

Plant Succession Across Landforms of Deglaciation 1740–2025 AD, Gígjökull Foreland, Iceland

You-Ning Kang¹ , Andrew J. Dugmore^{1†} ,
Robert G. Bingham¹ , Jakub D. Wiczorkowski¹ 

¹School of Geosciences, University of Edinburgh

Open Access

Article Type
Extended Report

Received
28 Jun 2026

Revised
17 Sep 2026

Accepted
23 Sep 2026

Published
19 Oct 2026

DOI
[10.2218/esjs.12320](https://doi.org/10.2218/esjs.12320)

ISSN
3049-7930

Abstract

Rapid climate change presents glacial forelands as ideal locations for studying plant succession and ecosystem development. This study investigates plant succession across recently de-glaciated landforms of kettleholes, moraines and sandur plains in the Gígjökull foreland, Iceland. In 2025, the changes in species richness and functional groups were examined over a chronosequence of surfaces formed from 1740 to 2010 AD. Results showed that species richness and functional group diversity increases with successional stage, but there were apparent differences between landforms. Most notably, kettleholes have the highest species richness whereas sandur plains have the lowest. Meanwhile, although kettleholes of younger successional stages show the lowest functional group diversity, this is the highest compared to moraines and sandur plains at older successional stages. Overall, these findings highlight the importance of geomorphological diversity in supporting resilient ecosystems.

Introduction

Global warming is accelerating glacial retreat, forming new terrains for species to colonise and creating new habitats (Cauvy-Fraunié & Dangles, 2019; Losapio *et al.*, 2021). While pioneer species benefit initially from these developments, late-stage species and high-level trophic consumers, do not (Losapio *et al.*, 2025). Additionally, some pioneer species, such as *Artemisia genipi* and *Saxifraga bryoides* will ultimately decline after a period of time (100 years after glacial retreat; Losapio *et al.*, 2021). Changing ecosystems have significant societal implications as they affect the types of ecosystem services available. Moreover, snow and ice cover are shifting to bare ground and vegetation. This exacerbates global warming and increased glacier melt due to a reduced albedo (Gibbard *et al.*, 2005). Understanding patterns in plant succession in pro-glacial areas is therefore not only a way to understand ecosystem development, but also the potential future changes in the surrounding geomorphology, natural hazards, water resources and overall resilience of the landscape (Losapio *et al.*, 2021). This paper investigates the impact of glacial processes on plant succession in the Gígjökull foreland in southern Iceland.

Iceland is experiencing rapid and intense warming (Intergovernmental Panel on Climate Change, 2013). Nearly all outlet glaciers from the principal icecaps have retreated by at least a kilometre over the last century, forming fresh surfaces and landforms (Synan *et al.*, 2021). Gígjökull's glacial foreland is an ideal site to study ecosystem change because of the well-dated exposed surfaces formed by deglaciation and outburst floods since the early 18th century high stands of the Little Ice Age (Kirkbride & Dugmore, 2008; Ficetola *et al.*, 2021). They represent different chronozones, which are units in chronostratigraphy where rocks around the world were formed during a specific time period (Ramezani & Hemming, 2026). Since successional stages vary by chronozone, the land surface across the Gígjökull foreland can be studied to understand plant community development (Glausen & Tanner, 2019). Understanding this will help contextualise the influence climate or geomorphological events to pro-glacial ecosystem development, offering insights for future landscape change and resource management (Bazzaz, 1979).

[†]Corresponding academic contact: andrew.dugmore@ed.ac.uk

Theories in Plant Succession

Plant succession was first described by Clements (1916) as involving six stages: nudation, migration, ecesis, competition, modification, and stabilisation (Walker & del Moral, 2003). ‘Nudation’ refers to when a disturbance event initiates succession. ‘Migration’ of species occurs when they have the biological traits, such as their germination and resource optimisation methods, to arrive in the environment. ‘Ecesis’ occurs when germination is successful, and ‘competition’ refers to the driving out of less-adapted species. In ‘modification’, surviving species, which also co-exist with other species, eventually modify the environment by altering pollination networks and the hydrology and geochemistry (Walker & del Moral, 2003). Over time, the plant community becomes ‘stabilised’ – species abundances in the community stop fluctuating.

However, the succession of plant communities does not always progress linearly or reach a dynamic equilibrium. Communities have been shown to be dynamic and their development unpredictable due to the changing interactions among coexisting species (Gleason, 1927). For example, the facilitation model suggests that pioneer species such as lichens and mosses modify barren substrate by accumulating organic matter and stabilising soil (Broady, 1993). This enables the later-successional and structurally more elaborate organisms like flowering plants and woody taxa to establish (Siqueira *et al.*, 1998), ultimately creating an increasingly heterogeneous community (Yarranton & Morrison, 1974). Additionally, some ecologists emphasise the influence of abiotic conditions, such as topography, soil depth and moisture gradients in the landscape, on enhancing or disrupting successional pathways (Matthews, 1992). Grime’s Competitors, Stress-tolerators and Ruderals (CSR) theory (2001) focuses on the physiological and morphological characteristics that increase a species’ competitiveness to dominate a landscape. This includes having an extensive root system and a rapid growth rate (Munoz *et al.*, 2016). The wide range of succession theories shows that plant succession pathways are diverse and can be described in many ways (Poorter *et al.*, 2023).

Quantifying Plant Succession

Plant succession can be quantified through measurement of species richness and functional group abundance across a chronosequence. In ecology, this refers to a group of sites that share the same parent material (Walker *et al.*, 2010). The chronosequence in this study consists of sites formed from glacial/fluvioglacial sediments over the last three centuries at times that have been determined using historical sources, lichenometry, and tephrochronology (Kirkbride & Dugmore, 2008). Chronosequences are useful because it allows ecosystem development to be tracked without needing long-term observation. Species richness is the count of species identified at a site and is the most fundamental, yet simplest, way to measure an ecosystem’s diversity (Gotelli & Colwell, 2001; Chao & Chiu, 2016). The more species there are, the more productive and resilient it is to climate change and disturbances (Waide *et al.*, 1999). Meanwhile, functional group cover takes an estimated percentage cover of each species identified, and categorises them based on their ecological functions. This is important because the relative abundance of a functional group reflects the extent to which a species affects an ecosystem, and is used to model future species responses to climate change (McLaren & Turkington, 2010).

Previous Successional Studies on Deglaciating Terrain

Glacial forelands have been popular locations for successional studies because de-glaciation can create a spatially ordered chronosequence; processes of abrasion, plucking, sub-glacial melting and sediment deposition by glaciers create heterogeneous terrains which provide patches of variable suitability for vegetation to inhabit and grow (Walker & del Moral, 2003). Moraines, which are accumulated glacial deposits (Clark *et al.*, 2004) for instance, have uneven terrains that may store seeds and provide protection against disturbances (Mayer & Erschbamer, 2011). Bedrock outcrops on the other hand, are formed by glacial erosion and they discourage plant growth, including pioneering species of moss and lichen (Garibotti *et al.*, 2011). Meanwhile, Ka’mierczak *et al.* (1995) demonstrated that kettleholes, which are depressional surfaces formed by the melting of dead ice (Pätzig *et al.*, 2012) support communities dominated by short-lived species. Here, competitive displacement drives high turnover rates; as outcompeted species decompose, the nutrients released facilitate the establishment of subsequent colonisers. Moreover, sandur plains consist of glacial outburst flood deposits of varying sizes (from coarse gravels to sand and silt), and a nutrient poor soil that discourage seed dispersal (Maizels, 1993; Marteinsdóttir *et al.*, 2018).

Despite the significant role of landforms on ecosystem development, there is a lack of studies on the interaction between physical and biotic factors, and their influence on plant growth, especially following glacier retreat and extinction (Tukiainen *et al.*, 2019; Losapio *et al.*, 2021). The earliest successional studies in glacial forelands were conducted in Scandinavia and North America, notably Cooper (1923) study at Glacier Bay, Alaska, which measured species richness on landforms of known ages (Chapin *et al.*, 1994). More recently, Glausen & Tanner (2019) examined successional changes in plant community structure at the Skaftafellsjökull glacier in southeastern Iceland.

They found that species richness was highest on the oldest landforms, before declining in younger landforms, where vegetation cover was dominated by bryophytes. The strong regional differences in plant succession emphasise the need for successional studies in multiple environments globally (Rosa, 2016). This approach helps identify alternative successional pathways, enhancing our understanding of interactions among species and different landscape qualities rather than focusing solely on the relationship between plant communities and terrain age (Matthews & Whittaker, 1987). Since there remains a limited number of studies on primary succession in sub-arctic glacial forelands (Tanner *et al.*, 2024), investigating succession in the Gígjökull foreland in Iceland is particularly valuable as it tackles both a geographical knowledge gap and an understudied site with a distinctive history of both glacial retreat and catastrophic flooding as a result of the 2010 eruption of Eyjafjallajökull.

Aim and Research Questions

As a result, our overarching aim is therefore to investigate plant succession in the Gígjökull foreland 1740–2025. This is broken down into two research questions: i) how do species richness and functional groups vary across successional stages? And ii) how do these relationships vary by landform type? To address these questions this paper identifies the species present at eight sites in the Gígjökull foreland formed 1740–2010, and estimate their percentage cover. The percentage cover of functional groups present is calculated based on the species identified to assess how species richness and functional groups vary across chronozones and successional stages, moraines, sandur and kettleholes.

Study Area: Geologic and Glacial History of the Gígjökull Foreland

Gígjökull is a steep, northern outlet glacier of the Eyjafjallajökull ice cap in the south of Iceland (Figure 1; Kirkbride & Dugmore, 2008). The Gígjökull foreland consists of a complex terrain of varied landforms. Multiple landscape-forming events have taken place since the 18th century AD ‘Little Ice Age’ high stands (Gudmundsson *et al.*, 2012; Dunning *et al.*, 2013); tephrochronological evidence suggests that there have been five episodes of glacial re-advance between 1700 and 1930 AD, combined with volcanogenic flooding in 1821–1823 (Kirkbride & Dugmore, 2008), forming various moraines and outwash deposits and kettleholes. The sediment-rich outburst floods from the most recent Eyjafjallajökull eruption in 2010 filled in the proglacial lake, forming a sandur plain with actively-forming kettleholes. The Gígjökull foreland’s heterogeneous terrains and chronozones are thus well suited to studying plant succession.

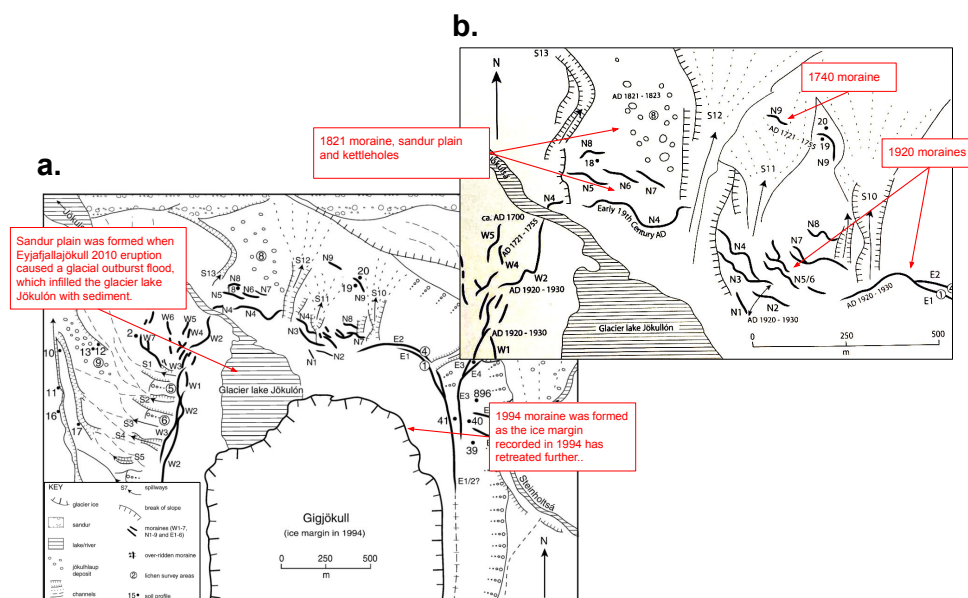


Figure 1: Dated geomorphic landforms in the Gígjökull foreland, adapted and annotated from Figure 3 from Kirkbride & Dugmore (2008), showing the 1740, 1821, 1920, 1994, and 2010 sites samples in 2025. (a) Overview of the glacial foreland; (b) zoomed-in view of the same area.

Methods

Site Description

Terrains formed in the 1740s, 1821, 1920s, 1994, and 2010 in the Gígjokull foreland were selected for this successional study because their locations and dates of formation are documented and dated by Kirkbride & Dugmore (2008) using tephrochronology. The sites on land surfaces from the 1740s, 1821, 1920s, and 1994 include moraines, and those from the 1821 and 2010 also contain sandur formations and kettleholes. In total, eight sites were sampled: four moraines (1740s, 1821, 1920s, and 1994), two sandur (1821 and 2010), and two kettleholes (1821 and 2010; Figures 2 and 3).

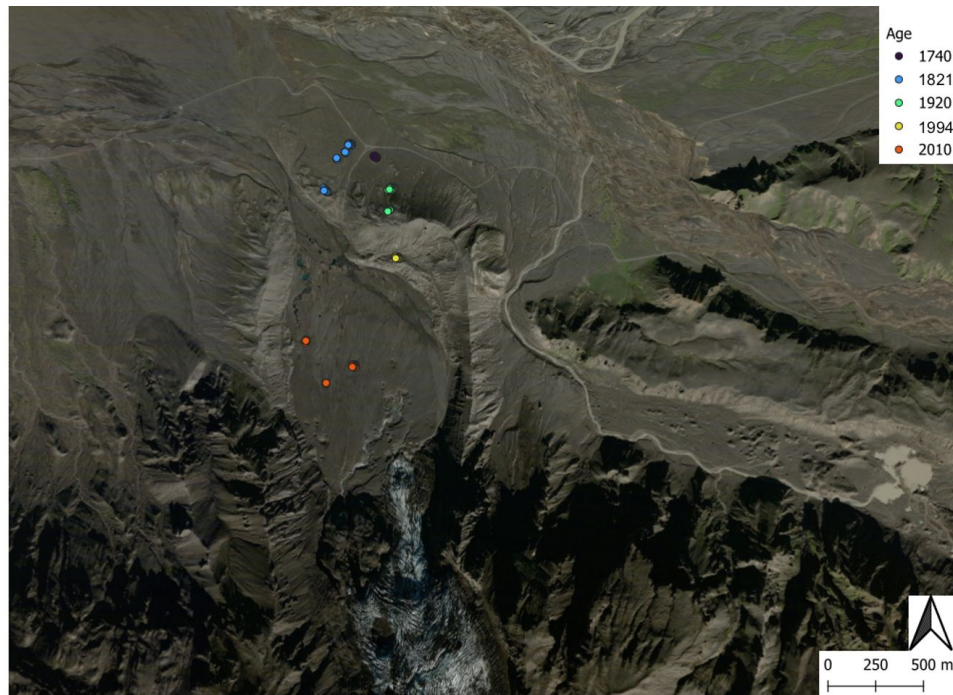


Figure 2: Site locations, coloured according to their year of formation and successional stage (1740, 1821, 1920, 1994, 2010), chosen with reference to Figure 1. Extra quadrats from sandur plains and kettleholes are included for the 1821 and 2010 sites.

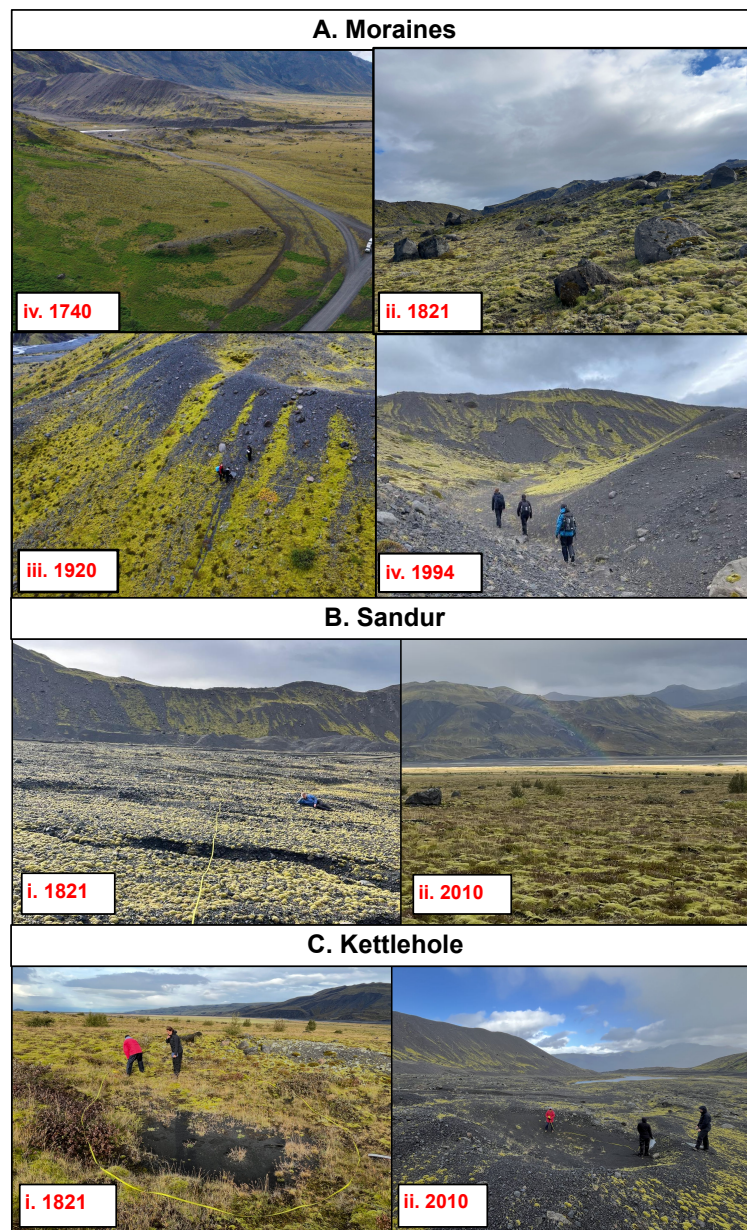


Figure 3: Photographs of the study sites: **A** Moraines from 1740, 1821, 1920, and 1994; **B** Sandur plains from 1821 and 2010; **C** Kettleholes formed after 1821 and 2010.

Sampling Method

To assess species richness and functional group cover at each site, three 25-meter transects were established, each positioned progressively further north. Along each transect, stratified sampling was conducted by recording plant species and estimating percentage cover within $50\text{ cm} \times 50\text{ cm}$ quadrats placed at 5 m intervals (Figure 4). This approach yielded a total of 15 quadrats per site.

Species Richness and Functional Group Cover

To assess species richness of each successional stage, the number of species present at each sample were counted and identified according to the catalogue 'Icelandic flora and fauna' by Kristinsson (2010). The count of species across all 15 quadrats at each site was averaged to represent the species richness for the site's chronozone and landform.

Functional group data is derived from the species count data. The plant functional groups of trees, shrubs, rushes, grasses, other flowering plants, and mosses; as well as lichens and fungi were included. Records of individual species cover in each quadrat were summed to determine the total percentage that each functional group cov-



Figure 4: The transect method for conducting the quadrat sampling illustrated on an 1821 moraine. The 50 cm $\times$ 50 cm quadrat was placed at 5 m intervals. There were three transects at each site.

ered in a sample. In the raw dataset, a note was made as to which landform the site and sample belonged, so that species richness and functional group cover variation between landforms could be established. ANOVA and relevant post-hoc tests were conducted to compare the differences in species richness across the different successional stages and landforms, which represent multiple independent groups.

Data Processing: Non-metric Multidimensional Scaling (NMDS)

Ordination is a statistical approach for modelling the variation of a community in relation to the environment, using species richness and functional group cover (Minchin, 1987). Non-metric Multi-dimensional Scaling (NMDS) is a popular ordination technique which visualise differences and gradients in community composition (Philippi *et al.*, 1998; Aggemyr *et al.*, 2018). This study used NMDS to quantify and visualise how species and functional groups between the successional stages and landform type vary. It is complemented by a PERMANOVA test to quantify the statistical significance of the patterns observed from NMDS (Dixon, 2003). Pairwise PERMANOVA is used as a secondary step to determine which specific pairs of samples are different from each other. Post-hoc tests are used to confirm whether overall trends are statistically significant (Dexter *et al.*, 2018). The use of the NMDS framework is justified by both the multivariate nature of the Gígjökull dataset, and its ability to enable a deeper analysis of functional group cover data, by examining how the trajectory of successional changes varies among sites, and which particular functional groups drive these changes.

Results

Species Richness Across Successional Years

A total of 48 species were identified across all sites. Landforms from 1740 AD supported the most species ($\mu = 12.9$), whereas those from 2010 supported the least ($\mu = 3.17$). There is a general trend of species richness increasing with time (Figure 5a). Along with the observed large variations of data (elongated violin plots and box and whisker plots), Welch's ANOVA test results shows that this trend is statistically significant ($p < 0.001$). Additionally, the mean species counted is strongly distinct between each chronozone ($F = 65.26$). In other words, the variation in data between the successional stages is greater than the variation within each stage. A pairwise comparison using Games-Howell's post-hoc test further identified data from the years 1740 and 2010 as the most distinctly different, as there was a gain of between 9–10 species between the early 18th and early 21st centuries. The difference between 1994 and 2010 was the next most pronounced, with a gain of between 3–4 species ($p < 0.0001$) in quarter of a century. Meanwhile, the differences observed between 1821 and 1920, and 1920 and 1994 are insignificant ($p > 0.05$).

Functional Group Cover Over the Years

The number of functional groups present increased in older successional stages. While only four groups were identified in 2025 on the 2010 surfaces, eight groups (fungi, lichen, moss, russ, grass, fungi, shrub, trees and other flowering plants) were present on those formed in 1740 (Figure 5b). The percentage cover of each functional group, when present, also increases. For example, in 2025, the percentage cover of other flowering plants was 0.39% for the 2010 surfaces compared to 5.24% for those from 1740. The total vegetation cover increased from 21.3% on the 2010 surfaces to 89.41% on the surfaces from 1740. In all successional stages, moss percentage is the highest, relative to other functional groups.

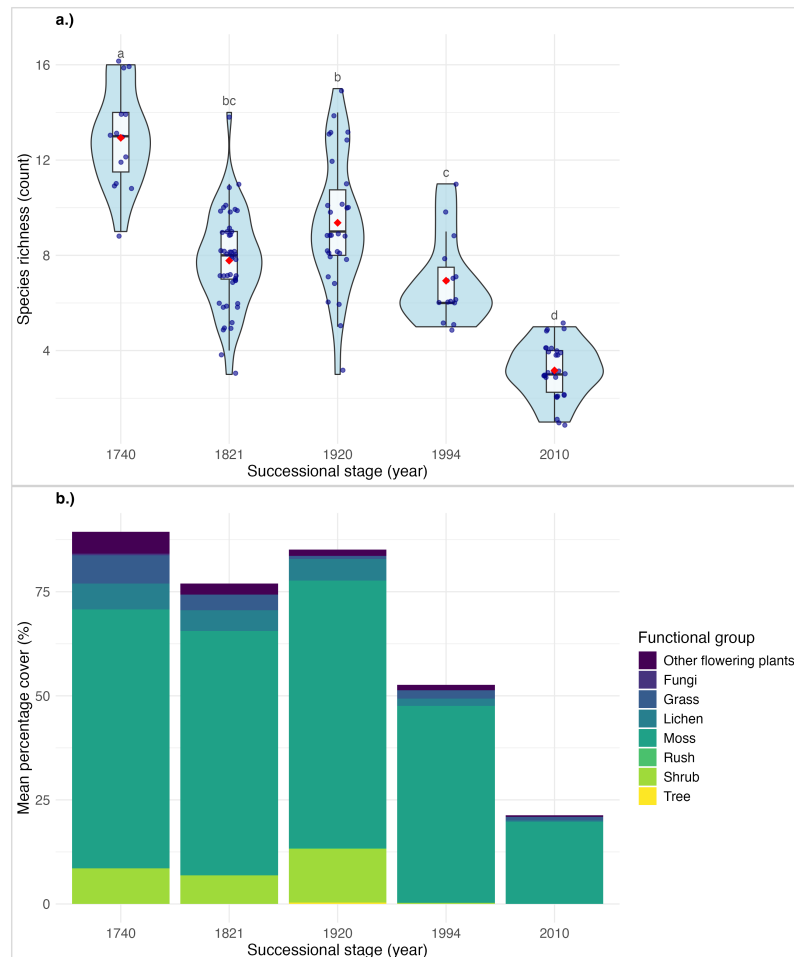


Figure 5: Species richness **A** and functional group **B** cover across successional years. In A, blue dots represent individual data points, red diamonds indicate means, and the violin plot (light blue) underneath shows the shape of the data distribution. Compact letter displays on the top of each violin indicate which years differ statistically; groups that share a letter are not statistically different.

The 1920 chronozone appears to be an anomaly in this trajectory. Not only does total vegetation cover rise from 76.95% in 1821 to 85.15%, shrub and tree cover also peak this year at 12.87% and 0.34% respectively. In comparison, shrub and tree cover in 1994 was 0.25% and 0%.

Functional Group Composition Across the Years

Plotting the NMDS results illustrated that functional group composition changes in a progression from early to late succession. Older successional stages (dark blue) cluster towards the bottom in the centre, whereas younger stages spread towards the top right (green and yellow; Figure 6). The composition of the 1920 community is distinct from other years because, though younger than that from 1821, it clusters below 1821 in the centre-bottom right of the ordination. This is driven by its higher shrub, tree and rush abundance. Nonetheless, a stress value of 0.182 indicates that the ordination of the data points is a good fit (stress < 0.02).

The plant community diverges after 1920 because the 1740, 1821 and 1920 ellipses intersect, whereas 1994 overlaps with 1821 and 2010, and 2010 overlaps only with 1994. This is reflected in the functional groups that drive

the change; fungi and lichens are more abundant in older stages (1740–1821), whereas mosses and grasses are represented more in younger stages (1994–2010). This is supported by the Pairwise PERMANOVA results, which showed that the functional group composition between earlier stages (1740 and 1821) did not differ significantly ($R^2 = 0.018$, $p = 0.358$). In contrast, the comparison between 1920 and 1994 showed a significant difference in community composition ($R^2 = 0.239$, $p = 0.010$). This indicates that there has been a significant change in functional group assemblages between the chronozones formed in 1920 and 1994.

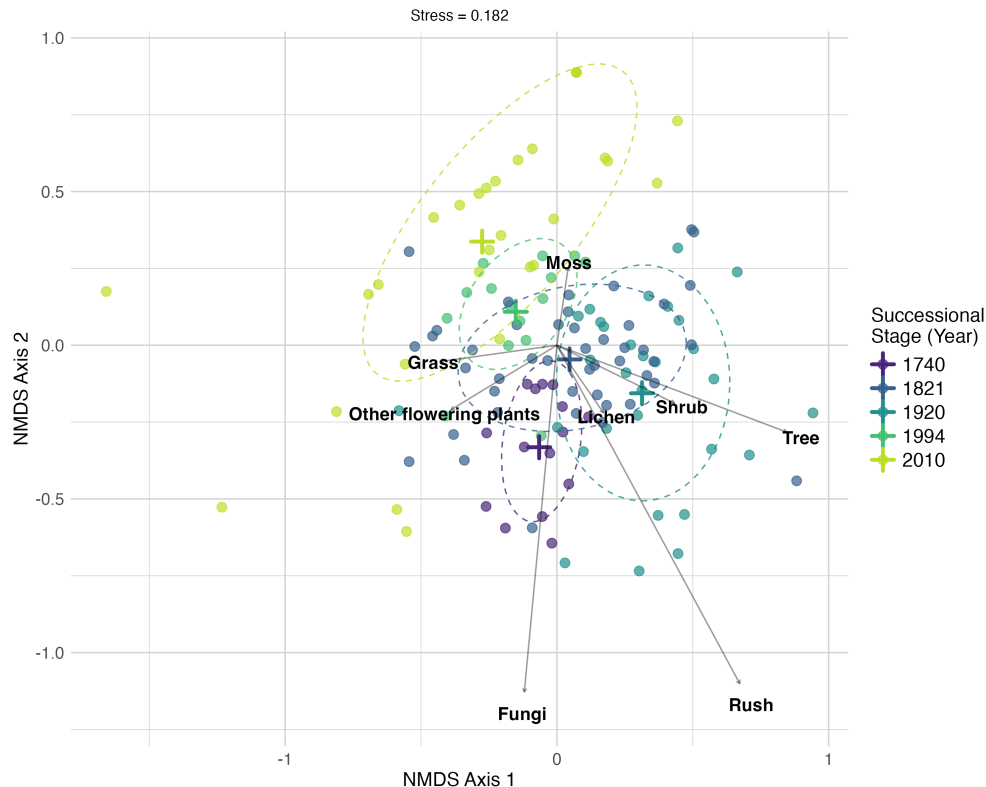


Figure 6: NMDS of functional group composition across successional stages. Each point represents a sample and distances reflect community dissimilarity (closer points = more similar). In the vector biplot, arrow length and direction indicate the functional groups driving compositional differences (longer arrows = stronger influence; arrows close together = species co-occurrence).

Species Richness by Landform

Species richness between the landforms in 1821 can be compared, as all three landforms exist for this year. ANOVA tests show that moraines support a significantly higher number of species than sandur plain ($\mu = 8.6$), but are not statistically different to kettleholes ($\mu = 8.1$) as $p = 0.130$ (Figure 7a). It is additionally noted that in 2010, species richness was lower for kettleholes than for sandur plain (2.67 compared to 3.67), but by 1821, their species richness exceeded that of sandur plains, with mean of 8.1 compared to 6.67, respectively (Figure 7b). For 2010, only kettleholes and sandur plains were compared as moraines were absent. The trajectory of species richness over time is also different between moraines, sandur plains and kettleholes ($p < 0.05$). While species richness peaks on the oldest surfaces across all landforms (1740 for moraines, 1821 for sandur and kettleholes), the rate of species richness change is greatest on kettleholes, followed by moraines and sandur.

Functional Group Composition by Landform

The functional group assemblages are distinct between moraines, sandur and kettleholes. Although moss is the dominant functional group in all landforms, kettleholes in 1821 have the most functionally diverse community, followed by moraines and sandur, despite being the least diverse in 2010 (Figure 7c, Figure 7d). Total vegetation cover also rose from 9.87% in 2010 to 84.3% in 1821, nearly matching sandur's increase from 33% to 85% (Figure 5).

Functional group composition changes are also the most gradual on moraines (Figure 7c), as the ellipses in the NMDS ordination plot overlap greatly, indicating similar plant communities across the years. Kettleholes' functional group assemblage also demonstrate minimal change as their 1821 and 2010 ellipses fully overlap. Sandur plains, by contrast, have distinct non-overlapping communities between 1821 and 2010.

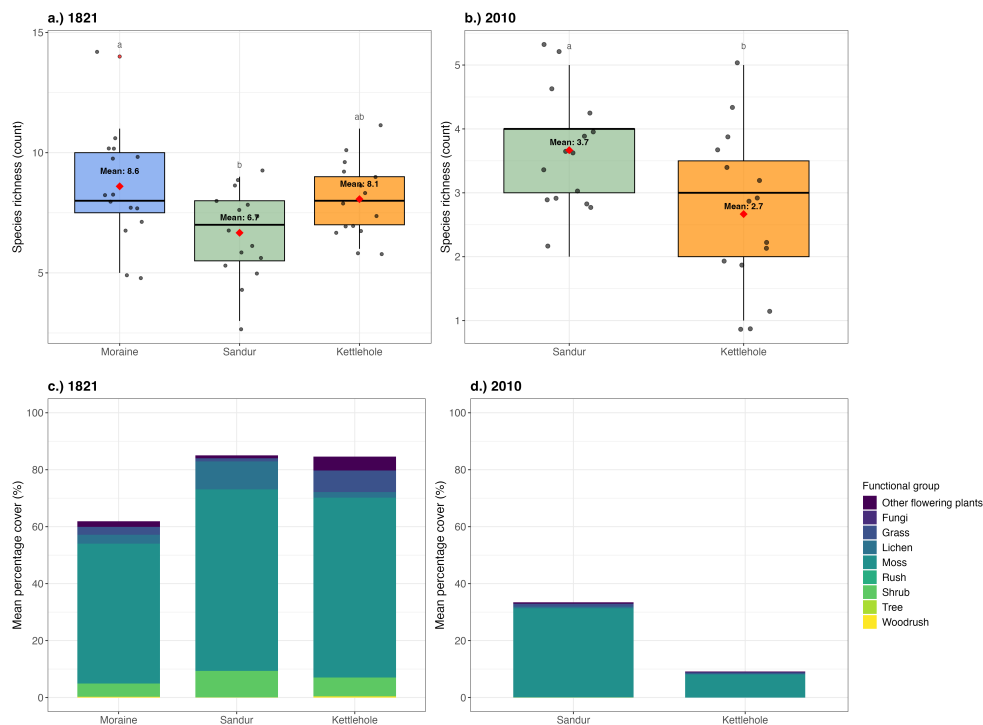


Figure 7: Species richness of moraines, sandur and kettleholes in 1821 **A** and in 2010 **B** and functional group percentage cover of moraines, sandur and kettleholes in 1821 **C** and 2010 **D**. Similar to Figure 5, compact letter displays were added to panels **A** and **B**.

Discussion

Results showed that species richness generally increases with successional stage (Figure 5), indicating an increasingly complex ecosystem as taxa accumulate over time. This aligns with older stages having greater functional group diversity, consisting of other flowering plants like the *Alchemilla alpina* and the *Galium verum*, which are non-graminoid herbaceous plants (forbs). (Figures 6 and 7). This suggests that the ecosystem is the most stable during mid to old successional stages (1821–1920) because resource-demanding species can establish and coexist. Younger successional stages (after 1920), on the other hand, are dominated by mosses and grasses (Figure 7). Given that moss species thrive in resource-poor environments, younger successional stages in Gígjökull likely support species that are highly resource-efficient. Mosses in particular are resilient to the disturbance events characteristic of glacial forelands and even benefit from the harsh environment by dispersing their spores via glacial wind (Tanner *et al.*, 2024). This allows them to colonise areas closer to the glacial edge.

The trajectory of increased species richness and functional group diversity across older successional stages further reflect the foundational role of moss in facilitating ecosystem development at Gígjökull. As mosses decompose, they contribute organic matter that forms the basic soils necessary for the establishment of more complex plant species (Turetsky *et al.*, 2010). Thus, the soil gradually matures over time, accumulating key nutrients, such as nitrogen and carbon, that support a greater diversity of species across functional groups with varying ecological requirements. This process likely explains the emergence of a distinct community composed of shrubs, trees, and fungi observed in the mid to late successional stage (1920; Figures 6 and 7), because the structural complexity of woody taxa requires greater quantity and heterogeneity of resources (Loveys *et al.*, 2010). In this way, plant succession in the Gígjökull foreland follows the classical successional theory, whereby pioneer species facilitate the emergence of further species. These findings align with findings by Tanner *et al.* (2024) in the Skaftafellsjökull glacial foreland, where functional group diversity declines towards more recent successional stages, with moss as the dominant functional group. This is relevant because it suggests that the plant community in Gígjökull may become increasingly complex over time if major disturbances do not occur, as pioneering, resource-efficient species lay the foundation for the more complex ecosystem.

Species richness and functional group patterns also varied across landforms. The 1821 moraines and kettleholes had the highest species richness (Figure 7a). Kettleholes exhibited the highest functional group diversity, which increased markedly from being significantly less diverse than sandur formed in 2010 to becoming the most functionally diverse of the three landforms (Figure 7b). This could be because the ecosystem within the kettlehole

is more sheltered from wind stress and exposure, and once formed, stabilises more rapidly, potentially due to its geomorphology; the depressional form allows for organic matter accumulation and water retention, fostering higher-quality soils that support more established communities (Ka'mierczak *et al.*, 1995). Therefore, even if initial species richness and functional group diversity was low, this becomes higher overtime. As aspect is significant for vegetation growth in higher latitude areas (Guo, 2001; Dearborn & Danby, 2017; see Figure 8 in Appendix 1), controlling sampling to north-facing slopes in kettleholes, as in moraines and sandur in future studies, may reveal higher mean species richness.

In contrast to the sheltered environments of established kettleholes, the gravel surfaces of unstable outwash deposits of sandur are constantly shaped and reshaped by disturbance events and exposed to harsher microclimatic conditions (9 in Appendix 1). This restricts colonisation because it limits the availability of suitable seeding sites and hinder the long-term persistence of species by impeding root growth (Tanner *et al.*, 2024). Consequently, functional group diversity reduces over time. Further analysis using NMDS supports this interpretation, because the turnover of plant communities between the 2010 and 1821 kettlehole is low (shown by their overlapping clusters) but high for sandur (clusters diverge strongly; see Appendix 1). Kettleholes thus exhibit 'functional redundancy': although species changed, the main functional groups stayed in similar proportions (Michalak *et al.*, 2020). In this way, kettleholes in Gígjökull are ecological hot spots, helping plant communities to survive and gain complexity.

The wide spread of species richness data in the 1920 moraine (Figure 5) reinforces the significance of landform in influencing plant successional patterns. While a moraine facilitates greater species richness due to poorly sorted glacial deposits and protruding boulders supporting root penetration, local abiotic factors are implied to contribute to the 1920 site's sudden abundance of shrubs and trees (Figure 7). Figure 10 in Appendix 1 notes that the 1920 site exhibits some gullies colonised by Nootka lupine (*Lupinus nootkatensis*) – an invasive species used in Iceland to enhance soil. Higher nitrogen and carbon content, along with altered soil structure at these sites due to the effect of the lupine (Benediktsson, 2015), may contribute to the growth of shrubs and trees. This suggests that variability within a landform can support the development of specific communities. However, further study is needed to confirm this effect, particularly because the 1920 moraine is substantially taller and wider than the other sites, meaning that the quadrats sampled there may not have represented it as accurately as at other locations. This may also benefit from somewhat greater shelter from winds flowing down the glacier. Additional transects and a greater sampling coverage may facilitate a more nuanced interpretation.

The combined findings of plant succession patterns over time and across different landforms suggest that more complex topographies are associated with greater species richness and functional group diversity. Microsites and resource niches cater for the needs of diverse species, which ultimately enhances ecosystem stability. This is important because if landform heterogeneity helps support multiple successional pathways, it may play an important role in supporting biodiversity under environmental change.

Opportunities for Future Research

All successional studies face a statistical challenge when estimating species richness. Inevitably, the number of species identified increases with the number of sites sampled (Bunge & Fitzpatrick, 1993). This means that the true species richness is not represented in this study, and the significance of this influence depends on the size of the species catalogue for each successional year and landform. Nonetheless, this limitation can only be addressed through increased sampling in further studies.

There are opportunities to improve the representation of Gígjökull foreland's ecosystem by sampling a wider variety of landforms, particularly those on still older chronozones and at sites closer to the glacier. The site selection in this paper captures only a part of the foreland's full heterogeneity; post-data collection, developed plant communities were observed near the glacier edge (Figure 11 in Appendix 1). Additionally, bird roosts – which are small, elevated patches of well-vegetated ground formed from bird dropping (Verbeek & Boasson, 1984) – are common in Southeast Iceland (Sigurðardóttir *et al.*, 2022). These features represent a biotic driver of localised vegetation development (Sigurðardóttir *et al.*, 2022). Such wildlife-shaped geomorphic features may equally promote vegetation growth in surfaces closer to the Gígjökull glacier edge, representing a valuable focus for future research.

In this way, further exploration may reveal other successional pathways that contrast sharply with the low species richness and functional group diversity of the final 2010 site. Given the relevance of soil in plant succession (Mori *et al.*, 2017), soil pH and moisture could be measured to deepen our current understanding of how landform affects species richness and functional group diversity.

Conclusion

Glacial processes shape plant succession at Gígjökull, by forming chronozones of different ages influencing species richness and functional group cover across successional stages and different landforms. By identifying species on terrains dated by Kirkbride & Dugmore (2008), representing a chronosequence from 1740, 1821, 1920, 1994 and 2010, we find that species richness and functional group diversity in 2025 increases with successional stage. The results from NMDS and PERMANOVA offer detailed analysis of how plant communities, based on their functional groups, developed over the years; by 2025, the years 1740–1920 and 1994–2010 exhibited distinct communities, highlighting two separate successional stages. While moss is the dominant functional group across all sites, the older successional stage is more abundant in the functional groups of fungi, lichen, grasses, and other additional flowering plants. Comparing the results by landform, the surfaces formed in 1821 showed that moraines and kettleholes are the most species rich (Figure 7). Kettleholes show notable functional diversity patterns; not only are those from 1821 the most diverse of the three, but the data from 2010 show they also begin with the lowest diversity. In contrast, sandur's initial high functional group cover became the lowest on the surfaces from 1821 (Figure 7).

These results show that plant succession at Gígjökull follows a classical successional pathway. The ecosystem gains stability over time as pioneering species such as moss creates conditions that support more complex species. This trajectory is, however, modulated by the heterogeneity of glacial landforms. Kettleholes serve as ecological hot spots that promote ecosystem development, whereas the dynamic nature of the gravel plains hinders it. Topographical variations within a single landform clearly contributes to ecosystem development.

This study highlights the fundamental role that glacial processes and time play in shaping ecosystem development, as glacial landforms both mediate and provide alternative successional pathways. Given that Iceland's ecosystems are unique yet simultaneously impacted by frequent disturbance events, which are exacerbated by rapid climate change, successional studies are crucial for enhancing our understanding of plant community development. Such research can inform land management practices to maintain geomorphological diversity, thereby fostering ecosystem resilience and the provision of ecosystem services to local communities.

Acknowledgements

First and foremost, thank you Dr. Andrew Dugmore for taking that extra time outside your office hours, over the last four months, to work on this paper with me. Your enthusiasm, dedication to teaching and overall sincere attitude to all things, are qualities I aspire to develop and hope to take with me wherever I go next.

To Dr. Robert Bingham - thank you for organising the Iceland field course for the BSc Geography students. Admittedly, I struggled to understand why we had to attend classes for a fourth-year course in third-year, but in hindsight it was clearly sensible, if not absolutely necessary. Getting thirty-six students and a whole team of staff from Edinburgh to Iceland is a mammoth of a task, and it was precisely your meticulous planning that has given me an experience that I will cherish for a lifetime.

Crucially, thank you Dr. Elizabeth Orr for your attentiveness and empathy. Beyond caring for my wellbeing in Iceland, our conversations throughout the year, on being a woman in geography, the struggles of being abroad as a foreigner far away from home, inspired me and motivated me to give my absolute best effort in everything. I leave my degree with no regrets because of you.

I must also thank the full teaching staff; Dave McGravie, Emily Lethbridge, Greta Wells, Carla Hyunh, Ryan Ing, Clara Nyqvist and Jakub Wieczorkowski for helping the course run smoothly. The everyday of supervising us lesser experienced undergraduates in the field, driving everyone around all day and just co-existing brought so much joy. I hope the course was just as enjoyable for you as it was for me. Special thanks to Jakub in particular, for not only providing your invaluable feedback and expertise in biogeography to our group in Iceland, but also to our entire cohort in our second-year field trip to the Cairngorms and third-year trip to Spain.

Finally, to my lovely group, which consisted of Martha Jones, Katie Chubb and Juliet Compagnon – thank you for standing in the rain and sun with me throughout data collection, whether that was on the steep slopes of the moraines or in the depths of (some) kettleholes. You made this trip all the more special and I am so lucky to have worked with you.

I consider it a true privilege to have studied at this university and to have travelled to Iceland to carry out this research. I hope this paper gives something of value back to our planet and to the communities of Iceland, however small it may be.

References

- Aggemyr, E., Auffret, A. G., Jädergård, L. & Cousins, S. A. O. 'Species Richness and Composition Differ in Response to Landscape and Biogeography' *Landscape Ecology* **33** 12 (2018) <https://doi.org/10.1007/s10980-018-0742-9>
- Bazzaz, F. A. 'The Physiological Ecology of Plant Succession' *Annual Review of Ecology and Systematics* **10** 1 (1979) <https://doi.org/10.1146/annurev.es.10.110179.002031>
- Benediktsson, K. 'Floral Hazards: Nootka Lupin in Iceland and the Complex Politics of Invasive Life' *Geografiska Annaler: Series B, Human Geography* **97** 2 (2015) <https://doi.org/10.1111/geob.12070>
- Broadly, P. A. 'Primary Succession on Land' *Antarctic Science* **5** 3 (1993) <https://doi.org/10.1017/s0954102093250428>
- Bunge, J. & Fitzpatrick, M. 'Estimating the Number of Species: A Review' *Journal of the American Statistical Association* **88** 421 (1993) <https://doi.org/10.1080/01621459.1993.10594330>
- Cauvy-Fraunié, S. & Dangles, O. 'A Global Synthesis of Biodiversity Responses to Glacier Retreat' *Nature Ecology & Evolution* **3** 12 (2019) <https://doi.org/10.1038/s41559-019-1042-8>
- Chao, A. & Chiu, C.-H. 'Species Richness: Estimation and Comparison' (Wiley 2016)
- Chapin, F. S., Walker, L. R., Fastie, C. L. & Sharman, L. C. 'Mechanisms of Primary Succession Following Deglaciation at Glacier Bay, Alaska' *Ecological Monographs* **64** 2 (1994) <https://doi.org/10.2307/2937039>
- Clark, C. D., Evans, D. J. A., Khatwa, A., et al. 'Map and GIS Database of Glacial Landforms and Features Related to the Last British Ice Sheet' *Boreas* **33** 4 (2004) <https://doi.org/10.1111/j.1502-3885.2004.tb01246.x>
- Clements, F. E. 'Plant Succession; An Analysis of the Development of Vegetation' (Carnegie Institution of Washington, 1916)
- Cooper, W. S. 'The Recent Ecological History of Glacier Bay, Alaska: The Present Vegetation Cycle' *Ecology* **4** 3 (1923) <https://doi.org/10.2307/1929047>
- Dearborn, K. D. & Danby, R. K. 'Aspect and Slope Influence Plant Community Composition More Than Elevation Across Forest-Tundra Ecotones in Subarctic Canada' *Journal of Vegetation Science* **28** 3 (2017) <https://doi.org/10.1111/jvs.12521>
- Dexter, E., Rollwagen-Bollens, G. & Bollens, S. M. 'The Trouble With Stress: A Flexible Method for the Evaluation of Nonmetric Multidimensional Scaling' *Limnology and Oceanography: Methods* **16** 7 (2018) <https://doi.org/10.1002/lom3.10257>
- Dixon, P. 'VEGAN, a Package of R Functions for Community Ecology' *Journal of Vegetation Science* **14** 6 (2003) <https://doi.org/10.1111/j.1654-1103.2003.tb02228.x>
- Dunning, S. A., Large, A. R. G., Russell, A. J., et al. 'The Role of Multiple Glacier Outburst Floods in Proglacial Landscape Evolution: The 2010 Eyjafjallajökull Eruption, Iceland' *Geology* **41** 10 (2013) <https://doi.org/10.1130/g34665.1>
- Ficetola, G. F., Marta, S., Guerrieri, A., et al. 'Dynamics of Ecological Communities Following Current Retreat of Glaciers' *Annual Review of Ecology, Evolution, and Systematics* **52** 1 (2021) <https://doi.org/10.1146/annurev-ecolsys-010521-040017>
- Garibotti, I. A., Pissolito, C. I. & Villalba, R. 'Spatiotemporal Pattern of Primary Succession in Relation to Meso-Topographic Gradients on Recently Deglaciated Terrains in the Patagonian Andes' *Arctic, Antarctic, and Alpine Research* **43** 4 (2011) <https://doi.org/10.1657/1938-4246-43.4.555>
- Gibbard, S., Caldeira, K., Bala, G., Phillips, T. J. & Wickett, M. 'Climate Effects of Global Land Cover Change' *Geophysical Research Letters* **32** 23 (2005) <https://doi.org/10.1029/2005gl024550>
- Glausen, T. G. & Tanner, L. H. 'Successional Trends and Processes on a Glacial Foreland in Southern Iceland Studied by Repeated Species Counts' *Ecological Processes* **8** 1 (2019) <https://doi.org/10.1186/s13717-019-0165-9>
- Gleason, H. A. 'Further Views on the Succession-Concept' *Ecology* **8** 3 (1927) <https://doi.org/10.2307/1929332>
- Gotelli, N. J. & Colwell, R. K. 'Quantifying Biodiversity: Procedures and Pitfalls in the Measurement and Comparison of Species Richness' *Ecology Letters* **4** 4 (2001) <https://doi.org/10.1046/j.1461-0248.2001.00230.x>
- Gudmundsson, M. T., Thordarson, T., Höskuldsson, Á., et al. 'Ash Generation and Distribution From the April-May 2010 Eruption of Eyjafjallajökull, Iceland' *Scientific Reports* **2** 1 (2012) <https://doi.org/10.1038/srep00572>
- Guo, Q. 'Early Post-Fire Succession in California Chaparral: Changes in Diversity, Density, Cover and Biomass' *Ecological Research* **16** 3 (2001) <https://doi.org/10.1046/j.1440-1703.2001.00410.x>
- Intergovernmental Panel on Climate Change *Climate Change 2013: The Physical Science Basis* 2013
- Ka'mierczak, E., van der Maarel, E. & Noest, V. 'Plant Communities in Kettle-Holes in Central Poland: Chance Occurrence of Species?' *Journal of Vegetation Science* **6** 6 (1995) <https://doi.org/10.2307/3236401>
- Kirkbride, M. P. & Dugmore, A. J. 'Two Millennia of Glacier Advances From Southern Iceland Dated by Tephrochronology' *Quaternary Research* **70** 3 (2008) <https://doi.org/10.1016/j.yqres.2008.07.001>
- Kristinsson, H. 'A Guide to the Flowering Plants and Ferns of Iceland' (2010)
- Losapio, G., Lee, J. R., Fraser, C. I., et al. 'Impacts of Deglaciation on Biodiversity and Ecosystem Function' *Nature Reviews Biodiversity* **1** 6 (2025) <https://doi.org/10.1038/s44358-025-00049-6>

- Losapio, G. *et al.* 'The Consequences of Glacier Retreat Are Uneven Between Plant Species' *Frontiers in Ecology and Evolution* **8** (2021) <https://doi.org/10.3389/fevo.2020.616562>
- Loveys, B. R., Egerton, J. J. G., Bruhn, D. & Ball, M. C. 'Disturbance Is Required for CO₂-dependent Promotion of Woody Plant Growth in Grasslands' *Functional Plant Biology* **37** 6 (2010) <https://doi.org/10.1071/fp09257>
- Maizels, J. 'Lithofacies Variations Within Sandur Deposits: The Role of Runoff Regime, Flow Dynamics and Sediment Supply Characteristics' *Sedimentary Geology* **85** 1-4 (1993) [https://doi.org/10.1016/0037-0738\(93\)90090-r](https://doi.org/10.1016/0037-0738(93)90090-r)
- Marteinsdóttir, B., Svavarsdóttir, K. & Thórhallsdóttir, T. E. 'Multiple Mechanisms of Early Plant Community Assembly With Stochasticity Driving the Process' *Ecology* **99** 1 (2018) <https://doi.org/10.1002/ecy.2079>
- Matthews, J. 'The Ecology of Recently Deglaciated Terrain: A Geoecological Approach to Glacier Forelands and Primary Succession' (Cambridge University Press 1992)
- Matthews, J. A. & Whittaker, R. J. 'Vegetation Succession on the Storbreen Glacier Foreland, Jotunheimen, Norway: A Review' *Arctic and Alpine Research* **19** 4 (1987) <https://doi.org/10.1080/00040851.1987.12002619>
- Mayer, R. & Erschbamer, B. 'Seedling Recruitment and Seed-/Microsite Limitation in Traditionally Grazed Plant Communities of the Alpine Zone' *Basic and Applied Ecology* **12** 1 (2011) <https://doi.org/10.1016/j.baae.2010.10.004>
- McLaren, J. R. & Turkington, R. 'Ecosystem Properties Determined by Plant Functional Group Identity' *Journal of Ecology* **98** 2 (2010) <https://doi.org/10.1111/j.1365-2745.2009.01630.x>
- Michalak, J. L., Stralberg, D., Cartwright, J. M. & Lawler, J. J. 'Combining Physical and Species-Based Approaches Improves Refugia Identification' *Frontiers in Ecology and the Environment* **18** 5 (2020) <https://doi.org/10.1002/fee.2207>
- Minchin, P. R. 'An Evaluation of the Relative Robustness of Techniques for Ecological Ordination' *Vegetatio* **69** 1-3 (1987) <https://doi.org/10.1007/bf00038690>
- Mori, A. S., Osono, T., Cornelissen, J. H. C., Craine, J. & Uchida, M. 'Biodiversity-Ecosystem Function Relationships Change Through Primary Succession' *Oikos* **126** 11 (2017) <https://doi.org/10.1111/oik.04345>
- Munoz, F., Violle, C. & Cheptou, P.-O. 'CSR Ecological Strategies and Plant Mating Systems: Outcrossing Increases With Competitiveness but Stress-Tolerance Is Related to Mixed Mating' *Oikos* **125** 9 (2016) <https://doi.org/10.1111/oik.02328>
- Pätzig, M., Kalettka, T., Glemnitz, M. & Berger, G. 'What Governs Macrophyte Species Richness in Kettle Hole Types? A Case Study From Northeast Germany' *Limnologica* **42** 4 (2012) <https://doi.org/10.1016/j.limno.2012.07.004>
- Philippi, T. E., Dixon, P. M. & Taylor, B. E. 'Detecting Trends in Species Composition' *Ecological Applications* **8** 2 (1998) [https://doi.org/10.1890/1051-0761\(1998\)008\[0300:dtisc\]2.0.co;2](https://doi.org/10.1890/1051-0761(1998)008[0300:dtisc]2.0.co;2)
- Poorter, L., Amissah, L., Bongers, F., *et al.* 'Successional Theories' *Biological Reviews* **98** 6 (2023) <https://doi.org/10.1111/brv.12995>
- Ramezani, J. & Hemming, S. R. 'Chronostratigraphy' in *Stratigraphy* (Elsevier 2026) <https://doi.org/10.1016/b978-0-443-26536-5.00018-4>
- Rosa, K. *One Hundred Years of Vegetation Succession in the Easton Glacial Foreland, Mount Baker, Washington* 2016
- Sigurðardóttir, S., Marteinsdóttir, B., Vigfúsdóttir, F. & Vilmundardóttir, O. K. 'Effects of Nutrient Transfer by Great Skuas (*Stercorarius Skua*) and Arctic Skuas (*Stercorarius Parasiticus*) on Vegetation and Soil at Breiðamerkurjökull, SE-Iceland' *Surtsey research* **15** (2022) <https://doi.org/10.33112/surtsey.15.5>
- Siqueira, J. O., Carneiro, M. A. C., Curi, N., da Silva Rosado, S. C. & Davide, A. C. 'Mycorrhizal Colonization and Mycotrophic Growth of Native Woody Species as Related to Successional Groups in Southeastern Brazil' *Forest Ecology and Management* **107** 1-3 (1998) [https://doi.org/10.1016/s0378-1127\(97\)00336-8](https://doi.org/10.1016/s0378-1127(97)00336-8)
- Synan, H. E., Melfi, M. A. & Tanner, L. H. 'Spatial and Temporal Dynamics of Growth of Woody Plant Species (Birch and Willows) on the Foreland of a Retreating Glacier in Southern Iceland' *Ecological Processes* **10** 1 (2021) <https://doi.org/10.1186/s13717-021-00282-9>
- Tanner, L., Kikukawa, G. & Weits, K. 'The Temporal and Spatial Dynamics of Succession in a Glacial Foreland in Southern Iceland: The Effects of Landscape Heterogeneity' *Land* **13** 7 (2024) <https://doi.org/10.3390/land13071055>
- Tukiainen, H., Kiuttu, M., Kalliola, R., Alahuhta, J. & Hjort, J. 'Landforms Contribute to Plant Biodiversity at Alpha, Beta and Gamma Levels' *Journal of Biogeography* **46** 8 (2019) <https://doi.org/10.1111/jbi.13569>
- Turetsky, M. R., Mack, M. C., Hollingsworth, T. N. & Harden, J. W. 'The Role of Mosses in Ecosystem Succession and Function in Alaska's Boreal forest This Article Is One of a Selection of Papers From the Dynamics of Change in Alaska's Boreal Forests: Resilience and Vulnerability in Response to Climate Warming.' *Canadian Journal of Forest Research* **40** 7 (2010) <https://doi.org/10.1139/x10-072>
- Verbeek, N. A. M. & Boasson, R. 'Local Alteration of Alpine Calcareous Vegetation by Birds: Do the Birds Create Hummocks?' *Arctic and Alpine Research* **16** 3 (1984) <https://doi.org/10.1080/00040851.1984.12004423>
- Waide, R. B., Willig, M. R., Steiner, C. F., *et al.* 'The Relationship Between Productivity and Species Richness' *Annual Review of Ecology and Systematics* **30** 1 (1999) <https://doi.org/10.1146/annurev.ecolsys.30.1.257>

- Walker, L. R. & del Moral, R. 'Primary Succession and Ecosystem Rehabilitation' (Cambridge University Press 2003)
- Walker, L. R., Wardle, D. A., Bardgett, R. D. & Clarkson, B. D. 'The Use of Chronosequences in Studies of Ecological Succession and Soil Development' *Journal of Ecology* **98** 4 (2010) <https://doi.org/10.1111/j.1365-2745.2010.01664.x>
- Yarranton, G. A. & Morrison, R. G. 'Spatial Dynamics of a Primary Succession: Nucleation' *The Journal of Ecology* **62** 2 (1974) <https://doi.org/10.2307/2258988>

Appendix 1

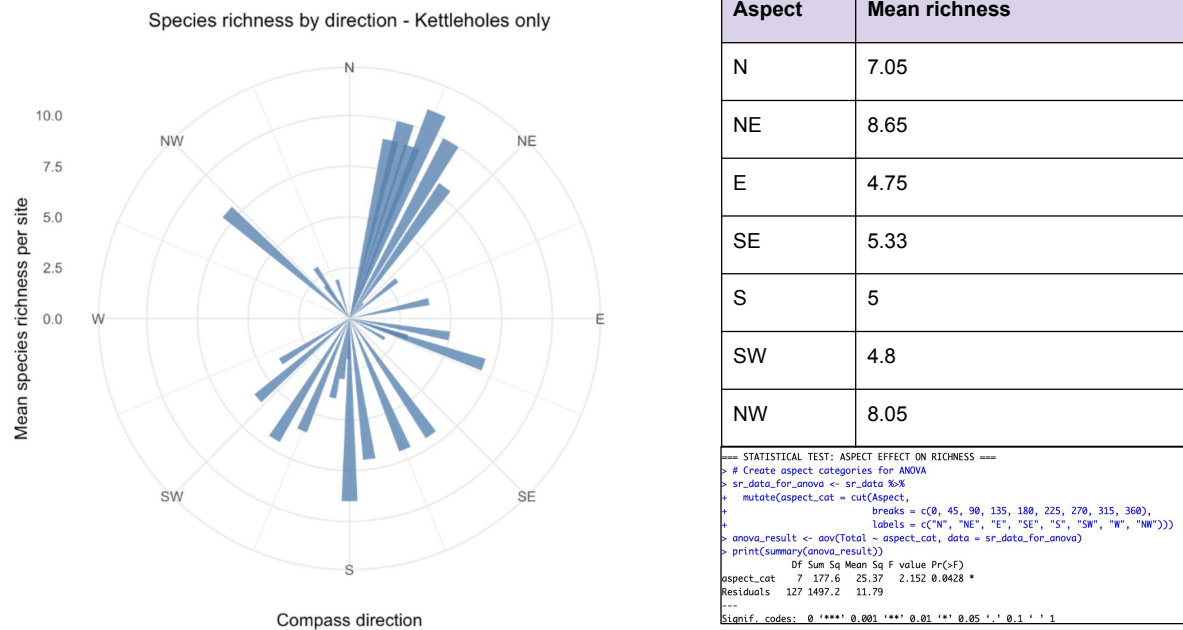


Figure 8: Compass plot showing the species richness of kettleholes by the aspect of the sample **A** and table of summary statistics **(B)** showing the mean richness by aspect. ANOVA results show that the mean richness by aspect is slightly significant as $p = 0.0428$.

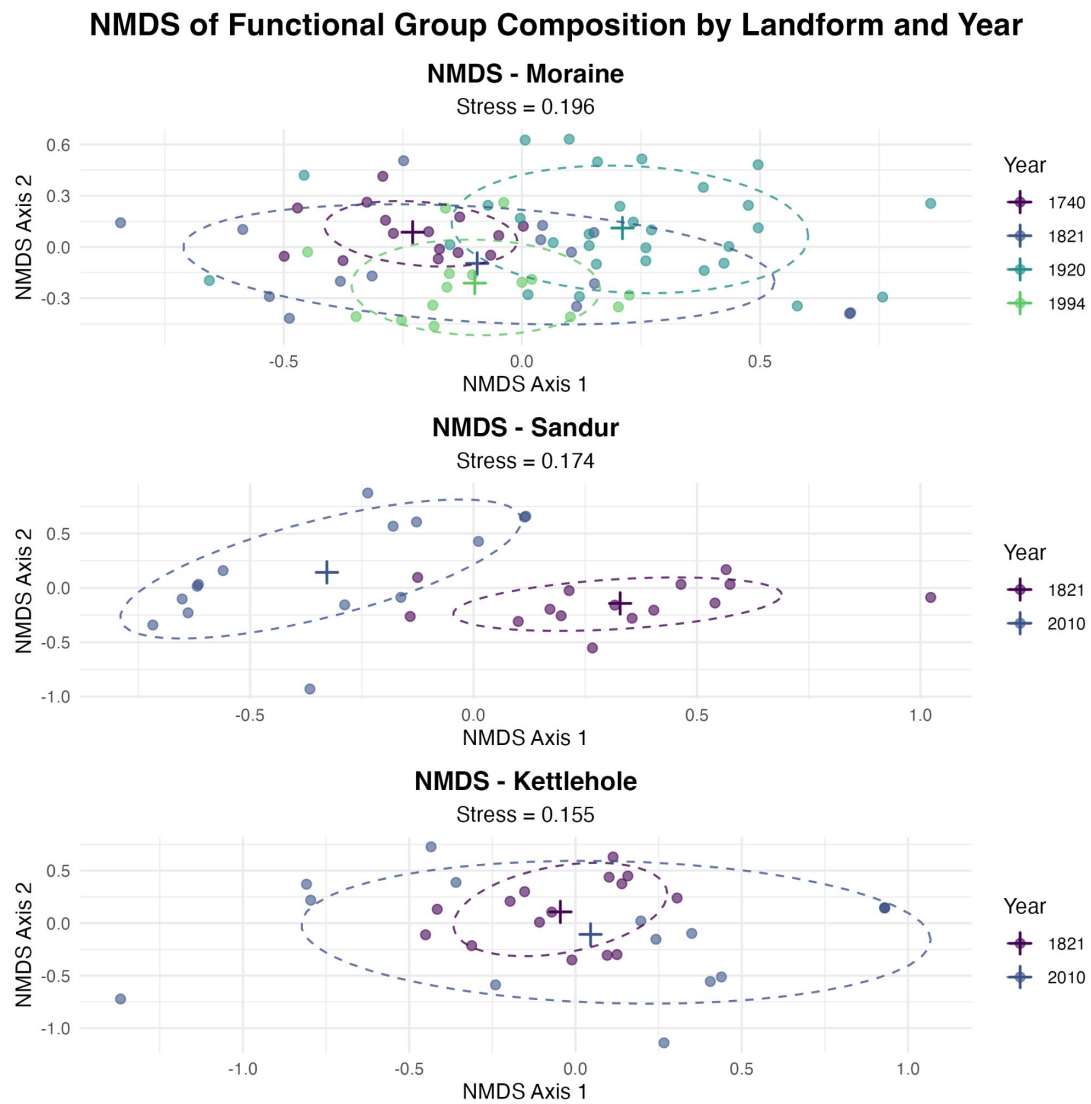


Figure 9: NMDS plot of functional groups across the moraine, sandur and kettlehole. It is noted that the ellipses of the data for years 1821 and 2010 in sandur diverge, whereas they fully overlap in kettlehole. All stress values are less than 0.2, indicating a good fit of the observations.

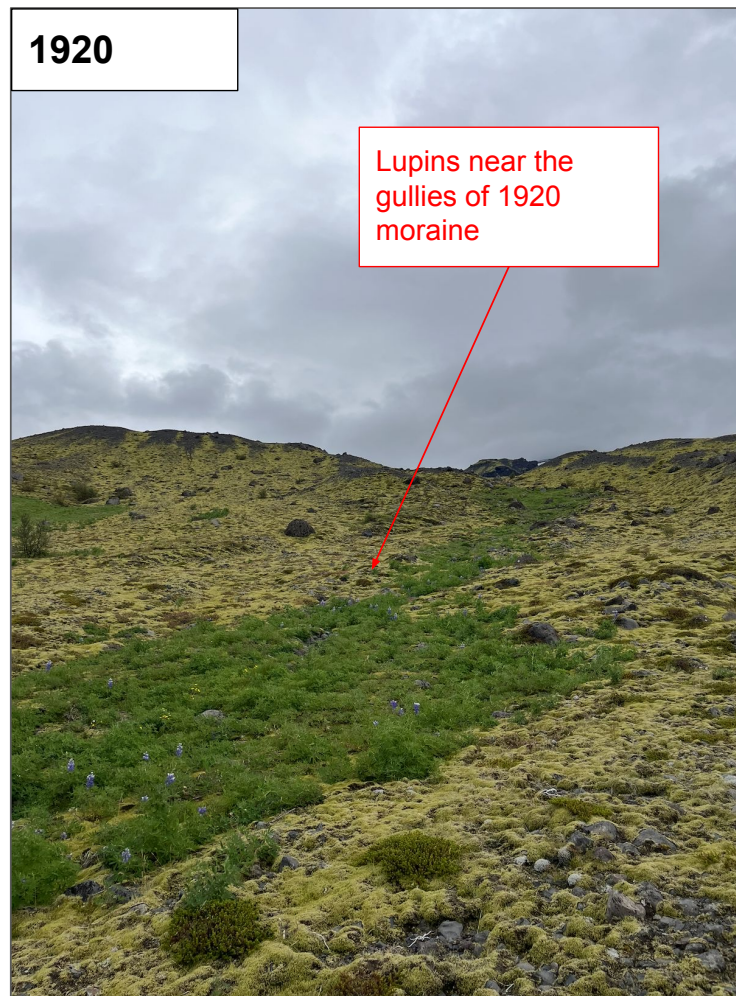


Figure 10: Site photograph of the 1920 moraine showing the Nootka lupine population along one of its gullies.

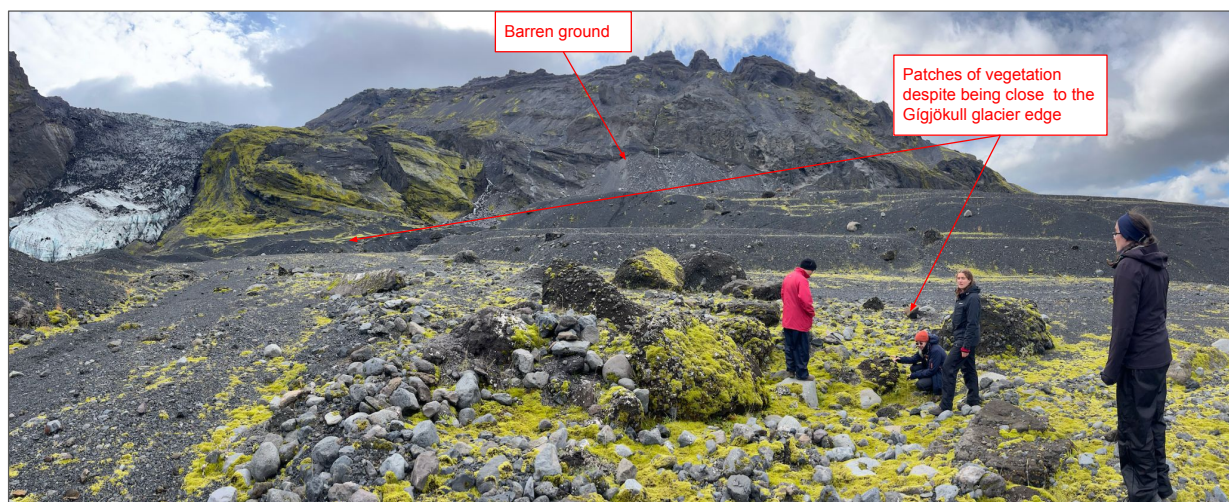


Figure 11: Site photograph in a location beyond the site closest to the gigjokull, taken during a walk after completing data collection. Patches of dense vegetation that were not in either kettleholes, sandur or moraines were observed. They may potentially be bird roosts that are common in South-East Iceland (Sigurðardóttir *et al.*, 2022). Observed woody taxa indicates diversity, contrasting the data from the latest kettlehole sampled.

Table 1: Raw data of the species identified and the corresponding functional group assignments of the species identified.

[illegible]

[illegible]

[illegible]