lavas formed in eruptions from 1300 to 1845.

Vascular plant dominance (VPD) represents an advanced successional stage where dwarf and taller shrubs become dominant in cover. *Vaccinium uliginosum, E.nigrum, Arcostaphyllus uva-ursi* were the dominant dwarf shrub species. The willows shrubs *Salix lanata* and *S.phylicifolia* and the native tree species *B.pubescens* comprised the taller shrub/tree cover (Table 5, Figure 3c). The parameters that were significantly higher within this stage were *Petligera* spp., *H.splendens*, vascular plant cover, grasses, shrubs/trees, vegetation height, TC, TN and lava age (Table 5 and 6). This stage was only found on lavas formed during the eruptions in 1206, 1300, and 1389 and the prehistorical lavas.

Highland conditions /Retrogression (H/R) by tephra deposition is an alternate stage where the successional trajectory has been altered due to greater environmental stress including thick tephra fall and/or are located at high elevation. On sites that had received thick tephra deposits the tephra has greatly reduced the cover of mosses but favoured the establishment of vascular plants (Figure 3d). Average vascular plant cover was 6.3% and species richness was similar to SC stage. On sites only receiving thin tephra additions, *Stereocaulon* spp. rapidly gained 45–50% cover such as on lavas formed in 1913 and 1878. *Anthelia* spp. cover was positively related to this stage and significantly different from the other SS's while vascular plant height, TC and TN were significantly lower (Tables 5 and 6, Figure 2).

Table 5. Relationship of plant groups vegetation parameters with successional stages. Average values (standard deviation in parenthesis) are shaded.

		Vegetation cover				*Anthelia* spp.				*Peltigera* spp.				*Stereocaulon* spp.			
SS	*n*	H/R	ICC	SC	VPD	H/R	ICC	SC	VPD	H/R	ICC	SC	VPD	H/R	ICC	SC	VPD
H/R	9	66.0 (21.3)				9.7 (8.9)				0.1 (0.3)				23.2 (19.5)			
ICC	8	0.808	66.0 (25.5)			0.003 **	1.8 (5.0)			0.045 *	0.0 (0.0)			0.148	9.1 (7.1)		
SC	8	0.002 **	0.035 *	86.7 (2.2)		0.003 ***	0.056	0.5 (0.6)		1	0.076	1.0 (1.8)		0.005 **	0.024 *	2.2 (3.2)	
VPD	7	0.002 **	0.019 *	0.423	87.5 (0.0)	0.008 **	0.077	0.769	0.8 (1.4)	0.001 ***	0.001 ***	0.006 **	7.1 (1.4)	0.001 ***	0.002 **	0.079	0.2 (0.3)
		R.lanuginosum				*H.splendens*				Vascular plants				Grasses			
SS	*n*	H/R	ICC	SC	VPD	H/R	ICC	SC	VPD	H/R	ICC	SC	VPD	H/R	ICC	SC	VPD
H/R	9	14.8 (14.3)				0.0 (0.0)				6.3 (5.2)				0.4 (0.6)			
ICC	8	0.003 **	59.2 (27.8)			1	0.0 (0.0)			0.001 ***	0.0 (0.0)			0.045 *	0.0 (0.0)		
SC	8	0.001 ***	0.308	74.3 (16.3)		0.346	0.382	0.1 (3.3)		0.148	0.001 ***	12.0 (8.0)		0.459	0.001 ***	0.5 (0.3)	
VPD	7	0.456	0.001 ***	0.001 ***	9.3 (7.7)	0.001 ***	0.002 **	0.004 **	19.1 (20.0)	0.001 ***	0.005 **	0.001 ***	75.3 (10.5)	0.002 **	0.001 ***	0.001 ***	9.4 (8.6)
		Sedges				Herbs				Dwarf shrubs				Shrubs and trees			
SS	*n*	H/R	ICC	SC	VPD	H/R	ICC	SC	VPD	H/R	ICC	SC	VPD	H/R	ICC	SC	VPD
H/R	9	0.2 (0.4)				0.8 (0.6)				4.4 (5.6)				0.5 (1.5)			
ICC	8	0.045 *	0.0 (0.0)			0.003 **	0.0 (0.0)			0.008 **	0.0 (0.0)			0.401	0.0 (0.0)		
SC	8	0.057	0.001 ***	0.9 (1.6)		0.808	0.001 ***	0.9 (0.9)		0.054	0.001 ***	11.6 (8.3)		0.401	1	0.0 (0.0)	
VPD	7	0.010 *	0.001 ***	0.146	4.8 (10.6)	0.239	0.001 ***	0.324	5.5 (11.7)	0.015 **	0.001 ***	0.093	39.4 (31.3)	0.002 **	0.002 **	0.002 **	36.5 (26.8)
		Vascular plant height				Moss thickness				MTR				Species richness			
SS	*n*	H/R	ICC	SC	VPD	H/R	ICC	SC	VPD	H/R	ICC	SC	VPD	H/R	ICC	SC	VPD
H/R	9	3.0 (2.6)				2.4 (1.1)				0.18 (0.18)				13.3 (6.7)			
ICC	8	0.003 **	0.0 (0.0)			1	3.2 (3.3)			0.001 ***	0.93 (0.47)			0.001 ***	0.3 (0.0)		
SC	8	0.012 **	0.001 ***	5.8 (2.1)		0.001 ***	0.003 **	13.7 (4.8)		0.026 *	0.004 **	0.40 (0.14)		0.082	0.001 ***	19.5 (5.4)	
VPD	7	0.001 ***	0.001 ***	0.004 **	13.4 (3.1)	0.671	0.954	0.009 **	5.4 (5.2)	0.168	0.001 ***	0.001 ***	0.06 (0.05)	0.022 *	0.001 ***	0.201	24.6 (8.5)

SS: Successional stage; H/R: Highland conditions/retrogression; ICC: Initial colonization and coalescence; SC: Secondary colonization – R.lanuginosum *dominance; VPD: Vascular plant dominance.*
*Signif. codes: 0.001 '***'; 0.01 '**'; 0.05 '*'.*

Table 6. Relationship of soil properties, MAT, MAP and lava age with successional stages. Average values (standard deviation in parenthesis) are shaded.

		Soil depth (cm)				SAR (mm yr^{-1})				Bulk density (g cm^{-3})			
SS	*n*	H/R	ICC	SC	VPD	H/R	ICC	SC	VPD	H/R	ICC	SC	VPD
H/R	9	36.2 (38.3)				1.39 (1.33)				0.51 (0.27)			
ICC	8	0.001 ***	0.3 (0.7)			0.003 **	0.10 (0.28)			-	-		
SC	8	0.885	0.001 ***	21.3 (13.1)		0.022 *	0.007 **	0.48 (0.29)		0.228	-	0.67 (0.14)	
VPD	7	0.112	0.001 ***	0.003 **	62.7 (22.5)	0.119	0.007 **	0.188	0.57 (0.21)	0.426	-	0.685	0.64 (014)

		pH (H_2O)				C (%)				N (%)			
SS	*n*	H/R	ICC	SC	VPD	H/R	ICC	SC	VPD	H/R	ICC	SC	VPD
H/R	9	6.2 (0.1)[1]				0.83 (0.65)				0.037 (0.033)			
ICC	8	-	-			-	-			-	-		
SC	8	0.024 **	-	6.4 (0.2)		0.002 **	-	2.50 (1.10)		0.030 *	-	0.074 (0.029)	
VPD	7	0.032 **	-	0.005 **	5.9 (0.2)	0.001 ***	-	0.013 *	5.22 (2.89)	0.001 ***	-	0.002 **	0.231 (0.130)

		MAT				MAP				Age (yrs)			
SS	*n*	H/R	ICC	SC	VPD	H/R	ICC	SC	VPD	H/R	ICC	SC	VPD
H/R	9	0.03 (1.1)				2336 (546)				253 (261)			
ICC	8	0.335	0.59 (1.3)			0.413	2603 (242)			0.001 ***	32 (17)		
SC	8	0.002 **	0.012 **	2.38 (0.8)		0.312	0.021 *	2207 (246)		0.06	0.001 ***	407 (206)	
VPD	7	0.001 ***	0.003 **	0.181	2.94 (0.3)	0.290	0.001 ***	0.132	2007 (65)	0.004 **	0.002 **	0.009 **	886 (247)

SS: Successional stage; H/R: Highland conditions/retrogression; ICC: Initial colonization and coalescence; SC: Secondary colonization – R.lanuginosum *dominance; VPD: Vascular plant dominance.*
*Signif. codes: 0.001 '***'; 0.01 '**'; 0.05 '*'.*
-: very little or no soil material in sampling sites.
[1] for H/R n=8 for pH H_2O.

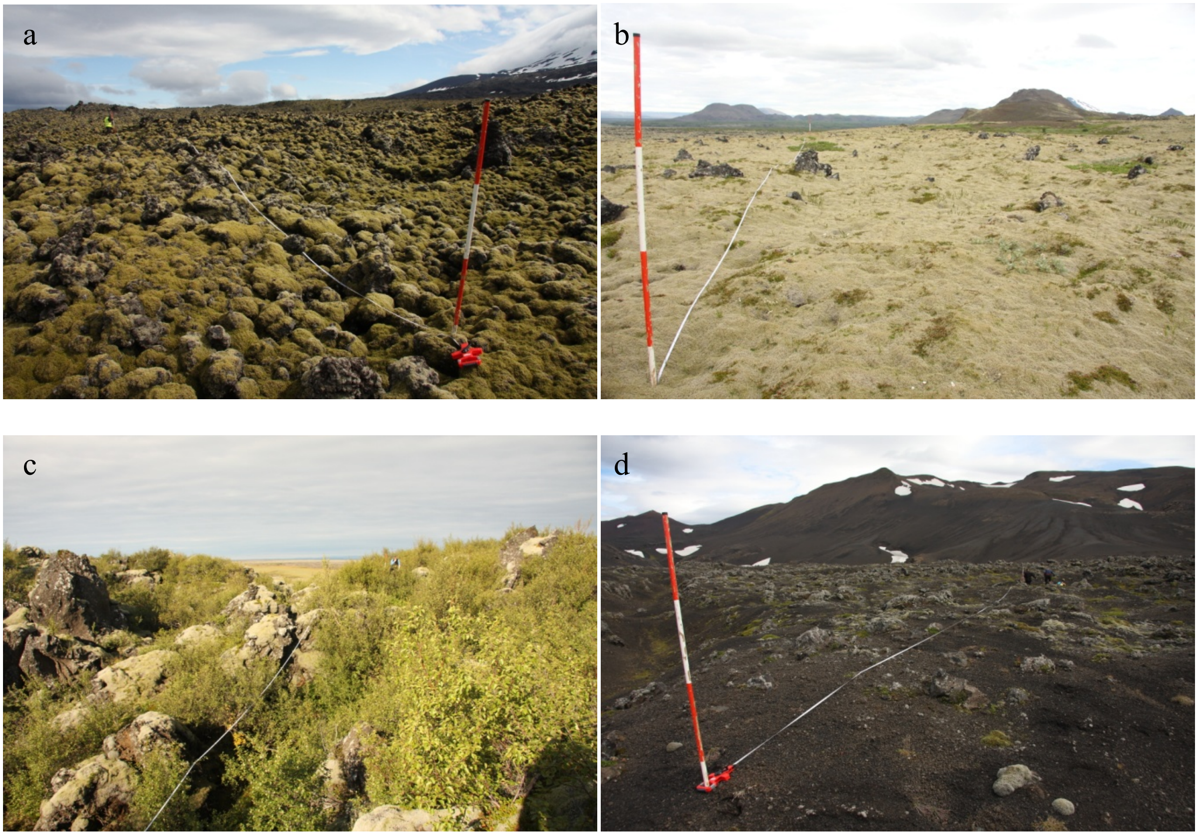

Figure 3. Examples of successional stages defined from the multivariate analysis: a) initial colonization and coalescence *stage with an example from the 1991 lava field west of Hekla, b)* secondary colonization − *R.lanuginosum* dominance *in the vegetation community on the 1300 lava field, c) an example from the same 1300 lava field where the succession has advanced to the* vascular plant dominance *stage with* B. pubescens *becoming dominant in the shrub cover, d)* highland conditions/retrogression by tephra deposition *stage with an example from the 1766 lava field that received a large amount of tephra during the 1947 eruption at Hekla.*

IV Discussion

1. Soil development and soil carbon accumulation

Time and climate appeared to be the most influential factors for soil development and pH, TC and TN concentrations differed significantly between successional stages. The soils developing on the lava fields of Hekla had rather typical properties of volcanic soils developing from basaltic parent material on well drained surfaces (Arnalds, 2004; Arnalds, 2015) as indicated by the dark brown and, less commonly, reddish brown colour of subsurface soil horizons. Soil pH values were generally >5.7 with lower values in the VPD SS compared to SC stage, indicating an increased influence of organic acids from plants lowering the pH. Bulk density values between 0.4–0.9 g/cm^{-3} reflected the low density porous tephra deposited on the lavas, acting as the parent material in the soil development. TC concentrations were generally under 5% (Table 4) and TN well below 0.5%. Concentrations increased gradually throughout the chronosequence and the highest values were comparable to common values in well drained volcanic soils in Iceland (Arnalds, 2004; Vilmundardóttir et al., 2015b).

Studies on soil development on lava flows have mainly focused on chemical weathering rates and nutrients but a few studies do report on soil carbon accumulation on lava flows but they have usually dealt with organic rich soils (Histosols) in warmer climates (Kamijo et al., 2002; Raich et al., 1997; Kitayama et al., 1997) or much older lava sequences (Nieuwenhuyse et al., 2000). Comparison with these studies shows that the soils on the Hekla lavas contain considerably less C and N concentrations compared to organic rich soils in Hawaii and Japan. On 37 and 125 yr-old lava flows in Japan, soils contained ~30% C (Kamijo et al., 2002) and in the Hawaiian archipelago C concentrations were 14% on 400–1400 yr old lava flows (Kitayama et al., 1997). Estimated C stocks were, however, more similar to our findings from Hekla. Kitayama et al. (1997) estimated the C stock to be 3.7 kg m^{-2} on 400 yr old lava and 7.0 kg C m^{-2} on 1400 yr-old lava substrate. Raich et al. (1997) reported 0.3–2.5 kg C m^{-2} on young (100–136 yr-old) lava flows in Hawaii. Kamijo et al. (2002) reported 0.3–0.6 kg C m^{-2} for the 125 yr old lava flow and 3.3–4.0 kg C m^{-2} on an older tephra rich lava. The C stock values are more similar to what we report from the Hekla lavas (Table 4) than the concentrations values, which is partly explained by higher bulk density values and higher rates of increase in soil depth in this study.

In south-east Iceland climate conditions are similar to those within the Hekla region and comparison of soil development can be made between the two surface types, lavas and glacial moraines. The lack of loose material on the lava flows affects the initial rates of soil development and carbon accumulation for obvious reasons. Ecosystem development on glacial moraines has an advantage over lava flows in a way that loose moraine material is available for plants for rooting and the large surface area of the finer grains has high weathering rates (Egli et al., 2008; Walker and Del Moral, 2003). Within the proglacial moraines of Skaftafellsjökull outlet glacier, birch and willow shrubland with *Racomitrium* moss cover was developing after 120 yrs since deglaciation (Vilmundardóttir et al., 2015b). Carbon concentrations in moraines exposed for 120 yrs were estimated to be 1.3–1.7% and carbon stocks 0.5–1.1 kg C m^{-2} (Vilmundardóttir et al., 2015a; Vilmundardóttir et al., 2017). Soil C stocks on 290 yr-old Hekla lavas (1.9 kg C m^{-2}, 1–15 cm) are similar to what was estimated for 120 yr-old moraines in Skaftafell (1.4 kg C m^{-2}, 1–20 cm) (Vilmundardóttir et al., 2015b) (Table 4). However, different sampling depths must be considered when making comparisons. It seems like the harsh conditions on the Hekla lavas are ameliorated by the general input of loose material, which steps up the pace of both plant succession and soil development. However, if tephra deposits are too thick and unstable, it may cause retrogression in the succession, the effects are reverted and soil properties are dominated by tephra and low organic content.

2. Vegetation succession on the Hekla lava sequence

Based on the results of this study, we propose a model of plant succession indicating a directional change in the relatively simple ecosystem developing over the last 860 years, as portrayed in Figure 4. Plant succession on the Hekla lava sequence has many similarities to volcanic regions over the world where the first stage(s) are characterized by mosses and lichens, with lichens of *Stereocaulon* spp. and *Racomitrium* mosses being important early colonizers (Clarkson, 1998; Marchese and Grillo, 2000; Korablev and Neshataeva, 2016). The initial colonization consists of *R.lanuginosum* and *Stereocaulon* spp., rapidly establishing on the coarse surface of the lavas and as their cover further coalesces, the moss becomes dominant. This is the initial succession found on lavas <70 yrs of age. The youngest lava from the 2000 eruption represents an incipient stage as the cover was only 20–40% on average, while the cover on the other lava fields in this group (1991, 1980 and 1947) was over 60%. This part of the colonization occurs rapidly as patches grow by lateral expansion and vertical thickening independent of the topography (Cutler et al., 2008a). On the lava flows of Mt. Etna, *Stereocaulon vesuvianum* along with *Racomitrium* mosses made up 80–90% on lavas emplaced in 1910–1780 (Marchese and Grillo, 2000). On the lava fields of Mauna Loa in Hawaii the cover of *Stereocaulon vulcani* and R.lanuginosum was 48% and 27% respectively after 5 years but it declined rapidly with increasing lava age and was almost absent after one century of development (Clarkson, 1998). These studies are, however, from sites in warmer climates and at higher altitudes than at Mt. Hekla. The decline in cover of these specific lichen and moss species has been associated with competition with vascular plants e.g. due to negative effects of shading and litter-fall for example (Tallis, 1959; Kurina and Vitousek, 1999). Cutler et al. (2008b) define two stages of succession during the initial phase of colonization on Hekla lavas: pioneer colonization and pioneer expansion. In this study, the multivariate analysis does not differentiate between the two stages. The successional sequence presented here follows Cutler's example and differentiates between the initial colonization stage found on the sparsely covered 2000 lava field and the coalescence stage of the older lava fields, i.e. the southwest parts of 1991 and 1980 (Figure 4).

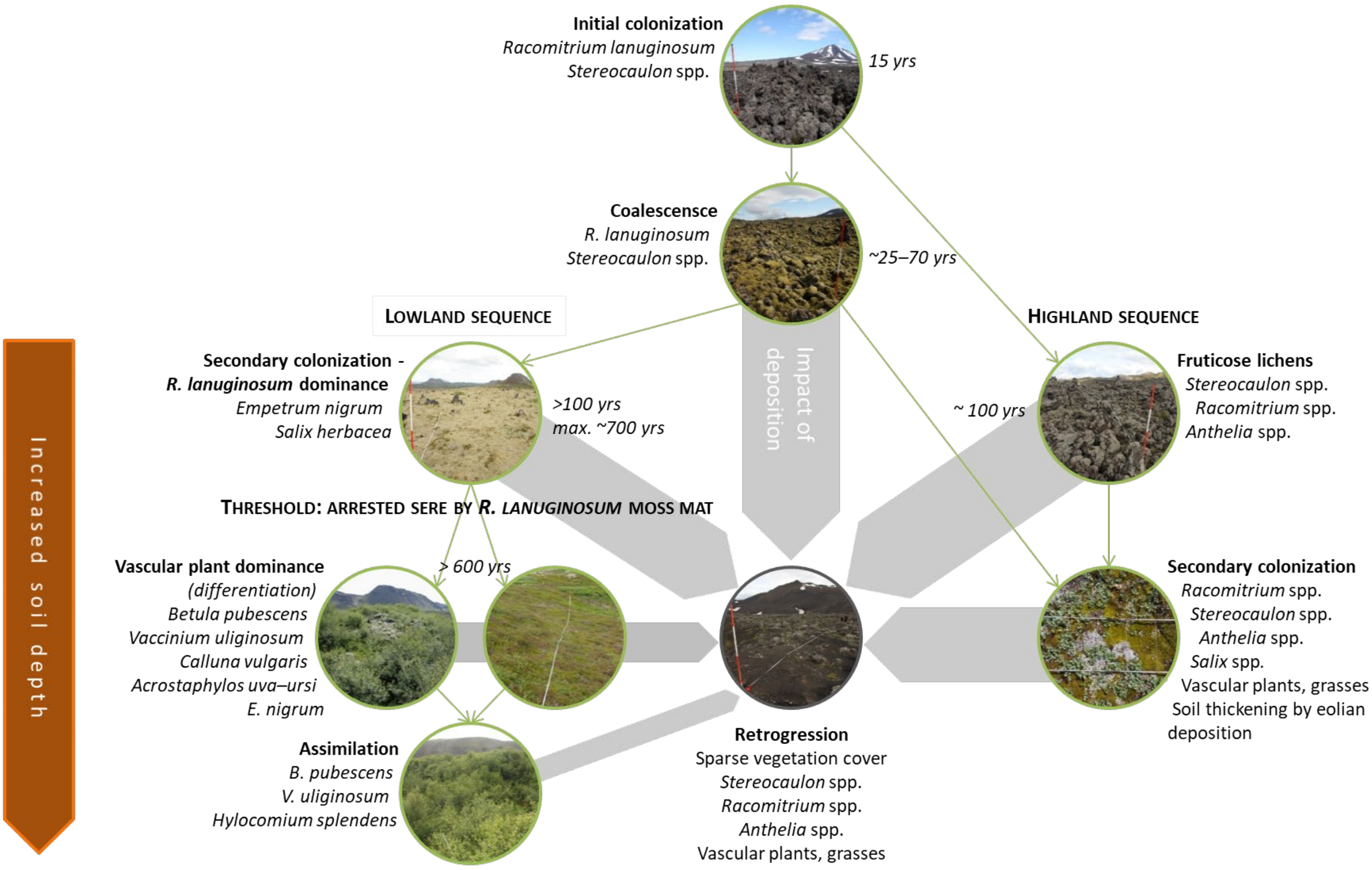

Figure 4. A simplified successional sequence on the Hekla lava fields for lowland and highland conditions. Connecting arrows represent progression between stages. Under lowland conditions, R.lanuginosum *becomes dominant in cover, inhibiting vascular plant establishment. Environmental drivers are needed for the succession to overcome this threshold and continue into vascular plant dominance and later into stage of assimilation dominated by birch. In the highlands, the fruticose lichen* Stereocaulon *spp. features a separate stage. Further succession leads to vascular plants colonizing the lavas, especially where there is thin or moderate deposition of tephra. Where deposition exceeds the tolerance limits for a given plant community, retrogression occurs and plant cover is severely reduced. The impact of deposition is higher for lower growing plant communities as indicated by the thickness of the grey arrows. Tolerance limits towards tephra fall increase downwards along the sequence. Soil depth increases after the initial colonization and coalescence stages.*

The successional sequence divides into lowland and highland conditions and is primarily driven by the input of loose material on the lavas building up soil depth, accumulating soil carbon and nitrogen. For lowlands, the dominance of *R.lanuginosum* and slow colonization of vascular plants characterizes the secondary colonization stage. The age of the lava fields spanned 170–700 yrs and the wide range suggests an arrested development in the successional sequence (Figure 4). This was first described from Hekla by Bjarnason (1991) and later by Cutler et al. (2008b) and is central in Jónsdóttir's study from Skaftáreldahraun, a lava flow field formed in the Laki eruption in 1783 (Jónsdóttir, 2009). The primary succession on the Hekla lava flows bears great resemblance to the development on the lava flows of the Tolbachinskii Dol Plateau on the Kamchatka peninsula, where temperature and altitude of the lava flows are similar to conditions around Hekla. There, Korablev and Neshataeva (2016) divided the ecological succession into three age groups, concluding that *R.lanuginosum* and *S.vesuvianum* remained important colonizers for many centuries in the first and second age groups featured on 35, 270, 800 and 1300 yr-old lavas. However, they do not mention inhibitive properties of this persistent plant cover. Comparison between the two studies indicates slightly faster progression from the SC to VPD on the Hekla lavas, comparable to Korablev and Neshtaeva's 2nd and 3rd stage.

The advance into the vascular plant dominance stage takes place where conditions are favourable for vascular plants, leading to the development of dwarf shrub heath and/or *Betula* shrubland with willows. Our results show that time correlated most strongly with vascular plant cover and plant height. MAT and SAR rates were positively related to vascular plant cover but there was not a significant difference of the environmental drivers between the SC and VPD successional stages. However, soil was significantly deeper in the VPD than the SC stage. Increased soil depth with input of loose material on the lavas, whether organic or inorganic, influences soil moisture and soil nutrients (Walker and Del Moral, 2003) and improves seed germination, growth and reproduction success (Marchese and Grillo, 2000; Clarkson, 1998; Korablev and Neshataeva, 2016). Surviving vegetation on *kipukas* (in Hawaiian, *óbrennishólmar* in Icelandic) plays a key role for vascular plant establishment. Korablev and Neshataeva (2016) noted that vascular plant dispersal was mostly limited to 1.5km distance to kipukas. On Mauna Loa, Hawaii, raft logs displaced by the flowing lava during emplacement and positioned on the lava surface acted as residual microhabitats providing soil, seeds and a rooting medium (Clarkson, 1998). This allowed for *Metrosideros* forest to form over 400 yrs. Such raft logs have not been reported from Hekla eruptions to our knowledge. On the Hekla lava sequence the development of birch shrubland needs up to ~600 years as it is found on the 1389 lava after 626 yrs of development. On the Tolbachinskii Dol Plateau, larch and poplar forests were forming after 1500–2000 years of development (Korablev and Neshataeva, 2016), again suggesting a slightly slower development compared to the Hekla lavas.

The lowland sequence can be expected to gradually develop towards birch woodlands, the assimilation stage (Figure 4), as it represents the climax lowland ecosystem in Iceland (Aradottir and Eysteinsson, 2005). The rate of progression into this stage is variable due to the extended dominance of *R.lanuginosum* and the proximity to seed sources. All the lava fields that feature developing birch woodlands are downwind from prevailing NE dry wind direction, which are known to control birch seed dispersal (Aradóttir et al., 1997; Aradóttir, 1992). The remains of the native birch woodlands are mostly confined to the south-west and west of Hekla mountain as a result of past and present land-use and soil erosion. Birch is found along the margins of the 1206, 1389 and 1845 historical lava flows and on kipukas within the lava fields. There are indications that birch shrubland can develop over shorter time period; on the 1845 lava flow birch shrubs are growing on the lava despite its young age (170 yrs) but native birch woodland is found north of the lava flow at 300–800 m distance. There is an interesting lack of birch woodlands in the southern part of the study area, which features some of the most extensive moss covered lava flows 461–715 yrs of age. There, the hyaloclastite mountain range north of these lava fields may act as a barrier for birch seed rain.

Conditions are harsher in the highlands north-east and east of Hekla mountain, with lower temperatures (Table A1), extended snow-lie and higher frequency of tephra fall from Hekla (Jónsson, 1990; Larsen and Gíslason, 2013). The initial phases of colonization and coalescence still apply since they are present on the lava fields from 2000 and 1991 at 600−700 m elevation south-west and west of Hekla mountain. However, within this part of the region, *Stereocaulon* spp. rapidly increases its cover over the first decades, gaining 45–50% cover on the lavas formed in 1913 and 1878. Bjarnason (1991) described these lichen-dominated lavas saying that at higher altitudes *Stereocaulon* (mainly *S. vesuvianum*) locally replaced *R.lanuginosum* in the carpet. Jónsdóttir (2009) similarly described the higher lichen cover proportion within the highland part of the Skaftáreldar lava flow field after 230 years of development but linked it with snow lie, thin *Racomitrium* moss mat and sheep grazing. On the other hand, *Stereocaulon* spp. cover in high latitude regions has been linked to exposed sites, as it tolerates wind pressure and abrasion by snow and ice-needles (Sheard, 1968). Our results indicate that Stereocaulon thrives best at higher elevation where MAT is lower compared to the lowlands. Further study is needed to explain the processes behind the two alternatives in the highland part of the sere. The *Stereocaulon*-covered lava fields have recently been suggested as a new EUNIS habitat class (European Nature Information System, E4.241 Icelandic lava field lichen heaths) by the IINH (Magnússon et al., 2016).

The successional trajectory on the lavas in the highlands does not indicate an arrested sere. Prevalent aeolian additions, tephra fall and a thinner moss mat create conditions for vascular plant colonization during the secondary colonization stage where *Salix* spp. and grasses are most prominent. Although not observed on the lava fields of Hekla, future development into heathland vegetation may occur, where low-growing dwarf shrubs or taller shrubs will be dominant in cover.

Retrogression can set back the ecosystem development if thick tephra deposition occurs eliminating the vegetation cover previously established. Korablev and Neshataeva (2016) conclude that within areas of heavy tephra fall (<50cm) plant colonization is dependent on the stability of the surface and distance to seed sources. A high degree of stochasticity is noted for plant composition in studies of primary succession on loose substrate in general (Walker and Del Moral, 2003; Marteinsdóttir et al., 2013). *R.lanuginosum* showed low tolerance to additions of loose material as its cover and thickening rates significantly decreased with increasing SAR. On the other hand, *Anthelia* spp., vascular plants, and herbs showed a positive relationship with SAR. The species present in exposed tephra deposits at Hekla indicate that plants colonizing these sites are more related to highland vegetation, since the highland sites and the sites with thick tephra fall do not differentiate in the ordination. Soils within this stage are characterized by high SAR rates and therefore considerable soil depth but low C and content.

3. The progression from R.lanuginosum *dominated mossland to vascular plant dominated plant communities*

The moss *R.lanuginosum* is a key species in primary succession on the Hekla lavas. It can monopolize the vegetation cover for a long time (Bjarnason, 1991; Cutler et al., 2008b) as described by Connell and Slatyer's (1977) inhibition model, which is rarely observed in primary succession (Walker et al., 2010). This is demonstrated in the SC stage where moss thickness reaches a maximum on lavas between 300–700 yrs of age with 12% average vascular plant cover. The progression into the VPD stage occurs at different rates, which renders the application of vegetation communities or successional stages to infer the age of the lavas underneath to be of limited use. Growing conditions at Hekla are ideal for *R.lanuginosum*, with the oceanic climate, ample precipitation, small chances of prolonged droughts, low competition with vascular plants and extremely permeable substrate (Tallis, 1958; Armitage et al., 2012; Tallis, 1959). A study of *R.lanuginosum* over climatic gradients in Europe showed a significant relationship between temperature, moss thickness and shoot turnover rate. Moss thickness and cover proportion was highest in Iceland when compared to Norway, the Faroes and the UK, showing that the cooler climate favours the moss. On the other hand, thickening and shoot turnover rates were the lowest for Iceland (Armitage et al., 2012). Our results show a positive relationship between moss thickness and MAT, indicating that the moss thrives at its lower tolerance limit to temperature. No apparent relationship was found between *R.lanuginosum* cover and MAT.

Mosses and lichens are generally thought to facilitate the establishment of vascular plants by regulating surface temperatures, improving soil moisture conditions, enhancing microbial activities stabilizing loose substrates and trapping seeds and sediments (Tsuyuzaki and Hase, 2005; Elmarsdottir et al., 2003; Bechberger et al.; Persson, 1964; Sohlberg and Bliss, 1984; Bardgett and Walker, 2004). However, the interaction between mat-forming mosses and vascular plants in cold regions is still poorly understood (Gornall et al., 2011). Environmental drivers may be key to overcome the threshold posed by the thick moss-mat but deposition of loose material and trampling is known to have a negative impact on moss cover and thickness (Vilmundardóttir et al., 2009; Van der Wal et al., 2005; Arnalds, 2013; Gísladóttir, 2006). In a study from Skaftáreldahraun, fine grained sediment additions, resembling thin tephra fall, resulted in higher germination rates compared to undisturbed moss-mat (Jónsdóttir, 2009). However, cutting off the top-most part of the moss stems, resembling the mechanisms of trampling, did not yield similar results. The seeds that germinated were mostly of the grass species *Festuca richardsonii* and the herb *Siliene acaulis* but birch seeds had a very low germination rate (Jónsdóttir 2009). Our results are in line with previous studies, as SAR was negatively associated with *R.lanuginosum* cover and MTR. The insulating effects of *R.lanuginosum* may also affect seedling survival as the moss was observed to maintain a frozen soil layer at 30 cm depth throughout June 2018.

The results from this study indicate that time and soil depth are the environmental factors separating the SC and VPD successional stages. Since the same lava flow can feature both stages soil depth must be of higher importance than time for the succession. Along with the soil depth, other important factors possibly influence the ecological succession on the lavas. These include the surface topography of lavas where depressions collect seeds, sediments and organic matter improving soil conditions and acting as safe sites for seeds to germinate (Jónsdóttir, 2009; Jumpponen et al., 1999; Egli et al., 2006; Vilmundardóttir et al., 2015b), the distance to seed sources and direction of dry winds controlling seed rain onto the lava flows (Aradóttir et al., 1997), and trampling and seed dispersal by livestock (Gísladóttir, 2001; Rockwell, 2016). Further study is needed to clarify how these environmental factors influence plant succession on the lava flows.

Tephra fall is known to influence ecosystems and their recovery is dependent on volcanic, biotic, climatic, seasonal and landscape/surface properties with complex feedback mechanisms (Arnalds, 2013; Eddudóttir et al., 2017). Vegetation height is the single most important factor for vegetation survival and the presence of woodlands has major implications for stabilization of thick tephra deposits and enhancing regrowth (Grishin et al., 1996). Tephra fall events from Hekla have caused a regression in the plant succession, as seen in the H/R SS, or driven the succession further into the VPD SS. Tolerance limits of plant communities and the mechanisms of ecosystem recovery on the Hekla lavas are still poorly explained. In addition to the original impact of tephra fall, erosion is a secondary impact that can be more severe than the effects of the initial deposition (Manville et al., 2009; Arnalds et al., 2013b;

Eddudóttir et al., 2016). Even very low winds can erode the low density tephra and persistent events of wind erosion are of concern for human health in Iceland (Bird and Gísladóttir, 2012; Gudmundsson, 2011; Hlodversdottir et al., 2016; Dagsson-Waldhauserova et al., 2014). Erosion shapes ecosystems in Iceland and possibly affects oceanic and atmospheric conditions in the sub-Arctic and Arctic areas (Arnalds et al., 2016). Understanding how plant communities tolerate and stabilize tephra fall is therefore very important in regions of frequent volcanism. The unique settings at Hekla with the well constrained age of the lava flows and high frequency in lava emplacement and tephra fall features the perfect placement for studies on the ecosystem response to tephra fall at higher latitudes.

V Conclusions

We have investigated plant succession and soil development on lava flows of the Hekla volcano that span the last 860 yrs. The comparison with young prehistoric lavas nearby indicates that climax vegetation is not reached over this period of time, although birch woodlands, the climax ecosystem of Iceland, are developing within parts of the oldest lava fields (<600 yrs). The soils were tephra rich, yet carbon concentrations increased along the chronosequence. Soils developing on the lava flows have a continued potential of accumulating soil carbon via natural plant succession, continued events of tephra fall and soil thickening. The C stocks on the Hekla lavas were comparable to estimated stocks in organic soils in Hawaii and Japan, indicating high potential for C accumulation and sequestration, given the soil cover is not eroded. The plant succession on the Hekla lavas features similarities to other volcanic regions, with the biggest resemblance to lava flows in the Kamchatka peninsula where similar successional stages have been described. We conclude that time is the primary factor influencing the development on the lava field, with climate and soil accumulation rate being secondary factors. Higher input rates of loose material (mainly tephra fall), were seen to act negatively on *R.lanuginosum* cover, moss thickening rates and impact plant composition. More research is needed to assess modern plant response to tephra fall and estimate tolerance limits for plant communities. The arrested development by *R.lanuginosum* makes applying vegetation composition for assessing age ineffective. Stratigraphic relationships, lava surface characteristics, such as smoothened topography, and tephra layers in soil are more informative when inferring the age of lava fields. Soil depth is the most important property for the plant succession to progress from secondary colonization stage dominated by *R.lanuginosum* into vascular plant dominance. The high frequency of lava flow formation and tephra deposition, well defined age constraints and delineation of lava flows provide ideal settings to study the impact of volcanism on the dynamics of ecosystem development in sub-Arctic environments.

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Appendix

Table A1. Overview of sampling sites: year of eruption (starting year), age of lava field (year measured – eruption year), elevation measured in the field, mean annual temperature (MAT) 1960−1990 (Bjornsson et al., 2007) and mean annual precipitation (MAP) 1971−2000 (Crochet et al., 2007). Four transects were located on lava fields where age was estimated based on relative arrangement of lava flows and tephra stratigraphy in soil.

Year of eruption	**Transect no.**	**Lava age (years)**	**Elevation (m)**	**MAT (°C)**	**MAP (mm)**
2000	25	15	628	0.1	2720
2000	32	16	694	-0.4	2900
1991	23	24	384	1.7	2400
1991	30	25	731	-0.5	2900
1980	11	35	489	0.9	2530
1980	17	36	440	1.3	2360
1980	37	36	784	-1.1	2730
1970	20	45	362	1.5	1680
1947	10	68	270	2.7	2290
1947	35	69	786	-1.2	2710
1913	18	102	506	0.2	1610
1913	36	103	746	-1.1	2630
1878	19	137	485	0.8	1600
1845	16	170	142	3.3	1780
1766	33	250	560	0.5	2710
1766	34	250	786	-1.2	2720
1725	12	290	330	2.3	2370
1725	46	291	434	1.3	2470
<1725	13	290	305	2.5	2320
1693	26	322	418	1.1	2420
1554	2	461	222	2.9	1980
1554	47	462	431	1.3	2440
1389	6	626	155	3.2	1980
1389	7	626	169	3.2	1910
1300	3	715	234	2.8	2030
1300	9	715	232	2.8	2300
1300	29	715	139	3.3	1970
1206	24	809	252	2.5	2060
1158	31	858	748	-0.5	2930
<874	14	1141	209	2.7	2080
<874	15	1141	220	2.7	2080
<874	1	1141	169	3.0	1980
Total no. of transects	32				