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Successes and failures following long-distance dispersal: Dynamics of mountain birch (*Betula pubescens* ssp. *tortuosa*) on a glacial outwash plain

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Dissertation submitted in partial fulfillment of a
Philosophiae Doctor degree in Biology

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Abstract

The colonisation of a forest-forming tree species into an early successional environment, following long-distance dispersal, presents a unique opportunity to study the dynamics of a founder population in a setting that differs from its origin. This thesis takes advantage of one such rare event and seeks to identify factors and processes determining the population's successes and failures. Around 1990, mountain birch (*Betula pubescens* ssp. *tortuosa*) established on Skeiðarársandur outwash plain in southeast Iceland. Nearest populations, and sources of origin, are ~10 km away. At the time of study, the first generation had recently reached reproductive maturity. Seed densities were high but when all losses were accounted for, only 2.7% of the crop remained viable and germinated. Most externally intact seeds did not contain developed embryos, despite being visually indistinguishable from filled seeds. Externally evident losses amounted to ~45%, mostly due to predation by gall midge larvae (*Semudobia betulae*). Even so, germinable seeds/m^2 ranged from 0.5–75.9. Birch establishment is strongly shaped by microsite quality and extreme early mortality is common. On Skeiðarársandur, seeds were most likely to germinate in thin moss and survivorship was exceptionally high in the first 1–2 years, mostly >50%. Despite Skeiðarársandur's apparent homogeneity, a comparison to 2008 population data revealed that a decade later, most measured variables (e.g. tree size, plant growth form, and seedling density) showed site-specific divergence. The mountain birch is predicted to act as an ecosystem engineer in this sparsely vegetated environment, leaving a transforming but spatially heterogeneous imprint on the ecosystem.

Útdráttur

Ilmbjörk (*Betula pubescens* ssp. *tortuosa*) nam skyndilega land á Skeiðarársandi um 1990, eftir að fræ hafði dreifst um 10 km leið frá Bæjarstaðarskógi og finnst nú á >35 km^2 svæði. Markmið verkefnisins var að nýta þetta einstaka tækifæri til að greina afdrif, viðgang og þróun fyrstu kynslóða einangraðs stofns í nýju umhverfi og bera saman við stofna í Skaftafelli og Morsárdal. Í upphafi rannsóknarinnar hafði stofninn nýlega náð kynþroska. Aðeins 2,7% fræja voru lífvænleg, einna helst vegna þess að þrátt fyrir að vera oftast ógreinanleg frá fylltum fræjum var þorri þeirra án kímplöntu. Fræ úr Morsárdal/Skaftafelli höfðu lægra hlutfall tómra fræja. Þroskunarferli þessara tómu fræja virðist endurspegla sóun auðlinda af hálfu móðurplöntunnar en mögulegar þroskunarfræðilegar, vistfræðilegar og þróunarfræðilegar skýringar eru settar fram og metnar. Fræskemmdir sáust á um 45% fræja, oftast af völdum birkihnúðmýs (*Semudobia betulae*). Fræframleiðsla á Skeiðarársandi var þó nægileg til að skila 0,5–75,9 spírunarhæfum fræjum á fermetra. Spírun var hlutfallslega mest í þunnum mosa. Lifun kímplantna var mjög há, oftast >50% fyrstu 1–2 árin, en ekki var marktækur munur á lifun milli yfirborðsgerða. Samanburður gagna frá árunum 2008 og 2018 sýndi verulegan framgang birkistofnsins á Skeiðarársandi en á óvart komu sterkar vísbendingar um að svæðisbundinn breytileiki væri að þróast, m.a. í vaxtarformi, stærðardreifingu og nýliðun. Tvær tilgátur eru ræddar til útskýringar, annars vegar að þrátt fyrir að Skeiðarársandur sýnist einsleitur, búi hann yfir svæðisbundnum breytileika og því ólíkum skilyrðum fyrir vöxt birkis og hins vegar að breytileikann megi rekja til svæðisbundins munar í arfleifð landnemakynslóðarinnar.

Dedication

Ritgerðin er tileinkuð Skarphéðni og Fríðu.

Náttúrufræðingar, samstarfsfólk, vinir, fyrirmyndir.

Þó þau séu farin af skrifstofunni eru þau með mér í felti.

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This thesis is based on the following papers. Within the thesis, the papers are referenced by their Roman numerals.

Paper I: Óskarsdóttir, G., Thórhallsdóttir, Th.E., Jónsdóttir, A.H., Birkisdóttir, H.M., Svavarsdóttir, K. (2022). Establishment of mountain birch (*Betula pubescens* ssp. *tortuosa*) on a glacial outwash plain: Spatial patterns and decadal processes. *Ecology and Evolution*, *12*, e9430. https://doi.org/10.1002/ece3.9430

Paper II: Óskarsdóttir, G., Thórhallsdóttir, Th.E., Svavarsdóttir, K. (202X). High seed losses in mountain birch (*Betula pubescens* ssp. *tortuosa*) and developmental, ecological, and environmental correlates. *Journal of Plant Ecology, accepted*.

Paper III: Óskarsdóttir, G., Svavarsdóttir, K., Speed, J.D.M., Thórhallsdóttir, Th.E. (202X). The recruitment niche of mountain birch (*Betula pubescens* ssp. *tortuosa*) and implications for native woodland restoration. *Manuscript*.

Contribution of the author.

Paper I: Investigation (equal), formal analysis (equal), visualization (lead), writing – original manuscript (lead), writing – review and editing (equal).

Paper II: Investigation (equal), formal analysis (lead), visualization (lead), writing – original manuscript (equal), writing – review and editing (equal).

Paper III: Investigation (lead), formal analysis (lead), visualization (lead), writing – original manuscript (lead), writing – review and editing (equal).

Reprint of paper I is published with kind permission from the publishers. In addition, some unpublished data are presented.

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This research is a part of a larger project, studying various ecological aspects of Skeiðarársandur and its mountain birch population. Being part of a great team of researchers and students has enriched this experience for me and helped me gain a more thorough understanding of the subject. For delightful cooperation and support, I sincerely thank Álfur Birkir Bjarnason, Benedikt Traustason, Bryndís Marteinsdóttir, Hlynur Steinsson, Hulda Margrét Birkisdóttir, Jóhannes Bjarki Urbancic Tómasson, Kristinn P. Magnússon, Ólafur Eggertsson, Snæbjörn Pálsson, Sydney Gunnarsson, Tryggvi Stefánsson, Victor Pajuelo Madrigal, and Vigdís Freyja Helmutsdóttir. Furthermore, I would like to adopt Anna Helga Jónsdóttir into the group, saying that she helped with statistics does her part no justice and I thank her for teaching me statistics and making it fun.

Behind this research lies a lot of field work, both on Skeiðarársandur and in Vatnajökull National Park. That work would neither have been doable, nor nearly as much fun, without the help of many fantastic people. I thank all my colleagues who helped out in the field in one way or another, the Skeiðarársandur team, as well as Hilmar Njáll Þórðarson, Rannveig Rögn Leifsdóttir, Sigurður Finnbogi Sæmundsson, Sólveig Magnea Guðjónsdóttir, and especially Hulda Margrét Birkisdóttir, who joined me on almost all my field trips. Furthermore, I would like to thank Vatnajökull National Park and the Skaftafell staff for their assistance regarding field work within the park. I would also like to thank Pálína Þorsteindóttir and Ólafur Sigurðsson in Svínafell for always providing us with accommodation for our field trips, no matter how short of a notice we gave them, even in peak tourist season. From the limited experience I have with running an AirBnB, I certainly do not take your exceptional hosting for granted.

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1 Introduction

The pace of change in the living world spans a wide course from very slow and continuous to large and abrupt. Similarly, there is a huge span of spatial scales where patterns of change are expressed. The science of ecology studies dynamics across scales, spatial and temporal, and each brings with it an understanding at some level (Levin, 1992). Today, in a time of rapid ecological changes worldwide due to anthropogenic activities (Rocha et al., 2015), an in-depth understanding of the natural processes that shape ecosystems is vital for their protection and management.

Abrupt ecosystem-scale changes may constitute a regime shift or state shift, i.e. the replacement of an earlier system by an entirely different one (Andersen et al., 2009; Biggs et al., 2018). The best-known examples usually involve negative changes in that the new system is less productive and diverse than the old one, following the passing of an ecological threshold or a tipping point (Mufungizi et al., 2023; Scheffer & Carpenter, 2003). However, the term can also apply to abrupt shifts to a more productive state (Biggs et al., 2018). Through history, there have of course been myriads of examples of sudden shifts to more productive states but in this context, the distinction between primary succession on barren surfaces and a regime shift may be blurred. In the early Holocene for example, forest regeneration in Europe seems to have been extremely rapid (Theuerkauf et al., 2014).

This thesis took advantage of a large-scale, rare event triggered by natural causes that is set to transform an extensive area on a sparsely vegetated glacial outwash plain in Iceland, Skeiðarársandur, into a birch woodland. It builds on data from previous studies on the birch population together with new data for gaining greater insights into its dynamics. I regard the population establishment as an incipient regime shift as it is 1) large scale (>35 km^2), 2) abrupt and possibly due to a single colonisation event or at the most very few ones, and 3) has taken place over a time scale of ca. three decades. The development of a birch ecosystem will take longer, but this spontaneous and successful colonisation presents a unique opportunity to study the dynamics of a founder population in an environmental setting that differs from its origin and test a variety of ecological theories and hypotheses.

1.1 Early ecosystem development and priority effects

Ecological succession is traditionally defined as the directional process by which biological communities assemble and change over time following natural or anthropogenic disturbance (Egerton, 2015; Chang & Turner, 2019). A critical phase in ecosystem development is the initial plant establishment (Walker & del Moral, 2003), commonly limited by the physical environment (Jones & del Moral, 2009) but, as more recently emphasised, influenced by stochasticity (Marteinsdóttir et al., 2018). Seed dispersal, for instance, is highly unpredictable (Fenner & Thompson, 2005), and neutral assembly patterns most strongly shape communities dominated by colonisation (Marteinsdóttir et al., 2018; Zillio & Condit, 2007). During early primary succession, seed dispersal is an important limiting factor (Walker & del Moral, 2003). A clear example of this can be found on large, barren outwash plains, where the nearest seed sources may be quite distant. Their colonisation is thus highly affected by stochastic factors like weather and long-distance dispersal events, which are generally rare (Doxford & Freckleton, 2012; der Weduwen & Ruxton, 2019; Marteinsdóttir et al., 2018).

When first colonisers influence the establishment of later-arriving species and thus, community assembly, they're said to cause priority effects (Fukami, 2015). The nature and strength of the priority effects are dependent on the traits of the species in question, but also on the arrival time, as well as the structure and species composition of the receiving ecosystem (Körner et al., 2007; Weidlich et al., 2020). For example, a tree species establishing in an early successional ecosystem will modify its structural dimensions, affect microclimate and soil processes (Jonczak et al., 2020; McElhinny et al., 2010), and attract both vertebrate and invertebrate animals (Kittipalawattanapol et al., 2021; Quinn et al., 2021), profoundly influencing the community's successional pathways (Mitchell et al., 2007). In this way, stochastic colonisation of such a species can have a significant and long-term impact on the ecosystem (Fukami, 2015).

This may also apply at the population level (Faillace et al., 2022) and in some instances, considering intraspecific trait variability may even be necessary to detect niche differentiation processes (Jung et al., 2010). Intraspecific trait variability may be attributable to both phenotypic plasticity and genetic diversity and in general, plants can display great variability in response to their environment (Violle et al., 2007). Regardless of its source, this variability affects species fitness and should thus be considered in community assembly (Jung et al., 2010). This may be particularly relevant for ecosystems consisting of few but large populations, harbouring great but sometimes cryptic intraspecific variation, which may indeed be the case in arctic and subarctic ecosystems (Brochmann & Brysting, 2008; Grundt et al., 2006; Steltzer et al., 2008).

1.2 The study species

Downy birch (*Betula pubescens* Ehrh.; Figure 1.1a) is one of around 50 species of *Betula*, a diverse genus of deciduous plants, ranging from 30 m forest trees to procumbent tundra shrubs (Ashburner & McAllister, 2013; Atkinson, 1992). The species itself has a notoriously variable growth form, which has been attributed to high phenotypic plasticity and hybridisation, for example with dwarf birch (*Betula nana*) (Thórsson et al., 2007; Verwijst, 1988). The naturally occurring hybrids are partially fertile (Anamthawat-Jónsson et al., 2020). Downy birch is commonly shrubby in highly oceanic, windy, and alpine sites, but taller and more often monocormic where conditions are more benign (Jónsson, 2004; Verwijst, 1988). For trees in general, there is evidence of greater physiological plasticity of shade-intolerant species compared to tolerant ones, but correlations between structural plasticity and shade tolerance are less known (Portsmuth & Niinemets, 2007; Van de Peer et al., 2017).

Towards the centre of its latitudinal range, downy birch is a shade-intolerant pioneer species, but due to its wide climatic tolerance, it forms stable and ecologically important woodlands towards the northern edge of its range (Atkinson, 1992). Downy birch is the most widespread birch in Europe and western Asia and extends farther north than any other broadleaf tree (Ashburner & McAllister, 2013). Due to its cascading effects on many ecological processes, significantly influencing ecosystem function and diversity, it has widely been regarded as an ecosystem engineer (Friggens et al., 2023; Mitchell et al., 2007; 2010).

Downy birch, like most birches, is regarded a masting species, with a highly temporally variable but regionally synchronised pattern of seed production (Masaka & Maguchi, 2001; Ranta et al., 2008; Gallego-Zamorano et al., 2018). It is monoecious and strongly self-incompatible (Atkinson, 1992; Hagman, 1971). The flowers are wind-pollinated catkins (Figure 1.1b). The fruit is a single seeded, two-winged achene (samara), that likely has a very thin layer (a few cells thick) of endosperm remaining at maturity (Håkansson, 1957), but throughout this thesis, I refer to it as a seed. Each seed contains a two-locular ovary, but one is always aborted (Dahl & Fredrikson, 1996).

Gall midges, of the genus *Semudobia*, are known to parasitise downy birch seeds (Holm, 1994a; Roskam, 1977). Flies lay their eggs in the catkins, between floral bracts and flowers, and larvae enter the seeds, feeding on their resources, leaving them inviable (Roskam, 1977). However, a seemingly more important check on the production of viable seed is the lack of a mature embryo, as a significant proportion of the seed crop are commonly partly filled or, even more commonly, empty, i.e., neither ovary shows any signs of development (Holm, 1994b; Sarvas, 1952). This has been reported for several *Betula* species and poor embryo development has been attributed to fertilisation limitation, due to lack of pollen, low pollen viability, or an incompatibility reaction of the mother plant (Bona et al., 2022; Sarvas, 1952; Weis & Hermanutz, 1993). However, producing empty seeds as a means of predator deception has been shown to have ecological and evolutionary benefits (Perea et al., 2013).

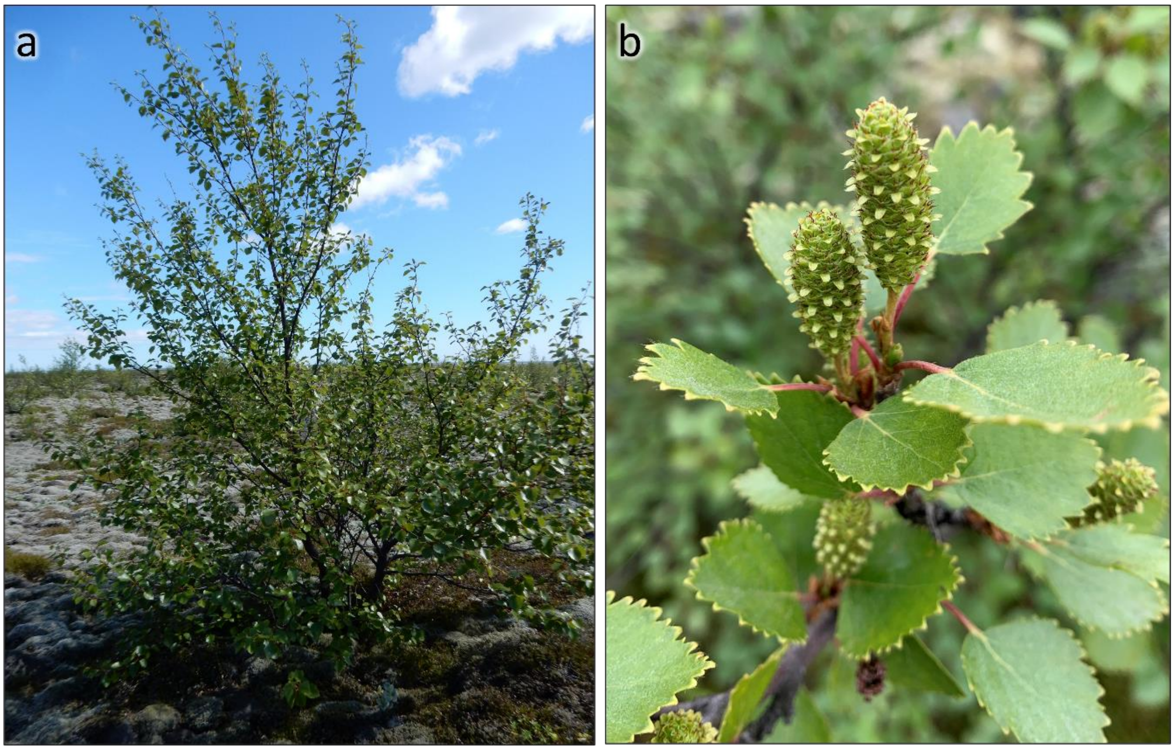

Figure 1.1. Young downy birch tree with polycormic structure (a), and its female catkins, not yet fully mature (b).

However, seed production of downy birch is generally prolific, and as a highly effective coloniser (Lidman et al., 2023), the species does not seem to be severely limited by availability of viable seed. On the other hand, as a small seeded species with small initial seedlings, plant establishment is strongly shaped by microsite conditions (Aradóttir & Halldórsson, 2018). Life histories of small seeded pioneers are often defined by extreme early mortality (Osumi & Sakurai, 2002; Marteinsdóttir et al. 2013). Due to its shade intolerance, downy birch is more likely to establish in poor or low-growing vegetation than in well vegetated sites but there, lack of protection from frost and drought can be a cause of severe mortality (Aradóttir, 1991).

Mountain birch (*Betula pubescens* ssp. *tortuosa* (Ledeb.) Nyman) is a subspecies of downy birch, generally found in the northernmost part of its range (Panarctic Flora, n.d.), forming the treeline against the tundra and in alpine regions (Atkinson, 1992). Its taxonomy has been disputed (Ashburner & McAllister, 2013) but provisionally, *B. p.* ssp. *tortuosa* seems to be widely applied towards the altitudinal and latitudinal limits of the species in Fennoscandia and Russia (Panarctic Flora, n.d.). In Iceland, all native birch is regarded as belonging to this subspecies (Kristinsson et al., 2018) and it has been the only native forest forming tree species during the Holocene (Hallsdóttir, 1995).

1.3 Icelandic mountain birch woodlands

The Icelandic mountain birch woodlands are ecologically important ecosystems with high conservation value (Icelandic law on nature protection, no. 60/2013; Ottósson et al., 2016). Most of them fall under the category “other wooded land” by FAO’s classification (2020), not the category “forest”, as mature trees are commonly <5 m tall. The tallest measured mountain birch in Iceland was 14.2 m in 2016 (Snorrason et al., 2016). Icelandic birch woodlands are very open, with a diverse sward layer (Ottósson et al., 2016).

The native woodlands have undergone extensive degradation and destruction since Norse settlement over 1,100 years ago. Several estimations on their extent at that time have been made, with results ranging from 8,000 km^2 (exclusively >2 m tall) (Ólafsdóttir et al., 2001) to 40,000 km^2 (no minimum height) (Bjarnason, 1974), the newest one estimating that woodlands (no minimum height) covered a little less than 24,000 km^2 at the time, or just under one-fourth of the country (Trbojević, 2016). According to pollen records, their cover rapidly and substantially decreased after the settlement, due to intense utilisation combined with volcanism and cold climatic periods (Gathorne-Hardy et al., 2009; Trbojević, 2016). The woodlands were nearly decimated by the early 20th century and now cover just over 1,500 km^2 or 1.5% of the country (Snorrason et al., 2016). The extensive land degradation that accompanied the loss of woodlands has resulted in soil erosion, biodiversity loss, and a severe decline in ecosystem function over vast areas (Barrio & Arnalds, 2022). Icelandic soils, consisting mostly of Andosols, are extremely vulnerable to erosion, emphasising the significant role that resilient vegetation plays in the Icelandic environments in protecting ecosystems and the habitats they foster (Arnalds, 2015).

The need to protect the remaining woodlands and restore degraded ones is now widely recognised (Aradóttir & Eysteinsson, 2005) and as part of the Bonn Challenge, the Icelandic government has pledged to initiate by 2030 the process of increasing cover of ecosystems dominated by mountain birch to 5% of the country, or on 350,000 ha (Bonn Challenge, n.d.). This will require major restoration efforts although with minimum intervention. An example of a large-scale woodland restoration is the Mt. Hekla restoration project (Hekluskógar) that was established in 2005 with the aim of restoring native birch woodland in the vicinity of an active volcano with one of the objectives to increase the ecosystem resilience to tephra deposits (Aradóttir, 2007). A slight natural expansion has also been occurring in the last few decades, following changes in land use (most notably a decrease in number of domesticated sheep which graze in open rangelands during summer) and climate change (Björnsson et al., 2023; Snorrason et al., 2016).

Herbivory has been recognised as a significant check on birch woodland expansion at the treeline ecotone (Speed et al., 2011), as well as a potential influencer on community composition following birch encroachment into the tundra (Scharn et al., 2022). However, using permanent plots in a long-term study in southeast Norway, researchers were able to identify gradual changes in growth conditions as a main driver for mountain birch forest line advancement of 0.72 m/year from 1937 to 2007 (Nygaard et al., 2022). In Iceland, the climatic envelope of mountain birch will expand with global warming and indications of range expansion have been reported, but simultaneous changes in land use impede direct calculations of treeline advances (Wöll, 2008). Examples of climate change indirectly facilitating mountain birch range expansion have also been noted, and the colonisation of mountain birch on Skeiðarársandur glacial outwash plain is such an example. Mountain birch population ecology and its recruitment on the plain are the research topics of this thesis.

1.4 The study area

Skeiðarársandur is a 1,000 km^2 glacial outwash plain in southeast Iceland (Figure 1.2), the largest one in front of an active glacier in the country and probably worldwide. Since the 14^{th} century or even sooner, glacial outburst floods intermittently flooded the plain (Thórarinsson, 1974), making it impossible for plants to persist and develop long-term communities. Some were associated with volcanic eruptions in either the Grímsvötn volcano or in other subglacial volcanoes in central Vatnajökull glacier (Figure 1.2). Outburst floods were also regularly triggered when continual melting of glacier ice by the geothermal area in Grímsvötn had filled the caldera enough to lift the glacier and allow floodwater to escape (Thórhallsdóttir & Svavarsdóttir, 2022). Much smaller floods were generated with the drainage of marginal ice dammed lakes, notably Grænalón, on the northwest side of Skeiðarárjökull glacier (Figure 1.2).

For centuries, Skeiðarársandur was a vast desert with only a few small vegetated patches (Thórhallsdóttir & Svavarsdóttir, 2022). In the first half of the 20th century, grasses dominated a small part of the west side of the otherwise extremely poorly vegetated plain (Björnsson, 2003). However, in the mid-20^{th} century, environmental conditions changed dramatically when the Skeiðarárjökull glacier (Figure 1.2) retreated past its huge Little Ice Age terminal moraine, channelling the outburst floods and shielding the middle of the plain from regular disturbance (Thórhallsdóttir & Svavarsdóttir, 2022). In addition, volcanic activity in Grímsvötn volcano (Figure 1.2) was lower during the second half of the last century than in the first half (Thórhallsdóttir & Svavarsdóttir, 2022), and the climate has been warmer in the last few decades than it was in the mid last century (Björnsson et al., 2023).

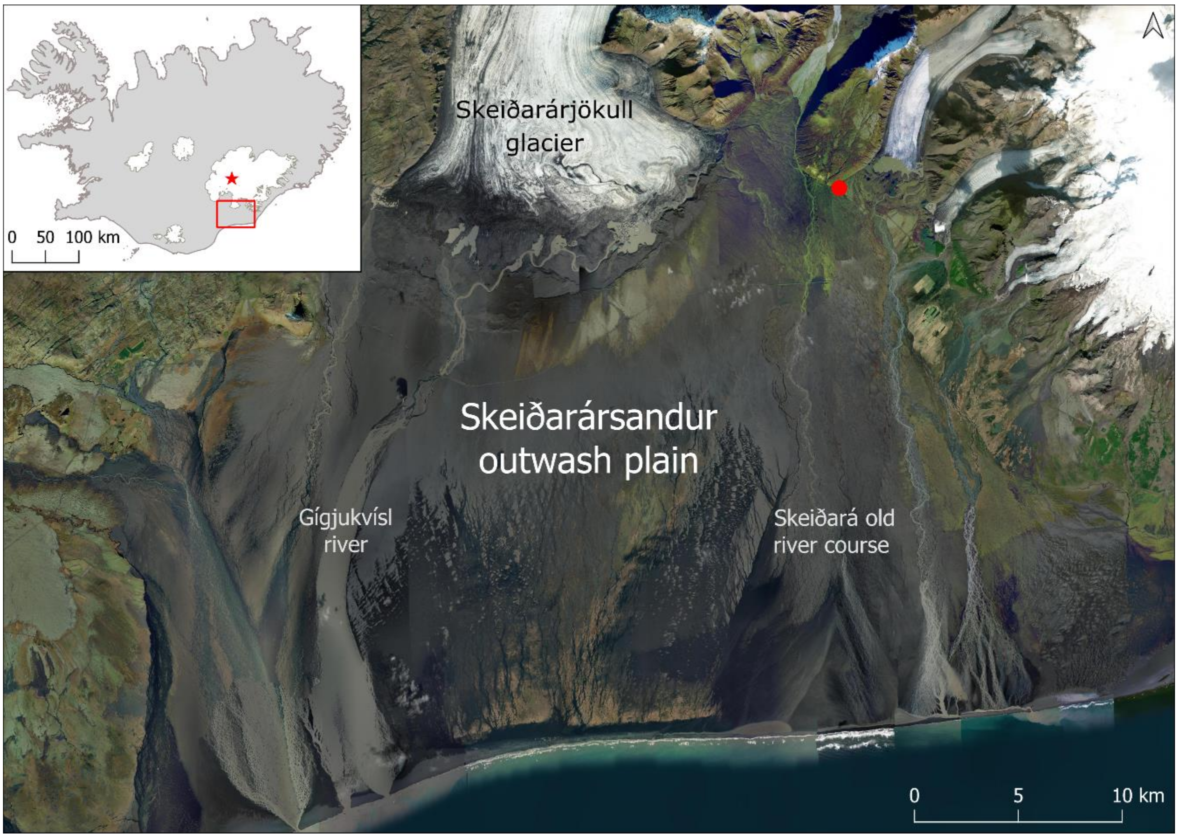

Figure 1.2. Location of Skeiðarársandur glacial outwash plain in Iceland. Red star shows location of Grímsvötn volcano, red dot shows location of Skaftafell weather station. Aerial photographs and map database: Open database of the National Land Survey of Iceland, accessed in January 2023 at https://www.lmi.is/is/landupplysingar/gagnagrunnar/nidurhal. Geographic information system: QGIS (http://qgis.osgeo.org).

These changes to the disturbance regime aided the establishment of early successional vegetation on the plain (Thórhallsdóttir & Svavarsdóttir, 2022). Still, it remains largely sparsely vegetated with over 70% of the area between Gígjukvísl river and the old Skeiðará river course having less than 10% vegetation cover in 2002 (Figure 1.2; Kofler, 2004). In the central upper zone of the plain (60–110 m a.s.l.; Figure 1.3), the substrate is coarser and more stable than in the sandier part seawards, making it more suitable for vegetation establishment (Figure 1.2). There, the sward layer is dominated by *Racomitrium ericoides* and *R. lanuginosum*, but lichens (mostly *Stereocaulon* spp.) and several low-growing vascular plant species (such as *Empetrum nigrum* and *Calluna vulgaris*) are also prominent.

The regional climate is maritime with high precipitation. Mean January and July temperatures are 0.9 and 10.9°C, respectively, and mean annual temperature is 5.2°C (values from Skaftafell, 1996–2020, unpublished data from the Icelandic Meteorological Office; Figure 1.2). The regional growing season is estimated to be about 110 days, from mid-May to early September (Marteinsdóttir et al., 2018), which is among the longest in Iceland (Thórhallsdóttir & Svavarsdóttir, 2022). Mean annual precipitation is around 1,700 mm and thereof, an average of just under 400 mm falls from May through August (values from Skaftafell, 2016–2020). Prevailing winds are from the northeast (Icelandic Meteorological Office, n.d.). Skeiðarársandur has been a summer grazing area for around 200 ewes and their lambs from ca. 1960 (A.M. Ragnarsdóttir, personal communication, June 2018).

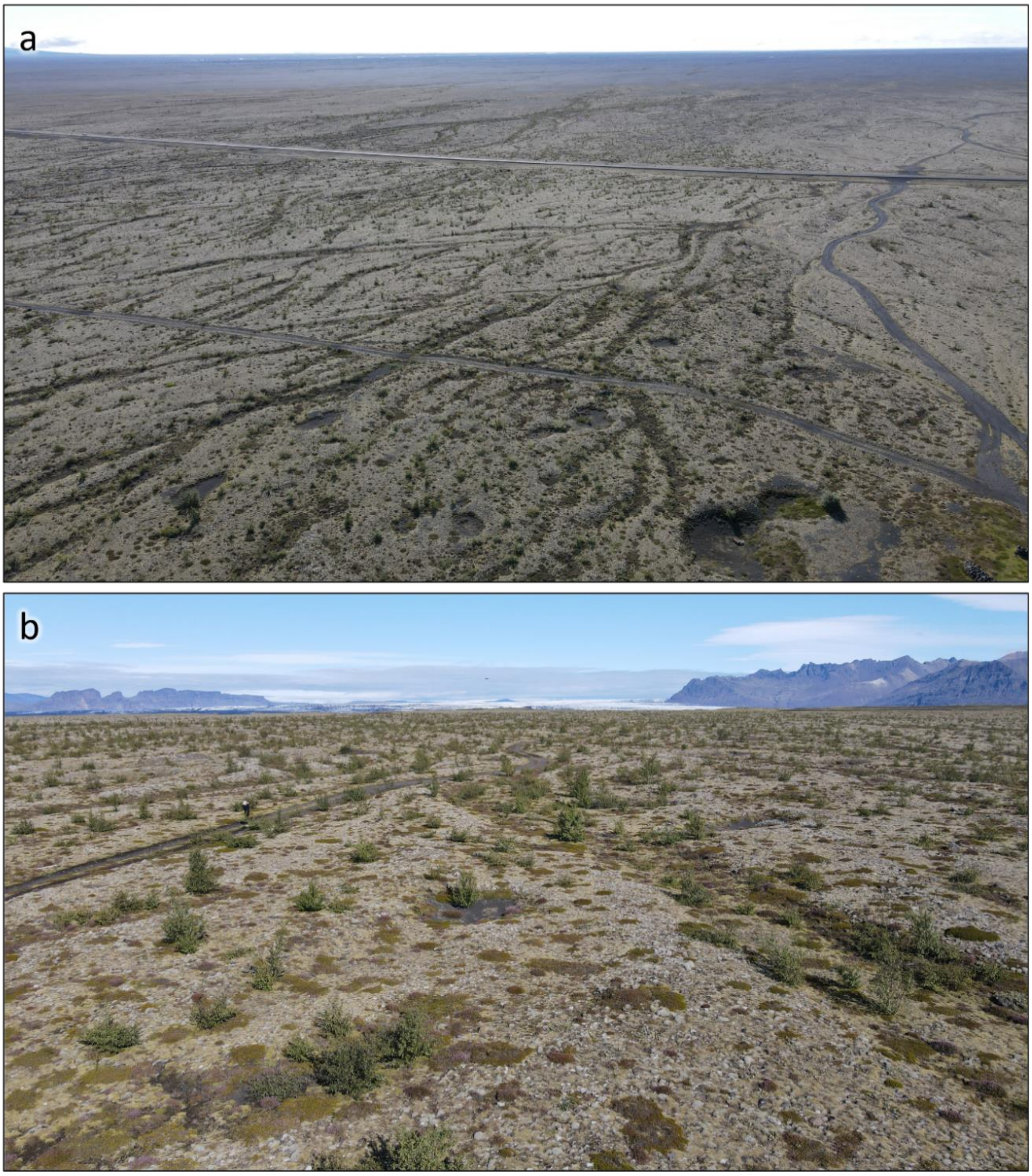

Figure 1.3. Aerial view of a part of Skeiðarársandur that has been colonised by mountain birch, looking south (a) and north (b). Both figures are taken in roughly the same location (63°58'14.2"N 17°09'32.4"W), but a is taken from a greater height than b. Photos: Ólafur G. Arnalds, June 2022.

Around 1990, mountain birch began colonising Skeiðarársandur's central upper zone (H.M. Birkisdóttir et al., unpublished data; Hiedl, 2009; Marteinsdóttir et al., 2007; Figure 1.3). The nearest seed sources are Skaftafell (10 km northeast), Bæjarstaðarskógur (11 km north-northeast) and Núpsstaðarskógur (16 km west). Thus, colonisation was only possible via long-distance dispersal. Genotyping by sequencing has revealed that the Skeiðarársandur population most likely originated from Bæjarstaðarskógur (Pálsson et al., 2023). At present, it has colonised an area of at least 35 km^2 (V.P. Madrigal et al., unpublished data) and has recently reached reproductive maturity (Hannesson, 2014; Hiedl, 2009).

1.5 Prior studies on mountain birch in the area

In Iceland, mountain birch woodlands are very fragmented and despite prolific seed production and dispersal potential, insufficient seed rain is regarded as an important limiting factor to their expansion (Aradóttir & Halldórsson, 2018). In addition, long-distance dispersal events such as the colonisation of Skeiðarársandur are globally rare (Doxford & Freckleton, 2012; der Weduwen & Ruxton, 2019). Consequently, the mountain birch establishment on Skeiðarársandur has sparked interest and inspired several research projects, most of them conducted by students at the University of Iceland under guidance of my supervisors, Professor Þóra Ellen Þórhallsdóttir and Dr. Kristín Svavarsdóttir.

The population ecology of the first-generation colonisers was studied in 2004 (Marteinsdóttir et al., 2007) and 2008 (Hiedl, 2009). At four sites studied in 2004, spread across most of the vegetated area in the central upper zone of the plain, mountain birch density ranged from 0.005 to 0.1 plants/m^2, their average height was 13 cm, and the tallest recorded plant was 72 cm (Marteinsdóttir et al., 2007). Furthermore, 3% of the sampled plants were flowering adults, catkin density was 0.007 catkins/m^2, and in 100 0.5 x 0.5 m quadrats studied, only one first-year seedling was found. In 2008, four sites were studied, three of them spatially comparable to 2004 sites (Hiedl, 2009). Then, mountain birch density ranged from 0.02 to 0.13 plants/m^2, mean height ranged from 6 to 16 cm, and the tallest recorded plant was 121 cm. Furthermore, 14% of the sampled plants were flowering adults, catkin density ranged from 0.002 to 1.3 catkins/m^2, but no first-year seedlings were found. Marteinsdóttir and Hiedl both conducted dendrochronological research and their results indicated that mountain birch first colonised Skeiðarársandur around 1990. Later, the more detailed study of H.M. Birkisdóttir (2018, unpublished data) supported those findings.

In 2013, Hannesson (2014) remeasured two of Marteinsdóttir's sites and concluded that tree height had increased and seed production surged. In 2015, recruitment was greater than in previous years but very clustered (Rúnarsdóttir, 2016). In the same year, mountain birch in kettleholes was also studied, but kettleholes are a prominent feature in the topography of the northern part of Skeiðarársandur. Generally, they seem to be a less suitable habitat for mountain birch than the flat terrain of the plain (Rúnarsdóttir, 2016).

Germination of mountain birch seeds has been tested for several years on Skeiðarársandur. Seeds from neighbouring populations in Skaftafell and Morsárdalur (near Bæjarstaðar-skógur) have been included for comparison. All tests were performed using the same methodology, including the exclusion of visibly damaged seeds and seeds infected by the gall midge *Semudobia betulae*. Throughout the current study, the same methods were used. Seed quality on Skeiðarársandur seemed to improve from the first test in 2008 and up to 2013, the latest test before my study (Halldórsdóttir, 2014; Hiedl, 2009; Jónsson, 2012; Ólafsdóttir, 2010). This might be due to increased tree size and fecundity with time since the first trees reached reproductive maturity, decreasing possible resource (Stephenson, 1981) or mate limitation (Bona et al., 2022; Holm, 1994b; Pannell et al., 2015) in the area. Seed germination has consistently been higher in the neighbouring populations than on Skeiðarársandur (Halldórsdóttir, 2014; Jónsson, 2012; Marteinsdóttir, 2004; Ólafsdóttir, 2010), indicating greater reproductive success in the more sheltered and less isolated populations (Mráz & Mrázová, 2021; Pannell et al., 2015).

The current study was a part of a larger project consisting of several work packages, all aiming at increasing knowledge on the patterns, processes, and origin of mountain birch on Skeiðarársandur, as well as its impact on the early successional ecosystem. The origin of the Skeiðarársandur mountain birch population was studied by assessing its genetic variation and relatedness with the three nearest woodlands and Pálsson et al. (2023) concluded that it most likely originated from Bæjarstaðarskógur, an old but small and isolated population ca. 11 km north-northeast of Skeiðarársandur. It is a highly regarded native birch stock in Iceland, with monocormic form and tall stature. Preliminary results on tree growth in relation to climatic factors on Skeiðarársandur suggest that in general, growth rates are comparable to other populations, but it seems to vary both temporally and spatially within the population and correlations to climate data are generally weak (H.M. Birkisdóttir, unpublished data).

Within the large project on Skeiðarársandur, ecological effects of the mountain birch colonisation were assessed for the belowground environment (Tómasson, 2023). Decomposition rate was positively related with tree density while the relationship with tree size varied, possibly due to small trees affecting the competitive balance between fungal guilds, slowing down carbon cycling (the Gadgil effect). Furthermore, soil fungal communities within the mountain birch colonisation sites differed substantially from those of mature forests, which may provide useful insights regarding mycorrhizal inoculation in forestry and woodland restoration in degraded areas (Tómasson, 2023). Lastly, Traustason (2022) compared several structural and reproductive traits between two mountain birch populations of contrasting growth form. Although mostly focused on populations outside of Skeiðarársandur, growth data from the plain (H.M. Birkisdóttir, unpublished data) were used in some of his analyses. He found that most life-history traits regarding reproduction and its success were comparable between populations, but a trade-off between annual shoot growth increment and reproductive effort was only found for the polycormic, decumbent population. Traustason (2022) concluded that resource availability and climatic factors were major drivers of reproductive success.

1.6 Aims of the research

The main objective of this thesis was to increase understanding of the population and reproduction ecology of the Skeiðarársandur mountain birch population. The persistence of a population requires that colonisers successfully leave descendants in the new range, and dispersal also controls its ability to move or adapt in response to environmental change (Hargreaves & Eckert, 2014). Thus, production of germinable seed and subsequent recruitment can be used to assess future development of the population, as well as its potential to adapt and expand its range. Moreover, due to high intraspecific variability of mountain birch and its potential to steer successional pathways of receiving ecosystems (Mitchell et al., 2007; 2010), unravelling the population's site-specific traits and development can provide the necessary foundation for assessing ecosystem development following woodland restoration.

Specific objectives were the following:

- To unravel spatial and temporal patterns of early population establishment of mountain birch on Skeiðarársandur, exploring whether early dynamics give insights into later emerging patterns. This was done with spatial comparisons within Skeiðarársandur and in the nearest established woodlands, as well as temporal comparisons, building on the 2008 survey of Hiedl (2009) (**Paper I**).

- To elucidate the reproductive success of the population and specifically, identify limiting factors and their relative importance. This was done by quantifying seed densities on the soil surface and in the seed bank, investigate losses from ovule development to pre-dispersal predation and fungal infections, and attempting to unravel their causes (**Paper II**).

- To assess local recruitment and its relation to surface characteristics. This was done by quantifying seed and seedling densities within different microsite types, as well as monitoring seedling survival for up to two years, thereby detailing the response of mountain birch to its immediate environment over three critical stages of recruitment: seed accumulation, germination, and early seedling survival (**Paper III**).

2 Methods

2.1 Study sites

Four sites were established within the mountain birch range on Skeiðarársandur with two more sites in Vatnajökull National Park to compare our study population to its nearest neighbouring woodland populations (Figure 2.1). In the western part of the mountain birch range on the plain, at the two western-most sites, mountain birch plants were small and sparse, but at the two eastern-most sites, trees were denser and larger (Figure 2.2a–d).

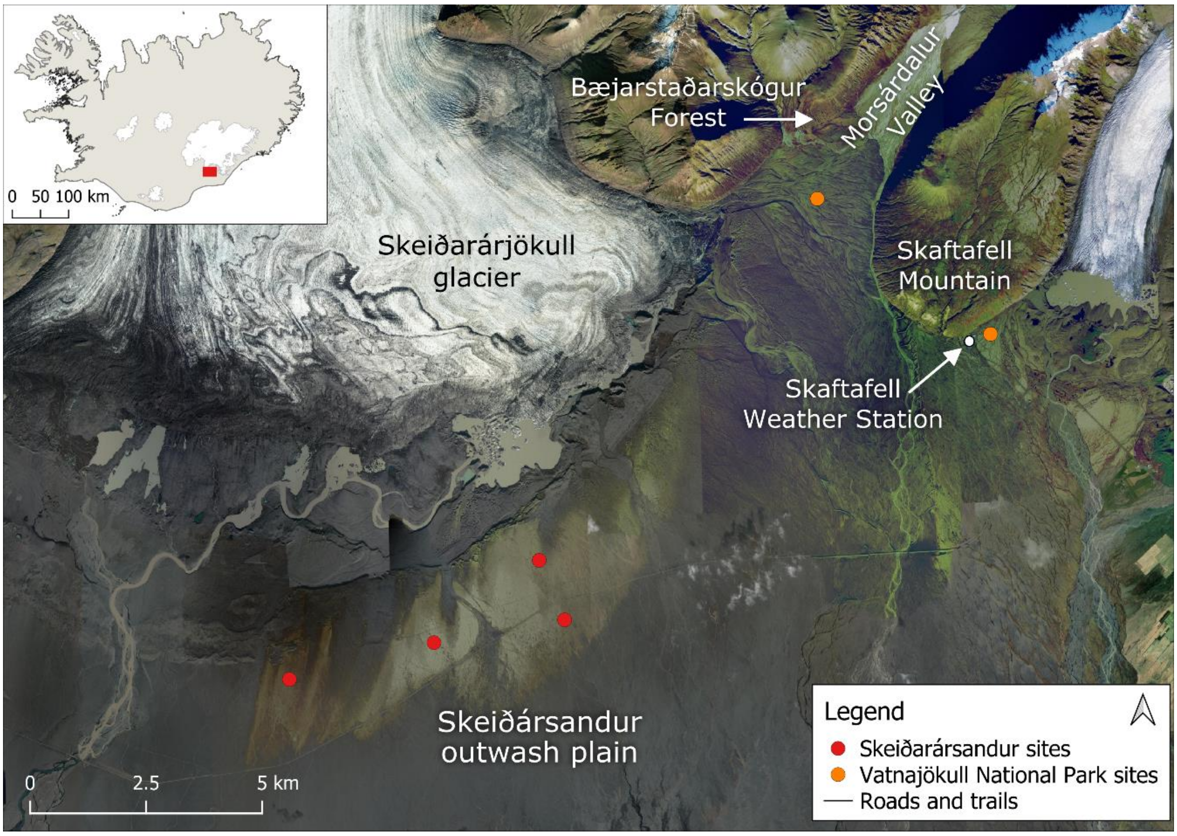

Figure 2.1 Location of the study area in southeast Iceland and the study sites within Skeiðarársandur and Vatnajökull National Park. Aerial photographs and map database: Open database of the National Land Survey of Iceland, accessed in January 2023 at https://www.lmi.is/is/landupplysingar/gagnagrunnar/nidurhal. Geographic information system: QGIS (http://qgis.osgeo.org).

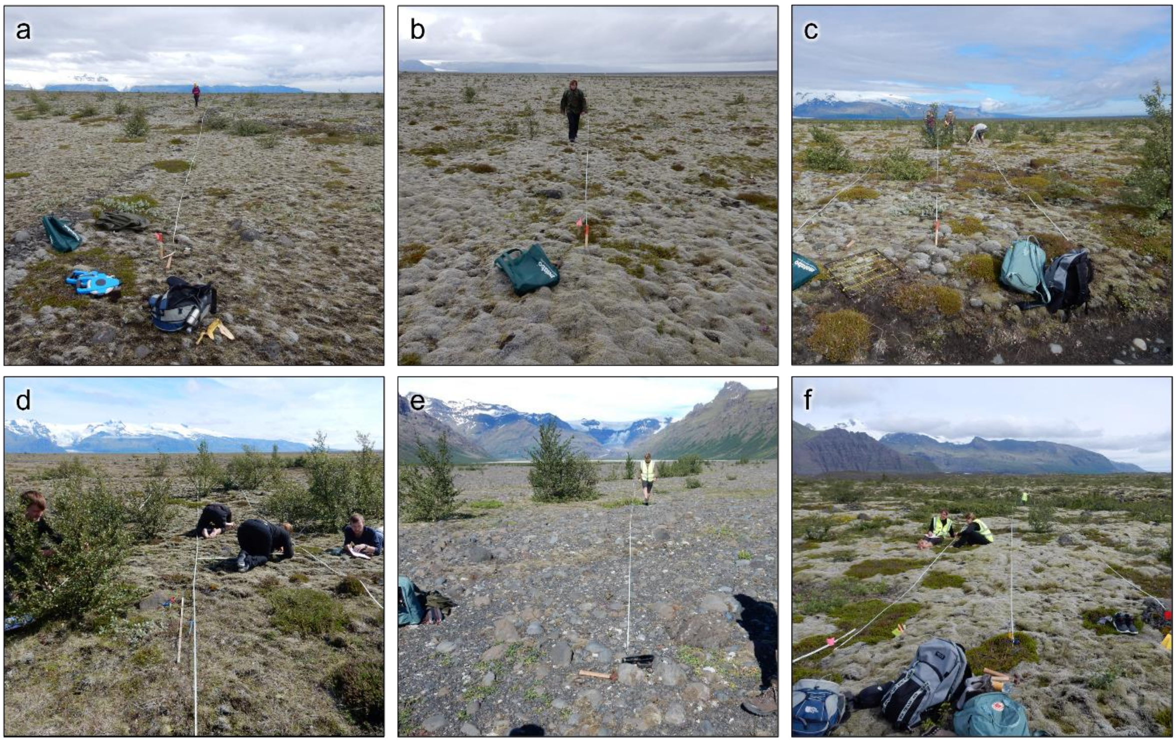

Figure 2.2 The study sites on Skeiðarársandur, progressing from west to southeast (a–d), the study site in Morsárdalur (e), and in Skaftafell (f). Photos were taken in June–July 2018.

Within Vatnajökull National Park, the site in Morsárdalur Valley was colonised by mountain birch around 1990 (Þ.E. Þórhallsdóttir & K. Svavarsdóttir, personal communication, June 2018), but still had low tree density (Figure 2.2e), while at the site in the proglacial area in front of Skaftafellsjökull, near Skaftafell weather station (Figure 2.1), mountain birch had begun to establish by the early 1960s (Persson, 1964) and tree density was greater than at the other sites (Figure 2.2f). Morsárdalur Valley is largely sparsely vegetated, but the ground at Skaftafell is mostly covered with *Racomitrium* moss and various dwarf shrubs (Figure 2.2e–f).

2.2 Data sampling

Maximum plant height, length of the longest shoot, and the number of female catkins were recorded for all mountain birch plants (excluding first-year seedlings) at all sites (Figure 2.1). Sampling on Skeiðarársandur was done in 2018 within 3 x 50 m transects (5–11 at each site) that had been established in 2008 (Hiedl, 2009). At each site, transects were laid out in a west-east direction, with a 100 m interval in a north-south direction, so that the whole north–south spread of mountain birch was covered, or to a maximum distance of 1 km from the first transect. Sites within the National Park had three equal sized transects each, laid down perpendicular to dry riverbanks, and were only sampled in 2018 (**Paper I**).

To evaluate pre-dispersal seed losses and quality, five catkins from each of 20 trees at each of the study sites (excluding the site on Skeiðarársandur shown in Figure 2.2b) were collected at the time of seed release in 2018–2020 (Figure 2.1). Trees were randomly chosen in 2018 but in the following years, catkins were collected from the same trees, or from the closest catkin-bearing trees if none were present on the original ones. For each tree, size and indices for growth habit and growth form were recorded. For each site and year, 50 randomly chosen seeds were classified by appearance into four groups: intact seed (not infected or damaged), seed predated by gall midge (*Semudobia betulae*), fungi infected seed, and physically damaged seed. Germination was tested for 20 intact seeds from each tree, each year. Additionally, results from 2017 germination testing on all previously mentioned sites except Morsárdalur were added to the dataset. In 2019, a sample of 10 intact seeds from each of 10 trees at three sites were measured for size and weight and then tested for germination. All seeds from all germination tests in 2019 and 2020 that did not germinate were dissected and split into two groups based on the presence or absence of a fully developed embryo (**Paper II**).

The seed rain and soil seed bank were quantified at two Skeiðarársandur sites, the western-most one and the southeastern one (Figure 2.1). At both sites, 500 m long transects were laid out in a north-south direction, split into four 125 m sections, and within each section, two sampling points were randomly chosen. At each sampling point, four 15 x 30 cm seed traps (synthetic turf mats) were laid out at the start of seed release in October 2018 and 2019, and collected in May the following year, to estimate the seed rain. Furthermore, five soil samples (Ø = 4.7 cm, depth = 5 cm) were taken at each sampling point in May 2019 and 2020 to quantify the soil seed bank. Mountain birch seeds were counted in all samples (N = 32 and N = 40 per site for seed rain and bank samples, respectively) and classified by appearance like described above for the catkin samples (**Paper II**). Furthermore, surface microsite type of each soil sample was recorded (**Paper III**).

Seedling establishment and survival were studied at the same two transects as described above for the seed quantity sampling. In summer 2018, at each sampling point within them, a 20 x 0.5 m plot was placed perpendicular to the transects. Each plot was split into 40 quadrats (0.5 x 0.5 m) and within each quadrat, all first-year seedlings (with cotyledons) on one hand, and all older seedlings with <5 leaves on the other hand, were recorded. At each site, around 200 first-year seedlings and 200 older seedlings were tagged, using a coloured wire, to monitor their survival (where seedlings were sparse, individuals outside of quadrats were also marked, and still, only about 100 older seedlings were found and marked at the western-most site). For each tagged and untagged plant, microsite type was recorded, and within two quadrats of every plot, the point-intercept method was used to record the microsite type (substrate characteristics) at 25 points. In 2019, all new first-year seedlings that were found in all plots and their closest vicinity were tagged and added to the dataset. The survival of seedlings was recorded in spring and autumn of 2019 and 2020 (**Paper III**).

2.3 Data analyses

To explore the variation in the data, several general and generalised linear models were used. More often than not, mixed models with random effects were used to account for non-independence in the dataset. Commonly used models included linear mixed effect models, negative binomial mixed models, and mixed effects logistic regressions. Several commonly used fixed effects were factor variables (e.g., site and year) and therefore, analysis of variance type II tests were used to explore the strength of their effects on the dependent variables. In case of significant effects in those models, estimated marginal means were used to identify the variation. Chi-square goodness-of-fit statistics were used to study the distribution of seeds and seedlings between microsite types. All data handling and analyses were conducted in *R* (R Core Team, 2022). Graphs were produced using the package *ggplot2* (Wickham, 2016).

3 Results

3.1 Mountain birch establishment on Skeiðarársandur: spatial patterns and decadal processes (Paper I)

All measured variables regarding the mountain birch population showed positive increments from 2008 to 2018, but despite the apparent homogeneity of Skeiðarársandur outwash plain, spatial divergence was evident in almost all of them, e.g. tree size, plant growth form, and seedling density. In 2018, the population could roughly be divided into two classes: largely monocormic trees with a high growth rate and high fecundity on one hand (present at the westernmost and the southeastern site, resembling the Morsárdalur population), and largely decumbent shrubby plants with lower growth rates and very limited second-generation recruitment (present at the middle and the northeastern site, more like the Skaftafell population) (Figure 3.1). Curiously, the two easternmost sites which had been very similar in 2008, did not fall into the same class in 2018 despite being only 500 m apart.

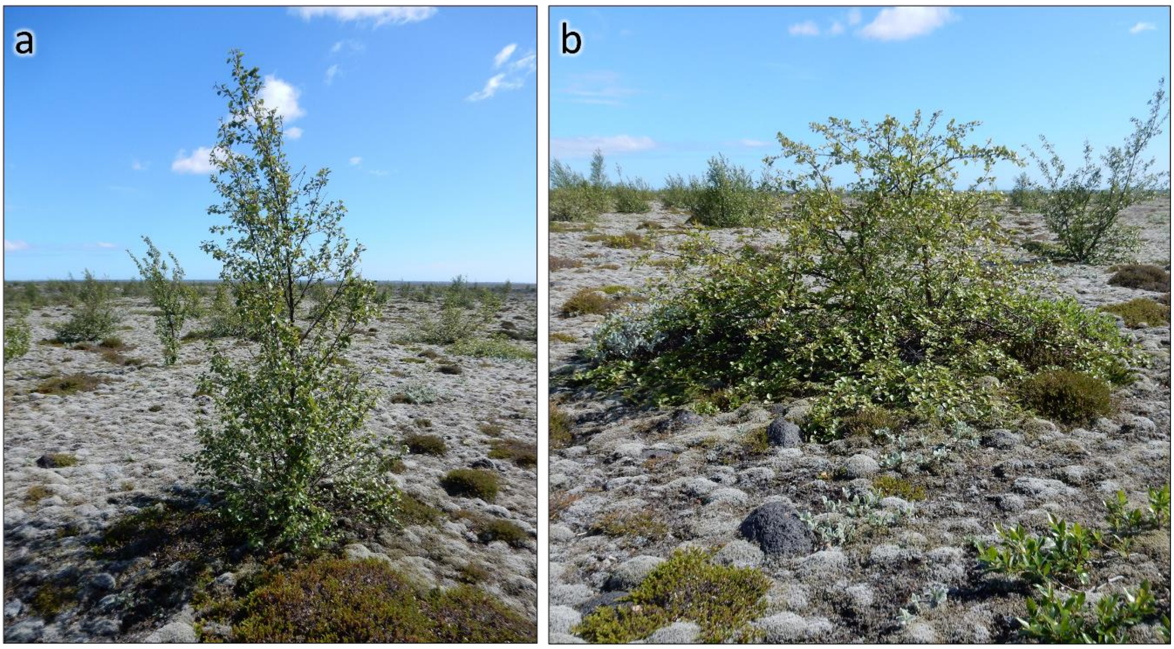

Figure 3.1. Examples showing the variable growth form of mountain birch on Skeiðarársandur, from mostly monocormic (a) to largely polycormic (b) plants.

3.2 Seed losses and their developmental, ecological, and environmental correlates (Paper II)

Germinable seeds only accounted for a very small proportion of the total seed crop, on average 2.7% on Skeiðarársandur and 9.2% at the two sites in Vatnajökull National Park (means of 2019 and 2020). Losses were mainly attributed to the failure of ovules to develop and infections by the gall midge *Semudobia betulae* (Figure 3.2a). Peculiarly, empty seeds were morphologically virtually indistinguishable from those containing a mature embryo (Figure 3.2b). While there were clear differences in unit area weight between empty and filled seeds, seed size and weight varied greatly within both groups and empty seeds had about the same range of variation in size as filled ones. For filled seeds, no correlation was found between unit area weight and germination, but increased germination with tree size was observed, while it decreased with proportion of filled seeds per tree. An overall great spatio-temporal difference was found in germination and proportions of filled seeds within the dataset. Seed density on Skeiðarársandur was high but varied greatly between years. Despite the massive collective losses, density of viable and germinable seeds on Skeiðarársandur was 0.5 seeds/m^2 in 2018 and 75.9 seeds/m^2 in 2019.

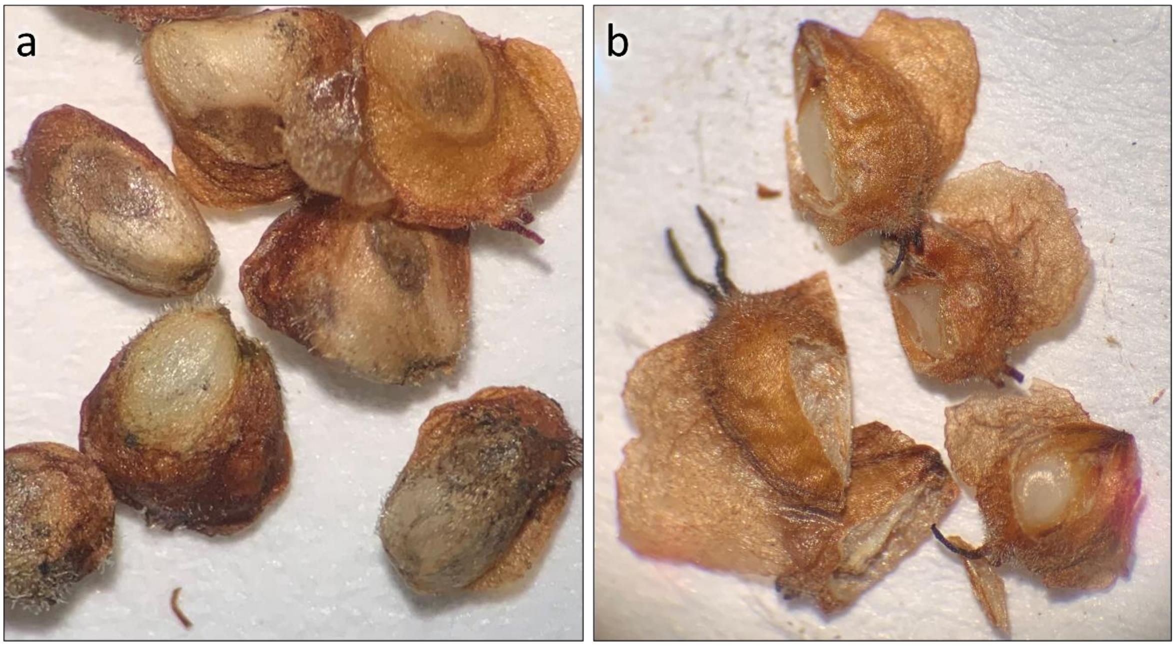

Figure 3.2. Mountain birch seeds predated by Semudobia betulaea *(a), which form conspicuous galls with a dark "weak spot" where they later exit the seeds, and dissected seeds that all looked similar before they were cut open (b), but only the three on the right are filled (revealed by the presence of a light-coloured embryo), the two in the bottom left are empty.*

3.3 Germination and survival of seedlings in relation to microsite types (Paper III)

At both sites, moss (mainly *Racomitrium* spp.) was the most prominent microsite type (Figure 3.3a), and it was generally <2 cm thick. Lichens were mainly *Stereocaulon* fruticose lichens which formed coarse-branched cushions on the plain, and dwarf shrubs were primarily *Empetrum nigrum* and *Calluna vulgaris*. Mountain birch seeds were most likely to be found in vegetated microsite types, where the vegetation structure had trapped windborne seeds. Seedlings were most likely to emerge in the most common microsite type, thin moss (Figure 3.3b). Significantly more first-year and older seedlings were found in moss than expected from random distribution, while fewer than expected were in unvegetated microsite types and those covered by dwarf shrubs. Seedling survival stayed surprisingly high throughout the study. Older seedlings had the highest survival, >90% at the end of the study, and in most cases, >50% of the first-year seedlings marked in 2018 and 2019 survived. Survival did not differ significantly between microsite types.

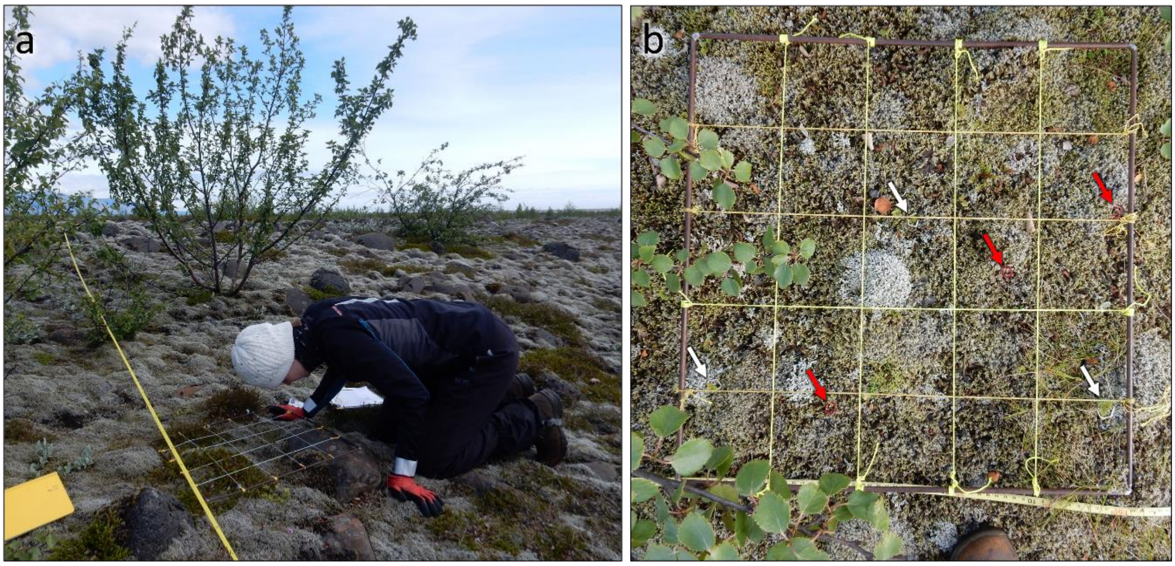

Figure 3.3. Typical substrate in the Skeiðarársandur study area, consisting mostly of low-growing vegetation (a), and an example of a quadrat in a seedling establishment plot (b), showing first-year and older seedlings marked with red and white wire, respectively (pinpointed with same-coloured arrows).

4 Conclusions

The overall aim of the research was to seize the opportunity provided by landscape-scale, natural colonisation, via long distance dispersal onto an early successional outwash plain, to increase the understanding of population ecology and recruitment of mountain birch in Iceland. In the time since the first tiny mountain birch seedlings were noticed on the plain in 1998 (Thórhallsdóttir & Svavarsdóttir, 2022), trees have dramatically changed the visual appearance of the >35 km^2 area where they have established, although through most of it, they are still sparse. Mountain birch forms persistent woodlands in Iceland, but in our study area on Skeiðarársandur it demonstrates the attributes *Betula pubescens* is known for towards the centre of its range, as a highly effective colonist (Atkinson, 1992; Portsmuth & Niinemets, 2007). The low-growing sward vegetation in the early successional environment present in the upper middle part of the plain has created favourable conditions for light-loving mountain birch establishment. Furthermore, its ability to grow in nutrient poor soils (Atkinson, 1992) likely alleviates potential limitations of the low soil fertility (Tómasson, 2023). At the subarctic treeline, mountain birch has been found to outcompete understory shrubs at nitrogen acquisition (Friggens et al., 2023), and if present in the nutrient-poor soil on Skeiðarársandur, this competitive advantage could further influence successional trajectories.

The persistence of a population requires that colonisers leave descendants in the new range (Hargreaves & Eckert, 2014). At the time of this study, the mountain birch population had recently reached reproductive maturity. Thus, the time from the first mountain birch colonisation on Skeiðarársandur around 1990 to the establishment of the first locally recruited generation can be estimated to be of the order of 25 years (Thórhallsdóttir & Svavarsdóttir, 2022). During the study, seed production of the first generation was prolific but varied greatly between years and study sites. Losses to the reproductive potential were huge, mostly attributable to lack of a developed embryo on one hand, and pre-dispersal predation by the gall midge *Semudobia betulae* on the other. The low proportion of filled seeds reflects constraints to successful reproduction. Considering the species' ability to develop fruits in the absence of pollination (Frolova, 1956; Johnsson, 1974; de Groot et al., 1997), the results suggest limited availability of viable pollen (Bona et al., 2022; Holm, 1994b; Sarvas, 1952). In small and isolated populations, mate limitation may favour the evolution of self-compatibility (Pannell et al., 2015), but no evidence of this was detected in the Skeiðarársandur population. Producing some empty seeds can however have important evolutionary and ecological benefits, as their presence may increase the proportion of filled seeds that escape predation (Perea et al., 2013). Despite extensive collective seed losses reported in the study, the density of viable seed appeared to be high, at least in some years. The great between-year variation in seed quantity and quality is typical for a masting species (Masaka & Maguchi, 2001; Gallego-Zamorano et al., 2018). For wind pollinated species in isolated and sparse populations, masting might increase pollination efficiency (Kelly et al., 2001), benefitting reproduction in environments like that on Skeiðarársandur, but none of the years where sufficient data were gathered to evaluate masting could be considered good seed years. Another benefit of masting is predator satiation (Zwolak et al., 2022), and patterns of annual variation in gall midge infestation on Skeiðarársandur seem to fit the widely described predator-prey relationship (Berryman, 2002).

For successful recruitment, seed production needs to be accompanied by available safe sites for progeny to germinate and establish (Aradóttir & Halldórsson, 2018). Mountain birch seeds are small and due to limited energy reserves (Atkinson, 1992), colonisation is strongly shaped by microsite quality and extreme early mortality is common (Aradóttir, 1991; Osumi & Sakurai, 2002). In Iceland, suitable microsite types for mountain birch seedlings include biological soil crust and thin moss, which provide sufficient protection without excessive shading (Aradóttir & Halldórsson, 2018; Elmarsdóttir et al., 2003). In the early successional environment on Skeiðarársandur, the prominent thin *Racomitrium* moss seemed to be very favourable for mountain birch germination, revealing high suitability of the study area for recruitment. Nonetheless, I was surprised by the overall high seedling survival during the study, although at the end of it, seedlings were still small and vulnerable to environmental stress such as severe frost, frost heaving, and prolonged drought. However, barring any unforeseen events, the recruitment strategy of mountain birch regarding dispersal efficiency and seed size and quality seems to be effective under the current circumstances, but great temporal variation in recruitment success highlights its stochasticity (Marteinsdóttir et al., 2018).

Birches have a wide distribution in the northern hemisphere (Ashburner & McAllister, 2013). In boreal forests, birch is a pioneer species that readily and abundantly establishes following disturbance (Lidman et al., 2023). Examples even exist of birch being removed in order to restore *Calluna* heaths (Wilton-Jones & Ausden, 2005). In Iceland, however, extensive deforestation and land degradation has created a great need for ecosystem restoration, including restoration of mountain birch woodlands (Aradóttir & Arnalds, 2001; Barrio & Arnalds, 2022). Ambitious government goals to initiate the process towards 5% birch woodland cover by 2030 (Bonn Challenge, n.d.) highlight the importance of understanding the recruitment ecology and range expansion potentials of mountain birch in Iceland. To that end, the colonisation of Skeiðarársandur has provided lessons and serves as an example of the species' ability to rapidly adjust its range when conditions become favourable, even without human intervention. However, in extensive parts of the country, its natural regeneration and expansion are currently limited by numerous and often interacting factors, including insufficient seed rain in areas far away from mountain birch stands, soil surface instability in severely degraded areas, and herbivory in areas grazed by domesticated sheep (Aradóttir & Halldórsson, 2018; Barrio et al., 2018). Thus, for the necessary scaling-up of woodland restoration in Iceland, emphasis should be placed on areas where minimal interventions are needed to facilitate establishment of mountain birch on a landscape-scale. For evaluating restoration success and its ecosystem impacts, Skeiðarársandur can continue to provide lessons. This early-successional ecosystem with low density of mature trees certainly has the potential to develop into a woodland, but if and how that occurs remains to be demonstrated. This presents a fruitful research setting for the long-term consequences of woodland development in barren, subarctic ecosystems.

Despite the apparent homogeneity of Skeiðarársandur, a decadal comparison revealed diverging trajectories within the mountain birch population, with significant between-site variation in most measured variables. While acknowledging that the role of soil heterogeneity is unresolved, I suggest that this divergence may be, at least in part, driven by intraspecific variation. Mountain birch has a notoriously variable appearance (Jónsson, 2004), which has been attributed to both high phenotypic plasticity and to hybridisation with *Betula nana* (Thórsson et al., 2007; Verwijst, 1988). The whole study area is well within the climatic range for monocormic tree form and as other factors that could influence stature such as grazing seemed limited, indications of intraspecific variation were detected in the study. In turn, the population diverges which can have profound consequences at the ecosystem level due to the engineering attributes of the species (Mitchell et al., 2007; 2010). Thus, intraspecific priority effects can be relevant, especially in the arctic and subarctic where the vascular flora is species poor but may harbour ecologically significant but often cryptic variation at the subspecies level (Brochmann & Brysting, 2008; Grundt et al., 2006; Steltzer et al., 2008). Ultimately, mountain birch colonisation on Skeiðarársandur is set to leave an ecosystem impact with a spatially heterogeneous intraspecific imprint and a long-term legacy.

The patterns and processes revealed in this study have implications in other global settings and environments and across multiple spatial scales. As in recently deglaciated landscapes and extensive new lava fields, plant colonisation on Skeiðarársandur is facilitated by long distance dispersal, but conditions for plant establishment are very different between the sandy sediments on the glacial outwash plain and the surface shaped by a retreating glacier or recent lava. The post-disturbance landscape on Skeiðarársandur has some similar attributes to recently burned boreal stands, where partial or complete removal of the understory has shaped availability of safe sites for different forest species (Anyomi et al., 2022), but the presence of organic forest soil and a local seed bank contrast the coarse mineral soil on the plain. In the outwash plain environment, dominated by low-growing vegetation, suitable microsites for mountain birch seem to be abundant and the recruitment pattern highly clustered, which suggests that the pattern is determined by dispersal limitation, as is typical for early successional species in early successional habitats (Turnbull et al., 2000). Skeiðarársandur is well within the climatic range of mountain birch, but population dynamics of this founder population seem to exhibit parallels to those commonly witnessed at range edges, for example regarding constraints on pre-dispersal reproduction at the forest tundra ecotone (Brown et al., 2019). Regardless of those constraints, the succession on Skeiðarársandur may even bear a resemblance to the early stages of rapid forest establishment in Europe in the early Holocene (Theuerkauf et al., 2014), as on the plain, the dominant species of native late successional woodlands has established in early succession and directs later trajectories.

Species expansion is usually gradual and potentials for long-distance dispersal are most often very limited (Doxford & Freckleton, 2012; der Weduwen & Ruxton, 2019). The landscape-scale establishment of mountain birch on Skeiðarársandur, followed by a swift transformation of the area from a community with slow rates of development, dominated by low stature vegetation, to a rapidly developing ecosystem with significantly different structural dimensions, can thus be regarded as an incipient regime shift (Andersen et al., 2009). Although the distinction from primary succession may be blurred, the rarity of such an event in subarctic Iceland with its severely fragmented woodlands, its scale, as well as its consequences, all fit within the regime shift concept of a large, persistent, and usually unexpected change in an ecosystem (Biggs et al., 2018). Today, as the occurrence of regime shifts driven by anthropogenic global change is escalating, with adverse impacts on ecosystem services worldwide (Rocha et al., 2015), understanding shifts to more productive and resilient states can increase our ability to successfully manage and restore ecosystems.

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Paper I

Establishment of mountain birch (*Betula pubescens* ssp. *tortuosa*) on a glacial outwash plain: Spatial patterns and decadal processes

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Establishment of mountain birch (*Betula pubescens* ssp. *tortuosa*) on a glacial outwash plain: Spatial patterns and decadal processes

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Abstract

Most of the Earth's surface has now been modified by humans. In many countries, natural and semi-natural ecosystems mostly occur as islands, isolated by land converted for agriculture and a variety of other land-uses. In this fragmented state, long-distance dispersal may be the only option for species to adapt their ranges in response to changing climate. The order of arrival of species may leave a lasting imprint on community assembly. Although mostly studied at and above the species level, such priority effects also apply at the intraspecific level. We suggest that this may be particularly important in subarctic and arctic ecosystems. Mountain birch (*Betula pubescens* ssp. *tortuosa*) is characterized by great intraspecific variation. We explored spatio-temporal patterns of the first two mountain birch generations on a homogeneous, early successional glacial outwash plain in SE Iceland that was the recipient of spatially extensive long-distance dispersal ca. 30 years ago. We evaluated the decadal progress of the young population by remeasuring in 2018, tree density and growth form, plant size, and reproductive effort on 30 transects (150 m^2) established in 2008 at four sites on the plain and two adjacent sites ca. 10 km away. All measured variables showed positive increases, but contrary to our predictions of converging dynamics among sites, they had significantly diverged. Thus, two of the sites (only 500 m apart) could not be distinguished in 2008, but by 2018, one of them had much faster growth rates than the other, a higher growth form index reflecting more upright tree stature, greater reproductive effort, and much greater second-generation seedling recruitment. We discuss two hypotheses that may explain the diverging dynamics, site-scale environmental heterogeneity, and legacies of intraspecific priority effects.

KEYWORDS

Betula pubescens ssp. tortuosa, early successional outwash plain, long-distance dispersal, mountain birch, priority effects, spatio-temporal patterns

TAXONOMY CLASSIFICATION

Autecology, Demography, Landscape ecology, Population ecology

1 | INTRODUCTION

One consequence of global climate change will be a shift in the distributions of plant populations (Hamann et al., 2021; Körner & Paulsen, 2004). Alpine populations are already shifting to higher elevations, and arctic and subarctic populations are moving polewards (Parmesan & Yohe, 2003). Changes in species distributions may be continuous, with populations contracting or expanding from an existing margin. Alternatively, discrete new populations may establish through long-distance dispersal (LDD) (Doxford & Freckleton, 2012; Hargreaves & Eckert, 2014). Anthropogenic activities have resulted in extensive habitat loss or degradation, leaving natural ecosystems as isolated islands (Haddad et al., 2015). Although LDD is considered a rare event (Weduwen & Ruxton, 2019), due to today's fragmented state of natural habitats, it may be the only means for many species to reach a suitable habitat.

Plants have little control over the spatial dispersion of their offspring and in most cases, seed dispersal is highly stochastic (Fenner & Thompson, 2005). The successful establishment of a plant population following LDD can be envisaged as having passed through a series of environmental filters (HilleRisLambers et al., 2012). Abiotic filters include climate, microtopography, soil nutrients, and water regime (Harper, 1977; Lett & Dorrepaal, 2018; Pinto et al., 2016). Among the myriad of biotic factors are established plants that can act as competitors, inhibitors, or facilitators (Aradóttir, 2004; Lett et al., 2017; Nystuen et al., 2019), organisms that limit the growth of the new population, e.g., herbivores (Speed et al., 2010; Thórsson, 2008), or symbionts that are crucial for successful establishment, e.g., mycorrhizae (Kokkoris et al., 2020). Each of the above will impose its own scale and degree of patchiness, but the final spatial configurations will determine whether the new species establishes in small discrete patches or as a large, spatially continuous population. The fate of the early colonizers and their offspring, i.e., the first locally recruited generation, will be determined by various spatial and temporal patterns and processes, including the highly stochastic peculiarities of the match or mismatch between the incoming seed rain and the constellation of safe sites (Aradóttir & Halldórsson, 2018) and the genetic constitution of the founder population (Burton et al., 2010; Hargreaves & Eckert, 2014).

The concept of priority effects refers to the legacy or historical contingency that the order of arrival and composition of early species imposes on the structure and function of biological communities (Chase, 2003; Fukami, 2015). The impact of a new arrival will depend on arrival time and the structure and species composition of the receiving ecosystem, e.g., on the suite of functional traits already represented (Körner et al., 2007; Weidlich et al., 2020). For example, a tree species establishing in an early successional, sub-arctic community consisting of low stature herbs and shrubs will change structural dimensions with its tall persistent woody build, affect microclimate with increased retention of winter snow (Helmutsdóttir, 2022) and altered light regime (D'Odorico et al., 2013), affect soil processes through increased litter deposition and enhanced microbial activity (Jonczak et al., 2020; McElhinny et al., 2010), and attract both vertebrate and invertebrate animals (Kittipalawattanapol et al., 2021; Quinn et al., 2021). The arrival of such an ecosystem engineer will have profound consequences at the ecosystem level and steer the community's successional pathways (Mitchell et al., 2007).

Where there is significant intraspecific structural or functional variation, priority effects may also operate at the population level (Faillace et al., 2022; Jung et al., 2010). We suggest that this may be particularly important in subarctic and arctic ecosystems that have low species richness but harbor ecologically important but sometimes cryptic variation at the subspecies level (Brochmann & Brysting, 2008; Dobbert et al., 2021; Grundt et al., 2006). The spatial configuration and genetic composition of the founder population and first locally recruited generation may thus leave a long-term legacy, i.e., shape the spatial dynamics of the community for a long time (García-Girón et al., 2022), but the strength of priority effects may depend on environmental heterogeneity (Tucker & Fukami, 2014).

Mountain birch (*Betula pubescens* subsp. *tortuosa*) displays great variation in growth form, ranging from polycormic decumbent shrubs to monocormic upright trees. We studied the early dynamics following a sudden, large-scale establishment of mountain birch through LDD onto a sparsely vegetated glacial outwash plain in subarctic Iceland. We report on decadal-scale spatio-temporal patterns of density, growth, fecundity, and first local seedling recruitment of the young population, and compare it to two neighboring mountain birch sites. Specifically, we explored whether early demographics of the first generation gave insights into later emerging patterns. Our predictions were that the population characteristics would converge across the flat and apparently homogeneous outwash plain.

2 | METHODS

2.1 | Study species

Betula pubescens Ehrh. is known through much of its natural range as an early successional forest species (Portsmuth & Niinemets, 2007). However, towards the northern limits of its distribution, it is the dominant tree in stable and regionally important ecosystems (Atkinson, 1992). Its wide habitat tolerance, rapid early growth, and precocious reproductive maturity make *B. pubescens* a highly effective colonizer (Jonczak et al., 2020). In Scotland, for example, it is regarded as a top-down ecosystem engineer, shaping the community both above- and below-ground (Mitchell et al., 2007). Colonization by *B. pubescens* can have substantial and long-lasting effects on soil, changing its nutrient supply, pH, and fungal community (Mitchell et al., 2010). Mountain birch (*B. pubescens* ssp. *tortuosa*) is a subspecies of *B. pubescens* native to Fennoscandia (Panarctic Flora, n.d.), generally found towards the altitudinal and latitudinal limits of the species (Atkinson, 1992; Holm, 1994). All native birch in Iceland is regarded as belonging to this subspecies (Kristinsson et al., 2018).

During early primary succession, light is generally abundant, and the shade-intolerant *B. pubescens* (Portsmuth & Niinemets, 2007) can establish due to its ability to grow in nutrient poor soils (Atkinson, 1992). However, surface instability may limit establishment in barren areas, and insufficient seed rain precludes colonization of areas far away from seed sources (Aradóttir & Halldórsson, 2018). In Iceland, these limitations apply over a regionally extensive land, for example, on large glacial outwash plains.

2.2 | Study area

The main research area is within the 1000 km^2 Skeiðarársandur (SKS) glacial outwash plain (63°58′N, 17°12′W, Figure 1a). Since the 14th century, at least, SKS has regularly received outburst floods, leaving it extremely barren by the late Little Ice Age. After the mid-20th century, the disturbance regime had changed, allowing the establishment of early successional vegetation (discussion in Thórhallsdóttir & Svavarsdóttir, 2022). Still, 70% of the central part of the plain between the rivers Gígjukvísl and Skeiðará had <10% vegetation cover in 2002 (Kofler, 2004), and most of SKS remains sparsely vegetated (Figure 1b). In the upper zone of the plain (60–110 m a.s.l.), the substrate is coarser and more stable than in the sandier part seawards. Within that upper zone, mountain birch has established across at least 35 km^2 (V. P. Madrigal et al., unpublished data), despite the nearest seed source being >10 km away. Age distributions based on dendrochronology indicate that mountain birch colonized the area around 1990 (H. M. Birkisdóttir et al., unpublished data; Hiedl et al., 2009; Marteinsdóttir et al., 2007).

Ecosystem development on the plain has been studied since shortly after mountain birch colonization and establishment (Hiedl et al., 2009; Kofler, 2004; Marteinsdóttir et al., 2007, 2010, 2013, 2018; Thórhallsdóttir & Svavarsdóttir, 2022). In 2008, Hiedl et al. (2009) gathered extensive data on the mountain birch population, summarizing its demographics at four sites in the west (S1), central (S2), northeast (S3), and southeast (S4) parts of the mountain birch area (Figure 1c). By then, the largest trees had reached reproductive maturity, but despite an extensive survey, no first-year seedlings were found (Hiedl et al., 2009). At S1 and S2, mountain birch plants were small and sparse, but at S3 and S4, trees were denser and larger (Figure 2). Despite differences in mountain birch density, a vegetation survey conducted in 2018 found similar vegetation composition at all sites (G. Óskarsdóttir et al., unpublished data), with the sward layer dominated by *Racomitrium lanuginosum* and *R. ericoides* (80%, 77%, and 66% average combined cover at S1, S3, and S4, respectively). Other common species included shrubs and dwarf shrubs (*Empetrum nigrum*, *Salix lanata*, *S. herbacea*, *Calluna vulgaris*), graminoids (*Juncus trifidus*, *Festuca richardsonii*, *F. vivipara*), and *Stereocaulon* lichens (Figure 2). For the past decades, SKS has been grazed in summer by around 200 ewes (Thórhallsdóttir & Svavarsdóttir, 2022).

In 2018, two sites were selected within Vatnajökull National Park (VNP) to compare the SKS population to its nearest neighboring mountain birch stands. Site VM is in Morsárdalur valley (Figure 1c), where mountain birch established around 1990 (Thórhallsdóttir & Svavarsdóttir, personal observations), but tree density is still low (Figure 2). Site VS is on the proglacial area in front of Skaftafellsjökull, near Skaftafell weather station (Figure 1c), where mountain birch had begun to establish by the early 1960s (Persson, 1964). While most of the young trees at VM and many on SKS have a largely upright and tree-like growth form, the mountain birch at VS is generally multistemmed and more procumbent (Figure 2). VM is largely sparsely vegetated, but the ground at VS is mostly covered with *Racomitrium* moss and various dwarf shrubs (Figure 2).

Southeast Iceland has a maritime climate with high precipitation. At Skaftafell weather station (86 m a.s.l.; Figure 1c), mean

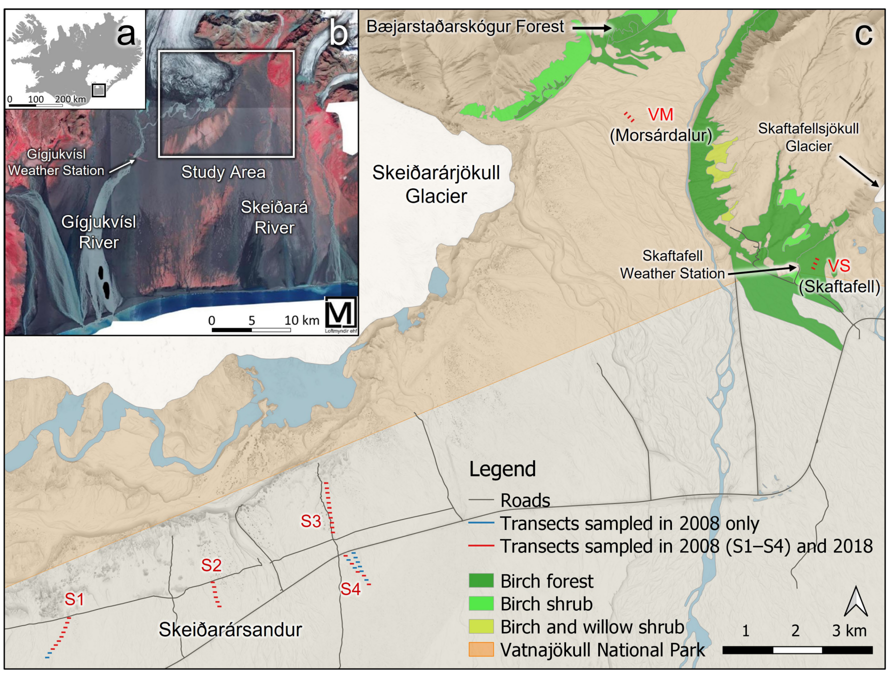

FIGURE 1 Location of Skeiðarársandur (SKS) in SE Iceland (a), the study area within SKS and Vatnajökull National Park (VNP) on an infrared aerial photo (vegetation in red) (b), and the sites/transects on SKS (S1–S4) and in VNP, Morsárdalur (VM) and Skaftafell (VS) (c). Site names are in red font. Map database: National Land Survey of Iceland (2020). Aerial photos: Loftmyndir ehf. (n.d.). Mountain birch map data: Icelandic Institute of Natural History (2019). Geographic information system: QGIS (QGIS Development Team, 2020).

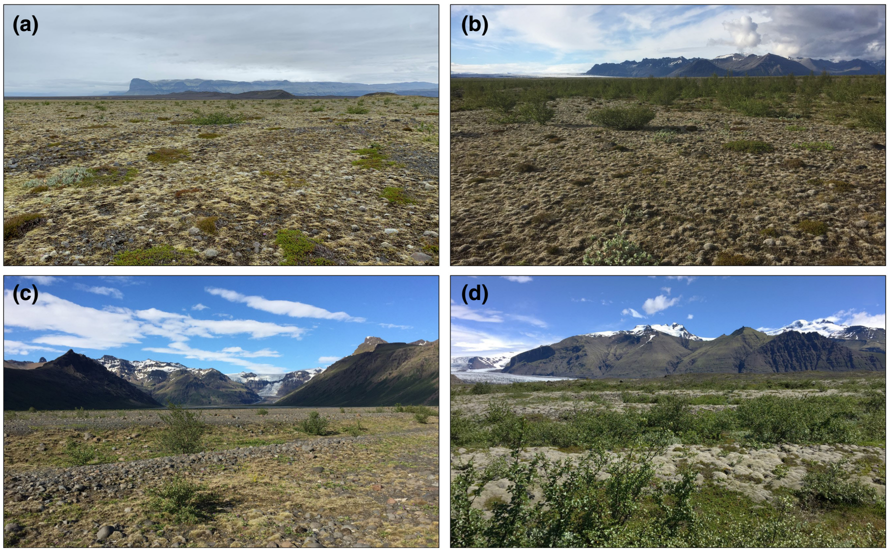

FIGURE 2 Examples of the study sites representing the range of conditions on Skeiðarársandur (a: S1, b: S4) and in Vatnajökull National Park (c: VM, d: VS). The maximum distance between sites is 16 km (S1–VS).

January and July temperatures are 0.9 and 10.9°C, respectively, the mean annual temperature is 5.2°C, and the mean annual precipitation is around 1650 mm (1996–2019, unpublished data from the Icelandic Meteorological Office, www.vedur.is). Six years of data (2014–2019) are available for a temperature station on SKS itself, 5–11 km from S1–S4 (Gígjukvísl, 58 m a.s.l., unpublished data from the Icelandic Meteorological Office, www.vedur.is; Figure 1b). Mean June–August temperatures were comparable for the two stations (10.3°C vs. 10.4°C for the same years in Skaftafell), but it is likely that Skaftafell has higher precipitation, due to proximity to high mountains, and generally lower windspeeds than Gígjukvísl (The Technical University of Denmark, 2021). Prevailing winds are from the northeast (Icelandic Meteorological Office, n.d.).

2.3 | Sampling design

To assess temporal changes in mountain birch demographics on SKS, we built on the 2008 survey of Hiedl et al. (2009) where at each of the four sites on SKS (S1–S4, Figure 1c), 150 m^2 (3 × 50 m) transects were established at 100 m intervals southwards, until the whole north–south spread of mountain birch had been covered, or to a maximum distance of 1000 m from the first transect. At S4, two adjacent N–S series of transects were established to increase the sample size. In total, 40 transects were established in 2008, of which 30 were resampled in 2018 (Figure 1c). The high plant density at S4 made complete resampling too time consuming, and a subset of five transects was selected, three from the western series and two from the eastern one, extending across the whole sampling area from north to south. At S1, GPS coordinates for the two southernmost transects of 2008 were missing, so only the remaining eight transects were resampled.

Both VNP sites comprised three 150 m^2 (3 × 50 m) transects, oriented perpendicular to dry riverbanks (Figure 1c). In total, 36 transects were sampled in 2018, covering 5400 m^2, thereof 4500 m^2 within SKS.

2.4 | Data sampling

In 2008, maximum plant height, length of the longest shoot, and the number of female catkins were recorded for all mountain birch plants within each transect. Since male catkins were not counted, *catkins* hereafter refers to female ones. We use *plant size* and *height* when referring to the length of its longest shoot and greatest height above ground, respectively (see Section 2.5 for further details). We use *trees* when referring to the largest plant category (≥20 cm) in our sample. For the remaining plants in the 2018 resampling, plant size only was measured for plants between 1 and 5 cm (here referred to as *larger seedlings, or L-seedlings*). Due to their large numbers, we counted but did not measure ≤1 cm plants (here referred to as *smaller seedlings, or S-seedlings*), and the size of all was assigned 1 cm. No first-year seedlings (plants with cotyledons) were quantified.

At the three northernmost transects at S4, the number of S-seedlings was so great that we counted a subsample in four 0.25 m^2 quadrats, placed at 33 cm intervals (widthwise) at every other metre (lengthwise) along each transect (n = 100 per transect). Estimated total number of S-seedlings was then extrapolated for each of those transects. Due to VM's small sample size of trees (n = 3, mean size = 126 cm), size and height of 40 additional randomly chosen trees (mean size = 110 cm) were measured in June 2019 and added to the 2018 dataset.

2.5 | Data analyses

For each transect, total density was calculated as the number of all individuals divided by area. Similarly, tree density was calculated using the number of individuals ≥20 cm, flowering adult density by using individuals with catkins, and finally, catkin density by using the total number of catkins. Plant height and the length of its longest shoot are interchangeable for upright trees, but since some plants in our study were prostrate or grew at an angle, we used the latter as a main measure of size. For the same reason, the ratio between plant height and shoot length was used as an index to study spatio-temporal variation in growth form.

We assessed the decadal-scale progress of the SKS population by comparing its status in 2008 and 2018 and exploring between-site variation. We also investigated between-site variation for 2008 separately on one hand, and for 2018 on the other, including the two VNP sites in the latter case. The following response variables were examined: density of all plants, trees, flowering adults, and catkins, presence and abundance of catkins per plant (between-site variation in 2008 not studied, and S-/L-seedlings excluded due to their very high numbers and low likelihood of persistence in the population), plant size (only trees included, due to increased number of young individuals between years), and plant growth form index (S-/L-seedlings excluded due to missing height data). The additional trees measured at VM in 2019 were only used in analyses of plant size and growth form (Sections 3.3 and 3.4).

All data handling and analyses were conducted in *R* v3.6.2. (R Core Team, 2019). Graphs were produced using the package *ggplot2* v3.2.1 (Wickham, 2016). Negative binomial (NB) regressions were fitted with the *MASS* package v7.3-57 (Venables & Ripley, 2002). Negative binomial mixed models (NBMM) and hurdle/zero-altered negative binomial mixed models (hurdle models) were fitted with the package *glmmTMB* v1.1.2.3 (Brooks et al., 2017). Linear mixed models (LMM) were fitted with the package *nlme* v3.1-142 (Pinheiro et al., 2019). Linear models (LM) were fitted with the package *stats* (R Core Team, 2019). Likelihood ratio tests (LRT) were performed using the package *lmtest* v0.9-38 (Zeileis & Hothorn, 2002). Analysis of variance (ANOVA) type II tests were conducted with the *car* package (Fox & Weisberg, 2019). Estimated marginal means (EMMs) were calculated and plotted using the package *emmeans* v1.4.5 (Lenth, 2020). Summary of all models is presented in Table S1.

2.5.1 | Density and catkin production

To explore spatio-temporal variations in mountain birch density, the density of trees, flowering adults, and their catkins, we used NBMM (with log link) with *year*, *site*, and their interaction as explanatory variables and *transect* (nested within sites) as a random effect (Table S1). Site differences for each year were explored using NB regressions. Since all transects were the same size, we used plant/catkin numbers instead of their calculated density for the NBMM and NB regressions. We used EMMs for temporal and spatial pairwise comparisons. For all models, sample sizes equalled the number of transects (S1 = 8, S2 = 6, S3 = 11, S4 = 5, VM = 3, VS = 3).

2.5.2 | Presence and abundance of catkins

Hurdle model (truncated negative binomial, with log link) with *transect* (nested within sites) as a random effect was used to explore how the presence and abundance of catkins related to plant size and differed between sites and years (Table S1). A hurdle model is a two-part model, consisting of a zero-part and a zero-truncated count-part. In the zero-part, the probability of a plant having catkins was estimated, using logistic regression. In the count-part, only flowering plants were included, and the number of catkins was estimated, using NB regression (Zuur et al., 2009).

Two hurdle models were built. The first one included only the SKS data from 2008 and 2018, aiming to identify whether the presence and abundance of catkins in relation to plant size had changed as the SKS population grew older, using *site*, *plant size*, *year*, and interaction between the two latter variables as fixed effects (Table S1). The second model included the 2018 data from SKS and VS (at VM, catkins occurred only on one of the sampled plants, thus the site was excluded), aiming to assess spatial variation in the presence and abundance of catkins in relation to plant size, using *site*, *plant size*, and their interaction as fixed effects (Table S1). In both models, for both model parts, we used backwards elimination for model reduction, with LRT ($\alpha < 0.05$; Zuur et al., 2009). Sample sizes equalled the number of mountain birch plants, excluding S- and L-seedlings (2008: S1 = 29, S2 = 17, S3 = 157, S4 = 52; 2018: S1 = 65, S2 = 25, S3 = 162, S4 = 205, VS = 393).

2.5.3 | Tree size

Spatio-temporal variation in tree size within SKS was studied using LMM with *transect* (nested within sites) as random effect and *year*, *site*, and their interaction as fixed effects (Table S1). The model had separate variance components for each year to account for different variances. Differences in tree size between SKS sites in 2008, on one hand, and all sites in 2018, on the other, were analyzed using comparable LMMs, but for those two models, the only fixed effect was *site*. For all LMMs, *tree size* values were log-transformed to meet model assumptions. We used EMMs for temporal and spatial pairwise comparisons. Sample sizes equalled the number of trees (2008: S1 = 13, S2 = 10, S3 = 115, S4 = 37; 2018: S1 = 40, S2 = 11, S3 = 128, S4 = 80, VM = 43, VS = 226).

The spatial differences in local recruitment may confound comparisons of tree growth among SKS sites and between years. For this reason, and to assess potential canopy height, we studied a sample of the 20 largest trees at each site separately. To study spatio-temporal patterns in the growth of those trees, we used LM with *year*, *site*, and their interaction as explanatory variables (Table S1). Spatial patterns on SKS in 2008, on one hand, and at all sites in 2018, on the other, were also studied using LM, including the variable *site*. The dependent variables were log-transformed if needed to meet model assumptions (see Table S1). We used EMMs for temporal and spatial pairwise comparisons. The sample size was 20 for each site.

2.5.4 | Plant growth form

For growth form comparisons on SKS in 2008 and 2018, we used LMM on *plant height/size ratio* with *year*, *site*, and their interaction as fixed effects and *transect* (nested within sites) as a random effect

(Table S1). Differences in the plant growth form index between sites on SKS in 2008, on one hand, and on SKS and VNP in 2018, on the other, were also explored using LMMs, but for those models, the only fixed effect was *site*. We used EMMs for temporal and spatial pair-wise comparisons. Sample sizes equalled the number of mountain birch plants, excluding S- and L-seedlings (2008: S1 = 29, S2 = 17, S3 = 157, S4 = 52; 2018: S1 = 65, S2 = 25, S3 = 162, S4 = 205, VS = 393).

3 | RESULTS

3.1 | Density and catkin production

Catkin production of the Skeiðarársandur (SKS) mountain birch greatly increased between 2008 and 2018, and all density-related variables had elevated values (Tables 1 and 2; Table S1). Significant between-site differences were found in all among-year comparisons (Tables 1 and 2). Densities were lower at the westernmost (S1 and S2) than at the easternmost sites (S3 and S4). For the most part, plant and catkin densities were very different between the two Vatnajökull National Park (VNP) sites, and while VM values were similar to values recorded for S1 and S2 in 2018, VS values were more similar to those recorded for S3 and S4 (Table 2).

3.2 | Presence and abundance of catkins

The hurdle model for the presence and abundance of catkins on SKS in 2008 and 2018 showed no significant interaction between *year* and *plant size* (Table 3). Therefore, the predicted probability of SKS plants' presence (zero-part of the model) and abundance (count-part of the model) of catkins in relation to plant size did not differ temporally, although their presence varied between years and sites. Backward elimination of the full model, as shown in Table 3 (using LRT), resulted in the best subset model, including *plant size* in both parts, as well as *year* and *site* in the zero-part (Table S3). According to EMMs on that model, the predicted probability of catkin presence

TABLE 1 ANOVA type II test results for NBMM and NB regressions of the number of mountain birch plants (excluding first-year seedlings), trees (≥20 cm), flowering adults, and their catkins at all Skeiðarársandur (SKS) sites in 2008 and 2018 and both Vatnajökull National Park (VNP) sites in 2018.

			All plants		Trees		Flowering		Catkins	
Data	Factor	*df*	χ^2	*p*	χ^2	*p*	χ^2	*p*	χ^2	*p*
SKS 2008 and 2018	Year	1	123.2	**<.001**	9.4	**.002**	36.8	**<.001**	23.6	**<.001**
	Site	3	102.8	**<.001**	32.9	**<.001**	26.7	**<.001**	41.9	**<.001**
	Year: Site	3	168.8	**<.001**	8.4	**.038**	4.5	.208	9.2	**.027**
SKS 2008	Site	3	26.3	**<.001**	28.8	**<.001**	32.8	**<.001**	33.8	**<.001**
SKS and VNP 2018	Site	5	294.8	**<.001**	115.3	**<.001**	83.8	**<.001**	28.4	**<.001**

Note: Significant values are in bold ($p < .05$). Sample sizes equalled the number of transects (S1 = 8, S2 = 6, S3 = 11, S4 = 5, VM = 3, VS = 3). Abbreviations: df, degrees of freedom; χ^2, chi-square value; *p*, *p*-value.

TABLE 2 Sampling effort and density (means ± standard errors) of all mountain birch plants (excluding first-year seedlings), trees (≥20 cm), flowering adults, and their catkins on Skeiðarársandur (S1–S4) in 2008 and 2018 and in Vatnajökull National Park (VM and VS) in 2018. Lowercase and uppercase letters in superscript denote significant differences between sites in 2008 and 2018, respectively (EMMs, $\alpha < 0.05$).

			Density (plants/m^2)			
Year	Site	Sampled area (m^2)	All plants	Trees	Flowering	Catkins
2008	S1	1200	0.033 ± 0.005^{ab}	0.011 ± 0.003^{a}	0.001 ± 0.001^{ab}	0.002 ± 0.002^{a}
	S2	900	0.021 ± 0.011^{a}	0.011 ± 0.009^{a}	0.001 ± 0.001^{ab}	0.013 ± 0.013^{a}
	S3	1650	0.125 ± 0.028^{c}	0.070 ± 0.015^{b}	0.016 ± 0.004^{c}	0.898 ± 0.401^{b}
	S4	750	0.081 ± 0.019^{bc}	0.049 ± 0.013^{b}	0.012 ± 0.004^{bc}	1.315 ± 0.552^{b}
2018	S1	1200	0.085 ± 0.017^{A}	0.033 ± 0.006^{AB}	0.014 ± 0.004^{A}	0.248 ± 0.120^{AB}
	S2	900	0.072 ± 0.014^{A}	0.012 ± 0.006^{A}	0.008 ± 0.004^{A}	0.211 ± 0.194^{BC}
	S3	1650	0.153 ± 0.031^{AB}	0.078 ± 0.015^{BC}	0.043 ± 0.008^{BC}	2.149 ± 0.711^{CD}
	S4	750	9.493 ± 3.550^{D}	0.107 ± 0.036^{C}	0.056 ± 0.022^{C}	11.104 ± 5.158^{D}
	VM	450	0.342 ± 0.173^{BC}	0.007 ± 0.007^{A}	0.002 ± 0.002^{AB}	0.138 ± 0.138^{ABC}
	VS	450	1.171 ± 0.517^{C}	0.502 ± 0.113^{D}	0.180 ± 0.000^{D}	2.353 ± 0.268^{BCD}

Note: Sample sizes equalled the number of transects (S1 = 8, S2 = 6, S3 = 11, S4 = 5, VM = 3, VS = 3).

TABLE 3 ANOVA type II test results for hurdle models of the presence and abundance of catkins at all Skeiðarársandur (SKS) sites in 2008 and 2018, and one Vatnajökull National Park site (VS) in 2018.

	SKS 2008 and 2018				SKS and VS 2018			
Model part	**Factor**	***df***	***χ²***	***p***	**Factor**	***df***	***χ²***	***p***
Zero	Year	1	7.6	**.006**	Size	1	180.0	**<.001**
	Size	1	148.5	**<.001**	Site	4	18.0	**.001**
	Site	3	13.4	**.004**	Size:Site	4	5.2	.267
	Year:Size	1	1.4	.236				
Count	Year	1	0.3	.578	Size	1	32.4	**<.001**
	Size	1	25.1	**<.001**	Site	4	23.9	**<.001**
	Site	3	7.5	.059	Size:Site	4	2.0	.745
	Year:Size	1	2.3	.133				

Note: Results from full models are shown. Significant values are in bold ($p < .05$). Sample sizes equalled the number of mountain birch plants, excluding S- and L-seedlings (2008: S1 = 29, S2 = 17, S3 = 157, S4 = 52; 2018: S1 = 65, S2 = 25, S3 = 162, S4 = 205, VS = 393).
Abbreviations: *df*, degrees of freedom; χ^2, chi-square value; *p*, *p*-value.

was higher at S2/S3 than at S4, and higher in 2018 than in 2008 (Table S4). However, only plant size had significant effects on predicted catkin abundance (Table S3).

For the spatial variation in 2018, including the VS data, *plant size x site* interaction was not significant (Table 3), and according to LRT, could be dropped from both parts of the model (Table S3). Therefore, in Figure 3, results for the reduced hurdle model (Table S1) on the presence and abundance of catkins on SKS and VS in 2018 are presented, using the variables *plant size* and *site* in both parts. Plant size had highly significant effects in both parts of the model (Table 3). Looking at each part of the model separately, the predicted probability of catkin presence was lower at S4 than at S2, S3, and VS (Figure 3a; Table S4), but of all flowering adults, catkin predicted abundance was highest at S4, with significant difference between S4 and S1/VS on one hand, and S3 and VS on the other (Figure 3b; Table S4).

3.3 | Tree size

The LMM for tree size on SKS in 2008 and 2018 revealed significant effects of fixed factors and their interaction (Table 4), reflecting different growth rates between sites (Figure 4a). LMM on the 2008 data (not shown in figure) revealed significant differences between sites (Table 4), with plants significantly smaller at S2 than at S3 (*z*-value = −3.442, $p = .012$) and S4 (*z*-value = −2.813, $p = .047$). In 2018, the difference between sites was also significant (Table 4), with plants on average larger at S4 and VM than at S1 and VS (Figure 4b).

For the 20 largest trees at each site, LM on the SKS data in 2008 and 2018 revealed significant effects of fixed factors and their interaction (Table 4). During the study period, the growth rate of the largest trees thus differed between sites (Figure 5). Between-site differences were also noticed when studying each year separately (Figure 5; Table 4). In 2018, neither VNP site was significantly different from S3, but a significant difference was found between all other sites (Figure 5).

3.4 | Plant growth form

Temporal patterns of the plant growth form index varied among SKS sites (Table 5; Figure 6a), and between-site variation was notable in both years (Table 5). In 2008 (data not shown in figure), index values were lower at S1 than at S2 (*z*-value = −3.334, $p = .013$) and S3 (*z*-value = −3.213, $p = .018$). In 2018, however, plants were most upright at S4 and VM, but least upright at site VS, which had significantly lower index values than all other sites, except S2 (Figure 6b).

4 | DISCUSSION

4.1 | From long-distance dispersal to self-sustaining population

For the first generation of mountain birch to establish on the plain, the plants had to pass through several environmental filters, one of which was seed dispersal (HilleRisLambers et al., 2012). Seed rain densities for wind dispersed seeds, such as *Betula pubescens*, decline steeply with distance from the mother plant (Aradóttir, 1991; Fenner & Thompson, 2005), and successful colonization kilometers away is rare (Doxford & Freckleton, 2012; Weduwen & Ruxton, 2019). Preliminary analyses of potential parent populations show that the mountain birch on Skeiðarársandur (S4) is derived from the woodland approximately 10 km northeast of the plain, predominantly from Bæjarstaðarskógur forest (K. P. Magnússon et al., unpublished data). Long-distance dispersal over roughly 10 km of mostly non-suitable habitats (barren and unstable sand) was needed for first generation establishment, showing the species' ability to shift its geographical range, even in a fragmented landscape (Hargreaves & Eckert, 2014).

Mountain birch density and catkin production on Skeiðarársandur greatly increased during the study period, although temporal patterns were mostly site-specific (Table 1, 2 and Table S1). Like most northern

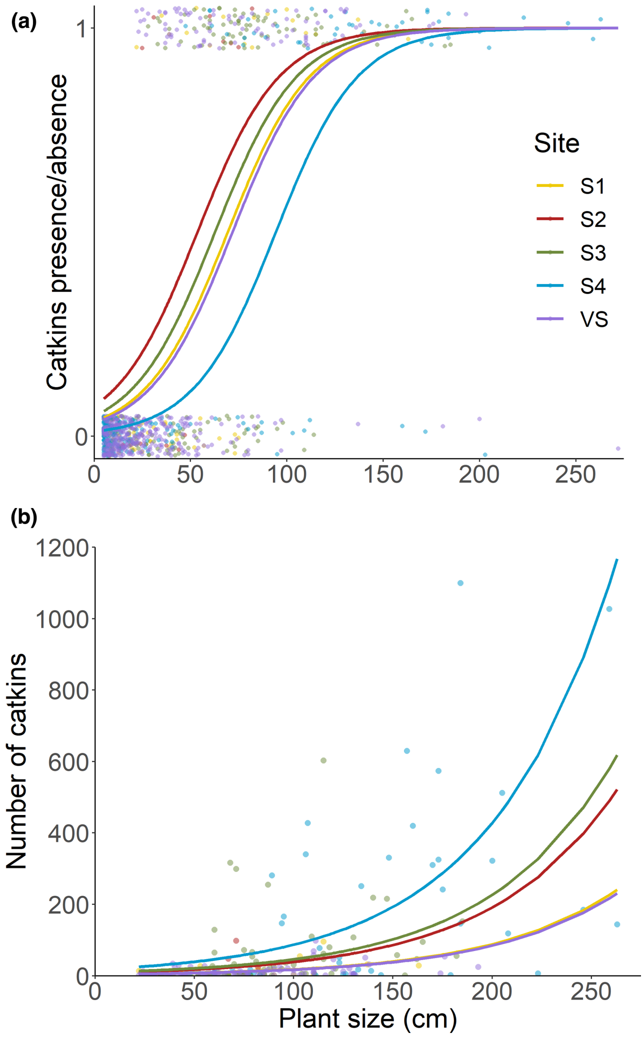

FIGURE 3 Predicted probability of mountain birch catkin presence (a), and abundance (b) in relation to plant size (length of its longest shoot) for the Skeiðarársandur sites (S1–S4) and one Vatnajökull National Park site (VS) in 2018. Results from the reduced model (see Tables S1 and S3) are shown. Sample sizes equalled the number of mountain birch plants, excluding S- and L-seedlings (2008: S1 = 29, S2 = 17, S3 = 157, S4 = 52; 2018: S1 = 65, S2 = 25, S3 = 162, S4 = 205, VS = 393).

hemisphere trees, mountain birch is regarded as a masting species, i.e., it intermittently produces large seed crops with synchrony across extensive geographic regions (Holm, 1994; Koenig & Knops, 2000; Zamorano et al., 2018). Therefore, the patterns in 2008 and 2018 might not be representative for other years. We do not have information on masting in the area, but the increased tree size in the study period (Figures 4a and 5), along with the rising predicted presence and abundance of catkins with plant size (Figure 3), all support a conclusion of greatly increased reproductive effort through the study period, noting that each catkin usually contains around 200 seeds (Holm, 1994). Looking further back, the increase becomes even more pronounced. In 2004, Marteinsdóttir et al. (2007) counted flowering adults and catkins in three areas, approximately corresponding to S1, S3, and S4. Despite a much larger research area (15,800 m^2), only 10 flowering adults were recorded (3% of the sample), with a total of 106 catkins, or 0.007 catkins/m^2. Using these data for comparison, catkin density had increased 150-fold by 2008, to 1.0 catkin/m^2, and almost 700-fold by 2018, to 4.7 catkins/m^2.

In 2004, most individuals in the then roughly 15-year-old population had not yet reached reproductive maturity, and both plant and seedling densities were low (Marteinsdóttir et al., 2007). In the full dataset from 2008 (6000 m^2), no first-year seedlings and only 25 S-seedlings (6% of sample) were recorded. However, in 2018, S-seedlings were estimated to be over 6000 (83% of the sample), and first-year seedlings were in the thousands. As we did not detect exceptional weather events or growing season trends through the study period (unpublished data from the Icelandic Meteorological Office, www.vedur.is), we propose that the recent surge in the seedling establishment is linked to the previously described surge in seed production, indicating greater limitation by seed than microsite early on in our study. If most of the newly established seedlings have a local origin, then this signals a turning point in the population's development since the persistence of a population requires that colonizers leave descendants in the new range (Hargreaves & Eckert, 2014). However, for a lasting impact, the long-term survival of those seedlings is needed. If some of these recruits persist, then the time from the initial colonization in ca. 1990 to the establishment

TABLE 4 ANOVA type II test results for LMMs of tree (≥20 cm) size (χ^2) and LMs of the size of the 20 largest trees (*F*) at all Skeiðarársandur (SKS) sites and both Vatnajökull National Park (VNP) sites in 2008 and 2018.

		SKS 2008 and 2018			SKS 2008			SKS and VNP 2018		
Data	Factor	*df*	χ^2/*F*	*p*	*df*	χ^2/*F*	*p*	*df*	χ^2/*F*	*p*
All trees	Year	1	50.3	**<.001**						
	Site	3	20.3	**<.001**	3	16.3	**<.001**	5	24.3	**<.001**
	Year:Site	3	9.7	**.021**						
20 largest trees	Year	1	112.7	**<.001**						
	Site	3	114.8	**<.001**	3	45.1	**<.001**	5	60.8	**<.001**
	Year:Site	3	7.4	**<.001**						

Note: Significant values are in bold ($p < .05$). Sample sizes in the LMMs equalled the number of trees (2008: S1 = 13, S2 = 10, S3 = 115, S4 = 37; 2018: S1 = 40, S2 = 11, S3 = 128, S4 = 80, VM = 43, VS = 226).

Abbreviations: *df*, degrees of freedom; χ^2, chi-square value; *F*, *F*-value; *p*, *p*-value.

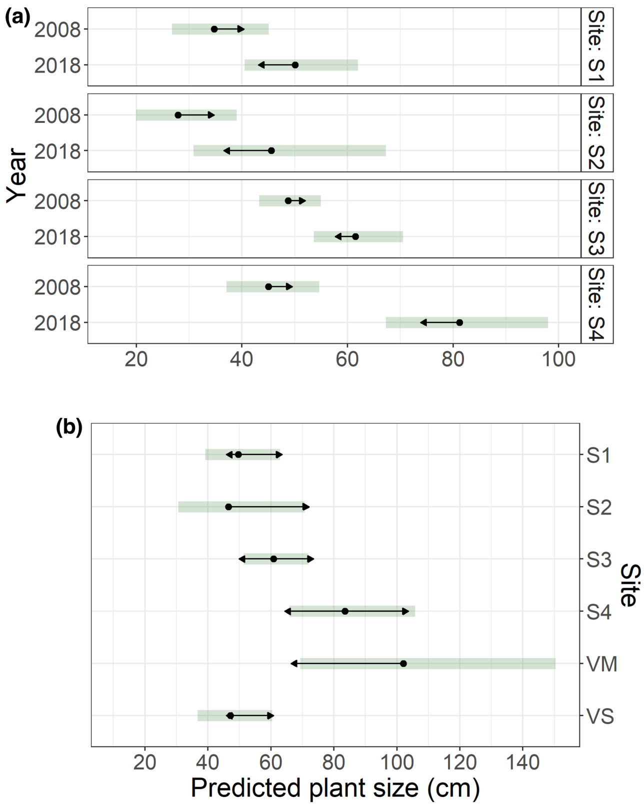

FIGURE 4 EMMs based on LMMs of mountain birch tree (≥20 cm) size (length of the longest shoot), showing (a) temporal change for each Skeiðarársandur site (S1–S4) between 2008 and 2018, and (b) spatial variation in 2018, including the Vatnajökull National Park sites (VM and VS). The bars show 95% confidence intervals for the EMMs, and the arrows comparisons among them. If an arrow from one mean overlaps an arrow from another group, the difference is not significant ($\alpha < 0.05$). Note that the x-axes differ between graphs, and a comparison between sites cannot be made using Figure 4a, because arrows are not comparable between them. Sample sizes equalled the number of trees (2008: S1 = 13, S2 = 10, S3 = 115, S4 = 37; 2018: S1 = 40, S2 = 11, S3 = 128, S4 = 80, VM = 43, VS = 226).

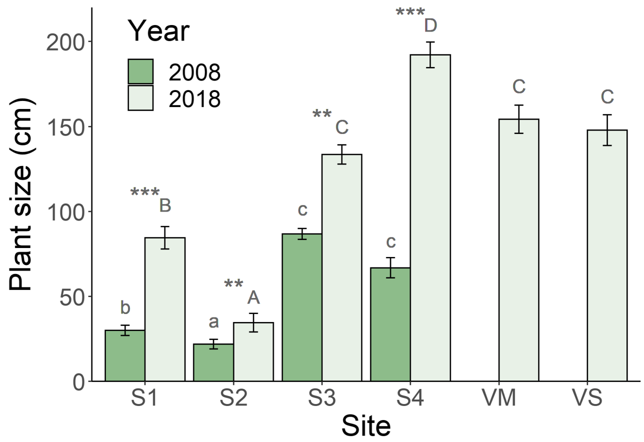

FIGURE 5 Average size (with standard errors) of the 20 largest mountain birch trees at each site in 2008 and 2018. Lowercase and uppercase letters denote significant differences between sites in 2008 and 2018, respectively, while asterisks denote significant differences between years for each site (EMMs, $\alpha < 0.05$). At S2 in 2008, the total sample size was only 19 plants.

of the first locally recruited generation can be estimated to be of the order of 25 years. It is certainly more than 15 years, and less than 30 years.

4.2 | Emerging spatial and temporal patterns

Most of the population variables showed significant variation among sites and years, and several also had *year x site* interactions. Sites S3 and S4 appeared quite alike in 2008, having similar growth form indices, and S3 had a slightly (although not statistically significant) greater mean tree size and density of plants, trees, flowering trees, and catkins (Table 2). By 2018, this had been reversed. Then, the 20 largest trees at S4 were significantly larger than at S3, plants had a significantly higher growth form index and five times greater (although not statistically different) density of catkins (Figures 5 and 6b, Table 2). Sites S1 and S2 are more difficult to place with respect to S3 and S4. Although our unpublished data (H. M. Birkisdóttir et al.) do not indicate that their oldest birch plants are younger, they were smaller and sparser in 2008, had a smaller increase in average tree size between years, and had lower catkin densities in 2018 (Table 2, Figures 4 and 5). An intriguing anomaly is that while the growth form index increased from 2008–2018 at S1 and S4, indicating a shift to more upright growth, it actually decreased at S2 and S3, with plants becoming more decumbent (Figure 6a). Roughly, the sites fall into two classes. S4 has largely monocormic trees with a high growth rate, high fecundity, and extremely high second-generation seedling densities. Two of the other sites (S2 and S3) have largely decumbent shrubby birch with lower growth rates, much lower catkin densities, and very limited second-generation recruitment. S1 partly resembles S2 and S3, but its shift in growth form index, increase in the size of the 20 largest trees, and its 2018 values of density of plants, trees, and flowering plants in comparison with S4 values in 2008 may indicate that it may fall more in line with S4, but with a time lag.

The two populations within Vatnajökull National Park are quite different. The young VM population had a similar average tree size and growth form as S4 in 2018 (Figures 4b and 6b), but the very low percentage of flowering at VM precludes comparison of reproductive traits. Meanwhile, the older VS population had very different traits. It had by far the highest tree density and the greatest density of flowering plants (Table 2), but in many other respects, it falls in line with S3. VS plants had the most decumbent growth form of all the populations, trees were significantly smaller than at S4 and VM, and they had the lowest number of catkins relative to size (Figures 3b, 4b, and 6b). Our results are in line with Thórsson et al. (2007), who contrasted the procumbent and shrubby plants in Skaftafell (VS) with the tall monocormic trees in the old forest in Bæjarstaðarskógur, close to VM. (Figure 6b). Mountain birch has a notoriously variable growth form, ranging from decumbent (sometimes virtually horizontal) polycormic shrubs to monocormic upright trees that in Iceland may reach

TABLE 5 ANOVA type II test results for LMMs of plant growth form index (largest shoot height to length ratio) at all Skeiðarársandur (SKS) sites in 2008 and 2018 and both Vatnajökull National Park (VNP) sites in 2018.

	SKS 2008 and 2018			SKS 2008			SKS and VNP 2018		
Factor	*df*	χ^2	*p*	*df*	χ^2	*p*	*df*	χ^2	*p*
Year	1	0.0	.965						
Site	3	27.4	**<.001**	3	14.1	**.003**	5	141.5	**<.001**
Year:Site	3	25.3	**<.001**						

Note: Significant values are in bold ($p < .05$). Sample sizes equalled the number of mountain birch plants, excluding S- and L-seedlings (2008: S1 = 29, S2 = 17, S3 = 157, S4 = 52; 2018: S1 = 65, S2 = 25, S3 = 162, S4 = 205, VM = 67, VS = 393).

Abbreviations: *df*, degrees of freedom; χ^2, chi-square value; *p*, *p*-value.

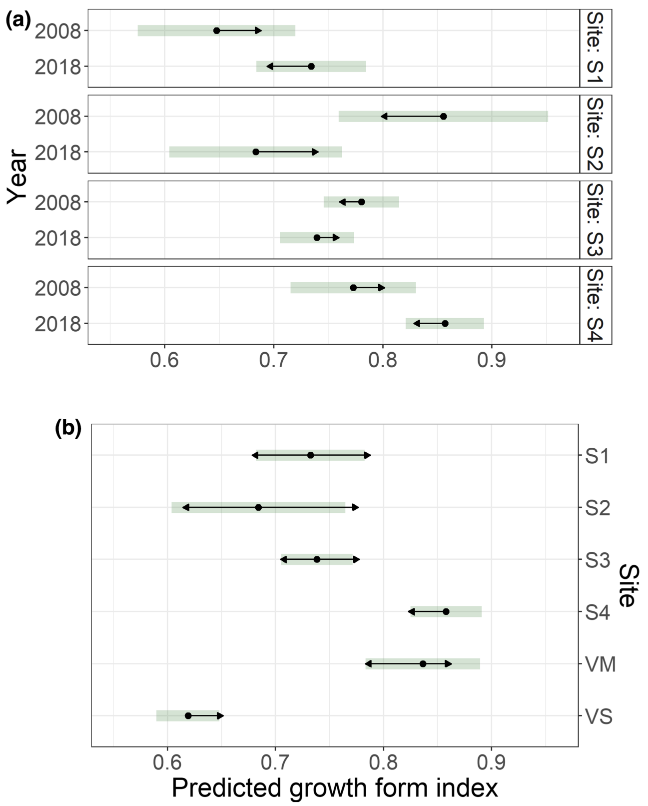

FIGURE 6 EMMs based on LMMs of mountain birch growth form index (largest shoot height to length ratio), showing (a) temporal change for each Skeiðarársandur site (S1–S4) between 2008 and 2018, and (b) spatial variation in 2018, including the Vatnajökull National Park sites (VM and VS). The bars show 95% confidence intervals for the EMMs, and the arrows comparisons among them. If an arrow from one mean overlaps an arrow from another group, the difference is not significant ($\alpha < 0.05$). Note that a comparison between sites cannot be made using Figure 6a, because arrows are not comparable between them. Sample sizes equalled the number of mountain birch plants, excluding S- and L-seedlings (2008: S1 = 29, S2 = 17, S3 = 157, S4 = 52; 2018: S1 = 65, S2 = 25, S3 = 162, S4 = 205, VM = 67, VS = 393).

10–12 m. The shrubby form is typical of highly oceanic, windy, and higher-elevation sites, with the tree form dominating in more benign locations, e.g., lowland valleys (Atkinson, 1992; Jónsson, 2004; Verwijst, 1988). This structural diversity has both been attributed to high phenotypic plasticity and to hybridisation with *Betula nana* (Thórsson et al., 2007; Verwijst, 1988).

For trees in general, greater physiological plasticity has been associated with shade-intolerant species colonizing early successional habitats (Portsmuth & Niinemets, 2007) but the plastic responses of tree architecture to local environmental conditions are generally not well known (Van de Peer et al., 2017). Neither has been investigated for *Betula pubescens*. Skeiðarársandur and vicinities have a milder climate and longer growing season than most of the rest of Iceland, and the old forest at Bæjarstaðarskógur harbors some of Iceland's tallest mountain birches. The study sites are, therefore, climatically well within the range occupied by the monocormic tree form. Jónsson (2004) concluded that the growth form variation in Icelandic mountain birch is accompanied by differences in growth rates, with the upright monocormic form having faster growth than the shrubby decumbent form. Positive correlation between growth rate and life expectancy has also been found (Jónsson, 2004), indicating that greater canopy height and stand age might be expected at VM and at least in parts of Skeiðarársandur than at VS.

In mountain birch, age/size at reproductive maturity varies among individuals and reflects environmental conditions (Aradóttir, 1991; Atkinson, 1992). Here, the predicted probability of catkin presence increased rapidly at all sites from a threshold plant size of ca. 50 cm (Figure 3a; VM excluded due to low flowering frequency). For catkin abundance per flowering plant, the difference between VS and S4 was especially apparent (Figure 3b), and although the density of flowering plants was more than three times greater at VS than S4, catkin density at VS was less than a quarter of the density at S4 (Table 2).

The number of flowers produced is generally positively correlated with plant size (Fenner & Thompson, 2005; Table 3), but this is unlikely to fully explain the difference in catkin abundance between S4 and VS (Figure 3b). Resources may also limit reproduction (Campbell & Halama, 1993). Soil carbon and nitrogen data (%) are available for S4 (J. B. U. Tómasson et al. unpublished data), and VS's close vicinity (Vilmundardóttir et al., 2015). All samples were very low in soil fertility, but it was slightly higher near VS in 2010–2011 ($C = 1.77 \pm 1.10$, $N = 0.101 \pm 0.064$ [means ± standard deviation], $n = 18$) than at S4 in 2018 ($C = 1.42 \pm 0.92$, $N = 0.044 \pm 0.015$, $n = 16$). Soil nutrients are therefore unlikely to explain the difference in catkin production of flowering trees between the two sites in 2018, and to elucidate the reproduction dynamics of the young population, more research is needed on temporal variation in flowering and possible explanations.

4.3 | Site divergence and possible environmental correlates

Two hypotheses may be advanced to explain the divergence across Skeiðarársandur, first that despite the highly similar climate and apparent homogeneity of the plain, there is sufficient environmental heterogeneity to induce the observed difference in growth and dynamics, and second that the population differs genetically among sites. We begin by considering the first hypothesis.

With time, the young mountain birch population on Skeiðarársandur has developed diverging patterns among sites (Tables 1, 4, and 5), roughly dividing them into two classes by 2018 (see Section 4.2). Since the temporal divergence was particularly noticeable for S3 and S4, we focus our discussion on those sites. In 2008, the two could not be distinguished in terms of plant densities or size distributions and were predicted to advance at comparable rates (Hiedl et al., 2009). Unexpectedly, this turned out not to be the case, resulting in them being characterized into different classes by 2018. Sites S3 and S4 are only 500 m apart and appear very alike to the human eye. One noticeable difference between them was the unequal increase in plant density (Table 2), largely explained by the huge number of seedlings at S4 in 2018.

Seedling establishment is one of the most crucial stages in a plant's life cycle and can be affected by a range of factors, including microhabitat (Lett et al., 2017; Nystuen et al., 2019), herbivores (Speed et al., 2010), soil moisture (Pinto et al., 2016), nutrient status (Harper, 1977), mycorrhizal associations (Kokkoris et al., 2020), and diverse combinations of interactions among factors (Lett & Dorrepaal, 2018). Preliminary results from vegetation analyses at the study sites (G. Óskarsdóttir et al., unpublished data) suggest that the sward layer at S3 and S4 is similar enough for microsite limitations to be comparable (see Section 2.2). *Racomitrium* mosses dominated the sward layer vegetation, and their average thickness was 1.3 cm at both sites. Effect of mosses on the seedling establishment is dependent on their traits and varies with climate (Lett et al., 2017). In Iceland, thin moss (<2 cm) has been shown to constitute a favorable microsite for mountain birch establishment (Aradóttir & Halldórsson, 2018). Thus, we conclude that the relatively few seedlings at S3 cannot be ascribed to the scarcity of microsites.

Another potential check on the seedling establishment is herbivory (Speed et al., 2010; Thórsson, 2008). Skeiðarársandur is not protected from grazing, but during summer, only 200 ewes graze the vast but mostly sparsely vegetated plain (Thórhallsdóttir & Svavarsdóttir, 2022). At our sites, low frequency of grazing marks attributed to sheep, recorded on 8% and 1% of mountain birch plants (S-seedlings excluded) in 2008 and 2018, respectively (G. Óskarsdóttir et al., unpublished data), suggests limited impact on the population. Furthermore, given the short distance and absence of barriers between S3 and S4, it is scarcely conceivable that the difference can be assigned to grazing.

The lack of obvious above-ground environmental differences between the two sites raises questions on possible variation in soil properties. Plant growth is often resource-limited (Ågren et al., 2012), especially in early succession (Marteinsdóttir et al., 2018; Vitousek et al., 1993). At both sites, trees were significantly larger in 2018 than in 2008, and within years, tree size was not statistically different between sites (Figure 4). However, spatial divergence in size of the largest trees (Figure 5) suggests that conditions for growth had indeed been more favorable at S4 than S3 in the study period, and resources may have been more limiting at S3 than S4. Comparison of soil properties between sites are needed to clarify this.

On Skeiðarársandur, the establishment of mountain birch is likely to increase rates of ecosystem development, e.g., by improving soil physical properties and nutrient status (Jonczak et al., 2020; Weidlich et al., 2020), increasing litter production and organic matter accumulation (McElhinny et al., 2010), ameliorating microclimate (D'Odorico et al., 2013), and changing above- and below-ground communities and successional processes (Kittipalawattanapol et al., 2021; Mitchell et al., 2007, 2010; Quinn et al., 2021). Consequently, the mountain birch population can leave a long-term legacy that steers the community's successional pathway for years and decades to come (García-Girón et al., 2022).

4.4 | Historical contingency and population development

The question of how the assembly of biological communities is influenced by past history remains a core issue in ecology (Chase, 2003; Fukami et al., 2016). Among key concepts are legacies or ecological memories, which have especially been explored in relation to disturbances and forest ecosystems (Johnstone et al., 2016), and in a sense, ecosystem succession can at least sometimes be considered as an expression of biological legacy. We contend that these issues also need to be considered at the intraspecific level, and that this may be particularly relevant for arctic and subarctic ecosystems. While the arctic/subarctic vascular flora is species poor compared to most other biomes (Grundt et al., 2006; Väre et al., 2013), it is now recognized that this may mask ecologically important but largely cryptic variation at the subspecies level (e.g., Brochmann & Brysting, 2008; Steltzer et al., 2008; Stubbs et al., 2020). Furthermore, these issues are likely to be particularly relevant in early succession, for example, when a tree species establishes in a community composed of low-growing vegetation. This qualifies as a priority effect in the sense of niche modification, as defined by Fukami (2015).

As already discussed (Section 4.3), a spatial divergence of the Skeiðarársandur population is evident in almost all the population variables recorded: plant growth form, tree size, and catkin as well as seedling densities (Figures 4 and 6, Table 2). There are two possible explanations for that spatial divergence. The first is that despite the apparent homogeneity of Skeiðarársandur outwash plain, there was sufficient underlying heterogeneity in the substrate at the site scale to significantly affect the aboveground structure (see Section 4.3). The millennial build-up of Skeiðarársandur is largely due to frequent and massive glacial outburst floods, with the largest Little Ice Age floods extending over more or less the entire 1000 km^2

plain (Thórhallsdóttir & Svavarsdóttir, 2022). While there is a well recognizable seawards gradient in soil grain size, it seems rather unlikely that soil properties can differ sufficiently in the short distance (500 m) between S3 and S4, to account for the demographical differences. The second explanation is that the birch on Skeiðarársandur has originated from genetically different sources. At this moment, we are unable to distinguish between the two.

Irrespective of the nature of the variation, we conclude that the young mountain birch population on Skeiðarársandur appears to be set on diverging trajectories. On one hand, there are the fast-growing, largely monocormic plants with massive recruitment of second-generation seedlings at S4, and on the other, the slower growing, polycormic plants with limited recruitment, most pronounced at S2. While acknowledging that the role of soil heterogeneity is unresolved, we suggest that the large-scale establishment of mountain birch on Skeiðarársandur is an example of how the stochastic colonization of a niche-modifying species is set to leave an ecosystem impact with a significantly different intraspecific imprint and a long-term legacy. This is all the more remarkable in light of the apparent homogeneity of the flat and featureless outwash plain environment.

In the context of distribution shifts due to global climate change, our study may provide lessons. Although directly (climate warming) and indirectly (glacier retreat) mediated by climate change, the colonization of mountain birch on Skeiðarársandur was a natural process (Thórhallsdóttir & Svavarsdóttir, 2022). The massive long-distance (≥10 km) dispersal, spatially extensive colonization (>35 km^2 area from ca. 1990–2016), and high, although spatially variable, recruitment of the second generation, all illustrate the mountain birch's ability to rapidly adjust its range in a shifting environment.

AUTHOR CONTRIBUTIONS

Guðrún Óskarsdóttir: Formal analysis (equal); investigation (equal); visualization (lead); writing – original draft (lead); writing – review and editing (lead). **Thora Ellen Thorhalsdottir:** Conceptualization (equal); data curation (equal); funding acquisition (equal); investigation (equal); methodology (equal); supervision (equal); visualization (supporting); writing – original draft (lead); writing – review and editing (lead). **Anna Helga Jónsdóttir:** Formal analysis (equal); visualization (supporting); writing – original draft (supporting); writing – review and editing (supporting). **Hulda Margrét Birkisdóttir:** Investigation (equal); writing – original draft (supporting); writing – review and editing (supporting). **Kristín Svavarsdóttir:** Conceptualization (equal); data curation (equal); funding acquisition (equal); investigation (equal); methodology (equal); supervision (equal); visualization (supporting); writing – original draft (lead); writing – review and editing (lead).

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Data are available in the Dryad public repository: https://doi.org/10.5061/dryad.4b8gthtgj.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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Supporting information

TABLE S1. Summary of models run.

Model ID	Model description	Model equation	Data	R-code
1Ai	Negative binomial mixed model	n(All plants per transect) ~ Year x Site + (1|Site/Transect)	SKS 2008 and 2018	glmmTMB (family = nbinom2 (link = ”log”)
1Aii	Negative binomial mixed model	n(Trees per transect) ~ Year x Site + (1|Site/Transect)	SKS 2008 and 2018	glmmTMB (family = nbinom2 (link = ”log”)
1Aiii	Negative binomial mixed model	n(Flowering adults per transect) ~ Year x Site+ (1|Site/Transect)	SKS 2008 and 2018	glmmTMB (family = nbinom2 (link = ”log”)
1Aiv	Negative binomial mixed model	n(Catkins per transect) ~ Year x Site + (1|Site/Transect)	SKS 2008 and 2018	glmmTMB (family = nbinom2 (link = ”log”)
1Bi	Negative binomial model	n(All plants per transect) ~ Site	SKS 2008	glm.nb
1Bii	Negative binomial model	n(Trees per transect) ~ Site	SKS 2008	glm.nb
1Biii	Negative binomial model	n(Flowering adults per transect) ~ Site	SKS 2008	glm.nb
1Biv	Negative binomial model	n(Catkins per transect) ~ Site	SKS 2008	glm.nb
1Ci	Negative binomial model	n(All plants per transect) ~ Site	SKS and VNP 2018	glm.nb
1Cii	Negative binomial model	n(Trees per transect) ~ Site	SKS and VNP 2018	glm.nb
1Ciii	Negative binomial model	n(Flowering adults per transect) ~ Site	SKS and VNP 2018	glm.nb
1Civ	Negative binomial model	n(Catkins per transect) ~ Site	SKS and VNP 2018	glm.nb
2Ai	Hurdle/zero-altered negative binomial mixed models	Catkins ~ Site + Size x Year + (1|Site/Transect), zi = ~ Site + Size x Year	SKS 2008 and 2018, S- and L-seedlings excluded	glmmTMB (family = truncated_nbinom2 (link = “log"))
2Aii	Hurdle/zero-altered negative binomial mixed models	Catkins ~ Size + (1|Site/Transect), zi = ~ Site + Size + Year	SKS 2008 and 2018, S- and L-seedlings excluded	glmmTMB (family = truncated_nbinom2 (link = “log"))
2Bi	Hurdle/zero-altered negative binomial mixed models	Catkins ~ Site x Size + (1|Site/Transect), zi = ~ Site x Size	SKS and VNP 2018, S- and L-seedlings excluded	glmmTMB (family = truncated_nbinom2 (link = “log"))
2Bii	Hurdle/z-altered negative binomial mixed models	Catkins ~ Site + Size + (1|Site/Transect), zi = ~ Site + Size	SKS and VNP 2018, S- and L-seedlings excluded	glmmTMB (family = truncated_nbinom2 (link = “log"))
3Ai	Linear mixed model	log(Size) ~ Year x Site, random = ~ 1|Site/Transect, weights = varIdent(form = ~ 1|Year)	SKS 2008 and 2018, trees	lme (method = "REML")
3Aii	Linear model	log(Size) ~ Year x Site	SKS 2008 and 2018, 20 largest trees each site	lm
3Bi	Linear mixed model	log(Size) ~ Site, random = ~ 1|Site/Transect	SKS 2008	lme (method = "REML")
3Bii	Linear model	log(Size) ~ Site	SKS 2008, 20 largest trees each site	lm
3Ci	Linear mixed model	log(Size) ~ Site, random = ~ 1|Site/Transect	SKS and VNP 2018	lme (method = "REML")
3Cii	Linear model	Size ~ Site	SKS and VNP 2018, 20 largest trees each site	lm
4A	Linear mixed model	Size/Height ~ Year x Site, random = ~ 1|Site/Transect, weights = varIdent(form = ~ 1|Year)	SKS 2008 and 2018, S- and L-seedlings excluded	lme (method = "REML")
4B	Linear mixed model	Size/Height ~ Site, random = ~ 1|Site/Transect	SKS 2008, S- and L-seedlings excluded	lme (method = "REML")
4C	Linear mixed model	Size/Height ~ Site, random = ~ 1|Site/Transect	SKS and VNP 2018, S- and L-seedlings excluded	lme (method = "REML")

Note: Trees = ≥20 cm plants, flowering adults = plants with female catkins, S-seedlings = ≤1 cm plants, L-seedlings = 1–5 cm plants. Since all transect were the same size (150 m^2), spatial and temporal variation in plant/catkin density (models 1Ai to 1Civ) was estimated using negative binomial regression on the number of plants/catkins. For models 2Aii and 2Bii, equations represent the best subset models for 2Ai and 2Bi, respectively, according to backwards elimination using a likelihood ratio test (see results in Table S3).

TABLE S2. Pairwise temporal comparisons for each site in models 1Ai to 1Aiv in Table S1, according to estimated marginal means.

Model ID	Contrasts	Estimate	SE	*t*-value	*p*
1Ai	S1 (2008–2018)	-0.940	0.276	-3.406	**0.001**
	S2 (2008–2018)	-1.329	0.356	-3.729	**0.005**
	S3 (2008–2018)	-0.221	0.196	-1.131	0.264
	S4 (2008–2018)	-4.646	0.285	-16.296	**<0.001**
1Aii	S1 (2008–2018)	-1.130	0.353	-3.206	**0.002**
	S2 (2008–2018)	-0.145	0.484	-0.299	0.766
	S3 (2008–2018)	-0.116	0.183	-0.635	0.528
	S4 (2008–2018)	-0.734	0.276	-2.655	**0.011**
1Aiii	S1 (2008–2018)	-2.835	1.034	-2.741	**0.009**
	S2 (2008–2018)	-1.943	1.076	-1.805	0.077
	S3 (2008–2018)	-0.965	0.243	-3.979	**<0.001**
	S4 (2008–2018)	-1.514	0.393	-3.848	**<0.001**
1Aiv	S1 (2008–2018)	-5.100	1.207	-4.226	**<0.001**
	S2 (2008–2018)	-2.790	1.001	-2.788	**0.008**
	S3 (2008–2018)	-1.100	0.626	-1.755	0.086
	S4 (2008–2018)	-2.210	1.044	-2.120	**0.039**

Note: Significant values are in bold (p<0.05).

TABLE S3. Results of model selection for models 2Ai and 2Bi in Table S1, according to backwards elimination using a likelihood ratio test.

Model ID	Part of model	Dropped term	AIC	Likelihood ratio test	
				χ^2	*p*
2Ai		None	2098.5		
	zero	Year x Plant size	2098.0	1.498	0.221
	zero	Year	2104.4	8.419	**0.004**
	zero	Site	2105.9	13.947	**0.003**
	zero	Plant size	2417.7	321.69	**<0.001**
	count	Year x Plant size	2098.4	2.431	0.119
	count	Year	2097.1	0.694	0.405
	count	Site	2098.2	7.089	0.069
	count	Plant size	2132.6	36.433	**<0.001**
2Bi		None	2446.0		
	zero	Site x Plant size	2444.8	6.813	0.146
	zero	Site	2457.6	20.794	**<0.001**
	zero	Plant size	2815.4	372.64	**<0.001**
	count	Site x Plant size	2438.5	1.655	0.799
	count	Site	2444.2	13.761	**0.008**
	count	Plant size	2469.2	32.761	**<0.001**

Note: Significant values are in bold (p<0.05).

TABLE S4. All pairwise comparisons for models 2Aii and 2Bii in Table S1, according to estimated marginal means.

Model ID	**Contrasts**	**Estimate**	**SE**	***t*-value**	***p***
2Aii (zero-part)	S1 – S2	0.736	0.580	1.268	0.584
	S1 – S3	0.228	0.389	0.585	0.937
	S1 – S4	-0.829	0.449	-1.849	0.252
	S2 – S3	-0.508	0.500	-1.017	0.739
	S2 – S4	-1.565	0.553	-2.829	**0.025**
	S3 – S4	-1.057	0.325	-3.250	**0.007**
	2008 – 2018	0.752	0.263	2.855	**0.004**
2Bii (zero-part)	S1 – S2	0.748	0.630	1.189	0.758
	S1 – S3	0.310	0.411	0.755	0.943
	S1 – S4	-1.178	0.475	-2.479	0.097
	S1 – VS	-0.170	0.391	-0.434	0.993
	S2 – S3	-0.438	0.559	-0.784	0.935
	S2 – S4	-1.927	0.612	-3.151	**0.015**
	S2 – VS	-0.918	0.541	-1.697	0.436
	S3 – S4	-1.489	0.368	-4.044	**<0.001**
	S3 – VS	-0.480	0.259	-1.855	0.343
	S4 – VS	1.009	0.354	2.850	**0.036**
2Bii (count-part)	S1 – S2	-0.965	0.792	-1.219	0.740
	S1 – S3	-1.083	0.478	-2.265	0.157
	S1 – S4	-1.635	0.549	-2.980	**0.025**
	S1 – VS	0.100	0.493	0.204	1.000
	S2 – S3	-0.118	0.705	-0.167	1.000
	S2 – S4	-0.670	0.771	-0.869	0.908
	S2 – VS	1.066	0.718	1.483	0.574
	S3 – S4	-0.552	0.418	-1.319	0.679
	S3 – VS	1.184	0.349	3.388	**0.007**
	S4 – VS	1.736	0.438	3.963	**0.001**

Note: For model 2Aii, pairwise comparisons were only performed for the zero-part, as neither site nor year were significant in the count-part. Significant values are in bold (p<0.05).

Paper II

High seed losses in mountain birch (*Betula pubescens* ssp. *tortuosa*) and developmental, ecological, and environmental correlates

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Abstract

Plants typically experience great losses from their reproductive potential represented by ovule production to the post-dispersal crop of viable seed. We examined seed density and viability in a founder population of mountain birch (*Betula pubescens* ssp. *tortuosa*), aiming to quantify losses at different stages and examine potential selection forces on reproduction success of the founder generation of an isolated population. At the time of study (2017–2020), the population had recently reached reproductive maturity, following its colonisation around 1990 through long distance dispersal onto an early successional outwash plain in southeast Iceland. Seed densities were high, but 89% of apparently intact seeds did not contain an embryo, despite being visually indistinguishable from filled seeds. Externally evident losses amounted to about 45% of the total seed crop and were mostly due to predation by the gall midge *Semudobia betulae*. When all losses were accounted for, 2.7% of the seed crop remained viable and germinated. Pollen limitation may partially explain high incidence of empty seeds. Excessive flower production is compatible with the predator satiation hypothesis but cannot explain pre-dispersal losses. Another adaptation to predation, masting, appears poorly developed in Iceland. Our results suggest the presence of constraints on the reproduction potential of the new island population, that are more limiting than in neighbouring populations, and we discuss their developmental, ecological, and environmental correlates.

Keywords

Betula pubescens ssp. *tortuosa* (Ledeb.) Nyman, Iceland, seed quality, seed losses, *Semudobia betulae*, sub-arctic.

Introduction

"A cardinal lesson from field biology is that the reproductive efforts of plants almost always fail."

Howe and Westley, 1997

In plants, losses of the reproductive potential can occur at any of the many stages from flowering to successful seed maturation and dispersal, and the number of germinated seeds at safe sites may only be a miniscule fraction of the ovules initiated by the mother plant (Howe and Westley 1997). Depending on their nature, magnitude, and expression, the losses may significantly but differentially affect offspring numbers and quality as well as the spatial and temporal recruitment patterns of the next generation (Clark et al. 2007; Brown et al. 2019).

At the initial stage, an obvious cause of failure is that the ovule is not fertilised, for example through lack of pollen (Weis and Hermanutz 1993; Bona et al. 2022). In angiosperms, the general rule for sexual reproduction is that flowers must be pollinated to set fruit (Stephenson 1981) and a second fertilisation event, following the union of egg and sperm nuclei, initiates the development of the (usually) triploid endosperm (Cailleau et al. 2010). Compared with gymnosperms, it may represent considerable savings of maternal resources as expenditure on seed reserves goes hand in hand with embryo establishment (Leslie and Boyce 2012). Many angiosperms habitually abort a large number of flowers (Stephenson 1981). Abortion soon after fertilisation may be triggered by late-acting self-incompatibility, lethal or sublethal alleles, or abnormal embryo sac development (Chen et al. 2022). Abortion at later stages or failure of the seed to reach full maturity may be due to external causes, i.e. lack of maternal resources to fill all fertilised ovules (Stephenson 1981). In cold climates, the short growing season may not suffice for seeds to reach maturity (Brown et al. 2019; Klady et al. 2010).

While the habit of producing far more flowers and ovules than mature seeds is widespread in plants, it is a wasteful process that needs examining in the light of ecological and evolutionary theory. The ovule oversupply hypothesis states that uncertain pollen receipt will favour plants that produce "too many" ovules, allowing the rare lucky recipient to capitalise by abundant seed production (Rosenheim et al. 2015). Excessive flower production may be an anti-predator strategy, with the profusion of flowers diluting predation pressures (Ezoe 2018; Baskin and Baskin 2019). Ghazoul and Satake (2009) suggested that late abortion of selfed or inbred ovules may increase the probability of outcrossed seeds escaping predation (the sacrificial sibling hypothesis). Pre-dispersal seed predation can have significant ecological (e.g., for population dynamics) and evolutionary consequences (e.g., for trait selection). In a review including 266 species, the mean percentage of predated seeds or fruits was 30.7% with trees tending to suffer greater damage than perennial herbs (Kolb et al. 2007). However, from his meta-analysis, Katz (2016) concluded that seed predation may have weaker demographic impacts than other types of insect herbivory, and although statistically significant, the average effects of seed predation are usually small (Clark et al. 2007). Some groups of plants, particularly wind-pollinated trees, are characterised by masting, the synchronised but highly fluctuating seed production between years. This has selective costs in terms of delayed reproduction, but two adaptive hypotheses have been proposed to explain its evolution. First, that the large spatial scale synchronicity leads to higher pollination efficiency through economy of scale and second that the massive seed output in mast years leads to predator satiation with more seeds escaping predation (Zwolak et al. 2022).

Throughout the Holocene, mountain birch (*Betula pubescens* ssp. *tortuosa* (Ledeb.) Nyman) has remained Iceland's only native forest-forming tree (Kristinsson et al. 2018). At the time of human settlement around 870 AD, birch woodland may have covered 20–30% of its 103,000 km² area but currently, it only has about 1.5% cover (Snorrason et al. 2016). Remaining woodlands are mostly small and isolated fragments. Some are now expanding and even establishing discrete new populations, probably both due to a warming climate and land use changes, especially cessation of livestock grazing (Snorrason et al. 2016). We took advantage of the sudden and large-scale long-distance colonisation of mountain birch onto a treeless glacial outwash plain about 30 years ago (ca 1990; Thórhallsdóttir and Svavarsdóttir 2022). The population has now reached reproductive maturity and this setting provides a unique opportunity to examine how selection forces operate in a new and spatially discrete founder population. We quantified losses and identified causes of failure from ovule development, through seed maturation, pre-dispersal predation and fungal infections to seed densities on the soil surface and in the seed bank, with comparison to the nearest two established birch woodland populations, one which has been identified as the source population (Pálsson et al. 2023). Our goal was to (1) sequentially unravel the magnitude and consequences of different factors limiting reproductive success and (2) to examine potential selection forces on the reproductive success in a new and isolated population.

Materials and methods

Study species: *Betula pubescens* reproduction and seed ecology

Betula pubescens is a deciduous tree with a wide distribution in the northern hemisphere (Ashburner and McAllister 2013). Towards the treeline in Scandinavia and west to central Siberia, it becomes the dominant or co-dominant woody species, particularly the shrub-like subspecies *tortuosa* (Atkinson 1992). *B. pubescens* is monoecious and wind pollinated. Finnish populations studied by Hagman (1971) were strongly self-incompatible, but the author could not ascertain whether the low percentage of filled seeds (1–1.3%) was due to contamination (i.e. pollination) or apomictic embryo development. The female birch flower contains a single viable ovule (Dahl and Fredrikson 1996). Birch seeds have been variously classified as without (Clapham et al. 1962; Wani 2020) or containing endosperm (Håkansson 1957). This discrepancy probably arises because only a very thin endosperm layer remains at maturity (Håkansson 1957; Kirkbridge et al. 2021). The fruit is a single seeded and two-winged achene (samara). The dispersal unit of birches should properly be termed a fruit as the seed is contained within the indehiscent fruit wall. However, following most authors, we will refer to it as seed.

A gall midge, *Semudobia betulae*, parasitises mountain birch seed in Iceland (Halldórsson et al. 2013). The fly lays its eggs between the floral bracts and flowers, and on hatching, larvae enter the seeds and form conspicuous galls (Roskam 1977). The larvae then feed on the seed resources, hibernate over winter, and pupate in spring. Infected seeds are inviable and identifiable by a circular "weak spot" in the seed coat (Roskam 1977).

Like many wind pollinated trees, birches have a masting habit (Sarvas 1955; Gallego-Zamorano et al. 2018). At least since the 1960s, some regional foresters in Iceland included visual assessments of the birch seed crop in their annual reports (Appendix S1) but unfortunately these records are patchy for the south which includes our sites. For northern woodlands, the record is complete from 1960 to 2014, with the seed crop size dividable into 8 categories (see Fig. S1 in Appendix S1 for details). If the categories large, very large, and unusually large are designated as representing masting, the average masting interval is nine years. For the south, the record is complete from 1963-1995 (33 yrs) but a large crop was only noted in 1981.

Study area and birch populations

The main study area is within the upper middle part of a 1,000 km^2 glacial outwash plain, Skeiðarársandur (SKS), in southeast Iceland (Fig. 1; 63°57’N, 17°11’W). It is at an early successional stage (Thórhallsdóttir and Svavarsdóttir 2022). Around 1990, long-distance seed dispersal from Vatnajökull National Park (VNP) resulted in the colonisation of mountain birch on the plain (Thórhallsdóttir and Svavarsdóttir 2022), >10 km downwind from the dominant wind direction (Icelandic Meteorological Office n.d.). Genetic analysis indicated that at least most of the population originated from Bæjarstaðarskógur forest, northeast of SKS (Pálsson et al. 2023). The massive, natural colonisation event involved seed dispersal well beyond reported dispersal distances (Liu and Evans 2021).

Three sites were established on the plain, SA close to the western edge of the mountain birch area and SB and SC ca 5 km east of SA (Fig. 1), all at around 100 m a.s.l. Mountain birch density, tree size, and catkin production were highest in the eastern section of the birch area and significantly declined westwards (Óskarsdóttir et al. 2022). Seed quality was studied at all sites and seed numbers quantified at SA and SB. Two additional seed quality sites were established within VNP, VM in Morsárdalur valley and VS on Skaftafell proglacial plain (Fig. 1). As at SKS, mountain birch colonised VM (120 m a.s.l.) around 1990. At VS (100 m a.s.l.), mountain birch had begun to establish by the early 1960s. Note that a previous study on the mountain birch population on the plain (Óskarsdóttir et al. 2022) was performed at the same locations as the current study, where SKS sites were referred to as S1 (SA), S2 (not included in this study), S3 (SC), and S4 (SB).

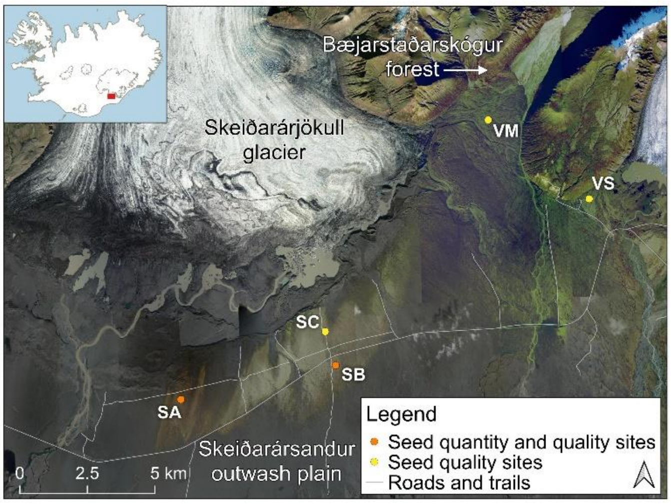

Fig. 1. Study sites on Skeiðarársandur (SA–SC) and in Vatnajökull National Park (Morsárdalur, VM, and Skaftafell, VS). Aerial photographs and map database: Open database of the National Land Survey of Iceland (Creative Commons Attribution 4.0 International License), accessed in January 2023 at https://www.lmi.is/is/landupplysingar/gagnagrunnar/nidurhal. Geographic information system: QGIS (http://qgis.osgeo.org).

The climate at SKS and VNP is maritime with high precipitation (values from Gígjukvísl at SKS and Skaftafell in 2016–2020, unpublished data from the Icelandic Meteorological Office). Mean temperatures were 0.9°C in January and 10.9°C in July, and the mean annual temperature was 5.2°C (Skaftafell 1996–2020). Mean annual precipitation was around 1,650 mm (Skaftafell 2016–2020).

Field sampling, seed classification, and germination tests

In 2018, 500 m long N-S transects were laid out at SA and SB (Fig. 1). Each transect was split into four 125 m blocks and within each, two sampling points were randomly chosen. To estimate the seed rain, four 15 cm x 30 cm seed traps (synthetic turf mats, with 5 mm x 55 mm fibres) were laid out at each sampling point at the start of seed release in October 2018 and 2019. The traps were placed at 4 m intervals along the transects and rotated so that the fibres inclined north-east, towards the prevailing wind direction (Icelandic Meteorological Office n.d.). The traps were collected in May the following year. Mountain birch seeds were counted in all traps (N = 32 per site) and classified by appearance into four groups that separated healthy-looking seeds from damaged ones and described the main causes of damage. The groups were: intact seed (not infected or damaged), seed predated by gall midge (*Semudobia betulae*), fungi infected seed, and physically damaged seed (see Appendix S2).

To quantify the soil seed bank, five soil samples (Ø = 4.7 cm, depth = 5 cm) were taken at each sampling point in May 2019 and 2020 (N = 40 per site). *Betula* seeds are not long-lived but can persist in the soil for at least a couple of years (summarised in Bonner et al. 2008). Thus, the soil samples included seeds produced from the autumn before they were collected and backwards in time but for simplicity, we will refer to them by their latest seed addition year in our analyses, i.e. 2018 and 2019 samples. The samples were taken at two m intervals perpendicular to the transect, 2 m north or south of it (direction was randomly chosen). Mountain birch seeds were counted in each sample and their visual quality assessed, as described above for the seed traps.

To assess seed quality, during October 2018–2020, five catkins were collected from each of 20 trees at all five sites (Fig. 1). In 2018, the trees were randomly selected and marked. In the following years, catkins were collected from the same trees, but if those had no or very few catkins, the nearest tree with catkins was sampled. The following variables were recorded: maximum tree height, length of the longest shoot, and the number of main trunks. Plant length was used as a measure of tree size, and a growth form index was derived as maximum height divided by length of the longest shoot (Óskarsdóttir et al. 2022). In the SKS population, dicormic plants generally had the same upright stature as monocormic ones, while plants with three or more trunks were most often shrub-like. Thus, a growth habit index was used to describe plants as either monocormic (1–2 trunks) or polycormic (≥3 trunks). The catkins from each tree were pooled, dried in paper bags, and stored at 2–4°C for at least two months, before seed germination was tested. For the tests, 50 seeds from each tree in each year were inspected under a stereo microscope and classified into the four quality groups described earlier for the seed rain and seed bank.

Subsequently, 20 intact seeds from each tree were selected for germination tests each year although a full sample size was not obtained for all trees in 2018. Each sample was split up into three lots of 6–7 seeds and placed in random order on wet filter papers within a germination chamber, with a temperature of 20°C and a light period of 16 hours, which is comparable to previous germination tests conducted for these populations (Marteinsdóttir

2004; Hiedl 2009). Germinated seeds were recorded at five-day intervals or less and removed. Tests were completed after a minimum of 31 days, when no germination had occurred for at least 3 days. In 2019 and 2020, all seeds that did not germinate were dissected, studied under a stereo microscope, and classified as follows: fully developed embryo, developed embryo but fungi infected, partially developed embryo, or no embryo (see Appendix S2). Additionally, germination of intact seeds, collected in 2017 from 20 unmarked trees at all sites except VM (ten trees at SB), was studied in the same way as in 2018–2020, but no further visual assessment was carried out.

Ten intact seeds from each of ten trees at sites SA, SB, and VS were selected from the 2019 seed crop, for size and weight measurements. Trees with the highest proportions of filled and/or germinated seeds in the 2019 germination test were chosen, as proportion of empty seeds was very high for most trees, but individual seeds were randomly selected. Seed length and width (excluding wings) was measured for each seed under a stereo microscope. Seed weight was measured to nearest 0.01 mg and germinability assessed as described above. All seeds that did not germinate were dissected and classified in the same way as in the 2019–2020 tests.

Data analyses

Initially, the three SKS sites were analysed separately but they all displayed the same patterns and temporal variability and grouping them had no effects on the results or conclusions. Therefore, SA, SB, and SC were treated as subsites within SKS in all subsequent analyses but were included as random factors in all models. All data handling and analyses were conducted in *R* v4.1.0. (R Core Team 2022).

To test between-year patterns in seed quantity for the seed rain and bank data, we used negative binomial mixed models (NBMM) with log link for seed numbers in samples, as they were all equally sized. We used *sampling point* (i.e., location within the 500 m long transects, nested within sites) as random intercept. NBMMs were fitted with the package *glmmTMB* v1.1.3 (Brooks et al. 2017).

To analyse patterns and correlates of seed quality, we used mixed effects logistic regressions (MELRs) with a dependent variable where each seed was either intact (1) or not (0). For seeds in catkins, predated seeds were studied in the same way. For these models, *year*, *site*, their interaction, as well as *plant size*, *growth form index*, and *growth habit index* were used as fixed effects and *tree identity* (nested within sites) was used as a random intercept. For the seed rain and seed bank data, between-year difference was tested with *sampling point* (nested within sites) as a random intercept. In case of significance for fixed effects, we used estimated marginal means (EMMs) for pairwise comparisons. MELRs were fitted with the package *lme4* v1.1-27.1 (Bates et al. 2015) and EMMs were calculated using the package *emmeans* v1.7.0 (Lenth 2020).

To test the spatio-temporal variance of seed germination in 2017–2020, we used a MELR with a dependent variable where each seed had either germinated (1) or not (0), including *year*, *site* and their interaction as fixed effects and *tree identity* (nested within sites) as random intercept. We used a similar MELR to identify potential impact factors for embryo presence in 2019–2020, adding *plant size*, *growth form index*, and *growth habit index* to the list of previously mentioned fixed effects. Seeds with partially developed embryos were grouped with empty ones and thus, a filled seed refers to the presence of a fully developed embryo. Factors affecting relative germination (i.e. germination of filled seeds), were tested similarly to those regarding embryo presence, but empty seeds were excluded from that MELR and the *proportion of filled seeds* for each tree was added to the fixed effects. Note that all germination results describe the germination of intact seeds, which were the ones exclusively chosen for germination testing.

As a measure of seed size, we used the formula for the area of an ellipse (*length/2 x width/2 x π*). Note that mountain birch seeds have varying shapes (see Appendix S2), and the formula should be regarded as an approximation. Using the seed size estimate, we also calculated seed unit area weight (mg/mm^2). To identify factors controlling seed weight, we used a linear mixed effects model (LMM) with *seed area*, *embryo presence/absence*, their interaction, and *site* as fixed effects and *tree identity* (nested within sites) as a random intercept. Additionally, the potential effects of *seed unit area weight* and *site* on relative germination was studied using MELR, with *tree identity* (nested within sites) as a random intercept. The LMM was fitted with the package *lme4* v1.1-27.1 (Bates et al. 2015).

Results

Seed appearance and density

The proportion of externally intact seeds varied from around 25–75% and averaged over all sites and years. Externally evident pre-dispersal catkin losses amounted to about 45% of the total seed crop (Fig. 2A). By far the greatest losses in catkins were attributed to infection by the gall midge. This was highest at most sites in 2018 but lowest in 2019 (Fig. 2A; Appendix S3). The MELRs for abundance of intact and gall midge infected seeds both revealed significant interactions between years and sites. In addition, number of gall midge infected seeds decreased with plant size, resulting in higher proportions of intact seeds in larger plants (Appendix S3). Adding an interaction term between sites and plant size to the model showed that decreased gall midge losses with plant size were independent of potential site-specific differences (χ^2 = 1.9, p = 0.39; ANOVA type II test). Furthermore, excluding the seeds collected from the largest tree in the dataset (>4 m) did not significantly change the effect of plant size on gall midge seed proportions (χ^2 = 5.9, p = 0.02; ANOVA type II test). For both intact and gall midge infected seeds, the only non-significant between-year difference was found between 2019 and 2020 at VM and VS (Fig. 2A). No significant between-site differences were found for gall midge infected seeds, and for intact seeds, the only significant between-site difference was found between SKS and VS in 2018 (Fig. 2A).

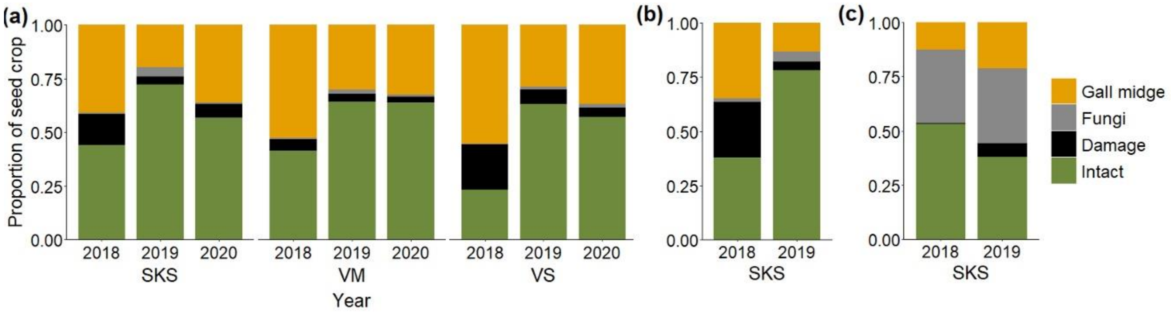

Fig. 2. Causes of losses across all sites and study years in catkins (A), the seed rain (B), and the soil seed bank (C). Sample size equalled the number of seeds inspected in catkin samples (50 seeds for each of 20 trees per site per year at VM and VS in Vatnajökull National Park, but three-fold that at SKS on Skeiðarársandur, due to it encompassing three subsites), seed rain samples (2018: N = 240, 2019: N = 5,094), and soil seed bank samples (2018: N = 154, 2019: N = 210).

Average seed rain density (using number of seeds in equally sized samples) was much greater in 2019 (1,769 seeds/m^2 on average, SE = 201) than in 2018 (83 seeds/m^2, SE = 15) (z = 24.69, SE = 0.13, p <0.001). The between-year differences were smaller in the seed bank than in the seed rain, but still also significantly greater in 2019 (1,513 seeds/m^2 on average, SE = 353) than in 2018 (1,110 seeds/m^2, SE = 312) (z = 2.18, SE = 0.24, p = 0.03).

Externally evident losses in the seed rain were mostly attributed to infections by the gall midge (24% on average) and physical damage (16% on average) (Fig. 2B). Both were higher in 2018 than in 2019, resulting in a great between-year difference in the proportion of externally intact seeds (z = 11.924, SE = 0.141, p <0.001). For the seed bank, externally evident losses were mostly attributed to fungal infections (34% on average) and infections by the gall midge (19% on average) (Fig. 2C). In contrast to the seed rain, the proportion of externally intact seeds was higher in 2018 than in 2019 (z = -3.778, SE = 0.227, p <0.001).

Seed development and germination

Only apparently intact seeds were selected for the germination tests, but even so, germination was extremely low (Fig. 3A). Averaged over all years, germination at SKS was only 5.0%. Average values were higher at VM (8.7%) and VS (19.8%) (Fig. 3A). The ultimate cause of loss was that despite their external morphology and size indicating a fully matured seed, most of them did not contain an embryo; 89% of intact seeds on average at SKS, 82% at VM, and 62% at VS (Fig. 3B). Most empty seeds seemed to have been aborted very early, as <1% had partially developed embryos (those were classified with empty seeds in our analyses). At SKS, proportions of viable seeds were significantly higher in 2019 than in 2020 but not at VM and VS (Fig. 3B).

The MELRs for germination of intact seeds in 2017–2020 and filled seeds in 2019–2020 revealed significant interactions between years and sites (Appendix S4), reflecting different between-year patterns in seed development and viability between sites (Fig. 3). In general, germination was highest in 2017 and lowest in 2018, and higher in VNP than on SKS (Fig. 3A).

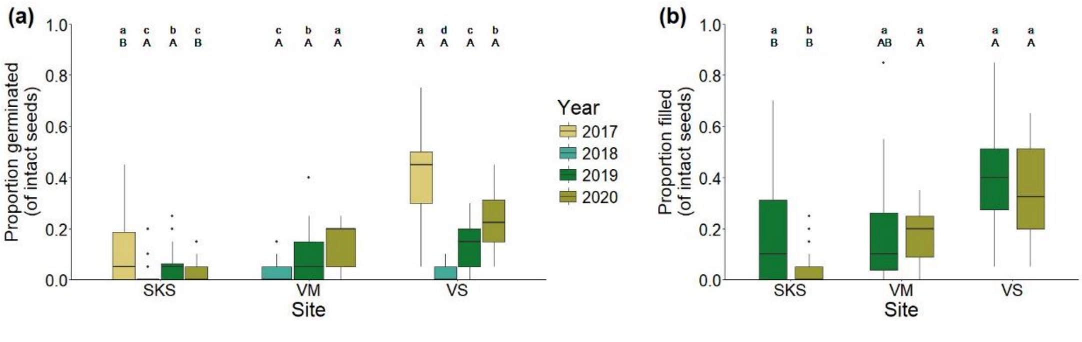

Fig. 3. Mean germination of all intact mountain birch seeds (not infected, parasitised, or damaged) per tree (A), and proportions of intact seeds with a fully developed embryo (B) across all study sites and years. Lowercase letters denote significant differences between years for each site and uppercase letters denote differences between sites for each year, based on estimated marginal means pairwise comparisons of mixed effect logistic regressions (Appendix S4). At VM and VS in Vatnajökull National Park, sample size was 20 seeds for each of 20 trees per site per year, but at SKS on Skeiðarársandur, seeds were collected from three subsites, making the sample size three times larger.

Germination and size of filled seeds

Relative germination (i.e., of filled seeds only) had a significant negative relationship with proportion of filled seeds (Fig. 4A) and a positive one with plant size (Fig. 4B, Appendix S4). Adding an interaction term between sites and plant size to the model on relative germination, to inspect whether the relationship with plant size could be explained by between-site difference, confirmed that this pattern was site-independent (χ^2 = 3.1, p = 0.22; ANOVA type II test). Of non-germinated filled seeds, around 14% had signs of fungal infection, but due to uncertainty in the visible estimation, these data were not analysed further.

Relative germination was higher in 2020 than in 2019 (Fig. 4) and varied between sites (Appendix S4). Over both years, 36% of filled seeds germinated at SKS, 63% at VM, and 48% at VS, and relative germination was significantly lower at SKS than the VNP sites (SKS/VM: z = -2.87, SE = 0.13, p = 0.01; SKS/VS: z = -2.91, SE = 0.13, p = 0.01; VM/VS: z = -0.10, SE = 0.32, p = 0.99; EMMs).

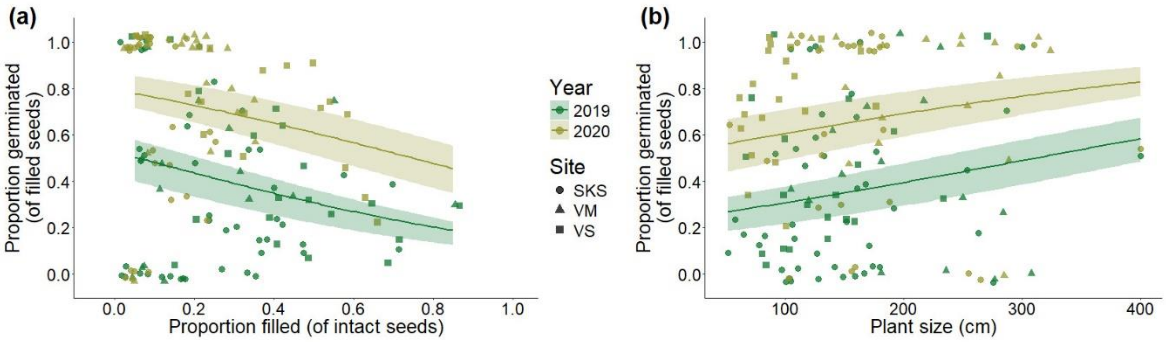

Fig. 4. Relationship between germination of filled seeds (relative germination) and their proportion for each tree (A) and plant size (B) at all study sites and years tested. SKS was located on Skeiðarársandur but VM and VS within Vatnajökull National Park. Predicted probabilities of relative germination for each year according to mixed effect logistic regressions (Appendix S4) have been projected onto the plots. Sample size equalled the number of trees with ≥1 filled seed (2019, SKS: N = 221, VM: N = 73, VS: N = 167; 2020, SKS: N = 55, VM: N = 74, VS: N = 135).

Seeds without an embryo were lighter than same size filled seeds (Fig. 5; *seed size x embryo presence*: χ^2 = 47.160; p <0.001; ANOVA type II test) but the relative germination was not significantly affected by unit area seed weight (χ^2 = 0.002; p = 0.965; ANOVA type II test). Only six out of the 300 dissected seeds were partially filled and were classed as empty. Seed weight did not differ between sites (χ^2 = 0.007; p = 0.936; ANOVA type II test), and neither did relative germination of the weighed seeds (χ^2 = 1.120; p = 0.290; ANOVA type II test) (Fig. 5).

Collective losses

Lack of embryo and infections by gall midge explained the greatest losses to the total viable seed crop (Fig. 6). Data were available for 2019 and 2020, when seeds were both classified prior to germination testing and inspected post-test for embryo presence. When all losses were accounted for, an average of 2.7% of the total seed crop at SKS remained viable and germinated (Fig. 6A), as opposed to an average of 9.2% at the VNP sites (Fig. 6B–C).

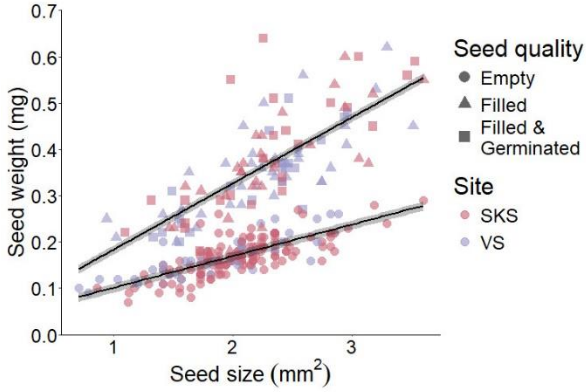

Fig. 5. The relationship between seed weight and size (length/2 x width/2 x π), for filled and empty seeds. The linear mixed model relationships for seeds with and without a fully developed embryo separately are shown. Sample size was ten seeds from ten trees at VS and at two of SKS's subsites (SA and SB).

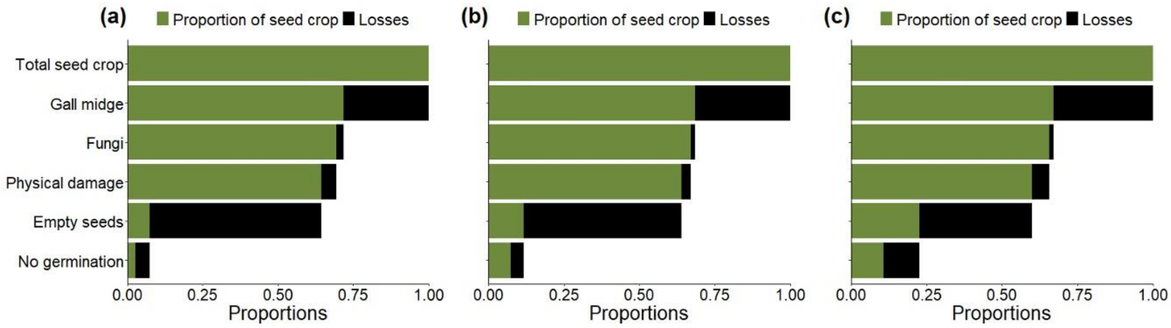

Fig. 6. Mean losses to the total mountain birch seed crop due to infections by gall midge and fungi, physical damage, lack of embryo, and poor germination in 2019 and 2020 at SKS on Skeiðarársandur (A), and at VM (B) and VS in Vatnajökull National Park (C).

Based on the incoming seed rain density, the mean proportion of intact seeds, and germination tests, the density of seeds with germination potential at SKS was estimated 0.5 seeds/m^2 in 2018 and 75.9 seeds/m^2 in 2019. Similarly, the density of filled seeds was estimated 255.0 seeds/m^2 (measured only in 2019).

Discussion

Germinable seeds constituted a small proportion of the total seed crop (Fig. 6). First, almost half of the pre-dispersal crop was lost, predominantly to the gall midge (Fig. 2). Furthermore, most apparently healthy seeds did not contain an embryo (Fig. 3B). This represented by far the greatest reduction of the reproductive potential in these sub-arctic mountain birch populations. As the proportion of seeds with partially developed embryos was very low, it appears that the termination of the remaining ovule in the female flower occurs very early, either before or soon after fertilisation. The actual reproductive success may have been lowered even further as a significant proportion of filled seeds failed to germinate after pre-treatment (Fig. 4). Despite the massive losses, the density of germinable seed at SKS was quite high, although annually variable. In 2019, the density of 255 filled seeds/m^2 was similar to what Sarvas (1948) reported for a *Betula pendula* stand in an average seed production year (340 filled seeds/m^2). These results raise several questions that we address below, such as the proximal (mechanistic) explanations of the high proportion of empty seeds and possible evolutionary implications or adaptive values.

The occurrence of empty seeds in birch

The greatest losses of reproductive potential are explained by the failure of the embryo to develop (Fig. 6). An embryo may be missing because the egg cell was not fertilised, either because of lack of pollen, low pollen viability, or because deposited pollen grains were rejected by incompatibility reaction of the mother plant (Stephenson 1981). Since the experimental addition of pollen very frequently increases seed output, it has long been believed that plant reproduction is pollen limited (Knight et al. 2005; Dawson-Glass and Hargreaves 2022). Pollen limitation has been reported in isolated and range edge *Betula* spp. populations and ascribed to either poor pollen availability or geitonogamous selfing (Sarvas 1952; Weis and Hermanutz 1993; Holm 1994a; Bona et al. 2022). Unfavourable weather may impede successful pollen dispersal, such as particularly heavy or prolonged rainfall that removes pollen from the air (Ranta et al. 2008). In southwest Iceland, birch pollen is released from early to mid-May and into mid-June (Icelandic Institute of Natural History n.d.) and the dispersal period is probably similar in the southeast. In our study area, precipitation in May 2018 was almost five times the average of the two preceding and two following years (values from Skaftafell 2016–2020, unpublished data from the Icelandic Meteorological Office). We propose that these heavy spring rains are responsible for the extremely poor seed quality and high incidence of empty seeds in 2018 (Fig. 3A).

Another cause of early reproductive failure is seed abortion which may have internal or external causes (Stephenson 1981). Late-acting self-incompatibility may lead to ovule abortion soon after fertilisation (Chen et al. 2022). Abortion at later stages has often been attributed to resource limitation, with seeds distally positioned in the fruit and furthest away from major veins being preferentially aborted (Stephenson 1981). Selfed or inbred seeds aborted at a relatively late stage may act as a predator sink (Ghazoul and Satake 2009). In Iceland, the female lays its eggs in late May to early July (Ottósson 1982). Therefore, while an excessive production of female flowers may be compatible with the predator satiation hypothesis, it cannot explain why these birches continue to spend resources on empty fruits long after the oviposition period of the gall midge.

When resources are limiting, there may be adaptive value in the mother plant aborting some offspring to ensure the successful maturation of the remaining seeds and for this there is ample experimental and observational evidence (Stephenson 1981). This may enhance overall offspring quality if the mother plant selectively aborts lower-quality embryos. However, Baskin and Baskin (2019) concluded that although selective seed abortion could increase vigour of young offspring, its demographic or evolutionary importance had not been demonstrated. Soil fertility in our study area is low (Vilmundardóttir et al. 2015; Tómasson 2023), but among the properties making mountain birch an effective coloniser is its ability to grow on nutrient-poor soils (Atkinson 1992). Still, this does not exclude the possibility of resource limitation and further research is needed to determine whether it could be limiting reproductive success in our populations.

In most sexually reproducing angiosperms, initiation of the endosperm occurs concomitantly with the formation of the zygote (Cailleau et al. 2010). Typically, unfertilised ovules remain small, do not develop a hard seed coat, and are easily distinguished from mature seeds with a viable embryo. While there were clear differences in unit area weight between our empty and filled mountain birch seeds, seed size and weight varied greatly within both groups and empty seeds had about the same range of variation in size as filled ones (Fig. 5). At first glance, high incidence of empty but normal looking seeds appears to represent a wasteful expenditure of resources on behalf of the mother plant (Leslie and Boyce 2012), but this same phenomenon (parthenocarpy; fruit development in the absence of an embryo) has been described in several *Betula* species (Frolova 1956; Johnsson 1974; de Groot et al. 1997). For example, the percentage of empty seeds in *B. pubescens* in north Sweden was 58.5% (Holm 1994b) and >50% in north Poland (Bona et al. 2022). For another masting species, *Ulmus laevis*, production of empty-seeded fruits has been shown to be energetically efficient, as they are low cost and can significantly reduce seed predation in mast years (Perea et al. 2013). To our knowledge, this simultaneous effect of parthenocarpy and masting on seed predation has not been tested for *B. pubescens*.

Pre- and post-dispersal seed predation

Predation by the gall midge was the second largest cause of loss of reproductive potential (Fig. 6). As expected, losses by fungi were higher in the soil seed bank than in the other sample types, but in 2018, proportions of intact seeds were even higher in soil samples than the other types (Fig. 2). High germination in 2017 (Fig. 3A) suggests that this pattern could be influenced by seeds from that year. We do not have data on losses to other seed predators than the gall midge, but birch seeds and catkins are important foods for two widespread birds in Iceland, the common redpoll (*Achanthis flammea*, Hilmarsson 2011) and the rock ptarmigan (*Lagopus mutus*, Dépré and Nielsen 2023). The redpoll is mostly confined to birch woodlands and is listed as a breeding and overwintering species in the Skaftafell and Bæjarstaðarskógur woodlands (Hilmarsson 2011), but we have not observed it on the SKS plain. The ptarmigan is common in our area, particularly in the birch woodlands but we have also often observed it in the upper parts of SKS. While post-dispersal seed predators present a potential evolutionary and ecological benefit to empty but normal looking seeds (Perea et al. 2013), they were outside of the scope of this study.

The negative trend in gall midge infections with tree size (Appendix S3) may reflect a greater ability of large trees than small ones to satiate seed predators (Bogdziewicz et al. 2023) or to synchronise, as small trees tend to produce seeds out of synchrony, leaving them more susceptible to seed predation than larger trees (Bogdziewicz et al. 2020). A positive correlation has been found between seed quantity and germinability for several masting species, including *B. pendula* and *B. papyrifera* (Sarvas 1952; Bjorkbom et al. 1965; Holm 1994b). Patterns of annual variation in gall midge infestation seem to fit widely described predator-prey relationships (Berryman 2002). In 2018, following a year of relatively high quality (and probably also quantity) seeds (Fig. 3A), the intensity of the predation was significantly greater at all sites than in the following years (Fig. 2). Holm (1994b) similarly found that the highest average gall midge infections were reported in the year after the study's best seed year.

A recent meta-analysis found strong evidence for the predator satiation effect of masting (Zwolak et al. 2022). The available records of seed crop sizes in Iceland (Appendix S1) indicate that masting is much weaker than in either Scandinavia (every 4–6 years in *B. pubescens*; Gallego-Zamorano et al. 2018) or Canada (ca 3 events for *B. alleghaniensis* in an 8-year record; Houle 1999). We hypothesise that there may be two proximal explanations. It may reflect a more limiting physical environment in Iceland that restricts resource budgets so that the trees are unable to respond to favourable weather cues. In the

SKS population, this could be due to low soil nutrient status, but that is unlikely to apply to established forests in the north that also had very sparse masting. Second, bad weather events (cold spells in spring, heavy rains or storms that tear catkins off plants) in an already marginal climatic setting, may prevent masting crops from being realised. As gall midge predation was a significant cause of loss in our populations, substantially greater than reported for *B. pubescens* in northern Sweden for example (1.4% averaged over six years in ten populations; Holm 1994b), sparse or weak masting may in the long run reduce the probability of seeds escaping predation.

Viability and germination of filled seeds

Averaged across our three populations, just over half of the filled seeds failed to germinate. Although we discounted all visibly fungal infected seeds prior to germination testing, 14% of the filled but non-germinated seeds had exterior fungal growth at the end of the germination period. This probably arose from internal infections, and it is very unlikely that those seeds were viable. Our seeds were stored at 2–4°C for at least eight weeks prior to testing (see Methods) which is the recommended pre-treatment for *B. pubescens* (Forest Research 2023). In our unpublished experiments, stratification or cold treatment of moist rather than dry seeds did not improve germination. We therefore conclude that the low germination percentages reflect poor viability rather than the lack of an appropriate dormancy-breaking treatment. In the arctic, the short and cool growing season may not suffice for the filling and full maturation of seeds (e.g. Klady et al. 2010; Brown et al. 2019) and this has also been established for *Betula glandulosa* close to its climatic limits (Hermanutz et al. 1989). Although the site conditions of our SKS mountain birch population might possibly be regarded as marginal, we found no correlation between unit area weight and germination (Fig. 5), which may indicate that incomplete maturation is not a likely explanation. However, the pattern of increase in relative germination with tree size coupled with decreases in the proportion of filled seeds per tree (Fig. 4) may implicate a role of resource budgets. Holm (1994b) also found a negative relationship for both the proportion of filled seeds and non-germinated filled seeds with altitude for *B. pendula*, indicating that when resources are scarce, few seeds are filled but their germination potential is high.

Potential constraints in a new island population

Our SKS birch population represents the first (founder) generation following long-distance dispersal into a treeless, early successional environment. Its establishment probably represents a very low number of successful colonisation events (Óskarsdóttir et al. 2022). In 1998, the SKS birch plants were tiny. By 2004, very few individuals had reached reproductive maturity (Marteinsdóttir 2004). Flowering was more frequent in 2008 but no first-year seedlings were found despite a very extensive survey (Hiedl 2009). By 2018, there were thousands of seedlings (Óskarsdóttir et al. 2022). Assuming that the (main) colonisation event took place in the early 1990's, about 25 years passed until the second, and first locally recruited, generation appeared.

Pannell et al. (2015) suggested that isolated populations recently established via long distance dispersal may be characterised by a small number of common S-alleles (that prevent self-fertilisation) and therefore be faced with low mate availability. As the mature Bæjarstaðarskógur forest is a rather small fragment, many of the individuals in the incoming seed rain may have been related. We suggest that if only a low fraction of the available pollen has mating potential, due to matching S-alleles, there should have been great differences between individual trees in the proportion of filled seeds with a few exceptions having better-quality seed crops. This was not the case. On the other hand, such a pattern would not emerge if most of the plants had a slightly leaky incompatibility system and were able to produce a small number of seeds through self-fertilisation. The very low proportion of filled seeds does not indicate the presence of active selfed or apomictic seed production. Hagman (1971) found very strong incompatibility reactions in his Finnish downy birches but as far as we know, self-compatibility has not been experimentally tested in Icelandic birch.

Selection pressures on the new SKS population must differ from those in its source population, given the disparate environmental conditions regarding competition for light (negligible on SKS, intense in Bæjarstaðarskógur), soil physical properties (coarse mineral *vs* organic forest soils) and soil fertility (very low *vs* higher). Pollen dispersal distances are also likely to differ (great in the open and exposed setting at SKS, smaller in the closed mature forest set in a steep-sided valley). The consistently and exceptionally low proportion of embryo-containing seeds reflects considerable barriers to successful reproduction, which seem more obstructive on the plain than in the neighbouring populations.

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Supporting information

Appendix S1. Summary information from annual reports on mountain birch seed crop.

At least since the 1960s, some regional foresters in Iceland included visual assessments of mountain birch seed crop in their annual reports but unfortunately these records are patchy for the south which includes our sites. From 1995–2021, 13 of 27 records are missing but three years were noted for good crops: 2020 (large), 2008 (very large) and 2003 (unusually large). The list is complete from 1963–1995 (33 years) but a large crop was only noted in 1981.

For northern woodlands, the record is complete from 1960 to 2014, with the seed crop size dividable into 8 categories (Fig. S1). If the categories large, very large, and unusually large are designated as representing masting, there were 6 (1+4+1) masting events through the 55-year period (1960–2014). This works out at an average interval of about 9 years, as does the incomplete 1995–2021 record for the south (3 good crops in 27 years but only 14 years on record. However, we consider it likely that a good crop would be noted for our reference forest of Bæjarstaðarskógur.

The linear distances between the north and south woodlands in Iceland are of the order of 200–250 km but comparisons of the records show that masting events are not synchronised. The most likely explanation is a difference in climate, as “good” summers do not co-occur.

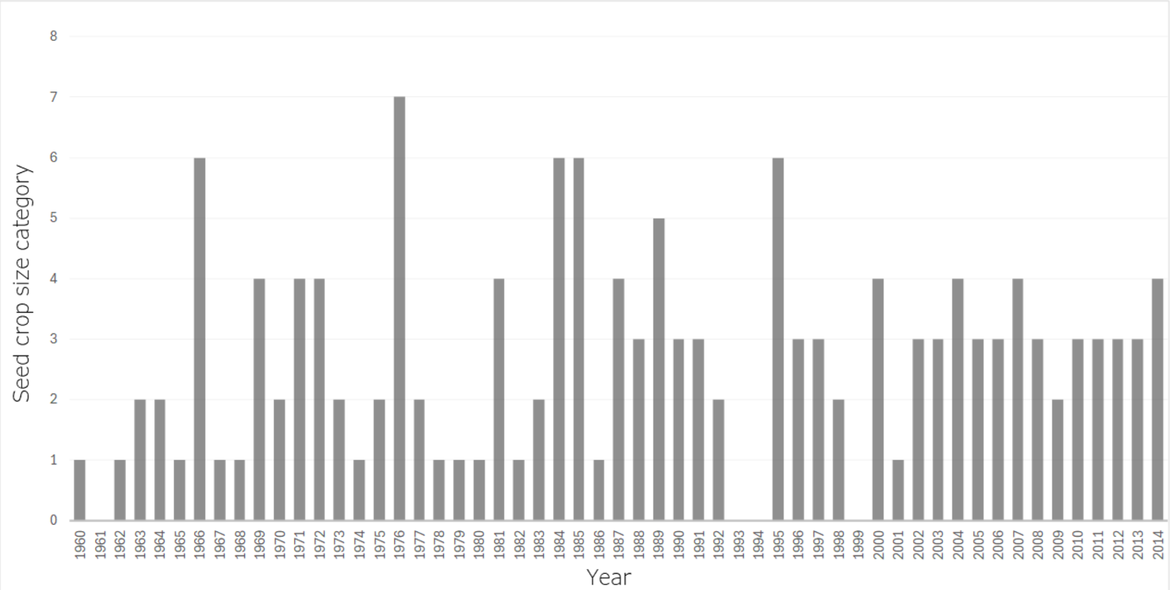
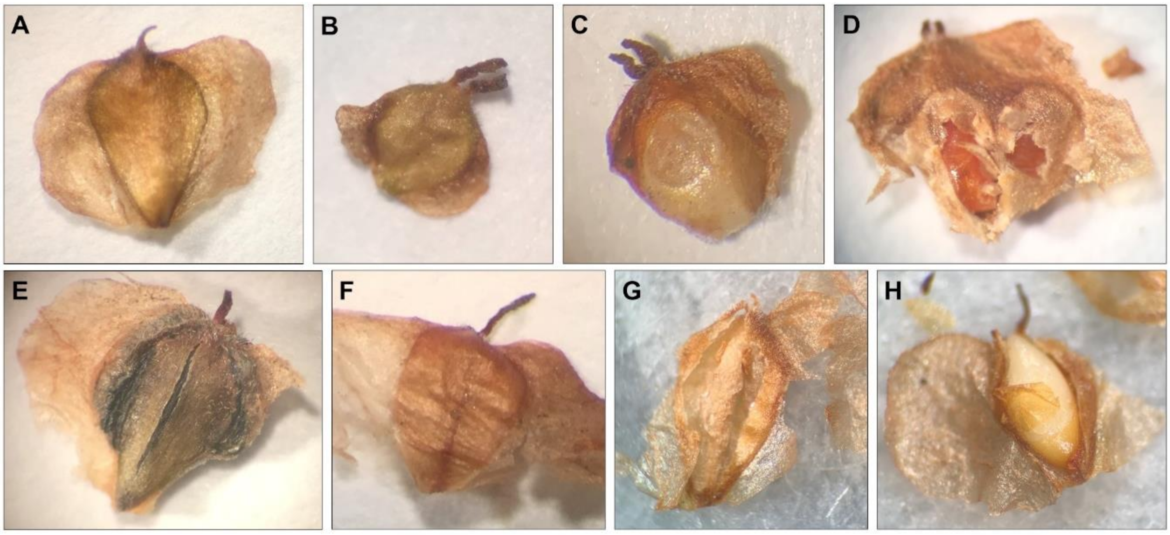


Fig. S1. Visual estimation of N-Icelandic mountain birch seed crop size from 1960 to 2014, according to regional foresters (see sources below). Seed crop categories were 0: none or virtually none (*ekkert* or *lítið sem ekkert*), 1: very small (*mjög lítið*), 2: small (*lítið*), 3: not much (*ekki mikið*), 4: considerable (*nokkuð, töluvert*), 5: large (*mikið*), 6: very large (*mjög mikið*), 7: unusually large (*óvenju mikið*). In our study, we consider categories 5–7 to be masting years.

Data sources for North Iceland and the above graph: Annual reports of north Iceland foresters https://www.skogur.is/is/um-skograektina/utgefid-efni/arsskyrslur-skogarvarda/nordurland.
Complete record 1960–2014.

Data sources for South (and SE) Iceland: Annual reports of south Iceland foresters: https://www.skogur.is/is/um-skograektina/utgefid-efni/arsskyrslur-skogarvarda/sudurland. Records for 1964–1995, 2002–2007 and 2016. For the years 2008 and 2017–2021, south Iceland seed crop sizes are mentioned in the annual publication of the Forestry Service (*Ársrit Skógræktarinnar*): https://www.skogur.is/is/um-skograektina/utgefid-efni/arsrit-sr

Appendix S2. Photos of mountain birch seeds, displaying variation between and within appearance groups.



Photos taken through the lens of a stereo microscope showing (A–B) intact mountain birch seeds (not infected or damaged) of different shapes and sizes, (C–D) seeds predated by Semudobia betulaea (C: unopened, D: opened, revealing two gall midges), (E) fungi infected seed, (F) damaged seed, and (G–H) opened intact seeds without (G) and with (H) a fully developed embryo. Magnification was around 40x but differed slightly between photos.

Appendix S3. Results from mixed effects logistic regressions on intact and gall midge infected mountain birch seeds.

ANOVA type II test results of mixed effects logistic regressions on intact (not infected or damaged) seeds and seeds infested by the gall midge Semudobia betulae at all sites and study years. Sample size equalled the number of seeds inspected in catkin samples (50 seeds for each of 20 trees per site per year at sites VM and VS in Vatnajökull National Park, but three-fold that at SKS on Skeiðarársandur, due to it encompassing three subsites). All sites were located in southeast Iceland. P-values in bold represent significant results.

	Intact seeds			Gall midge seeds		
Variables	*df*	X^2	*p*	*df*	X^2	*p*
Year	2	846.1	**<0.001**	*2*	519.3	**<0.001**
Site	2	0.8	0.668	2	2.0	0.374
Year x Site	4	67.9	**<0.001**	4	47.1	**<0.001**
Plant size	1	4.2	**0.040**	1	6.3	**0.012**
Growth form	1	0.1	0.745	1	0.6	0.428
Growth habit	2	2.8	0.249	2	2.5	0.290

Note: Abbreviations: *df*, degrees of freedom; χ^2, chi-square value; *p*, p-value.

Appendix S4. Results from mixed effects logistic regressions on the vitality of mountain birch seeds.

ANOVA type II test results of mixed effects logistic regressions of germination, seeds with a fully developed embryo (filled), and germination of filled seeds (relative germination) at all study sites. For germination and embryo presence at VM and VS in Vatnajökull National Park, sample size was 20 seeds for each of 20 trees per site per year, but at SKS on Skeiðarársandur, seeds were collected from three subsites, making the sample size three times larger than at the other sites. All sites were located in southeast Iceland. For relative germination (germination of filled seeds), sample size equalled the number of trees with ≥1 filled seed (2019, SKS: N = 221, VM: N = 73, VS: N = 167; 2020, SKS: N = 55, VM: N = 74, VS: N = 135). P-values in bold represent significant results.

	Germination of intact seeds (2017–2020)			Filled of intact seeds (2019–2020)			Relative germination (2019–2020)		
Variables	*df*	X^2	*p*	*df*	X^2	*p*	*df*	X^2	*p*
Year	3	146.1	**<0.001**	1	56.3	**<0.001**	1	45.5	**<0.001**
Site	2	10.1	**0.007**	2	12.1	**0.002**	2	11.5	**0.003**
Year x Site	5	28.6	**<0.001**	2	43.9	**<0.001**	2	0.9	0.651
Plant size				1	0.6	0.437	1	6.1	**0.013**
Growth form				1	2.9	0.087	1	0.8	0.381
Growth habit				1	1.4	0.242	1	0.6	0.421
Proportion of intact filled							1	12.2	**<0.001**

Note: Abbreviations: *df*, degrees of freedom; χ^2, chi-square value; *p*, p-value.

Paper III

The recruitment niche of mountain birch (*Betula pubescens* ssp. *tortuosa*) and implications for native woodland restoration

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Manuscript

Abstract

1. Restoring fragmented woodlands at large scales calls for scaling-up restoration practices. This requires a thorough understanding of the ecosystem involved, including identifying the recruitment niche of a target species, i.e. conditions required for plant recruitment from seed germination to seedling establishment. This calls for consideration of the plant-scale environment, and our study contributes to underpinning the science behind utilising natural regeneration in woodland restoration in subarctic environments.

2. We identified the recruitment niche of the only native forest-forming species in subarctic Iceland. From 2018 to 2020, we quantified mountain birch seed accumulation, germination, and early seedling survival in relation to microsite types on Skeiðarársandur outwash plain, southeast Iceland. At the time of study, the founding population in this early successional environment had recently reached reproductive maturity.

3. Mountain birch seeds were most likely to accumulate on vegetated surfaces, and to germinate in low-growing vegetation, with unimpeded light. Survival did not differ significantly between microsite types but was surprisingly high (generally >50%) for the first 1–2 years, although at that time, most seedlings were still very small.

4. Overall, thin moss (~1 cm) was most positively associated with recruitment and may be considered a key microsite type for mountain birch recruitment success. Due to high relative cover of suitable microsite types in the study area, the spatial pattern of the first locally recruited generation of mountain birch was determined at the earliest life history stage, by dispersal limitation.

5. *Synthesis and applications*. Our study highlights the importance of considering the recruitment niche of the target species during restoration, and to establish seed sources when dispersal limitation occurs, to effectively facilitate establishment. This allows for scaling-up restoration of severely fragmented woodlands, for which the pending restoration of Icelandic woodlands serves as a case study. The rapid mountain birch establishment on Skeiðarársandur shows that woodland restoration may not need major interventions, however they must be based on profound knowledge of colonising processes. Thus, restoration with minimal human assistance can be a practical, low-cost option.

Keywords

Betula pubescens ssp. *tortuosa*, early succession, germination, Iceland, recruitment niche, seed accumulation, seedling survival, large-scale restoration

Introduction

Overexploitation of resources has caused ecosystem degradation worldwide and generated an urgent need for large-scale ecosystem restoration (UN, 2015). Extensive scaling-up of restoration requires knowledge on the degraded as well as the target ecosystem, and when it is appropriate to work with individual species, an in-depth understanding of its "recruitment niche". The latter describes a subset of the regeneration niche (Grubb, 1977), describing conditions required for plant recruitment, from seed germination to seedling establishment (Larson et al., 2023). Plant recruitment is mostly shaped by the earliest stages of seedling establishment which are, in turn, largely conditioned by microsite quality (Graae et al., 2011). On bare soil, microsite conditions are shaped by abiotic structures and processes (Elmarsdóttir et al., 2003; Jones & del Moral, 2005). In vegetated areas, a plant's environment may be largely determined by its neighbours and their effects can be both positive and negative (Cavieres et al., 2007; Jeschke & Kiehl, 2008). Optimal conditions for seedling survival may also differ from those optimal for germination (Battaglia & Reid, 1993). For instance, in bare soil patches, there may be sufficient light for seedling emergence, but lack of protection from frost and drought can cause great seedling mortality (Aradóttir, 1991). Conversely, thick moss and litter cover may retain soil moisture better than bare soil, thus being conducive for seedling persistence, but may not facilitate germination (Battaglia & Reid, 1993; Tiebel et al., 2023). Thus, both life stages need to be considered when identifying the recruitment niche of a species (Larson et al., 2023).

An extreme example of an urgent, nation-wide restoration task can be found in Iceland. The distribution of mountain birch (*Betula pubescens* ssp. *tortuosa* (Ledeb.) Nyman), the only native forest-forming tree (Kristinsson et al., 2018), has declined drastically since human settlement over eleven hundred years ago, from an estimated cover of one fourth of the country (Trbojević, 2016) to below 1% around 1900, and with current distribution ca. 1.5% (Snorrason et al., 2016). As part of the Bonn Challenge, the Icelandic government pledged in 2021 to initiate mountain birch woodland restoration on 350,000 ha, eventually leading to them covering 5% of the country (Bonn Challenge, n.d.). Such scaling-up of restoration is an ambitious goal. Land-use in Iceland's sub-arctic environments has caused extensive and severe land degradation in the last millennium (Barrio & Arnalds, 2022). Together, extreme woodland fragmentation, harsh abiotic conditions in extensive degraded areas, and rangeland grazing severely limit the ability of the mountain birch woodlands to regenerate and expand their range (Aradóttir & Eysteinsson, 2005; Defourneaux et al., 2024). Thus, assisted natural regeneration on a landscape scale is an essential part of pending restoration actions.

Around 1990, long-distance seed dispersal (≥10 km) from Bæjarstaðarskógur forest in southeast Iceland, resulted in mountain birch colonisation on Skeiðarársandur glacial outwash plain, across an area that currently extends to over 35 km^2 (Thórhallsdóttir & Svavarsdóttir, 2022; Pálsson et al., 2023). Although the area did not suffer deforestation due to direct anthropogenic activities, there is strong evidence that Skeiðarársandur was at least partially vegetated with birch woodlands and riparian meadows at the time of human settlement in the 9th century AD (Thórhallsdóttir & Svavarsdóttir, 2022). Glacial outburst floods had left the 1000 km^2 plain extremely barren by the early 20th century (Björnsson, 2003), but a change in the disturbance regime in the mid-20th century allowed vegetation establishment (Thórhallsdóttir & Svavarsdóttir, 2022). Still, most of the area is at early successional stages and sparsely vegetated. Recently, the first generation of the mountain birch population reached reproductive maturity and seedling density consequently increased, although it was still low in most of the colonised area in 2018 (Óskarsdóttir et al., 2022).

Studying the natural colonisation of mountain birch on Skeiðarársandur through the lens of the species' recruitment niche provides a valuable opportunity to increase our understanding on its potential for natural regeneration and thus, our ability to scale up woodland restoration. By understanding which factors enabled the colonisation, restoration efforts could more effectively provide the conditions facilitating mountain birch recruitment and thereby, concentrate our restoration efforts. Thus, the objective of our study was to relate mountain birch seed germination and early seedling survival to microsite types, aiming to identify the recruitment niche of mountain birch. We distinguished three critical stages for successful recruitment: seed accumulation, germination, and early seedling survival. Specifically, we asked (1) whether and how the three stages of recruitment were constrained by the different microsite types, and (2) whether seed accumulation, germination, and seedling survival were positively associated with each other across microsite types, potentially allowing for identification of key microsites for successful regeneration.

Methods

Study Area

The study area is within the upper middle zone of Skeiðarársandur plain (Fig. 1). The surface is coarser and more stable in the study area than in the sandier part seawards, making way for vegetation establishment and mountain birch colonisation (Thórhallsdóttir & Svavarsdóttir, 2022). We selected two sites across the study area, to cover some of the spatial variability in the region. Logistical constraints prevented establishment of a greater number of sites. One was located towards the western limit of the mountain birch range (hereafter: **edge site**) and the other near the middle of the range (hereafter: **central site**), ca. 5 km east of the western one (Fig. 1). An earlier study at the same sites (Óskarsdóttir et al., 2022) showed that in 2018, mountain birch density, tree size, and seed production were significantly lower at the edge site (referred to as S1 in that study) than at the central one (referred to as S4), where great seedling density was reported.

The climate is maritime, with high precipitation. Mean annual temperature is 5.3°C (coldest quarter: 0.9°C, warmest quarter: 10.5°C) and mean annual precipitation is around 1,700 mm (2016–2020 data from Skaftafell weather station, around 10 km northeast of Skeiðarársandur, unpublished data from the Icelandic Met Office). Air temperature and precipitation in spring and summer 2016–2020 are summarised in Table S1.

Field Sampling

In late July 2018, we laid out a 500 m long N-S transect at each site. Each transect was split into four 125 m sections and within each at two randomly selected points, a 20 m x 0.5 m plot was established (Fig. 1). Each plot was split into 40 0.5 m x 0.5 m quadrats. Within each quadrat, we recorded all **first-year seedlings**, i.e. with cotyledons present, and all **older seedlings**, i.e. plants without cotyledons but with <5 leaves (Fig. S1). The number of leaves was recorded for all older seedlings. In mid-July 2019, all current first-year seedlings (within all quadrats and all plots) were recorded.

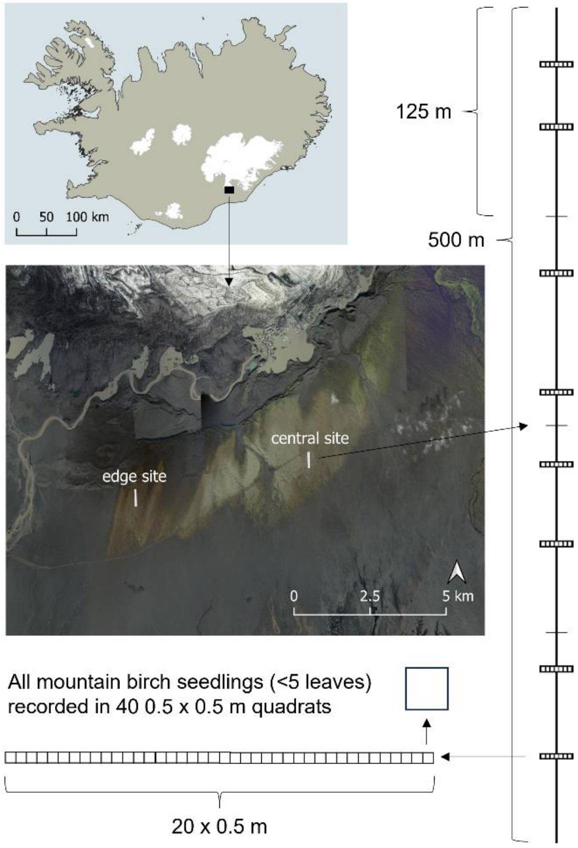

Fig. 1. The study area and sites within Skeiðarársandur, southeast Iceland, and a diagram of the sampling design. Aerial photographs and map database: Open database of the National Land Survey of Iceland (https://www.lmi.is/is/landupplysingar/gagnagrunnar/nidurhal). Geographic information system: QGIS (http://qgis.osgeo.org).

Within two quadrats in each plot, at metres 6 and 14, we recorded **microsite types** with the point-intercept method using 25 points. At each point, we identified the surface type under the pin, characterised into one of fourteen different microsite types (details in Appendix S1). We also recorded microsite types for all seedlings in both 2018 and 2019.

For monitoring survivorship, we aimed to tag ca 200 first-year seedlings and 200 older seedlings at each site (Fig. S1). Within most plots, seedling density was too low to reach our proposed sample size and thus, we also tagged several seedlings in their vicinity, within a radius of approximately 5 m. After subtracting lost seedlings, a total of 189 tagged first-year seedlings remained at the edge site but only 107 older seedlings, despite tagging all we found and losing only a few. At the central site, a total of 201 tagged first-year seedlings and 204 older seedlings remained throughout the study. In 2019, first-year seedlings were far less abundant than the previous year and thus, we tagged all first-year seedlings found within plots and their nearest vicinity, 65 and 97 at the edge and central site, respectively. In mid-June 2019, we recorded winter survival of seedlings marked in 2018. In early-September 2019, mid-June 2020, and late-August 2020, we recorded summer and winter survival of all tagged seedlings.

Finally, we quantified the soil seed bank at both sites. We took five soil samples (Ø = 4.7 cm, depth = 5 cm) in May 2019 and 2020 at 2 m intervals parallel to each plot, 2 m north or south of it (direction was randomly chosen and the middle sample was aligned with the transect) (N = 40 per site). Further details regarding data sampling are provided in Appendix S1.

Statistical Analyses

All data handling and analyses were conducted in the *RStudio* console (Posit Team, 2023) of *R* (R Core Team, 2022). To test whether the distribution of seeds and seedlings differed from expectations based on the prevalence of each microsite type, we used chi-square goodness-of-fit statistics, available in the *stats* package (R Core Team, 2022). The analyses were carried out separately for each site and for 2018–2019 first-year seedlings on one hand and older seedlings on the other. Observed values were the number of individuals in each microsite type. Expected values were calculated as the proportions of different microsite types recorded for soil samples (for seeds) and according to the results of microsite type frequencies in quadrats (for seedlings), multiplied by the total number of individuals. Microsite types with expected values <5 were combined (Conover, 1980; Bewick et al., 2003) into two groups: *other biotic* (vegetation and litter) or *other abiotic* (unvegetated) microsites. For the chi-square post-hoc tests, we used a Bonferroni correction, available within the *chisq.posthoc.test* package (Ebbert, 2023).

To test whether seedling survival differed between microsite types, we used mixed effects logistic regressions with a dependent variable where a seedling was either alive at the end of the study (1) or not (0). For first-year seedlings from 2018 and 2019 (analysed separately), we used *microsite* and *site* as fixed factors, as well as their interaction, to inspect whether the difference between microsite types differed between sites. For older seedlings, we added *number of leaves* at the beginning of our study to the fixed factors, and for all seedlings combined, *seedling cohort* was added to the list of fixed factors. For all the logistic regressions, *plots* (nested within sites) were used as a random factor. For all models, we used likelihood ratio tests to perform backwards elimination for model reduction. We used the package *lme4* (Bates et al., 2015) for performing the mixed effects logistic regressions, the *lmtest* package (Zeileis & Hothorn, 2002) for the likelihood ratio tests, the *car* package (Fox & Weisberg, 2019) for inspecting their results using analysis of variance (ANOVA) type II tests, and the package *emmeans* (Lenth, 2023) for pairwise comparisons between groups using estimated marginal means (EMMs).

Results

Microsite types and mountain birch recruitment

At both sites, moss (mostly *Racomitrium* spp.) was the most frequent microsite type (see details on microsite type classification in Appendix S1). Moss <1 cm thick had greater relative cover at the edge site than the central one, while the opposite was true for moss >1 cm (Table S2). At both sites, lichens were mostly fruticose *Stereocaulon* spp. which formed coarse-branched cushions on the plain. Of microsite types characterised by vascular plants, dwarf shrubs were the most prominent (Table S2), and the most common species were *Empetrum nigrum* and *Calluna vulgaris*.

Spatial distribution of both seeds and seedlings was clustered and varied between sites and years (Table 1). In 2018, the density of first-year seedlings was 17 times higher than of older seedlings at the edge site, while the difference was much smaller at the central site with around 1.5 times more first-year seedlings than the older ones. In 2019, first-year seedling density was substantially lower than the year before at both sites (Table 1).

Table 1. Mountain birch seed and seedling densities (individuals/m^2) at two sites (one close to the edge of the range and one towards its centre) on Skeiðarársandur, southeast Iceland (N = 8). First-year seedlings refers to all plants with cotyledons present, older seedlings refers to plants with <5 leaves. For seeds, the year refers to the latest year of seed production, sampled the following year.

		Seeds		**First-year seedlings**		**Older seedlings**	
Site		**edge**	**central**	**edge**	**central**	**edge**	**central**
2018	Mean	288	1,931	0.68	15.00	0.04	9.90
	Median	115	691	0.5	3.0	0	1.9
	Range	0–1,383	115–9,683	0–1.9	0.1–98.8	0–0.2	0–61.6
2019	Mean	504	2,522	0.04	1.05		
	Median	231	1,268	0	0.4		
	Range	0–1,729	346–8,876	0–0.2	0.1–5.1		

Seed accumulation and seedling presence

The spatial distribution of both seeds and seedlings deviated significantly from expectations based on the prevalence of each microsite type (Table S2). Despite the results for seeds at the edge site suggesting a distribution significantly different from random, the post hoc test did not detect any significant differences (p>0.05). However, seed distribution at the edge site was generally similar to that at the central site, where unvegetated microsites and moss <1 cm seemed to have fewer seeds than expected while more seeds were found in better vegetated microsites (Table S2). In all cases, seedlings were negatively associated with unvegetated microsite types, and for dwarf shrubs, the association was significantly negative for all seedlings except older seedlings at the edge site (Table S2). On the other hand, all seedling cohorts except first-year seedlings at the central site were significantly positively associated with moss >1 cm. The distribution of seedlings in moss <1 cm differed between seedling cohorts at the central site, where significantly more first-year seedlings occurred in the microsite type than expected, while the opposite was true for older seedlings (Table S2).

Early seedling survival

Throughout the study, survival of all seedling cohorts stayed high (Fig. 2). Survival of older seedlings at the end of the study was >90%, significantly higher than of first-year seedlings from 2018 (z = 8.977, SE = 0.029, p<0.001; EMMs) and 2019 (z = 7.815, SE = 0.035, p<0.001; EMMs), while the difference in survival between first-year seedlings from 2018 and 2019 was not significant (z = -0.209, SE = 0.195, p = 0.976; EMMs). Survival did not differ significantly between the recorded microsite types for any of the seedling cohorts (Table S3), and the between-site differences in survival were only significant for 2019 seedlings, where seedlings at the edge site suffered ca. 50% loss that summer, with most survivors persisting to the end of the study (Fig. 2). Note that considerably fewer seedlings were found (and tagged) in 2019 than in 2018. Survival of older seedlings at the end of the study showed a non-significant trend towards improvement (p = 0.06) with increasing number of leaves recorded at the start of it (Table S3).

Associations across recruitment stages

Significant associations between microsite types and mountain birch presence over the three stages of recruitment are summarised in Fig. 3 (green boxes) and other life history stages are also shown (blue boxes; see Óskarsdóttir et al., 2022; submitted). Regarding early seedling survival in different microsite types, results from the expected vs. observed occurrence of older seedlings (Table S2) were inconsistent with the direct seedling survival results (Table S3), which did not reveal any significant effects of microsites. Regardless of whether the preference of older seedlings for a specific microsite type is used as a metric for their survival or not, the microsite type that stood out across recruitment stages as being positively associated with mountain birch presence was moss >1 cm (Table S2). Dwarf shrubs and lichens had inconsistent effects across recruitment stages, with positive association to seed accumulation but negative to the presence of seedlings, both first-year and older ones. Overall, the associations between unvegetated microsites and mountain birch recruitment were negative (Table S2).

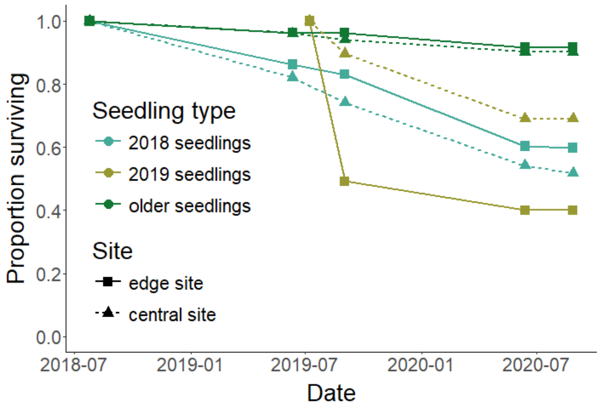

Fig. 2. Survivorship of seedling cohorts from late July 2018 to late August 2020 at the two study sites on Skeiðarársandur, southeast Iceland. Initial sample sizes were as follows: 2018 seedlings edge site=189, central site=201; 2019 seedlings edge site=65, central site=97; older seedlings edge site=107, central site=204.

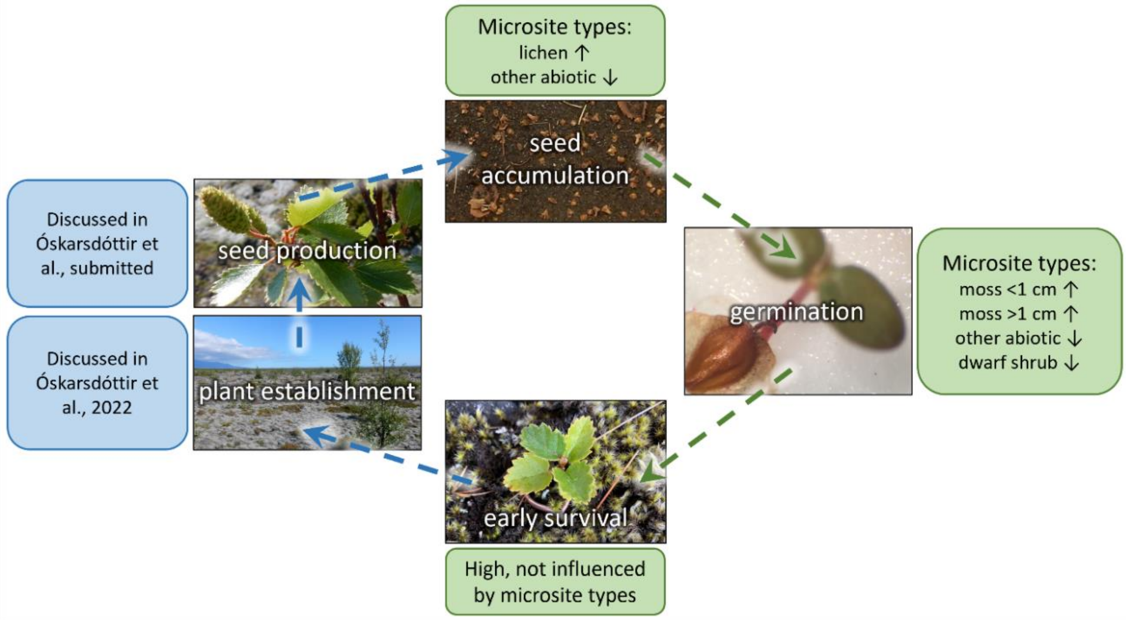

Fig. 3. Schematic model showing microsite types significantly influencing each of the three recruitment stages for the mountain birch population on Skeiðarársandur, southeast Iceland (green boxes, see Tables S2 and S3 for details). Two other life history stages have previously been studied and are also shown (blue boxes). Black arrows denote factors facilitating (upwards pointing) or inhibiting (downward) recruitment. Dotted arrows signalise movement between life history stages.

Discussion

The study identifies the recruitment niche for mountain birch across three life history stages (seed accumulation, germination, and early seedling survival) in relation to microsite types (Fig. 3). Seeds were more likely to accumulate on vegetated rather than barren surfaces, with plant aboveground structures acting as traps for windborne seeds. Furthermore, seeds were most likely to germinate in microsite types with low stature vegetation, where shelter was provided by plant neighbours, but light was not intercepted by taller canopies. Seedlings had high survivorship in the first one to two years, irrespective of microsite types. The study presents an applicable method of identifying the recruitment niche of target species for restoration, which allows us to identify key drivers of the pending succession and in turn, better predict and shape the outcome.

The seedlings of small seeded species such as mountain birch are very vulnerable to abiotic stress such as drought and frost, which can cause great losses during early establishment (Osumi & Sakurai, 2002). While larger seeds with greater reserves can support greater root growth, small-seeded species have the potential for rapid elongation of small initial root systems, maximising potential resource utilisation at suitable microsites (Larson et al., 2016). Therefore, colonisation patterns of species like mountain birch may be shaped by microsite quality to a greater degree than those of larger seeded plants. Importance of microsites was evident in our study, with different types significantly facilitating and hindering the first two stages of recruitment (Fig. 3).

First stage: seed accumulation

In general, accumulation of seeds was highest in microsite types with coarse microtopography, dominated by fruticose lichens or dwarf shrubs, and lowest where the microtopography was relatively smooth, such as in the barren microsite types (Table S2; Fig. 3), which is typical for any wind-dispersed matter (McElhinny et al., 2010). The between-site difference in seed densities (Table 1) at least partly reflects the spatial patterns of the population’s reproductive effort. For example, in 2018, density of flowering trees and catkins was four and 40 times higher at the central than the edge site, respectively (Óskarsdóttir et al., 2022). This suggests that although the distance between the two sites is smaller than the distance to the parent population in Bæjarstaðarskógur, between-site dispersal is limited, as indicated by reported common dispersal distances for mountain birch (Aradóttir et al., 1997; Liu & Evans, 2021). Great between-year differences in seed density were also observed (Table 1), as expected for a masting species (Gallego-Zamorano et al., 2018).

Second stage: germination

It has been suggested that the presence of moss on Skeiðarársandur drives subsequent vegetation development (Marteinsdóttir et al., 2013). Bryophytes can have both facilitating and limiting effects on seedling establishment (Jeschke & Kiehl, 2008). For mountain birch seedlings, moss up to 2 cm thick has been identified as a suitable microsite type (Aradóttir & Halldórsson, 2018), but a negative association has been reported between thick bryophyte layer and seed germination (Aradóttir, 1991; Jeschke & Kiehl, 2008; Jónsdóttir, 2009). *Racomitrium lanuginosum* and *R. ericoides* are the two dominating bryophytes on Skeiðarársandur and they are mostly <2 cm thick (Óskarsdóttir et al., unpublished data). This could be due to both slow growth (Armitage et al., 2012) and regular diebacks of moss stems caused by aeolian deposits, to which they are intolerant (Arnalds et al., 2010). Regardless of the cause of low moss thickness, it undoubtably shapes the suitability of the most prominent microsite type in the area for mountain birch regeneration, and more seedlings were found in moss than expected from a random occurrence (Table S2; Fig. 3).

The association between vascular plants and seedling presence seemed mostly negative, although results were only statistically negative for dwarf shrubs (Table S2). Under harsh conditions, nurse plants can facilitate seedling establishment (Cavieres et al., 2007) but where conditions are more benign, seedlings are more likely to experience competition with vascular plants (Graae et al., 2011; Elmarsdóttir et al., 2003). However, in monitoring plots close to our central site on Skeiðarársandur, interspecific competition was found to be unlikely to influence vascular plant species assembly (Marteinsdóttir et al., 2018). Shading by litter is another well-known limiting factor for seedling establishment (Tiebel et al., 2023) but in our study, litter had limited cover and no significant association with seedling presence. The reported negative association between unvegetated microsite types and seedling emergence agrees with other studies on recruitment in Iceland (Elmarsdóttir et al., 2003; Aradóttir & Halldórsson, 2018).

Third stage: seedling survival

A major and surprising finding in our study was the high survival rate of all seedling cohorts, mostly >50% for first-year seedlings after 1–2 years and >90% for older seedlings after 2 years (Fig. 2). Seedling survival can be highly dependent on microsite types, for example where frost heaving or drought stress are important limiting factors (Aradóttir, 1991; Tiebel et al., 2023) but generally, the smaller-scale heterogeneity affects survival less than it does colonisation (Table S3; Fig. 3; Renison et al., 2005). The significant association between microsite types and the presence of older seedlings (Table S2) likely reflects the strong influence of microsites on germination, still detectable for the older seedlings, rather than patterns of survival. Likewise, the contrasting association between moss of different thickness and the presence of older seedlings (Table S2) implies that thicker moss represents establishment at an earlier stage, such that these seedlings may have germinated when the moss was thinner (cf. Aradóttir & Halldórsson, 2018). During early primary succession, unfavourable local environmental conditions commonly cause low emergence and high seedling mortality rates (Aradóttir, 1991; Marteinsdóttir et al., 2010), and plant establishment is strongly shaped by physical microsite conditions (Jones & del Moral, 2005). Despite being an early-successional environment, our study area on Skeiðarársandur, with its mostly low-growing vegetation and maritime climate with high precipitation (Massad et al., 2020), seems to provide optimal conditions for mountain birch seedling establishment. Generally, pioneer species such as mountain birch are defined by extreme early mortality, with first-year seedling survival of <20% considered within the expected range (Osumi & Sakurai, 2002; Marteinsdóttir et al. 2013). For *Betula pubescens* specifically, a 7% one-year survival has been reported for seeded plants (Aradóttir, 1991) and 9% three-year survival for planted ones (Jessen et al., 2023). Although environmental conditions vary between these examples, they further support our conclusion that the survival rate in our study was exceptional.

During our study, one mortality event stood out, i.e. summer losses of first-year seedlings in 2019 at the edge site (Fig. 2). A close inspection of temperature and wind data from Skaftafell weather station from May through August in 2019 did not reveal any single weather event that could have explained the relatively high mortality of those seedlings (unpublished data from the Icelandic Met Office). However, precipitation for that period was only 263 mm, compared to 552 and 426 mm in the year before and after, respectively.

The humidity of microsites is one of the main factors influencing their suitability for seedlings (Battaglia & Reid, 1993; Lidman et al., 2023). Establishment of *Betula* seedlings is also linked to persistent moist conditions (Tiebel et al., 2023), which are better retained in the more vegetated microsite types than barren ones (Moreno et al., 2022). The moss layer was on average thinner at the edge site than the central one (Table S2) and thus, conditions there may have been overall less optimal for vulnerable first-year seedlings. Another possible influencing factor is the site's location, close to the edge of the vegetated area on Skeiðarársandur, where aeolian movement and deposition could be more prevalent and damaging to small plants than towards the centre (Arnalds et al., 2010).

The current study did not consider long-term survival of seedlings. In general, chances of seedling mortality are highest during the first year (Aradóttir, 1991; Osumi & Sakurai, 2002; Marteinsdóttir et al., 2013) but at the end of our study, most individuals were still very small and thus susceptible to environmental stress. With climate change, weather in the arctic and subarctic is expected to get warmer and moister (Björnsson et al., 2023) which might stimulate regeneration through escalated plant establishment and seed production (Fig. 3). However, complex biological interactions impede accurate predictions, for example through simultaneous advancements in pest outbreaks (Crossley et al., 2024).

Implications for woodland restoration

Our results show the potential of natural regeneration when favourable conditions arise, and the need for understanding the mechanisms involved to advance restoration measures. Learning from nature and considering the recruitment niche of target species in ecosystem restoration can allow us to facilitate establishment more effectively, at local to national scales. Biological soil crust and thin moss have been identified as safe sites for mountain birch (Aradóttir, 1991) and considering the high seedling survival in our study, we suggest that they can be considered key microsite types for recruitment success. The thickness of the moss also needs to be considered as moss >2 cm thick can severely affect recruitment at the germination stage (Aradóttir & Halldórsson, 2018). Other factors must also be considered, such as land-use, as grazing and browsing are known to strongly shape regeneration patterns and high herbivore density has been identified as a major factor limiting natural woodland expansion (Gullett et al., 2023; Barrio & Arnalds, 2022). Under moderate grazing, herbivore trampling can reduce moss thickness (Tuomi et al., 2020), potentially facilitating birch recruitment. On Skeiðarársandur, moss was overall too thin to inhibit germination and the low grazing pressure (around 200 ewes on the 1000 km^2 plain) was considered to have limited impact on regeneration (Óskarsdóttir et al., 2022).

In fragmented woodlands, insufficient seed rain is considered an important limiting factor for their expansion (Aradóttir & Halldórsson, 2018; Gullett et al., 2023). Despite great dispersal potential of birch (Lidman et al., 2023), events such as the long-distance, large-scale colonisation of Skeiðarársandur are rare. According to our results, the spatial pattern of the first locally recruited generation is determined at the earliest life history stage, by dispersal limitation (Fig. 3). Seed dispersal is a highly stochastic process (Fenner & Thompson, 2005), and stochasticity is increasingly recognised as an important aspect in early succession (Ulrich et al., 2016; Marteinsdóttir et al., 2018). This was clearly demonstrated on Skeiðarársandur, with great recruitment following a good seed year (2017) combined with moist conditions at the time of germination (spring 2018), but limited recruitment following a bad seed year (2018) combined with dry conditions in the first growing season (summer 2019) (Óskarsdóttir et al., submitted). This underscores the advantage of applied nucleation (establishing seed sources), to ensure that randomly occurring favourable conditions for recruitment are utilised, and this is an essential component of the scaling-up of restoration (Hulvey et al., 2017). Given the scale of the Icelandic pledge to initiate the process towards 5% cover of native woodlands by 2030, assisted natural regeneration must be emphasised (Shono et al., 2007). We advocate for using the pending restoration of native woodlands in Iceland as a case study for scaling-up restoration projects on landscape-scales. With the current high level of fragmentation and a single native forest forming tree species, the development of Icelandic woodlands presents an opportunity to identify key drivers of successes and failures that will likely shape the global task of restoring native ecosystems in the coming decades.

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Supporting information

Appendix S1. Additional information regarding field sampling

Seedling sampling within quadrats

Towards the northern end of the central site, birch densities were so high that it was impractical to count seedlings in all 40 quadrats. Instead, we laid out quadrats at every other metre and every metre in the northernmost (N = 10) and second northernmost (N = 20) plots, respectively. In all other plots, every quadrat was sampled.

Recording of microsite types

The microsite types used in the point-intercept sampling were moss >1 cm thick, moss <1 cm thick, biological soil crust, lichen, shrub, dwarf shrub, graminoid, forb, pteridophyte, litter, stone (Ø > 2 cm), gravel (Ø = 0.2–2 cm), sand (Ø < 0.2 cm), and bare soil. Pteridophyte and sand microsite types were not recorded across the quadrats and so were omitted from the analyses. The two categories of moss were considered sufficient since in our unpublished moss thickness data from the central site in 2018 (N = 414), only 12,6% of the measurements were >2 cm, and <1% were >3 cm. We followed Elmarsdóttir et al. (2003) in combining moss <1 cm and biological soil crust as the two microsite types were structurally similar at our sites.

Seedling tagging

Within most plots, seedling density was too low to reach our proposed sample size and thus, we also tagged several seedlings in their vicinity, within a radius of approximately 5 m. To avoid potential detectability bias, in plots with few seedlings, searches were carried out in a manner that allowed for the detection of even newly germinated individuals, while in plots with an abundance of seedlings, each quadrat was systematically searched and seedlings randomly tagged. For tagging, we used a 2 mm thick wire loop that was placed around each plant, with a little excess wire inserted into the ground to secure the loop.

Soil sampling

For soil samples, the sampling depth was selected considering both the thin layer of organic soil in the study area and the relatively short persistence of mountain birch seeds in the soil (summarised in Bonner et al., 2008). We recorded the microsite type of each sample and counted mountain birch seeds. To extract seeds from the soil samples, they were first carefully sieved to exclude fine textured soil (mesh opening size: 0.25 mm), then placed in a large glass containing water. Most seeds floated and were extracted using a pinsette. Most vegetation and litter also floated and was removed after the seed extraction. We then spread the remaining part of the soil sample, consisting mostly of sand and gravel, on a plastic tray and examined it thoroughly to extract any remaining seeds.

Seed and seedling density calculations

For each plot, we calculated the total density of seedlings as the number of all individuals divided by the sampled area (2.5 m^2 and 5 m^2 for the two northernmost plots at the central site, respectively, 10 m^2 for all other plots). We did the same for seeds, using the accumulated surface area of the five soil samples in each plot (0.00867 m^2).

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Fig. S1. A photo of a first-year mountain birch seedling (left) and an older seedling (right), tagged with wires for survival monitoring on Skeiðarársandur glacial outwash plain in southeast Iceland.

Table S1. Monthly mean values for air temperature, minimum and maximum temperatures, and total precipitation for the period May to August in 2016–2020 (unpublished data from Skaftafell weather station, Icelandic Met Office).

	Mean temp (°C)	Min temp (°C)	Max temp (°C)	Precipitation (mm)
May	7.2	-2.7	18.0	101
June	10.1	0.1	21.9	92
July	11.2	1.6	21.9	84
August	10.1	0.3	20.1	107
May–August	9.7			384*

*Sum of monthly values.

Table S2. Number of soil samples and points, determined using the point intercept method, at the two study sites on Skeiðarársandur, southeast Iceland (one close to the edge of the population range and one towards its centre), as well as the number of seeds and seedlings, and results of chi-square goodness-of-fit analyses for their occurrence in different microsite types. For seeds, expected values were obtained from microsite types recorded for the soil samples, while for seedlings, results of microsite type frequencies in quadrats were used. The difference of seed and seedling occurrence from expected values are also shown (+ denotes higher value than expected and - denotes lower). Bold font denotes a significant difference between expected and observed values (p<0.05), according to post hoc tests (with Bonferroni correction). For expected values <5, microsite types were combined in the categories other biotic (vegetated and litter) and other abiotic (unvegetated), and in those cases, results are shown within parentheses. Note that for seeds at the edge site, the expected value for the other biotic category was still <5. First-year seedlings in 2018 and 2019 are pooled.

	Expected values (%)				**Difference from expected (%)**					
	Soil samples		Point intercepts		Seeds		First-year seedlings		Older seedlings	
	edge	centre	edge	centre	edge	centre	edge	centre	edge	centre
N	80	80	400	400	55	309	271	534	119	354
χ^2					17.2	155.2	147.6	131.9	55.2	198.11
df					3	4	4	6	4	6
p-value					**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Microsite types										
Moss >1 cm	31,3	35	15	37,3	63 +	16 +	**158 +**	14 +	**135 +**	**88 +**
Moss <1 cm	48,8	31,3	64,5	29	29 -	13 -	9 -	**52 +**	1 -	**42 -**
Dwarf shrub	1,3	6,3	7,5	8,5	323 (+)	33 +	**95 -**	**74 -**	89 -	**71 -**
Bare soil	1,3	1,3	4,3	0,5	100 (-)	**100 (-)**	**84 (-)**	**100 (-)**	**100 (-)**	**100 (-)**
Stone	0	0	2,2	7,5			**100 (-)**	**100 (-)**	**100 (-)**	**100 (-)**
Gravel	15,0	18,8	1,8	7,5	63 (-)	**93 (-)**	**100 (-)**	**65 (-)**	**100 (-)**	**89 (-)**
Litter	0	0	1,5	2			53 (-)	15 -	100 (-)	100 +
Shrub	0	0	1,5	0,5			100 (-)	100 (-)	100 (-)	100 (-)
Lichens	2,5	7,5	1	6,3	44 (+)	**203 +**	60 (-)	5 -	100 (-)	14 -
Forb	0	0	0,8	0,3			100 (-)	100 (+)	100 (-)	100 (-)
Graminoid	0	0	0	0,8				100 (-)		100 (-)

Table S3. Results of model selection, according to backwards elimination using likelihood ratio test, as well as ANOVA type II test results for selected mixed logistic regressions on patterns of seedling survivorship on Skeiðarársandur, southeast Iceland, late July 2018 to late August 2020. If dropping a term increased the AIC and results of the likelihood ratio test were close to being significant (p<0.10), the term was included in the selected model. Significant results (p<0.05) are shown in bold font.

			Likelihood ratio test		Selected model			
	Dropped term	AIC	χ^2	*p-value*	Included term	χ^2	*df*	*p-value*
All plants (865)	None	960.2						
	Microsite type:Site	959.1	8.88	0.11				
	Site	957.2	0.15	0.69				
	Seedling cohort	1070	116.9	**<0.001**				
					Microsite type	9.10	7	0.25
					Seedling cohort	87.16	2	**<0.001**
2018 seedlings (390)	None	548.3						
	Microsite type:Site	546.2	5.90	0.21				
	Site	546.0	1.81	0.18				
					Microsite type	5.77	7	0.57
2019 seedlings (162)	None	212.0						
	Microsite type:Site	211.8	5.79	0.12				
	Site	214.3	4.51	**0.03**				
					Microsite type	1.12	5	0.95
					Site	6.79	1	**0.009**
Older seedlings (310*)	None	197.3						
	Microsite type:Site	195.6	0.22	0.64				
	Site	195.1	1.51	0.22				
	No. of leaves	196.7	3.59	0.06				
					Microsite type	8.32	5	0.14
					No. of leaves	3.56	1	0.06

*Originally, we tagged 311 older seedlings, but since only one seedling was present in the microsite type "dwarf shrub" at one site, it was excluded from this analysis.