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RESEARCH ARTICLE

Natural colonization as a means to upscale restoration of subarctic woodlands in Iceland

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The global climate and biodiversity crisis has led to extensive restoration initiatives, calling for cost-effective strategies harnessing the potential of natural processes. Natural colonization of target species is a key process in the scaling up of woodland restoration, and effective planning and implementation of restoration strategies requires a mechanistic understanding of colonization processes. In this study, we investigated patterns and processes of natural colonization of mountain birch (*Betula pubescens* ssp. *tortuosa*), the only native woodland-forming tree species in Iceland, into adjacent treeless lands under diverse conditions, and its implications for low-intensity restoration strategies. Accordingly, we assessed spatial patterns of seedling densities on transects extending from 10 birch woodlands in Iceland and analyzed the impact of local environments on colonization dynamics. Seedling densities generally decreased rapidly with distance from the seed source to around 40 m. In many study areas, however, birch seedlings were registered at high enough densities to potentially form woodlands, up to 140 m from a standing seed source. We identified a range of biotic and abiotic determinants of colonization, with the largest number affecting the early-establishment phase of birch colonization, including safe site availability, wind speed and dominant direction, and grazing. Our results demonstrate a good potential for natural colonization as a restoration strategy for birch woodlands in subarctic environments, and they can furthermore be used to identify areas where birch colonization is likely to occur naturally and determine appropriate interventions that can facilitate birch colonization in areas where it is less likely.

Key words: ***Betula pubescens*** **ssp.** ***tortuosa*****, birch woodlands, Iceland, mountain birch, natural colonization, passive restoration, safe sites, seedling establishment**

Implications for Practice

- Natural colonization of mountain birch is generally greatest within the first 40 m of the woodland edge, but occasional long-range dispersal creating nascent foci further away may play an important role in woodland expansion.
- Targeting of areas for passive and low-intensity woodland restoration should take into consideration the availability of microsites for seedling establishment, which for relatively small-seeded tree species are characterized by low-growing vegetation and stable biocrust surfaces on mineral soils.
- Restoration interventions to facilitate natural colonization should address the limiting factors in each case, including planting of a seed source to induce seed dispersal far from the woodland edge, revegetation to stabilize eroded surfaces unfit for establishment, and the removal or strategic introduction of disturbances such as grazers.

Introduction

The continuing degradation of Earth's ecosystems is among the biggest threats facing humanity in the twenty-first century (Barnosky et al. 2012). It has been estimated that more than 70% of natural ecosystems have been altered or lost due to anthropogenic disturbances (IPCC 2019). This is particularly the case for primary forests and woodlands, with estimated losses of 47 million ha in the last 20 years (FAO 2022). Their restoration is of great importance to ensure the provision of valuable ecosystem services (Suding et al. 2015; Temperton et al. 2019). Globally, there are numerous ongoing efforts to increase the cover of natural woodlands and restore degraded woodland ecosystems, including the Bonn Challenge, a global

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initiative aiming to restore 350 million ha of deforested and degraded lands by 2030 (World Conservation Union 2020).

Much of woodland restoration has focused on large-scale tree planting, which is both an economically and logistically infeasible strategy for the extensive effort that is currently needed (Ferreira et al. 2023). Nor is it a guarantee for the success of such restoration projects, as tree planting projects often fail to consider ecological principles for the creation of new, self-sustaining populations (Holl et al. 2011; McCallum et al. 2018; Hua et al. 2022). To scale up woodland restoration globally, cost-effective restoration strategies that harness the potential for woodland expansion through natural colonization from existing seed sources and planted tree nuclei are needed, that is, natural regeneration, assisted natural regeneration, and applied nucleation (Gann et al. 2019).

Effective facilitation of natural colonization in restoration requires a thorough understanding of limiting factors at the successive life history stages of targeted plant species. The process of seed dispersal is, in the case of anemochorous species, affected by distance from seed source, landscape patterns, topography, wind direction, and a range of other biotic and abiotic factors and their interactions (Wilson 1993; Auffret et al. 2017; Beckman & Sullivan 2023). Successful colonization furthermore requires habitat patches with suitable safe sites for seedling establishment and survival (Fowler 1988; Duncan et al. 2009). An improved understanding of the precise limitations to recruitment is necessary for more accurate predictions of colonization rates and patterns and the design of effective restoration approaches.

Several passive and low-intensity restoration frameworks rely on natural colonization to a large degree. A completely passive framework, in the context of woodland restoration, typically arises from initial management actions with little or no subsequent intervention, such as land protection or abandonment, leading to successional trajectories toward target ecosystems (Holl & Aide 2011). Strategies relying entirely on natural colonization, however, can lead to invasion of species other than the target species, and predicting restoration outcomes is in most cases not possible (Crouzeilles et al. 2020; Pizza et al. 2023). Assisted natural regeneration removes potential barriers to seedling establishment and enhances survival by selected interventions, for example, protection against active disturbances such as erosion and grazing and active removal of tall-growing competing vegetation (Shono et al. 2007). Applied nucleation, on the other hand, overcomes dispersal limitations by establishing tree clusters that serve as future seed sources (Benayas et al. 2008). These strategies are generally less costly than more extensive planting (Campanhã Bechara et al. 2021), but applying them can be challenging without a comprehensive mechanistic understanding of factors affecting seedling establishment and survival (Corbin & Holl 2012; McCallum et al. 2018). Existing research on the drivers and dynamics of natural colonization is skewed toward the tropical and temperate regions of the world (Chazdon & Guariguata 2016; Bauld et al. 2023; Pedersen et al. 2023) with studies from subarctic regions being more limited. Successional processes are generally thought to be slower in the subarctic and Arctic than in warmer regions (Cargill & Chapin 1987; Jones & Henry 2003), which might lead to the erroneous notion that restoration strategies relying on natural colonization are not efficient in the subarctic. Large-scale studies addressing mechanisms of colonization under diverse conditions are needed, particularly in the subarctic region, to investigate the efficacy of natural colonization for upscaling woodland restoration.

Mountain birch (*Betula pubescens* ssp. *tortuosa*) is a key woodland-forming tree species in the subarctic. In Iceland, mountain birch woodlands covered an estimated 30% of the land area before settlement but were decimated over the next millennium to less than 1%, primarily due to unsustainable overexploitation of the woodlands for fuel and grazing by domestic sheep, the latter being a known limitation of tree line expansion in the northern hemisphere (Arnalds 1987; Speed et al. 2011). In recent decades, the total area of birch woodlands in Iceland has increased through natural regeneration to an estimated 1.5% cover, driven mainly by revegetation efforts for soil stabilization and protection from sheep grazing (Snorrason et al. 2016; Óskarsson & Traustason 2023). Iceland is one of the countries that have accepted the Bonn Challenge, pledging to increase the cover of mountain birch woodlands by approximately 3500 km^2 to obtain a total coverage of 5% (Government of Iceland 2022). Large-scale restoration efforts of mountain birch ecosystems have recently also been initiated in other countries, including *Cairngorm Connect* and the *Mountain Birch Project* in Scotland (Gullett et al. 2023; Mossy Earth, 2023). These extensive restoration initiatives call for effective guidance on the potential of natural colonization for upscaling woodland restoration.

The overall objective of our study was to elucidate patterns and processes of natural colonization of birch into adjacent open lands to support the development of strategies for scaling up woodland restoration. We compared patterns of colonization from existing seed sources in 10 areas encompassing all main lowland regions of Iceland and related them to biotic and abiotic variables that may enhance or limit colonization. We hypothesized (1) that colonization would be limited by seed rain and effects of local biotic and abiotic environments on establishment processes, and (2) a shift in factors that limit birch colonization: from competitive constraints and safe site limitations close to the woodland edge toward seed limitation further from the woodland edge.

Methods

Study Areas

We selected areas with active birch colonization in the vicinity of old woodland stands, that is, where woodland mapping (Snorrason et al. 2016) and the presence of birch seedlings observed in initial field visits indicated active colonization. Another criterion for the selection of study areas was that the oldest part of the woodland was at least 60 years old, based on examination of historical aerial photos. Most of the woodlands were older, however, and in many cases remnants of more extensive woodlands existing before Iceland's settlement in the eighth century. The 10 selected study areas were spread throughout the lowland areas of Iceland that still have birch remnants (Fig. 1), encompassing variability in birch growth form, climate, soil properties and dominant habitat of the adjacent treeless land that may affect the distribution patterns of birch (Table 1; Fig. 2).

Study Species

Downy birch (*Betula pubescens* Ehrh.) has a wide distribution across Europe and western Asia, reaching further north than any other broadleaved tree (Atkinson 1992). It may be an effective early colonizer due to its ability to grow in both nutrient poor and nutrient rich soils. In its central range, downy birch is often regarded as a pioneer species (Atkinson 1992). *Betula pubescens* has an extremely variable growth form, and toward the treeline and in mountain habitats, the tree form is replaced by a low stature shrub. This growth form dominates extensive and stable woodlands in alpine and subarctic environments. The taxonomy of *B. pubescens* has not been completely resolved, but we follow Elven et al. (Panarctic Flora n.d.) in regarding the mountain birch of Fennoscandia, Iceland, and Greenland as *B. pubescens* subsp. *tortuosa* (Ledeb.) Nyman and refer to our Icelandic populations as mountain birch in the remainder of this article. Like all species of birch, *B. pubescens* has a masting habit, but there are indications that masting may be relatively weakly expressed in Icelandic populations (Óskarsdóttir et al. 2024).

Study Design and Field Data

Data collection was carried out between July and September 2021. In each area, four 100 m long and 2 m wide belt transects, divided into 10 m long (20 m^2) segments, were laid out at least 100 m apart perpendicular to the woodland edge into the adjacent open landscape, using random starting points generated along the woodland edge prior to fieldwork. The transects were laid out in pairs, going in different cardinal directions. If active colonization was registered in the last 90–100 m interval of a transect, the transect was extended by another 10 m until no more seedlings were registered (Fig. S1). Along each transect, all birch seedlings with mature leaves were registered and their size measured as the length of the longest shoot from the stem base at the soil surface. Due to the frequently crooked and bent trunks, this is common practice when working with mountain birch in Iceland (Snorrason & Einarsson 2006). The birch seedlings were divided into three size classes: I: less than 2 cm, II: 2–20 cm, and III: greater than 20 cm, thus including both seedlings

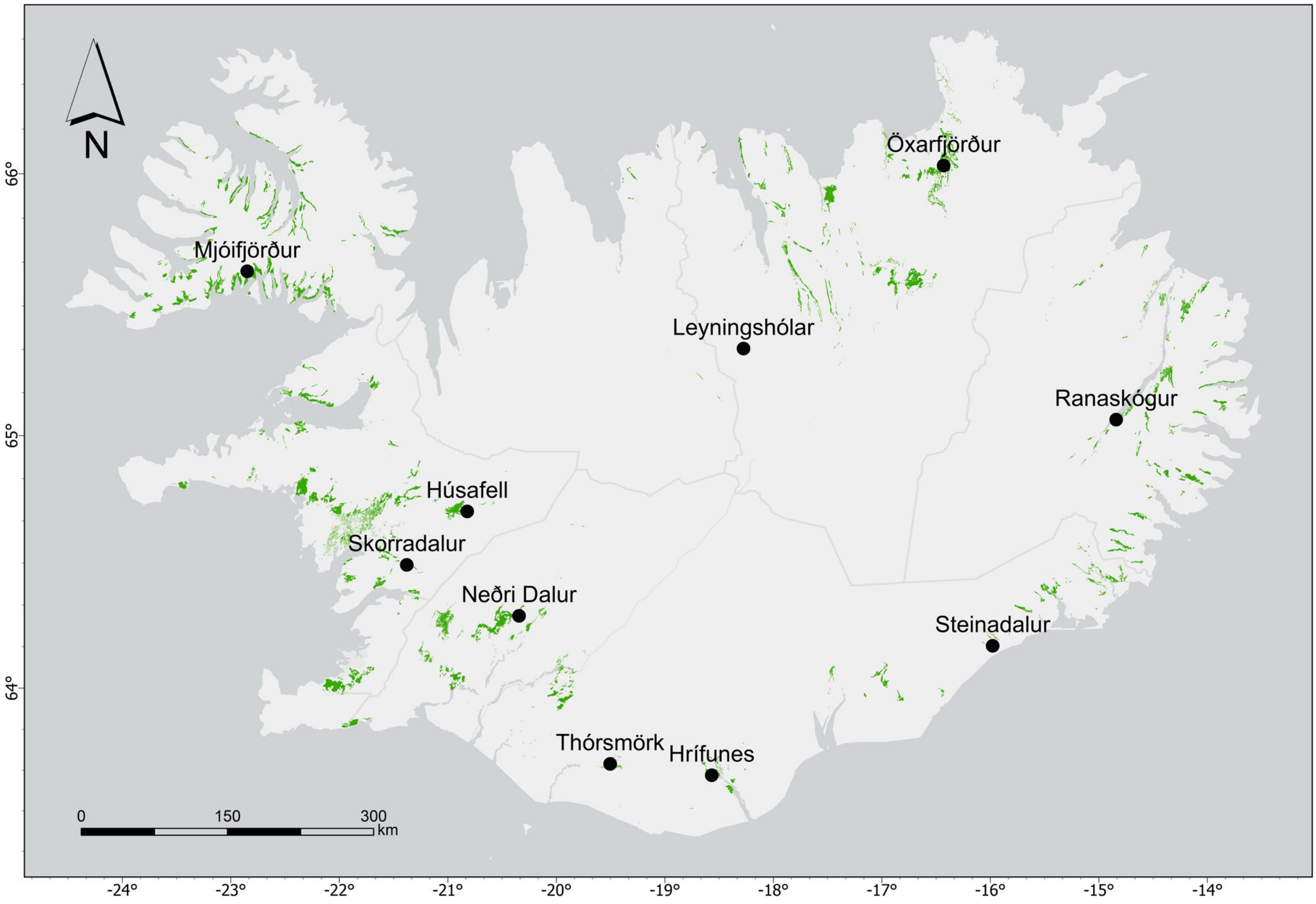

Figure 1. Locations of the 10 study areas across lowland Iceland. The present distribution of mountain birch woodlands is shown in green. Map databases: mountain birch map data, Icelandic Forest Service (2023); Geographic Information System, ArcGIS Pro (version 3.0.3).

Table 1. Geographical location (as global co-ordinates) and selected environmental and climate data for the 10 study areas across Iceland, based on 5-year averages (2016–2021). Precipitation was only measured at seven of the weather stations. Dominant wind direction abbreviations: N, North; S, South; E, East; NE, North-East. Soil type abbreviations: BA, Brown Andosol; H, Histosol; HA, Histic Andosol; GA, Gleyic Andosol; GV, Gravelly Vitrisol; MV, Cambric Vitrisol.

Study area	*Latitude N*	*Longitude W*	*Elevation range (m a.s.l.)*	*Mean temperature May–August (C°)*	*Mean annual precipitation (mm)*	*Mean wind speed Sep-Dec (m/s)*	*Dominant wind direction*	*Soil type*	*Dominant habitat of adjacent treeless land*
Leyningshólar	65.342	−18.275	127–367	9.4	450	3.5	N	BA-HA-GA	Moss and lichen fjell fields
Öxarfjörður	66.024	−16.430	23–137	8.9	—	4.2	S	BA	Heathlands
Ranaskógur	65.069	−14.839	19–210	5.5	905	7.6	S	BA-HA-GA	Braided floodplains
Steinadalur	64.159	−15.965	7–624	9.4	1162	6.5	N	MV-GV	Braided floodplains
Hrífunes	63.649	−18.569	96–223	9.9	1477	4.9	E	BA	Moss heaths
Thórsmörk	63.686	−19.543	175–504	9.1	—	2.6	E	BA	Moss and lichen fjell fields
Neðri Dalur	64.286	−20.338	87–305	9.9	1107	5.5	NE	BA	Moss heaths
Skorradalur	64.482	−21.343	61–273	9.7	966	4.1	NE	BA-HA-GA	Heathlands
Húsafell	64.712	−20.823	132–375	9.1	807	3.9	NE	MV-GV	Lava fields
Mjóifjörður	65.635	−22.855	1–341	6.8	—	8.1	NE	BA-HA-H	Heathlands

and older saplings. All catkin-bearing trees within 5 m of the transects were also registered.

To characterize what constitutes safe sites for birch seedling establishment, the microsite occupied by each seedling in size class I was recorded, in total 15 different types comprising a variety of soil textures, mosses of different thickness, and vascular plants (Table 2). The microsite types were based on former studies on plant establishment in different microsites in subarctic environments (Elmarsdóttir et al. 2003; Aradóttir & Halldórsson 2018). The microsite cover along the transects was measured using the point-intercept method (Floyd & Anderson 1987) in 50 × 50 cm quadrats at 10 m intervals along

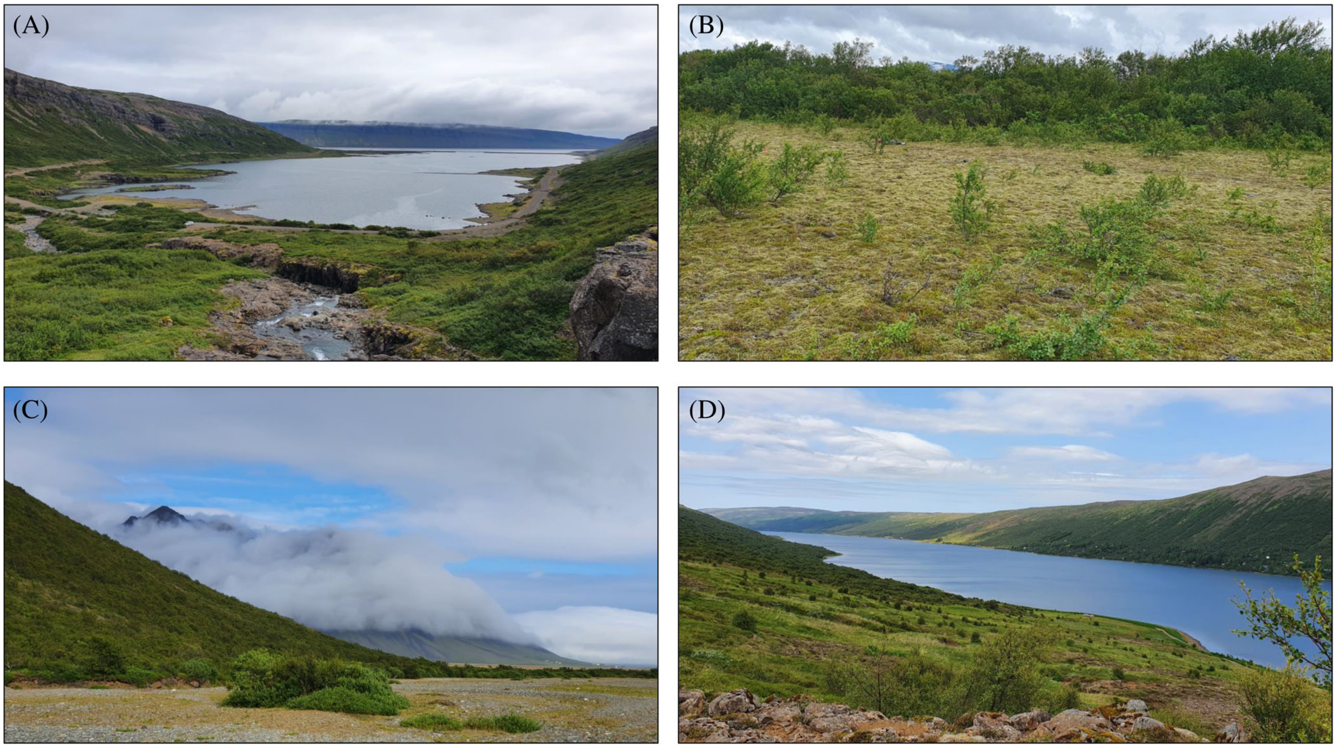

Figure 2. Examples of the visual variations in landscape and colonization patterns among the study areas in Iceland, (A) Mjóifjörður; (B) Húsafell; (C) Steinadalur; (D) Skorradalur.

Table 2. Summary of the microsite types distinguished in the study. All types are modified from Aradóttir and Halldórsson (2018).

Microsite type	*Description*
Soil	All types of exposed mineral soils, not overlain by other types of cover
Sand	Loose sand, grains mostly less than 0.2 cm in diameter
Gravel	Grain size 0.2–2 cm diameter
Pebbles	Grain size 2–5 cm diameter
Rocks	greater than 5 cm in diameter
Biocrust	Biological soil crust dominated by liverworts (especially *Anthelia juratzkana*)
Moss less than 1 cm	Bryophyte layer, less than 1 cm thick, dominated by *Racomitrium* ssp.
Moss 1–2 cm	Bryophyte layer, 1–2 cm thick
Moss greater than 2 cm	Bryophyte layer, greater than 2 cm thick
Lichens	All lichens except crustose lichens on rocks
Graminoids	Grasses, sedges, and rushes
Forbs	Herbaceous eudicots
Dwarf shrubs	Most commonly *Vaccinium* ssp., *Empetrum nigrum*, and *Calluna vulgaris*
Shrubs	All shrubs, dominated by *Salix* spp.
Ferns and horsetails	Seedless vascular plants: ferns, horsetails, moonwort, and lycopods

the transects. We recorded microsites at 25 regularly spaced points within the quadrats. To account for rare microsite types, which were not recorded by the 25 points, all additional microsite types present within each quadrat were recorded.

Local climate data were obtained from nearest weather stations (unpublished data from the Icelandic Met Office, www.vedur.is), including annual precipitation, mean wind speed, and dominant wind direction from September to December (the main period for birch seed dispersal), and mean growing season (May to August), temperature. All variables were based on 5-year averages (2016–2021). The following site-specific ecological variables were obtained from other sources: elevation (National Land Survey of Iceland 2021), soil type (Arnalds & Óskarsson 2009), dominant height of the woodland canopy and total woodland area (Icelandic Forest Service 2023), and presence of domestic sheep (binomial variable: 0 = absence, 1 = presence, information based on personal communication with respective landowners).

Data Analyses

All data were analyzed in R version 4.1.0 (R Development Core Team 2023). Initial data exploration based on the protocol by Zuur et al. (2010) was applied to assess all explanatory variables before performing statistical analyses.

Birch colonization patterns were analyzed within each 20 m^2 segment along the transects. We explored area-specific differences in colonization patterns of birch by comparing seedling densities in the different size classes. This was done by fitting generalized linear models (GLM) based on Poisson distributions with a log-link function using the package *lme4* (Bates et al. 2015), using seedling densities as response variables and study area as predictor. We applied estimated marginal means (EMMs) for spatial pairwise comparisons using the package *emmeans* (Lenth 2020). Observed seedling densities were interpreted in the context of "regenerating woodlands" (defined as 100–1100 stems/ha by Gullett et al. 2023), which was used as a reference for *woodland-forming natural colonization*.

Motivated by Law et al. (2009) and Häbel et al. (2019), we applied the Gaussian colonization kernel, p, to the observed birch densities to explore the effect of dominant woodland height and distance to seed source on colonization:

$$p = h^{\alpha} \times e^{\left(\frac{-\delta \times dist^2}{h^{\beta}}\right)} \qquad (1)$$

In Equation (1), h is the dominant height of the local woodland canopy, *dist* is the Euclidean distance between a given density of seedlings and the seed source, and α, β, and δ are model parameters to be determined. We used maximum-likelihood and least-square methods to fit the model parameters.

We calculated the establishment potential of birch in a given microsite as the number of seedlings registered in a microsite within a 20 m^2 transect segment, multiplied by the proportional cover of that microsite on the segment. To test whether different microsites showed significant positive or negative associations with seedling densities, zero-augmented generalized linear mixed models (GLMM) with gamma distributions were generated to fit the continuous positive structure of the data using the *glmmTMB* package in R (Brooks et al. 2017). The response variable was the proportion of seedlings in the different microsites relative to the observed cover of each microsite type, and the explanatory variable was microsite type. Transect nested within the study area was used as a random factor to account for the non-independence of segments within the same transects and transects within the same areas.

The effect of the different biotic and abiotic environmental variables on seedlings in the different size classes was modeled using two types of hurdle models (zero-augmented GLMMs). Hurdle models are commonly used when dealing with count data including excess zeros (in our case transect segments with no seedlings) and are considered appropriate for modeling complex ecological responses (Zeileis et al. 2008). We fitted negative binomial distributions with a logit-link function to the data, using the different factors as explanatory variables for all size classes (for full list, see Table S1). The first model type used a transect segment, that is, distance from the woodland edge, as an interaction to address the possible synergetic effect of distance with some of the predictor variables (i.e. the variables expected to have varying effects depending on distance to the woodland edge) for the following: catkin-bearing trees, presence of domestic grazers, woodland area, and dominant height of the woodland. The second model type included segment as a random variable (see Table S2 for full model structures). Models were built so that they facilitated testing the factors one at a time. Transect nested within the study area was included as a random explanatory variable in all models. We furthermore used the interaction between wind speed and dominant wind direction as a predictor variable in one model. The models were checked for heteroscedasticity by generating and visually assessing the quantile residuals using the *statmod* package (Giner & Smyth 2016). Model overdispersion was assessed using the *DHARMa* package (Hartig 2022).

Results

More than 5000 birch seedlings were recorded on the 40 transects surveyed. Per study area, the average seedling densities ranged from less than 0.01 to 1.41 seedlings/m^2 for size class I, 0.03 to 1.85 for size class II, and 0.01 to 0.19 for size class III (Table 3). Steinadalur, Húsafell, and Thórsmörk had significantly higher class I seedling densities than the remaining seven areas. Average seedling densities in class I were lowest in the northern study areas, particularly at Leyningshólar and Öxarfjörður. On the other hand, along with Ranaskógur in the east of the country, these areas had higher average densities of seedlings in size class III than the other areas, possibly indicating a higher survival rate (Table 3).

The Gaussian colonization kernels applied to combined seedling densities showed maximum seedling densities close to the woodland edge, and this maximum became higher with greater dominant height of the adjacent woodlands (Fig. 3). Patterns of seedling density along the transects, however, varied greatly among woodlands; some of the study areas had the highest seedling densities close to the woodland edge while others had low densities (mostly <1 seedlings/m^2) but colonization reached a distance of 100 m or more from the woodland edge (Fig. 4). In most of the study areas, however, seedling densities beyond 40 m were within or exceeded the defined success criteria of *woodland-forming natural colonization* (i.e. densities between 100 and 1100 trees/ha), and some areas had the highest seedling densities in clusters far from the edge, e.g. in Leyningshólar. The maximum distance of active colonization ranged from 40 m within one transect in Ranaskógur in the East, to as far as 140 m from the woodland edge in Steinadalur in the South.

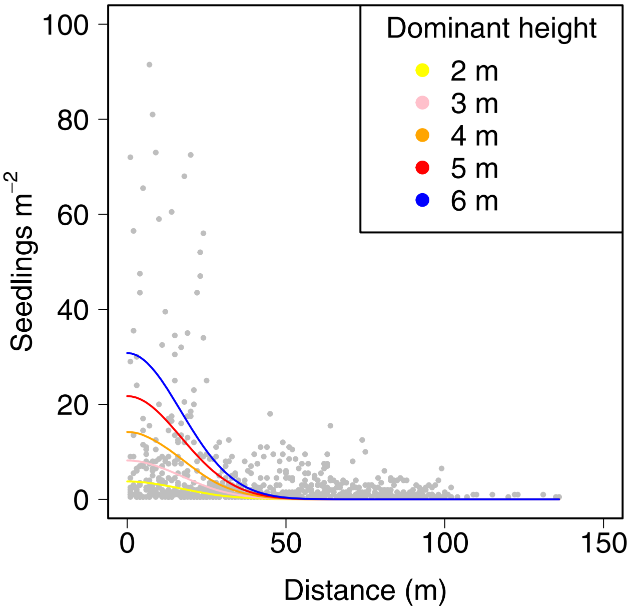

Figure 3. Gaussian colonization kernels indicating the trends of combined seedling densities as functions of distance to the woodland edge for different adjacent dominant woodland heights at 10 areas around Iceland. Gray dots are observed values for all study areas.

The establishment potential of birch seedlings in size class I was 24 (±3.1) seedlings/m^2 for *moss less than 1 cm*, 14 (±2.8) for *moss 1–2 cm*, and 7 (±2.4) for *biocrust*, and seedling densities showed significant positive association with these microsites ($p < 0.05$, Fig. 5, Table S3, Table S4). With the exception of *shrubs*, all microsites characterized by taller vegetation or thicker sward than those previously mentioned had a relatively low establishment potential, ranging from 2 (±1.5) to 4 (±2.1) seedlings/m^2. Thereof, three microsite types showed significant negative associations with birch seedling density, that is, *dwarf shrubs*, *forbs*, and *moss greater than 2 cm*. Furthermore, seedling densities also displayed a near-significant negative associations with *shrubs*, *rocks*, and *lichens* microsites.

Table 3. Density (mean ± SE) of seedlings in size classes I–III on transects taken from the woodland edge at the 10 different study areas. n = total sample size. Letters denote significance in density between study areas (EMM, $\alpha < 0.05$).

			Density (seedlings/m^2)		
Area	*Area sampled (m^2)*	n	*Size class I*	*Size class II*	*Size class III*
Leyningshólar	620	144	<0.01 ± <0.01^{a}	0.08 ± 0.01^{b}	0.14 ± 0.05^{de}
Öxarfjörður	580	203	<0.01 ± 0.01^{ab}	0.16 ± 0.07^{c}	0.18 ± 0.04^{e}
Ranaskógur	340	891	0.17 ± 0.09^{d}	1.85 ± 0.85^{f}	0.44 ± 0.23^{f}
Steinadalur	820	2.601	1.45 ± 0.92^{g}	1.71 ± 0.47^{f}	0.08 ± 0.03^{c}
Hrífunes	640	363	0.08 ± 0.03^{c}	0.31 ± 0.1^{e}	0.18 ± 0.05^{e}
Thórsmörk	820	1.220	1.26 ± 0.53^{f}	0.18 ± 0.04^{c}	0.06 ± 0.01^{bc}
Neðri Dalur	760	600	0.48 ± 0.14^{e}	0.22 ± 0.05^{cd}	0.09 ± 0.03^{cd}
Skorradalur	680	45	0.02 ± 0.01^{ab}	0.03 ± 0.01^{a}	0.01 ± 0.01^{a}
Húsafell	620	1.073	1.41 ± 0.51^{fg}	0.28 ± 0.1^{de}	0.03 ± 0.01^{ab}
Mjóifjörður	520	117	0.04 ± 0.02^{bc}	0.08 ± 0.03^{b}	0.16 ± 0.05^{de}

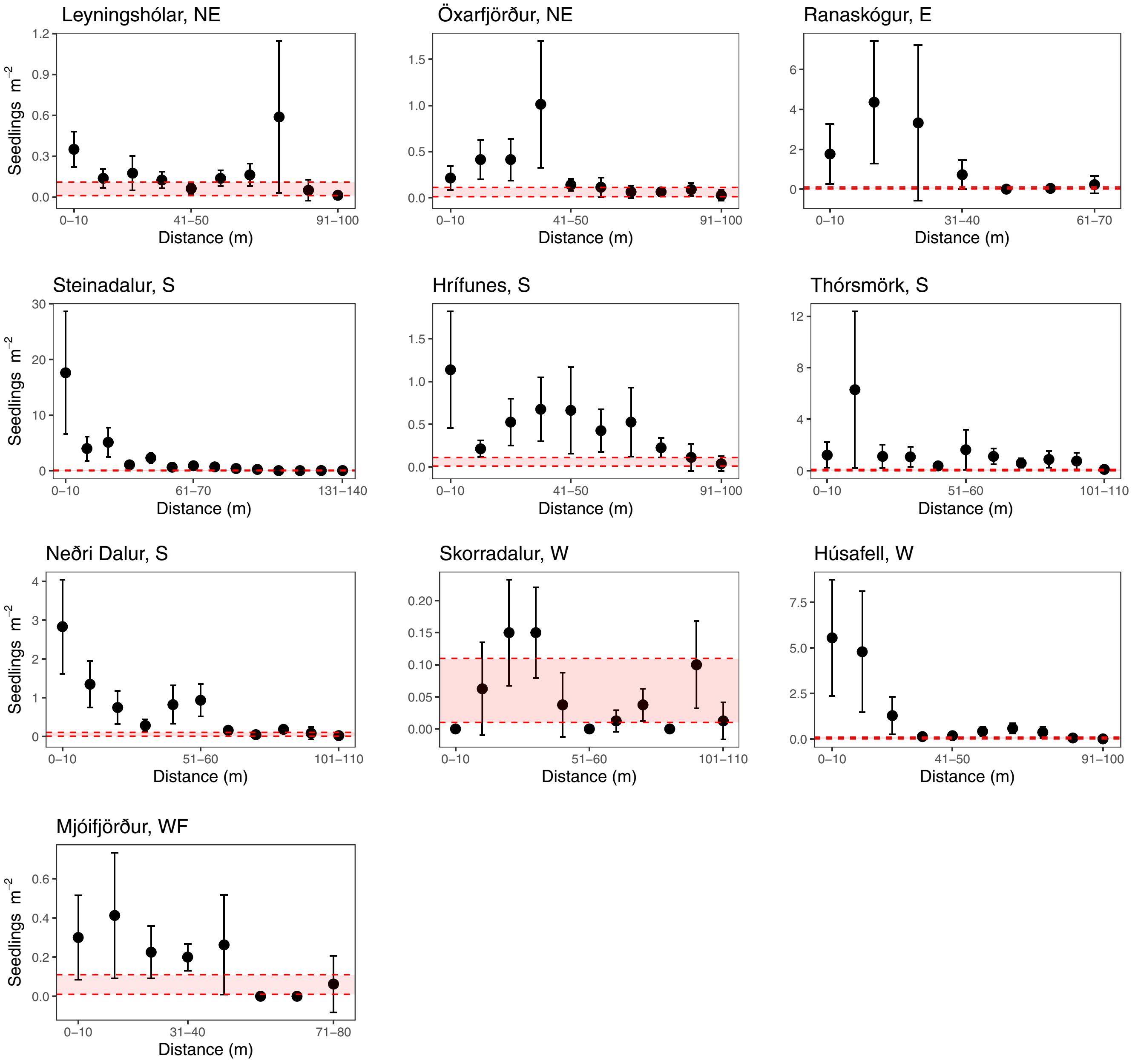

Figure 4. Average mountain birch seedling densities on the study areas for pooled size classes (mean ± SD) plotted against distance from the woodland edge for 10 study areas around Iceland. The areas in red represent the success criteria for *woodland-forming natural colonization*, ranging from 0.01 to 0.11 trees/m^2 (or 100 to 1100 trees/ha) as defined by Gullett et al. (2023). Note different *x* and *y* axis-scales.

Several of the site-specific factors showed significant associations with birch seedling densities in the three different size classes, with the largest number of significant variables for size class I seedlings (Table S1; Fig. 6). Apart from distance from the woodland edge and safe site availability as detailed above, the main associations of seedling densities in size class I were with the soil type Brown Andosol, eastern and northeastern winds, and mean wind speed (Fig. 6). The presence of catkin-bearing trees within transects had a significant negative association with seedling densities for size class I, but a near-significant positive relationship was detected when the interaction with distance from the woodland edge was included. On its own, sheep grazing did not display any association with seedling densities in any size class, although a near-significant positive effect was observed for seedlings in size class I. When the presence of sheep was included as an interaction variable together with distance to the woodland edge, however, the association was significantly negative. Densities of seedlings in size class II were significantly associated with easterly winds and elevation, while the only factor with a significant association with densities of birch plants in size class III was wind speed, with increasing elevation displaying a near-significant negative relationship.

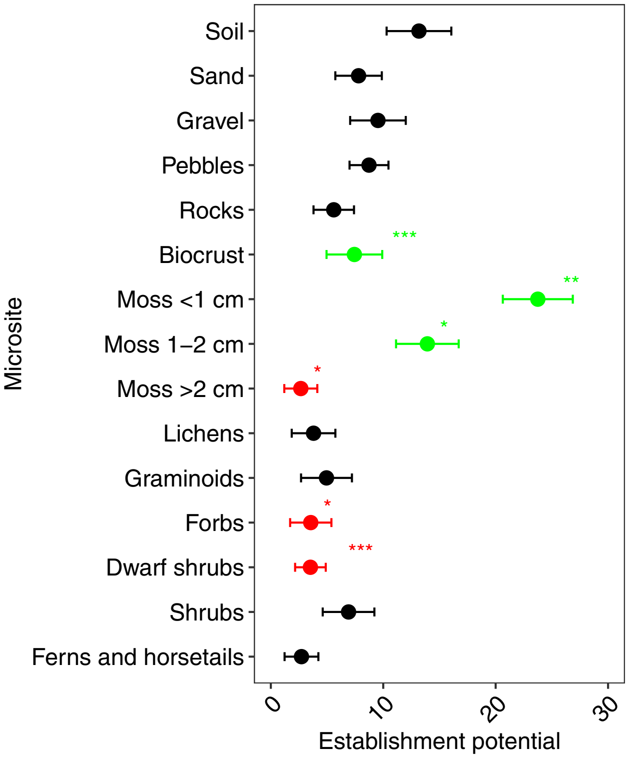

Figure 5. Establishment potential (mean ± SE), defined as the number of seedlings in size class I occupying a microsite multiplied by its proportional cover, derived from GLMMs (see Table 3 for an overview of the different categories). Asterisks indicate significance (*$p < 0.05$, **$p < 0.01$, and ***$p < 0.001$) for pairwise comparisons of means. Color indicates whether the association was significantly positive (green), negative (red), or nonsignificant (black).

Discussion

This study provides insights into the spatial patterns and processes of natural colonization for a key woodland-forming species in the subarctic, showing natural colonization as a dynamic and variable process that is highly dependent on local environments. Seedling densities across all study sites were associated with many of the same factors: distance to seed source, availability of safe sites and soil conditions, wind, elevation, and grazing, confirming our first hypothesis of constraining effects of local biotic and abiotic environments. Furthermore, our results indicate a temporal variation in birch colonization or seedling mortality among the study areas. Some areas had high average densities of young seedlings (class I) that suggest recent or active ongoing colonization, while others had low densities of class I seedlings but higher densities of older seedlings (size classes II and III), suggesting past colonization events and possibly changes in conditions affecting establishment over time.

Colonization Patterns

The emerging patterns from the Gaussian colonization kernels suggest that the highest seedling densities can be expected within 40 m distance to the seed source, although they decline with increasing distance already after 10 m. This pattern reflects the characteristic unimodal curve of wind-dispersed tree species (Harper 1977; Hughes & Fahey 1988) and indicates an increasing seed rain limitation with distance from the seed source. In most of our study areas, however, observed seedling densities beyond 40 m were within or exceeded the range of density, defined as *woodland-forming colonization*, 100–1100 trees/ha by Gullett et al. (2023), in some cases extending up to 140 m from the nearest seed source. This indicates that optimal conditions further from the woodland edge, such as high availability of suitable microsites, can result in effective colonization, partly confirming our second hypothesis.

Comparing seedling densities among the 10 study areas revealed distinct patterns. The unimodal pattern described above applied to about half of the study areas, while the other areas, which incidentally all had average seedling densities of less than 1 seedling/m^2, had more erratic density patterns, and some of the study areas also had sections of peak seedling densities at different distances from the woodland edge. This points to alternative processes; first, the unidirectional and often exponential decline with distance reflects the short dispersal of most seeds from most trees in most years (Levin et al. 2003). Secondly, the observed erratic decline in seedling density points to more constraints from the local environment on colonization, that is, lack of safe sites for seedling establishment rather than seed limitation per se, as seedling densities were similarly low at most distances from the woodland edge. Peak densities observed far from the woodland edge might also reflect singular events in unusual conditions, such as years of high seed production, when relatively high seed rain may extend to greater distances from the woodland edge. This colonization pattern could furthermore have been driven by occational long distance dispersal of seeds by strong winds in the fall or early winter into sites with optimal conditions for seedling establishment, including secondary dispersal across snow surfaces (Matlack 1989). Such events may be rare, e.g. depending on the frequency of masting years (Sarvas 1956), but have the potential to leave a strong legacy by creating nascent foci for colonization that can greatly increase the speed of expansion (Moody & Mack 1988; Óskarsdóttir et al. 2022).

Constraints on Early Establishment

Early establishment is often considered to be the most challenging life stage of plants (Hanbury-Brown et al. 2022), particularly for relatively small-seeded trees like birch that are highly sensitive to competition and disturbances, and because of this, experience high mortality rates in their first year (Atkinson 1992). In our study, the number of limiting factors was greatest for seedlings in size class I, including prevailing wind direction and average wind velocity during seed dispersal season, presence of sheep grazing, safe sites for seed establishment, and soil characteristics. Optimal wind conditions are a perquisite for successful colonization of wind-borne species, so it is not surprising that the effect of wind could be detected both in recent and past birch establishment patterns (i.e. also for seedlings in size classes II and III). Our results thus agree with a previous study showing

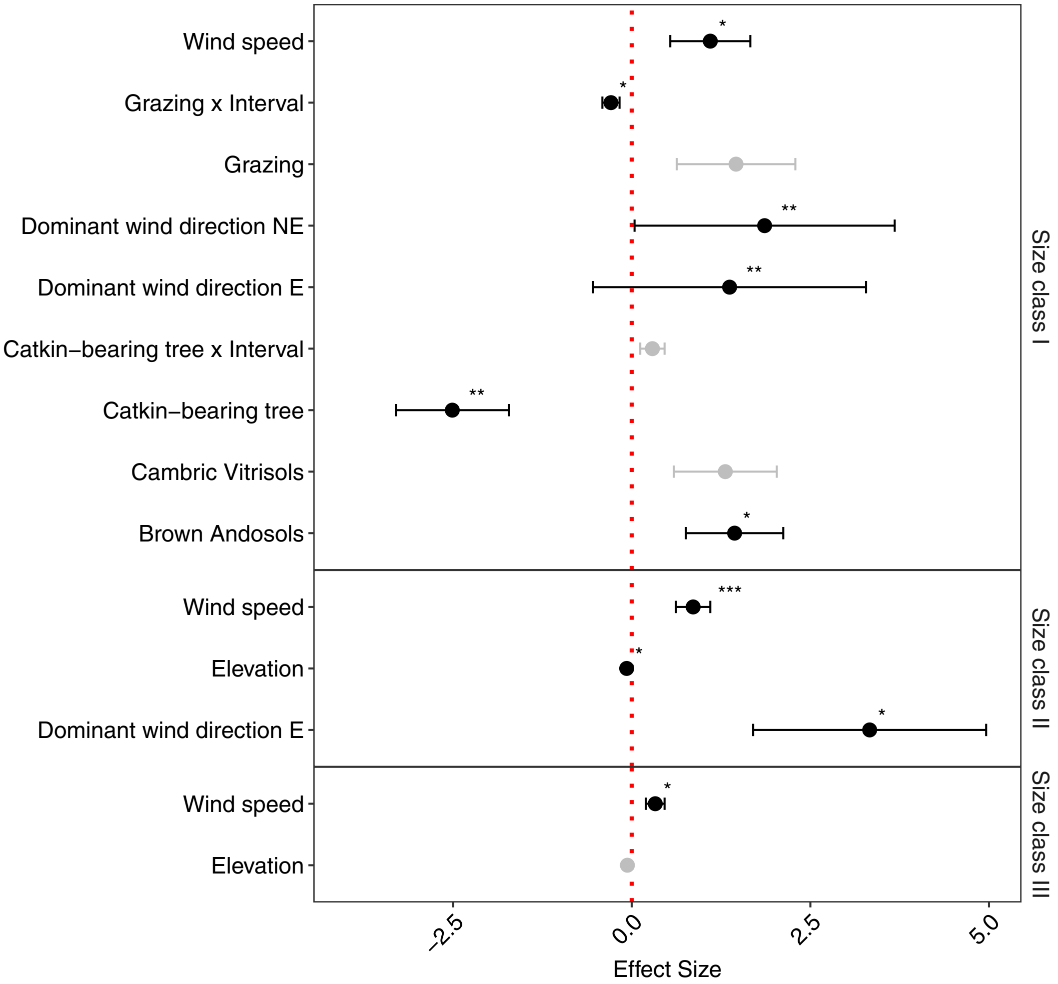

Figure 6. Effect-size plot (±95% CI) from the minimum zero-inflated GLMM hurdle models with negative binomial distributions on the influence of different explanatory variables on the density of seedlings in different size classes. Results are reported for separate models for each response variable (size classes) and explanatory variable. Explanatory variables are only included if a statistically significant (black, $*p < 0.05$, $**p < 0.01$, and $***p < 0.001$) or near-significant result (gray, $p < 0.1$) was detected. All of the listed model intercepts were significant ($p < 0.05$).

a positive correlation of birch establishment in South Iceland with the frequency of strong, dry easterly and northeasterly winds (Aradóttir et al. 1997). Understanding the effect of prevailing wind directions, a highly variable local factor, on establishment can aid in site selection and spatially targeting tree clusters in applied nucleation.

The presence of catkin-bearing trees had a strong negative association with class I seedling density, likely due to competition and shade casting. On the other hand, catkin-bearing trees had a near-significant positive association to seedling densities when using distance from the woodland edge as an interaction in the models. This indicates that their presence can enhance establishment further from the edge, implying that nuclei, or even single catkin-bearing trees, can promote seedling establishment, presumably through increased local seed rain.

The density of small seedlings (size class I) did not have a significant association with grazing ($p < 0.1$), but the interaction of grazing with distance from the woodland edge was significant ($p < 0.05$). Browsing animals can have both facilitating and impeding effects on tree establishment, depending on the condition of the surrounding habitats. By trampling and browsing they can damage or kill young plants (Barrio et al. 2018), but also create disturbances, which in habitats with thick moss sward and tall vegetation can create windows of opportunity for seedling establishment by reducing competition and creating suitable microsites (Ross et al. 2016; Marteinsdóttir et al. 2017). Our results remain inconclusive on the direct effect of browsing on the establishment of birch, as we did not consider the effect of grazing in particular habitats.

Although the early-establishment phase proved the most crucial part of mountain birch colonization, future woodland development will come from surviving seedlings, that is, seedlings in the larger size classes in our study (classes II and III). In the northern and eastern study areas, size classes II and III generally had higher densities than in the other areas. This is likely correlated with local environmental conditions, such as more days with snow cover, which prevents frost heaving (Aradóttir 2004), or lower densities of grazers. It is important to study the survival of individual seedlings in different environments as well as possible drivers, to fully elucidate these patterns.

Microsite Limitations for Natural Colonization

The availability of suitable microsites was one of the main factors affecting the density of the smallest seedlings (size class I), which is consistent with a number of other studies (Douterlungne et al. 2015; Boeken 2018; Holmgren et al. 2022). To our knowledge, our study is the first comparing safe site availability at such a large scale and among so many varying landscapes and habitats. The establishment potential for birch was generally highest in microsites characterized by a thin, bryophyte layer, including mosses less than 2 cm, and in biocrust, and lower in areas with a high cover of competing vegetation, thick moss layers, and rocky surfaces.

Mosses and biocrust can act as ecological engineers in subarctic ecosystems, stabilizing barren soils and supplying moisture and nutrients (Ficko et al. 2022), thus facilitating colonization of many vascular plant species. Our results confirm, though, that the window of opportunity for birch establishment in moss closes when the moss reaches a sward thickness of greater than 2 cm (Aradóttir & Halldórsson 2018; Vilmundardóttir et al. 2018).

Earlier studies from the subarctic have shown barren microsite types such as soil, gravel, and pebbles to be unfavorable for the establishment of birch and other vascular plants in eroded and revegetated areas due to their susceptibility to cryoturbation (Elmarsdóttir et al. 2003; Aradóttir & Halldórsson 2018). The suitability of these barren microsite types varied more in our study, reflecting a higher diversity of landforms, habitats, and site conditions. The average establishment potential was higher in *gravel*, *pebbles*, and *soil* microsites than in *rocks* and *sand* that represent habitats with unstable surfaces and provide low seed-soil contact (Johnson & Fryer 1992; Aradóttir & Halldórsson 2018). We did not find a significant association between these microsite types and seedling densities, which suggests suitability for birch establishment in barren microsites in some sites but not in others. Areas with exposed mineral soils where small seedlings are vulnerable to cryoturbation and in sandy, unstable soils where seedlings are susceptible to soil erosion are examples of habitats where barren microsites will not benefit establishment (Aradóttir 2004; Aradóttir & Halldórsson 2018). An example of the opposite relationship was observed in Steinadalur, which is dominated by a large, braided riverbed with a typically coarse and stable surface and plenty of moisture (Jones & del Moral 2005). In the northern and inland study areas, more persistent snow cover throughout winter protects the soil surface, thus reducing the risk of cryoturbation that can cause seedling mortality (Cargill & Chapin 1987).

Areas with continuous dense vegetation sward dominated by thick moss, forbs, and dwarf shrubs may restrict natural colonization of birch, a relatively small-seeded tree that is shade-intolerant and sensitive to competition and allelopathy (Weih & Karlsson 1999). In study areas dominated by dense vegetation of forbs and dwarf shrubs, seedling densities were sparse and mostly limited to scattered, eroded patches in the landscape. However, there was not a significant negative association between seedling density and the microsite-type *shrubs*, and seedling density was higher on average in the *shrubs* microsite than in other vascular plant microsites. This suggests that shrubs such as different species of *Salix* might facilitate seedling establishment or survival in subarctic environments, a phenomenon seen both for birch and other plant species in tundra vegetation (Carlsson & Callaghan 1991).

Natural Colonization of Birch for Scaling Up Woodland Restoration

Our results suggest that strategies utilizing natural colonization for woodland restoration can be efficient in subarctic environments if constraints to the early-establishment phase are overcome, implying that the Icelandic Bonn Challenge pledge may be feasible if certain management actions are undertaken. Our results can furthermore aid in spatial planning and upscaling of restoration projects involving wind-borne tree species by determining where existing woodlands are likely to expand naturally and where and which interventions may be appropriate to facilitate and accelerate natural regeneration.

For applied nucleation of birch, or of mixed clusters including birch, it is important to consider the spatial arrangements of planted woodland isles as well as the interpolated distance between isles to enhance optimal densities of natural colonization. In our study, the most efficient colonization takes place within the first 40 m of a seed source, with many areas having woodland-forming densities much further from the woodland edge. Such information, indicating potential distance for natural colonization, is useful for planning restoration involving applied nucleation to determine the optimal planting distance between woodland isles to obtain the most cost-efficient utilization of natural colonization (Corbin & Holl 2012). This distance, however, is likely driven by local environments, as our study confirmed, especially optimal wind conditions. Long-range dispersal can create additional opportunities for induced unassisted nucleation, and these clusters of trees far from the woodland edge demonstrate the potential of nucleation in accelerating the spread of key woodland-forming species (Howe & Smallwood 1982; Óskarsdóttir et al. 2022).

Our results suggest that for passive restoration of birch woodlands, relatively open lands dominated by a thin layer of moss and/or biocrust are optimal. This encompasses many different naturally occurring habitats in the subarctic, such as moss heaths, fjell fields, and braided floodplains, highlighting a good spatial potential for natural colonization or assisted woodland restoration in areas with these habitats. Where the soil surface is too coarse or unstable for natural colonization, revegetation measures that facilitate biocrust formation or other interventions to stabilize eroding surfaces may be a necessary first step toward woodland restoration (Aradóttir & Halldórsson 2018; Ficko et al. 2022). In areas with a continuous cover of tall-growing vegetation, natural colonization can be assisted by cutting gaps and by light scarification of the topsoil layer (Magnússon &

Magnússon 1990) or periodic regenerative grazing to create safe sites in areas with dense vegetation or a thick layer of mosses. In areas where there are otherwise conditions for woodland expansion through natural colonization, it may be beneficial to protect them from sheep grazing, a management action that may be an efficient passive restoration strategy for mountain birch (Óskarsson & Traustason 2023). Birch woodlands in Iceland can, however, also expand despite low grazing pressure (Óskarsdóttir et al. 2022). Thus, the effects of grazing on the inhibition or facilitation of birch colonization need to be studied further.

Aligning restoration practices with the natural process of woodland colonization is crucial to achieve the best possible restoration outcomes. Where natural recovery (i.e. "passive restoration") is possible or can be enhanced, this should be prioritized rather than active restoration efforts such as tree planting (Gann et al. 2019; Di Sacco et al. 2021). Identifying the ecological conditions in which natural colonization can be a viable restoration approach should therefore be of high priority for politicians and restoration practitioners, both because it offers a more economically feasible alternative to reforestation and because it supports natural ecosystem recovery. This, in combination with research on the temporal scale of woodland expansion, can aid practitioners and land managers in understanding the potential of natural colonization for woodland expansion under various environmental conditions.

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LITERATURE CITED

Aradóttir ÁL (2004) Does the Nootka Lupin facilitate or impede colonization and growth of native birch in Iceland? Pages 184–190. In: Santen EV (ed) Wild and cultivated lupins from the tropics to the poles. Proceedings of the 10th International Lupin Conference, Laugarvatn Iceland, 19–24 June 2002. International Lupin Association, Canterbury, New Zealand

Aradóttir ÁL, Halldórsson G (2018) Colonization of woodland species during restoration: seed or safe site limitation? Restoration Ecology 26:73–83. https://doi.org/10.1111/rec.12645

Aradóttir ÁL, Robertson A, Moore E (1997) Circular statistical analysis of birch colonization and the directional growth response of birch and black cottonwood in south Iceland. Agricultural and Forest Meteorology 84:179–186. https://doi.org/10.1016/S0168-1923(96)02385-4

Arnalds A (1987) Ecosystem disturbance in Iceland. Arctic and Alpine Research 19:508–513. https://doi.org/10.1080/00040851.1987.12002633

Arnalds O, Óskarsson H (2009) Íslenskt jarðvegskort (A soil map of Iceland). Náttúrufræðingurinn 78:107–121

Atkinson MD (1992) Biological flora of the British Isles. *Betula pendula* Roth (*Betula verrucosa* Ehrh.) and *B. pubescens* Ehrh. Journal of Ecology 80: 837–870. https://doi.org/10.2307/2260870

Auffret AG, Rico Y, Bullock JM, Hooftman DAP, Pakeman RJ, Soons MB, Suárez-Esteban A, Traveset A, Wagner HH, Cousins SAO (2017) Plant functional connectivity – integrating landscape structure and effective dispersal. Journal of Ecology 105:1648–1656. https://doi.org/10.1111/1365-2745.12742

Barnosky AD, Hadly EA, Bascompte J, Berlow EL, Brown JH, Fortelius M, et al. (2012) Approaching a state shift in Earth's biosphere. Nature 486:52–58. https://doi.org/10.1038/nature11018

Barrio IC, Hik DS, Thórsson J, Svavarsdóttir K, Marteinsdóttir B, Jónsdóttir IS (2018) The sheep in wolf's clothing? Recognizing threats for land degradation in Iceland using state-and-transition models. Land Degradation & Development 29:1714–1725. https://doi.org/10.1002/ldr.2978

Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48. https://doi.org/10.18637/jss.v067.i01

Bauld J, Guy M, Hughes S, Forster J, Watts K (2023) Assessing the use of natural colonization to create new forests within temperate agriculturally dominated landscapes. Restoration Ecology 31:e14004. https://doi.org/10.1111/rec.14004

Beckman NG, Sullivan LL (2023) The causes and consequences of seed dispersal. Annual Review of Ecology, Evolution, and Systematics 54:403–427. https://doi.org/10.1146/annurev-ecolsys-102320-104739

Benayas JMR, Bullock JM, Newton AC (2008) Creating woodland islets to reconcile ecological restoration, conservation, and agricultural land use. Frontiers in Ecology and the Environment 6:329–336. https://doi.org/10.1890/070057

Boeken BR (2018) Competition for microsites during recruitment in semiarid annual plant communities. Ecology 99:2801–2814. https://doi.org/10.1002/ecy.2484

Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Maechler M, Bolker BM (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. The R Journal 9:378–400. https://doi.org/10.32614/RJ-2017-066

Campanhã Bechara F, Trentin BE, Lex Engel V, Estevan DA, Ticktin T (2021) Performance and cost of applied nucleation versus high-diversity plantations for tropical forest restoration. Forest Ecology and Management 491: 119088. https://doi.org/10.1016/j.foreco.2021.119088

Cargill SM, Chapin FS (1987) Application of successional theory to tundra restoration: a review. Arctic and Alpine Research 19:366–372. https://doi.org/10.1080/00040851.1987.12002617

Carlsson BA, Callaghan TV (1991) Positive plant interactions in tundra vegetation and the importance of shelter. Journal of Ecology 79:973. https://doi.org/10.2307/2261092

Chazdon RL, Guariguata MR (2016) Natural regeneration as a tool for large-scale forest restoration in the tropics: prospects and challenges. Biotropica 48: 716–730. https://doi.org/10.1111/btp.12381

Corbin JD, Holl K (2012) Applied nucleation as a forest restoration strategy. Forest Ecology and Management 265:37–46. https://doi.org/10.1016/j.foreco.2011.10.013

Crouzeilles R, Beyer HL, Monteiro LM, Feltran-Barbieri R, Pessôa ACM, Barros FSM, et al. (2020) Achieving cost-effective landscape-scale forest restoration through targeted natural regeneration. Conservation Letters 13:e12709. https://doi.org/10.1111/conl.12709

Di Sacco A, Hardwick KA, Blakesley D, Brancalion PHS, Breman E, Cecilio Rebola L, et al. (2021) Ten golden rules for reforestation to optimize carbon sequestration, biodiversity recovery and livelihood benefits. Global Change Biology 27:1328–1348. https://doi.org/10.1111/gcb.15498

Douterlungne D, Ferguson BG, Siddique I, Soto-Pinto L, Jímenez-Ferrer G, Gavito ME (2015) Microsite determinants of variability in seedling and cutting establishment in tropical forest restoration plantations: microsite variability in restoration trials. Restoration Ecology 23:861–871. https://doi.org/10.1111/rec.12247

Duncan RP, Diez JM, Sullivan JJ, Wangen S, Miller AL (2009) Safe sites, seed supply, and the recruitment function in plant populations. Ecology 90: 2129–2138. https://doi.org/10.1890/08-1436.1

Elmarsdóttir A, Aradóttir AL, Trlica MJ (2003) Microsite availability and establishment of native species on degraded and reclaimed sites: establishment of native plants in Iceland. Journal of Applied Ecology 40:815–823. https://doi.org/10.1046/j.1365-2664.2003.00848.x

FAO (Food and Agriculture Organization) (2022) The state of the world's forests 2022. In: Forest pathways for green recovery and building inclusive, resilient, and sustainable economies. FAO, Rome, Italy

Ferreira MC, de Oliveira Cordeiro AO, Sampaio AB, Schmidt IB, Vieira DLM (2023) Direct seeding versus seedling planting: survival, biomass, growth, and cost up to 6 years for four tropical seasonal tree species. Restoration Ecology 31:e13807. https://doi.org/10.1111/rec.13807

Ficko SA, Haughland DL, Naeth MA (2022) Assisted dispersal and retention of lichen-dominated biocrust material for arctic restoration. Restoration Ecology 31:e13793. https://doi.org/10.1111/rec.13793

Floyd DA, Anderson JE (1987) A comparison of three methods for estimating plant cover. Journal of Ecology 75:221–228. https://doi.org/10.2307/2260547

Fowler NL (1988) What is a safe site?: neighbor, litter, germination date, and patch effects. Ecology 69:947–961. https://doi.org/10.2307/1941250

Gann GD, McDonald T, Walder B, Aronson J, Nelson CR, Johnson J (2019) International principles and standards for the practice of ecological restoration. Second edition. Restoration Ecology 27:1–46. https://doi.org/10.1111/rec.13035

Giner G, Smyth GK (2016) Statmod: probability calculations for the inverse gaussian distribution. The R Journal 8:339–351. https://doi.org/10.32614/RJ-2016-024

Government of Iceland (2022) Land og líf. Landgræðsluáætlun og landsáætlun í skógrækt. Stefna og framtíðarsýn í landgræðslu og skógrækt til ársins 2031 (Land and life. A master plan for land restoration and forestry. Strategy and vision until 2031). Government of Iceland, Reykjavík, Iceland.

Gullett PR, Leslie C, Mason R, Ratcliffe P, Sargent I, Beck A, et al. (2023) Woodland expansion in the presence of deer: 30 years of evidence from the Cairngorms Connect landscape restoration partnership. Journal of Applied Ecology 60:2298–2308. https://doi.org/10.1111/1365-2664.14501

Häbel H, Myllymäki M, Pommerening A (2019) New insights on the behaviour of alternative types of individual-based tree models for natural forests. Ecological Modelling 406:23–32. https://doi.org/10.1016/j.ecolmodel.2019.02.013

Hanbury-Brown AR, Ward RE, Kueppers LM (2022) Forest regeneration within earth system models: current process representations and ways forward. New Phytologist 235:20–40. https://doi.org/10.1111/nph.18131

Harper JL (1977) Population biology of plants. Academic Press, New York

Hartig F (2022) DHARMa: residual diagnostics for hierarchical (multi-level/-mixed) regression models. R package version 0.4.6. https://cran.r-project.org/web/packages/DHARMa/vignettes/DHARMa.html (accessed 14 Feb 2024)

Holl KD, Aide TM (2011) When and where to actively restore ecosystems? Forest Ecology and Management 261:1558–1563. https://doi.org/10.1016/j.foreco.2010.07.004

Holl KD, Zahawi RA, Cole RJ, Ostertag R, Cordell S (2011) Planting seedlings in tree islands versus plantations as a large-scale tropical forest restoration strategy. Restoration Ecology 19:470–479. https://doi.org/10.1111/j.1526-100X.2010.00674.x

Holmgren M, Scheffer M, Huston MA (2022) The interplay of facilitation and competition in plant communities. Ecology 78:1966–1975. https://doi.org/10.1890/0012-9658(1997)078[1966:TIOFAC]2.0.CO;2

Howe HF, Smallwood J (1982) Ecology of seed dispersal. Annual Review of Ecology and Systematics 13:201–228. https://doi.org/10.1146/annurev.es.13.110182.001221

Hua F, Bruijnzeel LA, Meli P, Martin PA, Zhang J, Nakagawa S, Miao X, Wang W, McEvoy C, Peña-Arancibia JL, Brancalion PHS, Smith P, Edwards DP, Balmford A (2022) The biodiversity and ecosystem service contributions and trade-offs of forest restoration approaches. Science 376: 839–844. https://doi.org/10.1126/science.abl4649

Hughes JW, Fahey TJ (1988) Seed dispersal and colonization in a disturbed northern hardwood forest. Bulletin of the Torrey Botanical Club 115:89–99. https://doi.org/10.2307/2996139

IFS (Icelandic Forest Service) (2023) Náttúrulegt birki á Íslandi (Natural birch woodlands in Iceland). https://iceforestservice.maps.arcgis.com/apps/webappviewer/index.html?id=de3bbce4966b4290847ba4ae0c87d3f3 (accessed 28 Oct 2023)

IPCC (Intergovernmental Panel on Climate Change) (2019) IPCC special report on climate change, desertification, land degradation, sustainable land management, food security, and greenhouse gas fluxes in terrestrial ecosystems. https://www.ipcc.ch/srccl/ (accessed 1 May 2024)

World Conservation Union (2020) The Bonn challenge. https://www.bonnchallenge.org/ (accessed 4 Dec 2023)

Johnson EA, Fryer GI (1992) Physical characterization of seed microsites—movement on the ground. The Journal of Ecology 80:823–836. https://doi.org/10.2307/2260869

Jones CC, del Moral R (2005) Effects of microsite conditions on seedling establishment on the foreland of Coleman Glacier, Washington. Journal of Vegetation Science 16:293–300. https://doi.org/10.1111/j.1654-1103.2005.tb02367.x

Jones GA, Henry GHR (2003) Primary plant succession on recently deglaciated terrain in the Canadian high Arctic. Journal of Biogeography 30:277–296. https://doi.org/10.1046/j.1365-2699.2003.00818.x

Law R, Illian J, Burslem DFRP, Gratzer G, Gunatilleke CVS, Gunatilleke IAUN (2009) Ecological information from spatial patterns of plants: insights from point process theory. Journal of Ecology 97:616–628. https://doi.org/10.1111/j.1365-2745.2009.01510.x

Lenth R (2020) Estimated marginal means, aka least-squares means. R package version 1.4.5. https://cran.r-project.org/web/packages/emmeans/index.html (accessed 10 Jan 2024)

Levin SA, Muller-Landau HC, Nathan R, Chave J (2003) The ecology and evolution of seed dispersal: a theoretical perspective. Annual Review of Ecology, Evolution, and Systematics 34:575–604. https://doi.org/10.1146/annurev.ecolsys.34.011802.132428

Magnússon SH, Magnússon B (1990) Birkisáningar til landgræðslu og skógræktar (Seeding of birch for land reclamation and woodland establishment). Ársrit Skógræktarfélags Íslands 1990:9–18

Marteinsdóttir B, Barrio IC, Jónsdóttir IS (2017) Assessing the ecological impacts of extensive sheep grazing in Iceland. Icelandic Agricultural Sciences 30:55–72. https://doi.org/10.16886/IAS.2017.07

Matlack GR (1989) Secondary dispersal of seed across snow in *Betula lenta*, a gap-colonizing tree species. Journal of Ecology 77:853–869. https://doi.org/10.2307/2260990

McCallum KP, Lowe AJ, Breed MF, Paton DC (2018) Spatially designed revegetation—why the spatial arrangement of plants should be as important to revegetation as they are to natural systems. Restoration Ecology 26:446–455. https://doi.org/10.1111/rec.12690

Moody ME, Mack RN (1988) Controlling the spread of plant invasions: the importance of nascent foci. The Journal of Applied Ecology 25:1009–1021. https://doi.org/10.2307/2403762

Mossy Earth (2023) The Mountain Birch Project: locating, distributing, and propagating a rare high-altitude tree. Mossy Earth. https://www.mossy.earth/projects/the-mountain-birch-project (accessed 23 Dec 2023)

National Land Survey of Iceland (2021) ÍslandsDEM (digital surface model).

Óskarsdóttir G, Thórhallsdóttir TE, Jónsdóttir AH, Birkisdóttir HM, 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

Óskarsdóttir G, Thórhallsdóttir TE, Svavarsdóttir K (2024) High seed losses in mountain birch (*Betula pubescens* ssp. *tortuosa*) and developmental, ecological, and environmental correlates. Journal of Plant Ecology 17:rtae049. https://doi.org/10.1093/jpe/rtae049

Óskarsson H, Traustason B (2023) Aldarfriðun Þórsmerkur-og Goðalandsskóga. Breytingar á skógarþekju (Conservation of the Þórsmerkur and Godaland forests. Changes in forest cover). Skógræktarritið 2023:4–22

Panarctic Flora (n.d.) 610206b *Betula pubescens* subsp. *tortuosa* (Ledeb.) Nyman. http://panarcticflora.org/results?biogeographic=&bioclimatic=&region=&name=betula%2Bpubescens#paf-610206b (accessed 29 Aug 2024)

Pedersen NK, Schmidt IK, Kepfer-Rojas S (2023) Drivers of tree colonization, species richness, and structural variation during the initial three decades of natural forest colonization in abandoned agricultural soils. Forest Ecology and Management 543:121138. https://doi.org/10.1016/j.foreco.2023.121138

Pizza RB, Foster J, Brudvig LA (2023) Where should they come from? Where should they go? Several measures of seed source locality fail to predict plant establishment in early prairie restorations. Ecological Solutions and Evidence 4:e12223. https://doi.org/10.1002/2688-8319.12223

R Development Core Team (2023) R: a language and environment for statistical computing. R Foundation for Statistical Computing. http://www.Rproject.org

Ross LC, Austrheim G, Asheim LJ, Bjarnason G, Feilberg J, Fosaa AM, et al. (2016) Sheep grazing in the North Atlantic region: a long-term perspective on environmental sustainability. Ambio 45:551–566. https://doi.org/10.1007/s13280-016-0771-z

Sarvas R (1956) Investigations into the flowering and seed quality of forest trees. Communicationes Instituti Forestalis Fenniae 45:1–37

Shono K, Cadaweng EA, Durst PB (2007) Application of assisted natural regeneration to restore degraded tropical forestlands. Restoration Ecology 15: 620–626. https://doi.org/10.1111/j.1526-100X.2007.00274.x

Snorrason A, Einarsson SF (2006) Single-tree biomass and stem volume functions for eleven tree species used in Icelandic forestry. Icelandic Agricultural Sciences 19:15–24

Snorrason A, Traustason B, Kjartansson BÞ, Heiðarsson L (2016) Náttúrulegt birki á Íslandi – ný úttek á útbreiðslu þess og ástandi (The natural birch woodlands in Iceland – a new assessment on distribution and state). Náttúrufræðingurin 86:97–111

Speed JDM, Austrheim G, Hester AJ, Mysterud A (2011) Growth limitation of mountain birch caused by sheep browsing at the altitudinal treeline. Forest Ecology and Management 261:1344–1352. https://doi.org/10.1016/j.foreco.2011.01.017

Suding K, Higgs E, Palmer M, Callicott JB, Anderson CB, Baker M, et al. (2015) Committing to ecological restoration. Science 348:638–640. https://doi.org/10.1126/science.aaa4216

Temperton VM, Buchmann N, Buisson E, Durigan G, Kazmierczak L, Perring MP, Sá Dechoum M, Veldman JW, Overbeck GE (2019) Step back from the forest and step up to the Bonn challenge: how a broad ecological perspective can promote successful landscape restoration. Restoration Ecology 27:705–719. https://doi.org/10.1111/rec.12989

Vilmundardóttir OK, Sigurmundsson FS, Møller Pedersen GB, Belart JMC, Kizel F, Falco N, Benediktsson JA, Gísladóttir G (2018) Of mosses and men: plant succession, soil development and soil carbon accretion in the sub-Arctic volcanic landscape of Hekla, Iceland. Progress in Physical Geography: Earth and Environment 42:765–791. https://doi.org/10.1177/0309133318798754

Weih M, Karlsson PS (1999) The nitrogen economy of mountain birch seedlings: implications for winter survival. Journal of Ecology 87:211–219. https://doi.org/10.1046/j.1365-2745.1999.00340.x

Wilson MF (1993) Dispersal mode, seed shadows, and colonization patterns. Vegetatio 107:261–280. https://doi.org/10.1007/BF00052229

Zeileis A, Kleiber C, Jackman S (2008) Regression models for count data in *R*. Journal of Statistical Software 27:1–25. https://doi.org/10.18637/jss.v027.i08

Zuur AF, Ieno EN, Elphick CS (2010) A protocol for data exploration to avoid common statistical problems: data exploration. Methods in Ecology and Evolution 1:3–14. https://doi.org/10.1111/j.2041-210X.2009.00001.x

Supporting Information

The following information may be found in the online version of this article:

Table S1. Full list of predictor variables used in the generalized linear mixed models, with response variables being density of seedlings in the different size classes.
Table S2. Summary of the results from the different models.
Table S3. Results from the zero-augmented generalized linear mixed models (GLMM) with Gamma distribution on the effect of microsite on the establishment potential of mountain birch.
Table S4. Seedling occurrence and mean cover of different microsites for seedlings in size class I.
Figure S1. Transect design used in the study.

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