Doctoral Thesis

October 2025

Patterns and processes of birch establishment in space and time

Implications for large-scale woodland restoration

Anna Mariager Behrend

Landbúnaðarháskóli Íslands
Agricultural University of Iceland

Patterns and processes of birch establishment in space and time

Implications for large-scale woodland restoration

Anna Mariager Behrend

150 ECTS thesis submitted in partial fulfilment of
a doctoral degree in Restoration Ecology

Academic advisors:
Professor Ása L. Aradóttir, Agricultural University of Iceland
Dr. Kristín Svavarsdóttir, Land and Forest Iceland
Professor Þóra Ellen Þórhallsdóttir, University of Iceland

Opponents:
Professor Alison J. Hester, The James Hutton Institute (Scotland)
Professor Susana Bautista, University of Alicante (Spain)

Faculty of Environmental and Forest Sciences
Agricultural University of Iceland
Reykjavik, October 2025

This thesis should be cited as:

Behrend, A. M. (2025). *Patterns and processes of birch establishment in space and time; Implications for large-scale woodland restoration.* PhD thesis, Agricultural University of Iceland, 76 pages. ISBN 978-9935-512-61-1.

Vitna skal til þessarar ritgerðar sem:

Behrend, A. M. (2025). *Mynstur og ferli við landnám birkis; þekkingarsköpun fyrir stórfellda endurheimt birkiskóga.* Doktorsritgerð, Landbúnaðarháskóli Íslands, 76 bls. (á ensku, með íslenskum útdrætti). ISBN 978-9935-512-61-1.

Faculty of Environmental and Forest Sciences
Agricultural University of Iceland
Hvanneyri
IS-311 Borgarnes
Telephone: 433 5000

Clarification of contribution

I hereby declare that the ideas behind this research, the writing of the following thesis and the four accompanying papers are my own work, done under the supervision and with assistance of Professor Ása L. Aradóttir, Dr. Kristín Svavarsdóttir, Professor Þóra Ellen Þórhallsdóttir and two additional collaborators, Professor Arne Pommerening and Dr. Emmanuel P. Pagneux. This work has not been previously submitted to a higher degree, neither in part nor in whole.

The contribution of Anna Mariager Behrend to the papers included in this thesis are as follows:

Paper I: Anna Mariager Behrend is the main author. Behrend designed the study in collaboration with the other authors. Behrend assembled the data. Behrend analysed the data with support from Emmanuel P. Pagneux. Behrend drafted the manuscript which was reviewed and supervised by all co-authors.

Paper II: Anna Mariager Behrend is the main author. Behrend designed the study in collaboration with the other authors. Behrend performed the fieldwork. Behrend performed data analysis with support from the other authors. Behrend drafted the manuscript which was reviewed and supervised by all co-authors. Behrend corresponded with the scientific journal.

Paper III: Anna Mariager Behrend is the main author. Behrend performed the fieldwork. Behrend designed the study and analysed the data in an equal collaboration with Arne Pommerening. Behrend drafted the manuscript which was reviewed and supervised by both co-authors.

Paper IV: Anna Mariager Behrend is the main author. Behrend designed the study in collaboration with the other authors. Behrend performed the fieldwork. Behrend analysed the data with support from Ása L. Aradóttir. Behrend drafted the manuscript which was reviewed and supervised by all co-authors.

Anna Mariager Behrend

Photo: Solveig Sánchez

Abstract

The continuous global ecosystem loss and degradation calls for extensive ecological restoration. Iceland has lost more than 95% of its original native mountain birch (*Betula pubescens* ssp. *tortuosa*) woodlands since the country's settlement in the 9th century CE. This has prompted an ambitious pledge for their restoration by the Icelandic government with the acceptance of the Bonn Challenge, aiming to increase the native birch woodland cover from 1.5 to 5%. This is only going to be possible through passive and low-intensity restoration strategies, and such strategies must be grounded in an in-depth knowledge of colonization processes of the targeted woodland species.

The overall aim of this thesis was to improve knowledge on the patterns, processes and drivers of mountain birch woodland expansion through natural processes in order to guide their restoration. The thesis encompasses studies at different scales, including field surveys, seeding experiments and remote sensing, based on ten study areas covering most lowland areas of Iceland.

Analysis of aerial photos from different years showed that the studied birch woodlands expanded on average by 1,5% annually over a period of 38-65 years. Areas that had been protected from grazing generally had higher expansion rates than those open for grazing, and the area with the highest expansion rate had also undergone revegetation. This expansion has mainly happened through natural colonization, as revealed by surveys of colonization patterns: a process mainly limited by local environmental factors at the early seedling establishment phase. This includes microsite availability, wind and soil type, and disturbance in the form of presence of domestic grazers. Seedling densities were greatest within 20 m of the woodland edge, indicating dispersal limitation, with varying patterns among areas. However, most areas had densities of more than 100 seedlings m^{-2} out to at least 100 m from the woodland edge. The results also show a positive effect of greater woodland heights on the effective colonization range of birch, and on the morphology of saplings growing at the woodland edge. Seeding experiments confirmed the importance of favourable microsites (safe sites) for recruitment. Recruitment of mountain birch was furthermore highly variable among different land classification types (habitat types), dependent on safe site availability and partly on origin of the seed source used. These are factors that can be controlled in restoration to improve conditions for birch establishment and survival.

The results show the feasibility of upscaling mountain birch woodland restoration by applying knowledge on natural processes to promote natural colonization and regeneration. The increased knowledge on birch colonization processes supports more targeted guidance on how natural recovery processes can be enhanced by limited interventions.

Keywords: *Betula pubescens* ssp. *tortuosa*, birch woodlands, mountain birch, natural colonization, recruitment niche, restoration ecology, spatiotemporal ecosystem expansion

Ágrip

[Mynstur og ferli við landnám birkis; þekkingarsköpun fyrir stórfellda endurheimt birkiskóga].
Hnignun og tap vistkerfa jarðar kallar á víðtæka vistheimt. Þetta á einnig við á Íslandi, sem hefur glatað yfir 95% af upprunalegu birkiskógum sínum frá landnámi. Íslensk stjórnvöld hafa sett sér metnaðarfull markmið um endurheimt birkiskóganna og hyggjast auka útbreiðslu þeirra úr 1,5% í 5%. Svo stórfelld vistheimt er aðeins raunhæf með lágmarksinngripum þar sem treyst er á sjálfgræðslu en þá verður að vera fyrir hendi þekking á landnámsferlum birkis og takmarkandi þáttum.

Megintilgangur þessarar rannsóknar var að auka þekkingu á mynstrum, ferlum og helstu drifkröftum aukinnar útbreiðslu birkiskóga með sjálfgræðslu. Rannsóknirnar byggðu bæði á tilraunum og samanburðarathugunum og spönnuðu breiðan kvarða í rúmi, allt frá næsta umhverfi kímplantna og upp í samanburð á tíu birkiskógum á Vesturlandi, Vestfjörðum, Norðurlandi, Austurlandi, Suðausturlandi og Suðurlandi. Í tíma spanna rannsóknirnar frá lifun og vexti kímplantna upp í áratuga ferli þar sem byggt var á samanburði á loftmyndum.

Greining á loftmyndum sýndi að birkiskógarnir höfðu að meðaltali stækkað útbreiðslusvæði sitt um 2% á ári yfir 38–65 ára tímabil. Útbreiðsluhraði var alla jafna meiri á svæðum sem höfðu verið friðuð fyrir beit en á beittu landi. Hröðust var útbreiðslan á friðuðu landi sem hafði verið örfoka en þar sem uppgræðsla hafði verið stunduð. Þessi stækkun birkiskóganna skýrist að mestu af sjálfgræðslu eins og kom skýrt fram í vettvangsrannsóknum við skógarjaðra. Þær sýndu ennfremur að landnám birkis takmarkaðist einkum af staðbundnum umhverfisþáttum á fyrstu stigum landnáms, svo sem framboði á öruggum setum, vindafari og jarðvegsskilyrðum, auk rasks vegna búfjárbeitar. Þéttleiki birkiplantna var mestur innan við 20 m frá skógarjaðri, sem bendir til þess að fræframboð hafi verið takmarkandi þáttur. Landnámsmynstur voru breytileg á milli svæða en á flestum var þéttleiki birkis yfir 100 plöntur á m^2 í a.m.k. 100 m fjarlægð frá skógarjaðri. Niðurstöðurnar sýndu einnig jákvætt samband á milli hæðar trjánna og stærðar landnámssvæða og jafnframt á milli hæðar skóga og vaxtarlags ungplantna við jaðrana. Sáingartilraunir staðfestu mikilvægi hagstæðra öruggra seta fyrir landnám birkis. Landnám var enn fremur afar breytilegt eftir vistgerðum, framboði á öruggum setum og að hluta til einnig eftir uppruna fræsins sem var notað. Þessum þáttum má stýra í vistheimt til að bæta aðstæður fyrir landnám og lifun birkis.

Niðurstöður ritgerðarinnar sýna að sjálfgræðsla birkis er áhrifarík leið til að auka umfang birkiskóga. Aukin þekking á landnámsferlum birkis og öðrum þáttum er hafa áhrif á útbreiðslu birkiskóganna styðja einnig markvissari leiðsögn um hvernig hægt sé að auka nýliðun og sjálfgræðslu birkis með takmörkuðum inngripum og þannig stuðla að endurheimt birkskóganna.

Lykilorð: *Betula pubescens* ssp. *tortuosa*, birkiskógur, ilmbjörk, sjálfgræðsla, nýliðun, endurheimt vistkerfa, útbreiðsla vistkerfa í tíma og rúmi

Photo: Berglind Guðjónsdóttir

Dedication

To Alenka Louise
You and your generation deserve a beautiful world
I will do what I can

Acknowledgements

I would first and foremost like to thank my fantastic supervisors and committee members: Professor **Ása L. Aradóttir**, Dr. **Kristín Svavarsdóttir** and Professor **Þóra Ellen Þórhallsdóttir**. I have been very fortunate to have such brilliant scientist and strong, pleasant and helpful women in my doctoral committee. I am positive that you have provided me with the best possible baseline for a future career in academia and ecological restoration. A special thanks goes to my main academic advisor Ása for being the best mentor I could wish for, for always being available for any little inquiry, and for all of the opportunities you gave me during my time as a PhD-student to grow academically.

I believe that I owe a special thanks to my former mentors, **Karsten Raulund-Rasmussen** and **Hreinn Óskarsson**. Karsten for pointing me in the direction of restoration ecology as a field of science, and Hreinn for introducing me to the Icelandic birch woodlands, which I have now dedicated a good portion of my professional life to conserve and restore. If not for both of you, I would never have gone in the direction I have, so thank you sincerely.

I thank **Arne Pommerening** for our close collaboration on several of the papers in this thesis, and for hosting a very pleasant research stay in Umea. Thank you to **Guðrún Óskarsdóttir** for helping me with my seeding experiments, for all of your constructive criticism on my research and for a fruitful collaboration on seed quality in different mountain birch populations. Thank you **Emmanuel P. Pagneux** for all of your help and guidance on remote sensing and GIS. Thank you to **Jacob M. Kasper** for being my statistical web of knowledge. I thank **Ólafur Arnalds** for valuable lessons on land degradation and soil. Thank you to everyone at the *BirkiVist* research project for stimulating conversations and seminars during my time as doctoral student. It has been great to learn about the extents of restoration ecology from such a diverse group of experts.

A big thanks to everyone who helped me in the field over the years (it was not always easy); **Árni Hafstað Arnórsson, Caroline Behrend Rasmussen, Kata Valsdóttir, Margrét Guðbrandsdóttir, Muez Hailu** and **Tobias Behrend Eugen-Olsen**. A special thanks to my field assistant **Berglind Guðjónsdóttir** who accompanied me on nearly all of my field trips, and tirelessly taught me about Icelandic culture and language while on the road. Thank you to the wonderful people in the PhD-office for help and moral support throughout the years: **Jónína S. Þorláksdóttir, Laura Barbero-Palacios, Mathilde Deforneaux, Ruth Phoebe Tchana Wandji, Stephen Hurling** and **Sumjidmaa Sainnemekh**. Thank you to all employees at Landbúnaðarháskóli Íslands who gave me the opportunity to teach classes, supervise students, and were generally friendly and welcoming (and insisted on speaking Icelandic to me so that I would learn). It has meant a lot for me to be part of such a pleasant academic work environment.

Thank you to family and friends near and far for your love and support. To my **ICE-SAR family**, and to everyone who came and visited me in Iceland over the years. To the **Arnórsson-Sánchez** family for making Iceland feel like home. To my dear friends, **Greg Gaede** and **Michelle Pröstler**, for countless sleepovers and general distractions from life as a doctoral student. To my parents, **Louise Behrend** and **Mads Mariager**, who always encouraged me to follow my own path and supported and fed my enthusiasm for nature and science. Děkuji **Ondřej Kupka** for keeping our home together throughout periods of both mental and physical absence, and for lending an ear to my frustration and enthusiasm for the better part of four years. **Alenka Louise Kupka**, mit livs lys, thank you for reminding me to stay present in the moment, and for motivating me to fight for a better world.

A final and very big thank you to my PhD partner **Sólveig Sánchez**. I could not have done this without you. The world lies ahead of us, and I am sure we will continue to do great things together.

List of original papers

This thesis is based upon four original scientific papers, referred to in the text by Roman numerals. Two are published, one has been submitted to a scientific journal, and one is in the form of a manuscript.

I. **Behrend, A. M.**, Pagneux, E. P., Svavarsdóttir, K., Thórhallsdóttir, T. E., & Aradóttir, Á. L. (202X). Spatio-temporal patterns of subarctic woodland expansion to guide future restoration. [submitted]

II. **Behrend, A. M**., Aradóttir, Á. L., Svavarsdóttir, K., Thórhallsdóttir, T. E., & Pommerening, A. (2024). Natural colonization as a means to upscale restoration of subarctic woodlands in Iceland. *Restoration Ecology*, 33(1), e14332. https://doi.org/10.1111/rec.14332. [published]

III. **Behrend, A. M.**, & Pommerening, A. (2025). Growing at the edge: modelling sapling colonization, performance, and effective range of mountain birch (*Betula pubescens* ssp. *tortuosa*). *Ecological Modelling*, 503, 111073. https://doi.org/10.1016/j.ecolmodel.2025.111073. [published]

IV. **Behrend, A. M.**, Aradóttir, Á. L., Thórhallsdóttir, T. E., & Svavarsdóttir, K. (202X). Assessing safe-site limitations to support recruitment niche-based restoration frameworks. [manuscript]

Reprints of *Paper II* and *III* are published with kind permission from the publishers. Submitted and unsubmitted manuscripts may be subjected to change.

List of figures

Figure 1. The massive and hilly rockslide of Leyningshólar, North Iceland, with a mosaic of patchy mountain birch woodlands, heathlands and sparsely vegetated ground. In the background, scree slopes due to water and/or wind erosion can be seen. 5

Figure 2. Different Icelandic mountain birch woodland ecosystems; (a) tall birch trees from an old woodland in Thórsmörk, South Iceland; (b) low-growing shrubby birch woodlands in Mjóifjörður, Westfjords; (c) birch trees in a mixed woodland with *Sorbus aucuparia* and *Salix phylicifolia.* 6

Figure 3. Overview of the *BirkiVist* study areas with symbol colour referring to sites used in different papers. Also shown in green is the current distribution of natural birch woodlands in Iceland (Snorrason et al. 2016).. 13

Figure 4. Mountain birch regenerating in different microsites; (a) in pebbles on a braided floodplain; (b) in thin moss; (c) in lichens on a lava field; (d) in biological soil crust, formed by lichen and liverworts in a disturbed habitat; (e) in a heathland dominated by forbs and dwarf shrubs. 15

Figure 5. Overview of the four habitat types where seeding experiments were established; (a) Oroboreal *Carex bigelowii-Racomitrium* moss-heath; (b) Moss and lichen fjell field; (c) Icelandic *Empetrum-Thymus* grassland; (d) North Atlantic *Vaccinium-Empetrum-Racomitrium* heath.. 16

Figure 6. Nightingale Rose diagrams showing lateral woodland increase (m year-1) in 12 cardinal directions for all nine study areas over the studied time period. Dark blue diagrams represent study areas that were covered in their entirety by the outlined area of interest, while light blue diagrams are areas where the woodland extents were cut due to lack of aerial photo data.. 22

Figure 7. Site-specific relationships between seedling densities and distance from the woodland edge for the 10 study areas included in *Paper II.* The area in red falls within the success-criteria for natural colonization, i.e. from 100 to 1100 seedlings ha^{-1}, as defined by Gullet et al. (2023) 23

Figure 8. Establishment potential, calculated as the number of birch seedlings (mean ± SE) in a given microsite multiplied by the proportional aerial cover, for each microsite type included in *Paper I.* Numbers are based on the results from all 10 study areas. Color indicates whether the association was significantly positive (green), negative (red) or non-significant (black).. 24

Figure 9. Morphology indices for the four regions in Iceland as described in *Paper III.* Letters denote significant differences between geographic regions (Bonferroni test, $p < 0.05$). 25

Figure 10. Correlation between $dist_{max}$ and median (± SE) morphology index (S_i)....................................25

Figure 11. Conceptual model building on the results found in *Paper IV* on how a species environment can be altered by different restoration interventions to better match their recruitment niche..................28

Figure 12. Conceptual figure of key recommendations to restore mountain birch woodlands derived from the results of this thesis. 30

List of Abbreviations

Abbreviation	Full description
DEM	Digital Elevation Model
GLM	Generalized Linear Model
GLMM	Generalized Linear Mixed Model
LMM	Linear Mixed-Effects Model
LSM	Least Squares Method
m.a.s.l	Meters Above Sea Level
MLM	Maximum Likelihood Method

Table of content

1. Introduction 1
1.1 The ecology of restoration 1
1.2 Restoration of woodland ecosystems 3
1.3 Ecosystem degradation and restoration efforts in Iceland 4
1.4 Ecology of the study species, mountain birch (*Betula pubescens* ssp. *tortuosa*) 5
1.5 Importance and current state of mountain birch woodlands in Iceland 7
1.6 Challenges and knowledge gaps in restoration of mountain birch woodlands 8
1.7 *BirkiVist* – Restoration of birch woodlands in the 21st century 9

2. Thesis objectives 11

3. Methods 13
3.1 Study areas 13
3.2 Remote sensing data 14
3.3 Field data 14
3.4 Seeding experiments 16
3.4.1 Germination tests 16
3.4.2 Experiments 16
3.5 Data analysis 17
3.5.1 Aerial photo analysis (*Paper I*) 17
3.5.2 Field data analysis (*Paper II* and *III*) 17
3.5.3 Seeding experiment data analysis (*Paper IV*) 19

4. Main findings and discussion 21
4.1 Spatio-temporal rates and patterns of birch woodland expansion (*Paper I*) 21
4.2 Natural colonization of mountain birch: drivers and spatial patterns (*Paper II*) 22
4.3 Morphology of individual saplings and effective range of birch colonization (*Paper III*) ... 24
4.4 A recruitment niche-based restoration framework for mountain birch (*Paper IV*) 26
4.5 Implications for ecological restoration 28
4.6 Recommendations for restoring subarctic mountain birch woodlands 29
4.6.1 Protect existing woodlands and woodland remnants 29
4.6.2 Prioritize restoration strategies relying on natural processes 29
4.6.3 Examine habitat suitability for appropriate interventions 31
4.6.4 Implement active restoration when necessary 31
4.6.5 Ensure soil stability 31

4.6.6 Minimize habitat loss 31
4.6.7 Consider spatial arrangements in applied nucleation 32
4.6.8 Use local seed material whenever possible 32
4.6.9 Use relevant reference ecosystems 32
4.6.10 Long-term monitoring is mandatory 33

5. Conclusions 35
6. Future work 37
7. Funding 39
8. References 41
9. Appendices 51

1. Introduction

Ecosystem degradation is defined as the deterioration of land conditions caused by human-induced climate change and disturbances (Olsson et al. 2019). It has been estimated that more than 70% of Earth's ecosystems have been degraded or transformed by anthropogenic disturbances (Arneth et al. 2019). This continuous degradation of Earth's natural ecosystems is among the biggest environmental threats that humanity is facing in the 21st century (Barnosky et al. 2012). Conservation ecology has long been recognized as an important framework for combatting ecosystem degradation and biodiversity loss. At this rapid rate of ecosystem degradation and loss, however, conserving the remaining ecosystems will be insufficient; it is crucial to reverse land degradation and restore degraded ecosystems.

The process for combatting large-scale ecosystem degradation is ecological restoration (Young et al. 2005). Ecological restoration has become an inherent part of conservation ecology (Perring et al. 2015, Suding et al. 2015) focusing on the protection and restoration of nature (Gann et al. 2019). It has a growing importance in addressing current global environmental challenges, such as climate change, loss of biodiversity and land degradation (Temperton et al. 2019, Hua et al. 2022). The United Nations has declared 2021 – 2030 to be the Decade on Ecosystem Restoration (UNEP/FAO 2020). The Bonn Challenge, commenced in 2011, is a global initiative aiming to bring 350 million hectares of degraded and deforested lands into restoration by 2030 (IUCN 2020). The newly adopted EU Nature Restoration Regulation commits European countries to restore hundreds of millions of hectares of degraded land (The European Commission 2024).

1.1 The ecology of restoration

Ecological restoration is defined as the process of assisting recovery of ecosystems that have been degraded, damaged or destroyed (Gann et al. 2019). The scientific discipline underpinning the practice of ecological restoration, restoration ecology, has its conceptual basis in ecological theory and relies on the natural ecological processes of ecosystem recovery and expansion (Young et al. 2005, Chazdon et al. 2021). One of the most critical processes of terrestrial ecosystem development is colonization; the spread and succesful establishment of a species into new areas (Chapin et al. 2011). Successful colonization is limited by a number of ecological processes, including seed dispersal; a critical stage in the colonization process in which seeds move away from their parent locations (Beckman and Sullivan 2023). Limitations to colonization include distance to a nearby seed source and habitat limitations, i.e. the availability of safe sites for seedling establishment (Duncan et al. 2009). Furthermore, colonization is dependent on the successful establishment of individual plants, i.e. the process where seeds successfully germinate, grow and survive as self-sustaining individuals (Chapin et al. 2011). These key ecological processes are limited by a range of ecological filters, which each individual needs to go through for successful establishment (Hanbury-Brown et al. 2022). These include disturbance regime, which can either facilitate or impede colonization depending on the context (Suding et al. 2004) and interspecific competition, particularly in the early-establishment phase of a plant's life, where it may be easily outcompeted by already established individuals of other species (Grubb 1977).

In restoration, selected interventions to overcome barriers to these processes can be applied. Although ecological knowledge is the foundation for restoration ecology, it is difficult to predict and/or generalize the outcome of interventions, as there are many variables that may affect recovery, both biotic and abiotic (Hobbs & Harris 2001). To successfully apply and upscale restoration globally, an in-depth understanding of the ecological processes driving restoration success is therefore necessary.

Ecological processes act at different spatial scales, from landscape, to site, to microsite scale (Parker 1997). Most often, when restoration is performed on a site-level, the ecological processes considered are those within the site, such as abiotic factors including soil conditions and local climate (Gomes Marques et al. 2022, Pedersen et al. 2023) and species interactions (Boeken 2018). However, processes external to the site often have an effect on the contained ecological processes as well. This includes long-distance seed dispersal from neighbouring communities (Óskarsdóttir et al. 2022), topographical constraints in the surrounding landscape (Greenwood et al. 2014, Dobbert et al. 2021) and climatic events occurring outside a site which may affect its environment, such as floods or volcanic eruptions (Thórhallsdóttir & Svavarsdóttir 2022). Restoration outcome can also be influenced by the performance of individuals (Hanbury-Brown et al. 2022). Restoration should therefore be based on an understanding of the linkages between these scale-dependent processes.

Ecological restoration involves a continuum of approaches on a scale from passive to active (Chazdon et al. 2021). Active or intensively assisted restoration includes extensive human interventions to influence the arrival of biota or ecosystem recovery, such as planting, introduction of species and soil amendments (Holl & Aide 2011, Gann et al. 2019). Active ecosystem restoration can be necessary when ecosystems have surpassed a critical threshold where recovery needs to be assisted (Suding et al. 2015). However, it is often associated with high economic costs and does not guarantee restoration success (Kimball et al. 2015, Crouzeilles et al. 2017).

On the other end of the continuum is passive restoration, or natural recovery, which is based entirely on minimal interventions, the primary one being removal of disturbances to enhance natural or unassisted ecosystem recovery (Holl & Aide 2011, Chazdon et al. 2021). Passive restoration strategies commonly rely on natural regeneration and colonization (Chazdon & Guariguata 2016, Bauld et al. 2023), i.e., on the targeted ecosystems' ability to recover and expand on their own through natural processes. This strategy can be very cost-efficient at large scales, but may be a slow process, where biotic and abiotic filters such as competition and microclimate can prevent emergence and establishment of seedlings (Fowler 1988). In general, the main challenge in passive restoration arises when ecological conditions do not support the processes of natural recovery, i.e., there are barriers slowing down or preventing ecosystem recovery. Under those conditions restoration may hinge on active interventions.

In practice, most restoration projects require some intervention and therefore incorporate a spectrum of intervention strategies ranging from unassisted to intensely assisted recovery (Chazdon et al. 2021). An example could be protection from grazing or browsing wildlife, which may prevent ecosystem recovery and expansion (Hope et al. 1996). Although this is widely accepted as being a passive restoration strategy, it still requires an initial intervention and monitoring to determine if more restoration activities are needed (Gann et al. 2019). Viewing restoration activities as a spectrum may be especially relevant in forest and woodland ecosystems, in which restoration almost always needs some intervention to succeed (Holl & Aide 2011).

1.2 Restoration of woodland ecosystems

It has been estimated that 47 million hectares of primary forests and woodlands have been lost globally in the past 20 years (Olsson et al. 2019). Their conservation and restoration are of crucial importance to maintain the wide range of ecosystem services they provide (Hua et al. 2022). So far, this has to a large degree relied on afforestation practices, such as large-scale tree planting, which is not a feasible strategy considering the scale and scope of restoration that is currently needed (Ferreira et al. 2023). Tree planting is, on its own, no guarantee for success, as important ecological criteria for tree establishment and survival are often overlooked in this practice (Holl et al. 2011, Hua et al. 2022). Extensive tree planting can furthermore introduce issues such as the spread of invasive species (Moyano et al. 2024) and superior alien genotypes (Bischoff et al. 2010).

Restoration strategies relying on the natural processes of woodland recovery and expansion, such as natural regeneration and colonization, have become common in recent decades due to their lower costs (Crouzeilles et al. 2020), a resulting increase in ecosystem resilience (Chazdon & Guariguata 2016), and potentially higher restoration success (Crouzeilles et al. 2017). There are several common factors that affect colonization success. One essential factor is a seed source, which if absent needs to be provided. Instead of large-scale planting of trees, planting in small clusters to establish a seed source and promote natural colonization can be an effective, low-cost strategy, known as applied nucleation (Corbin & Holl 2012). Even with a seed source present, colonization can still be halted by a variety of factors in the local environment, including impediment from surrounding vegetation, i.e. low soil-seed interface (Collis-George & Hector 1966), or soil degradation, which can cause upheaving of tree seedlings (Jiao et al. 2009). In such cases, colonization can be accelerated by interventions that remove barriers to colonization, known as assisted natural regeneration (Shono et al. 2007). This may include restoration activities such as mulching, i.e. adding organic materials that improve soil health (Wu et al. 2024) and measures to improve soil stability, consequently creating safe sites for seedling establishment

(Aradóttir & Halldórsson 2018). These interventions are applied with the goal of promoting recovery and expansion through natural processes.

Another method to introduce key plant species in restoration is direct seeding, where seeds are dispersed mechanically or by hand to establish standing seed sources, or entire woodlands (Cole et al. 2011). Although it is considered a cost-effective alternative to planting, there may be difficulties with implementing direct seeding on a large scale. These include many of the same barriers that exists for natural regeneration, but furthermore include the challenge of sourcing large quantities of viable seed material, and for dispersed seeds to establish within the already established ground cover (Souza et al. 2022).

1.3 Ecosystem degradation and restoration efforts in Iceland

Iceland, a subarctic oceanic island, has undergone severe ecosystem degradation since its settlement in the 9th century (Arnalds 1987). This can mainly be attributed to anthropogenic drivers such as overexploitation of resources, including chopping and burning wood for coal production and intensive year-round grazing (Thórsson, 2010), leading to severe wind and water erosion, which can remove entire layers of soil and vegetation (Greipsson 2012) and frequent sand and dust storms (Arnalds 2010). Iceland is a volcanic island, and about 58% of the country's land area comprises the highlands, where sandy deserts and glaciers are dominant, sustaining little vegetation cover (Thórhallsdóttir 1998).

According to Arnalds et al. (2023), 45% of Iceland's land area can be considered as being in poor or very poor condition, the main drivers identified as continuous land pressures since the settlement, and more recently wetland drainage, and the presence of eroded scree slopes (**Figure 1**). A factor still continuously challenging the already fragile state of the Icelandic terrestrial ecosystems is grazing by domestic sheep (Arnalds & Barkarson 2003, Barrio et al. 2018). The grazing sheep roam both the highland and lowland regions of Iceland during the summer months, causing damage to ecosystems that are already severely degraded (Arnalds et al. 2023). The domestic sheep is generally thought to be a grass/roughage eater (Hoffman 1989), but in the subarctic North sheep have been shown to limit treeline expansion (Speed et al. 2011, Potthoff 2017).

Iceland's terrestrial ecosystems are furthermore experiencing major problems with invasive species. Most notably perhaps is the Nootka lupine (*Lupinus nootkatensis*), a legume introduced in the 1940s with the purpose of combatting desertification (Magnusson 2010). Nootka lupine has spread at high rates throughout the country, outcompeting the native vegetation in woodlands, heathlands, and grasslands (Magnusson et al. 2008). The land area covered by lupine is expected to increase rapidly with increased habitat suitability within the next 40-60 years, depending on the level of warming the subarctic ecoregion will experience (Vetter et al. 2018).

Figure 1. The massive and hilly rockslide of Leyningshólar, North Iceland, with a mosaic of patchy mountain birch woodlands, heathlands and sparsely vegetated ground. In the background, scree slopes due to water and/or wind erosion can be seen.

With the challenges that Iceland has faced for centuries, and continues to face, land degradation and desertification remain among the country's biggest environmental challenges (Runólfsson 1987). Iceland has a long history of dealing with these issues, and the country is home to one of the first official soil conservation agencies in the world, the Soil Conservation Service of Iceland (SCSI, now part of Land and Forest Iceland). Since its foundation in 1907, the SCSI has been the leading governmental soil conservation authority in Iceland, working with the restoration of degraded terrestrial ecosystems in both research and practice (Aradóttir et al. 2013). One of the largest terrestrial restoration projects in Iceland is the Hekluskógar restoration project, initiated in 2006 with the aim of restoring 90.000 ha of birch woodlands in predominantly barren and degraded lands in the vicinity of the active Mount Hekla volcano (Aradóttir 2007).

1.4 Ecology of the study species, mountain birch (*Betula pubescens* ssp. *tortuosa*)

Mountain birch (*Betula pubescens* ssp. *tortuosa*) is a subspecies of downy birch (*Betula pubescens* Ehr.) native to northern Fennoscandia, Russia, Scotland, Greenland, and Iceland (Böcher 1977, Atkinson 1992). Mountain birch is the only native woodland forming tree species in Iceland, and all birch in Iceland is regarded as belonging to this species (Kristinsson et al. 2018). In mixed temperate and boreal forests, birch is considered as an early successional species (Lidman et al. 2021). However, in Iceland, mountain birch woodlands form climax communities with trees reaching up to 14 meters in height (Snorrason et al. 2016). Mountain birch is an efficient early colonizer due to its ability to establish both in nutrient rich and poor soils (Atkinson 1992). With abundant light (Grime & Jeffrey 1965) and optimal wind conditions, including strong, prevailing winds (Aradóttir et al. 1997) mountain birch woodlands can expand rapidly via natural colonization, with long distance dispersal events additionally forming the basis for new woodland establishment (Óskarsdóttir et al. 2022). Their rapid expansion is enhanced by the warming climate in the arctic and subarctic regions, with climatic projections for the future supporting higher rates of birch woodland expansion, and an increased altitudinal treeline (Truong et al. 2007, de Wit et al. 2014).

The morphology of mountain birch is highly variable and ranges from taller, straight, monocormic trees (**Figure 2a**) to low-stature polycormic individuals (**Figure 2b**, Jónsson 2004). This can be attributed to genetic isolation (Pálsson et al. 2023), hybridisation with the shrubby dwarf birch, *Betula nana* (Leduc et al. 2025) and local environments, particularly the negative thigmotropism of strong winds (Telewski 2012) and high winter snow cover (Verwijst 1988). Natural woodlands in Iceland most often consist only of mountain birch but can sometimes be seen forming more heterogenous communities mixed with other native tree species such as rowan (*Sorbus aucuparia*), Eurasian aspen (*Populus tremula*), and different willow species (*Salix lanata* and *Salix phylicifolia*, **Figure 2c**).

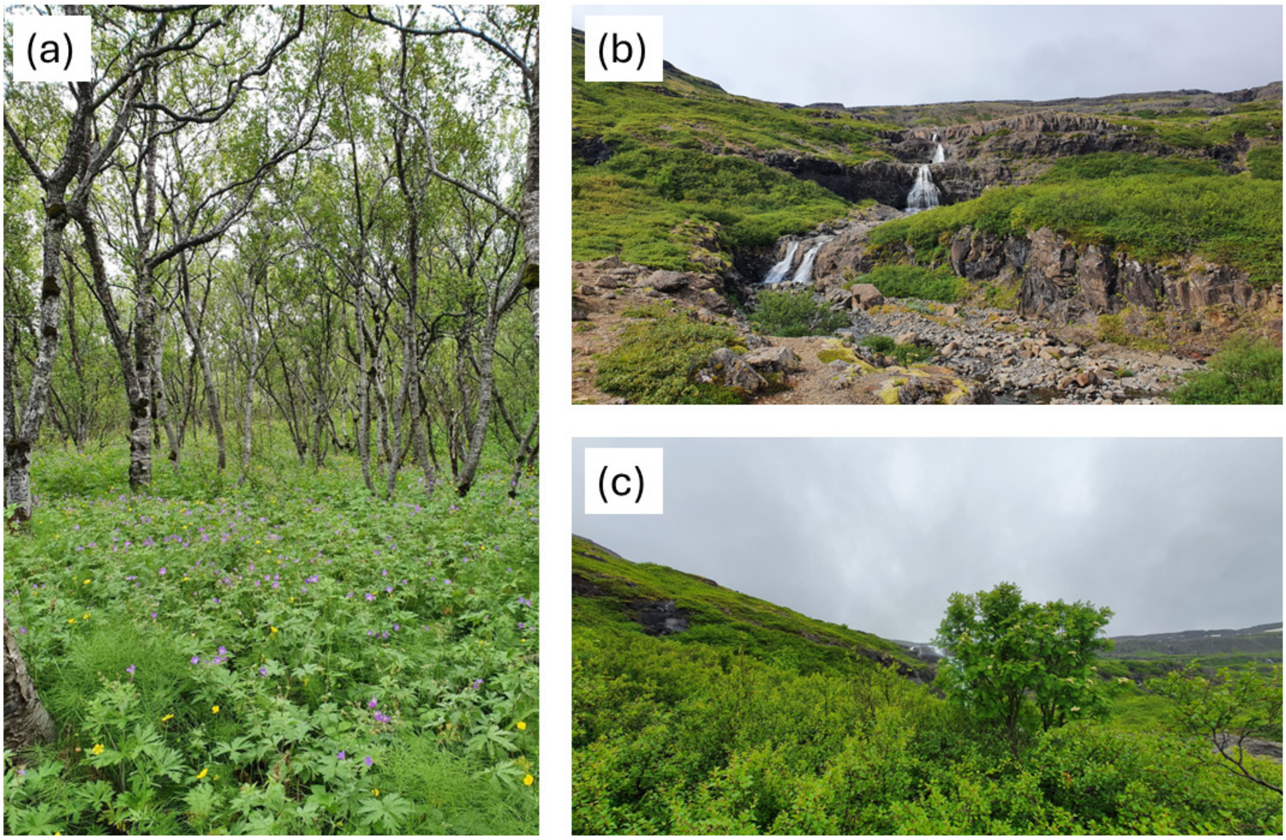


Figure 2. Different Icelandic mountain birch woodland ecosystems; (a) tall birch trees from an old woodland in Thórsmörk, South Iceland; (b) low-growing shrubby birch woodlands in Mjóifjörður, Westfjords; (c) birch trees in a mixed woodland with *Sorbus aucuparia* and *Salix phylicifolia*.

Mountain birch is a relatively small-seeded, anemochorous tree species (Atkinson 1992). This fact, combined with the often harsh, subarctic environments and degraded lands in Iceland, means that the process of natural colonization can be challenging. Small birch seedlings are susceptible to soil erosion and cryoturbation in winter, causing high mortality rates in the early-establishment phase of colonization (Aradóttir 2004, Aradóttir & Halldórsson 2018). Establishment of birch is highly dependent on safe sites, especially biological soil crust or low-growing vegetation that provide both a stable surface and minimal interspecific competition (Aradóttir & Halldórsson 2018). Both establishment and survival are furthermore challenged by sheep grazing and trampling (Speed et al. 2010). Mountain birch is a masting species, which means that seed quantity varies substantially between years, with high synchrony across geographical regions (Sarvas 1956, Holm 1994). This large interannual variation in seed production can lead to episodic colonization events (Óskarsdóttir et al. 2022).

1.5 Importance and current state of mountain birch woodlands in Iceland

Natural mountain birch woodlands covered an estimated 30% of Iceland before human settlement, but had been decimated to less than 1% cover in the early 1900s (Sigurðsson 1977, Eysteinsson & Aradóttir 2004). This is believed to have been caused primarily by unsustainable overexploitation of the woodlands for fuel, combined with extensive year-round grazing by domestic sheep, preventing natural regeneration (Arnalds 1987, Gísladóttir 2011). Today, the cover of mountain birch woodlands has increased to 1.5% of Iceland, with a warmer climate and reduced sheep grazing likely to have accelerated the process (Snorrason et al. 2016, Óskarsson & Traustason 2023). Birch woodlands and woodland remnants are spread across the entire island (Snorrason et al. 2016).

The remaining birch woodlands in Iceland provide important ecosystem services such as protection from dust storms and soil erosion (Eysteinsson & Aradóttir 2004), enhanced water infiltration (Orradóttir et al. 2008), biodiversity of specialized woodland organisms (Oddsdóttir et al. 2008) and climate change mitigation, storing extensive amounts of carbon in their soils (Hunziker et al. 2019, Sánchez et al. 2025). Thus, they are of high ecological and socioeconomic importance, and their protection and restoration are of high prioritization to the Icelandic government. In 2022, Iceland accepted the Bonn Challenge with the goal of restoring a total 3.41% land cover with birch woodlands, or in metrics 341.000 ha, with the initial planning for how this is to be executed by 2030 (IUCN 2020). To achieve these ambitious goals of restoration, large-scale tree planting is not a feasible strategy; it is necessary to harness the potential for woodland expansion through natural colonization from existing seed sources and planted tree nuclei.

1.6 Challenges and knowledge gaps in restoration of mountain birch woodlands

Successional processes in the subarctic and arctic regions are usually slow due to a harsher climate than much of the rest of the world (Cargill & Chapin 1987). Birch woodlands, however, are known to rapidly colonize new land and expand in the subarctic if optimal conditions are present, which is for example seen on the Skeiðarársandur glacial outwash plain in southeast Iceland (Óskarsdóttir et al. 2022). Large-scale, long-term investigations are needed to make general statements about expansion rates, and whether these are related to regional differences in climate and topography. Such information can be obtained from image classification analysis of remote sensing sources such as historical aerial photos (Chugtai et al. 2021). Knowledge on the drivers and past rate of woodland expansion on a landscape scale can provide valuable insight for decision making in restoration, and for projections of future woodland spread in different environments (Dickinson et al. 2016, Qiu et al 2023).

Natural colonization can be an efficient passive restoration strategy resulting in rapid woodland expansion if the right conditions are met (Chazdon et al. 2017, Crouzeilles et al. 2020, Pedersen et al. 2023). Birch woodlands and woodland remnants are distributed across a large part of lowland Iceland (Snorrason 2016). Thus, theoretically, there is potential for their expansion by natural colonization from existing seed sources. Effective implementation of natural colonization in restoration requires understanding of the underlying mechanistic factors behind establishment success and/or failure (Hanbury-Brown et al. 2022). For example, successful establishment is both dependent on distance to a seed source and local environment and microtopography, factors that often interact either as facilitating or inhibiting (Lett & Dorrepaal 2018). Although several case studies have been carried out on this subject for mountain birch, a collective understanding on their colonization patterns in varying habitats and local conditions is still lacking.

For successful large-scale woodland restoration, spatial arrangements are of great importance (McCallum et al. 2018). This particularly goes for restoration strategies relying on natural colonization, as this process depends on an available seed source (Bauld et al. 2023). In such cases, applied nucleation can be a pertinent restoration strategy (Corbin et al. 2016). For successful spatial arrangements of planted tree nuclei forming the basis for applied nucleation, the effective range of natural colonization is of great interest, as this can inform on optimal planting distances between tree nuclei for successful restoration. This is an understudied subject, particularly for wind-dispersed tree species, whose dispersal patterns can be highly stochastic (Beckmann & Sullivan 2023). Dispersal distances of windborne tree species are known to be affected by the morphology of individual trees, as the sheltering effect of surrounding woodlands diminishes with a decreasing canopy height (Wu et al. 2018). This is particularly relevant for mountain birch with its marked variation in growth form (Jónsson 2004). Assessment of the maximum dispersal distance of seeds from woodlands can aid in restoration planning by providing a mechanistic understanding of dispersal processes.

A recruitment niche for a given species is an expression of their biotic and abiotic requirements for successful establishment (Grubb 1977). This is determined by the local microenvironment, especially ground cover characteristics at the microsite level (Aradóttir & Halldórsson 2018) and microsites that are suitable for germination and establishment have been called 'safe sites' (Fowler 1988). In Icelandic nature, birch establishment can be affected by common disturbances such as erosion and cryoturbation (Aradóttir & Arnalds 2001, Aradóttir 2004), this has so far only been studied on one or few sites rather than a suite of different habitats. A more comprehensive assessment would support a general understanding of what constitutes safe sites for birch establishment. Investigating the availability of suitable microsites for birch establishment in common habitat types, which is accessible from land cover classification data in Iceland, would aid in determining where natural colonization will occur naturally, and where active disturbances need to be controlled to facilitate natural colonization (Douterlungne et al. 2015, Souza et al. 2022). This type of knowledge is very useful in both active and passive restoration frameworks, including assisted natural regeneration and direct seeding. It can furthermore assist in the development of habitat suitability models to predict where active restoration efforts will be most cost-efficient, and where existing birch woodlands can be expected to expand naturally (Griffiths et al. 2011, Bryn et al. 2013).

1.7 BirkiVist – Restoration of birch woodlands in the 21st century

The research presented in this thesis is a part of the trans disciplinary research project *BirkiVist*, or *EcoBirch – restoration of birch woodlands in the 21st century: challenges, approaches and benefits.* The project's overall purpose was to increase knowledge on the ecological, societal, and cultural significance of mountain birch woodlands in Iceland, and provide improved guidelines for their restoration. The work forming the basis of this doctoral thesis is part of the *BirkiVist* work package 1 *Ecological challenges and opportunities/approaches* which aimed to shed light on the biotic and abiotic factors that enhance or impede restoration of birch from natural colonization. Furthermore, it aimed at investigating rates and patterns of birch woodland spread by natural colonization from existing seed sources. The ultimate goal of the *BirkiVist* research project was to synthesize the acquired ecological knowledge and compare it with existing studies on mountain birch woodlands in the subarctic to develop conceptual models for the future spread and distribution of mountain birch in Iceland. This will strengthen both planning and implementation of future restoration projects involving mountain birch, not only in Iceland but in the entire subarctic.

2. Thesis objectives

The aim of this PhD thesis was to expand knowledge and understanding of the patterns and processes driving natural colonization of mountain birch in Iceland, and on the basis of obtained results provide implications for the upscaling of birch woodland restoration in the subarctic. The thesis is divided into four parts, which have the following overall objectives:

I. Determine spatio-temporal rates, patterns and drivers of birch woodland expansion in Iceland (*Paper I*)

II. Disentangle spatial patterns and drivers of natural colonization of mountain birch from existing seed sources to aid in the upscaling of subarctic woodland restoration (*Paper II*)

III. Evaluate the effect of sheltering on the morphology of mountain birch saplings colonizing the woodland edge, and quantify the effective spatial range of natural colonization of mountain birch (*Paper III*)

IV. Characterize the recruitment niche for mountain birch in selected common subarctic habitat types with and without restoration interventions, and investigate the usability of safe site occurrence to predict natural colonization of birch (*Paper IV*)

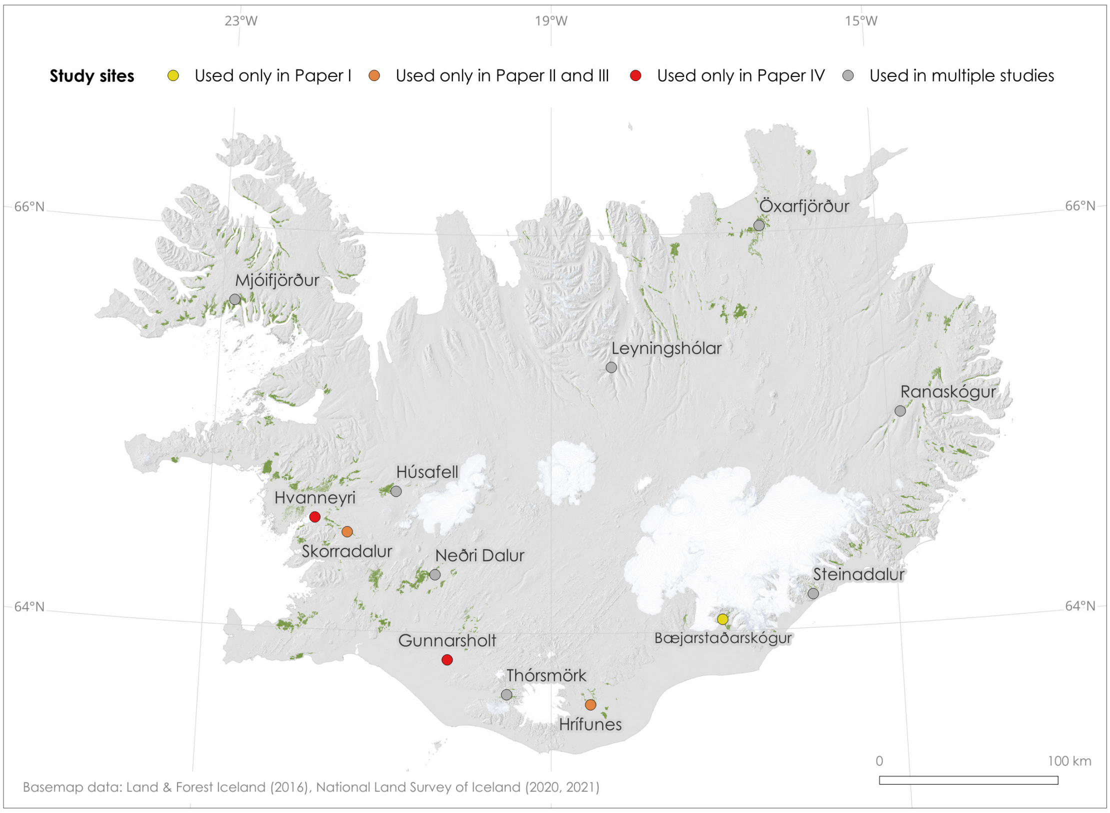
Each objective is addressed in a separate scientific paper, referred to in the text by Roman numerals.

3. Methods

This thesis is based upon both remote sensing data (*Paper I*), field survey data (*Paper II* and *III*), and experimental data (*Paper IV*), all assembled and analysed within the time period of the candidates' doctoral studies. This section provides a brief explanation of the materials and methods used. For further details, I refer to the individual papers.

3.1 Study areas

Most of the different work packages of the *BirkiVist*-project centre around 10 study areas with natural mountain birch woodlands distributed across Iceland, covering a wide variety of habitat types, management regimes and local climate and topography, with the common denominators that (i) parts of the birch woodlands were at least 60 years old as identified on historical aerial photos, and (ii) ongoing active colonization could be detected in their vicinity based upon initial field visits (**Figure 3**). The data for *Paper II* and *III* of this thesis are based on these 10 study areas. In *Paper I*, however, two of these areas were excluded due to poor quality of the available remote sensing data, but one additional study area, Bæjarstaðarskógur, was included instead. The seeding experiments forming the basis of *Paper IV* were conducted in the *BirkiVist* area Neðri Dalur, and in two additional study areas, Hvanneyri and Gunnarsholt.



Basemap data: Land & Forest Iceland (2016), National Land Survey of Iceland (2020, 2021)

Figure 3. Overview of the *BirkiVist* study areas with symbol colour referring to sites used in different papers. Also shown in green is the current distribution of natural birch woodlands in Iceland (Snorrason et al. 2016).

3.2 Remote sensing data

Historical and newer aerial photos formed the basis for the analysis carried out in *Paper I,* which had the objective to elucidate the spatio-temporal patterns of mountain birch woodland expansion in Iceland. Historical aerial photos (1954 - 1999) were assembled from the National Land Survey of Iceland (Landmælingar Íslands) and newer aerial photos (2000 - 2022) were assembled from Loftmyndir ehf. The aerial photos were imported into ArcGIS Pro, and an area of interest based on the extent of the available photos was outlined, setting the spatial base for the analysis. The photos were georeferenced, spline transformed and resampled to the resolution of the aerial photo with the highest pixel resolution of the individual study area (values ranging from 0.6 x 0.6 to 1.2 x 1.2 m).

3.3 Field data

The fieldwork forming the basis of *Paper II* and *III* was carried out between July and September 2021. The cutoff between the woodland edge and adjacent treeless lands was pre-defined from the most recent aerial photograph of each of the 10 *BirkiVist* study areas, and woodland edge polylines were created in ArcGIS Pro. Along these lines, four points were placed using stratified random sampling; two and two in pairs going in different cardinal directions from the woodland edge, with at least 100 meters distance between each other. These points served as starting points for transects which were put out perpendicularly to the woodland edge, stretching min. 100 m into the open landscape. Along these transects, all individual birch seedlings were counted in 1 x 2 m intervals. If a seedling was found in the last 10 m of the transect, it was continued for another 10 m until no seedlings were found in the last 10 m interval of the transect.

The seedling size was measured, and they were divided into three size classes based on the length of the longest living stem: I (<2 cm), II (2–20 cm), and III (>20 cm). For seedlings in size class III (called saplings in *Paper III*), total height and diameter from the stem base was also measured.

Since the suitability of an area for natural colonization of birch is strongly related to the availability of suitable microsites for establishment (Aradóttir & Halldórsson 2018), I investigated what constituted safe sites for birch seedling establishment by recording microsite occupancy of each individual seedling in size class I, distinguishing between 15 different microsite types (see *Paper II*, Table 2 for full description of the different microsite types). Expecting the ability of mountain birch to colonize a microsite to be dependent on microsite availability (**Figure 4**), the cover of microsites was furthermore recorded on every 10 meters of the transect using a 0.5 x 0.5 m quadrat with 25 regularly distributed points.

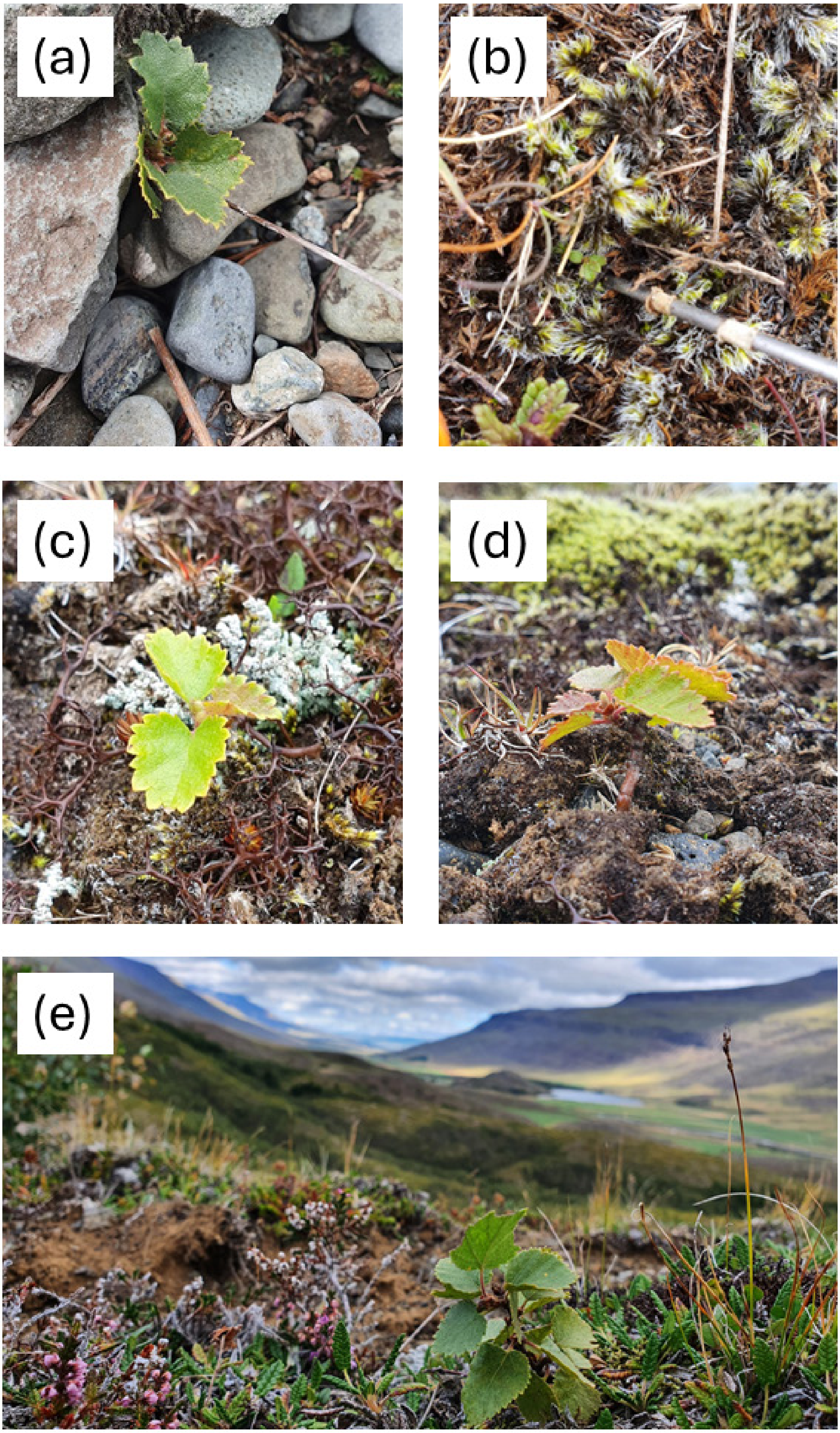


Figure 4. Mountain birch regenerating in different microsites; (a) in pebbles on a braided floodplain; (b) in thin moss; (c) in lichens on a lava field; (d) in biological soil crust, formed by lichen and liverworts in a disturbed habitat; (e) in a heathland dominated by forbs and dwarf shrubs.

3.4 Seeding experiments

An experimental approach was applied to investigate objective IV of this thesis: field experiments in three different locations involving direct seeding of birch and the application of different restoration treatments.

3.4.1 Germination tests

For the experiments, I used both a local seed source and a standard seed source to investigate the possible improved adaptability of a local seed source (McKay et al. 2005, Miller et al. 2017). The germination rate of all seed sources was tested in a germination chamber with a constant air temperature of 20 °C and a light cycle of 16 hours per day, to determine the amount of bulk to be distributed to obtain the same number of viable seeds per plot. 40 seemingly healthy (i.e. not obviously predated or mouldy) seeds from each seed source were tested in total. Germination was recorded every three days for three weeks, until germination had ceased.

3.4.2 Experiments

Four common subarctic habitat types were chosen based on their estimated land cover in Iceland, and their hypothesized applicability for birch woodland restoration (**Figure 5**). Five blocks were established in each habitat type, in every study area (i.e. 15 blocks per habitat type in total). The blocks where at least 25 m apart. Three 0.5 x 0.5 m plots were established within each block; one was seeded with local seeds, one with the standard seed source, and one with local seeds and an applied disturbance, encompassing vegetation cutting and soil scarification. In one study area, where the local seed source was sparse, the standard seed source was used in the disturbed plots instead. The experiments were established and

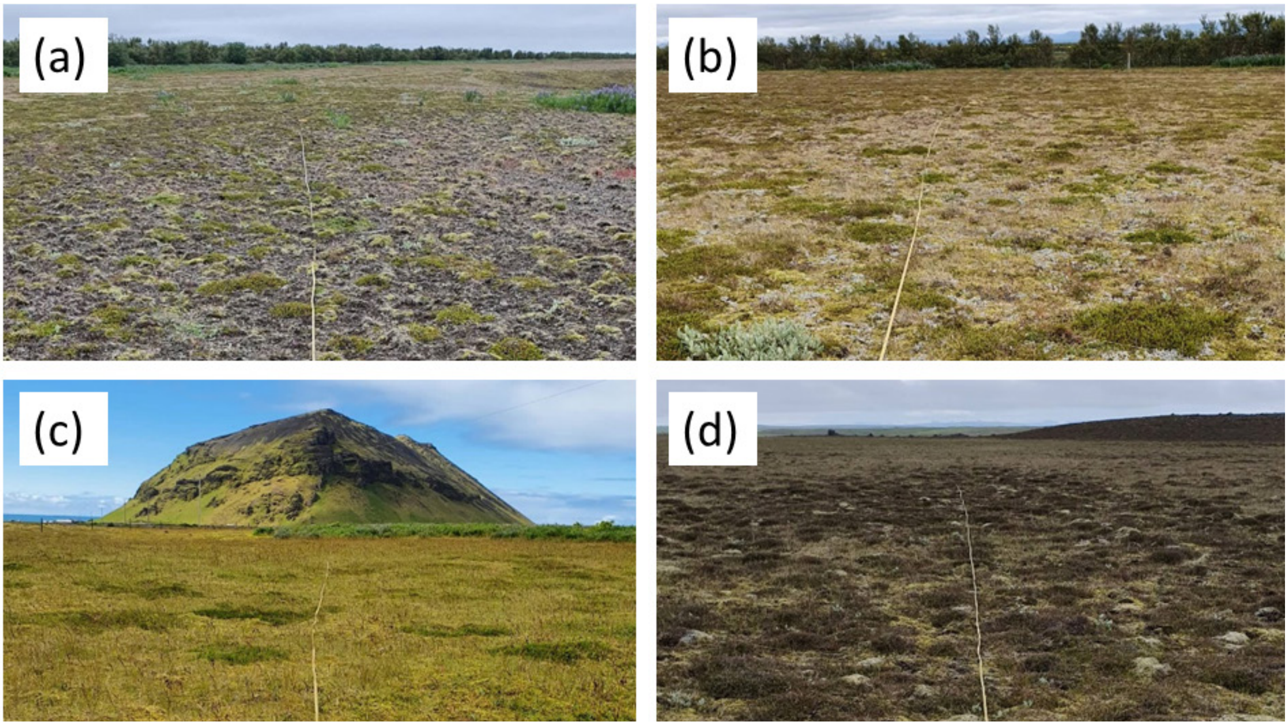


Figure 5. Overview of the four habitat types where seeding experiments were established; (a) Oroboreal *Carex bigelowii-Racomitrium* moss-heath; (b) Moss and lichen fjell field; (c) Icelandic *Empetrum-Thymus* grassland; (d) North Atlantic *Vaccinium-Empetrum-Racomitrium* heath.

seeded in winter 2021, and birch emergence and survival surveyed twice the following two years, in July and September, to account for both early and late germination.

3.5 Data analysis

All data analysis for this thesis was performed in R studio (R Development Core Team 2023) except for the analysis of rates and spatio-temporal patterns of birch woodland expansion in *Paper I,* for which most of the analysis was performed in ArcGIS Pro (ESRI 2023).

3.5.1 Aerial photo analysis (Paper I)

Image segmentation and unsupervised classification analysis was applied to all aerial photographs using 10 classes of brightness (for panchromatic photos) and colour (for colour photos). The overall accuracy and Kappa coefficient of agreement was calculated for each individual image classification. The total area of birch woodland was calculated for each year on each study area, and the average annual absolute growth rate (ha) and rate of increase (percentage year^{-1}) was calculated.

I calculated the main directions of woodland expansion by performing a near-analysis in ArcGIS Pro on points with 10 m intervals at the edge of the woodlands in the newest aerial photo and extracted the distance from these points to the edge of the woodlands in the oldest aerial photos. From this I calculated the lateral rate of expansion (m year^{-1}) in 12 cardinal directions and fitted the data into Nightingale Rose diagrams.

To assess the potential effects of restoration efforts on woodland expansion rates, I fitted a LMM to the data on birch woodland increase, using restoration intervention, i.e. protection from grazing and in one case also revegetation, as a binomial predictor variable (0 = no intervention, 1 = intervention) and study area as a random variable.

3.5.2 Field data analysis (Paper II and III)

I investigated the spatial patterns of birch colonization based on the assembled field data in two separate papers.

In *Paper II*, I examined the general spatial patterns of natural colonization by fitting the Gaussian regeneration kernel to observed seedling densities:

$$p = h^{\alpha} \times e^{\frac{-\delta \times dist^2}{h^{\beta}}} \tag{I}$$

where h is the dominant height of the local woodland canopy, *dist* is the Euclidean distance between a given density of seedlings to the seed source, and *a, β* and *δ* are model parameters which were determined using MLM and LSM.

I furthermore investigated site-specific colonization patterns by calculating average seedling densities in 10 x 2 m transect intervals, interpreting observed seedling densities in the context of the criteria of *successful natural colonization* defined by Gullett et al. (2023), ranging between 100 and 1100 seedlings ha^{-1}.

Applying zero-augmented GLMMs with negative binomial distributions I tested whether the association between observed seedling densities and different biotic and abiotic ecological factors, including precipitation, mean wind speed and dominant wind direction from September–December (the main period for birch seed dispersal) and presence of domestic sheep, was significantly positive or negative. The colonization potential of birch in different microsites was calculated as the number of seedlings registered in a given microsite, multiplied by the proportional cover of that microsite within a transect-segment. Zero-augmented GLMMs with gamma distributions were applied to test positive and negative associations between microsite type and seedling density.

In *paper III* I used individual-based modelling to investigate colonization of birch from the woodland edge in relation to a possible sheltering effect from surrounding woodlands, and the resulting performance of individual saplings (i.e. their morphology). I explored these different variables on a regional scale. Specifically, I applied the hyperbolic colonization kernel to observed seedling densities:

$$p_j = \frac{m_j^{\alpha}}{1+\left(\frac{dist}{\delta}\right)^2} \tag{II}$$

This kernel type uses the same parameters as the Gaussian colonization kernel but is based on the hyperbolic tangent function instead of the exponential function.

From the hyperbolic kernel function, I derived a formula describing the effective spatial range of birch colonization, $dist_{\max}$. I defined this as the 5% percentile of the most effective colonization along all converged kernel functions:

$$p_j^{(0.05)} = 0.05 \times \max\left(m_j^{\alpha}\right) \tag{III}$$

$dist_{\max}$ was then derived as:

$$dist_{\max} = \delta \times \sqrt{\frac{m_j^{\alpha}}{p_j^{(0.05)}} - 1} \tag{IV}$$

I furthermore assessed the performance of individual saplings by calculating the morphology index of saplings with a length of >20 cm:

$$s_i = \frac{h_i}{l_i} \tag{V}$$

Where h_i is the total height of the individual sapling and l_i is the length from stem base to the longest growing shoot. I tested for regional differences using a LMM with morphology index as response variable and region as predictor variable, while transect ID and distance from woodland edge was used as random variables. Spatial pairwise comparisons were made using the Bonferroni test. I investigated the effect of different ecological variables on the morphology index, using the same variables listed in section 3.6.2. I furthermore correlated the regional kernel parameters α and δ with morphology indexes.

3.5.3 Seeding experiment data analysis (Paper IV)

Seedling emergence (combined emergence from 1st and 2nd seedling cohorts) and survival was modelled using GLMMs with a Poisson distribution, with habitat type, disturbance and seed source as fixed variables, and plot ID nested within study area as a random factor. I furthermore fitted a binomial GLMM to data on restoration success, i.e. plots either with or without emergence and/or survival.

In similar way as in *Paper II*, the potential for establishment and survival in different microsites was calculated as number of seedlings in a given microsite multiplied by the proportional microsite cover, and the association between microsite type and seedling density was tested using zero-augmented GLMMs. I used study area and plot ID as random variables, and habitat type and disturbance as fixed variables, and I fitted two different models: one using emergence (both cohorts) as response variable, and another using survival. The effect of the applied disturbance on microsite cover in individual plots was investigated using Wilcoxon's rank sum tests.

4. Main findings and discussion

4.1 Spatio-temporal rates and patterns of birch woodland expansion (*Paper I*)

The results presented in *Paper I* show that mountain birch woodlands in Iceland have been expanding with an overall unidirectional rate of increase over the past 38-65 years. The temporal rate of expansion varied from 0.4% to 3.3% per year, with a mean annual expansion rate of 1.5%. Compared to similar studies on natural woodland expansion from other regions of the world (Laliberte et al. 2004, Weisberg et al. 2007, Girard et al. 2008), this expansion rate is quite high. Elevated air temperatures, which are projected to be four times higher in the subarctic and Arctic regions than the rest of the world (Nolan et al. 2018), are likely to have amplified these rapid expansion rates. This is supported by the clear regional differences in expansion rates; the colder North and Westfjords regions of Iceland expanded at lower rates than the warmer South, West and Eastern regions.

There were substantial differences in the spatio-temporal patterns of birch woodland expansion; while some woodlands expanded predominantly in one main direction, others displayed an equal expansion rate in several, or all, cardinal directions (**Figure 6**). This suggests diverging patterns of woodland increase: some woodlands expanded into adjacent barren habitats, while others increased in density/canopy cover, rather than total occupied area. These patterns may be ascribed to local environmental variation, including available space for colonization (Bauld et al. 2023) and dominant wind direction and gust strengths (Aradóttir et al. 1997). Furthermore, the suitability of surrounding habitats, including the availability of microsites for natural colonization and regeneration, have most likely played a role in these patterns, which differed vastly between study areas (Dobbert et al. 2021). There was a high variability in the lateral expansion rate of the woodlands, ranging from 0.1 to 16 m year^{-1}. This is likely an effect of expansion limitations in the landscape, including topographical obstacles such as steep slopes and rivers, anthropogenic features such as summerhouse areas, and lack of safe sites for natural colonization (Potthoff 2017, Borda-Niño et al. 2020).

The results also showed that woodlands protected from sheep grazing, and in one case having also undergone revegetation efforts, expanded at higher rates than those who had not. This suggests that protecting existing woodlands and woodland remnants from sheep grazing is an important first step in promoting restoration of natural woodlands, as expansion through natural colonization can lead to significant increases in woodland area through cost-effective means. It is, however, important to initiate restoration efforts in areas with unfavourable conditions. This encompasses ongoing anthropogenic disturbances, such as land development for housing lots, and grazing by domestic and wild herbivores (Thomson et al. 2016, Barrio et al. 2018, Gullett et al. 2023).

.

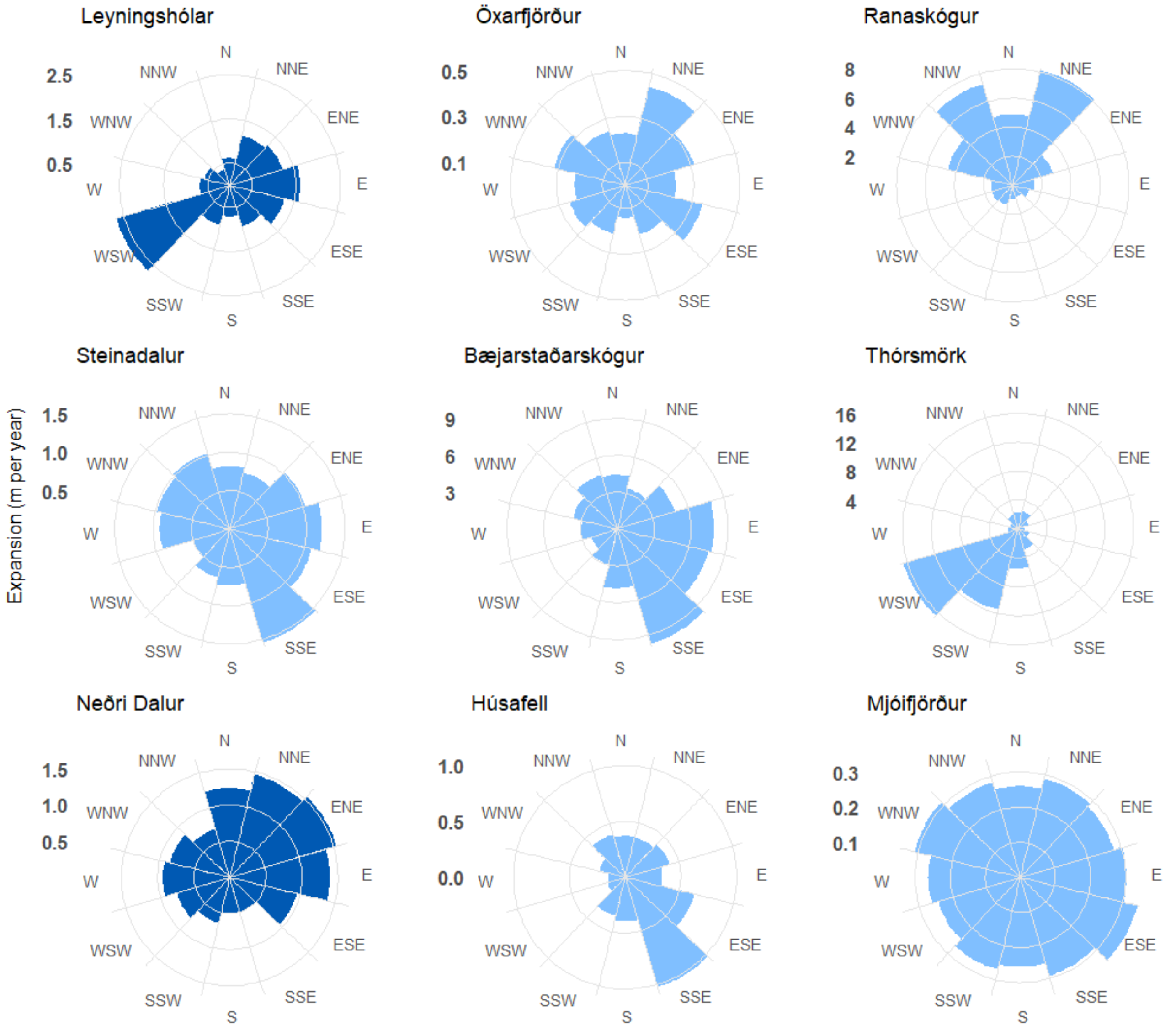


Figure 6. Nightingale Rose diagrams showing lateral woodland increase (m year^{-1}) in 12 cardinal directions for all nine study areas over the studied time period. Dark blue diagrams represent study areas that were covered in their entirety by the outlined area of interest, while light blue diagrams are areas where the woodland extents were cut due to lack of aerial photo data.

4.2 Natural colonization of mountain birch: drivers and spatial patterns (*Paper II*)

The results presented in *Paper II* show that the density of birch seedling originating from natural colonization differed among study areas: some sites had high densities of seedlings in size class I, implying active ongoing natural colonization, while others had low class I seedling densities, but high class II and III seedling densities, suggesting past colonization events, possibly reflecting temporal changes in conditions suitable for establishment (Miles 1973, Hanbury-Brown et al. 2022) or differences in timing of masting events.

The colonization patterns of the 10 study areas were highly variable (**Figure 7**). While a few reflected classic unimodal seed dispersal curves characteristic for anemochorous tree species (Levin et al. 2003), many sites either had equal densities across distances from the woodland edge, or peak densities further from the

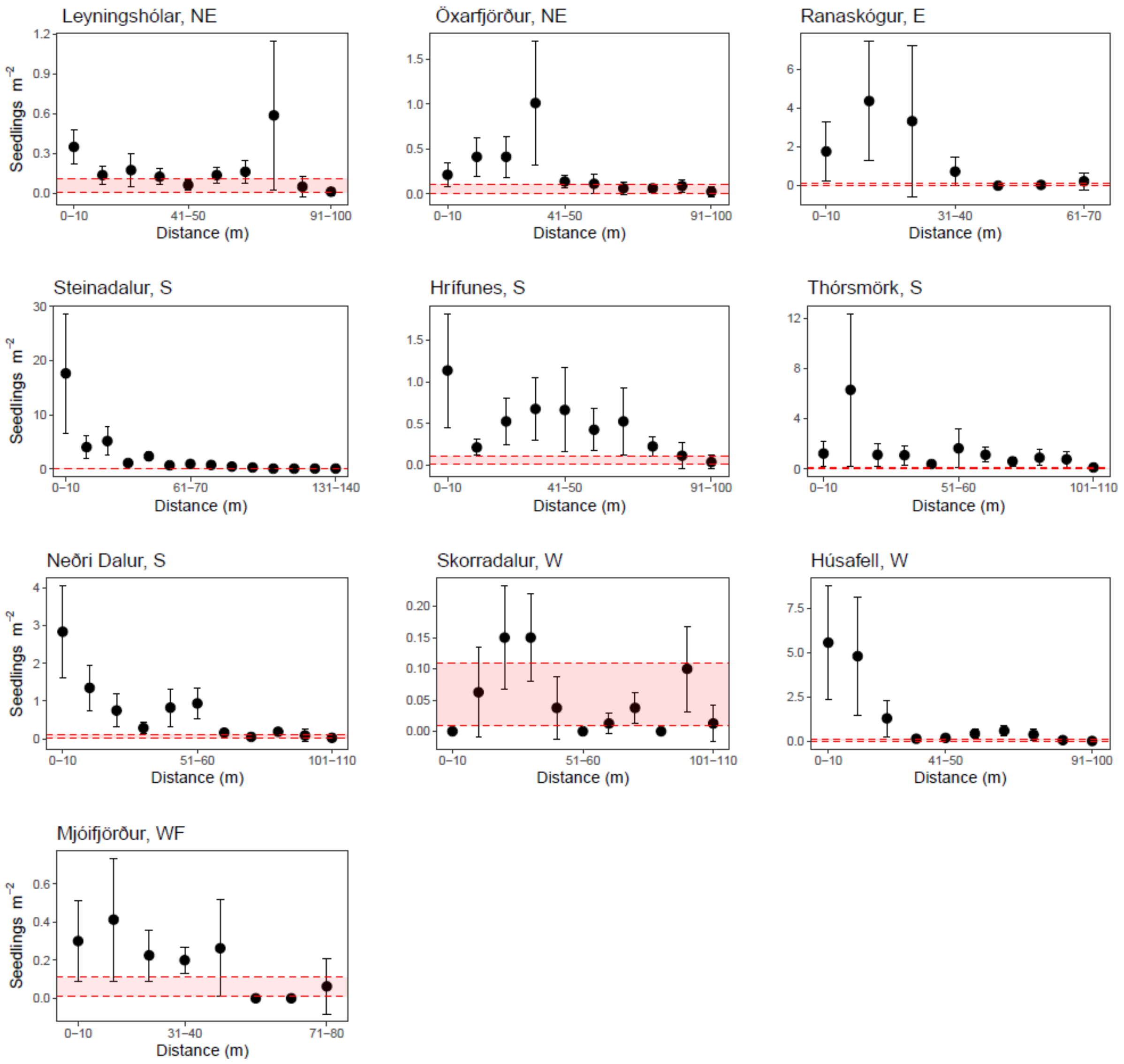


Figure 7. Site-specific relationships between seedling densities and distance from the woodland edge for the 10 study areas included in *Paper II*. The area in red falls within the success-criteria for natural colonization, i.e. from 100 to 1100 seedlings ha^{-1}, as defined by Gullet et al. (2023).

edge, i.e. at 40-80 m from the nearest standing seed source. Most of the study areas furthermore fulfilled the requirement of *successful natural colonization* (Gullet et al. 2023) at most distances, to a maximum of 140 meters from the woodland edge in one study area. In most of the study areas, seedling densities were highest 0-20 m from the woodland edge. These results support restoration strategies relying on natural colonization as being generally favourable for mountain birch.

Other than distance to seed source, colonization patterns were significantly associated with several of the tested ecological factors, both abiotic and biotic. Factors affecting seedlings in the smallest size class (class I), or what can be defined as the "early establishment phase" of natural colonization, included wind speed, dominant wind direction, soil type and the presence of domestic sheep. These factors act as environmental filters that seedlings must go through to establishment and survive to the following year (Marteinsdóttir et al. 2018, Hanbury-Brown et al. 2022). Another significant positive driver of birch colonization in the statistical models was the presence of catkin-bearing trees along the transects. These individual trees are postulated to have provided seed sources far from the woodland edge, and may explain the sudden high densities far from the woodland edge observed in several of the study areas. Few of the tested factors showed significant associations to densities of class I and II seedlings. This is most likely due to the fact that the environmental filters a seedling must go through to survive cannot be assessed on a single survey alone; these processes must be monitored over time to properly disentangle their effects on birch survival.

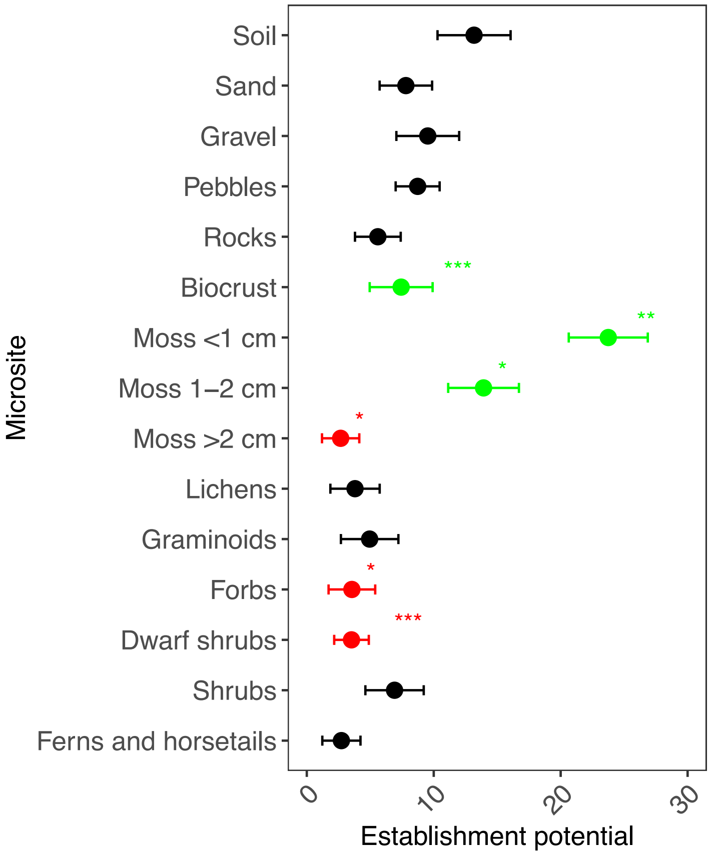


Figure 8. Establishment potential, calculated as the number of birch seedlings (mean ± SE) in a given microsite multiplied by the proportional aerial cover, for each microsite type included in *Paper I*. Numbers are based on the results from all 10 study areas. Color indicates whether the association was significantly positive (green), negative (red) or non-significant (black).

Another limiting factor to the potential of colonization of mountain birch was the availability of different microsites along transects. Seedling densities were highest in microsite types characterized by low-growing vegetation such as mosses <2 cm, and in biological soil crusts, or biocrusts, while they were lowest in microsites characterised by moss >2 cm and tall-growing vegetation, such as dwarf shrubs, forbs and grasses (**Figure 8**). Even with sufficient seed rain, establishment of birch seedlings is strongly limited by the availability of safe sites (Aradóttir & Halldórsson 2018). Interacting with the availability of seed, this effect can become more prominent with increased distance from the woodland edge, since seed rain for wind-borne species decreases exponentially with distance from nearest seed source (Willson 1993, Beckmann & Sullivan 2023).

4.3 Morphology of individual saplings and effective range of birch colonization (*Paper III*)

Distinct regional patterns of mountain birch morphology for saplings growing at the edge of the woodlands emerged from the results of *Paper III*, ranging from low-growing trees of basitonic growth in the Westfjords, to the straightest and tallest stems in the Eastern region of Iceland (**Figure 9**). This is a postulated effect of the increased sheltering from prevailing winds experienced by saplings growing at the edge of taller woodlands (i.e. in the North and East), as opposed to those growing at the edge of shrubby, low growing woodlands (Telewski 2012, Wu et al. 2018).

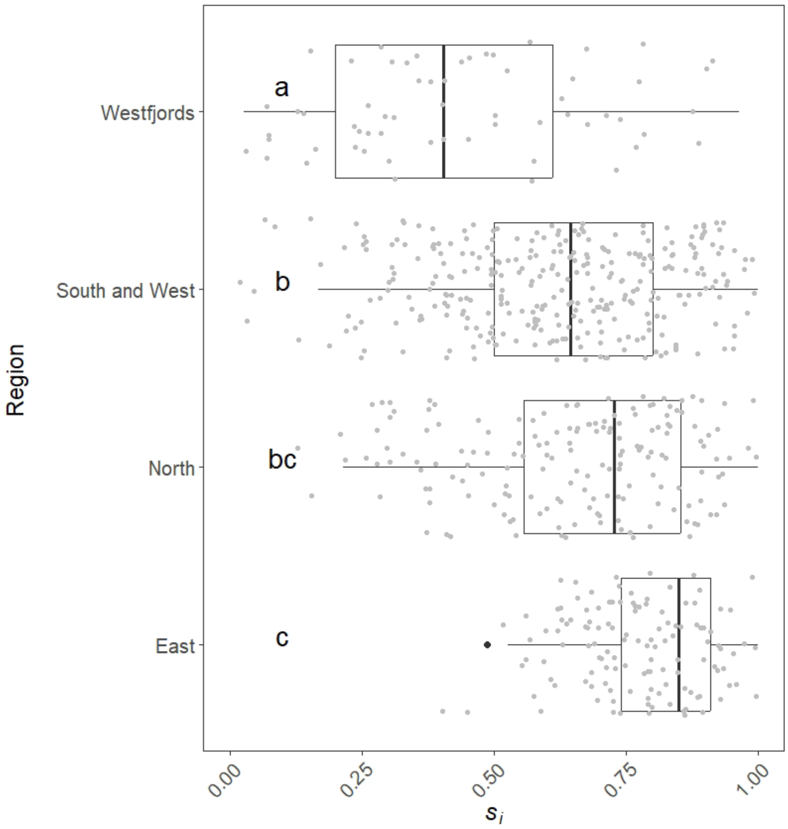


Figure 9. Morphology indices for the four regions in Iceland as described in *Paper III*. Letters denote significant differences between geographic regions (Bonferroni test, $p < 0.05$).

The morphology of individual saplings was affected by several local environmental factors, including mean annual wind speed and elevation. The height of surrounding woodlands facilitates sapling growth by providing shelter (Eränen & Kozlov 2006), while varying wind speeds and elevations can initiate local adaptations of trees and shrubs (Dobbert et al. 2021). The best fitting model only explained 42% of the variation, suggesting untested factors that could be at play, such as genetic adaptation to the environment (Espeland et al. 2017).

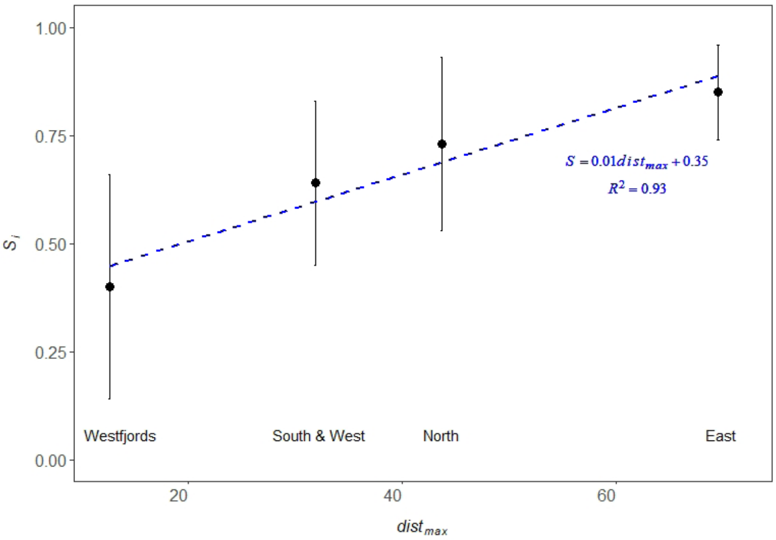


Figure 10. Correlation between $dist_{\max}$ and median (± SE) morphology index (S_i).

There were clear regional patterns for birch colonization when modelling natural colonization as a function of distance to seed source and dominant woodland height. Taller woodlands had a higher effective colonization range, or $dist_{\max}$, than low growing woodlands, with the relationship being significant and highly correlated (**Figure 10**).

Seed material and local environments are likely to shape both colonization patterns and morphology of individual birch saplings (McCallum et al. 2018, Arroyo-Rodríguez et al. 2023). Although there was a sheltering effect in this study, it generally wasn't very big, with the dominant woodland heights ranging only from 2 – 6 m in height (Snorrason et al. 2016). However, the difference in $dist_{\max}$ between regions suggest that there is a substantial difference in the effective colonization range of mountain birch depending on the height of the sheltering woodlands. This is important to consider when planting woodland isles for applied nucleation. The effective colonization range of mountain birch varied from a few meters to nearly 70 meters depending on the height of the surrounding woodlands, suggesting that for woodlands consisting of trees closer to 6 m in height, the planting distance of tree nuclei should be substantially longer than for woodlands with a 2 m high canopy. $dist_{\max}$ thus provides a very practical measure that can be implemented in applied nucleation of mountain birch woodlands, and for other target species in forest restoration in general.

4.4 A recruitment niche-based restoration framework for mountain birch (*Paper IV*)

The results of the seeding experiments presented in *Paper IV* were in agreement with the results of *Paper II* regarding microsite suitability for mountain birch. The highest densities of both emerging and surviving seedlings were found in moss <1 cm, biocrust and dead moss and grass. The same was the case for seedling survival, which was furthermore high in grass microsites in disturbed plots. As densities of emerged seedlings were also high and positively associated with other tall-growing microsite types such as forbs, dwarf shrubs and ferns and horsetails, this suggests a facilitating effect. Emergence was furthermore positively associated with the presence of biocrust, which can be considered a rare microsite type.

The results show that an active disturbance, i.e. cutting the existing vegetation layer followed by soil scarification, promoted both establishment and survival of seedlings in three out of the four habitat types, i.e. habitat types 1.3, 5.3, and 10.4, where the vegetation layer was typically dominated by thick moss swards, grasses and herbaceous plants. This was not the case for habitat type 10.8, which was dominated by dwarf shrubs and barren lands/low growing vegetation. Here, the vegetation may have had a facilitative effect through sheltering (Elgar et al. 2014, Andivia et al. 2017), which was no longer in effect after cutting the vegetation. Disturbance applied to habitat types characterized by tall vegetation such as grasses, forbs and dwarf shrubs, had a facilitating effect, i.e. significant positive associations with seedling densities. Positive associations were not observed for the same microsite types in undisturbed plots. These results imply that it is not vegetation height *per se* that negatively affects birch recruitment, but rather the thick moss swards associated with many subarctic habitats, preventing the birch seeds from reaching substrate appropriate for germination (Aradóttir & Halldórsson 2018, Vilmundardóttir et al. 2018). The fact that no seedlings were recorded in moss thicker than 2 cm in any of the targeted habitat types supports this. Reducing sward thickness can create a window of opportunity for birch establishment by improving the soil-seed interface necessary for germination (Collis-George & Hector 1966), which might be an effective restoration intervention in habitats dominated by thick mosses.

Negative associations, and generally low seedling densities, were observed in undisturbed habitats dominated by barren microsite types such as soil, gravel and rocks. This was expected, as although these microsites may be suitable for germination, they are susceptible to soil erosion (Jiao et al. 2009) and cryoturbation, which contribute to seedling mortality (Goulet 1995, Bianchi et al. 2019). The disturbed plots were often left covered in a layer of dead moss and grass, which had a significant positive effect on seedling emergence and survival. Dead moss and grass has likely facilitated recruitment by protecting seedlings from frost heaving on bare-ground microsites (Goulet 1995, Wu et al. 2024), and thus it might be more beneficial not to remove litter in assisted natural regeneration but rather leave it for enhanced seedling survival.

Restoration success, i.e. whether there was observed emergence and survival in plots of different treatments, was significantly different among habitat types and influenced by the applied disturbance, but not by seed source. However, in the long-term, the choice of seed source in restoration is important to consider, because of potential adaptation to local environments (Espeland et al. 2017). Furthermore, introduced genetic materials may outcompete local genotypes, leading to the spread of a superior alien genotype (Bischoff et al. 2010). Although our results showed no significant effect of seed source material on neither survival nor restoration success, there were significantly higher densities of emerged seedlings of local seed material. The effect of these higher densities can possibly be detected in future surveys of the experiments. Therefore, additional long-term monitoring is necessary to conclude on the effect of seed source, and the long-term outcome of these experiments in general (Gann et al. 2019, Lindenmayer 2020).

Collectively, this study outlines the environmental filters of the different phases of mountain birch establishment, and how these can be altered by different management decisions and restoration interventions (**Figure 11**). There are, however, still several factors that need to be studied further in this context, such as the high differences in germination and survival among study areas, which were substantially higher in Gunnarsholt than in the two other study areas for all habitat types. There are several site-specific factors that may have contributed to this difference, including annual precipitation and temperature (Ranno et al. 2021) and soil conditions, including moisture contents (Lidman et al. 2023) and dust deposition, which differed substantially between the study areas (Kullman 1986, Arnalds 2010).

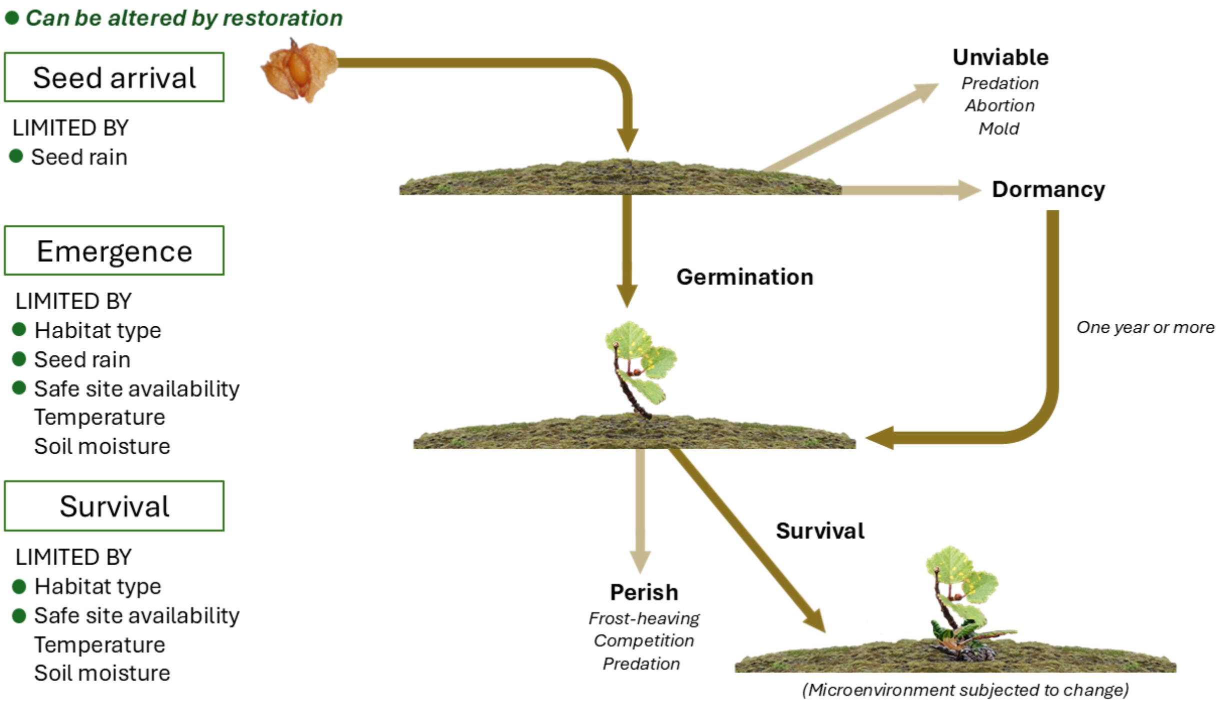


Figure 11. Conceptual model building on the results found in *Paper IV* on how a species environment can be altered by different restoration interventions to better match their recruitment niche.

4.5 Implications for ecological restoration

The urgent need to upscale restoration of natural ecosystems, including subarctic mountain birch woodlands, emphasises the necessity of understanding the patterns and driving forces of successful ecosystem recovery and expansion. In this thesis, I worked at various scales to understand how an ecosystem expands through natural processes and explored how this can be aided by a suite of restoration measures. Birches (*Betula* spp.) have a wide distribution in the Northern hemisphere, both in mixed woodlands and as the dominant tree species (Beck et al. 2016). Despite ecological differences amongst different species of birch, they share many of the same requirements for establishment and survival (Willis et al. 2015, Holmström et al. 2017, Lidman et al. 2023). Thus, the results of this thesis can aid in birch woodland restoration not only in the Icelandic context, but in other parts of the Northern hemisphere.

This study has implications for various woodland restoration strategies on the passive-active continuum (Chazdon et al. 2021); The results of *Paper I* and *Paper II* suggest that passive or low-intensity restoration strategies, such as fencing and initial revegetation measures, can be effective for mountain birch woodland restoration. However, these can only be considered suitable strategies if the ecological requirements of the target species are present in the given environments. More active restoration strategies such as applied nucleation and assisted natural regeneration will accelerate recovery and expansion, and can be optimized by spatial arrangements, habitat suitability assessment and improvements of the microenvironment, as seen in *Paper III* and *IV*. My results furthermore imply that successful restoration requires planning on both a landscape and site level, and ideally also taking the microsite level into consideration.

The mountain birch woodlands in Iceland have suffered extensive degradation since the human settlement of Iceland (Sigurðsson 1977) and an improved understanding of their establishment in space and time can aid large-scale restoration to accomplish ambitious national restoration goals. Future expansion of the birch woodlands through restoration will benefit native biodiversity which is crucial in times where alien plant species threaten native ecosystems, thus greatly reducing and even eradicating native biodiversity (Vetter et al. 2018, Wasowicz et al. 2025). Expansion of the birch woodlands will also improve ecosystem services, including contribution to national climate change mitigation goals, as an immense amount of carbon is stored in birch woodland soils in Iceland (Sánchez et al. 2025). Furthermore, spatially targeted birch woodland restoration can aid in protecting settlements from volcanic ash and dust storms, which is an important issue to address both economy and health wise (Arnalds et al. 2016).

4.6 Recommendations for restoring subarctic mountain birch woodlands

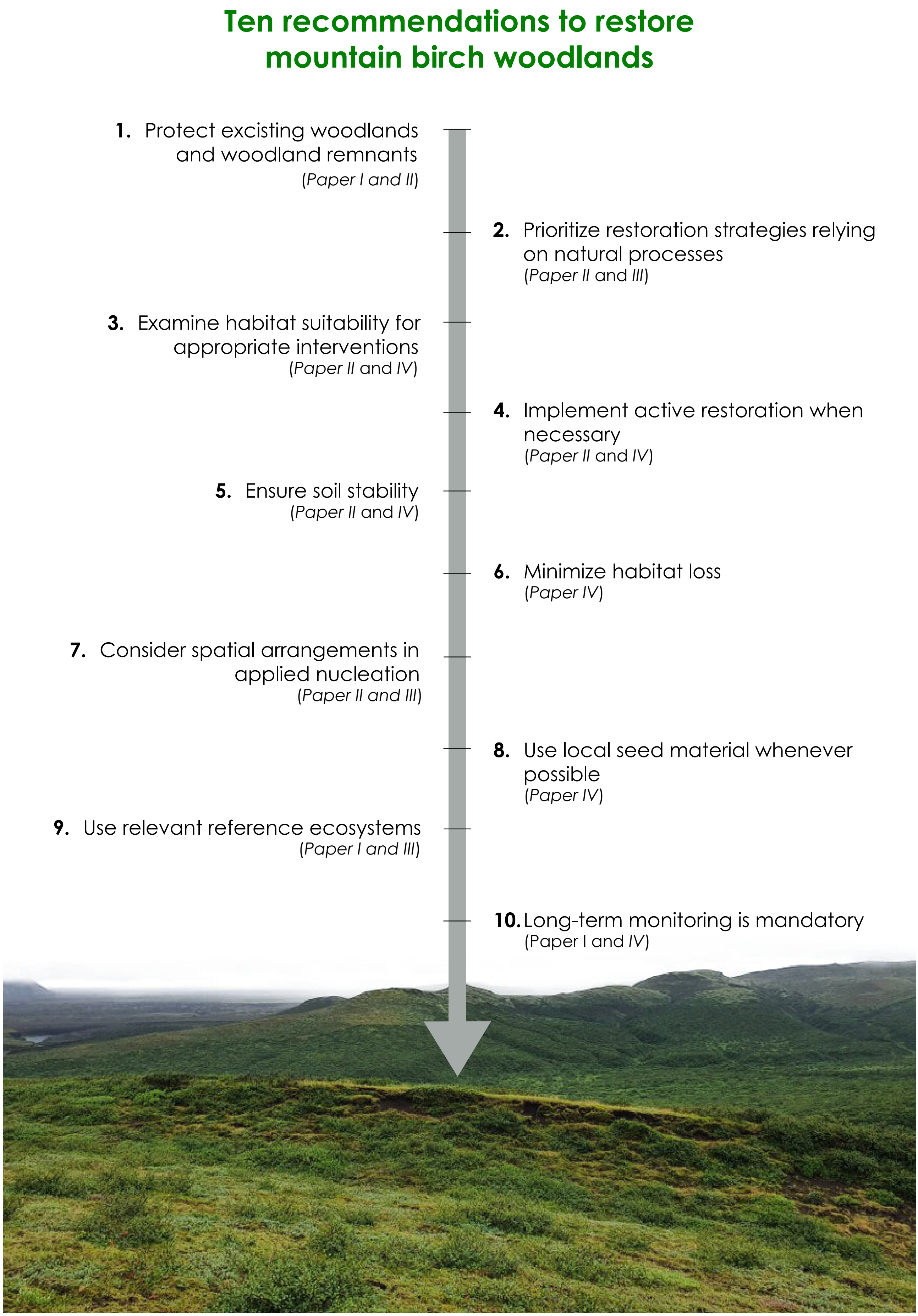
Based on current results in the context of existing published literature on mountain birch, it is possible to derive some general recommendations on the practices of mountain birch woodland restoration (**Figure 12**). These recommendations are grounded in the International Principles and Standards for Ecological Restoration by the Society of Ecological Restoration (SER, Gann 2019).

4.6.1 Protect existing woodlands and woodland remnants

Existing woodlands and woodland remnants provide valuable seed sources for the upscaling of restoration through natural colonization. Thus, an important first step in mountain birch woodland restoration is to protect the already existing woodlands and woodland remnants from livestock grazing and other anthropogenic disturbances. Although it may be necessary to reintroduce mountain birch in some areas to upscale woodland restoration, the ecological properties of existing ancient woodlands cannot be replaced by new plantings. Incipient mountain birch populations may take decades to become self-sustainable (Óskarsdóttir et al. 2022), and reproductive maturity varies a lot in mountain birch, but is generally thought to happen when the trees are 10-15 years old (Perala & Alm 1990). Thus, existing woodlands and woodland remnants, and even single catkin-bearing trees, can act as important seed sources for low-intensity or passive restoration strategies and should therefore be protected.

4.6.2 Prioritize restoration strategies relying on natural processes

The results of *Paper II* and *III* indicate a good potential of birch woodland expansion in Iceland through natural colonization. Restoration frameworks that focus on utilizing natural processes for recovery and expansion should therefore be prioritized in the context of mountain birch woodlands, as these strategies are generally more cost-effective (Douterlungne et al. 2015, Crouzeilles et al. 2020) and often result in more heterogenous and resilient ecosystems than planted woodlands (Chazdon & Guariguata 2016, Bauld et al. 2023). Understanding of the factors that facilitate and prevent colonization can help to assess the possibility of relying solely on natural colonization, or if interventions are needed to promote colonization (Elgar et al. 2014).



Ten recommendations to restore mountain birch woodlands

1. Protect excisting woodlands and woodland remnants (*Paper I and II*)
2. Prioritize restoration strategies relying on natural processes (*Paper II* and *III*)
3. Examine habitat suitability for appropriate interventions (*Paper II* and *IV*)
4. Implement active restoration when necessary (*Paper II* and *IV*)
5. Ensure soil stability (*Paper II* and *IV*)
6. Minimize habitat loss (*Paper IV*)
7. Consider spatial arrangements in applied nucleation (*Paper II and III*)
8. Use local seed material whenever possible (*Paper IV*)
9. Use relevant reference ecosystems (*Paper I and III*)
10. Long-term monitoring is mandatory (Paper I and *IV*)

Figure 12. Conceptual figure of key recommendations to restore mountain birch woodlands derived from the results of this thesis.

4.6.3 Examine habitat suitability for appropriate interventions

The success of all terrestrial ecosystem restoration depends in part on the suitability of targeted habitats for recruitment (Griffiths et al. 2011, Baguette et al. 2012). Both when relying on existing seed sources of mountain birch, or planting of tree clusters (applied nucleation) to overcome dispersal limitations, the outcome depends on the suitability of surrounding habitats for birch recruitment. This, as my results have shown, includes availability of suitable microsites for seedling establishment, topography and local environments (such as soil type, topography, disturbance regime). Interventions to promote establishment, survival and future ecosystem expansion should be determined based on assessment of the suitability of the restoration area.

4.6.4 Implement active restoration when necessary

Restoration interventions may facilitate natural colonization and natural regeneration that is impeded, either by anthropogenic disturbances (Myers-Smith et al. 2011) or unsuitable habitats within and around the woodlands (Griffiths et al. 2011) as was found in *Papers II* and *IV*. Where such impediments exist, natural processes cannot drive restoration on their own, and some active efforts are needed. These may include measures such as fencing for grazing protection, revegetation, or targeted disturbances, all of which can promote natural colonization on a given site by increasing safe site availability. This is, however, far from necessary for most sites, and thus active restoration should be implemented only when necessary.

4.6.5 Ensure soil stability

The lack of birch seedlings found in microsites common to eroded soils demonstrate how challenging mountain birch recruitment is in soils susceptible to frost heaving and erosion. This is going to be an unavoidable challenge to overcome in Iceland, as 45% of terrestrial lands in Iceland are currently comprised of landscapes characterised by such soils (Arnalds et al. 2023). Therefore, a necessary first step of birch woodland restoration in many areas will be to stabilize eroding soils. This can comprise fertilization, with or without seeding with grasses, a practice that has been carried out in Iceland for decades (Greipsson & El-Mayas 1999) but could also involve assisted dispersal of biological soil crusts (Bowker 2007, Ficko et al. 2023), which has proven to promote establishment of birch.

4.6.6 Minimize habitat loss

The large-scale birch woodland restoration efforts pledged by the Icelandic government will inevitably cause loss of other tundra habitat types that are important for subarctic ecosystem functioning (Myers-Smith et al. 2011, Moyano et al. 2024). Therefore, when planning a birch woodland restoration project, it is crucial to consider the possible losses of important habitats this may involve, including key habitat types for ground nesting birds (Pálsdóttir et al. 2022) and habitats harbouring threatened plant species (Reji Chacko et al. 2023).

Furthermore, as my results show, most habitat types dominated by tall-growing vegetation, including some heathland types, will need an active implemented disturbance to be suitable for spontaneous establishment of mountain birch, or via direct seeding. Such costs can be lowered by focussing on habitat types where birch is likely to expand naturally without interventions, where applied nucleation is viable or where revegetation to ensure soil stability is needed to promote natural colonization.

4.6.7 Consider spatial arrangements in applied nucleation

The results of *Papers II* and *III* indicate that the effective spatial range for natural colonization of birch depends on the dominant canopy height of the woodlands. This measurement can be used directly in a restoration framework, to determine the optimal distance between planted woodland isles in applied nucleation (Corbin & Holl 2012). This is an important aspect for optimal spatial arrangement in restoration to make good use of available resources and the local conditions which should always be considered in active restoration frameworks (McCallum et al. 2018). The distance between planted woodland isles should depend on the height and stature of the trees for sheltering and effective dispersal (Eränen & Koslov 2006, Greenwood et al. 2014), which is a product of both local environments and genetics (Dubois et al. 2020). In practice, the results suggest that woodlands with an effective spatial range of 10 meters should be placed closer than woodlands with a range of 70 meters.

4.6.8 Use local seed material whenever possible

Although there was no evidence of enhanced survival of individual birch seedlings or restoration success when using local seed material in *Paper IV*, local seed sources did have a positive effect on density of emerged seedlings across all study areas. This implies some level of local environmental adaptation which could result in an increased long term restoration success. The resulting effect of this can possibly be detected in future surveys of the experiments, which would be needed to conclude on this.

Other reasons for using local plant material include genetic adaptation to local environments (Espeland et al. 2017) and for avoiding the spread of an alien genotype that may outcompete the local (Bischoff et al. 2010). Possible exceptions are where there exists genetic isolation, and including more genetic diversity could benefit a populations fitness (Jadwiszczak et al. 2017).

4.6.9 Use relevant reference ecosystems

Woodland ecosystems can differ immensely in their ecology across geographical regions, including species composition of both trees and the understory vegetation, overstory height of the woodlands, soil properties and hydrology (Suganuma & Durigan 2015, Gann et al. 2019). These factors can affect various aspects of restoration, including the patterns and general potential of natural colonization, and the morphology of individual trees growing at the edge of the woodlands. Thus, it is important to account for ecological differences in structural woodland complexity that may affect rates, patterns and processes of woodland expansion (Stockton & Gillette 1990, Jónsson 2004, Óskarsdóttir et al. 2022). This should be done at regional scale at minimum, and account for genetic adaptation of local populations.

4.6.10 Long-term monitoring is mandatory

Monitoring is an often-overlooked step in the restoration planning process (Lindenmayer 2020). It is, however, a very important step, as it allows for an evaluation on whether or not an implemented strategy has worked (Gann et al. 2019). Monitoring and evaluation is particularly important in order to guide future restoration of forests and woodlands, because of the long timeframe of recovery for these ecosystems. Longer-term monitoring of field experiments elucidating the different processes of birch woodland restoration, such as those forming the basis of *Paper I* and *IV,* is therefore important. Furthermore, remote sensing offers a valuable opportunity for large-scale monitoring, including assessments of historical aerial photos as was done in *Paper I* of this thesis, satellite images, or drone images for a more detailed current-state assessment (Dickinson et al. 2016, Reis et al. 2019, Qiu et al. 2023).

5. Conclusions

The overall aim of this thesis was to increase the understanding of the patterns, processes and drivers of mountain birch establishment and their implications for restoration through studies on various spatial and temporal scales.

Analysis of spatio-temporal patterns and rates of birch woodland expansion provided realistic time frames of the speed of woodland expansion from existing woodlands and woodland remnants. The results indicate that protection from sheep grazing, and revegetation of eroded areas, can benefit birch woodland expansion, implying that low intensity restoration efforts can induce woodland expansion. The most limiting factor for mountain birch colonization on a site scale was proximity to a seed source, including single catkin-bearing trees. The birch did, however, establish at high densities further from seed sources than was anticipated, if other conditions for colonization were optimal. Where dispersal limitations exist, it is important to consider spatial arrangements of introduced seed sources for optimal natural colonization. Natural colonization was also driven by local environmental factors, such as soil type and stability, direction of dry prevailing winds, disturbance regime and the availability of suitable microsites for seedling establishment. The most suitable microsites for mountain birch establishment across a variety of habitat types were found to be low-growing mosses, biological soil crusts and litter, whereof the occurrence of litter was mainly facilitated by an applied disturbance. Thus, where the availability of suitable microsites is low, restoration initiatives appropriate for the local conditions can be applied to increase the share of suitable microsites, and facilitate birch establishment. By utilizing land classification data, such as habitat types, and defining their restoration potential based on the availability of suitable microsites, it may be possible to predict future colonization on a nationwide scale. Furthermore, it can aid in identifying so-called “restoration hotspots” where passive and low-intensity strategies are likely to be most successful, and where active interventions are needed to induce recovery and expansion.

Studying the patterns of birch establishment and birch woodland expansion on different scales, provides insights into the processes and requirements of a key woodland tree species in the subarctic. This lays a foundation that can be used to guide the planning and implementation of birch woodland restoration. The results of this thesis can furthermore contribute to strategies for restoration of ecosystems involving other birch species, both in ecosystems where they act as early colonizers in mixed forests, and as dominant species in woodlands at northern high latitudes.

6. Future work

Although the results of this doctoral thesis fill some essential knowledge gaps and provide key information on the patterns and processes of mountain birch colonization in space and time, more research is needed on the subject, particularly on the practical implications for restoration. It is proposed that future research on the topic focus on:

- Experimental investigation of the efficiency of active restoration methods that can enhance the potential of birch establishment from existing seed sources on a large scale, such as water ponding, soil scarification and periodic regenerative grazing.
- Controlled experiments in different land cover classification units, e.g. habitat types, to quantify the enhancing/impeding effect of varying grazing pressures on birch establishment. This is crucial to determine where grazing should be controlled, introduced, or excluded altogether to facilitate restoration of birch.
- Linking the spatio-temporal expansion of birch woodlands directly to relevant environmental factors to determine what has, and what will, determine birch woodland expansion in different climate and management scenarios.
- Investigating the patterns of masting for mountain birch, and the possible environmental drivers of seed quality and dormancy. This is an important factor to consider when planning for and estimating the efficiency of passive restoration projects involving birch.
- Experiments on restoration of moss and biological soil crust. Implementing this as a first step in birch woodland restoration will prevent further degradation through soil erosion and cryoturbation and thus enhance birch establishment and survival.
- Developing habitat suitability models on a national scale for Iceland, for (I) the potential of birch woodland expansion through natural colonization, and (II) highlighting hotspots for active restoration with limited efforts/interventions.
- Synthesizing all available knowledge (both ecological and socioeconomic) and develop guidelines on sustainable birch woodland restoration in the subarctic for scientists, practitioners, landowners and governmental institutions.

7. Funding

This work was funded by the Icelandic Government's Strategic Research and Development Program for Societal Challenges, 2020-2023 (grant number 200090-5601-5603). Additional funding was provided by the Agricultural University of Iceland and the I.F. Lemvigh-Müller Foundation.

8. References

Andivia, E., Villar-Salvador, P., Tovar, L., Rabasa, S., & Rey Benayas, J. M. (2017). Multiscale assessment of woody species recruitment in Mediterranean shrublands: Facilitation and beyond. *Journal of Vegetation Science*, *28*(3), 639–648. https://doi.org/10.1111/jvs.12520

Aradóttir, Á. L. (2004). Does the Nootka lupine facilitate or impede colonization and growth of native birch in Iceland? In: *E. van Santen & G. D. Hill (Eds.), Wild and Cultivated Lupins from the Tropics to the Poles. Proceedings of the 10th Interannual Lupin Conference Laugarvatn, Iceland, June 19-24, 2022*, 184–190.

Aradóttir, Á. L. (2007). Restoration of birch and willow woodland on eroded areas. In: *Halldórsson, G., Oddsdóttir, E. S., & Eggertson, Ó. (Eds.) Effects of afforestation on ecosystems, landscape and rural development*, 67-74. Nordic Council of Ministers, Copenhagen, Denmark.

Aradóttir, Á. L. & Arnalds, Ó. (2001). Ecosystem degradation and restoration of birch woodlands in Iceland. In: *Nordic Mountain Birch Ecosystems, Wielgolaski, F.E. (Eds.). UNESCO, Paris, and Parthenon Publishing, Carnforth, 2001*, chap. 24.

Aradóttir, Á. L., & Halldórsson, G. (2018). Colonization of woodland species during restoration: Seed or safe site limitation? *Restoration Ecology*, *26*, S73–S83. https://doi.org/10.1111/rec.12645

Aradóttir, Á. L., Petursdottir, T., Halldorsson, G., Svavarsdottir, K., & Arnalds, O. (2013). Drivers of ecological restoration: Lessons from a century of restoration in Iceland. *Ecology and Society*, *18*(4), art33. https://doi.org/10.5751/ES-05946-180433

Aradóttir, Á. L., 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*(1–2), 179–186. https://doi.org/10.1016/S0168-1923(96)02385-4

Arnalds, A. (1987). Ecosystem disturbance in Iceland. *Arctic and Alpine Research*, *19*(4), 508. https://doi.org/10.2307/1551417

Arnalds, Ó. (2010). Dust sources and deposition of aeolian materials in Iceland. *Icelandic Agricultural Sciences, 23*, 3-21.

Arnalds, Ó., & Barkarson, B. H. (2003). Soil erosion and land use policy in Iceland in relation to sheep grazing and government subsidies. *Environmental Science and Policy, 6*, 105-113. https://doi.org/10.1016/S1462-9011(02)00115-6

Arnalds, Ó., Dagsson-Waldhauserova, P., & Olafsson, H. (2016). The Icelandic volcanic aeolian environment: Processes and impacts — A review. *Aeolian Research*, *20*, 176–195. https://doi.org/10.1016/j.aeolia.2016.01.004

Arnalds, Ó., Marteinsdóttir, B., Brink, S. H., & Þórsson, J. (2023). A framework model for current land condition in Iceland. *PLOS ONE*, *18*(7), e0287764. https://doi.org/10.1371/journal.pone.0287764

Arneth, A., F. Denton, F. Agus, A. Elbehri, K. Erb, B. Osman Elasha, M. Rahimi, M. Rounsevell, A. Spence & R. Valentini (2019). Framing and Context. In: *Climate Change and Land: an IPCC special report on climate change, desertification, land degradation, sustainable land management, food security, and greenhouse gas fluxes in terrestrial ecosystems* [P.R. Shukla, J. Skea, E. Calvo Buendia, V. Masson-Delmotte, H. O. Pörtner, D.C. Roberts, P. Zhai, R. Slade, S. Connors, R. van Diemen, M. Ferrat, E. Haughey, S. Luz, S. Neogi, M. Pathak, J. Petzold, J. Portugal Pereira, P. Vyas, E. Huntley, K. Kissick, M. Belkacemi, J. Malley, (eds.)].

Arroyo-Rodríguez, V., Rito, K. F., Farfán, M., Navia, I. C., Mora, F., Arreola-Villa, F., Balvanera, P., Bongers, F., Castellanos-Castro, C., Catharino, E. L. M., Chazdon, R. L., Dupuy-Rada, J. M., Ferguson, B. G., Foster, P. F., González-Valdivia, N., Griffith, D. M., Hernández-Stefanoni, J. L., Jakovac, C. C., Junqueira, A. B., … Martínez-Ramos, M. (2023). Landscape-scale forest cover drives the predictability of forest regeneration across the Neotropics. *Proceedings of the Royal Society B: Biological Sciences*, *290*(1990), 20222203. https://doi.org/10.1098/rspb.2022.2203

Atkinson, M. D. (1992). *Betula Pendula* Roth (*B. Verrucosa* Ehrh.) and *B. Pubescens* Ehrh. *The Journal of Ecology*, *80*(4), 837–870. https://doi.org/10.2307/2260870

Baguette, M., Blanchet, S., Legrand, D., Stevens, V. M., & Turlure, C. (2013). Individual dispersal, landscape connectivity and ecological networks. *Biological Reviews*, *88*(2), 310–326. https://doi.org/10.1111/brv.12000

Barnosky, A. D., Hadly, E. A., Bascompte, J., Berlow, E. L., Brown, J. H., Fortelius, M., Getz, W. M., Harte, J., Hastings, A., Marquet, P. A., Martinez, N. D., Mooers, A., Roopnarine, P., Vermeij, G., Williams, J. W., Gillespie, R., Kitzes, J., Marshall, C., Matzke, N., … Smith, A. B. (2012). Approaching a state shift in Earth's biosphere. *Nature*, *486*(7401), 52–58. https://doi.org/10.1038/nature11018

Barrio, I. C., Hik, D. S., Thórsson, J., Svavarsdóttir, K., Marteinsdóttir, B., & Jónsdóttir, I. S. (2018). The sheep in wolf's clothing? Recognizing threats for land degradation in Iceland using state-and-transition models. *Land Degradation & Development*, *29*(6), 1714–1725. https://doi.org/10.1002/ldr.2978

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*(8), e14004. https://doi.org/10.1111/rec.14004

Beck, P., Caudullo, G., de Rigo, D., Tinner, W., 2016. *Betula pendula*, *Betula pubescens* and other birches in Europe: distribution, habitat, usage and threats. In: San-Miguel-Ayanz, J., de Rigo, D., Caudullo, G., Houston Durrant, T., Mauri, A. (Eds.), *European Atlas of Forest Tree Species*. Publ. Off. EU, Luxembourg, pp. e010226

Beckman, N. G., & Sullivan, L. L. (2023). The causes and consequences of seed dispersal. *Annual Review of Ecology, Evolution, and Systematics*, *54*(1), 403–427. https://doi.org/10.1146/annurev-ecolsys-102320-104739

Bianchi, E., Bugmann, H., & Bigler, C. (2019). Early emergence increases survival of tree seedlings in Central European temperate forests despite severe late frost. *Ecology and Evolution*, *9*(14), 8238–8252. https://doi.org/10.1002/ece3.5399

Bischoff, A., Steinger, T., & Müller-Schärer, H. (2010). The importance of plant provenance and genotypic diversity of seed material used for ecological restoration. *Restoration Ecology*, *18*(3), 338–348. https://doi.org/10.1111/j.1526-100X.2008.00454.x

Boeken, B. R. (2018). Competition for microsites during recruitment in semiarid annual plant communities. *Ecology*, *99*(12), 2801–2814. https://doi.org/10.1002/ecy.2484

Borda-Niño, M., Meli, P., & Brancalion, P. H. S. (2020). Drivers of tropical forest cover increase: A systematic review. *Land Degradation & Development*, *31*(11), 1366–1379. https://doi.org/10.1002/ldr.3534

Bowker, M. A. (2007). Biological soil crust rehabilitation in theory and practice: An underexploited opportunity. *Restoration Ecology, 15(1)*, 13-23. https://doi.org/10.1111/j.1526-100X.2006.00185.x

Bryn, A., Dourojeanni, P., Hemsing, L. Ø., & O'Donnell, S. (2013). A high-resolution GIS null model of potential forest expansion following land use changes in Norway. *Scandinavian Journal of Forest Research*, *28*(1), 81–98. https://doi.org/10.1080/02827581.2012.689005

Böcher, T. W. (1977). Birch woodlands and tree growth in southern Greenland. *Ecography*, *2*(4), 218–221. https://doi.org/10.1111/j.1600-0587.1979.tb01292.x

Cargill, S. M., & Chapin, F. S. (1987). Application of successional theory to tundra restoration: A review. *Arctic and Alpine Research*, *19*(4), 366–372. https://doi.org/10.2307/1551401

Chapin, F. S., Matson, P. A., & Vitousek, P. M. (2011). Principles of terrestrial ecosystem ecology. Springer New York. https://doi.org/10.1007/978-1-4419-9504-9

Chazdon, R. L., Bodin, B., Guariguata, M., Lamb, D., Walder, B., Chokkalingam, U. & Shono, K. (2017). *Partnering with nature: The case for natural regeneration in forest and landscape restoration*. FERI Policy Brief. Montreal, Canada.

Chazdon, R. L., & Guariguata, M. R. (2016). Natural regeneration as a tool for large-scale forest restoration in the tropics: Prospects and challenges. *Biotropica*, *48*(6), 716–730. https://doi.org/10.1111/btp.12381

Chazdon, R. L., Falk, D. A., Banin, L. F., Wagner, M., J. Wilson, S., Grabowski, R. C., & Suding, K. N. (2021). The intervention continuum in restoration ecology: Rethinking the active–passive dichotomy. *Restoration Ecology*, e13535. https://doi.org/10.1111/rec.13535

Chughtai, A. H., Abbasi, H., & Karas, I. R. (2021). A review on change detection method and accuracy assessment for land use land cover. *Remote Sensing Applications: Society and Environment*, *22*, 100482. https://doi.org/10.1016/j.rsase.2021.100482

Cole, R. J., Holl, K. D., Keene, C. L., & Zahawi, R. A. (2011). Direct seeding of late-successional trees to restore tropical montane forest. *Forest Ecology and Management*, *261*(10), 1590–1597. https://doi.org/10.1016/j.foreco.2010.06.038

Collis-George, N., & Hector, J. B. (1966). Germination of seeds as influenced by matric potential and by area of contact between seed and soil water. *Soil Research, 4*(2), 145-164.

Corbin, J. D., & Holl, K. D. (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

Corbin, J. D., Robinson, G. R., Hafkemeyer, L. M., & Handel, S. N. (2016). A long-term evaluation of applied nucleation as a strategy to facilitate forest restoration. *Ecological Applications*, *26*(1), 104–114. https://doi.org/10.1890/15-0075

Crouzeilles, R., Beyer, H. L., Monteiro, L. M., Feltran-Barbieri, R., Pessôa, A. C. M., Barros, F. S. M., Lindenmayer, D. B., Lino, E. D. S. M., Grelle, C. E. V., Chazdon, R. L., Matsumoto, M., Rosa, M., Latawiec, A. E., & Strassburg, B. B. N. (2020). Achieving cost-effective landscape-scale forest restoration through targeted natural regeneration. *Conservation Letters*, *13*(3), e12709. https://doi.org/10.1111/conl.12709

Crouzeilles, R., Ferreira, M. S., Chazdon, R. L., Lindenmayer, D. B., Sansevero, J. B. B., Monteiro, L., Iribarrem, A., Latawiec, A. E., & Strassburg, B. B. N. (2017). Ecological restoration success is higher for natural regeneration than for active restoration in tropical forests. *Science Advances*, *3*(11), e1701345. https://doi.org/10.1126/sciadv.1701345

de Wit, H. A., Bryn, A., Hofgaard, A., Karstensen, J., Kvalevåg, M. M., & Peters, G. P. (2014). Climate warming feedback from mountain birch forest expansion: Reduced albedo dominates carbon uptake. *Global Change Biology*, *20*(7), 2344–2355. https://doi.org/10.1111/gcb.12483

Dickinson, Y., Pelz, K., Giles, E., & Howie, J. (2016). Have we been successful? Monitoring horizontal forest complexity for forest restoration projects. *Restoration Ecology*, *24*(1), 8–17. https://doi.org/10.1111/rec.12291

Dobbert, S., Pape, R., & Löffler, J. (2021). How does spatial heterogeneity affect inter- and intraspecific growth patterns in tundra shrubs? *Journal of Ecology*, *109*(12), 4115–4131. https://doi.org/10.1111/1365-2745.13784

Douterlungne, D., Ferguson, B. G., Siddique, I., Soto-Pinto, L., Jímenez-Ferrer, G., & Gavito, M. E. (2015). Microsite determinants of variability in seedling and cutting establishment in tropical forest restoration plantations: Microsite variability in restoration trials. *Restoration Ecology*, *23*(6), 861–871. https://doi.org/10.1111/rec.12247

Dubois, H., Verkasalo, E., & Claessens, H. (2020). Potential of birch (*Betula pendula* Roth and *B. pubescens* Ehrh.) for forestry and forest-based industry sector within the changing climatic and socio-economic context of western Europe. *Forests*, *11*(3), 336. https://doi.org/10.3390/f11030336

Duncan, R. P., Diez, J. M., Sullivan, J. J., Wangen, S., & Miller, A. L. (2009). Safe sites, seed supply, and the recruitment function in plant populations. *Ecology*, *90*(8), 2129–2138. https://doi.org/10.1890/08-1436.1

Elgar, A. T., Freebody, K., Pohlman, C. L., Shoo, L. P., & Catterall, C. P. (2014). Overcoming barriers to seedling regeneration during forest restoration on tropical pasture land and the potential value of woody weeds. *Frontiers in Plant Science*, *5,* 200. https://doi.org/10.3389/fpls.2014.00200

Eränen, J. K., & Kozlov, M. V. (2006). Physical sheltering and liming improve survival and performance of mountain birch seedlings: A 5-year study in a heavily polluted industrial barren. *Restoration Ecology*, *14*(1), 77–86. https://doi.org/10.1111/j.1526-100X.2006.00107.x

Espeland, E. K., Emery, N. C., Mercer, K. L., Woolbright, S. A., Kettenring, K. M., Gepts, P., & Etterson, J. R. (2017). Evolution of plant materials for ecological restoration: Insights from the applied and basic literature. *Journal of Applied Ecology*, *54*(1), 102–115. https://doi.org/10.1111/1365-2664.12739

ESRI 2023. ArcGIS Pro Desktop: Release 3.1.

European Commission (2024). EU Nature Restoration Regulation. https://environment.ec.europa.eu/topics/nature-and-biodiversity/nature-restoration-regulation_en. Accessed the 6th of August 2025.

Eysteinsson, T., & Aradóttir, Á. L. (2004). Restoration of birch woodlands in Iceland. In J. Stanturf & P. Madsen (Eds.), *Restoration of Boreal and Temperate Forests* (Vol. 20047067, pp. 195–209). CRC Press. https://doi.org/10.1201/9780203497784.pt5

Ferreira, M. C., De Oliveira Cordeiro, A. O., Sampaio, A. B., Schmidt, I. B., & Vieira, D. L. M. (2023). Direct seeding versus seedling planting: Survival, biomass, growth, and cost up to 6 years for four tropical seasonal tree species. *Restoration Ecology*, 31(4), e13807. https://doi.org/10.1111/rec.13807

Ficko, S. A., Haughland, D. L., & Naeth, M. A. (2023). Assisted dispersal and retention of lichen-dominated biocrust material for arctic restoration. *Restoration Ecology*, *31*(4), e13793. https://doi.org/10.1111/rec.13793

Fowler, N. L. (1988). What is a safe site?: Neighbor, litter, germination date, and patch effects. *Ecology*, 69(4), 947–961. https://doi.org/10.2307/1941250

Gann, G. D., McDonald, T., Walder, B., Aronson, J., Nelson, C. R., Jonson, J., Hallett, J. G., Eisenberg, C., Guariguata, M. R., Liu, J., Hua, F., Echeverría, C., Gonzales, E., Shaw, N., Decleer, K., & Dixon, K. W. (2019). International principles and standards for the practice of ecological restoration. Second edition. *Restoration Ecology*, *27*(S1). https://doi.org/10.1111/rec.13035

Girard, F., Payette, S., & Gagnon, R. (2008). Rapid expansion of lichen woodlands within the closed-crown boreal forest zone over the last 50 years caused by stand disturbances in eastern Canada. *Journal of Biogeography*, *35*(3), 529–537. https://doi.org/10.1111/j.1365-2699.2007.01816.x

Gísladóttir, G., Erlendsson, E., & Lal, R. (2011). Soil evidence for historical human-induced land degradation in West Iceland. *Applied Geochemistry*, *26*, S28–S31. https://doi.org/10.1016/j.apgeochem.2011.03.021

Gomes Marques, I., Faria, C., Conceição, S. I. R., Jansson, R., Corcobado, T., Milanović, S., Laurent, Y., Bernez, I., Dufour, S., Mandák, B., Ennouni, H., Sahli, A., Ater, M., Dorado, F. J., Caperta, A. D., David, T. S., Solla, A., & Rodríguez-González, P. M. (2022). Germination and seed traits in common alder (*Alnus* spp.): The potential contribution of rear-edge populations to ecological restoration success. *Restoration Ecology*, *30*(3). https://doi.org/10.1111/rec.13517

Goulet, F. (1995). Frost heaving of forest tree seedlings: a review. *New forests, 9,* 67-94. https://doi.org/10.1007/BF00028927

Greenwood, S., Chen, J., Chen, C., & Jump, A. S. (2014). Strong topographic sheltering effects lead to spatially complex treeline advance and increased forest density in a subtropical mountain region. *Global Change Biology*, *20*(12), 3756–3766. https://doi.org/10.1111/gcb.12710

Greipsson, S. (2012). Catastrophic soil erosion in Iceland: Impact of long-term climate change, compounded natural disturbances and human driven land-use changes. *CATENA*, *98*, 41–54. https://doi.org/10.1016/j.catena.2012.05.015

Greipsson, S., & El-Mayas, H. (1999). Large-scale reclamation of barren lands in Iceland by aerial seeding. *Land Degradation & Development*, *10*(3), 185–193. https://doi.org/10.1002/(SICI)1099-145X(199905/06)10:3<185::AID-LDR327>3.0.CO;2-R

Griffiths, G. H., Vogiatzakis, I. N., Porter, J. R., & Burrows, C. (2011). A landscape scale spatial model for semi-natural broadleaf woodland expansion in Wales, UK. *Journal for Nature Conservation*, *19*(1), 43–53. https://doi.org/10.1016/j.jnc.2010.05.002

Grime, J. P. & Jeffrey, D. W. (1965). Seedling establishment in vertical gradients of sunlight. *Journal of Ecology*, 53, 621-642.

Grubb, P. J. (1977). The maintenance of species-richness in plant communities: The importance of the regeneration niche. *Biological Reviews*, *52*(1), 107–145. https://doi.org/10.1111/j.1469-185X.1977.tb01347.x

Gullett, P. R., Leslie, C., Mason, R., Ratcliffe, P., Sargent, I., Beck, A., Cameron, T., Cowie, N. R., Hetherington, D., MacDonell, T., Moat, T., Moore, P., Teuten, E., & Hancock, M. H. (2023). Woodland expansion in the presence of deer: 30 years of evidence from the Cairngorms Connect landscape restoration partnership. *Journal of Applied Ecology*, *00*, 1–11. https://doi.org/10.1111/1365-2664.14501

Hanbury-Brown, A. R., Ward, R. E., & Kueppers, L. M. (2022). Forest regeneration within Earth system models: Current process representations and ways forward. *New Phytologist*, *235*(1), 20–40. https://doi.org/10.1111/nph.18131

Hobbs, R. J., & Harris, J. A. (2001). Restoration ecology: Repairing the earth's ecosystems in the new millennium. *Restoration Ecology*, *9*(2), 239–246. https://doi.org/10.1046/j.1526-100x.2001.009002239.x

Hofmann, R. R. (1989). Evolutionary steps of ecophysiological adaptation and diversification of ruminants: A comparative view of their digestive system. *Oecologia*, *78*(4), 443–457. https://doi.org/10.1007/BF00378733

Holl, K. D., & Aide, T. M. (2011). When and where to actively restore ecosystems? *Forest Ecology and Management*, *261*(10), 1558–1563. https://doi.org/10.1016/j.foreco.2010.07.004

Holl, K.D., Zahawi, R.A., Cole, R.J., Ostertag. R., & Cordell, S. (2011). Planting seedlings in tree islands versus plantations as a large-scale tropical forest restoration strategy. *Restoration Ecology, 19*(4), 470–479. https://doi.org/10.1111/j. 1526-100X.2010.00674.x

Holm, S. O. (1994). Reproductive patterns of *Betula pendula* and *B. pubescens* coll. Along a regional altitudinal gradient in northern Sweden. *Ecography*, *17*(1), 60–72. https://doi.org/10.1111/j.1600-0587.1994.tb00077.x

Holmström, E., Karlsson, M., & Nilsson, U. (2017). Modelling birch seed supply and seedling establishment during forest regeneration. *Ecological Modelling*, *352*, 31–39. https://doi.org/10.1016/j.ecolmodel.2017.02.027

Hope, D., Picozzi, N., Catt, D. C., & Moss, R. (1996). Effects of reducing sheep grazing in the Scottish highlands. *Journal of Range Management, 49*(4), 301–310. https://doi.org/10.2307/4002587

Hua, F., Bruijnzeel, L. A., Meli, P., Martin, P. A., Zhang, J., Nakagawa, S., Miao, X., Wang, W., McEvoy, C., Peña-Arancibia, J. L., Brancalion, P. H. S., Smith, P., Edwards, D. P., & Balmford, A. (2022). The biodiversity and ecosystem service contributions and trade-offs of forest restoration approaches. *Science*, *376*(6595), 839–844. https://doi.org/10.1126/science.abl4649

Hunziker, M., Arnalds, O., & Kuhn, N. J. (2019). Evaluating the carbon sequestration potential of volcanic soils in southern Iceland after birch afforestation. *SOIL*, *5*(2), 223–238. https://doi.org/10.5194/soil-5-223-2019

IUCN (International Union for Conservation of Nature) (2020). *The Bonn Challenge*. https://www.bonnchallenge.org/, accessed 4th of June 2024.

Jadwiszczak, K., Kłosowski, S., Zalewska, I., Banaszek, A., & Chrzanowska, A. (2017). Genetic diversity and sexual reproduction in relict populations of *Betula nana*. *Silva Fennica*, *51*(2). https://doi.org/10.14214/sf.5643

Jiao, J., Zou, H., Jia, Y., & Wang, N. (2009). Research progress on the effects of soil erosion on vegetation. *Acta Ecologica Sinica*, *29*(2), 85–91. https://doi.org/10.1016/j.chnaes.2009.05.001

Jónsson, T. H. (2004). Stature of sub-arctic birch in relation to growth rate, lifespan and tree form. *Annals of Botany*, *94*(5), 753–762. https://doi.org/10.1093/aob/mch200

Kimball, S., Lulow, M., Sorenson, Q., Balazs, K., Fang, Y.-C., Davis, S. J., O'Connell, M., & Huxman, T. E. (2015). Cost-effective ecological restoration. *Restoration Ecology*, *23*(6), 800–810. https://doi.org/10.1111/rec.12261

Kristinsson, H., Hlíðberg, J. B., & Thórhallsdóttir, T. E. (2018). *Flóra Íslands. Blómplöntur og byrkningar* [Flora of Iceland. Angiosperms and ferns] (p. 742). Vaka-Helgafell.

Kullman, L. (1986). Demography of *Betula pubescens* ssp. *tortuosa* sown in contrasting habitats close to the birch tree-limit in Central Sweden. *Vegetatio*, *65*(1), 13–20. https://doi.org/10.1007/BF00032122

Laliberte, A. S., Rango, A., Havstad, K. M., Paris, J. F., Beck, R. F., McNeely, R., & Gonzalez, A. L. (2004). Object-oriented image analysis for mapping shrub encroachment from 1937 to 2003 in southern New Mexico. *Remote Sensing of Environment*, *93*(1–2), 198–210. https://doi.org/10.1016/j.rse.2004.07.011

Leduc, G. B., Thórsson, Æ. T., & Anamthawat-Jónsson, K. (2025). Species integrity and ploidy stability despite extensive gene flow via introgressive hybridization: The case of *Betula* species in Iceland. BMC Plant Biology, 25(1), 462. https://doi.org/10.1186/s12870-025-06482-1

Lett, S., & Dorrepaal, E. (2018). Global drivers of tree seedling establishment at alpine treelines in a changing climate. *Functional Ecology*, *32*(7), 1666–1680. https://doi.org/10.1111/1365-2435.13137

Levin, S. A., Muller-Landau, H. C., Nathan, R., & Chave, J. (2003). The ecology and evolution of seed dispersal: A theoretical perspective. *Annual Review of Ecology, Evolution, and Systematics*, *34*(1), 575–604. https://doi.org/10.1146/annurev.ecolsys.34.011802.132428

Lidman, F. D., Holmström, E., Lundmark, T., & Fahlvik, N. (2021). Management of spontaneously regenerated mixed stands of birch and Norway spruce in Sweden. *Silva Fennica*, *55*(4). https://doi.org/10.14214/sf.10485

Lidman, F. D., Karlsson, M., Lundmark, T., Sängstuvall, L., & Holmström, E. (2023). Birch establishes anywhere! So, what is there to know about natural regeneration and direct seeding of birch? *New Forests*. https://doi.org/10.1007/s11056-023-09971-z

Lindenmayer, D. (2020). Improving restoration programs through greater connection with ecological theory and better monitoring. *Frontiers in Ecology and Evolution*, *8*, 50. https://doi.org/10.3389/fevo.2020.00050

Magnusson, B. (2010). *NOBANIS - Invasive Alien Species Fact Sheet - Lupinus nootkatensis*. Icelandic Institute of Natural History, Reykjavík.

Magnusson, B., Magnusson, S. H., and Sigurdsson, B. D. (2008). Plant succession in areas colonized by the introduced Nootka lupin in Iceland. In *Lupins for Health and Wealth 12th International Lupin Conference*, Fremantle, Western Australia, 14-18 September 2008, eds J. A. Palta and J. D. Berger (Canterbury: International Lupin Association).

Marteinsdóttir, B., Svavarsdóttir, K., & Thórhallsdóttir, T. E. (2018). Multiple mechanisms of early plant community assembly with stochasticity driving the process. *Ecology*, *99*(1), 91–102. https://doi.org/10.1002/ecy.2079

McCallum, K. P., Lowe, A. J., Breed, M. F., & Paton, D. C. (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*(3), 446–455. https://doi.org/10.1111/rec.12690

McKay, J. K., Christian, C. E., Harrison, S., & Rice, K. J. (2005). "How local is local?"-A review of practical and conceptual issues in the genetics of restoration. *Restoration Ecology*, *13*(3), 432–440. https://doi.org/10.1111/j.1526-100X.2005.00058.x

Miles, J. (1973). Early mortality and survival of self-sown seedlings in Glenfeshie, Inverness-Shire. *Journal of Ecology*, *61*(1), 93. https://doi.org/10.2307/2258919

Miller, B. P., Sinclair, E. A., Menz, M. H. M., Elliott, C. P., Bunn, E., Commander, L. E., Dalziell, E., David, E., Davis, B., Erickson, T. E., Golos, P. J., Krauss, S. L., Lewandrowski, W., Mayence, C. E., Merino-Martín, L., Merritt, D. J., Nevill, P. G., Phillips, R. D., Ritchie, A. L., … Stevens, J. C. (2017). A framework for the practical science necessary to restore sustainable, resilient, and biodiverse ecosystems: A framework for practical restoration science. *Restoration Ecology*, *25*(4), 605–617. https://doi.org/10.1111/rec.12475

Moyano, J., Dimarco, R. D., Paritsis, J., Peterson, T., Peltzer, D. A., Crawford, K. M., McCary, M. A., Davis, K. T., Pauchard, A., & Nuñez, M. A. (2024). Unintended consequences of planting native and non□native trees in treeless ecosystems to mitigate climate change. *Journal of Ecology*, *112*(11), 2480–2491. https://doi.org/10.1111/1365-2745.14300

Myers-Smith, I. H., Forbes, B. C., Wilmking, M., Hallinger, M., Lantz, T., Blok, D., Tape, K. D., Macias-Fauria, M., Sass-Klaassen, U., Lévesque, E., Boudreau, S., Ropars, P., Hermanutz, L., Trant, A., Collier, L. S., Weijers, S., Rozema, J., Rayback, S. A., Schmidt, N. M., … Hik, D. S. (2011). Shrub expansion in tundra ecosystems: Dynamics, impacts and research priorities. *Environmental Research Letters*, *6*(4), 045509. https://doi.org/10.1088/1748-9326/6/4/045509

Nolan, C., Overpeck, J. T., Allen, J. R. M., Anderson, P. M., Betancourt, J. L., Binney, H. A., Brewer, S., Bush, M. B., Chase, B. M., Cheddadi, R., Djamali, M., Dodson, J., Edwards, M. E., Gosling, W. D., Haberle, S., Hotchkiss, S. C., Huntley, B., Ivory, S. J., Kershaw, A. P., … Jackson, S. T. (2018). Past and future global transformation of terrestrial ecosystems under climate change. *Science*, *361*(6405), 920–923. https://doi.org/10.1126/science.aan5360

Oddsdóttir, E. S., Svavarsdóttir, K., & Halldórsson, G. (2008). The influence of land reclamation and afforestation on soil arthropods in Iceland. *Icelandic Agricultural Sciences*, *21*, 3–13.

Olsson, L., H. Barbosa, S. Bhadwal, A. Cowie, K. Delusca, D. Flores-Renteria, K. Hermans, E. Jobbagy, W. Kurz, D. Li, D.J. & Sonwa L. (2019). *Land Degradation*. In: *Climate Change and Land: an IPCC special report on climate change, desertification, land degradation, sustainable land management, food security, and greenhouse gas fluxes in terrestrial ecosystems* [P.R. Shukla, J. Skea, E. Calvo Buendia, V. Masson-Delmotte, H.-O. Pörtner, D. C. Roberts, P. Zhai, R. Slade, S. Connors, R. van Diemen, M. Ferrat, E. Haughey, S. Luz, S. Neogi, M. Pathak, J. Petzold, J. Portugal Pereira, P. Vyas, E. Huntley, K. Kissick, M. Belkacemi, J. Malley, (eds.)].

Orradóttir, B., Archer, S. R., Arnalds, O., Wilding, L. P., & Thurow, T. L. (2008). Infiltration in Icelandic andisols: The role of vegetation and soil frost. *Arctic, Antarctic, and Alpine Research*, *40*(2), 412–421. https://doi.org/10.1657/1523-0430(06-076)[ORRADOTTIR]2.0.CO;2

Óskarsdóttir, G., Thórhallsdóttir, T. 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*(10), e9430. https://doi.org/10.1002/ece3.9430

Óskarsson, H., & Traustason, B. (2023). Aldarfriðun Þórsmerkur- og Goðalandsskóga. Breytingar á skógarþekju [Permanent protection of Þórsmérkur and Goðalandsskógar. Changes in forest cover]. *Skógræktarritið 2023, 1*, 4-22.

Parker, V. T. (1997). The scale of successional models and restoration objectives. *Restoration Ecology*, *5*(4), 301–306. https://doi.org/10.1046/j.1526-100X.1997.00031.x

Pálsdóttir, A. E., Gill, J. A., Alves, J. A., Pálsson, S., Méndez, V., Ewing, H., & Gunnarsson, T. G. (2022). Subarctic afforestation: Effects of forest plantations on ground-nesting birds in lowland Iceland. *Journal of Applied Ecology*, *59*(10), 2456–2467. https://doi.org/10.1111/1365-2664.14238

Pálsson, S., Wasowicz, P., Heiðmarsson, S., & Magnússon, K. P. (2023). Population structure and genetic variation of fragmented mountain birch forests in Iceland. *Journal of Heredity*, *114*(2), 165–174. https://doi.org/10.1093/jhered/esac062

Pedersen, N. K., Schmidt, I. K., & 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

Perala, D. A., & Alm, A. A. (1990). Reproductive ecology of birch: A review. *Forest Ecology and Management, 32 (1)*, 1-38. https://doi.org/10.1016/0378-1127(90)90104-J.

Perring, M.P., Standish, R.J., Price, J.N., Craig, M.D., Erickson, T.E., Ruthrof, K.X., Whiteley, A.S., Valentine, L.E. & Hobbs, R.J. (2015). Advances in restoration ecology: Rising to the challenges of the coming decades. *Ecosphere, 6(8), 1-25*. http://dx.doi.org/10.1890/ES15-00121.1

Potthoff, K. (2017). Spatio-temporal patterns of birch regrowth in a Western Norwegian treeline ecotone. *Landscape Research*, *42*(1), 63–77. https://doi.org/10.1080/01426397.2016.1260701

Qiu, Y., Xu, Z., Xu, C., & Holmgren, M. (2023). Can remotely sensed vegetation patterns signal dryland restoration success? *Restoration Ecology*, *31*(3). https://doi.org/10.1111/rec.13760

R Development Core Team (2023) R: A language and environment for statistical computing. R Foundation for Statistical Computing.

Ranno, V., Blandino, C., & Giusso del Galdo, G. (2021). A comparative study on temperature and water potential thresholds for the germination of *Betula pendula* and two Mediterranean endemic birches, *Betula aetnensis* and *Betula fontqueri*. *Seed Science Research, 30*(4), 249–261. https://doi.org/10.1017/S0960258520000483

Reis, B. P., Martins, S. V., Fernandes Filho, E. I., Sarcinelli, T. S., Gleriani, J. M., Leite, H. G., & Halassy, M. (2019). Forest restoration monitoring through digital processing of high resolution images. *Ecological Engineering*, *127*, 178–186. https://doi.org/10.1016/j.ecoleng.2018.11.022

Reji Chacko, M., Oehri, J., Plekhanova, E., & Schaepman-Strub, G. (2023). Will current protected areas harbor refugia for threatened Arctic vegetation types until 2050? A first assessment. *Arctic, Antarctic, and Alpine Research*, *55*(1), 2203478. https://doi.org/10.1080/15230430.2023.2203478

Runólfsson, S. (1987). Land reclamation in Iceland. *Arctic and Alpine Research*, *19*(4), 514–517. https://doi.org/10.1080/00040851.1987.12002634

Sanchez, S., Arnalds, Ó., Thórsson, J., Dahlgren, R., & Aradóttir, Á. L. (2025). Soil carbon stocks of regenerating Icelandic native birch woodlands: Effects of space and time. *Science of the Total Environment*, 958, 178063. https://doi.org/10.1016/j.scitotenv.2024.178063

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

Shono, K., Cadaweng, E. A., & Durst, P. B. (2007). Application of assisted natural regeneration to restore degraded tropical forestlands. *Restoration Ecology*, *15*(4), 620–626. https://doi.org/10.1111/j.1526-100X.2007.00274.x

Sigurðsson, S., (1977). Birki á Islandi [Birch in Iceland]. *Skógarrnal, Reykjavik,* 146-172.

Snorrason, A., Traustason, B., Kjartansson, B. Þ., & 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

Souza, D. C. (2022). Forest restoration by direct seeding: A global bibliometric analysis. *Restoration Ecology, 30(8),* e13631. https://doi.org/10.1111/rec.13631

Speed, J. D. M., Austrheim, G., Hester, A. J., & Mysterud, A. (2010). Experimental evidence for herbivore limitation of the treeline. *Ecology*, *91*(11), 3414–3420. https://doi.org/10.1890/09-2300.1

Speed, J. D. M., Austrheim, G., Hester, A. J., & Mysterud, A. (2011). Growth limitation of mountain birch caused by sheep browsing at the altitudinal treeline. *Forest Ecology and Management*, *261*(7), 1344–1352. https://doi.org/10.1016/j.foreco.2011.01.017

Stockton, P. H., & Gillette, D. A. (1990). Field measurement of the sheltering effect of vegetation on erodible land surfaces. *Land Degradation & Development*, *2*(2), 77–85. https://doi.org/10.1002/ldr.3400020202

Suding, K. N., Gross, K. L., & Houseman, G. R. (2004). Alternative states and positive feedbacks in restoration ecology. *Trends in Ecology & Evolution, 19*(1), 46–53. https://doi.org/10.1016/j.tree.2003.10.005

Suding, K., Higgs, E., Palmer, M., Callicott, J. B., Anderson, C. B., Baker, M., Gutrich, J. J., Hondula, K. L., LaFevor, M. C., Larson, B. M. H., Randall, A., Ruhl, J. B., & Schwartz, K. Z. S. (2015). Committing to ecological restoration. *Science*, *348*(6235), 638–640. https://doi.org/10.1126/science.aaa4216

Suganuma, M. S., & Durigan, G. (2015). Indicators of restoration success in riparian tropical forests using multiple reference ecosystems. *Restoration Ecology, 23*(3), 238–251. https://doi.org/10.1111/rec.12168

Telewski, F. W. (2012). Is windswept tree growth negative thigmotropism? *Plant Science*, *184*, 20–28. https://doi.org/10.1016/j.plantsci.2011.12.001

Temperton, V. M., Buchmann, N., Buisson, E., Durigan, G., Kazmierczak, L., Perring, M. P., Sá Dechoum, M., Veldman, J. W., & Overbeck, G. E. (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*, rec.12989. https://doi.org/10.1111/rec.12989

Thompson, J. R., Lambert, K. F., Foster, D. R., Broadbent, E. N., Blumstein, M., Almeyda Zambrano, A. M., & Fan, Y. (2016). The consequences of four land-use scenarios for forest ecosystems and the services they provide. *Ecosphere*, *7*(10), e01469. https://doi.org/10.1002/ecs2.1469

Thórhallsdóttir, T. E. (1998). Flowering phenology in the central highland of Iceland and implications for climatic warming in the Arctic. *Oecologia*, *114*(1), 43–49. https://doi.org/10.1007/s004420050418

Thórhallsdóttir, T. E., & Svavarsdóttir, K. (2022). The environmental history of Skeiðarársandur outwash plain, Iceland. *Journal of the North Atlantic*, *2022*(43). https://doi.org/10.3721/037.006.4303

Thórsson, J. (2010). *Desertification of high latitude ecosystems: conceptual models, time series analyses and experiments.* Doctoral dissertation, Texas A&M University.

Truong, C., Palmé, A. E., & Felber, F. (2007). Recent invasion of the mountain birch *Betula pubescens* ssp. *tortuosa* above the treeline due to climate change: Genetic and ecological study in northern Sweden. *Journal of Evolutionary Biology*, *20*(1), 369–380. https://doi.org/10.1111/j.1420-9101.2006.01190.x

UNEP (United Nations Environment Programme) & FAO (United Nations Food and Agriculture Organization) (2020). The decade on ecosystem restoration https://www.decadeonrestoration.org/, accessed 4th of June 2024

Verwijst, T. (1988). Environmental correlates of multiple-stem formation in *Betula pubescens* ssp. *tortuosa*. *Vegetatio*, *76*(1–2), 29–36. https://doi.org/10.1007/BF00047385

Vetter, V. M. S., Tjaden, N. B., Jaeschke, A., Buhk, C., Wahl, V., Wasowicz, P., & Jentsch, A. (2018). Invasion of a legume ecosystem engineer in a cold biome alters plant biodiversity. *Frontiers in Plant Science*, *9*, 715. https://doi.org/10.3389/fpls.2018.00715

Vilmundardóttir, O. K., Sigurmundsson, F. S., Møller Pedersen, G. B., Belart, J. M.-C., Kizel, F., Falco, N., Benediktsson, J. A., & 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*(6), 765–791. https://doi.org/10.1177/0309133318798754

Wasowicz, P., Óskarsdóttir, G., & Þórhallsdóttir, Þ. E. (2025). Lodgepole pine (*Pinus contorta* Douglas ex Loudon) invasion in subarctic Iceland: Evidence from a long-term study. *NeoBiota*, 97, 47–66. https://doi.org/10.3897/neobiota.97.134047

Weisberg, P. J., Lingua, E., & Pillai, R. B. (2007). Spatial patterns of pinyon–juniper woodland expansion in central Nevada. *Rangeland Ecology & Management*, *60*(2), 115–124. https://doi.org/10.2111/05-224R2.1

Willis, J. L., Walters, M. B., & Gottschalk, K. W. (2015). Scarification and gap size have interacting effects on northern temperate seedling establishment. *Forest Ecology and Management, 347*, 237–247. https://doi.org/10.1016/j.foreco.2015.02.026

Willson, M. F. (1993). Dispersal mode, seed shadows, and colonization patterns. *Vegetatio*, *107/108*, 261–280. https://doi.org/10.1007/BF00052229

Wu, G., Li, M., Leite, P. A. M., Dang, Z., & Zhao, J. (2024). Restoration approach for alpine extremely degraded landscapes: Testing direct seeding and mulching with grass clippings. *Restoration Ecology*, *32*(3), e14074. https://doi.org/10.1111/rec.14074

Wu, T., Zhang, P., Zhang, L., Wang, J., Yu, M., Zhou, X., & Wang, G. G. (2018). Relationships between shelter effects and optical porosity: A meta-analysis for tree windbreaks. *Agricultural and Forest Meteorology*, *259*, 75–81. https://doi.org/10.1016/j.agrformet.2018.04.013

Young, T. P., Petersen, D. A., & Clary, J. J. (2005). The ecology of restoration: Historical links, emerging issues and unexplored realms. *Ecology Letters*, *8*(6), 662–673. https://doi.org/10.1111/j.1461-0248.2005.00764.x

9. Appendices

I

Spatio-temporal patterns of subarctic woodland expansion to guide future restoration

Anna M. Behrend[1], Emmanuel P. Pagneux[1], Kristín Svavarsdóttir[2], Thóra E. Thórhallsdóttir[3], Ása L. Aradóttir[1]

[1] Agricultural University of Iceland, Faculty of Environmental and Forest Sciences, Keldnaholt, Árleynir, 112 Reykjavík, Iceland

[2] Land and Forest Iceland, Keldnaholt, Árleynir, 112 Reykjavík, Iceland

[3] University of Iceland, Faculty of Life and Environmental Sciences, Sæmundargötu 2, 102 Reykjavík, Iceland

Abstract

Restoration of native woodlands is of high global importance. Upscaling of restoration efforts is, however, hampered by lack of knowledge on temporal rates, patterns and drivers of woodland expansion. Analysis of historical aerial photos provide the opportunity to study ecosystem expansion that can inform future restoration. Having lost most of its original woodland cover, Iceland provides an appropriate setting for such analyses. The key objective of our study was to assess rates and spatio-temporal patterns of native woodland expansion, and furthermore to investigate whether protection from livestock grazing had accelerated the temporal rates of woodland expansion. We used image segmentation and unsupervised classification analysis of historical and recent aerial photos to monitor woodland expansion over 38-65 years in nine study areas in Iceland with native mountain birch (*Betula pubescens* ssp. *tortuosa*) woodlands representing different management histories. The area occupied by these woodlands expanded on average 1.5 ha or nearly 2% per year, in the time from the oldest to the youngest aerial photo. Patterns of woodland increase varied among study areas, with strong lateral expansion in some woodlands while others mainly increased in canopy cover within their current range. The annual rate of increase was greater in areas with a management history of fencing to exclude livestock grazing or revegetation of adjacent eroded areas. This easily applicable method enables a quantification of the rates and spatio-temporal patterns of subarctic woodland expansion that can be used to guide decision-making in restoration.

Keywords: aerial photos, *Betula pubescens* ssp. *tortuosa,* landscape ecology, mountain birch, remote sensing, spatio-temporal patterns, woodland expansion, woodland restoration

Introduction

Forests and woodlands have experienced dramatic global declines since the industrial revolution (IPCC 2019, FAO 2022). Primary forests and woodlands have been degraded and converted to other land uses, with an estimated loss of 47 million hectares in the last 20 years (FAO 2022). This is accompanied by loss of biodiversity and important ecosystem services, such as water regulation, recreational opportunities, and climate change mitigation (Mori et al. 2017, Sanchez et al. 2025). Conserving the remaining primary forest and woodland ecosystems is not sufficient; additional large-scale restoration efforts are needed to increase their extent (UNEP & FAO 2020).

Cost-effective large-scale restoration of forest and woodland ecosystems requires harnessing their potential for expansion through natural regeneration. Woodlands can expand rapidly where conditions for seedling establishment are favorable in the vicinity of seed sources (Girard et al. 2008, Óskarsdóttir et al. 2022, Behrend et al. 2025). Where ecosystem degradation has surpassed critical thresholds, however, recovery must be assisted through restoration interventions (Suding et al. 2015), such as revegetation efforts and establishment of seed sources (Aradóttir & Halldórsson 2018), or protection from anthropogenic disturbances such as grazing (Leu et al. 2021, Gullett et al. 2023). Ecosystem recovery can also be facilitated by land abandonment (Bryn et al. 2013, Kepfer-Rojas et al. 2015) and even natural disturbances (Girard et al. 2008). Deciding on appropriate restoration approaches requires clear objectives and in-depth knowledge of the target ecosystems and recovery trajectories (Gann et al. 2019). For passive and low-intensity restoration frameworks such as assisted natural regeneration and applied nucleation, this includes knowledge on the rates, spatio-temporal patterns and drivers of ecosystem expansion (Griffiths et al. 2011, García et al. 2020, Arroyo-Rodríguez et al. 2023).

Quantitative data on the spatio-temporal rates and patterns of woodland expansion is limited, with much of the existing studies focusing on deforestation dynamics (Borda-Niño et al. 2019). There is a growing interest in using landscape-scale approaches such as quantification of spatial vegetation patterns by remote sensing to guide restoration efforts and define restoration targets (Dickenson et al. 2016). Historical landscape data such as aerial photos are useful to study spatial and temporal patterns of vegetation, including woodlands (Kadmon & Harari-Kremer 1999, Weisberg et al. 2007), shrublands (Laliberte et al. 2004), seagrass (Dalby et al. 2022) and the interaction between shrubland expansion and snow cover (Zong et al. 2022). Analysis of temporal changes in woodland cover, combined with climate data and spatial data on distribution of land classification data, such as habitat types, and land-use can help to identify future restoration 'hotspots' where interventions are most likely to succeed (Griffiths et al. 2011, Arroyo-Rodríguez et al. 2023). The direction of woodland expansion can provide valuable information on the driving forces behind expansion, and about habitat suitability, which eventually can guide management decisions for woodland restoration and conservation (Weisberg et al. 2007, Gimona et al. 2012). These analyses can aid in predicting recovery and expansion of woodland ecosystems with and without applied restoration interventions (Qiu et al. 2023).

Woodland restoration studies in the subarctic are generally underrepresented in literature, with studies skewed towards the temperate and boreal regions of the northern hemisphere (Gatica-Saavedra et al. 2017). Birch woodlands, key ecosystems in the subarctic, have been subject to depletion and degradation. In Iceland, mountain birch woodlands (*Betula pubescens* ssp. *tortuosa*, hereafter referred to as birch woodlands) currently cover only 1.5% of the land area, a drastic reduction from an estimated 30% at the time of settlement in the ninth century (Snorrason et al. 2016). Their restoration is of high priority, and the Icelandic government has accepted the Bonn Challenge by pledging to initiate restoration of birch woodlands on 3.5% of Iceland by 2030 (IUCN 2020, Government of Iceland 2022). Woodland restoration efforts in Iceland have often relied on planting (Eysteinsson 2004) which is economically and logistically unfeasible for such ambitious restoration goals. Emphasis on approaches that rely on assisted or unassisted natural regeneration has been growing (Aradóttir & Eysteinsson 2005, Aradóttir 2007), and recent studies indicate their effectiveness in a subarctic context (Aradóttir & Halldórsson 2018, Behrend et al. 2025).

The main objective of our study was to investigate the spatio-temporal patterns and rates of native birch woodland expansion in Iceland, that can be used to guide future restoration efforts. We performed an image classification analysis of historical and recent aerial photographs from nine areas with birch woodlands across Iceland, to assess increases in total woodland area and rates of expansion over time, evaluating the distance and direction of expansion in different cardinal directions. Furthermore, we investigated whether birch woodland expansion had been accelerated by management interventions, such as protection from livestock grazing and revegetation.

Methods

Study areas

The study included nine areas with birch woodlands distributed around Iceland (**Figure 1**). They were selected on the basis of available information on the current distribution of birch woodlands (Snorrason et al. 2016), including only woodlands that were at least 60 years old as determined from historical aerial photos. Another selection criterion was ongoing natural colonization in the vicinity of the existing woodlands as verified by field visits. The study areas ranged in latitude from 63.7° - 66.0°N and in longitude from 22.9° - 14.8°W (**Table 1**). They varied substantially in climate and topography; some were in wind-protected valleys and fjords while others were on extensive, flat plains including lava fields and braided floodplains (**Table 1**). Five of the nine areas had been fenced and protected from livestock grazing for several decades, although grazing had in some cases been resumed in recent years, and one area had also undergone revegetation.

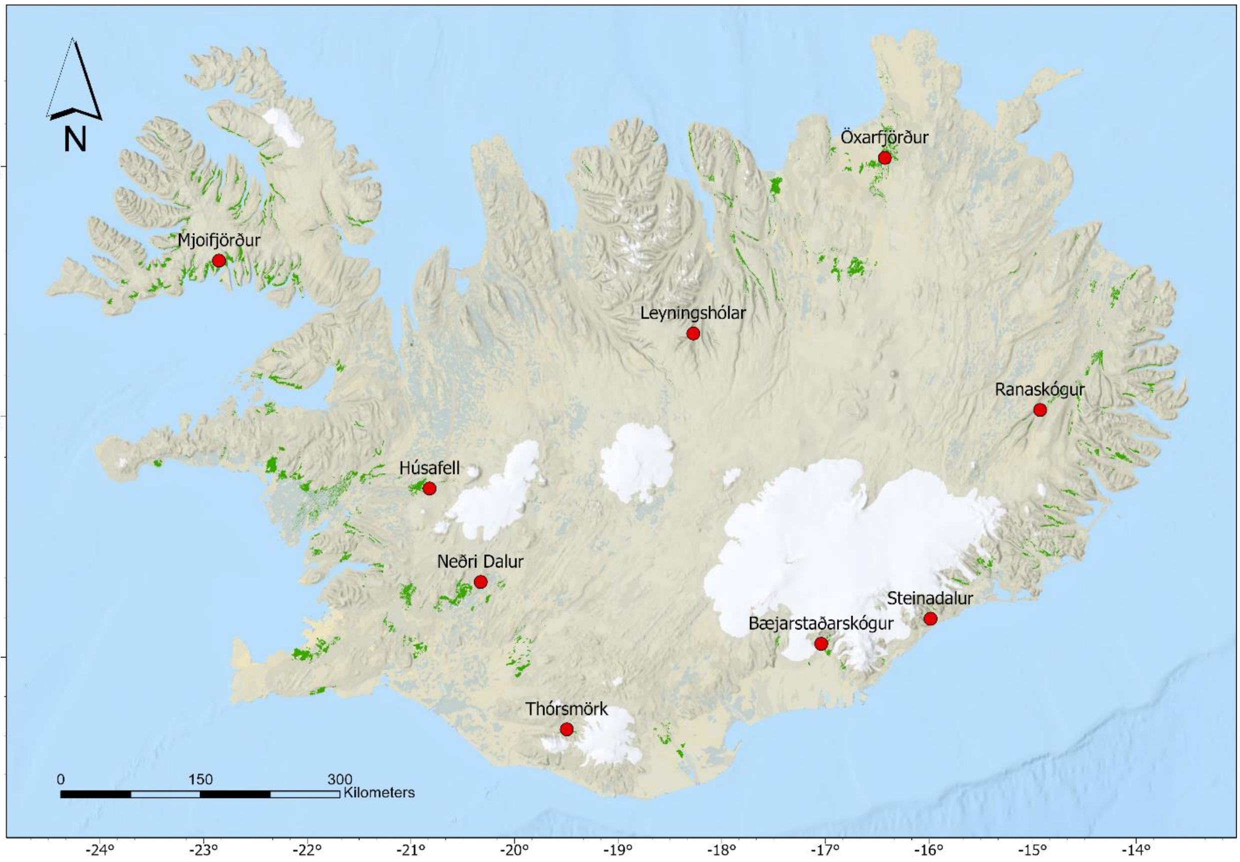


***Figure 1**. Study areas (red circles) where expansion of birch woodlands was assessed by analysis of historical and recent aerial photos. Green patches represent the current distribution of natural mountain birch woodlands (Icelandic Forest Service, 2023). Base data: NLSI (2020, 2021).*

Table 1. *Overview of the areas included in this study, and area-specific characteristics. Altitudinal range was derived from the Digital Elevation Model ÍslandDEM V1.0 (National Land Survey of Iceland, 2021). Temperatures are based on 30-year averages (1992-2022) obtained from the closest weather station (unpublished data from the Icelandic Meteorological Office). Management status was obtained from various sources.*

Study area	**Lat**	**Long**	**Oldest aerial photo**	**Latest aerial photo**	**Area of interest (ha)**	**Altitudinal range (m.a.s.l)**	**Average temperature May – August (C°)**	**Management status (protection from grazing)**
Leyningshólar	65.342	-18.275	1954	2018	285	127 – 367	7.5	Protected since 1965
Öxarfjörður	66.024	-16.430	1955	2019	368	23 - 137	7.3	Not protected
Ranaskógur	65.069	-14.839	1967	2021	286	19 - 210	7.2	Protected since 1952
Neðri Dalur	64.286	-20.338	1955	2020	252	87 - 305	9.9	Not protected
Bæjarstaðarskógur	64.060	-17.023	1975	2019	821	106 - 679	9.9	Protected 1967
Steinadalur	64.159	-15.965	1957	2021	1104	7 - 624	9.9	Not protected
Thórsmörk	63.686	-19.543	1960	2019	836	175 - 504	9.9	Protected since 1920, fences renewed and surrounding areas revegetated around 1990
Húsafell	64.712	-20.823	1957	2022	943	132 – 375	8.9	Protected 1974-2001
Mjóifjörður	65.635	-22.855	1984	2022	342	1 - 341	8.8	Not protected

Aerial photographs

The expansion of birch woodlands was evaluated based on a comparative analysis of series of older (1954–1999) and more recent (2000–2022) aerial photos from the nine study areas (**Table 1**). The older aerial photos were obtained from the National Land Survey of Iceland and more recent ones from Loftmyndir ehf. The older aerial photos were typically panchromatic (1 band), varying in pixel size from 1.1 to 18.7 m. Newer photos were colored (3-4 bands) and had pixel sizes ranging from 0.6 to 5.2 m (**Table S1**).

Spatial analyses were performed in ArcGIS Pro version 3.1.3 (ESRI 2023). For a visual overview of the analyses we refer to **Figure S1** in the supplementary materials which presents a workflow of the analyses and GIS functions applied to the data.

Georeferencing and resampling

The aerial photos were georeferenced in ArcGIS Pro, using the most recent available pan-Icelandic imagery mosaic from Loftmyndir ehf. as the reference dataset (0.6 × 0.6 m pixel size). For each photo, we used a minimum of 20 control points, placed primarily around visible patches of woodlands. Spline transformation was applied to ensure optimized georeferencing accuracy at the woodland patch locations (Verykokou & Ioannidis, 2018).

Because of the varying spatial resolution of the original aerial photos and pixel distortions caused by georeferencing, we super sampled all the photos to a unique, regular pixel size (0.6 × 0.6 m). Rather than compromising the quality of the newest aerial photo mosaics, super sampling resamples images with a lower resolution so that they rise to the pixel-level of the image with the highest resolution (Zhang et al 2020, **Table S1**).

Image classification

To isolate birch woodlands from other types of land cover within the areas of interest, we opted for the Kk-Nearest Neighbor unsupervised classification algorithm (Cover & Hart 1967). The classification was based on either the brightness (in panchromatic photos) or color (in color photos) of the aerial photos. Unsupervised classification is less time-consuming than supervised, but accuracy can be compromised because the algorithm does not incorporate any expert knowledge (Ahmad & Quegan 2013). In our case, unsupervised classification was deemed suitable for two main reasons: (1) mountain birch is the only native woodland forming tree species in Iceland, and generally dominates the native woodlands and shrublands, and (2) the most typical surrounding vegetation types differ in brightness from birch woodlands (i.e., pine plantations are darker and lupine fields, heathlands, and grasslands are brighter). The standard number of vegetation classes was 10, which was sufficient to segregate birch woodlands from other vegetation types. To improve the unsupervised classification analyses, the photographs were post-segmented using expert judgement: a rough extent of the birch woodlands was manually digitized and used to cut out areas that were obviously outside these (**Figure 2**). After implementing the image segmentation to the results of the unsupervised analysis, both accuracy and reliability of the classification increased substantially, and thus we applied this methodology to all aerial photos.

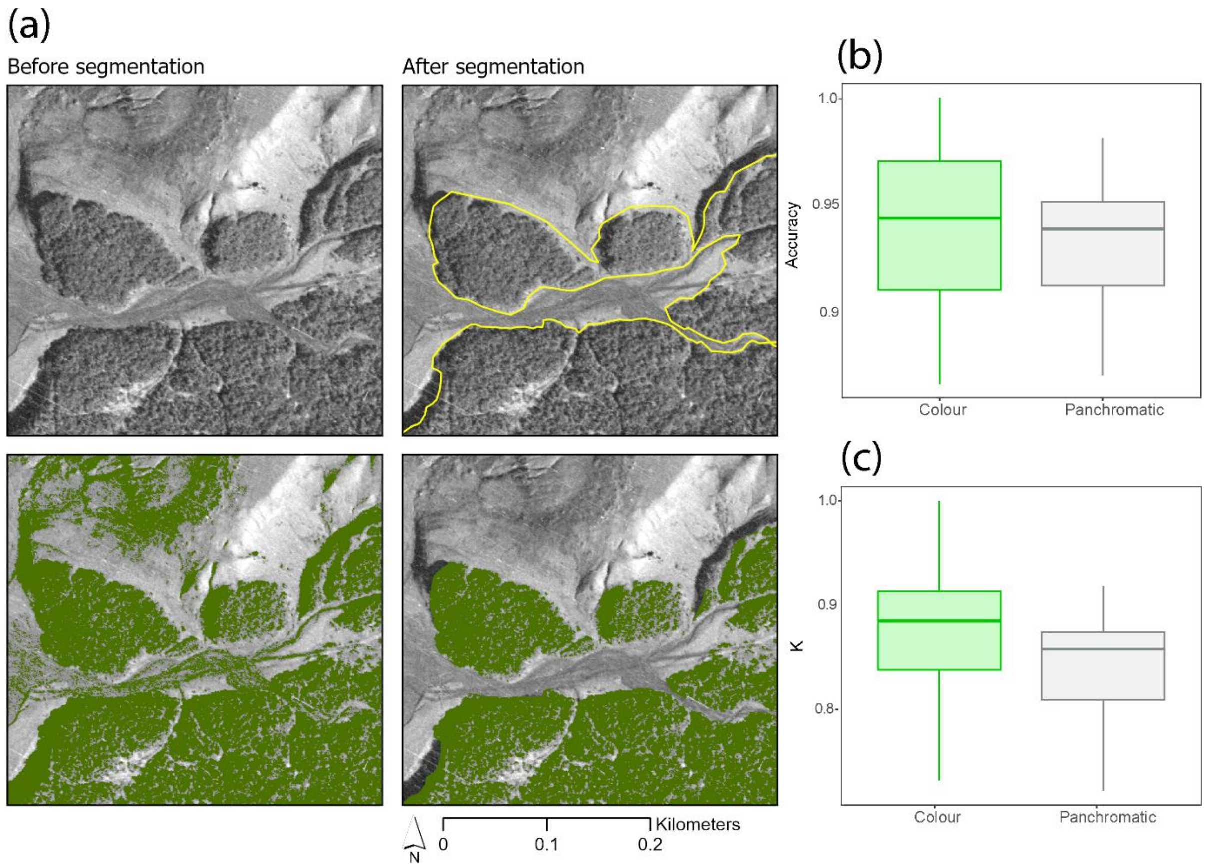


Figure 2. *(a) A detailed example of a pre- and post-classified panchromatic aerial image used in the analysis (Thórsmörk, 1960). Dark green pixels represent the classification of mountain birch woodlands. The classification to the left is based on the entire aerial photo and clearly emphasizes the need for the rough outlining of the woodlands for increased accuracy, as dark patches and shadow cast are wrongly classified as birch woodlands. The classification on the right is based on the image classification cut to the extent of the rough outline of the woodlands. (b) Mean (±SD) overall accuracy of the aerial photo classification. (c) Mean (±SD) Kappa coefficient of agreement (κ) for all classifications.*

Accuracy assessment

Stratified random sampling was conducted to assess accuracy of the image classification. We aimed for an expected accuracy of 85% with a 10% margin of error, resulting in a sample size of 49 validation points per class (Cochran 1977, Foody 2009). To minimize type-2 errors, we excluded land cover patches <0.005 ha from the sampling domain (Tuominen & Pekkarinen 2005). Assessment results indicate a similar overall accuracy (OA) for both panchromatic and color photos, with mean values slightly below 95% and a minimum OA of 80%. The Kappa coefficient of agreement (κ) ranged from 0.72 to 0.91 for panchromatic photos and from 0.73 to 1 for color photos (**Figure 2**).

Statistical Analyses

For each study area, we calculated the annual growth rate of total birch woodland area as

$$\bar{\imath}_k = \frac{y_k - y_{k-1}}{t_k - t_{k-1}} = \left(\frac{\Delta y}{\Delta t}\right)_k \qquad \text{Eq. 1}$$

Where y represents total woodland area at years k and $k-1$, and t indicates the years the aerial photos were taken (Pommerening & Grabernik 2019). Annual growth rate was calculated for each time period between two consecutive aerial photographs. We furthermore calculated the mean annual percentagewise increase in total woodland area for each study area.

For each study area, we extracted the distance and direction of birch woodland expansion at a spatial resolution of 10 meters and an angular resolution of 1° azimuth between the years covered by the oldest and most recent aerial photographs. We then calculated the annual average distances for every 30° interval and projected the results onto 12-direction Nightingale Rose diagrams. For some of the study areas, the outermost limits of the woodlands were included in the area of interest, whereas others only represented a part of a larger woodland, depending on the availability of aerial photos. For the latter, the results represent minimum expansion rates.

To test potential differences in growth rate between study areas with different management regimes, we applied a linear mixed-effect model with the *lme4* package in R (Bates et al. 2015). We used the percentage increase in total woodland area as response variable, and protection as a binomial predictor variable (0 = area not protected from grazing, 1 = area protected). Study area was included as a random variable. We did not consider time periods or type of management interventions, but assigned the value 1 to all study areas that had undergone protection from livestock grazing, with or without revegetation.

Statistical analyses were performed using R version 4.1.0 (R Development Core Team, 2023). All figures were done using the *ggplot2* package in R (Wickham et al. 2009), and maps were produced in ArcGIS Pro.

Results

The initial size of the birch woodlands in our study areas ranged from 25 to 262 ha (**Table 2**). The combined extent of birch woodlands in the nine study areas more than doubled, from 866 to 1917 ha, from the oldest to the newest aerial photos, i.e. over 38-65 years. The total percentagewise increase ranged from 35% over 65 years in Húsafell to 436% over 59 years in Thórsmörk. On average, the minimum annual growth rate was 2.0 ha year^{-1}, corresponding to a 1.5% annual increase in total woodland area. The growth rate varied substantially between study areas, with mean values ranging from 0.6 to 5.4 ha year^{-1}. In five out of nine study areas, the total extent of birch woodlands increased by more than 100% from the oldest aerial photo to the newest one (average 57 years).

Table 2. *Increases in area of mountain birch woodlands over time for the nine study areas. For all study areas except Leyningshólar and Neðri Dalur, the most recent available aerial photos did not fully cover the woodland expansion, hence for those the results represent minimum expansion rates.*

Study area	**Size of woodland in oldest aerial photo (ha)**	**Size of woodland in newest aerial photo (ha)**	**Total increase (ha)**	**Total increase (%)**	**Mean (± SD) annual growth rate (ha year^{-1})**	**Mean annual increase (%)**
Leyningshólar	25	51	26	106	0.6 ± 0.44	0.9
Öxarfjörður	113	198	85	75	1.1 ± 0.33	0.5
Ranaskógur	42	126	84	205	1.9 ± 0.45	2.3
Neðri Dalur	36	107	71	201	1.3 ± 0.27	1.7
Bæjarstaðarskógur	50	140	90	180	2.1 ± 0.38	2.7
Steinadalur	207	472	265	56	3.4 ± 0.96	0.6
Thórsmörk	72	384	312	436	5.4 ± 1.70	3.3
Húsafell	262	352	90	35	1.6 ± 0.73	0.4
Mjóifjörður	61	87	26	42	0.7 ± 0.13	1.0

All nine study areas increased in woodland size over time, but with different temporal patterns. Three areas, Bæjarstaðarskógur, Neðri Dalur and Mjóifjörður displayed linear patterns with constant, steady increases over the whole study period (**Figure 3**). Another three, Öxarfjörður, Steinadalur and Húsafell also had linear increases, but with periods of no or limited growth at some point during the studied time period. Finally, three study areas had exponential rates of increase: Leyningshólar, Ranaskógur and Thórsmörk, all of which had been protected from livestock grazing at some point in time (**Table 1**).

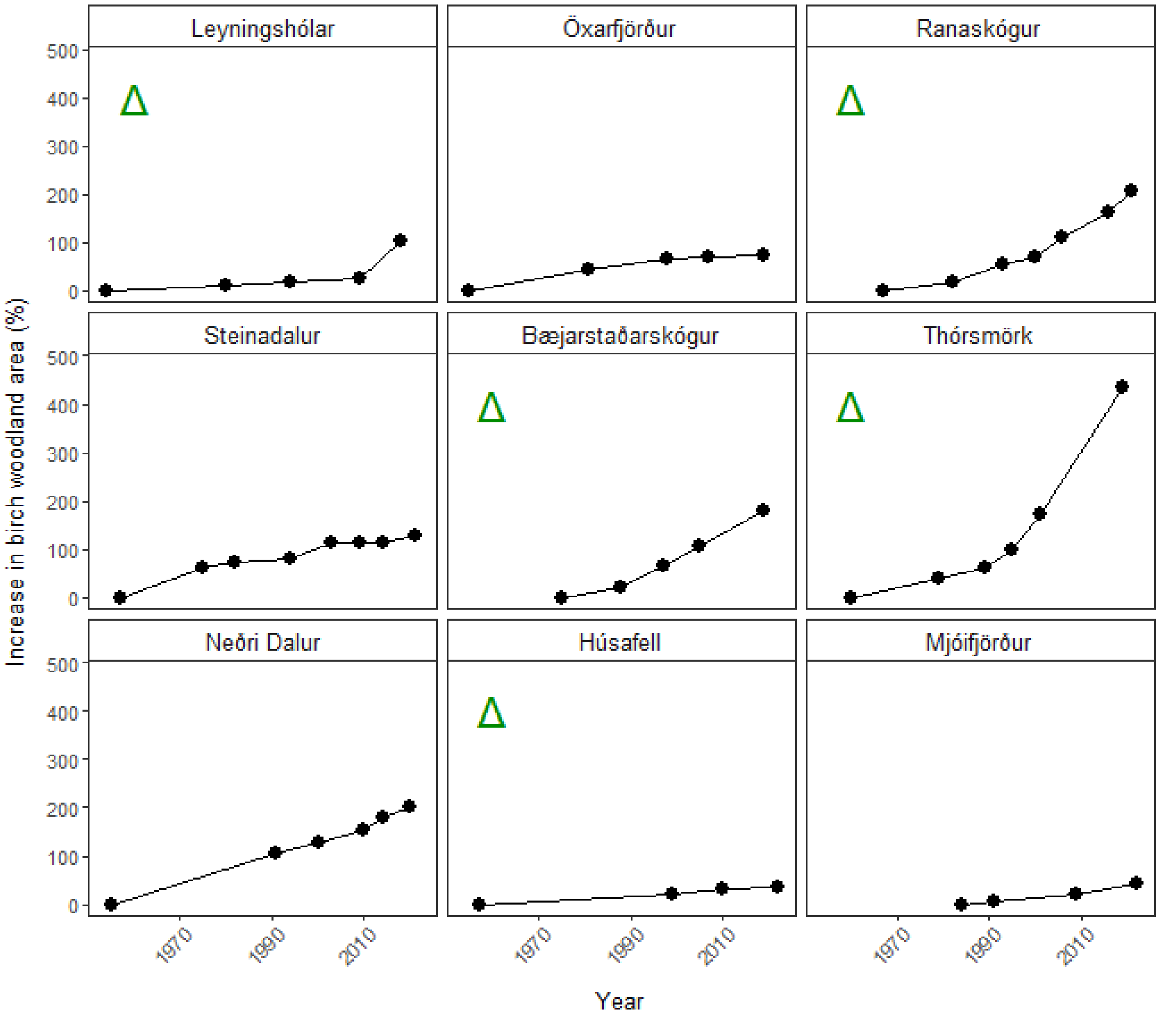


Figure 3. *Percentagewise increase in mountain birch woodlands for the nine study areas, based on successive aerial photos at each study area. Green triangles indicate study areas protected from sheep grazing.*

The spatio-temporal patterns of birch woodland expansion varied substantially between study areas; from being strongly directional to having relatively even rates of expansion in all cardinal directions (**Figure 4**). The most common directions of maximum woodland expansion were SSE for Steinadalur, Bæjarstaðarskógur and Húsafell, WSW for Leyningshólar and Thórsmörk, and NNE for Öxarfjörður, Ranaskógur and Neðri Dalur. In study areas where woodlands were expanding upslope, such as Mjóifjörður (a fjord) and Steinadalur (a valley), expansion was slower than in study areas with less of an altitude range. Other landscape features seemingly restricting expansion were natural obstacles such as the ocean and rivers, and anthropogenic ones such as roads, pine plantations and summerhouse plots (**Figure 5**). The highest observed rate of lateral increase was in Thórsmörk, (max. 16.5 m year^{-1}) followed by Bæjarstaðarskógur and Ranaskógur (max. 9.7 and 8.2 m year^{-1}, respectively).

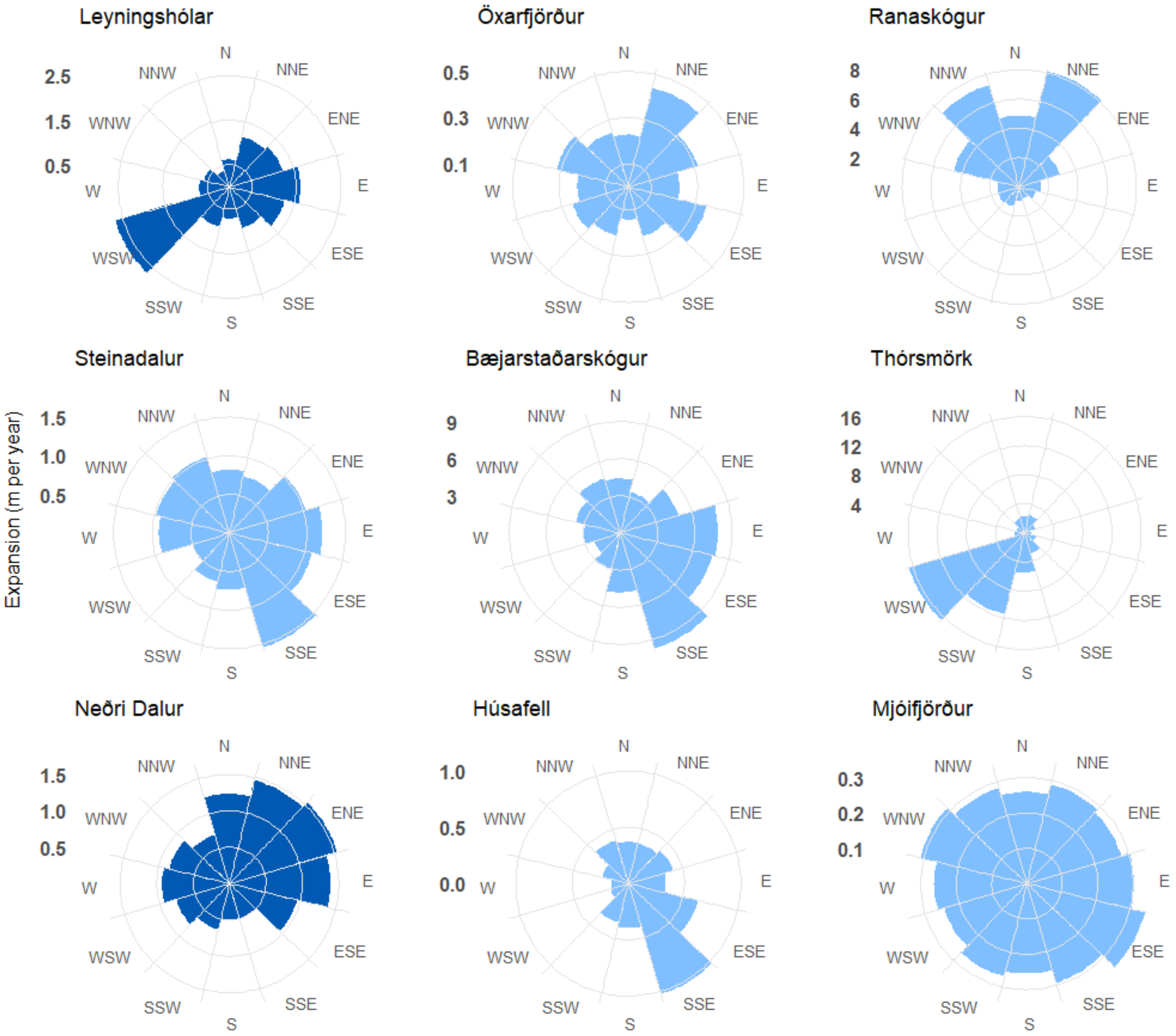


Figure 4. *Average annual distances (m year*$^{-1}$*) of birch woodland expansion in 12 cardinal directions at nine study areas in Iceland. Light blue diagrams represent study areas where woodland expansion was determined by the edges of available aerial imagery and thus the values given represent minimum expansion rates, while diagrams where extension was determined from the complete aerial extent are indicated in dark-blue. Note different scales of the axes showing annual expansion rates.*

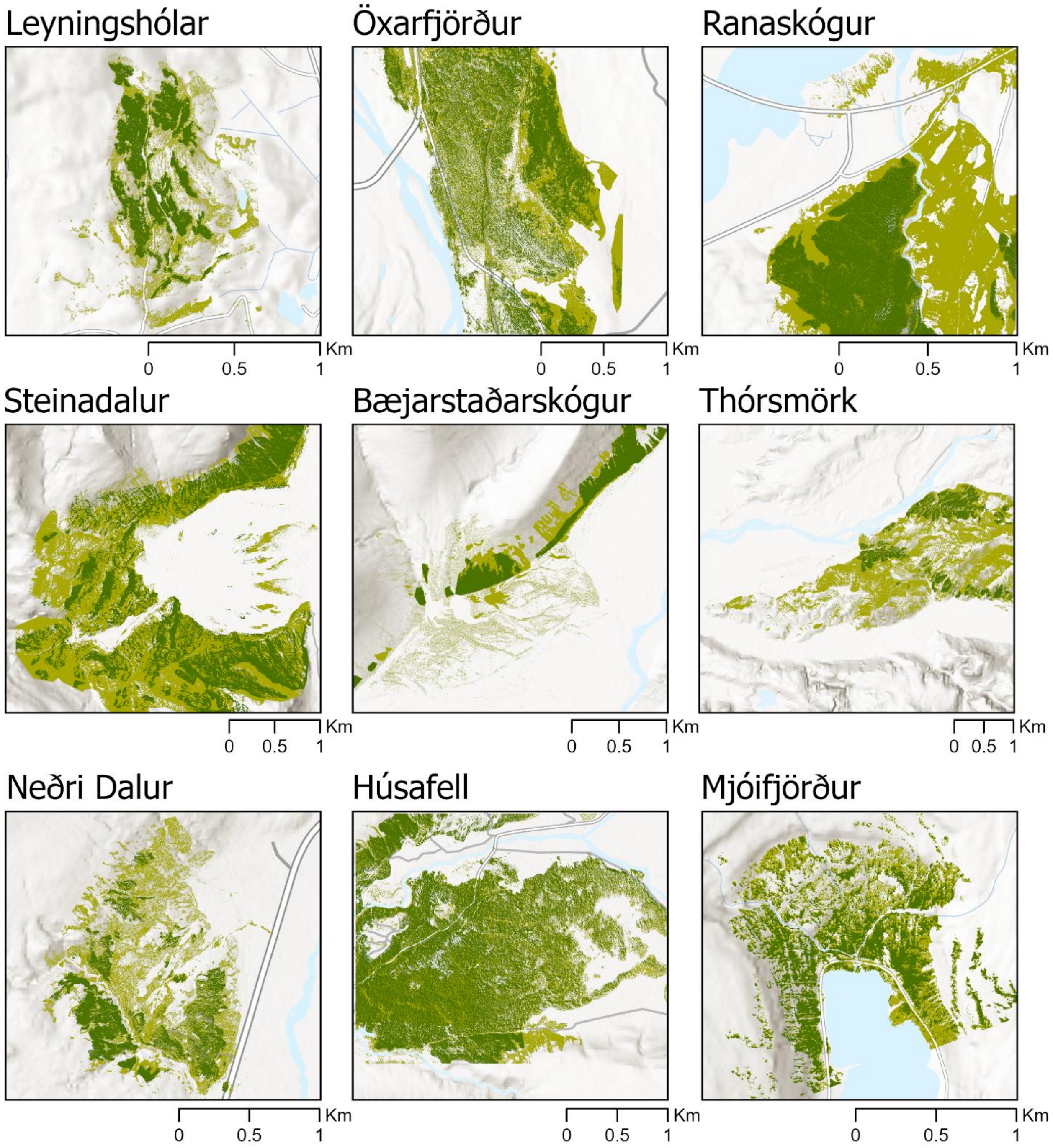


Figure 5. *Mountain birch woodland cover based on the oldest (dark green) and the newest (light green) aerial photo in all nine study areas*

Average expansion rates of birch woodlands in study areas that had been protected from livestock grazing, with or without revegetation efforts, were overall higher than birch woodlands in areas without protection ($p < 0.05$, **Figure 3, Table S2**). On average, woodlands protected from livestock grazing (Leyningshólar, Ranaskógur, Bæjarstaðarskógur, Thórsmörk and Húsafell) increased in size by 2% year^{-1} on average, whereas woodlands that were open to livestock grazing increased by half of that, or 1% year^{-1}. Thórsmörk, the only study area that underwent revegetation together with grazing exclusion, increased much faster than the other protected areas, by 5.4 ha year^{-1} compared to 0.6 - 3.4 ha year^{-1} for the other study areas.

Discussion

Using an easily applicable method of image classification analysis, we demonstrated high rates of expansion of the studied birch woodlands in Iceland over the past six decades. While varying substantially among study areas, the mean annual increase in total woodland extent was 1.5%, or approximately 2 ha per year. This shows potential for relatively rapid expansion, compared to other northern regions in both the temperate (Laliberte et al. 2004, Weisberg et al. 2007) and boreal forest zones (Girard et al. 2008).

Constraints of the applied method

The approach used in our study was efficient and the image classification had a high overall level of accuracy. However, there were some challenges with its application. The analysis on woodland expansion was limited by the availability of aerial photos, resulting in incomplete coverage of potential expansion. Therefore, the data present minimum expansion rates, which should be kept in mind when interpreting the results.

The varying quality of historical aerial photos poses challenges in this type of analysis, including a risk of either over- or underestimating woodland cover in aerial photos of poor quality, even after super-sampling (Tuominen & Pekkarinen 2005, Dickinson et al. 2016). This is furthermore complicated by shadow-casting on slopes, which may also lead to either over- or underestimations of the target ecosystem (Dickinson et al. 2016). Here, availability of aerial photos from adjacent years made it possible to omit photos with too much shadow cast and thus mostly avoid this limitation. It may, however, present a challenge for similar studies conducted in slopy terrains. For such cases, adjusting the image resolution to a coarser scale may be an appropriate solution (Meddens et al. 2011), although this may lead to underestimation of target ecosystem cover. Increased resolution of aerial photos with future technological advances will, however, likely reduce this challenge. Furthermore, aerial photos and LiDAR data from drones which are now frequently used for ecosystem monitoring on both small and large scales, offer an even higher resolution which should increase the accuracy of comparable analyses in the future (Qiu et al. 2023).

Spatio-temporal patterns and drivers of native birch woodland expansion

Climate change effects are expected to be stronger in the arctic and alpine ecoregions than in the rest of the world (Walsh et al. 2011, IPCC 2018), resulting in tree lines expanding at higher rates (Harsch et al. 2009, Nolan et al. 2018) and a general increase in woody vegetation (Myers-Smith et al. 2011, Mekonnen et al. 2021). Variable annual rates of expansion between study areas suggest effects of regional differences in climate on birch woodland expansion. Woodland expansion was overall slower in the colder (North and Westfjords) than the warmer regions of Iceland (South, West and East). In both field and controlled experiments, mountain birch survival and growth has benefitted from increasing temperatures (de Wit et al. 2014, Ranno et al. 2021), and warmer climate may benefit the overall woodland expansion rate (Nolan et al. 2018).

The presence of domestic grazers that appear to have affected woodland expansion patterns in our study, seen in different expansion rates between grazed study areas and those protected from grazing, agrees with earlier findings (Speed et al. 2010, Gullet et al. 2023). Domestic sheep is the main large herbivore in Iceland and has greatly contributed to extensive land degradation and soil erosion (Arnalds & Barkarson 2003). Although the rate of birch woodland expansion was higher in areas protected from grazing, woodland expansion also occurred in areas that were open to grazing by the domestic sheep. This suggests complex dynamics between grazing pressure and land condition where the animals can have both impeding and facilitating effects on colonization of woody species, depending on environmental conditions and grazing pressures (Olofsson & Post 2018, Óskarsdóttir et al. 2022, Vuorinen et al. 2022). An impeding effect is seen when the young seedlings are grazed directly by the sheep (Hoogesteger & Karlsson 1992), while a facilitating effect can occur through disturbances such as trampling and grazing of vegetation that is too dense to allow for natural colonization; these activities can disturb thick sward and expose mineral soils, thus creating safe sites for seedling establishment (Murphy et al. 2022).

At least six out of nine study areas displayed continuous patterns of expansion. These results suggest that, regardless of management regime, these areas have all offered conditions favoring expansion for at least a part of the studied time-period, including suitable safe sites for birch colonization (Behrend et al. 2025). This is particularly true for areas showing a linear increase in woodland area. The three study areas displaying exponential expansion patterns, Leyningshólar, Ranaskógur and Thórsmörk, have possibly experienced changes in disturbance regimes that may have induced elevated rates of increase. Thórsmörk, for example, was fully fenced off from sheep grazing in 1990 followed by extensive revegetation of eroded areas. Both of these interventions are likely to have contributed to the 268 ha increase in birch woodlands in Thórsmörk, and the continued very active birch colonization (Behrend et al., 2025). The woodlands in Húsafell and Öxarfjörður showed a linear temporal expansion pattern that eventually flattened out. Thus, expansion proceeded at a more or less constant rate until a maximum value was reached at a point in time, mostly through an increased canopy cover rather than spatial expansion per se. This pattern might simply reflect that the woodlands in the outlined area of interest were unable to expand much more due to spatial constraints, i.e. landscape features preventing further expansion (del Monte-Luna et al. 2004). Alternatively, this could be related to anthropogenic disturbances such as woodland clearing for summerhouses, livestock grazing and planting of non-native trees; all common land use changes in Iceland that impact expansion of the natural birch woodlands. The possible effects of grazing are demonstrated in areas not protected from sheep grazing, such as Steinadalur and Mjóifjörður, where annual rates of increase were slower than average, or halted for periods of time.

Our results reveal the impacts of the surrounding landscape and topography on the rates and patterns of woodland expansion. This is particularly evident for lateral woodland expansion; study areas with one main direction of woodland expansion seem to represent either settings where expansion is influenced by prevailing dry winds that favor directional seed dispersal (Aradóttir et al. 1997) or where suitable conditions for expansion are limited to certain sections of the study area. The latter reflects the effects of topography (Mekonnen et al. 2021) and higher habitat suitability (Griffiths et al. 2011, Baguette et al. 2013). On the other hand, study areas with a limited lateral woodland expansion and varying main directions of dispersal, such as Mjóifjörður and Steinadalur, had an increase in canopy cover within the woodlands rather than an expansion of woodland area. This pattern could, however, also reflect geographical limitations; these areas were situated in valleys or fjords with steep slopes which may be difficult for woody species to colonize if partially barren and unstable surface (Bochet et al. 2009, Borda-Niño et al. 2019, Arnalds et al. 2023). Protection from livestock grazing and revegetation could promote faster woodland expansion on these slopes until the area has been fully occupied; a pattern observed in several of our study areas.

Implications for ecological restoration

The United Nations have declared 2021–2030 as the Decade on Ecosystem Restoration (UNEP/FAO 2020). Together with other recent environmental initiatives, such as the Bonn challenge (IUCN 2020) and the Kunming Montreal Global Biodiversity Framework (Convention on Biological Diversity, 2022), they call for extensive upscaling of restoration projects and for maximum utilization of existing ecosystems for passive and low-intensity restoration. Aerial photos present an often-unutilized opportunity to study spatio-temporal ecosystem changes, knowledge that can be used to guide future restoration efforts (de Almeida et al. 2020). The methodology applied here could be used to explore spatio-temporal patterns of other ecosystem types, making it a cost-effective alternative or supplement to field studies.

Restoration relying on planting nursery grown seedlings can be costly but is nevertheless often done at large scales without considering the existing biotic and abiotic environments (Kimball et al. 2015), regularly resulting in poor survival rates (Ferreira et al. 2023, Preece et al. 2023). Thus, it is worth considering the extensive capital, both financial and human, that can be saved by harnessing the potential for woodland expansion through natural regeneration from existing seed sources, or by applying restoration strategies such as applied nucleation and assisted natural regeneration in combination with land-use management (Shono et al. 2007, Corbin & Holl 2012). The extent of woodland in our study areas more than doubled over six decades with an average annual increase of 1.5%. Achieving a comparable increase in woodland cover by planting at conventional planting densities of 1500-2000 trees ha^{-1} as recommended for mountain birch in Iceland (personal communication, Land and Forest Iceland) would have required substantial resources and manpower, and serves as evidence that natural recovery or passive restoration can contribute to birch woodland restoration.

Our results furthermore indicate that management interventions such as protection from grazing can at least double woodland expansion rates, suggesting a potential to enhance woodland expansion. Monitoring the temporal development of ecosystems can inform whether interventions are needed to enhance restoration, thus supporting decision-making about restoration strategies and help to predict their efficiency under different conditions. For example, in environments without local seed sources, applied nucleation would be an appropriate strategy to establish these, while areas lacking safe sites for seedling establishment may need interventions to increase habitat suitability (Aradóttir & Halldórsson 2018). Integrating data on suitability of different habitats for natural regeneration with the presence and expansion rates of current birch woodlands could inform decision making on where to expect unassisted natural recovery and where restoration interventions are needed.

Conclusions

The level of upscaling needed to obtain ambitious global restoration goals calls for improved understanding of the patterns and drivers of natural ecosystem development. Our results, revealing rapid rates of birch woodland expansion in Iceland, also apply to these key ecosystems in the rest of the subarctic. Birch woodland growth rates, patterns of lateral expansion and main directions seem to be driven by local environmental factors, including climate and topography, and there were strong indications of an enhanced increase in woodland area in study areas protected from grazing. Our study suggests that protection of woodlands and woodland remnants from anthropogenic disturbances such as grazing by domestic animals and site-development could increase ecosystem expansion rates and enhance the outcome of passive and low-intensity restoration efforts.

Author contributions

Anna M. Behrend: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Methodology (equal); Writing – original draft (lead); Writing – review and editing (equal). **Emmanuel P. Pagneux**: Conceptualization (equal); Data curation (supporting); Formal analysis (supporting); Methodology (equal); Writing – original draft (supporting); Writing – review and editing (equal). **Kristín Svavarsdóttir**: Conceptualization (equal); Data curation (supporting); Writing – review and editing (equal). **Thóra E. Thórhallsdóttir**: Conceptualization (equal); Writing – review and editing (equal). **Ása L. Aradóttir**: Conceptualization (equal); Writing – original draft (supporting); Writing – review and editing (equal).

Data availability statement

The data used in this study are available in the Mendeley Data repository [Link will be provided upon manuscript acceptance].

Conflict of interest

The authors declare no conflict of interest.

Supporting information

The supporting information associated with this paper is available in the online version.

References

Ahmad, A., & Quegan, S. 2013. Comparative analysis of supervised and unsupervised classification on multispectral data. – Appl. Math. Sci. 7: 3681–3694.

Aradóttir, Á. L. 2007. *Restoration of birch and willow woodland on eroded*. In: Halldórsson, G., Oddsdóttir, E. S., & Eggertson, Ó. (eds.) Effects of afforestation on ecosystems, landscape and rural development, 67-74. Nordic Council of Ministers, Copenhagen, Denmark.

Aradóttir, Á. & Eysteinsson, T. 2005. Restoration of birch woodlands in Iceland. – In: Stanturf, J. A. & Madsen, P. (eds), Restoration of boreal and temperate forests. CRC Press, pp.195-209.

Aradóttir, A. L. & Halldorsson, G. 2018. Colonization of woodland species during restoration: Seed or safe site limitation? – Restor. Ecol. 26: S73–S83.

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

Arnalds, Ó. & Barkarson, B. H. 2003. Soil erosion and land use policy in Iceland in relation to sheep grazing and government subsidies. - Env. Sci. Policy 6: 105-113

Arnalds, Ó., Marteinsdóttir, B., Brink, S. H. & Thórsson, J. 2023. A framework model for current land condition in Iceland. - PLOS ONE 18: e0287764.

Arroyo-Rodríguez, V., Rito, K. F., Farfán, M., Navia, I. C., Mora, F., Arreola-Villa, F., Balvanera, P., Bongers, F., Castellanos-Castro, C., Catharino, E. L. M., Chazdon, R. L., Dupuy-Rada, J. M., Ferguson, B. G., Foster, P. F., González-Valdivia, N., Griffith, D. M., Hernández-Stefanoni, J. L., Jakovac, C. C., Junqueira, A. B., … Martínez-

Ramos, M. 2023. Landscape-scale forest cover drives the predictability of forest regeneration across the Neotropics. - Proc. R. Soc. B. 290: 20222203.

Baguette, M., Blanchet, S., Legrand, D., Stevens, V. M., & Turlure, C. 2013. Individual dispersal, landscape connectivity and ecological networks. – Biol. Rev. 88: 310–326.

Bates, D., Mächler, M., Bolker, B., & Walker, S. 2015. Fitting linear mixed-effects models using lme4. - J. Stat. Softw. 67: 1–48.

Behrend, A. M., Aradóttir, Á. L., Svavarsdottir, K., Thórhallsdóttir, T. E. & Pommerening, A. 2025. Natural colonization as a means to upscale restoration of subarctic woodlands in Iceland. – Restor. Ecol, e14332.

Bochet, E., García-Fayos, P. & Poesen, J. 2009. Topographic thresholds for plant colonization on semi-arid eroded slopes. - Earth Surf. Process. Landf. 34: 1758–1771.

Borda-Niño, M., Meli, P., & Brancalion, P. H. S. 2020. Drivers of tropical forest cover increase: A systematic review. - Land Degrad. Dev. 31: 1366–1379. https://doi.org/10.1002/ldr.3534

Bryn, A., Dourojeanni, P., Hemsing, L. Ø. & O'Donnell, S. 2013. A high-resolution GIS null model of potential forest expansion following land use changes in Norway. - Scand. J. For. Res. 28: 81–98.

Cochran, W.G. 1977 Sampling Techniques. 3rd ed., New York, John Wiley.

Convention on Biological Diversity 2022. Kunming-Montreal Global biodiversity framework. Conference of the parties to the convention on biological diversity, Montreal, Canada

Corbin, J. D. and Holl, K. D. 2012. Applied nucleation as a forest restoration strategy. - For. Ecol. Manage. 265: 37-46

Cover, T. & Hart, P. 1967. Nearest neighbor pattern classification. - IEEE Trans. Inf. Theory 13: 21-27.

Dalby, O., Pucino, N., Tan, Y. M., Jackson, E. L., Macreadie, P. I., Coleman, R. A., Young, M. A., Ierodiaconou, D., & Sherman, C. D. H. 2023. Identifying spatio-temporal trends in seagrass meadows to inform future restoration. - Restor. Ecol. 31: e13787. https://doi.org/10.1111/rec.13787

de Almeida, D. R. A., Stark, S. C., Valbuena, R., Broadbent, E. N., Silva, T. S. F., De Resende, A. F., Ferreira, M. P., Cardil, A., Silva, C. A., Amazonas, N., Zambrano, A. M. A. & Brancalion, P. H. S. 2020. A new era in forest restoration monitoring. - Restor. Ecol. 28: 8–11.

de Wit, H. A., Bryn, A., Hofgaard, A., Karstensen, J., Kvalevåg, M. M. & Peters, G. P. 2014. Climate warming feedback from mountain birch forest expansion: Reduced albedo dominates carbon uptake. - Glob. Change Biol. 20: 2344–2355.

del Monte-Luna, P., Brook, B. W., Zetina-Rejón, M. J., & Cruz-Escalona, V. H. 2004. The carrying capacity of ecosystems. – Glob. Ecol. Biogeogr. 13: 485–495. https://doi.org/10.1111/j.1466-822X.2004.00131.x

Dickinson, Y., Pelz, K., Giles, E. & Howie, J. 2016. Have we been successful? Monitoring horizontal forest complexity for forest restoration projects. - Restor. Ecol. 24: 8–17.

ESRI 2023. ArcGIS Pro Desktop: Release 3.1.

Eysteinsson, T. 2017. Forestry in a treeless land. Lustgården 84:27-34.

Food and Agriculture Organization (FAO) 2022. The State of the World's Forests 2022. Forest pathways for green recovery and building inclusive, resilient, and sustainable economies. FAO, Rome.

Ferreira, M. C., De Oliveira Cordeiro, A. O., Sampaio, A. B., Schmidt, I. B. & Vieira, D. L. M. 2023. Direct seeding versus seedling planting: Survival, biomass, growth, and cost up to 6 years for four tropical seasonal tree species. – Restor. Ecol. 31: e13807.

Foody, G. M. 2009. Sample size determination for image classification accuracy assessment and comparison. - Int. J. Remote Sens. 30: 5273–5291.

Gann, G. D., McDonald, T., Walder, B., Aronson, J., Nelson, C. R., Jonson, J., Hallett, J. G., Eisenberg, C., Guariguata, M. R., Liu, J., Hua, F., Echeverría, C., Gonzales, E., Shaw, N., Decleer, K. & Dixon, K. W. 2019. International principles and standards for the practice of ecological restoration. Second edition. - Restor. Ecol. 27: 1-46.

García, C., Espelta, J. M. & Hampe, A. 2020. Managing forest regeneration and expansion at a time of unprecedented global change. - J. Appl. Ecol. 57: 2310–2315.

Gimona, A., Poggio, L., Brown, I. & Castellazzi, M. 2012. Woodland networks in a changing climate: Threats from land use change. Biol. Cons. 149: 93–102.

Girard, F., Payette, S. & Gagnon, R. 2008. Rapid expansion of lichen woodlands within the closed-crown boreal forest zone over the last 50 years caused by stand disturbances in eastern Canada. - J. Biogeogr. 35: 529–537.

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]. Reykjavík, Iceland

Griffiths, G. H., Vogiatzakis, I. N., Porter, J. R. & Burrows, C. 2011. A landscape scale spatial model for semi-natural broadleaf woodland expansion in Wales, UK. - J. Nat. Conserv. 19: 43–53.

Gullett, P. R., Leslie, C., Mason, R., Ratcliffe, P., Sargent, I., Beck, A., Cameron, T., Cowie, N. R., Hetherington, D., MacDonell, T., Moat, T., Moore, P., Teuten, E. & Hancock, M. H. 2023. Woodland expansion in the presence of deer: 30 years of evidence from the Cairngorms Connect landscape restoration partnership. - J. Appl. Ecol. 00: 1-11.

Hoogesteger, J., & Karlsson, P. S. 1992. Effects of defoliation on radial stem growth and photosynthesis in the mountain birch (*Betula pubescens* ssp. *tortuosa*). - Funct. Ecol.

6: 317-323.

Icelandic Forest Service (IFS) 2023 Náttúrulegt birki á Íslands [Natural birch woodlands in Iceland] https://iceforestservice.maps.arcgis.com/apps/webappviewer/index.html?id=de3bbce4966b4290847ba4ae0c87d3f3 (accessed 12th of November 2024)

Intergovernmental Panel on Climate Change (IPCC) 2018. IPCC Special Report on the Impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gass emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development and efforts to eradicate poverty. https://www.ipcc.ch/sr15/, accessed on 3rd of July 2024

Intergovernmental Panel on Climate Change (IPCC) 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 on 20th of May 2024

International Union for Conservation of Nature (IUCN) 2020. The Bonn challenge. https://www.bonnchallenge.org/ accessed 4th of December 2023

Kadmon, R. & Harari-Kremer, R. 1999. Studying Long-Term Vegetation Dynamics Using Digital Processing of Historical Aerial Photographs. - Remote Sens. Environ. 68 - 164–176.

Kepfer-Rojas, S., Verheyen, K., Johannsen, V. K. & Schmidt, I. K. 2015. Indirect effects of land-use legacies determine tree colonization patterns in abandoned heathland. - Appl. Veg. Sci. 18: 456–466.

Kimball, S., Lulow, M., Sorenson, Q., Balazs, K., Fang, Y.-C., Davis, S. J., O'Connell, M. & Huxman, T. E. 2015. Cost-effective ecological restoration. – Restor. Ecol. 23: 800–810.

Laliberte, A. S., Rango, A., Havstad, K. M., Paris, J. F., Beck, R. F., McNeely, R., & Gonzalez, A. L. 2004. Object-oriented image analysis for mapping shrub encroachment from 1937 to 2003 in southern New Mexico. - Remote Sens. Environ. 93: 198–210. https://doi.org/10.1016/j.rse.2004.07.011

Leu, S., Ben-Eli, M. & Mor-Mussery, A. 2021. Effects of grazing control on ecosystem recovery, biological productivity gains, and soil carbon sequestration in long-term degraded loess farmlands in the Northern Negev, Israel. - Land Degrad. Dev. 32: 2580–2594.

Loftmyndir ehf. Aerial Photography Service. Accessed 21/06/2022 at https://mp.map.is/service.

Meddens, A. J. H., Hicke, J. A. & Vierling, L. A. 2011. Evaluating the potential of multispectral imagery to map multiple stages of tree mortality. - Remote Sens. Environ. 115: 1632–1642.

Mekonnen, Z. A., Riley, W. J., Berner, L. T., Bouskill, N. J., Torn, M. S., Iwahana, G., Breen, A. L., Myers-Smith, I. H., Criado, M. G., Liu, Y., Euskirchen, E. S., Goetz, S. J., Mack, M. C. & Grant, R. F. 2021. Arctic tundra shrubification: A review of mechanisms and impacts on ecosystem carbon balance. - Environ. Res. Lett. 16: 053001.

Mori, A. S., Lertzman, K. P. & Gustafsson, L. 2017. Biodiversity and ecosystem services in forest ecosystems: A research agenda for applied forest ecology. - J. Appl. Ecol. 54: 12-27.

Murphy, T. R., Hanley, M. E., Ellis, J. S., & Lunt, P. H. 2022. Optimizing opportunities for oak woodland expansion into upland pastures. - Ecol. Solut. Evid. 3: e12126.

Myers-Smith, I. H., Forbes, B. C., Wilmking, M., Hallinger, M., Lantz, T., Blok, D., Tape, K. D., Macias-Fauria, M., Sass-Klaassen, U., Lévesque, E., Boudreau, S., Ropars, P., Hermanutz, L., Trant, A., Collier, L. S., Weijers, S., Rozema, J., Rayback, S. A., Schmidt, N. M., … Hik, D. S. 2011. Shrub expansion in tundra ecosystems: Dynamics, impacts and research priorities. - Environ. Res. Lett. 6: 045509.

National Land Survey of Iceland. Aerial Photography Gallery. Accessed 21/06/2022 at https://www.lmi.is/is/vefsjar/korta-og-loftmyndasofn/loftmyndasafn

National Land survey of Iceland 2021. ÍslandsDEM v1.0 [Digital Elevation Model]. Retrieved 14/05/2022 from https://dem.lmi.is/mapview/?application=DEM

Nolan, C., Overpeck, J. T., Allen, J. R. M., Anderson, P. M., Betancourt, J. L., Binney, H. A., Brewer, S., Bush, M. B., Chase, B. M., Cheddadi, R., Djamali, M., Dodson, J., Edwards, M. E., Gosling, W. D., Haberle, S., Hotchkiss, S. C., Huntley, B., Ivory, S. J., Kershaw, A. P., … Jackson, S. T. 2018. Past and future global transformation of terrestrial ecosystems under climate change. - Science, 361: 920–923.

Olofsson, J. & Post, E. 2018. Effects of large herbivores on tundra vegetation in a changing climate, and implications for rewilding. - Phil. Trans. R. Soc. B 373: 20170437.

Óskarsdóttir, G., Thórhallsdóttir, T. 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. - Ecol. Evol. 12: e9430.

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

Pommerening, A. & Grabarnik, P. 2019. Individual-based methods in forest ecology and management. Springer Nature, Cham.

Preece, N. D., Van Oosterzee, P. & Lawes, M. J. 2023. Reforestation success can be enhanced by improving tree planting methods. - J. Environ. Manage. 336: 117645.

Qiu, Y., Xu, Z., Xu, C. & Holmgren, M. 2023. Can remotely sensed vegetation patterns signal dryland restoration success? - Restor. Ecol. 31: e13760,

R Development Core Team 2023. R: A language and environment for statistical computing. R Foundation for Statistical Computing.

Ranno, V., Blandino, C., & Giusso del Galdo, G. 2021. A comparative study on temperature and water potential thresholds for the germination of *Betula pendula* and two Mediterranean endemic birches, *Betula aetnensis* and *Betula fontqueri*. - Seed Sci. Res. 30: 249–261.

Sanchez, S., Arnalds, Ó., Thórsson, J., Dahlgren, R., & Aradóttir, Á. L. 2025. Soil carbon stocks of regenerating Icelandic native birch woodlands: Effects of space and time. - Sci. Total Environ. 958: 178063.

Shono, K., Cadaweng, E. A. & Durst, P. B. 2007. Application of Assisted Natural Regeneration to Restore Degraded Tropical Forestlands. - Restor. Ecol. 15: 620–626.

Snorrason, A., Traustason, B., Kjartansson B. T. & Heiðarsson, L. 2016. Náttúrulegt birki á Íslandi – Ný uttekt á útbreiðslu þess og ástandi [The natural birch woodlands in Iceland – a new assessment on distribution and state]. - Náttúrufræðingurin 86: 97-111.

Speed, J. D. M., Austrheim, G., Hester, A. J. & Mysterud, A. 2010. Experimental evidence for herbivore limitation of the treeline. - Ecol. 91: 3414–3420.

Suding, K., Higgs, E., Palmer, M., Callicott, J. B., Anderson, C. B., Baker, M., Gutrich, J. J., Hondula, K. L., LaFevor, M. C., Larson, B. M. H., Randall, A., Ruhl, J. B. & Schwartz, K. Z. S. 2015. Committing to ecological restoration. - Science 348: 638–640.

Tuominen, S. & Pekkarinen, A. 2005. Performance of different spectral and textural aerial photograph features in multi-source forest inventory. - Remote Sens. Environ. 94: 256–268.

United Nations Environment Programme (UNEP) & FAO 2020. The Decade on Ecosystem

Restoration. https://www.decadeonrestoration.org/, accessed 4th of June 2024

Verykokou, S. & Ioannidis, C. 2018. Oblique aerial images: A review focusing on georeferencing procedures. - Int. J. Remote Sens. 39: 3452–3496.

Vuorinen, K., Austrheim, G., Tremblay, J.-P., Myers-Smith, I. H., Hortman, H. I., Frank, P., Barrio, I. C., Dalerum, F., Björkman, M. P., Björk, R. G., Ehrich, D., Sokolov, A., Sokolova, N., Ropars, P., Boudreau, S., Normand, S., Prendin, A. L., Schmidt, N. M., Pacheco, A., … Speed, J. D. M. 2022. Growth rings show limited evidence for ungulates' potential to suppress shrubs across the Arctic. - Environ. Res. Lett. 17: 034013

Walsh, J. E., Overland, J. E., Groisman, P. Y. & Rudolf, B. 2011. Ongoing Climate Change in the Arctic. - AMBIO 40: 6–16.

Weisberg, P. J., Lingua, E. & Pillai, R. B. 2007. Spatial Patterns of Pinyon–Juniper Woodland Expansion in Central Nevada. - Rangel. Ecol. Manage. 60: 115–124.

Wickham, H. 2016. ggplot2. Elegant graphics for data analysis. Springer-Verlag https://ggplot2.tidyverse.org

Zhang, J., Shao, M., Yu, L. & Li, Y. 2020. Image super-resolution reconstruction based on sparse representation and deep learning. Signal Process. - Image Commun. 87: 115925.

Zong, S., Lembrechts, J. J., Du, H., He, H. S., Wu, Z., Li, M. & Rixen, C. 2022. Upward range shift of a dominant alpine shrub related to 50 years of snow cover change. - Remote Sens. Environ. 268: 112773.

Supplementary materials

Behrend, A. M., Pagneux, E. P., Svavarsdóttir, K., Thórhallsdóttir, T. E., & Aradóttir, Á. L. (2025). Spatio-temporal patterns of subarctic woodland expansion to guide future restoration. [submitted]

Table S1. Overview of aerial photos used in the analysis. Abbreviations: LMI = National Land Survey of Iceland; LOFT = Loftmyndir efh. The georeferencing transformation method used on all aerial photo was Spline with a minimum of 20 reference points.

Field site	Year	Source	Type of photo	Nr of bands	Pixel size (m)	Pixel size after super sampling (m)	Overall accuracy	K	Birch woodland area (ha)
Neðri Dalur	1955	LMI	Panchromatic	1	1.5	0.6	93.9	85.8	35.5
	1991	LMI	Panchromatic	1	5.9	0.6	90.8	81	72.5
	2000	LMI	Colour	3	1.2	0.6	93.9	86.3	81.2
	2010	LOFT	Colour	3	1.2	0.6	97.9	95.7	89.5
	2014	LOFT	Colour	3	1.2	0.6	91.8	80.8	99.5
	2020	LOFT	Colour	3	0.6	0.6	97.9	94.3	106.9
Húsafell	1957	LMI	Panchromatic	1	1.5	0.6	87.1	77.5	261.5
	1999	LMI	Colour	3	1.2	0.6	89.9	82.6	312.2
	2010	LOFT	Colour	3	1.2	0.6	93.7	88.3	348.8
	2022	LOFT	Colour	3	0.6	0.6	86.9	77.1	352.4
Thórsmörk	1960	LMI	Panchromatic	1	6.3	0.6	95.9	85.8	71.6
	1979	LMI	Panchromatic	1	18	0.6	96.9	87.9	100.9
	1989	LMI	Panchromatic	1	12.3	0.6	98.1	87.8	115.2
	1995	LMI	Panchromatic	1	12	0.6	92.9	83.6	142.3
	2001	LOFT	Colour	3	1.1	0.6	87.8	77.7	195.6
	2019	LOFT	Colour	3	0.6	0.6	94.9	89.3	383.9
Steinadalur	1957	LMI	Panchromatic	1	10.8	1.2	92.9	85.7	205.9
	1975	LMI	Panchromatic	1	16.2	1.2	90.8	80.7	330.7
	1982	LMI	Panchromatic	1	19	1.2	87.8	75.6	333
	1994	LNI	Panchromatic	1	12.9	1.2	93.9	87.6	372.7
	2003	LOFT	Colour	3	1.2	1.2	94.9	89.7	418.7
	2009	LOFT	Colour	3	1.4	1.2	93.9	87.7	434.9
	2014	LOFT	Colour	3	1.2	1.2	95.9	88.7	441.6
	2021	LOFT	Colour	3	2.7	1.2	95.9	88.7	467.8
Mjóifjörður	1984	LMI	Panchromatic	1	17.2	0.6	93.9	87.3	61
	1991	LMI	Panchromatic	1	12.9	0.6	93.9	85.9	65.2
	2009	LOFT	Colour	3	1.3	0.6	97.9	95.9	73.4
	2022	LOFT	Colour	3	1.4	0.6	91.8	83.3	86.5
Leyningshólar	1954	LMI	Panchromatic	1	5.9	0.6	91.8	79.6	24.8
	1980	LMI	Panchromatic	1	17.4	0.6	95.9	91.8	27.6
	1994	LMI	Panchromatic	1	13.5	0.6	93.9	87.4	29.4
	2009	LOFT	Colour	3	1.2	0.6	87.9	87	31.4
	2018	LOFT	Colour	3	0.6	0.6	86.7	73.2	50.2
Öxarfjörður	1955	LMI	Panchromatic	1	1.1	0.6	88.8	73.5	113.4

	1981	LMI	Panchromatic	1	1.7	0.6	93.9	86.4	164.1
	1998	LMI	Colour	3	1.4	0.6	90.8	75.8	188.9
	2007	LOFT	Colour	3	5.2	0.6	96.9	91.8	192.3
	2019	LOFT	Colour	3	0.6	0.6	88.8	88.7	198.2
Ranaskógur	1967	LMI	Panchromatic	1	2.2	0.6	96.2	81.2	41.4
	1982	LMI	Panchromatic	1	1.8	0.6	91.8	78.3	48.1
	1993	LMI	Panchromatic	1	1.5	0.6	88.8	72.2	65.1
	2000	LMI	Colour	3	2.6	0.6	97.9	95.8	69.5
	2006	LOFT	Colour	3	2.6	0.6	95.9	91.4	76.3
	2016	LOFT	Colour	3	2.6	0.6	91.8	80.2	95.6
	2021	LOFT	Colour	3	0.6	0.6	1	1	110.8
Bæjarstaðarskógur	1975	LMI	Panchromatic	1	19.8	0.6	94.9	86.1	50.2
	1988	LMI	Panchromatic	1	11.9	0.6	96.9	90.4	60.8
	1997	LMI	Panchromatic	1	18.7	0.6	91.4	83.3	83.4
	2005	LOFT	Colour	3	1.2	0.6	1	1	103.1
	2019	LOFT	Colour	3	0.6	0.6	97.1	85.4	140.3

Table S2. Results from the linear mixed-effect model on the effect of protection from livestock grazing on birch woodland absolute growth rate (AGR).

	E	**Std. error**	**t-value**	***p***
Intercept	1.39	0.34	4.13	<0.01
Restoration 1	1.53	0.59	2.59	<0.05

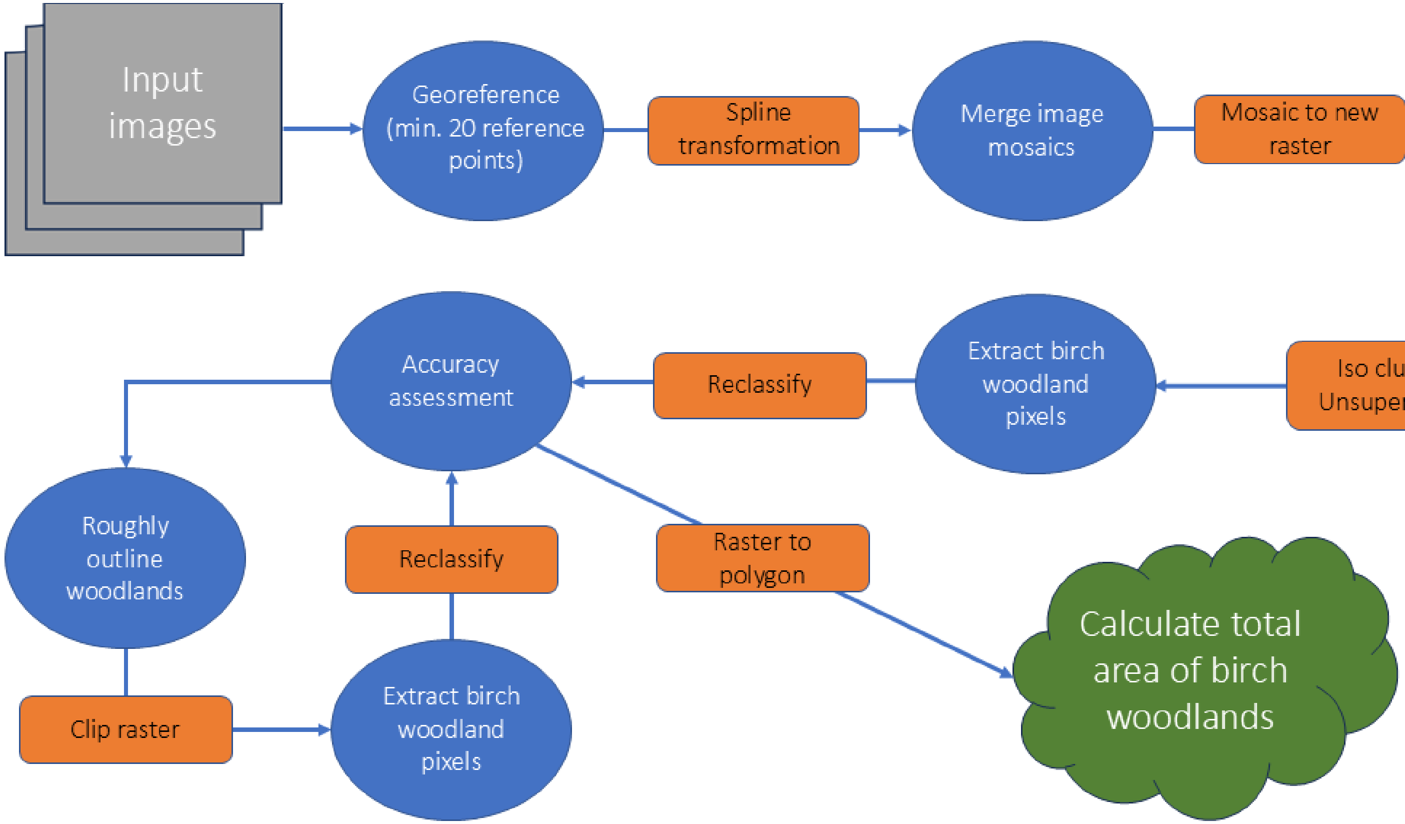


Figure S1. Schematic workflow of the aerial photo analysis, from the input of images to the final calculation of total area of birch woodlands. Blue circles represent different steps in the analysis, and orange quadrants are the tools used in ArcGIS Pro (version 3.0.3) to obtain next step in the analysis.

II

RESTORATION ECOLOGY
The Journal of the Society for Ecological Restoration

RESEARCH ARTICLE

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

Anna M. Behrend[1,2], Ása L. Aradóttir[1], Kristín Svavarsdóttir[3], Thóra E. Thórhallsdóttir[4], Arne Pommerening[5]

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

---

Author contributions: AMB, ALA, KS, TET designed and conceived the study; AMB performed the fieldwork, with contributions from ALA, KS, TET; AMB, AP analyzed the data; AMB drafted the manuscript; all authors reviewed and edited the manuscript and gave their final approval for publication.

[1] Faculty of Environmental and Forest Sciences, Agricultural University of Iceland, Árleynir 22, 112, Reykjavík, Iceland
[2] Address correspondence to A. M. Behrend, email annamariager@lbhi.is
[3] Land and Forest Iceland, Árleynir 22, 112, Reykjavík, Iceland
[4] Faculty of Life and Environmental Sciences, University of Iceland, Sæmundargötu 2, 102, Reykjavík, Iceland
[5] Faculty of Forest Sciences, Department of Forest Ecology and Management, Swedish University of Agricultural Sciences, Skogmarksgränd 17, 901 83, Umeå, Sweden

doi: 10.1111/rec.14332
Supporting information at:
http://onlinelibrary.wiley.com/doi/10.1111/rec.14332/suppinfo

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

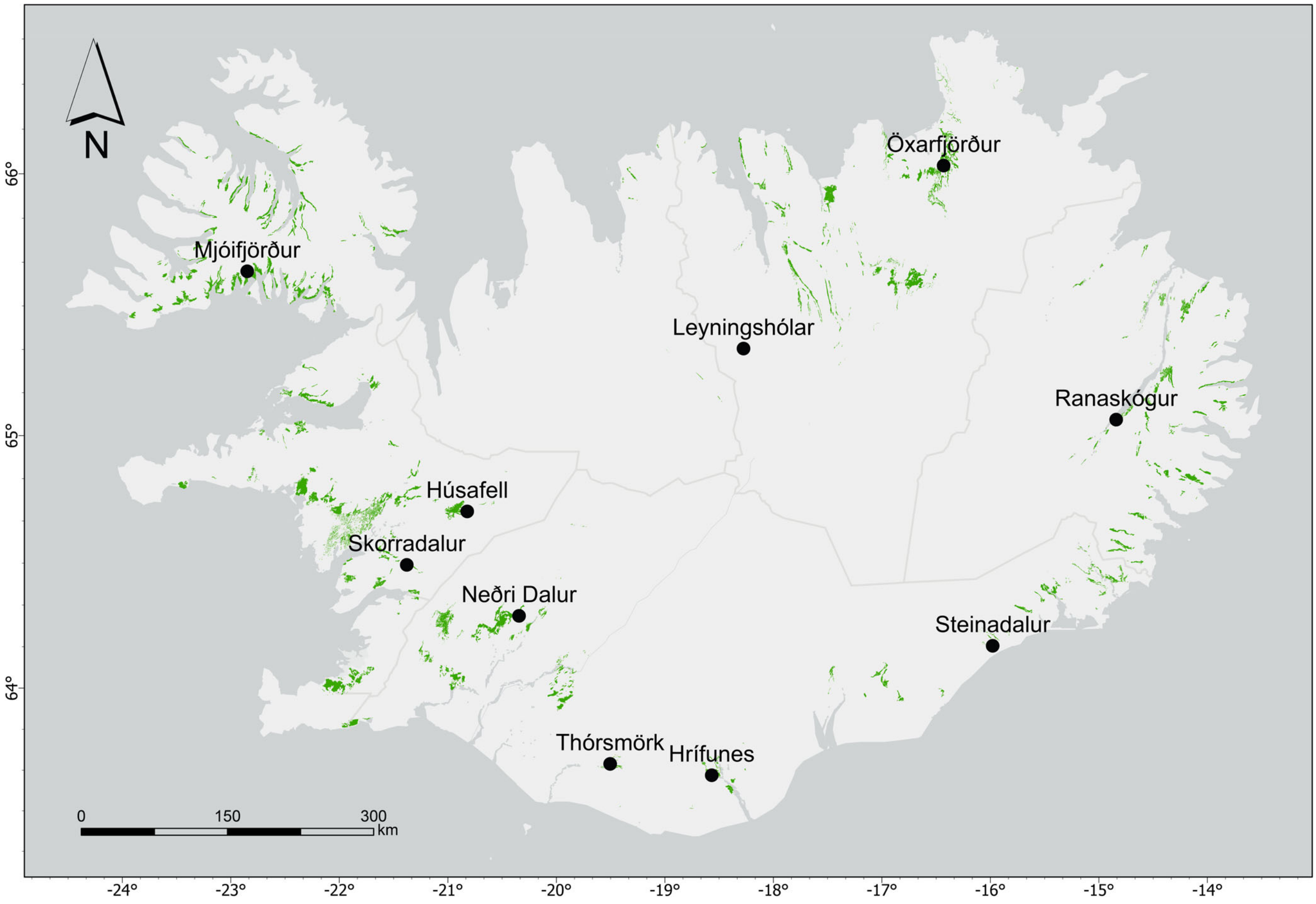


Figure 1. Locations of the 10 study areas across lowland Iceland. The present distribution of mountain birch woodlands is shown in green. Map databases: mountain birch map data, Icelandic Forest Service (2023); Geographic Information System, ArcGIS Pro (version 3.0.3).

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

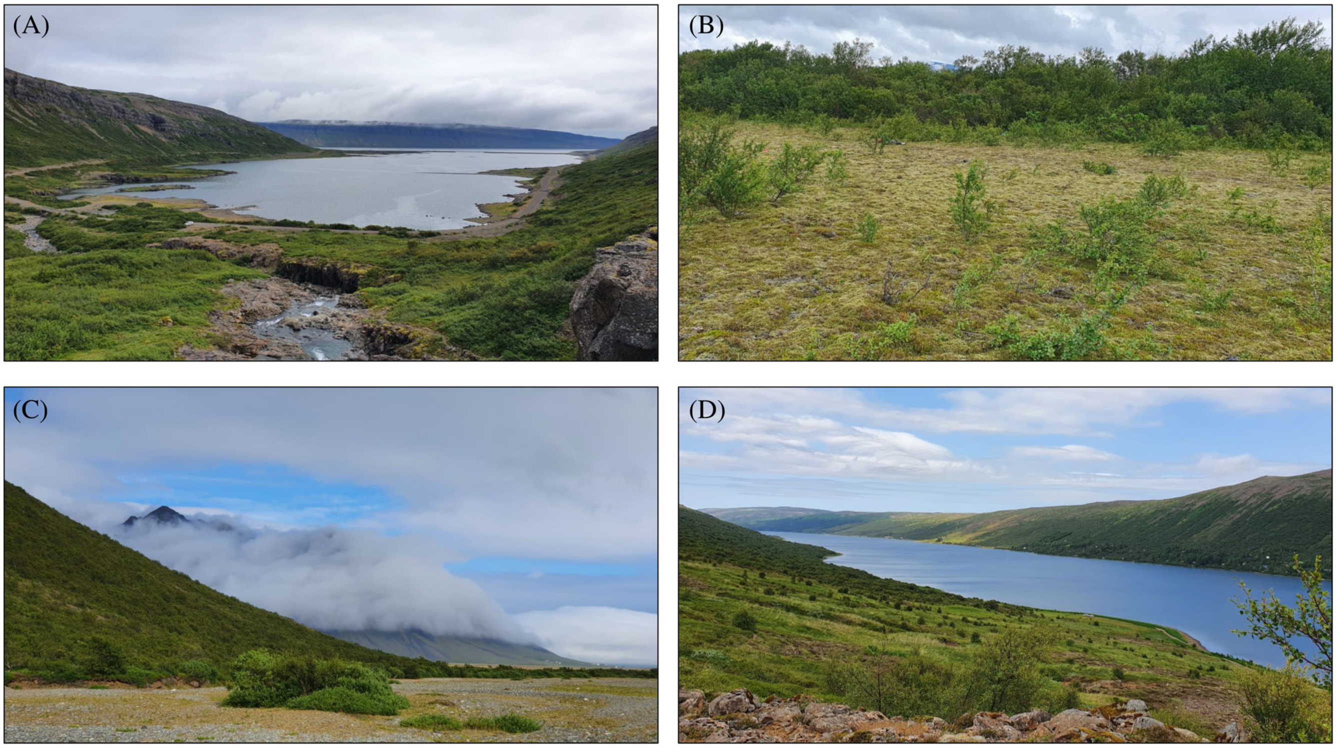


Figure 2. Examples of the visual variations in landscape and colonization patterns among the study areas in Iceland, (A) Mjóifjörður; (B) Húsafell; (C) Steinadalur; (D) Skorradalur.

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.

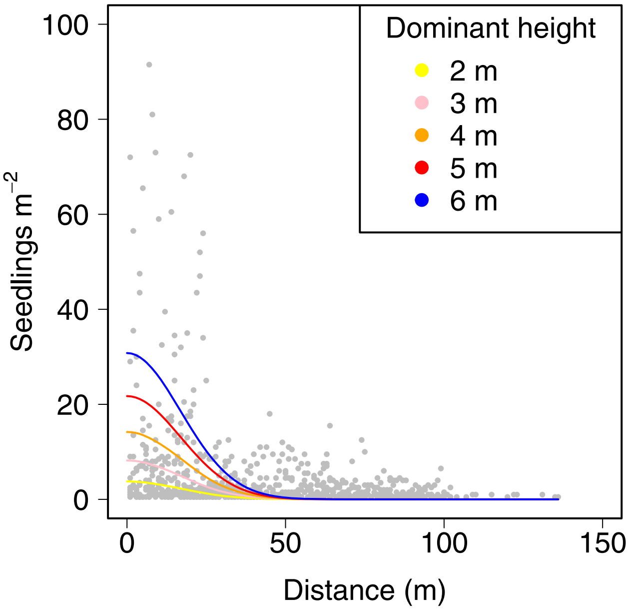


Figure 3. Gaussian colonization kernels indicating the trends of combined seedling densities as functions of distance to the woodland edge for different adjacent dominant woodland heights at 10 areas around Iceland. Gray dots are observed values for all study areas.

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}

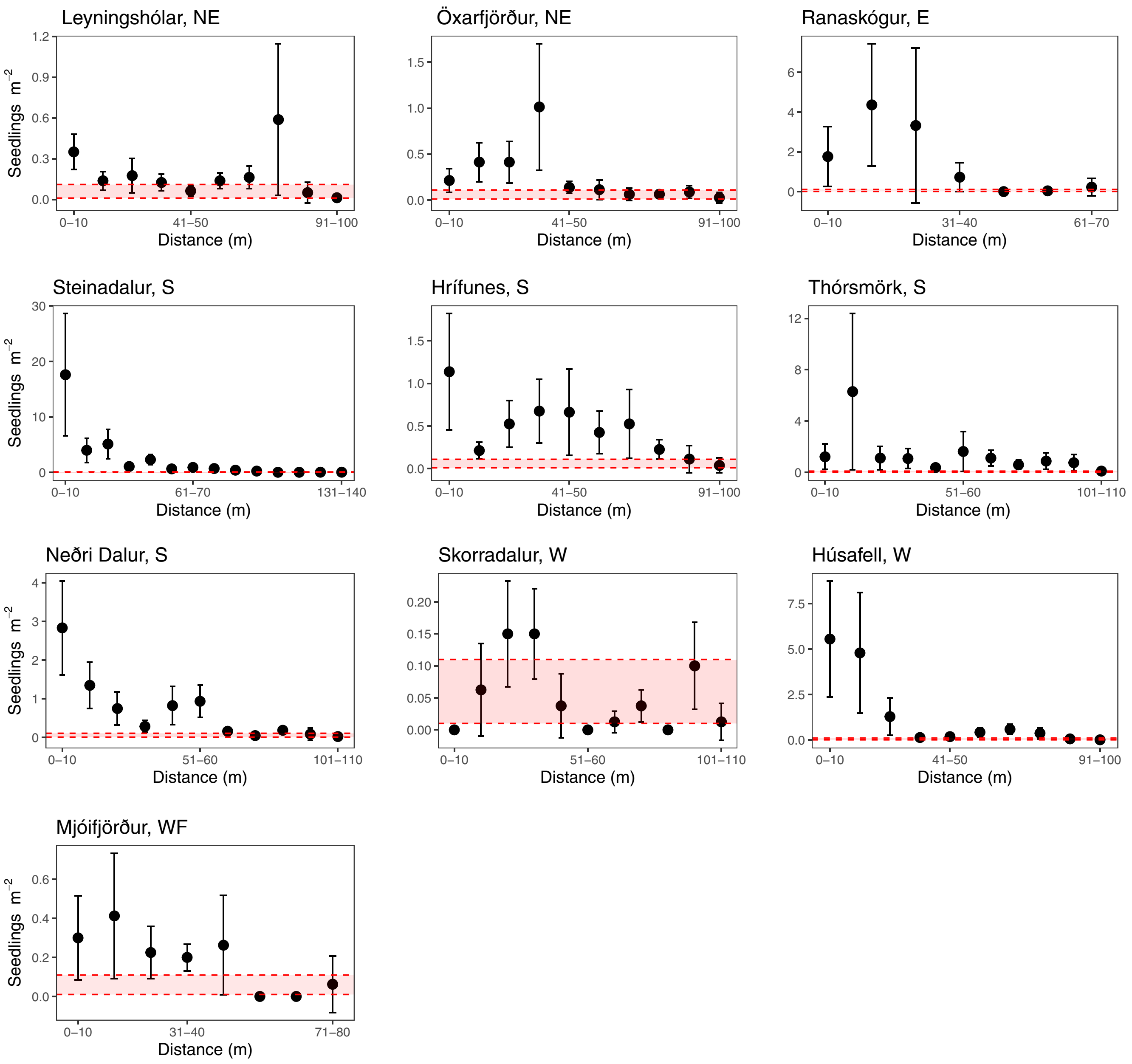


Figure 4. Average mountain birch seedling densities on the study areas for pooled size classes (mean ± SD) plotted against distance from the woodland edge for 10 study areas around Iceland. The areas in red represent the success criteria for *woodland-forming natural colonization*, ranging from 0.01 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.

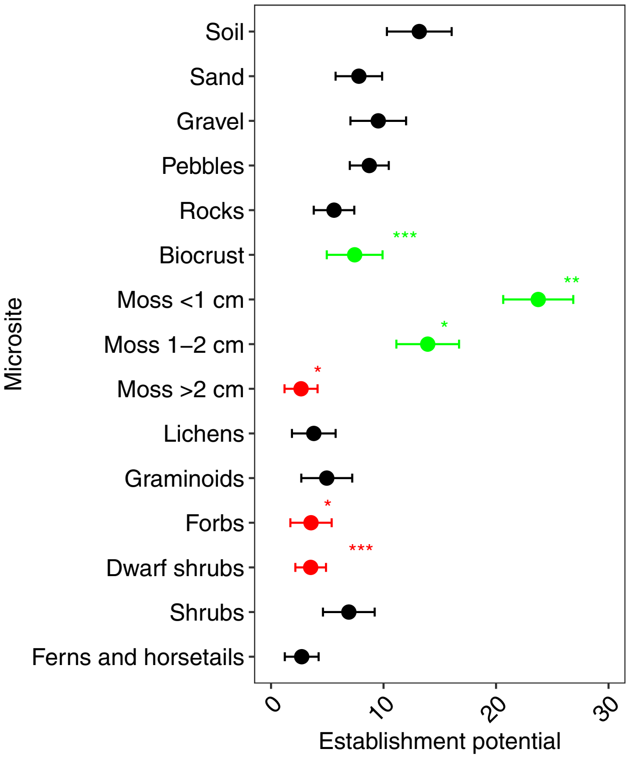


Figure 5. Establishment potential (mean ± SE), defined as the number of seedlings in size class I occupying a microsite multiplied by its proportional cover, derived from GLMMs (see Table 3 for an overview of the different categories). Asterisks indicate significance (*$p < 0.05$, **$p < 0.01$, and ***$p < 0.001$) 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

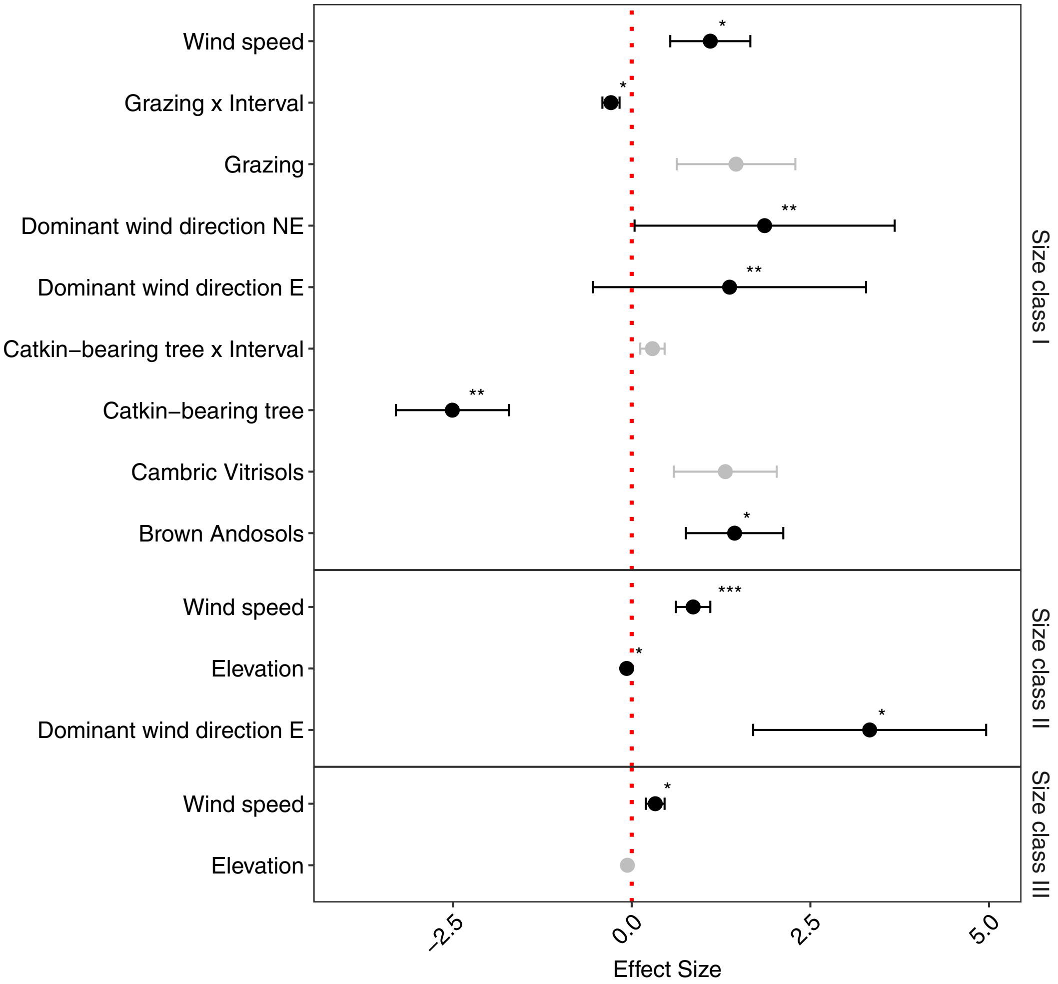


Figure 6. Effect-size plot (±95% CI) from the minimum zero-inflated GLMM hurdle models with negative binomial distributions on the influence of different explanatory variables on the density of seedlings in different size classes. Results are reported for separate models for each response variable (size 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.

Acknowledgments

We gratefully acknowledge Á. H. Arnórsson, B. Guðjónsdóttir, K. Valsdóttir, M. Guðbrandsdóttir, and S. Sánchez for assistance in fieldwork. We thank the Icelandic Met Office, the Icelandic Forest Service, and Loftmyndir efh. for permitting use of their data for our analysis. Furthermore, we wish to thank J. M. Kasper for assistance with analysis. This study is part of the research project *Eco-Birch - restoration of birch woodlands in the 21st century: challenges, approaches and benefits*, funded by the Icelandic Government's Strategic Research and Development Program for Societal Challenges, 2020–2023, grant no. 200090-5601-5603. The data used in this study are available in the Mendeley Data repository, https://data.mendeley.com/datasets/54yx9m6gv8/1.

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.

Coordinating Editor: Karel Prach

Received: 30 June, 2024; First decision: 8 August, 2024; Revised: 23 September, 2024; Accepted: 22 October, 2024

Supplementary materials

Behrend, A. M., Aradóttir, Á. L., Svavarsdóttir, K., Thórhallsdóttir, T. E., & Pommerening, A. (2025). Natural colonization as a means to upscale restoration of subarctic woodlands in Iceland. *Restoration Ecology*, *33*(1), e14332. https://doi.org/10.1111/rec.14332

Table S1. Full list of predictor variables used in the generalized linear mixed models (GLMM, negative binomial distributions with logit-link), with response variables being density of seedlings in the different size classes. Transect nested within field site was included as random variables in all models. All variables were on a study area-specific level.

Variable	Unit	Definition
Birch density	n m^{-2}	Number of birch plants in three different size groups (I = <2 cm, II = 2-20 cm, III = >20 cm)
Interval	Categorical (1-14)	10m distance intervals from the closest (1) to the furthest (14) from the woodland edge
Site	Site ID	Individual site (10 in total)
Catkin presence outside transects	Binomial variable (0 or 1)	Presence or absence of catkin-bearing trees within the 20 m^2 segments up to 5 m from the edge of the transect.
Microsite occupancy	Categorical	Microsite occupied by seedlings. Only measured for seedlings in *size group I* (<2 cm). See **Table 2** for description of the different types
Microsite cover	Cover (%)	Cover of the different types of microsites (**Table 2)** estimated per 10 m long (20 m^2) transect segment based on 25 points within a 50 x 50cm quadrat.
Grazing presence	Binomial variable (0 or 1)	Presence or absence of sheep grazing on a transect-specific level.
Average temperature May-August	C°	5-year average (2016 – 2021)
Total annual precipitation	mm	5-year average (2016 – 2021)
Wind speed Sep-Dec	m s^{-1}	5-year average (2016 – 2021)
Dominant wind direction	Categorical (N, NE, E, SE, S, SW, S, NW)	Dominant wind direction calculated from 5-year averages (2016-2021).
Elevation	m	Mean elevation of transects (from beginning to end of transect).
Soil type	Categorical	Soil type in which the transects were taken.
Dominant height of woodland canopy	m	Measured by the national survey on native mountain birch woodlands in Iceland by the Icelandic Forest Service.
Woodland size	m^2	Measured by the national survey on native mountain birch woodlands in Iceland by the Icelandic Forest Service.

Table S2. Summary of the results from the different models. The same models were run separately with all three size classes as response variables, except for catkin-bearing trees, which was only used as a predictor variable for seedlings in size class I. All models had the following standard R code: *glmmTMB(family = truncated_nbinom2(link = "log"), ziformula = ~ 1*. Values in bold indicate significant values, with asteriks indicating level of significance for the model intercpet (p < 0.05 *; p < 0.01 **; p < 0.001, ***).

Explanatory variable(s)	**Model equation**	**Intercept (for models performed on different size classes of birch plants)**		
Models with interval as interaction		**I**	**II**	**III**
Catkin-bearing trees 5≥ meters outside transect interval	n(birch plants) ~ Catkin.inside * Interval + (1 | Field.site/Transect.unique)	**4.25*** **	-	-
Dominant height of woodland canopy (m)	n(birch plants) ~ Dominant.height.woodland * Interval + (1 | Field.site/Transect.unique	**2.88*** **	**3.06*** **	1.27
Area of woodland (ha)	n(birch plants) ~ Area.of.woodland * Interval + (1 | Field.site/Transect.unique	**3.33*** **	**2.75*** **	1.13
Grazing	n(birch plants) ~ Grazing.presence * Interval + (1 | Field.site/Transect.unique	**2.73*** **	**2.49*** **	0.66
Model without interval as interaction				
Interval	n(birch plants) ~ Interval + (1 | Interval) + (1 | Field.site/Transect.unique)	**3.65*** **	**2.61*** **	0.52
Catkin-bearing trees 5≥ meters outside transect interval	n(birch plants) ~ Catkin.outside + (1 | Field.site/Transect.unique	**3.79*** **	-	-
Models with interval as random effect				
Mean temperature May-August (C°)	n(birch plants) ~ Temp.mean + (1 | Interval) + (1 | Field.site/Transect.unique)	2.01	**2.84***	**1.73***
Total annual precipitation (mm)	n(birch plants) ~ Precipitation + (1 | Interval) + (1 | Field.site/Transect.unique)	2.8	0.51	-0.23
Mean wind speed Sep-Dec ($m\ s^{-1}$)	n(birch plants) ~ Wind.speed + (1 | Interval) + (1 | Field.site/Transect.unique)	0.99	-1.07	-1.42
Dominant wind direction	n(birch plants) ~ Dominant.wind.direction + (1 | Interval) + (1 | Field.site/Transect.unique)	0.05	**2.39****	1.16
Mean wind speed x Dominant wind direction	n(birch plants) ~ Dominant.wind.direction * Wind.speed + (1 | Interval) + (1 | Field.site/Transect.unique)	**-6.49***	**-2.58***	**-1.83***
Elevation	n(birch plants) ~ Elevation + (1 | Interval) + (1 | Field.site/Transect.unique)	1.44	**2.45*** **	0.87
Soil type	n(birch plants) ~ Soil.type + (1 | Interval) + (1 | Field.site/Transect.unique)	**1.44***	1.2	0.2

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 (seedling density in size class I relative to microsite cover). Significant values are highlighted in bold.

<table>
<tr><th colspan="5">Model formula: glmmTMB(potential ~ Microsite + (1|Field.site/Transect.unique/Interval), family = ziGamma(link = "log"), ziformula=~1, data = data)</th></tr>
<tr><th></th><th>Estimate</th><th>SE</th><th>z-value</th><th>P value</th></tr>
<tr><td>Biocrust[a]</td><td>1.69</td><td>0.3</td><td>5.6</td><td>< 0.001</td></tr>
<tr><td>Soil</td><td>0.58</td><td>0.34</td><td>1.72</td><td>0.08</td></tr>
<tr><td>Sand</td><td>0.02</td><td>0.48</td><td>0.04</td><td>0.96</td></tr>
<tr><td>Gravel</td><td>0.07</td><td>0.31</td><td>0.23</td><td>0.82</td></tr>
<tr><td>Pebbles</td><td>-0.29</td><td>0.32</td><td>-0.92</td><td>0.36</td></tr>
<tr><td>Rocks</td><td>-0.67</td><td>0.39</td><td>-1.7</td><td>0.09</td></tr>
<tr><td>Lichens</td><td>-0.62</td><td>0.36</td><td>-1.73</td><td>0.08</td></tr>
<tr><td>Mosses <1 cm</td><td>0.82</td><td>0.28</td><td>2.92</td><td>< 0.01</td></tr>
<tr><td>Mosses 1-2 cm</td><td>0.61</td><td>0.31</td><td>1.98</td><td>< 0.01</td></tr>
<tr><td>Mosses >2 cm</td><td>-0.77</td><td>0.34</td><td>-2.25</td><td>< 0.05</td></tr>
<tr><td>Grasses & sedges</td><td>-0.39</td><td>0.34</td><td>-1.17</td><td>0.24</td></tr>
<tr><td>Forbs</td><td>-0.89</td><td>0.4</td><td>-2.23</td><td>< 0.05</td></tr>
<tr><td>Ferns & Horsetails</td><td>-1.38</td><td>0.91</td><td>-1.51</td><td>0.7</td></tr>
<tr><td>Dwarf shrubs</td><td>-1.28</td><td>0.37</td><td>-3.51</td><td>< 0.001</td></tr>
<tr><td>Shrubs</td><td>-0.28</td><td>0.75</td><td>-1.72</td><td>0.08</td></tr>
</table>

[a] Intercept in the overall model: Biocrust. To test for the effect of biocrust on birch establishment potential, levels were rearranged in R using the *relevel*-function. The Aikake Information Criteria (AIC) was similar (± 1) in the two models. Sample size equals the number of 10 m intervals along transects for each study area (Hrífunes = 40, Húsafell = 41, Leyningshólar =37, Mjóifjörður = 23, Neðri Dalur = 42, Ranaskógur = 40, Skorradalur = 41, Steinadalur = 46, Thórsmörk = 43, Öxarfjörður = 40).

Table S4. Seedling occurrence and mean cover of different microsites for seedlings in size class I.

	Leyningshólar		**Öxarfjörður**		**Ranaskógur**		**Steinadalur**		**Hrífunes**		**Thórsmörk**		**Neðri Dalur**		**Skorradalur**		**Húsafell**		**Mjóifjörður**		**Total**
	n	Cover (%)	n	Cover (%)	n	Cover (%)	n	Cover (%)	n	Cover (%)	n	Cover (%)	n	Cover (%)	n	Cover (%)	n	Cover (%)	n	Cover (%)	
Soil	1	30.3	0	3.3	1	0	0	0	6	3.9	6	3.9	63	3.6	1	2.5	45	1.1	0	2.4	123
Sand	0	0	1	9.2	0	0.2	31	1.1	0	0	1	0.9	0	0	0	0	139	26.2	0	0	172
Gravel	0	14.6	0	0.3	4	7.5	44	3.5	0	1.6	33	18.6	32	5.2	1	0.2	35	7.8	6	19.6	155
Pebbles	0	9.9	0	0.3	8	6.6	68	11	0	0.3	10	9.2	51	1.6	2	1.1	69	14	5	9.2	213
Rocks	0	24.7	0	17.7	0	12.7	11	14.9	0	0	3	9.1	29	2.7	0	6.3	8	8.4	1	23.9	52
Biocrust	0	1.2	1	2.7	1	2.3	6	8.8	9	3.9	38	4.5	18	0.4	4	0.2	22	3.4	0	0	99
Lichens	0	1	5	7.3	0	19.8	2	0.5	0	0.5	1	1.3	4	0.4	0	0.2	280	18.4	0	6.3	292
Mosses <1 cm	1	0.3	0	3.1	13	6.6	222	3.4	13	7.2	289	15.3	97	4.9	2	2	34	3	1	3	672
Mosses 1-2 cm	0	0.2	0	3.9	0	7	123	6.4	18	4.5	298	8.5	24	4	3	0.5	49	0.5	0	0.5	515
Mosses >2 cm	0	1.5	0	8.9	0	10.2	4	32.3	1	51.1	2	10.3	4	26.8	0	9.7	3	1.4	0	10.1	14
Graminoids	0	1.5	0	4.2	1	14.8	4	1.6	0	4.5	16	7.3	15	3	0	26.4	7	4.6	0	0.5	43
Forbs	0	4.8	0	0.6	2	9.8	4	0.7	0	2.7	8	3.3	4	3.1	0	7.8	3	2.4	0	0	21
Ferns & Horsetails	0	0	0	0	1	0.9	0	0	0	0.5	1	0.9	0	0.1	0	4.5	0	0.2	0	0	2
Dwarf shrubs	0	10.2	0	37.7	2	1.4	3	15.4	2	18.1	28	4.3	21	41.7	0	38.3	36	8.4	3	24.2	95
Shrubs	0	0	0	0.8	0	0.2	0	0.3	0	1.3	15	2.7	0	2.4	0	0.5	1	0.3	0	0.3	16
Total	2		7		33		522		49		749		362		13		731		16		2484

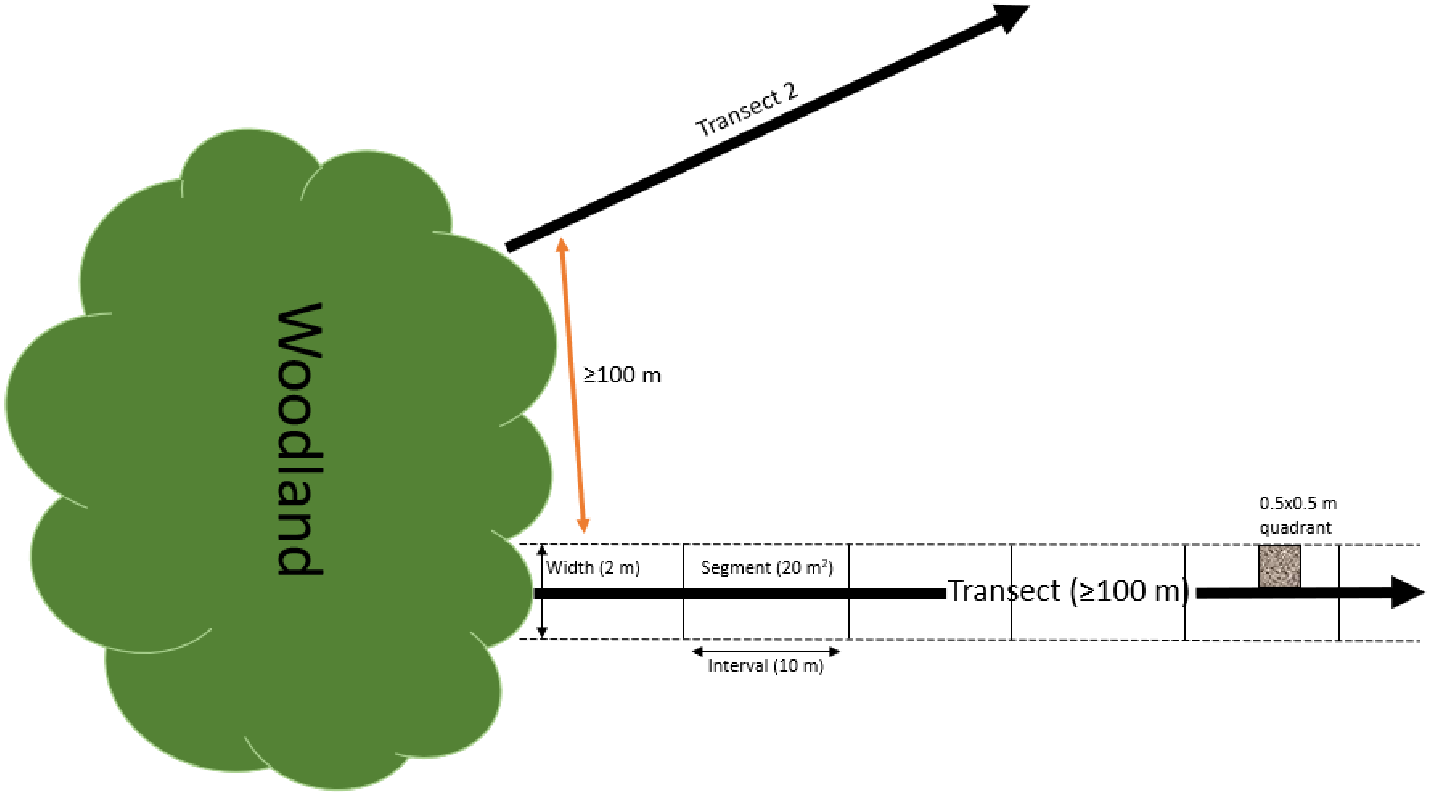


Figure S1. Transect design used in the study. The width of the transect was 2 meters, and the intervals used in the subsequent modelling was 10 m (thus, transect segments were 20 m^2). The figure furthermore depicts the position of the quadrats used to assess microsite cover, which was placed at 10 m intervals on the transects, starting at 5 m, and always on the left side of the transect line. The starting point of each transect was generated prior to fieldwork using a stratified random sampling approach in ArcGIS pro, using the outline of the woodland edge based on recent aerial photos, and always minimum 100 meters apart. At two of the study areas, one or more transects did not reach a 100 m length due to obstacles such as fences, roads, water bodies, or cultivated land. To ensure a minimum area of 200 m^2 per transect, the width of these transects was increased from 2 to 4 m and continued for as long as possible.

III

Ecological Modelling 503 (2025) 111073

Contents lists available at ScienceDirect

Ecological Modelling

journal homepage: www.elsevier.com/locate/ecolmodel

Growing at the edge: Modelling sapling colonization, performance, and effective range of mountain birch (*Betula pubescens* ssp. *tortuosa*)

Anna Mariager Behrend [a], Arne Pommerening [b,*]

[a] *Faculty of Environmental and Forest Sciences, Agricultural University of Iceland, Árleynir 22, 112, Reykjavík, Iceland*
[b] *Faculty of Forest Sciences, Department of Forest Ecology and Management, Swedish University of Agricultural Sciences, Skogmarksgränd 17, Umeå 901 83, Sweden*

ARTICLE INFO

Keywords:
Betula pubescens (ssp. *tortuosa*)
Effective colonization range
Colonization kernel
Natural colonization
Sheltering effect
Tree morphology
Restoration ecology

ABSTRACT

Colonization of trees from existing woodlands into adjacent open lands is a critical process of passive restoration, leading to the formation of secondary woodlands. Important drivers of this process include sheltering from surrounding woodlands, which can affect both the spatial range of colonization and the performance of individual saplings. In this study we analysed the effects of sheltering and canopy height on the patterns of natural colonization and individual sapling performance of mountain birch (*Betula pubescens* ssp. *tortuosa*) in different regions of Iceland. We measured sapling densities and individual sapling morphology along transects, and modelled colonization using hyperbolic kernel functions. We subsequently used these colonization kernels to define and calculate the effective spatial range for mountain birch colonization. The results showed a clear effect of regional environments on the performance of mountain birch saplings. The effective spatial range of colonization varied greatly between regions, ranging from 16.6 m in areas with birch of low stature, to 67.4 m in the region with the tallest, straightest stems. We furthermore saw that individual sapling performance was a direct product of sheltering, as one kernel function parameter was significantly correlated with the tree morphology index used in this study. Our results highlighted the importance of sheltering from surrounding woodlands on both colonization patterns and on individual sapling performance, though sheltering effects are generally low in Iceland. This should be considered in research as well as practice by combining natural colonization with efficient localized planting. The effective spatial range can aid in finding an appropriate balance between these two restoration methods.

1. Introduction

Progressive succession of barren tundra habitats to woodlands is a key process in the challenging formation of climax ecosystems in the subarctic North (Cargill and Chapin, 1987; Hester et al., 1991). Although open areas with appropriate microclimatic conditions naturally develop into woodlands with time, colonization processes in this harsh environment can be slow and sometimes arrested for decades if not aided (Thórhallsdóttir, 1998; Gretarsdottir et al., 2004; Hofgaard and Wilmann, 2002). In restoration practice, this process is traditionally facilitated and accelerated by large-scale tree planting. Although planting can be an efficient method for rapid active restoration, it often either leads to large homogenous monocultures, or to failures due to a lack of knowledge of the mechanistic drivers of successful forest establishment (Holl et al., 2011; Crouzeilles et al., 2017; McCallum et al., 2018). Afforestation by natural regeneration offers a more economic alternative (Campanhã Bechara et al., 2021) and follows the often-preferred principle of *passive restoration*. Such a process typically results in more natural ecosystems with heterogeneous structures that benefit biodiversity and ecosystem resilience more than traditional plantations (Chazdon and Guariguata, 2016; Crouzeilles et al., 2020). The results of passive restoration, however, are often less predictable than planting, because they depend on many environmental factors including short-term weather events that are difficult to control (Peringer and Rosenthal, 2011; Pedersen et al., 2023). Naturally both active and passive restoration methods are not mutually exclusive and particularly harsh environments such as those in the subarctic North may require combinations as part of adaptive management.

The colonization of new habitats by trees depends in part on their ability to spread through vegetative propagation or seed dispersal. Within woodlands, this propagation usually faces less environmental resistance and can be characterized by *regeneration kernels* (Law et al.,

---

* Corresponding author.
E-mail address: arne.pommerening@slu.se (A. Pommerening).

https://doi.org/10.1016/j.ecolmodel.2025.111073
Received 13 November 2024; Received in revised form 21 February 2025; Accepted 23 February 2025
Available online 1 March 2025

2009; Pommerening and Grabarnik, 2019), a comparatively recent mathematical-statistical concept that is frequently used in individual-based ecology and modelling. Regeneration kernels essentially are akin to probability density functions and describe the combined influence of abiotic and biotic factors on the spatial establishment potential of plants, including both facilitation and inhibition. As colonization typically describes the migration of plants from woodlands into open habitats unoccupied by trees, we propose a related concept, i.e. the modelling of *colonization kernels*. Some of the most crucial ecological factors for colonization in open habitats are sheltering from prevailing winds by adjacent woodlands and the intensity of the emitted seed cloud, which depends on woodland canopy height (Eränen and Kozlov, 2006; Greenwood et al., 2014; Pedersen et al., 2023). Both effects, however, are notoriously difficult to disentangle, as they encompass the combined effects of the height of the forest canopy, wind directions and velocities. The effect of forest canopy height on wind sheltering can in turn be confounded by larger quantities of seed (due to larger tree crowns) released at larger heights above the soil surface the larger the forest canopy height is (Thomson et al., 2011). Usually, colonization is restricted to an area close to the woodland edge (Willson, 1993). For birch species, a wind-born genus, colonization patterns can greatly differ and include high, constant rates of lateral woodland movement over time as well as the sporadic establishment of tree clusters at some distance from the nearest seed source (Potthoff, 2017; Aradóttir and Halldórsson, 2018; Maletha et al., 2021; Óskarsdóttir et al., 2022).

Wind sheltering of regenerated tree saplings by adjacent woodlands furthermore influences survival and overall sapling performance (Potthoff, 2017; Wu et al., 2018).

The performance of individual saplings is often characterized by their morphology, which can give important clues in terms of possible resistance to environmental influences, particularly wind (Rowe and Speck, 2005). Both biotic and abiotic stress can cause the morphology of individual saplings within a population to differ in terms of straightness, total height, stem diameter, and number of stems per individual (Dassot et al., 2015; MacFarlane and Kane, 2017; Zhang et al., 2017). This process can, for example, result in a shrubby, multi-stemmed appearance (basitonic growth) in some trees when they are affected by certain abiotic and biotic factors (Tanentzap et al., 2012). It is generally not considered an advantage for a tree to grow horizontally or to develop multiple stems, as this is usually associated with decreased vigour and shorter life spans (Verwijst, 1988; Jonsson, 2004). Other than that, this growth pattern is caused by or is an adaptation to windy climates and minimises wind-induced forces affecting trees (Niklas and Spatz, 2012). Such adaptations are indeed a phenomenon observed in many different tree species as a response to extreme environments, including a high number of days with snow cover (Tremblay and Bégin, 2005), major wind events (Telewski, 2012) and browsing by ungulates (Hoogesteger and Karlsson, 1992; Speed et al., 2011). This is particularly true for different subspecies of birch forming woodlands in the subarctic and Arctic regions (Aradóttir et al., 1997; Jonsson, 2004; Dobbert et al., 2021).

Quantifying sapling establishment and performance in open areas can provide valuable knowledge for the restoration management of key species, such as birch. This information furthermore provides valuable insights into passive restoration strategies that rely on the expansion of existing woodlands and planted woodland isles by natural colonization (Corbin and Holl, 2012; Aradóttir and Halldórsson, 2018). Using colonization kernels and a morphology index as summary characteristics and indicators, we analysed patterns of spatial establishment and sapling morphology of mountain birch (*Betula pubescens* ssp. *tortuosa*) trees in ten different woodlands in Iceland, and studied how these were affected by the environmental conditions of adjacent woodlands. Based on preliminary field observations, we proposed the following two hypotheses:

1. Natural colonization of birch is largely restricted to an effective range close to the woodland edge, a phenomenon primarily driven by a sheltering effect from prevailing winds and a seed dispersal effect exerted by the existing woodland.
2. The sheltering effect exerted by adjacent woodlands supports apical dominance and stem straightness of birch saplings growing at the woodland edge. Conversely, where the sheltering effect is low, sapling morphology is expected to deviate from the aforementioned characteristics.

2. Materials and methods

2.1. Study species

Mountain birch (*Betula pubescens* ssp. *tortuosa*) is a subspecies of downy birch (*Betula pubescens* Ehrh.), which is native to large parts of the subarctic North (Panarctic Flora, 2024). In Iceland, mountain birch is the only native woodland-forming tree, and all native birch in Iceland is considered to be of this subspecies (Kristinsson et al., 2018). With abundant light and seed rain (Grime and Jeffrey, 1965; Aradóttir and Halldórsson, 2018), the shade-intolerant mountain birch is an efficient colonizer due to its ability to establish in nutrient-poor soils and on open ground (Atkinson, 1992). This ability is limited, however, by active soil erosion and cryoturbation, which can cause high seedling mortality (Aradóttir, 2004; Aradóttir and Halldórsson, 2018). The colonization efficiency can furthermore differ substantially with prevailing wind conditions (Aradóttir et al., 1997).

The morphological appearance of mountain birch can range from completely upright single-stemmed trees up to 14 m in total height, to shrubby plants with basitonic, concave stems growing laterally near the ground (Jonsson, 2004). Mountain birch morphology is partially driven by the influence of wind (Jonsson, 2004), grazing pressure (Speed et al., 2011), soil conditions (Verwijst, 1988), and partially by genetic isolation of distinct populations, a phenomenon previously studied and confirmed in the fragmented Icelandic mountain birch woodlands (Pálsson et al., 2023).

2.2. Field measurements

We collected data from ten different mountain birch woodlands in Iceland, covering the entire ecoregion (Fig. 1). The areas varied in climate, topography, and land use history (Table 1), but as a common denominator, all of them had ongoing natural colonization starting at the woodland edge and extending into the adjacent open landscapes. As part of our analysis, we classified the ten study areas according to four distinct regions: North, East, South and West, and Westfjords of Iceland. This distinction was made partly based on a study on genetic variations between isolated mountain birch populations (Pálsson et al., 2023) and partly based on a study on land condition that indicated a high correlation of ecological conditions within these regions (Arnalds et al., 2023).

All birch saplings were measured in a spatially explicit way: four transects (at least 100 × 2 m) were laid out at each study area (Behrend et al., 2024). Three transects were taken in the same cardinal direction and a single transect extended into another direction. A minimum distance of at least 100 m was maintained between transects, and, using ArcGIS Pro (version 3.0.3), the transects were randomly placed along the defined woodland edge prior to fieldwork. If active colonization was registered on the last 10 m of the transect, sampling continued for another 10 m until no more saplings were registered in a subsequent 10-m interval.

All birch saplings along the transects were counted, and densities were calculated on a 1-m scale (saplings m^{-2}). If the length of a sapling's longest shoot exceeded 20 cm, both length and total height were measured (Fig. 2). At this length, birch saplings are at least a few years old, and the effects of local environments start to show in their morphology (Atkinson, 1992). Environmental data were gathered at the weather station closest to each of the ten areas (2016 – 2021,

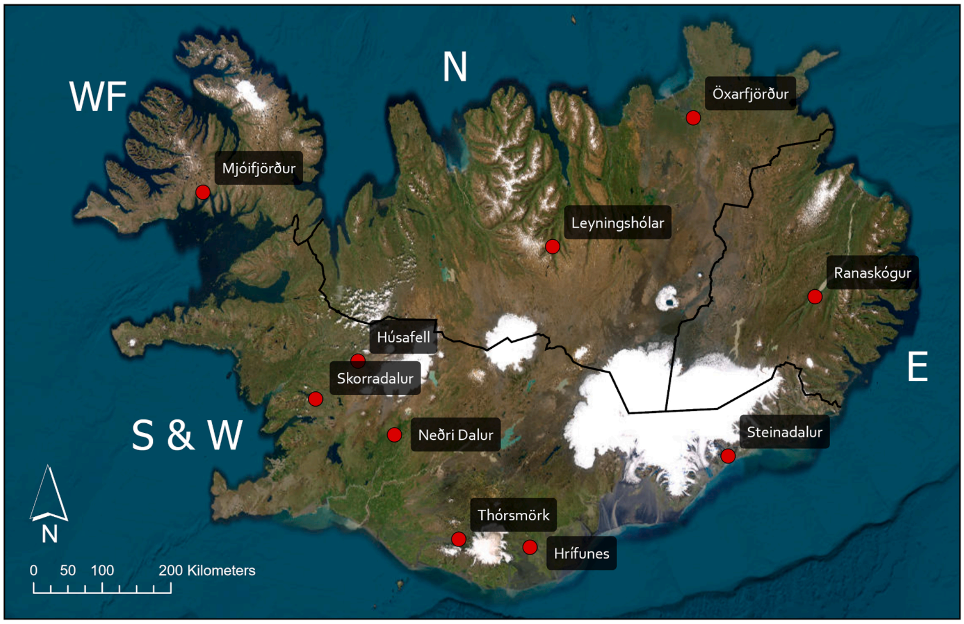


Fig. 1. Map of Iceland including the ten study areas used in our study with the geographical regions used in the analyses, outlined in black: N = North; E = East; S and W = South & West; WF = Westfjords.

Table 1
Environmental and topographical variables for the different study areas.

Region	Study area	Altitude range (m.a.s.l)	Mean temperature May-August (C°)	Mean annual precipitation (mm)	Mean wind speed (m/s)
North	Leyningshólar	127 - 367	9.4	449.7	3.5
	Öxarfjörður	23 - 137	8.9	–	4.2
East	Ranaskógur	19 - 210	5.5	905.2	7.6
South and West	Steinadalur	7 - 624	9.4	1161.8	6.5
	Hrífunes	96 – 223	9.9	1476.8	4.9
	Thórsmörk	175 – 504	9.1	–	2.6
	Neðri Dalur	87 – 305	9.9	1107.0	5.5
	Skorradalur	61 - 273	9.7	965.9	4.1
	Húsafell	132 - 375	9.1	807.2	3.9
Westfjords	Mjóifjörður	1 - 341	6.8	–	8.1

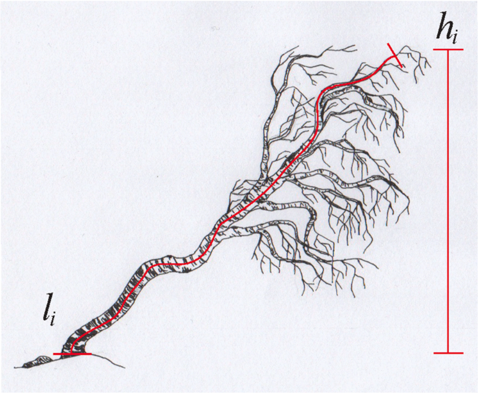


Fig. 2. Measurements performed on each individual birch plant *i* with a length of >20 cm.

unpublished data from the Icelandic Met Office, www.vedur.is). Elevations of the sampled transects were obtained from the Digital Elevation Model *ÍslandDEM V1.0* in ArcGIS Pro (National Land Survey of Iceland, 2021).

2.3. *Morphology*

We characterised the morphology of birch plants with a length larger than 20 cm, i.e. individuals that can be considered saplings or trees rather than seedlings, by ratio s_i of total tree height, h_i, and the length of the longest growing stem, l_i, of tree *i*, a method previously applied in studies on the morphology of Icelandic mountain birch to indicate the shrubby appearance and lateral growth frequently occurring in this species (Jonsson, 2004; Óskarsdóttir et al., 2022; Fig. 2):

$$s_i = \frac{h_i}{l_i} \tag{1}$$

In contrast to tree length, total tree height is defined as the distance between the tip of the most terminal leader and the soil surface, measured along a perpendicular line dropped from the top (van Laar and Akça, 2007; Fig. 2). In the remainder of the text, we refer to the ratio in Eq. (1) as *tree morphology index*.

Low s_i values of sapling *i* indicate that $l_i > h_i$ and consequently the tree stem is not straight. Large values of s_i of tree *i* imply straight stem development with a maximum of 1 when $l_i = h_i$.

We tested for spatial differences in tree morphology by applying a linear mixed-effect model. Defining s_{ijk} as the morphology index of individual tree *i* on transect *j* in region *k*, the model can be written as

$$s_{ijk} = \beta_0 + u_{ijk} + v_{jk} + \beta_1 x_k + \epsilon_{ijk}, \tag{2}$$

where β_0 is the overall, fixed model intercept and β_1 is the fixed model parameter. The model includes two random effects: u_{ijk} is the random effect of i^{th} distance from the woodland edge in transect j and region k, v_{jk} is the random effect of transect j in region k whilst x_k is region k. ϵ_{ijk} is the error term for each individual observation expressing the remaining variance. We performed comparisons between regions using the Bonferroni correction for multiple testing.

To further test for the effects of the existing woodlands on the performance of trees colonizing parts of the adjacent open landscape, we applied a multiple regression model with the morphology index as response variable and various explanatory variables, including dominant woodland height (m), elevation of transect (m.a.s.l), wind speed (m s^{-1}, 5-year averages), grazing (presence/absence, binomial variable), average temperature (°C, 5-year averages) and total woodland area (ha). Additionally, we tested for interactions between wind speed and cardinal direction of the transect. We used backwards stepwise selection to select the model with the best overall fit, based on the Akaike Information Criteria (Table S1). The model with the best fit according to AIC included the variables dominant woodland height (m), elevation (a) and wind speed (w), and had the following structure:

$$s_{jk} = \beta_0 + \beta_1 \times m_{jk} + \beta_2 \times a_{jk} + \beta_3 \times w_k + \epsilon_{jk} \tag{3}$$

Dominant woodland height and elevation were measured at transect level (index j), whilst wind speed was only available at the level of regions (index k). As before, parameter β_0 is the overall, fixed model intercept whilst $\beta_{1,\ldots,3}$ are further fixed model parameters and ϵ_{jk} is the error term.

2.4. *Hyperbolic colonization kernels*

To analyse environmental effects on the colonization patterns of birch saplings outside existing woodlands, we devised the new concept of a colonization kernel and applied it to densities of birch saplings on individual transects, j. In the initial phase of the analysis, we fitted three basic kernel functions to the data: the Gaussian, exponential, and hyperbolic kernels (Pommerening and Grabarnik, 2019). All three kernel types included dominant height of the most adjacent birch stand, m_j, and distance, $dist_j$, between individual trees and the nearest edge of the birch stand as explanatory variables. The kernel functions differ in the number of model parameters that scale the range of interaction. The hyperbolic colonization kernel, p_j, also referred to as fractional kernel, accommodated our data best when fitting the function to regional data. Nonlinear regression for the Gaussian and exponential kernel functions representing the Westfjords region did not converge. Therefore, we continued the analysis with the hyperbolic colonization kernel

$$p_j = \frac{m_j^{\alpha}}{1 + \left(\frac{dist_j}{\delta}\right)^2}. \tag{4}$$

In Eq. (4), $dist_j$ is the Euclidean distance between a given 1-m section of transect j and the nearest woodland edge in meters, since the trees were recorded in sections. As before, variable m in our study denotes the dominant height of the existing adjacent woodland in metres, whilst α, and δ are model parameters. Dominant height is a forest stand characteristic defined as the height corresponding to the quadratic mean stem diameter of the 100 largest trees per hectare (van Laar and Akça, 2007). Parameter δ scales the spatial range of the kernel function, i.e. the attenuation of the curve with distance. Parameter α scales maximum resource absorption as a function of dominant stand height and governs the strength of the colonization kernel (Pommerening and Grabarnik, 2019). Another advantage of the hyperbolic kernel was that it has only two model parameters compared to the other kernel functions we tried. As a result there were no "competing" parameters accounting for distance or dominant height twice and therefore the subsequent correlation and modelling analysis would yield unambiguous results.

To characterise the general patterns of how natural colonization of birch relates to regional differences in tree morphology indices, we fitted kernel functions to transects pooled according to the four different regions, i.e. we estimated one kernel model for every region. The model parameters were estimated using nonlinear regression based on both the least-square and the maximum-likelihood method.

To examine the possible effect of sheltering on tree morphology indices, we applied linear regressions to the relationship between morphology index of the different regions, and the kernel model parameters.

Hyperbolic colonization kernels, as applied in our study, model the density of tree establishment as a function of the dominant height of existing woodlands and of distance from the woodland edge. Accordingly, there is a distance along the transects where establishment density reaches spatial independence, i.e. where tree density does not any longer depend on distance. This point in the different transects is ecologically interesting and can be considered the *effective spatial range* of birch colonization from existing woodlands into the open landscape surrounding them (Fig. 3).

To determine the effective spatial range of mountain birch colonization, we identified the maximum value of m_j^{α}, i.e. maximum kernel density at the woodland edge where $dist_j = 0$, across all study areas and transects. In plant ecology, benchmarks for dispersal and colonization are often based on observed maximum values (Beckman and Sullivan, 2023; Lososová et al., 2023), and $\max\left(m_j^{\alpha}\right)$ indicates the highest birch colonization density observed across all fitted kernel functions. This is where birch colonization was most successful. We used this absolute density estimate as a reference for our entire study. This seemed justified as our study areas covered a wide range of habitats across Iceland so that $\max\left(m_j^{\alpha}\right)$ is likely to reflect the country's maximum.

In analogy to statistical hypothesis testing, we calculated the effective spatial range of birch colonization, $dist_{\max}$, as the distance at which the kernel function value corresponds to 5 % of the maximum colonization kernel function values observed in our study:

$$p_j^{(0.05)} = 0.05 \times \max\left(m_j^{\alpha}\right) \tag{5}$$

The effective spatial range, $dist_{\max}$, can then be calculated as

$$dist_{\max} = \delta \times \sqrt{\frac{m_j^{\alpha}}{p_j^{(0.05)}} - 1} \tag{6}$$

and is derived from the hyperbolic colonization kernel (Appendix A). We

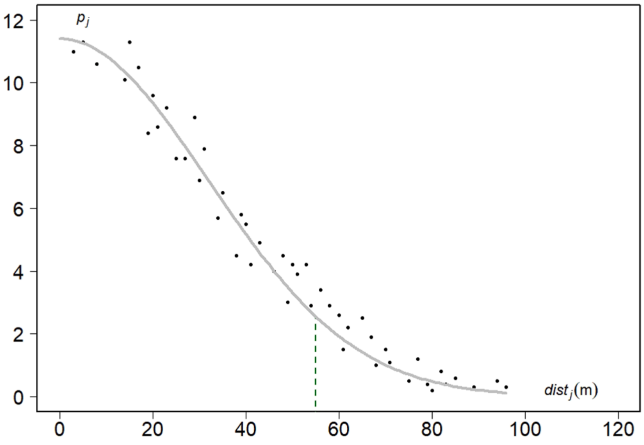


Fig. 3. Illustrating the concept of $dist_{\max}$: the curve represents the hyperbolic colonization kernel, and the green dashed line indicates $dist_{\max}$ of the kernel calculated according to Eq. (6).

calculated $dist_{\max}$ for the pooled data from the four different regions.

All data handling and analysis were performed in R version 4.3.2 (R Development Core Team, 2023).

3. Results

A total of 5501 birch plants were counted across all study areas, growing at a distance ranging from 1 to 140 m from the woodland edge. 740 of these plants were longer than 20 cm in total length (l_i) and were therefore included in morphology measurements for calculating the tree morphology index of Eq. (1). One of the ten study areas, Skorradalur in the South and West region, did not have sufficient data in any of their transects for kernel function regressions to converge, thus this area was not considered in the analysis.

3.1. *Tree morphology*

There was considerable variation in the morphology index (Eq. (1)) of mountain birch trees in our study, with values ranging from 0.03 (almost complete lateral growth) to 0.96 (almost complete upright) (Fig. 4**)**. Values of the morphology index were significantly lower in the Westfjords ($p < 0.05$, Table 2) compared to the Northern, Southern and Western, and Eastern regions, with a mean morphology index of 0.42, indicating a strong influence of environmental factors thus preventing stem straightness. As expected, the trees with the straightest stems were found in the East of Iceland, with a mean morphology index of 0.82. The morphology index values in the East did not differ significantly from the Northern region, which had mean values of 0.69, but did significantly differ from the South and Western region with an index of 0.64.

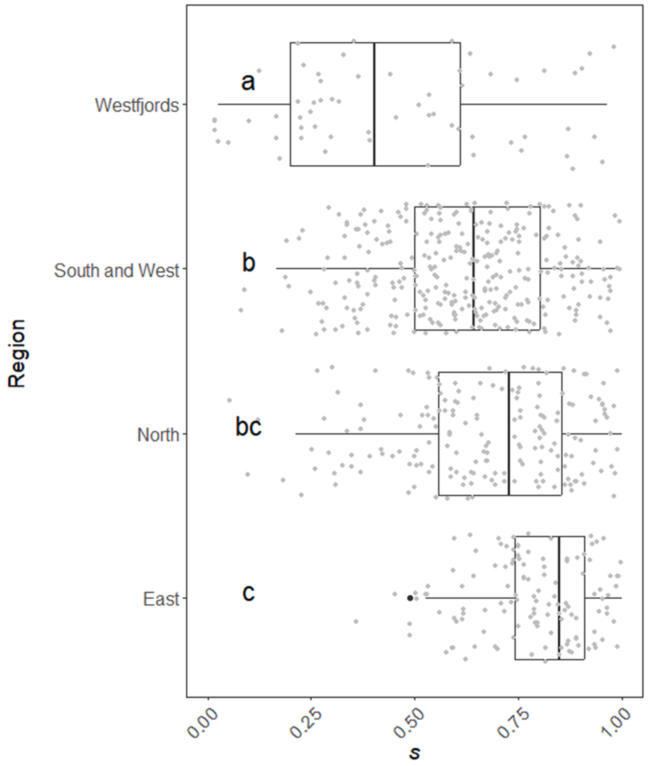


Fig. 4. Boxplots illustrating the variation in morphology index, *s*, between regions included in this study. Letters indicate significant differences in morphology index between geographic regions (Bonferroni test, $p < 0.05$). Sample size for the different regions: Westfjords, $n = 67$; South and West, $n = 331$; North, $n = 192$; East, $n = 150$.

Table 2
Results from the linear mixed-effects models testing for the effect of region on the morphology index of mountain birch trees.

Comparison	Estimate	Std. Error	*z* value	*p*
N – E	−0.18	0.08	−2.31	0.09
S & W – E	−0.22	0.07	−3.20	**< 0.01**
WF – E	−0.51	0.08	−6.09	**< 0.001**
S & W – N	−0.05	0.05	−1.00	0.74
WF – N	−0.34	0.07	−5.07	**< 0.001**
WF – S & W	−0.29	0.06	−4.94	**< 0.001**

3.2. *Regional colonization patterns and effective spatial range*

We were able to determine the effective spatial range, $dist_{\max}$, for all four aforementioned regions. The value of $dist_{\max}$ was highest in the East, with an effective spatial range of 67.4 m, while the North and South and West regions had markedly lower values of 44.8 m and 30.6 m, respectively (Fig. 5). The Westfjords region displayed the shortest effective spatial range with a value of 16.6 m. $dist_{\max}$ was, furthermore, highly correlated with the birch morphology index ($R^2 = 0.92$).

When examining the hyperbolic kernel curves fitted to the four different regions, there were distinct patterns reflecting both the differences in the morphology index of the trees and the dominant woodland heights of the study areas (Fig. 6, Table S2). Surprisingly, the kernel functions had the largest maximum in the South and West region, followed by the Eastern region. The East, which had the highest value of $dist_{\max}$, had high densities close to the woodland edge, with the curve flattening less with increasing distance to the woodland edge than in the South and West region. Upon initial examination, the curves from the North and the Westfjords look very similar, although there was a difference in dominant woodland height of three meters. However, despite generally low densities in the transects from the Northern region, birch saplings tended to disperse more widely, possibly indicating some sheltering effect or more benign germination and growth conditions. This is furthermore reflected in the higher $dist_{\max}$ value for the Northern region. When applying linear regressions to the morphology indices and the kernel function parameters (see Eq. (4)) individually, the results revealed significant relationships for δ ($p < 0.05$), but not for α ($p = 0.07$, Fig. 7).

3.3. *Environmental correlations with the morphology index*

The best performing multiple linear regression model involving morphology index *s* (Eq. (1)) in mountain birch only explained 34 % of the variation between study areas. In this model, elevation, dominant height of adjacent woodlands and mean annual wind speeds were

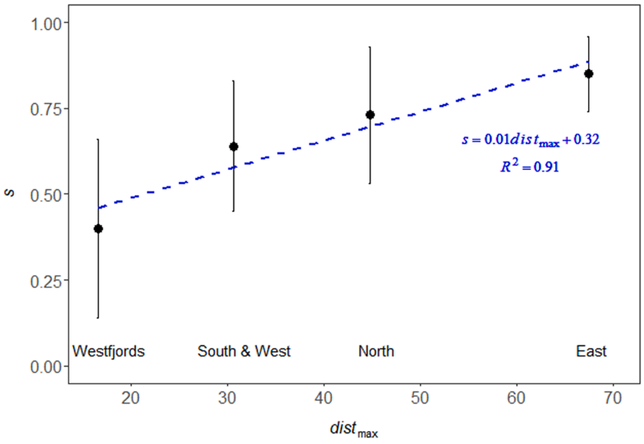


Fig. 5. Correlation between $dist_{\max}$ and median (± standard deviation) morphology index, *s*.

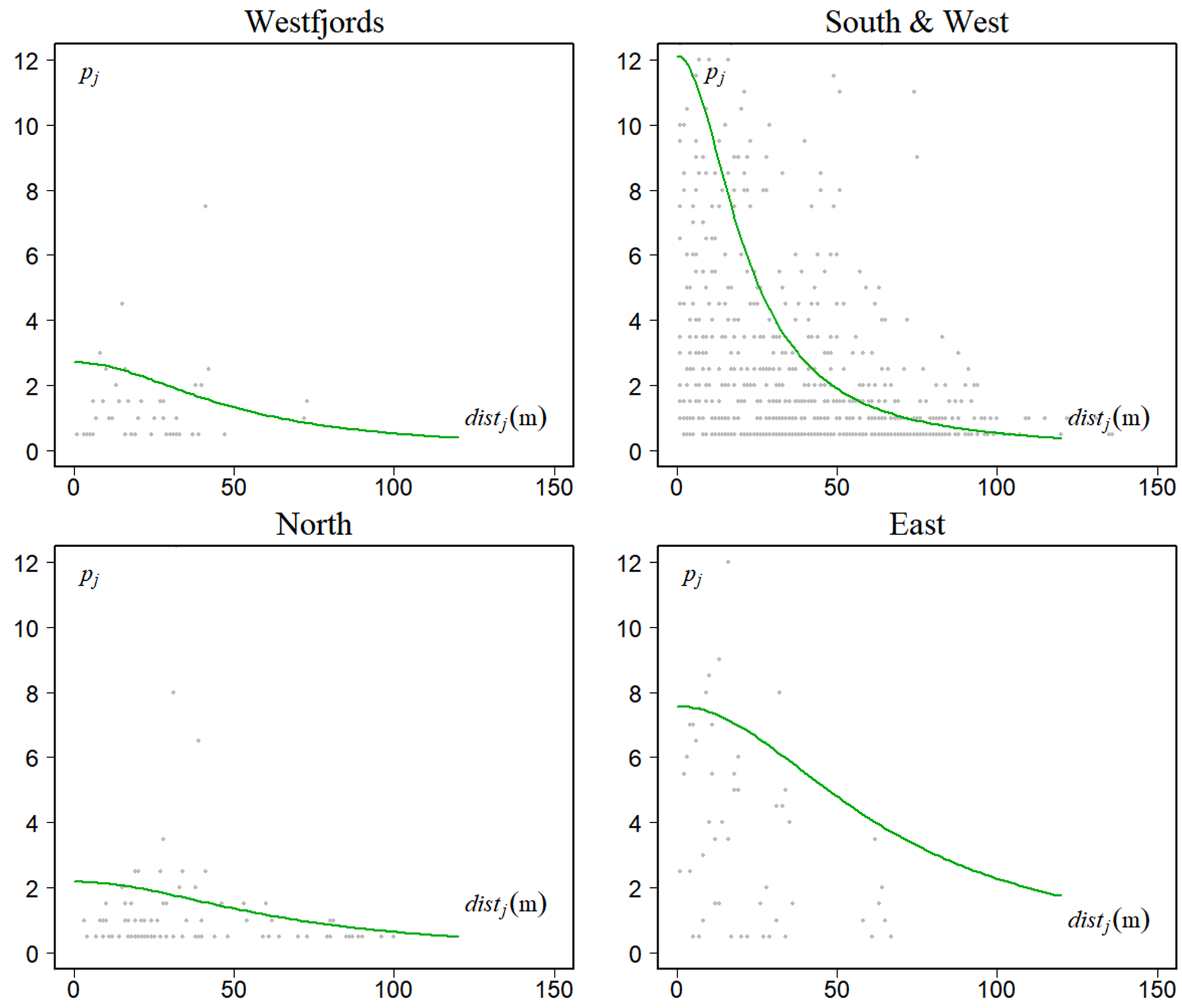


Fig. 6. Hyperbolic colonization kernels for the four different regions.

included as explanatory variables. Decreasing morphology indices were observed with increasing values of elevation (t-value = −9.81, $p <$ 0.001, Fig. 8A) and mean annual wind speed (t-value = −5.89, $p <$ 0.001, Fig. 8B) while dominant height of the adjacent woodlands had a small but significant positive association with the morphology index (t-value = 4.47, $p = <$ 0.001, Fig. 8C, Table S3).

4. Discussion

In times of global ecosystem loss and degradation, understanding the patterns and driving forces of native ecosystem expansion is more important than ever for guiding effective restoration, and thus for mitigating the effects of climate change and the ongoing global biodiversity crisis (Barnosky et al., 2012; Cardinale et al., 2012; IPCC, 2019). Accordingly, in our study we investigated individual sapling performance and patterns of colonization of mountain birch from existing subarctic birch woodlands into adjacent treeless lands. We found evidence that the performance of individual birch saplings is affected by regional differences in environment including wind gusts, elevation and dominant height of the surrounding woodlands. Furthermore, we quantified the effective spatial range of birch colonization from existing woodlands into the adjacent treeless habitats, a phenomenon driven in part by the height of nearby woodlands.

The results of our analysis revealed that mountain birch saplings growing at the woodland edge are adapted to the adverse effects of wind and weather whilst benefitting from a moderate facilitation effect provided by adjacent woodlands, which is directly related to the morphology of individual trees. Our models analysing the between-area differences in the morphology index, however, explained less than half of the variation in tree morphology between regions. This is likely a result of the variation in the morphology of trees growing at different distances from the woodland edge, i.e. a consequence of the amount of shelter each individual tree receives and other germination and growing conditions at the four regions. This interpretation is supported further by the regression analysis involving the parameters of the colonization kernel and regional morphology indices, as tree morphology was significantly correlated with kernel parameter δ, which determines the spatial range of interaction. Another emerging result of our study was to understand that tree morphology is an indicator and summary characteristic of regional patterns of environmental resistance to colonization. For trees that are well sheltered either by tall surrounding woodlands or by high densities of other saplings or both, we would consequently

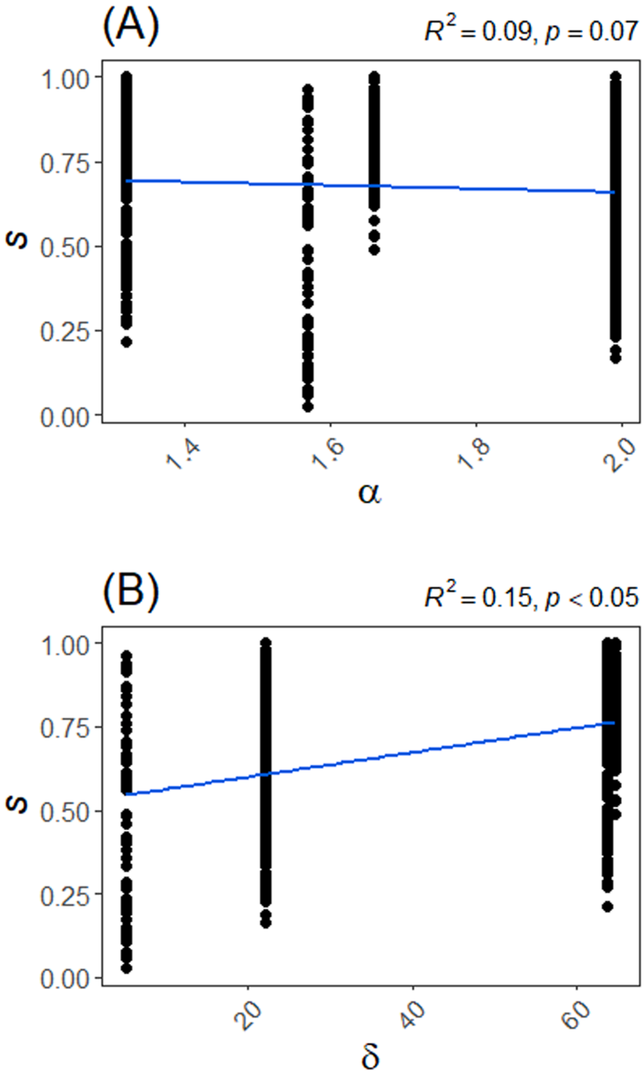


Fig. 7. Correlations between morphology index (s) and regional kernel parameters (A) α, and (B) δ.

expect straight stems and high values of the morphology index. The good indicator performance of the morphology index is an important finding, since where environmental resistance is large, restoration needs to provide supporting measures, e.g. planting, fencing or artificial shelter.

As we hypothesized, the majority of birch colonization was restricted to the area close to the woodland edge, because the sheltering effect from surrounding woodlands was highest here, and the seed cloud the most intense (Howe and Smallwood, 1982). This hypothesis was supported by the shapes of the colonization kernels from all four regions. Our study confirms that distance from a standing seed source and sheltering are two of the critical factors determining natural colonization potential of mountain birch. Based on the results of our study, different processes are involved that do not allow a generalization of outcomes such as effective distance and density across regions; both establishment and individual performance of saplings are dependent on local environments, which should be considered in restoration planning and perhaps be implemented in an application model within a geographic information system (GIS) for practical use. In practice, our results mean that woodlands producing colonizing trees in the adjacent open landscape that have a low morphology index values must have a lower sheltering capacity and will likely take longer to expand naturally. As a consequence, tree nuclei planted to facilitate natural colonization need to be placed closer together in such situations. Morphology index measurements can in the future be accompanied by detailed localised wind speed measurements, e.g. by using methods ranging from simple tatter flags (Quine, 2000) to eddy covariance (Aubinet et al., 2012). Such observations will subsequently allow a prediction of environmental resistance before restoration even begins so that the best restoration method can be applied right from the start.

The overall low sapling densities in the Westfjords is in large parts likely to be the result of the rough weather conditions in this region; with more days of frost and woodlands at higher elevations than in the other aforementioned regions (unpublished data from the Icelandic Met Office), saplings are likely to experience higher mortality (Goulet, 1995). One potential adaptation to these environments is vegetative propagation, which for shrubs and subarctic tree species is a common reproductive adaptation to challenging environments (Leakey, 1985). This is also a common phenomenon in *B. pubescens* Ehrh. (Kennedy et al., 1980). It is thus possible that sapling densities were occasionally underestimated in the Westfjords, where this phenomenon was observed in the field on multiple occasions.

The process of natural colonization depends on many ecological factors affecting the various life stages of trees, from establishment to survival and subsequent growth (Hanbury-Brown et al., 2022), and there are several underlying factors that may affect the morphology and consequently the performance of individual saplings, which we did not include in our study. Both biotic factors such as soil nutrient composition, and abiotic factors such as herbivory, are known to affect the growth of different species of birch (Hoogesteger and Karlsson, 1992; Óskarsson et al., 2006; Luostarinen et al., 2017) and these are site-specific attributes that are likely to differ between our study areas. Furthermore, the remaining populations of mountain birch in Iceland have experienced historical isolation since the degradation of birch woodlands in the country (Pálsson et al., 2023), suggesting the possibility of adaptation through genetic divergence which may affect growth patterns and the morphology index.

Applying the hyperbolic kernel function to woodland colonization patterns proved a useful new tool for characterizing spatial colonization densities and for quantifying the effective spatial range of natural colonization of mountain birch. Our analysis showed that patterns of natural colonization of birch in Iceland can differ greatly in different regional environments. According to our results, the range of effective colonization of mountain birch lies between 16.6 and 67.4 m, depending on regional environments and the main canopy height of the trees constituting nearby woodlands. We found evidence of some sheltering effect of adjacent woodlands on sapling densities and individual sapling performance, although the effect was not very strong. This is certainly owed to the low main canopy heights of existing birch woodlands in Iceland and to the general openness of Icelandic landscapes with hardly any really large woodland block creating meaningful shelter effects and regional differences. Mountain birch trees can grow up to 14 m in total height in certain regions of Iceland (Snorrason et al., 2016), and for woodlands with such a canopy height, the sheltering and seed dispersal effect might be stronger.

The effective spatial range for natural colonization, $dist_{\max}$, provides a very practical measure to be taken up in spatial woodland restoration, which is important for successful application and maximum utilization of resources (McCallum et al., 2018). $dist_{\max}$ can indicate optimal planting distance between woodland isles in applied nucleation (Corbin and Holl, 2012) and additionally provides support in determining the expected outcome of more passive frameworks, such as assisted natural regeneration, for existing woodlands of different heights and structure (Shono et al., 2007). These woodland restoration frameworks are gaining more momentum in recent years due to lower costs (Kimball et al., 2015; Ferreira et al., 2023) and potentially higher restoration success (Crouzeilles et al., 2017). Characteristic $dist_{\max}$ can also assist in the planning of combinations of natural regeneration and localised planting eventually paving the way towards precision restoration where

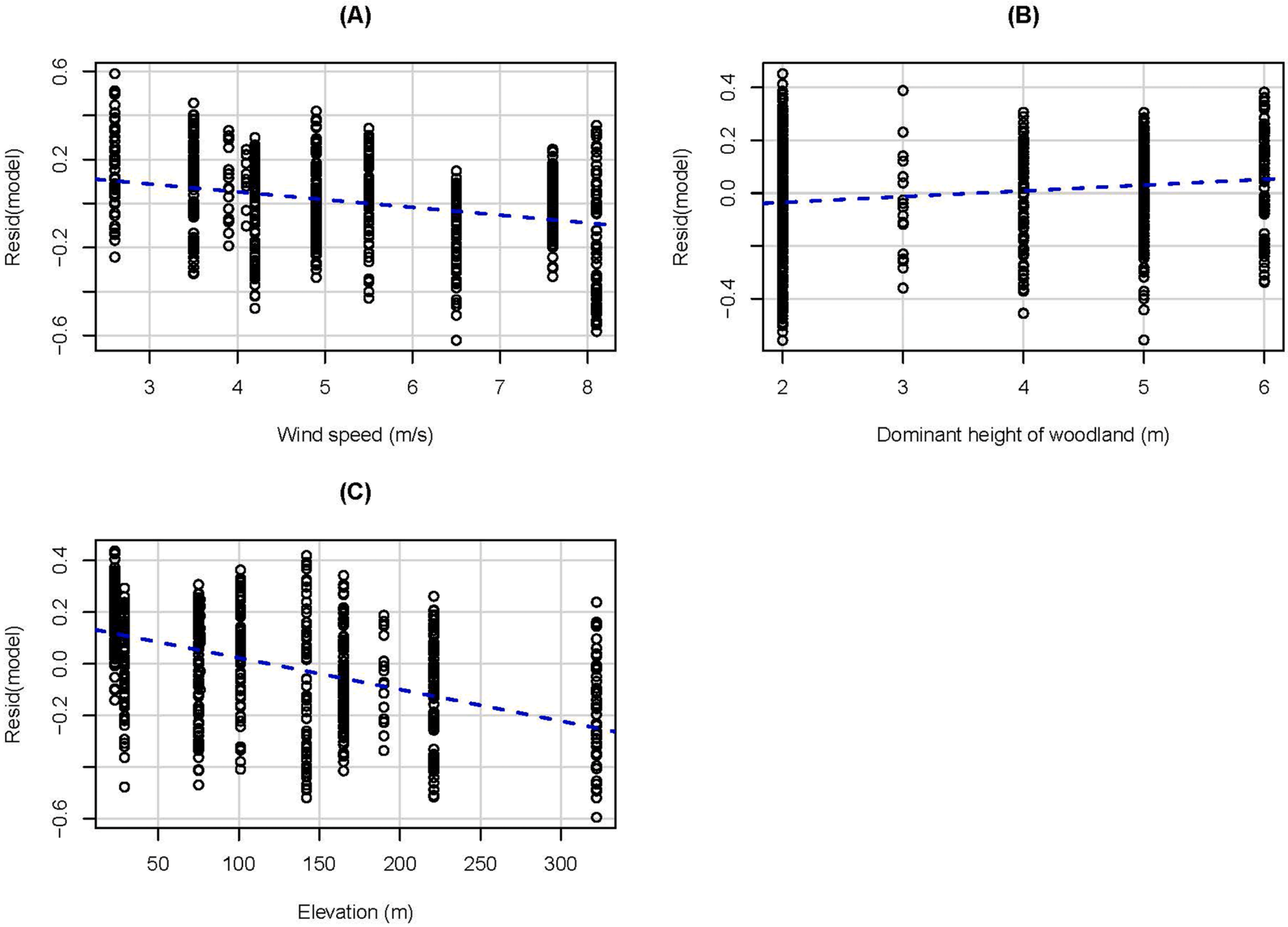


Fig. 8. Partial residual plots of multiple regression models testing for the effects of (A) mean annual wind speed, (B) dominant woodland height and (C) elevation on the morphology index of birch saplings.

the greatest effect is achieved with the lowest input.

The concept of $dist_{\max}$ can also be applied to other tree species involving different dispersal strategies. Zoochores are, for example, known to spread several thousand meters on average, depending on their target host (Camargo et al., 2020; Axer et al., 2021). Thus, $dist_{\max}$ measurements and modelling should be carried out separately for each species or even provenance and location.

In a restoration context, a few surviving saplings per m^2 are often considered to be sufficient for successful natural colonization (Bauld et al., 2023; Gullett et al., 2023). Depending on the objectives of a given restoration framework, $dist_{\max}$ can be adapted to accommodate different optimum sapling densities depending on species, environment and the time frame of the project. It is important to note, that absolute thresholds can be challenging to determine in ecological studies, due to the complexity and variability of natural ecosystems (Huggett, 2005). Nonetheless, identifying trends across multiple areas can contribute to our understanding of ecological thresholds and help inform future decision-making in conservation and restoration.

5. Conclusions

The baseline of any restoration work should always be a thorough understanding of the natural dynamics that drive the successful recovery and expansion of ecosystems. Our study revealed that there are clear effects of regional environmental factors both on the overall colonization by mountain birch and on individual sapling performance in Iceland. Seed availability and sheltering by landscape and surrounding woodlands are the most important determinants of colonization success. However, the sheltering effect is generally low in Iceland where in the presence of continuous high wind speeds existing woodlands are rare and small. In this situation, combining natural colonization with limited localised planting is most likely the best restoration approach. Using our new colonization kernels in conjunction with a morphology index revealed that the effective spatial range of colonization ranged from 16.6 m in the exposed Westfjords region to 67.4 m in the more sheltered Eastern region. This quantitative information can now be applied to precisely plan the proposed combination of natural colonization and localised planting at any given site.

Funding

This study is part of the research project *EcoBirch — restoration of birch woodlands in the 21st century: challenges, approaches and benefits*, funded by the Icelandic Government's Strategic Research and Development Program for Societal Challenges, 2020–2023, grant no 200,090–5601–5603.

CRediT authorship contribution statement

Anna Mariager Behrend: Writing – original draft, Visualization, Software, Methodology, Formal analysis, Data curation, Conceptualization. **Arne Pommerening:** Writing – original draft, Visualization, Software, Methodology, Formal analysis, Conceptualization.

Declaration of competing interest

The authors declare that they have no conflict of interest.

Acknowledgements

The authors wish to thank Ása L. Aradóttir, Kristín Svavarsdóttir and Thóra Ellen Thórhallsdóttir who helped planning and provided support for the fieldwork related to this publication. Furthermore, we thank Árni Hafstað Arnórsson, Berglind Guðjónsdóttir, Katrín Valsdóttir, Margrét Guðbrandsdóttir and Sólveig Sánchez for fieldwork-assistance.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2025.111073.

Data availability

Data and R code used in this study is available in Mendeley Data: https://data.mendeley.com/datasets/cbjfw9kh3t/1.

References

Aradóttir, Á.L., 2004. Does the Nootka lupin facilitate or impede colonization and growth of native birch in Iceland? Santen E.v. (eds.). 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, pp. 184–190.

Aradóttir, Á.L., Halldórsson, G., 2018. Colonization of woodland species during restoration: seed or safe site limitation? Restor. Ecol. 26, 73–83. https://doi.org/10.1111/rec.12645.

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

Arnalds, Ó., Marteinsdóttir, B., Brink, S.H., Þórsson, J., 2023. A framework model for current land condition in Iceland. PLoS One 18, e0287764. https://doi.org/10.1371/journal.pone.0287764.

Atkinson, M.D., 1992. *Betula pendula* Roth (*B. verrucosa* Ehrh.) and *B. pubescens* Ehrh. J. Ecol. 80, 837–870. https://doi.org/10.2307/2260870.

Aubinet, M., Vesala, T., Papale, D., 2012. Eddy Covariance: a Practical Guide to Measurement and Data Analysis. Springer Science and Business Media, 2012.

Axer, M., Schlicht, R., Wagner, S., 2021. Modelling potential density of natural regeneration of European oak species (Quercus robur L., Quercus petraea (Matt.) Liebl.) Depending on the distance to the potential seed source: methodological approach for modelling dispersal from inventory data at forest enterprise level. For. Ecol. Manage 482, 118802. https://doi.org/10.1016/j.foreco.2020.118802.

Barnosky, A.D., Hadly, E.A., Bascompte, J., Berlow, E.L., Brown, J.H., Fortelius, M., Getz, W.M., Harte, J., Hastings, A., Marquet, P.A., Martinez, N.D., Mooers, A., Matzke …, N., Smith, A.B., 2012. Approaching a state shift in Earth's biosphere. Nature 486, 52–58. https://doi.org/10.1038/nature11018.

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. Restor. Ecol. 31, e14004. https://doi.org/10.1111/rec.14004.

Beckman, N.G., Sullivan, L.L., 2023. The causes and consequences of seed dispersal. Annu. Rev. Ecol. Evol. Syst. 54 (1), 403–427. https://doi.org/10.1146/annurev-ecolsys-102320-104739.

Behrend, A.M., Aradóttir, Á.L., Svavarsdottir, K., Thórhallsdóttir, T.E., Pommerening, A., 2024. Natural colonization as a means to upscale restoration of subarctic woodlands in Iceland. Restor. Ecol. e14332. https://doi.org/10.1111/rec.14332.

Camargo, P.H.S.A., Pizo, M.A., Brancalion, P.H.S., Carlo, T.A., 2020. Fruit traits of pioneer trees structure seed dispersal across distances on tropical deforested landscapes: implications for restoration. J. Appl. Ecol. 57 (12), 2329–2339. https://doi.org/10.1111/1365-2664.13697.

Campanhã Bechara, F., Trentin, B.E., Lex Engel, V., Estevan, D.A., Ticktin, T., 2021. Performance and cost of applied nucleation versus high-diversity plantations for tropical forest restoration. For. Ecol. Manage 491, 119088. https://doi.org/10.1016/j.foreco.2021.119088.

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace, G.M., Tilman, D., Wardle, D.A., Kinzig, A.P., Daily, G.C., Loreau, M., Grace, J.B., Larigauderie, A., Srivastava, D.S., Naeem, S., 2012. Biodiversity loss and its impact on humanity. Nature 486, 59–67. https://doi.org/10.1038/nature11148.

Cargill, S.M., Chapin, F.S., 1987. Application of successional theory to tundra restoration: a review. Arct. Alp. Res. 19, 366–372. https://doi.org/10.2307/1551401.

Chazdon, R.L., Guariguata, M.R., 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, J.D., Holl, K.D., 2012. Applied nucleation as a forest restoration strategy. For. Ecol. Manage 265, 37–46. https://doi.org/10.1016/j.foreco.2011.10.013.

Crouzeilles, R., Beyer, H.L., Monteiro, L.M., Feltran-Barbieri, R., Pessôa, A.C.M., Barros, F.S.M., Lindenmayer, D.B., Lino, E.D.S.M., Grelle, C.E.V., Chazdon, R.L., Matsumoto, M., Rosa, M., Latawiec, A.E., Strassburg, B.B.N., 2020. Achieving cost-effective landscape-scale forest restoration through targeted natural regeneration. Conserv. Lett. 13, e12709. https://doi.org/10.1111/conl.12709.

Crouzeilles, R., Ferreira, M.S., Chazdon, R.L., Lindenmayer, D.B., Sansevero, J.B.B., Monteiro, L., Iribarrem, A., Latawiec, A.E., Strassburg, B.B.N., 2017. Ecological restoration success is higher for natural regeneration than for active restoration in tropical forests. Sci. Adv. 3, e1701345. https://doi.org/10.1126/sciadv.1701345.

Dassot, M., Constant, T., Ningre, F., Fournier, M., 2015. Impact of stand density on tree morphology and growth stresses in young beech (Fagus sylvatica L.) stands. Trees 29, 583–591. https://doi.org/10.1007/s00468-014-1137-4.

Dobbert, S., Pape, R., Löffler, J., 2021. How does spatial heterogeneity affect inter- and intraspecific growth patterns in tundra shrubs? J. Ecol. 109, 4115–4131. https://doi.org/10.1111/1365-2745.13784.

Eränen, J.K., Kozlov, M.V., 2006. Physical sheltering and liming improve survival and performance of mountain birch saplings: a 5-year study in a heavily polluted industrial barren. Restor. Ecol. 14, 77–86. https://doi.org/10.1111/j.1526-100X.2006.00107.x.

Ferreira, M.C., De Oliveira Cordeiro, A.O., Sampaio, A.B., Schmidt, I.B., Vieira, D.L.M., 2023. Direct seeding versus sapling planting: survival, biomass, growth, and cost up to 6 years for four tropical seasonal tree species. Restor. Ecol. 31, e13807. https://doi.org/10.1111/rec.13807.

Goulet, F., 1995. Frost heaving of forest tree saplings: a review. New Forest 9, 67–94. https://doi.org/10.1007/BF00028927.

Greenwood, S., Chen, J., Chen, C., Jump, A.S., 2014. Strong topographic sheltering effects lead to spatially complex treeline advance and increased forest density in a subtropical mountain region. Glob. Change Biol. 20, 3756–3766. https://doi.org/10.1111/gcb.12710.

Gretarsdottir, J., Aradóttir, Á.L., Vandvik, V., Heegaard, E., Birks, H.J.B., 2004. Long-term effects of reclamation treatments on plant succession in Iceland. Restor. Ecol. 12 (2), 268–278. https://doi.org/10.1111/j.1061-2971.2004.00371.x.

Grime, J.P., Jeffrey, D.W., 1965. Sapling establishment in vertical gradients of sunlight. J. Ecol. 53, 621–642. https://doi.org/10.2307/2257624.

Gullett, P.R., Leslie, C., Mason, R., Ratcliffe, P., Sargent, I., Beck, A., Cameron, T., Cowie, N.R., Hetherington, D., MacDonell, T., Moat, T., Moore, P., Teuten, E., Hancock, M.H., 2023. Woodland expansion in the presence of deer: 30 years of evidence from the Cairngorms Connect landscape restoration partnership. J. Appl. Ecol. 00, 1–11. https://doi.org/10.1111/1365-2664.14501.

Hanbury-Brown, A.R., Ward, R.E., Kueppers, L.M., 2022. Forest regeneration within Earth system models: current process representations and ways forward. New Phytol. 235, 20–40. https://doi.org/10.1111/nph.18131.

Hester, A.J., Miles, J., Gimingham, C.H., 1991. Succession from heather moorland to birch woodland. II. Growth and competition between Vaccinium myrtillus, Deschampsia flexuosa and Agrostis capillaris. J. Ecol. 79 (2), 317. https://doi.org/10.2307/2260715.

Hofgaard, A., Wilmann, B., 2002. Plant distribution pattern across the forest-tundra ecotone: the importance of treeline position. Écoscience 9, 375–385. https://doi.org/10.1080/11956860.2002.11682725.

Hoogesteger, J., Karlsson, P.S., 1992. Effects of defoliation on radial stem growth and photosynthesis in the mountain birch (Betula pubescens ssp. tortuosa). Funct. Ecol. 6 (3), 317. https://doi.org/10.2307/2389523.

Howe, H.F., Smallwood, J., 1982. Ecology of seed dispersal. Annu. Rev. Ecol. Syst. 13, 201–228. https://doi.org/10.1146/annurev.es.13.110182.001221.

Holl, K.D., Zahawi, R.A., Cole, R.J., Ostertag, R., Cordell, S., 2011. Planting saplings in tree islands versus plantations as a large-scale tropical forest restoration strategy. Restor. Ecol. 19, 470–479. https://doi.org/10.1111/j.1526-100X.2010.00674.x.

Huggett, A.J., 2005. The concept and utility of 'ecological thresholds' in biodiversity conservation. Biol. Conserv. 124, 301–310. https://doi.org/10.1016/j.biocon.2005.01.037.

Intergovernmental Panel on Climate Change (IPCC) (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 on 14th of August 2024).

Jonsson, T.H., 2004. Stature of sub-arctic birch in relation to growth rate, lifespan and tree form. Ann. Bot. 94, 753–762. https://doi.org/10.1093/aob/mch200.

Kennedy, D., Cameron, A.D., Brown, I.R., 1980. Vegetative propagation of two birch species. Arboric. J. 4, 168–176. https://doi.org/10.1080/03071375.1980.10590610.

Kristinsson, H., Hlíðberg, J.B., Thórhallsdóttir, T.E., 2018. Flóra Íslands. Blómplöntur og Byrkningar [Flora of Iceland. Angiosperms and Ferns]. Vaka-Helgafell.

Kimball, S., Lulow, M., Sorenson, Q., Balazs, K., Fang, Y.C., Davis, S.J., O'Connell, M., Huxman, T.E., 2015. Cost-effective ecological restoration. Restor. Ecol. 23, 800–810. https://doi.org/10.1111/rec.12261.

Laar, A.v., Akça, A., 2007. Single-tree measurements. Forest Mensuration. Springer, Netherlands, Dordrecht, pp. 63–93.

Law, R., Illian, J., Burslem, D.F.R.P., Gratzer, G., Gunatilleke, C.V.S., Gunatilleke, I.A.U.N., 2009. Ecological information from spatial patterns of plants: insights from point process theory. J. Ecol. 97, 616–628. https://doi.org/10.1111/j.1365-2745.2009.01510.x.

Leakey, R.R.B., 1985. The capacity for vegetative propagation in trees. Cannell, M.G.R., and Jackson, J.E. (eds.). Attributes of Trees As Crop Plants. Abbotts Ripton. Institute of Terrestrial Ecology, pp. 110–133.

Lososová, Z., Axmanová, I., Chytrý, M., Midolo, G., Abdulhak, S., Karger, D.N., Renaud, J., Van Es, J., Vittoz, P., Thuiller, W., 2023. Seed dispersal distance classes and dispersal modes for the European flora. Glob. Ecol. Biogeogr. 32 (9), 1485–1494. https://doi.org/10.1111/geb.13712.

Luostarinen, K., Hakkarainen, K., Kaksonen, H., 2017. Wood anatomy of seed and basal bud originated downy birches (*Betula pubescens* Ehrh.) grown at four different sites. Silva Fennica 51, 1694. https://doi.org/10.14214/sf.1694.

MacFarlane, D.W., Kane, B., 2017. Neighbour effects on tree architecture: functional trade-offs balancing crown competitiveness with wind resistance. Funct. Ecol. 31, 1624–1636. https://doi.org/10.1111/1365-2435.12865.

Maletha, A., Maikhuri, R.K., Bargali, S.S., 2021. Population structure and regeneration pattern of himalayan birch (Betula utilis D.Don) in the timberline zone of Nanda Devi Biosphere Reserve, Western Himalaya, India. Geol. Ecol. Landsc. 7, 248–257. https://doi.org/10.1080/24749508.2021.1952767.

McCallum, K.P., Lowe, A.J., Breed, M.F., Paton, D.C., 2018. Spatially designed revegetation — Why the spatial arrangement of plants should be as important to revegetation as they are to natural systems. Restor. Ecol. 26, 446–455. https://doi.org/10.1111/rec.12690.

National Land Survey of Iceland, 2021. ÍslandsDEM [digital surface model].

Niklas, K.J., Spatz, H.C., 2012. Plant Physics. The University of Chicago Press, Chicago.

Óskarsdóttir, G., Thórhallsdóttir, T.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. Ecol. Evol. 12, e9430. https://doi.org/10.1002/ece3.9430.

Óskarsson, H., Sigurgeirsson, A., Raulund-Rasmussen, K., 2006. Survival, growth, and nutrition of tree saplings fertilized at planting on Andisol soils in Iceland: six-year results. For. Ecol. Manage 229, 88–97. https://doi.org/10.1016/j.foreco.2006.03.018.

Pálsson, S., Wasowicz, P., Heiðmarsson, S., Magnússon, K.P., 2023. Population structure and genetic variation of fragmented mountain birch forests in Iceland. J. Hered. 114, 165–174. https://doi.org/10.1093/jhered/esac062.

Panarctic Flora. (2024). 610206b *Betula pubescens* subsp. *tortuosa* (Ledeb.) Nyman. http://panarcticflora.org/results?biogeographic=andbioclimatic=andregion=andname=betula±pubescens#paf-610206b.

Pedersen, N.K., Schmidt, I.K., 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. For. Ecol. Manage 543, 121138. https://doi.org/10.1016/j.foreco.2023.121138.

Peringer, A., Rosenthal, G., 2011. Establishment patterns in a secondary tree line ecotone. Ecol. Modell. 222, 3120–3131. https://doi.org/10.1016/j.ecolmodel.2011.05.025.

Pommerening, A., Grabarnik, P., 2019. Individual-based Methods in Forest Ecology and Management. Springer Nature, Cham.

Potthoff, K., 2017. Spatio-temporal patterns of birch regrowth in a Western Norwegian treeline ecotone. Landsc. Res. 42, 63–77. https://doi.org/10.1080/01426397.2016.1260701.

Quine, C.P., 2000. Estimation of mean wind climate and probability of strong winds for wind risk assessment. Forestry 73, 247–258. https://doi.org/10.1093/forestry/73.3.247.

R Core Team, 2022. R: a language and environment for statistical computing. R Foundation for Statistical Computing. https://www.R-project.org.

Rowe, N., Speck, T., 2005. Plant growth forms: an ecological and evolutionary perspective. New Phytol. 166, 61–72. https://doi.org/10.1111/j.1469-8137.2004.01309.x.

Shono, K., Cadaweng, E.A., Durst, P.B., 2007. Application of assisted natural regeneration to restore degraded tropical forestlands. Restor. Ecol. 15, 620–626. https://doi.org/10.1111/j.1526-100X.2007.00274.x.

Snorrason, A., Traustason, B., Kjartansson, B.Þ., Heiðarsson, L., 2016. Náttúrulegt birki á Íslandi – Ný uttek á útbreiðslu þess og ástandi [The natural birch woodlands in Iceland – a new assessment on distribution and state]. Náttúrufræðingurin 86, 97–111.

Speed, J.D.M., Austrheim, G., Hester, A.J., Mysterud, A., 2011. Growth limitation of mountain birch caused by sheep browsing at the altitudinal treeline. For. Ecol. Manage 261, 1344–1352. https://doi.org/10.1016/j.foreco.2011.01.017.

Tanentzap, A.J., Mountford, E.P., Cooke, A.S., Coomes, D.A., 2012. The more stems the merrier: advantages of multi-stemmed architecture for the demography of understorey trees in a temperate broadleaf woodland: demography of multi-stemmed trees. J. Ecol. 100, 171–183. https://doi.org/10.1111/j.1365-2745.2011.01879.x.

Telewski, F.W., 2012. Is windswept tree growth negative thigmotropism? Plant Sci. 184, 20–28. https://doi.org/10.1016/j.plantsci.2011.12.001.

Thomson, F.J., Moles, A.T., Auld, T.D., Kingsford, R.T., 2011. Seed dispersal distance is more strongly correlated with plant height than with seed mass. J. Ecol. 99 (6), 1299–1307. https://doi.org/10.1111/j.1365-2745.2011.01867.x.

Thórhallsdóttir, T.E., 1998. Flowering phenology in the central highland of Iceland and implications for climatic warming in the Arctic. Oecologia 114, 43–49. https://doi.org/10.1007/s004420050418.

Tremblay, J., Bégin, Y., 2005. The effects of snow packing on tree growth forms on an island in a recently created reservoir in northern Québec, Canada. Écoscience 12, 530–539. https://doi.org/10.2980/i1195-6860-12-4-530.1.

Verwijst, T., 1988. Environmental correlates of multiple-stem formation in Betula pubescens ssp. Tortuosa. Vegetatio 76, 29–36. https://doi.org/10.1007/BF00047385.

Willson, M.F., 1993. Dispersal mode, seed shadows, and colonization patterns. Vegetatio 107/108, 261–280. https://doi.org/10.1007/BF00052229.

Wu, T., Zhang, P., Zhang, L., Wang, J., Yu, M., Zhou, X., Wang, G.G., 2018. Relationships between shelter effects and optical porosity: a meta-analysis for tree windbreaks. Agric. For. Meteorol. 259, 75–81. https://doi.org/10.1016/j.agrformet.2018.04.013.

Zhang, Z., Papaik, M.J., Wang, X., Hao, Z., Ye, J., Lin, F., Yuan, Z., 2017. The effect of tree size, neighbourhood competition and environment on tree growth in an old-growth temperate forest. J. Plant Ecol. 10, 970–980. https://doi.org/10.1093/jpe/rtw126.

Supplementary materials

Behrend, A. M., & Pommerening, A. (2025). Growing at the edge: Modelling sapling colonization, performance, and effective range of mountain birch (*Betula pubescens* ssp. *tortuosa*). *Ecological Modelling*, *503*, 111073. https://doi.org/10.1016/j.ecolmodel.2025.111073

Table S1. Results of model selection of the multiple regression model on birch morphology index, based on backwards stepwise selection.

Dropped term	**df**	**SS**	**AIC**
None			-2551.4
Dominant height of woodland	1	0.11	-2549.7
Wind speed	1	1.91	-2492.5
Altitude	1	2.89	-2475.4

Table S2. Parameters of the hyperbolic colonization kernel functions pooled into four distinct geographic regions.

	α	δ
Westfjords	1.57	5.18
South & West	1.99	22.09
North	1.32	63.77
East	1.66	64.62

Table S3. Results from the best multiple linear regression model for the morphology index of mountain birch.

	Estimate	**Std. Error**	***t* value**	***p***
Intercept	0.93	0.05	17.76	**< 0.001**
Wind speed	-0.04	0.006	-5.89	**< 0.001**
Dominant height of woodland	0.02	0.004	4.47	**<0.001**
Elevation	-0.001	0.0001	-9.81	**< 0.001**

IV

Assessing safe-site limitations to support recruitment niche-based restoration frameworks

Anna M. Behrend[1], Thóra Ellen Thórhallsdóttir[2], Kristín Svavarsdóttir[3], Ása L. Aradóttir[1]

[1]Agricultural University of Iceland, Faculty of Environmental and Forest Sciences, Árleynir 22, 112 Reykjavík, Iceland

[2]University of Iceland, Faculty of Life and Environmental Sciences, Sæmundargötu 2, 102 Reykjavík, Iceland

[3]Land and Forest Iceland, Árleynir 22, 112 Reykjavík, Iceland

Abstract

Low-intensity restoration approaches, including seed-based restoration, may be important when upscaling woodland restoration globally. To improve restoration outcomes, it is necessary to obtain a better understanding of the limitations to tree seedlings emergence and survival, or species recruitment niches, and to what degree this can be affected by restoration interventions. Using mountain birch (*Betula pubescens* ssp. *tortuosa*) as a study species, we investigated if interventions could alter the local microenvironment to match a species' recruitment niche. Furthermore, we identified suitable microsites, or safe sites, for birch recruitment across habitat types with the aim to generalize where restoration efforts should be focused for the best possible outcome. We set up seeding experiments in three study areas in lowland South and West Iceland, located within four different common subarctic habitat types in each area, and measured emergence and survival over two growing seasons. The experiment included plots with or without an applied disturbance and two types of seed sources, a local vs a standard one. There were strong area-specific recruitment patterns, with one study area having significantly higher densities of emerging seedlings in the first growing season. An applied disturbance increased both emergence, survival and restoration success in three out of four habitat types, with birch seedling recruitment being highly microsite limited in both disturbed and undisturbed plots. Seedling emergence was greater for the local seed sources than the standard one, but there was no effect of seed source on survival and restoration success. Our study shows that restoration interventions can alter microenvironments to support the recruitment niche of a target species in woodland restoration, by increasing the abundance of suitable microsites. This can aid in standardizing habitat types as a predictor of restoration success, with the potential to utilize land cover classification data to upscale woodland restoration. Our results furthermore support the importance of a recruitment-niche based framework in seed-based restoration.

Keywords

Betula pubescens ssp. *tortuosa*, ecological restoration, microsites, natural colonization, natural regeneration, recruitment niche, seed-based restoration

Introduction

Ecological restoration of forest and woodland ecosystems is of high global priority because of the many ecosystem services they provide (Chazdon 2008, Mori et al. 2017). As natural recovery of these ecosystems can take decades, there is considerable social pressure to accelerate this process through interventions. In heavily degraded or deforested areas, this is commonly undertaken through large-scale tree planting (Bastin et al. 2019). This is, however, an unfeasible strategy considering the large-scale efforts currently needed to comply with global restoration and conservation pledges such as the Bonn Challenge (IUCN 2020) and the Kunming-Montreal Global Biodiversity Framework (CBD, 2022). As alternatives to large-scale planting, woodland restoration approaches that aim at utilizing spontaneous or assisted natural regeneration of target species are gaining momentum, being more cost-effective and targeted towards restoring the structural complexity of natural ecosystems (Chazdon & Guariguata 2016, Strassburg et al. 2018, Crouzeilles et al. 2020). These typically involve strategic low-intensity restoration efforts, such as protection from disturbances (Shono et al. 2007), revegetation (Deshaies et al. 2009, Aradóttir & Halldórsson 2018), and planting of woodland isles to establish seed sources where none are present (Corbin & Holl 2012). There are, however, large uncertainties involved in the process of natural regeneration, and predicting the outcome of restoration efforts based on such approaches is challenging (Meli et al. 2017, Kim et al. 2022). Failed restoration efforts often arise from a lack of understanding of the biotic and abiotic attributes limiting successful regeneration and subsequent ecosystem development and expansion (Holl & Aide 2011, Crouzeilles et al. 2017). To successfully apply these approaches based on natural regeneration to effectively upscale native forest and woodland restoration, it is essential to understand the factors that limit and drive recruitment of the target species.

A species' recruitment niche, a subset of the regeneration niche as described by Grubb (1977) refers to the biotic and abiotic requirements of a species for emergence and survival. In addition to the effects of factors such as temperature and precipitation (Valdez et al. 2019, Svejcar et al. 2023), one of the primary abiotic barriers to plant recruitment is the availability of suitable microsites for seedling establishment (Duncan et al. 2009, Wandrag et al. 2019). The specific qualities of suitable microsites, or safe sites, differ between plant species, but common denominators are soil stability, limited competition from surrounding vegetation (Aradóttir & Halldórsson 2018, Boeken 2018, Behrend et al. 2025) and, in some cases, positive effects of a sheltering neighbor (Fowler 1988). A given microsite type may impact establishment and survival in a different manner (Renison et al. 2005).

Where availability of suitable microsites is limited, strategic interventions may be needed to enhance natural regeneration. This may apply to areas with ongoing natural and anthropogenic disturbances (Jutila & Grace 2002, Renison et al. 2005), areas with surface characteristics that provide low soil-seed contact (Collis George & Hector 1966), or areas with high interspecific competition (Holmgren 1997). For example, in mesic areas with dense competing vegetation, an applied disturbance can create safe sites and thus enhance seedling establishment (Willis et al. 2015, Lidman et al. 2023), while in areas dominated by land cover experiencing cryoturbation or soil erosion, revegetation efforts can improve soil stability and hence create safe sites (Aradóttir & Halldórsson 2018). Basing decisions about interventions in seed-based restoration on an understanding of the recruitment niche of key plant species involved in the recovery of the target ecosystems should lead to more focused restoration efforts (Young et al. 2005, Larsson et al. 2023). Furthermore, it may be beneficial to consider possible effects of seed origin that may affect restoration outcomes due to differences in environmental and genetic adaptability among populations of the target species (Broadhurst et al. 2008, Bischoff et al. 2010, Espeland et al. 2017).

Iceland has set an ambitious goal in relation to the Bonn Challenge, that is to increase the cover of mountain birch (*Betula pubescens* ssp. *tortuosa*) woodlands by 3500 km^2 or to about 5% of Iceland (Government of Iceland 2022). These ecosystems were severely degraded and, in many places, destroyed following the country's settlement in the 9th century, decreasing in cover from approximately 25-30% of Iceland to less than 1% in the early 1900s (Arnalds 1987), but are currently estimated to cover 1.5% (Snorrason et al, 2016). Restoration on such a large scale is only possible through approaches relying in large part on natural and assisted birch regeneration, which calls for improved understanding of the ecological constraints of birch recruitment. These have been investigated in various studies (Aradóttir & Halldórsson 2018, Liu & Evans 2021, Lidman et al. 2023, Óskarsdóttir et al. 2025). To our knowledge, however, it has not been investigated how microsite composition across different habitat types affect the recruitment patterns of birch. The distribution of microsites for natural regeneration on land classification units such as habitat types could aid scaling up restoration by making predictions on where natural regeneration is likely to occur naturally, and where active restoration might need to take place.

The aim of our study was to assess the recruitment potential of mountain birch in common subarctic habitat types in Iceland, with a particular focus on availability of safe sites and characterization of the species recruitment niche, and furthermore to evaluate whether modifying the microenvironment can increase the abundance of microsites that match the species' recruitment niche. We investigated this through seeding experiments in different subarctic habitat types where a disturbance was applied to alter the local microenvironment. Additionally, we compared the performance of two different seed sources, *i.e.* a local seed source and a standard seed source. Our goal was ultimately to improve understanding of the ecological processes for supporting low intensity seed-based restoration strategies, i.e., natural and assisted regeneration, applied nucleation and direct seeding.

Specifically, we asked the following questions:

- (I) What are the characteristics of microsites suitable for birch recruitment in different subarctic habitat types?
- (II) Can selected restoration interventions enhance colonization by increasing the abundance of microsites that match the specie's recruitment niche?
- (III) Can abundance of favorable microsites be used as a predictor of natural colonization in different habitat types?

Materials and methods

Selection of habitat types

Habitat types in Iceland have been mapped using the European Nature Information System (EUNIS 2024) with some amendments (Ottósson et al. 2016). The selection of habitat types for the seeding experiments was based on the Habitat Map Fact Sheets from the Natural Science Institute of Iceland. Our study focused on four common habitat types that are likely to be targeted for birch woodland expansion: fjell field, moss heath and two types of heathlands that cover in total approximately 14 800 km^2, or 14%, of Iceland (see details for these habitat types in **Table 1**). They vary in vegetation cover, height and species composition and include a range of microsite types that are likely to be found in similar dryland habitat types in Iceland.

Table 1. *Summary of the four habitat types where seeding experiments were established in three study areas in West and South Iceland, their estimated land cover in Iceland, and a short description based on the Icelandic Institute of Natural History (now Natural Science Institute of Iceland) Habitat Map Fact Sheets (Ottósson et al. 2016). For more details on habitat types, we refer to the Habitat Map Fact Sheets.*

Habitat type	Land cover	Description	Picture
1.3 - Oroboreal *Carex bigelowii-Racomitrium* moss-heaths	~ 3.000 km^2	Semi-vegetated, stony hillsides; found in both lowlands and mountains where rainfall is abundant, but snowfall is low. The ecosystem is characterized by a high coverage of the mosses *Racomitrium lanuginosum* and *R. ericoides*. The cover is fragmented, however, with patches of eroded surfaces and rocks. There is sparse vascular plant cover, and lichens are quite prominent. Vegetation is generally very low-growing.	
5.3 - Moss and lichen fjell fields	~ 5.300 km^2	Surface often rocky, low stature vegetation. High cover of Racomitrium spp with considerable cover of both vascular species and lichens. Both highland and lowland regions.	
10.4 - Icelandic *Empetrum-Thymus* grasslands	~ 1.500 km^2	Grassy heathlands with sedges, grasses, mosses and other heathland species, often on sloping ground. The habitat is covered in vegetation which is rather low growing. Vascular plants are dominant, but there is also a lot of moss and lichens.	
10.8 - North Atlantic *Vaccinium-Empetrum-Racomitrium* heaths	~ 5.000 km^2	Dry and stony heathlands with *Empetrum nigrum*, *Vaccinium uliginosum*, *Calluna vulgaris* and other low-growing heather species, often on considerable slopes, ridges or bulges. The vegetation is generally low growing, dominated by vascular plants and mosses, with occasional lichens.	

Study areas

The experiments were established in three areas distributed across the West and South lowland regions of Iceland (**Figure 1**): Hvanneyri, Neðri Dalur and Gunnarsholt. All three consist mainly of habitat types dominated by low-growing vegetation, such as mosses (mainly

Racomitrium spp.) and dwarf shrubs (such as *Calluna vulgaris*, *Empetrum nigrum* and *Vaccinium uliginosum*), and agricultural fields. All three study areas had several large patches of the selected habitat types.

The areas were situated at an elevation between 11 and 80 m.a.s.l. The dominant soil type in Neðri Dalur and Gunnarsholt was brown Andosols, while the soils of Hvanneyri were a mixture of Histosols and brown and histic Andosols (Arnalds & Óskarsson 2009). The nearest weather stations, located no more than 8 km from the corresponding study areas, have average July temperatures between 10.9 and 11.6 °C, and January temperatures between -2.0 and -3.5 °C, with total annual precipitation values between 1264.5 and 1540.3 mm (**Figure S1**, unpublished data from the Icelandic Met Office, 1973-2023 averages). None of the study areas were, to our knowledge, used for summer grazing of sheep during the experiments.

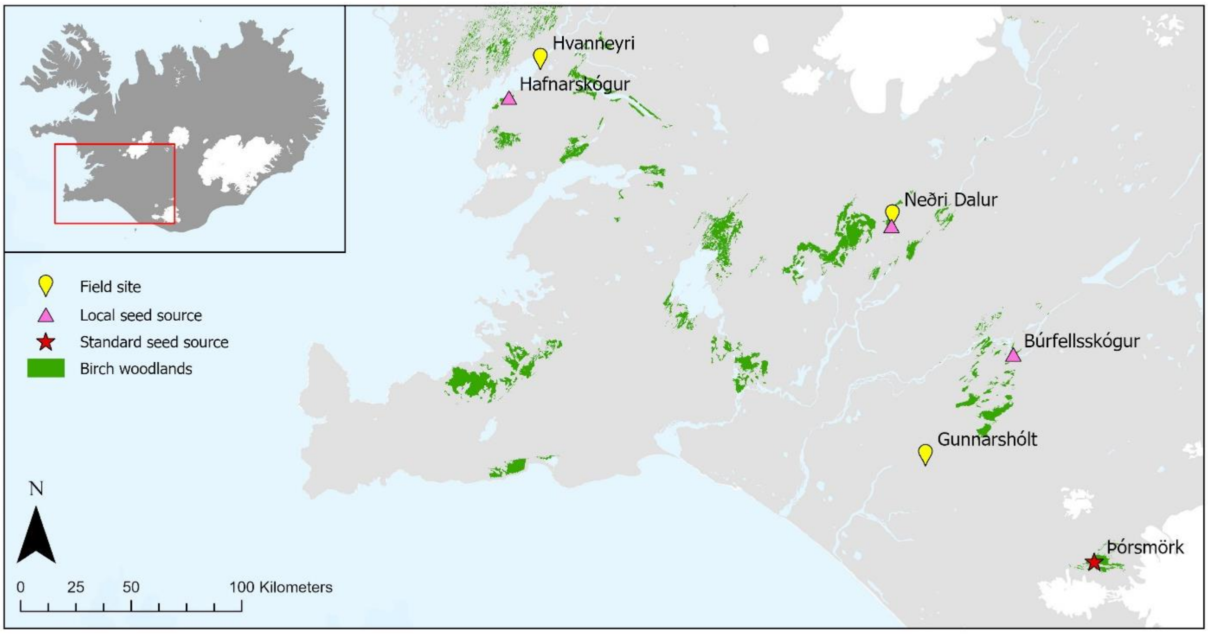


Figure 1. *Location of the three study areas with the seeding experiments (yellow) in West and South Iceland and their respective local seed sources (pink). The standard seed source was obtained from Thórsmörk (red star). The current distribution of natural birch woodlands is shown in green.*

Seed sources and germination tests

To examine the effect of seed source for the recruitment potential of mountain birch, we seeded the experimental plots with (i) a seed source local to each study area and (ii) a seed source provided by the Icelandic Forest Service (now Land and Forest Iceland) that was used in all three areas (from here on referred to as standard seed source). The local seed sources were collected in woodlands between 1 and 28 km from a corresponding study area: Hafnarskógur near Hvanneyri, Búrfellsskógur near Gunnarsholt, and the woodlands within the property of Neðri Dalur farm (**Figure 1**). The seed was collected from 10 different trees in each area in October 2021. The standard seed source originated from the valley Thórsmörk in South Iceland.

The seeds were refrigerated for three weeks before germination tests began. The tests were performed in a germination chamber over three weeks from November to December 2021. Six petri dishes per seed source, i.e., 24 dishes in total, were prepared with filter paper, and strips of filter paper connecting the dish to the water supply. In each petri dish, 40 healthy-looking (non-moldy and not visibly predated) seeds from the same source were evenly distributed. Thus, we tested 240 seeds from each population in total. To avoid bias within the germination chamber, the petri dishes were distributed evenly over three zones within the chamber: left, middle and right, containing two petri dishes from each seed source. The air temperature in the germination chamber was set at 20°C, and the water temperature at 13°C. The chamber was set to a 16-hour light period. During the test, germinating seeds were monitored twice a week, counted and removed. The test was terminated after three weeks when there had been no germination for five days.

Average germination rates were calculated for each seed source and subsequently used to determine the amount of seed bulk to be distributed per plot (**Table S1**).

Experimental design and measurements

Experimental plots were established in October and seeded in December 2021. Within all three study areas, five blocks (approx. 1 m^2, with the longer side 2 m) were randomly selected in each habitat type. The blocks were established at a minimum of 10 m apart (**Figure S2**), each within a at least 10 m^2 patch of the chosen habitat type.

Three plots (0.5 x 0.5 m) were laid out in a row within each block, with a 25 cm buffer zone between them and treatments randomized amongst them (**Figure S2**). The treatments were: no disturbance with a local seed source, no disturbance with a standard seed source, and disturbance with a local seed source, with the exception of Neðri Dalur where the standard seed source was used for the disturbed plots due to very low germination rate of Neðri Dalur's local seed source (**Table S1**). Disturbance was applied to the designated plots by cutting all the vegetation at ground level and subsequently raking the entire plot to expose the underlying soil (Magnusson & Magnusson 1990).

We decided on a density of 1500 viable seeds per plot, based on the availability of the bulk of the different seed sources. The number of healthy-looking seeds in 1 gram of each of the seed sources, i.e. seeds that were not obviously damaged or predated, was inspected to calculate the correct amount of bulk to be distributed, to have a similar number of viable seeds per plot. Seeds were distributed evenly across the entire plot surface area and pressed to the ground with the inside of the paper bag in which they had been stored in an attempt to prevent them from being immediately swept away by wind.

Seedling emergence and survival were surveyed in July and September 2022 and 2023, a total of four times. The September surveys were designed to account for late emergence. In 2022, emergence was assessed by counting seedlings, and individual seedlings of this first cohort were marked to assess their survival. In 2023, surviving seedlings were counted, as well as new emergence of a second seedling cohort.

To determine safe sites for emergence and survival, we registered the microsite occupied by each individual seedling, distinguishing between 15 different microsite types (**Table 2**). To account for microsite occupancy relative to cover, we measured the cover of different microsites within each plot during the July surveys, using the point-intercept method of 25 evenly distributed points within a 0.5 x 0.5 m quadrat.

Table 2*. Microsite types included in this study, adapted from Aradóttir & Halldórsson (2018).*

Microsite	Description
Soil	Mineral soil
Sand	Loose sand, mostly <0.2 cm in diameter
Gravel	Gravel 0.2–2 cm in diameter
Pebbles	Rocks 2–5 cm in diameter
Rocks	Rocks >5 cm in diameter
Biocrust	Biological soil crust dominated with liverworts (especially *Anthelia* spp.)
Moss <1 cm	Bryophyte layer, <1 cm thick
Moss 1–2 cm	Bryophyte layer, 1–2 cm thick
Moss >2 cm	Bryophyte layer, >2 cm thick
Lichens	All lichens
Grasses	All grasses
Sedges and rushes	All sedges and rushes (mostly *Luzula* spp.)
Forbs	All forbs
Dwarf shrubs	All dwarf shrubs
Dead moss and grass	Dead moss and grass, mostly generated by an applied disturbance

Statistical analysis

Out of the 60 established blocks, two were excluded from statistical analyses. One block in habitat type 5.3 in Hvanneyri could not be located with enough precision from July 2022 onward, and thus neither emergence nor survival could be assessed; and a block in habitat type 1.3 in Gunnarsholt was by mistake established close (<20 m) to a cluster of birch trees and may have received external seed rain. Thus, the total number of blocks included in the analysis were 58, or 174 plots.

Seedlings densities were calculated for each plot and averaged per treatment (i.e. considering habitat type, disturbance and seed source). We distinguished between seedling emergence of the 1st and 2nd cohorts (from 2022 and 2023 respectively), and survival of the 1st cohort (in 2023).

Due to the nested, non-normally distributed structure of our data, we modelled seedling emergence (mean seedling densities in emergence of the 1st and 2nd cohort) using generalized linear mixed-effect models (GLMMs) with a Poisson distribution. Habitat type, disturbance and seed source were used as fixed variables, and plot ID nested within study area as a random variable. One model was fitted for emergence, and another for survival.

In the context of woodland restoration, one surviving seedling per m^2 may be considered more than sufficient as this would represent more than fivefold density used for planting. Therefore, we also fitted binomial GLMMs to the data on emergence and survival, where we assigned each plot a value of either 0 (restoration failure, i.e. no seedlings) or 1 (restoration success, i.e. one or more seedlings). The same model variables used in the seedling emergence (density) models were applied. For all models performed, we tested interactions between fixed variables and performed backwards stepwise selection based on the Aikake Information Criteria (AIC) to select the model with the best fit.

To analyze the composition of microsite cover in the different habitat types, both with and without an applied disturbance, we performed Wilcoxon's rank sum tests on the effect of the applied disturbance on the cover of each microsite within a habitat type.

The number of emerged and surviving seedlings in different microsites in disturbed and undisturbed areas respectively was calculated by averaging seedling densities across all study areas. Furthermore, to account for the disproportional cover of microsites within a plot, we divided densities by the proportional cover of the given microsite within each plot. To test microsite limitations, we fitted a GLMM with negative binomial distribution with a log-link function on (I) seedling densities of the 1st and 2nd cohort emergence, and (II) survived seedlings of the 1st cohort. Models were fitted for disturbed and undisturbed plots separately for improved interpretation. Plot ID nested within study area was used as a random variable. Furthermore, habitat type was included as a random variable, as we were interested in the association to microsite type across habitat types. Three microsite types (*sand*, *moss >2 cm*, and *shrubs)* were excluded from this analysis, as no seedlings were registered in them in any of the surveys.

We examined model fits by plotting predicted vs observed values, and by examining the distribution of the residuals. Furthermore, all models were examined for over- and underdispersion.

All data analyses were performed in R studio version 4.3.2 (R Core Team 2023). Binomial and Poisson distributed GLMMs were performed using the *lme4* package (Bates et al. 2015), while negative binomial GLMMs were performed using the *glmmTMB* package (Brooks et al. 2017). Likelihood ratio tests were performed using the package *lmtest* (Zeileis & Hothorn 2002). Overdispersion of the GLMMs was assessed using the *DHARMa* package (Hartig 2022). All plots were made using the package *ggplot2* (Wickham 2016).

Results

Of the 1753 seedlings emerging in the first cohort of the experiment in 2022, 585 seedlings, or 33%, survived until autumn 2023. Additionally, 428 new seedlings emerged in 2023 (second cohort). Although we applied the same treatments to same habitat types across all study areas, the outcome differed substantially between study areas (**Table 3**).While Hvanneyri and Neðri Dalur had overall mean seedling densities of 4 seedlings m^{-2} in undisturbed and 6 seedlings m^{-2} in disturbed plots in the second growing season, the numbers for Gunnarsholt were on average 7 times higher in undisturbed plots (28 seedlings m^{-2}), and 16 times higher in disturbed plots (98 seedlings m^{-2}). km^2

Habitat type 10.8 had the highest densities of emerging and surviving seedlings across all treatments and study areas (**Table 3**). Both emergence and survival in undisturbed plots of habitat type 1.3 were generally low, although higher in Gunnarsholt than in the two other study areas. Emergence in undisturbed plots in habitat 5.3 was highest in Neðri Dalur but very low at the other sites, while emergence in disturbed plots of this habitat type was by far the highest in Gunnarsholt. No seedlings were found in undisturbed plots in habitat type 10.4, however emergence occurred in most disturbed plots of the same habitat type across all study areas.

Table 3. *Overview of seedling emergence and survival (mean ± SE seedlings m^{-2}) of mountain birch seedlings in different habitat types (see* ***Table 1.*** *for details) and disturbance treatments in three study areas in West and South Iceland. For plots receiving disturbance treatment, the local seed source was used in Hvanneyri and Gunnarsholt, while the standard seed source was used in Neðri Dalur.*

		Neðri Dalur			Hvanneyri			Gunnarsholt		
		1st growing season	2nd growing season		1st growing season	2nd growing season		1st growing season	2nd growing season	
Habitat type and disturbance	Seed source	Emergence 1^{st} cohort	Survival	Emergence 2^{nd} cohort	Emergence 1^{st} cohort	Survival	Emergence 2^{nd} cohort	Emergence 1^{st} cohort	Survival	Emergence 2^{nd} cohort
1.3										
No disturbance	Local	0	-	0	0	-	0	1 (± 0.2)	1 (± 0.2)	30 (± 2.3)
No disturbance	Standard	0	-	0	0	-	0	1 (± 0.1)	1 (± 0.1)	3 (± 0.2)
Disturbance	Local/standard	0	-	1 (± 0.1)	1 (± 0.1)	0	1 (± 0.1)	97 (± 6.1)	28 (± 2.5)	3 (± 0.2)
5.3										
No disturbance	Local	3 (± 0.2)	1 (± 0.1)	0	0	-	0	0	-	0
No disturbance	Standard	4 (± 0.5)	1 (± 0.1)	1 (± 0.1)	1 (± 0.1)	1 (± 0.1)	0	0	-	0
Disturbance	Local/standard	3 (± 0.4)	1 (± 0.1)	2 (± 0.2)	0	-	2 (± 0.1)	298 (± 26.6)	101 (± 9.2)	38 (± 3.4)
10.4										
No disturbance	Local	0	-	0	0	-	0	0	-	0
No disturbance	Standard	0	-	0	0	-	0	0	-	0
Disturbance	Local/standard	1 (± 0.1)	1 (± 0.1)	14 (± 1)	30 (± 1.9)	5 (± 0.2)	3 (±0.3)	54 (± 4.9)	18 (± 1.9)	4 (± 0.4)
10.8										
No disturbance	Local	0	-	0	1 (± 0.1)	1 (± 0.1)	1 (± 0.1)	74 (± 8.8)	10 (± 0.4)	38 (± 2.3)
No disturbance	Standard	1 (± 0.1)	1 (± 0.1)	3 (± 0.5)	3 (± 0.5)	2 (± 0.3)	12 (± 1)	13 (± 0.7)	8 (± 0.4)	29 (± 0.7)
Disturbance	Local/standard	10 (± 1.1)	3 (± 0.3)	3 (± 0.3)	6 (± 0.5)	2 (± 0.2)	4 (± 0.4)	183 (± 8.8)	72 (± 1.6)	35 (± 3.5)

The effect of seed source was less prominent than the other factors, with similar densities of both emerging and surviving seedlings observed across treatments (**Table 3**). The only noticeable effect was in Gunnarsholt, where the local seed source performed better in terms of emergence of both the 1st and 2nd seedling cohorts.

In both years, birch seedling emergence was significantly associated with disturbance ($p < 0.001$), seed source ($p < 0.001$) and habitat type ($p < 0.05$) (**Table 4**). Undisturbed plots had significantly fewer seedlings than disturbed (E = -1.43, $p < 0.001$, **Table S2**), and seedling emergence was significantly lower when using the standard seed source than the local (E = -0.56, $p < 0.001$). The interaction between disturbance and habitat type was only significant for 10.8, i.e., there was a significantly higher seedling emergence in undisturbed than disturbed plots in 10.8 (E = 3.07, $p < 0.001$). This interaction was insignificant for the other habitat types.

Table 4. *Summary of ANOVA type II test results for generalized linear mixed-effect models (GLMM) regressions with a Poisson distribution of the total birch seedling emergence (1st and 2nd cohort) in three study areas in SW Iceland using habitat type, disturbance and seed source as fixed variables, and plot ID nested within study area as a random variable. Significant values are highlighted in bold.*

		Emergence	
Factor	df	$\chi2$	p
Habitat type	3	15.4	**< 0.01**
Disturbance	1	79.1	**< 0.001**
Habitat type:Disturbance	3	10.4	**< 0.001**
Seed source	1	33.8	**< 0.001**

Binomial GLMMs on restoration success, i.e. proportion of plots with at least one emerged or one surviving seedling (which corresponds to a minimum of two seedlings m^{-2}), revealed significant effects of both disturbance and habitat type (**Table 5**). More specifically, there was a negative association between undisturbed habitats and restoration success (emergence: E = -4.02, $p < 0.001$, survival: E = -3.11, $p < 0.001$, **Table S3**). The only habitat type displaying a significant positive effect was 10.8 (emergence: E = 2.63, $p < 0.01$, survival: E = 3.17, $p < 0.01$, **Table S4**). Seed source had no significant effect on neither success in emergence nor survival.

Table 5. *Summary of ANOVA type II test results for the binomial GLMM regressions on restoration success, both for seedling emergence and survival, using habitat type, disturbance and seed source as fixed variables, and plot ID nested within study area as a random variable. Significant values are highlighted in bold.*

		Emergence		Survival	
Factor	df	χ2	p	χ2	p
Habitat type	3	10.1	**< 0.05**	9.5	**< 0.05**
Disturbance	1	23.6	**< 0.001**	18.9	**< 0.001**
Seed source	1	0.01	0.951	0.7	0.389

The applied disturbance affected the microsite composition differently amongst habitat types. In all habitat types, the cover of the microsite types of *soil* and *dead moss and grass* was significantly higher in disturbed than undisturbed plots (**Figure 2**). This increase typically corresponded to a decrease in *dwarf shrubs*, although this decrease was only significant in habitat types 1.3 and 10.8. In all four habitat types, the disturbance also affected the cover of *moss >2 cm*, i.e. reducing the thick sward layer. However, it was only significant in habitat type 10.8. Habitat type 10.4 furthermore had a significantly increased cover of thinner mosses (*moss <1 cm* and *1-2 cm*) in disturbed plots, and habitat type 10.8 had a significantly reduced cover of *lichens*.

Mean seedling emergence of the 1st and 2nd cohort in undisturbed plots was highest in the *moss <1 cm* microsite (2 seedlings m^{-2}) and had a significant positive association (**Figure 3a**), i.e. seedlings were more likely to emerge in this microsite than expected if their distribution was random. Emergence was furthermore positively associated with the microsite types *biocrust* and *dead moss and grass*. The same microsite types had significant positive associations with seedling density in disturbed plots, along with *soil*, which also had rather high mean densities (9 seedlings m^{-2}, **Figure 3b**). In general, seedling densities were lower in microsite types characterized by tall-growing vegetation, such as *grasses*, *forbs*, *ferns & horsetails* and *dwarf shrubs*. Seedling densities were, however, higher in these microsites in disturbed than in undisturbed plots, and furthermore displayed significant positive associations to these microsites (**Figure 3b**).

Density of surviving seedlings of the 1st cohort in undisturbed plots were highest in microsites characterized by thin, soil stabilizing substrates, such as *biocrust* (3 seedlings m^{-2}), *moss <1 cm* (4 seedlings m^{-2}) and *lichens* (4 seedlings m^{-2}), with similarly high densities in *grasses* and *dwarf shrubs* (3 seedlings m^{-2}, **Figure 4a**), although none of these microsites showed a significant positive relation to seedling density. The microsite types of *soil* and *gravel* had an average of less than 1 surviving seedling m^{-2}, with the relationship furthermore displaying a significant negative association. In disturbed plots, *moss <1 cm* (20 seedlings m^{-2}), *grasses* (12 seedlings m^{-2}) and *dead moss and grass* (9 seedlings m^{-2}) had the highest density of surviving seedlings, with significant positive associations (**Figure 4b**).

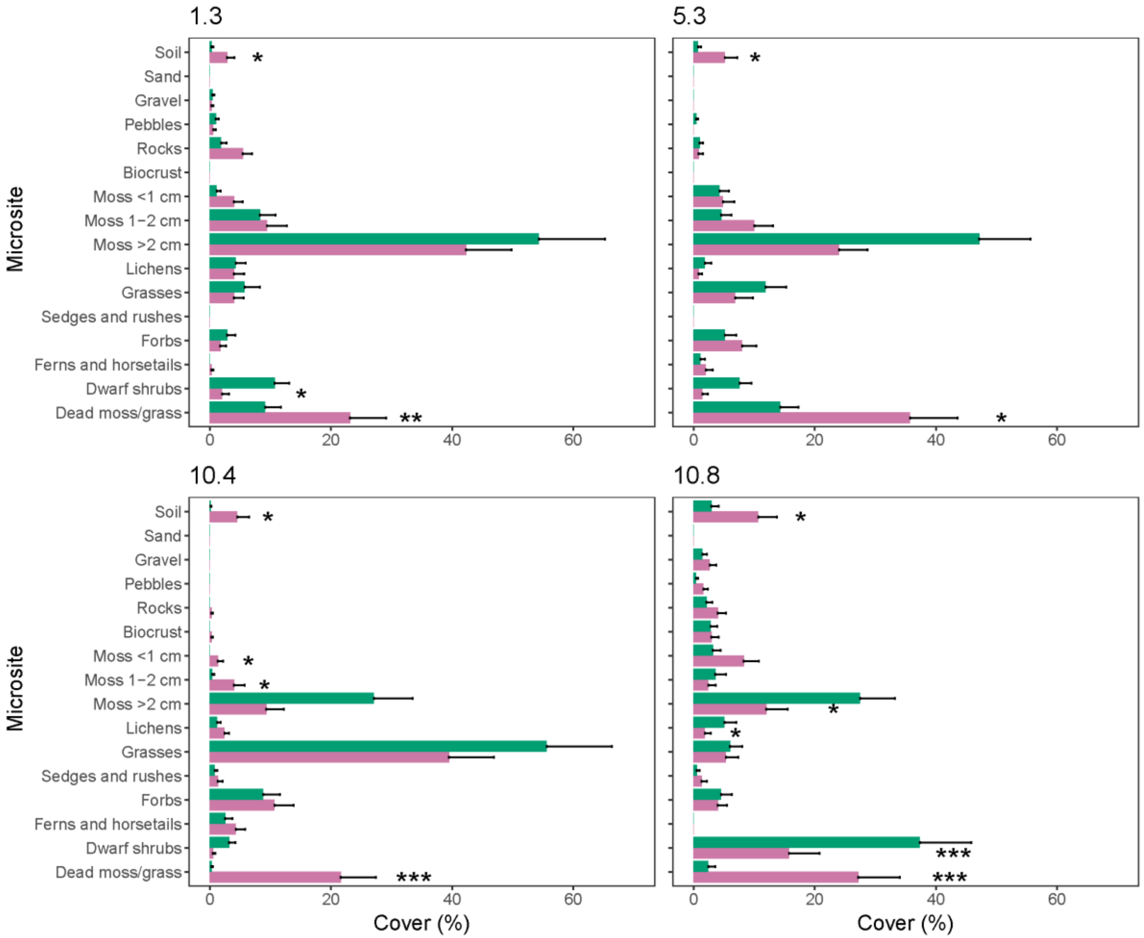


Figure 2. *Mean (± SE) cover of microsites in undisturbed (turquoise) and disturbed (magenta) plots combined over four habitat types (see details on them in Table 1). Asterisks indicate level of significance in Wilcoxon's rank sum tests on the effect of disturbance on microsite cover (* = p < 0.05, ** = p < 0.01, *** = p < 0.001). Values are based on the first survey year, 2022.*

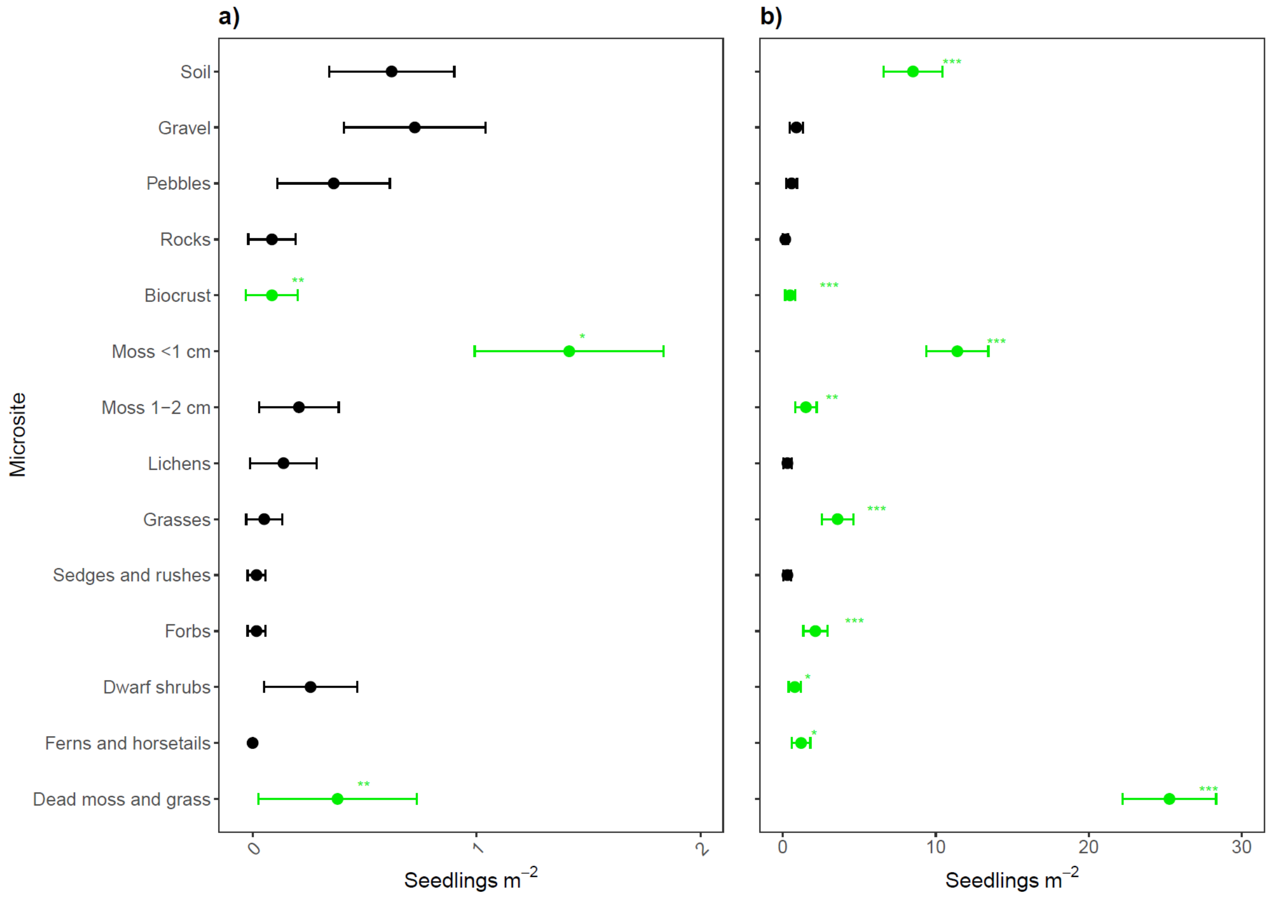


Figure 3. *Mean (± SE) density of emerging seedlings from the 1st and 2nd cohort in different microsite types in a) undisturbed and b) disturbed plots. Color indicates the association of seedling density to individual microsite types (green = significantly positive association, black = insignificant association) and asterisks indicate level of significance (* = p < 0.05, ** = p < 0.01, *** = p < 0.001). Note different scales on the horizontal axes. Three microsite types were excluded from this analysis: sand, shrubs and moss >2 cm.*

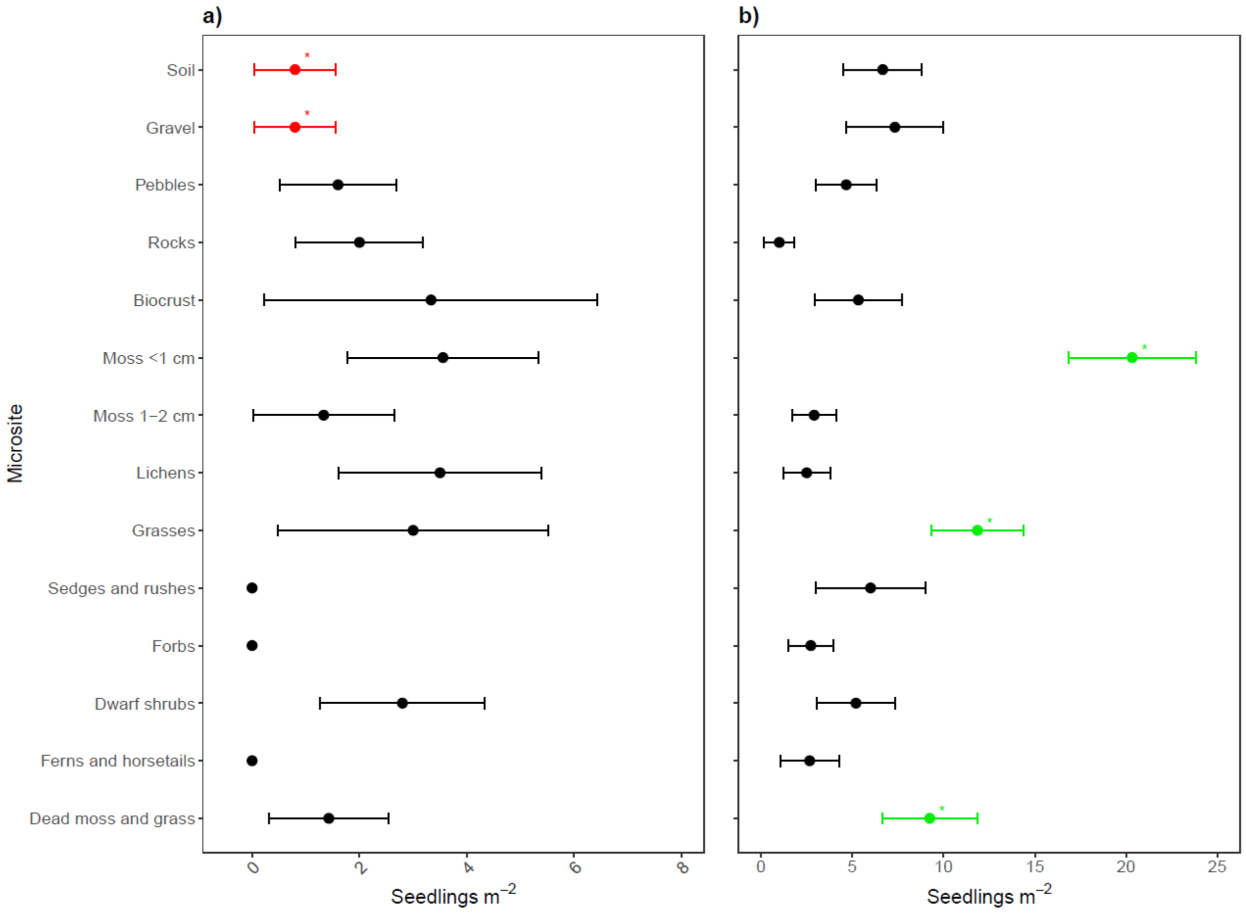


Figure 4. *Mean (± SE) density of surviving seedlings from the 1st and 2nd cohort in different microsite types in a) undisturbed and b) disturbed plots. Color indicates the association of seedling densities to microsite type (green = significantly positive association, red = significant negative association, black = insignificant association) and asterisks indicate level of significance (* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$). Note different scales on the horizontal axes.*

Discussion

What are the characteristics of microsites suitable for birch recruitment in different subarctic habitat types?

Our study showed that recruitment of mountain birch, as for many other tree species, is highly microsite limited (Johnson & Fryer 1992, Jones & del Moral 2005, Douterlungne et al. 2015). The microsite types *biocrust*, *moss <1 and 1-2 cm* and *dead moss and grass* were favorable for birch recruitment across habitat types. These offer optimal conditions for birch establishment, including soil stability, an appropriate soil-seed interface (Collis-George & Hector 1966) and possibly facilitation (Gavini et al. 2019).

Dead moss and grass was present in undisturbed habitats, but its cover increased significantly following the applied disturbance. This turned out to be highly beneficial for both seedling establishment and survival, most likely by providing some protection to the exposed mineral soils from frost heaving (Goulet 1995, Douterlungne et al. 2015) and possibly by increasing moisture at the soil surface (De Atrip & O'Reilly 2007, Lidman et al. 2023). This is further supported by the negative association of the microsite type *soil* to densities of surviving seedlings. Establishment of plants has been found to be high in exposed mineral soils (Jones & del Moral 2005, Lidman et al. 2023, Hernández & Pérez 2024). Combined with the harsh subarctic climate, this barren microsite will, however, likely result in high rates of mortality. This can be prevented by, when applying a disturbance, covering the exposed area with the plant cuttings or mulch after seeding.

The occurrence of the microsite type *biocrust* was so low that it can be considered rare. However, the significant positive association between this microsite type and emergence indicates that although mean seedling densities were low, they were high relative to the microsite cover. Thus, biocrust may facilitate high rates of recruitment in the context of ecological restoration (Aradóttir & Halldórsson 2018, Behrend et al. 2025). Their presence can be supplemented by assisted dispersal and inoculation, especially in degraded habitats; a subject that has been researched increasingly in recent years (Ficko et al. 2022, Lamarre et al. 2023).

Can selected restoration interventions enhance colonization by increasing the abundance of microsites that match a species' recruitment niche?

Disturbance in the form of cutting the aboveground vegetation and raking to expose the soil surface was the most significant factor affecting seedling establishment of birch in our experiment. Although the results varied between habitat types, the overall effect of this type of disturbance was to boost the emergence of birch; a relatively small seeded, light-sensitive species (Grime & Jeffrey 1965). In disturbed plots, tall vegetation had a facilitating rather than impeding effect on recruitment. This suggests that the main inhibitor to recruitment altered by the applied disturbance was the removal of the thick sward, which was significantly reduced by the disturbance in three out of four habitat types. The absence of any recorded birch seedlings in the *moss >2 cm* microsite in all experimental plots support this. The disturbance applied presumably also improved the soil seed interface (Collis-George & Hector 1966). With an observed fast regrowth of taller vascular plants such as *Galium boreale* and *Alchemilla alpina* during the two years of our study, it remains to be seen if the surviving birch seedlings are competitive enough for continuing survival and growth.

Our results indicate that the effect of disturbance on recruitment is context dependent. This was seen in habitat type 10.8, where the interaction between habitat type and the applied disturbance was significant, both for emergence and survival of seedlings. Undisturbed plots of habitat type 10.8 mainly consisted of different species of dwarf shrubs, but with a higher cover of barren and low growing microsite types (including biocrust) than the other three habitat types. This implies that, if a patch is already dominated by safe sites such as biocrust and thin moss, an active disturbance may be a limiting rather than an facilitating factor for birch recruitment. Thus, our results support that an essential first step in terrestrial restoration planning is to assess habitat suitability before implementing any interventions (Gann et al. 2019).

In seed-based restoration, the choice of seed source can affect restoration outcomes (Bischoff et al. 2010). Our results suggest that local population are superior when it comes to seedling emergence, but not survival, or general restoration success. In agreement with earlier studies, it is an advantage to use local seed material in restoration due to genetics and environmental adaptations (Renison et al. 2005, Vander Mijnsbrugge et al. 2010, Havens et al. 2015). Additionally, by considering the choice of seed source and mainly using local seed material, the spread of superior alien genotypes can be avoided (Bischoff et al. 2010).

Can abundance of favorable microsites be used as a predictor of natural colonization in different habitat types?

Recruitment of birch proved to be highly microsite limited, with several significant relationships of emergence and survival to certain microsite types. The abundance of suitable microsites can thus be used as a predictor for the potential of natural colonization of mountain birch. Iceland has been divided into habitat types based on the EUNIS classification system (EUNIS 2024). This land cover classification system does not exist in all countries, but similar data could be utilized in a corresponding way to investigate habitat suitability for restoration. Land cover classification data makes it possible to standardize the potential for natural regeneration of targeted restoration species through an assessment of the availability of safe sites, which is a limiting factor for many dryland plant species (Fowler et al. 1988). This framework can be applied to any tree species with strong recruitment limitations. Habitat suitability based on microsite cover can be measured with the same methodology used to assess microsite cover in our study. Such a survey should ideally cover a substantial number of field sites, and perhaps even regions, to account for the variability in local climate and abiotic factors, including soil. Such information can furthermore support the development of habitat suitability models with basis in species recruitment niches (Guerra-Coss et al. 2021); a tool which can utilize data on large spatial scales to inform ecosystem restoration by identifying suitable areas for passive and active restoration (Griffiths et al. 2011, Yuen et al. 2023).

Differences between study areas

Although we were able to delineate general drivers of birch establishment success across habitat types, the outstanding difference in both emergence and survival between Gunnarsholt and the two other study areas begs an explanation. Temperatures may affect recruitment from seed, either positively by breaking dormancy (Gosling et al. 2009) and by increasing survival and optimal growth conditions (Canham & Murphy 2016, Hannak & Eggertsson 2020), or negatively through low winter temperature causing frost heaving of seedlings and resulting mortality (Goulet 1995). Precipitation is an important environmental factor in recruitment, as it increases soil moisture which benefits establishment of many tree species (Andrus et al. 2018, Lidman et al. 2023). Both factors interact with microsite cover (Andivia et al. 2017, Frost et al. 2018), making the exact effects challenging to disentangle. There was little inter-annual variation in both variables between sites; the slightly higher monthly winter-precipitation in Neðri Dalur and Hvanneyri compared to Gunnarsholt could have contributed to the more equal rates of second-year emergence observed between study areas, and the generally cold winter of 2022 may have contributed to equal rates of mortality. As a rule of thumb, seedlings are most vulnerable during their first year. Seeding or planting gradually over several years can thus reduce mortality caused by extreme weather events.

An alternative explanation of the diverging results between study areas could be related to the soil. The differences between Gunnarsholt and the remaining areas are mainly observed in the disturbed plots where soils are more exposed, which supports this. This can be both from differences in the soil-seed interface, i.e. some study areas having a rockier surface than others, allowing for less germination (Holmgren 1997, Renison et al. 2005), and from difference in soil nutrients. Dust deposit is higher in Gunnarsholt than in the other study areas, being in close proximity to the Hekla Volcano (Arnalds 2010). This proximity results in a nutrient-rich layer of aeolian deposit which might benefit seedling emergence. This was not examined directly in the field, and no conclusion can thus be drawn from this. Further investigation into the experiments in the coming years would aid in disentangling these effects, which should be included in future considerations on the suitability of habitat restoration of birch woodlands.

Implications for ecological restoration

Larson et al. (2023) advocates using a recruitment niche-based framework for improving seed-based restoration strategies. Our study supports such a framework, with a particular focus on the limitations of suitable microsites for recruitment of target restoration species, such as mountain birch in Iceland. The results are in agreement with the recruitment niche identified by Óskarsdóttir et al. (2025) for mountain birch in a young mountain birch population on a glacial outwash plain in Southeast Iceland, showing that it applies more generally. The microsite types found to be suitable for birch recruitment in our study are common to a variety of different habitat types in Iceland, and in the subarctic region in general. These include braided floodplains, glacial moraines and fjell fields (Ottósson et al. 2016), indicating a good spatial potential for seed-based restoration of mountain birch.

Studying the suitability of dryland habitat types for natural regeneration can aid in identifying where restoration can occur with minimal or no human interventions through low-intensity restoration efforts such as assisted natural regeneration (Griffiths et al. 2011, Yuen et al. 2023). By optimizing spatially targeted ecological restoration, extensive human and economic capital can be saved (Kimball et al. 2015), and restoration can be upscaled efficiently. During the planning phase, however, it is important to consider the possible habitat losses that may follow expansion of woodlands in the arctic and subarctic (Myers-Smith et al. 2011), particularly heathlands which are important habitat types for ground-nesting birds in Iceland (Pálsdóttir et al. 2022). It might therefore be a good strategy to focus active restoration efforts on degraded habitat types, if available, that may need some revegetation before woodland establishment can take place (Aradóttir & Halldórsson 2018).

In many countries, including Iceland, it is a standard practice to use mainly one or few seed sources in both restoration and afforestation contexts. Thus, seed-based restoration practices should be revisited by environmental agencies and restoration practitioners to consider the use of more diverse seed sources, which could improve the outcome of seed-based restoration. Local seed materials need not necessarily be from a seed source in the close vicinity of a restoration site. It is, however, important to identify correct seed transfer zones (Jørgensen et al. 2016), as well as using indicators for genetic adaptation to environments in different populations, which has been shown for historically isolated populations of mountain birch in Iceland (Pálsson et al. 2023).

Conclusions

The results of this study show that it is crucial to consider the recruitment niche of target-species for successful restoration. If this is ignored, substantial restoration efforts could be wasted. We show that certain microsite types are highly favorable for recruitment of mountain birch, which in all habitat types comprise thin mosses, biocrusts and dead moss and grass, and for habitats with tall vegetation allowing for facilitation, as long as the underlying sward layer is thin, allowing for sufficient soil-seed contact for seed germination; an attribute that can be manipulated through an applied disturbance. As significant relationships were seen for seedling emergence and survival in several microsite types across habitat types, the abundance of favorable microsite can act as a predictor of successful natural colonization. Our results confirm that recruitment can be facilitated by restoration interventions that shift the microenvironment towards the recruitment niche of a target species, in this case mountain birch. This may have diverging effects in different habitat types, which is why habitat is an important attribute to consider. Our results can aid in optimizing the planning of seed-based restoration frameworks, and restoration strategies relying on natural regeneration such as applied nucleation and assisted natural regeneration, and aid in modelling the potential future spread of native ecosystems through natural colonization.

References

Andivia, E., Villar-Salvador, P., Tovar, L., Rabasa, S., & Rey Benayas, J. M. (2017). Multiscale assessment of woody species recruitment in Mediterranean shrublands: Facilitation and beyond. *Journal of Vegetation Science*, *28*(3), 639–648. https://doi.org/10.1111/jvs.12520

Andrus, R. A., Harvey, B. J., Rodman, K. C., Hart, S. J., & Veblen, T. T. (2018). Moisture availability limits subalpine tree establishment. *Ecology 99*(3), 567-575. https://doi.org/10.1002/ecy.2134

Aradóttir, A. L., & Halldorsson, G. (2018). Colonization of woodland species during restoration: Seed or safe site limitation? *Restoration Ecology*, *26*, S73–S83. https://doi.org/10.1111/rec.12645

Arnalds, A. (1987). Ecosystem disturbance in Iceland. *Arctic and Alpine Research*, *19*(4), 508. https://doi.org/10.2307/1551417

Arnalds, Ó. (2010). Dust sources and deposition of aeolian materials in Iceland. *Icelandic Agricultural Sciences, 23*, 3–21.

Arnalds, Ó., & Óskarsson, H. (2009). Íslenskt jarðvegskort [A soil map of Iceland]. *Náttúrufræðingurinn, 78*, 107-121.

Bastin, J.-F., Finegold, Y., Garcia, C., Mollicone, D., Rezende, M., Routh, D., Zohner, C. M., & Crowther, T. W. (2019). The global tree restoration potential. *Science*, *365*(6448), 76–79. https://doi.org/10.1126/science.aax0848

Bates, D., Mächler, M., Bolker, B., Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67(1), 1–48.

Behrend, A. M., Aradóttir, Á. L., Svavarsdóttir, K., Thórhallsdóttir, T. E., & Pommerening, A. (2025). Natural colonization as a means to upscale restoration of subarctic woodlands in Iceland. *Restoration Ecology, e14332*. https://doi.org/10.1111/rec.14332

Bischoff, A., Steinger, T., & Müller-Schärer, H. (2010). The importance of plant provenance and genotypic diversity of seed material used for ecological restoration. *Restoration Ecology*, *18*(3), 338–348. https://doi.org/10.1111/j.1526-100X.2008.00454.x

Boeken, B. R. (2018). Competition for microsites during recruitment in semiarid annual plant communities. *Ecology*, *99*(12), 2801–2814. https://doi.org/10.1002/ecy.2484

Broadhurst, L. M., Lowe, A., Coates, D. J., Cunningham, S. A., McDonald, M., Vesk, P. A., & Yates, C. (2008). Seed supply for broadscale restoration: Maximizing evolutionary potential. *Evolutionary Applications*, *1*(4), 587–597. https://doi.org/10.1111/j.1752-4571.2008.00045.x

Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Maechler, M., Bolker, B. M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, 9(2), 378–400.

Canham, C. D., & Murphy, L. (2016). The demography of tree species response to climate: Seedling recruitment and survival. *Ecosphere*, *7*(8), e01424. https://doi.org/10.1002/ecs2.1424

Chazdon, R. L. (2008). Beyond deforestation: Restoring forests and ecosystem services on degraded lands. *Science*, *320*(5882), 1458–1460. https://doi.org/10.1126/science.1155365

Chazdon, R. L., & Guariguata, M. R. (2016). Natural regeneration as a tool for large-scale forest restoration in the tropics: Prospects and challenges. *Biotropica*, *48*(6), 716–730. https://doi.org/10.1111/btp.12381

Collis-George, N., & Hector, J. B. (1966). Germination of seeds as influenced by matric potential and by area of contact between seed and soil water. *Soil Research*, *4*(2), 145-164.

Corbin, J. D., & Holl, Karen D. (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

Convention on Biological Diversity (CBD) 2022. Kunming-Montreal Global Biodiversity Framework. Conference of the parties to the convention on biological diversity, Montreal, Canada. https://www.cbd.int/gbf (Accessed on 13th of September 2025)

Crouzeilles, R., Beyer, H. L., Monteiro, L. M., Feltran-Barbieri, R., Pessôa, A. C. M., Barros, F. S. M., Lindenmayer, D. B., Lino, E. D. S. M., Grelle, C. E. V., Chazdon, R. L., Matsumoto, M., Rosa, M., Latawiec, A. E., & Strassburg, B. B. N. (2020). Achieving cost-effective landscape-scale forest restoration through targeted natural regeneration. *Conservation Letters*, *13*(3), e12709. https://doi.org/10.1111/conl.12709

Crouzeilles, R., Ferreira, M. S., Chazdon, R. L., Lindenmayer, D. B., Sansevero, J. B. B., Monteiro, L., Iribarrem, A., Latawiec, A. E., & Strassburg, B. B. N. (2017). Ecological restoration success is higher for natural regeneration than for active restoration in tropical forests. *Science Advances*, *3*(11), e1701345. https://doi.org/10.1126/sciadv.1701345

De Atrip, N., & O'Reilly, C. (2007). Effect of seed coverings and seed pretreatments on the germination response of *Alnus glutinosa* and *Betula pubescens* seeds. *European Journal of Forest Research*, *126*(2), 271–278. https://doi.org/10.1007/s10342-006-0146-2

Deshaies, A., Boudreau, S., & Harper, K. A. (2009). Assisted revegetation in a subarctic environment: Effects of fertilization on the performance of three indigenous plant Species. *Arctic, Antarctic, and Alpine Research*, *41*(4), 434–441. https://doi.org/10.1657/1938-4246-41.4.434

Douterlungne, D., Ferguson, B. G., Siddique, I., Soto-Pinto, L., Jímenez-Ferrer, G., & Gavito,

M. E. (2015). Microsite determinants of variability in seedling and cutting establishment in tropical forest restoration plantations: Microsite variability in restoration trials. *Restoration Ecology*, *23*(6), 861–871. https://doi.org/10.1111/rec.12247

Duncan, R. P., Diez, J. M., Sullivan, J. J., Wangen, S., & Miller, A. L. (2009). Safe sites, seed supply, and the recruitment function in plant populations. *Ecology*, *90*(8), 2129–2138. https://doi.org/10.1890/08-1436.1

Espeland, E. K., Emery, N. C., Mercer, K. L., Woolbright, S. A., Kettenring, K. M., Gepts, P., & Etterson, J. R. (2017). Evolution of plant materials for ecological restoration: Insights from the applied and basic literature. *Journal of Applied Ecology*, *54*(1), 102–115. https://doi.org/10.1111/1365-2664.12739

European Nature Information System (EUNIS). https://eunis.eea.europa.eu/habitats.jsp. (Accessed on 13th of July 2024)

Ficko, S. A., Haughland, D. L., & Naeth, M. A. (2023). Assisted dispersal and retention of lichen-dominated biocrust material for arctic restoration. *Restoration Ecology*, *31*(4), e13793. https://doi.org/10.1111/rec.13793

Fowler, N. L. (1988). What is a safe site? Neighbor, litter, germination date, and patch effects. *Ecology*, *69*(4), 947–961. https://doi.org/10.2307/1941250

Frost, G. V., Epstein, H. E., Walker, D. A., Matyshak, G., & Ermokhina, K. (2018). Seasonal and long-term changes to active-layer temperatures after tall shrubland expansion and succession in Arctic tundra. *Ecosystems, 21*, 507-520. https://doi.org/10.1007/s10021-017-0165-5

Gann, G. D., McDonald, T., Walder, B., Aronson, J., Nelson, C. R., Jonson, J., Hallett, J. G., Eisenberg, C., Guariguata, M. R., Liu, J., Hua, F., Echeverría, C., Gonzales, E., Shaw, N., Decleer, K., & Dixon, K. W. (2019). International principles and standards for the practice of ecological restoration. Second edition. *Restoration Ecology*, *27*(S1). https://doi.org/10.1111/rec.13035

Gavini, S. S., Suárez, G. M., Ezcurra, C., & Aizen, M. A. (2019). Facilitation of vascular plants by cushion mosses in high-Andean communities. *Alpine Botany*, *129*(2), 137–148. https://doi.org/10.1007/s00035-019-00222-6

Gosling, P. G., McCartan, S. A., & Peace, A. J. (2009). Seed dormancy and germination characteristics of common alder (*Alnus glutinosa* L.) indicate some potential to adapt to climate change in Britain. *Forestry*, *82*(5), 573–582. https://doi.org/10.1093/forestry/cpp024

Goulet, F. (1995). Frost heaving of forest tree seedlings: a review. *New forests*, *9*, 67-94. https://doi.org/10.1007/BF00028927

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]. Reykjavík, Iceland.

Griffiths, G. H., Vogiatzakis, I. N., Porter, J. R., & Burrows, C. (2011). A landscape scale spatial model for semi-natural broadleaf woodland expansion in Wales, UK. *Journal for Nature Conservation*, *19*(1), 43–53. https://doi.org/10.1016/j.jnc.2010.05.002

Grime, J. P. & Jeffrey, D. W. (1965). Seedling establishment in vertical gradients of sunlight. *Journal of Ecology*, 53, 621-642.

Grubb, P. J. (1977). The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological Reviews*, *52*(1), 107–145. https://doi.org/10.1111/j.1469-185X.1977.tb01347.x

Guerra-Coss, F. A., Badano, E. I., Cedillo-Rodríguez, I. E., Ramírez-Albores, J. E., Flores, J., Barragán-Torres, F., & Flores-Cano, J. A. (2021). Modelling and validation of the spatial distribution of suitable habitats for the recruitment of invasive plants on climate change scenarios: An approach from the regeneration niche. *Science of The Total Environment*, *777*, 146007. https://doi.org/10.1016/j.scitotenv.2021.146007

Havens, K., Vitt, P., Still, S., Kramer, A. T., Fant, J. B., & Schatz, K. (2015). Seed sourcing for restoration in an era of climate change. *Natural Areas Journal*, *35*(1), 122–133. https://doi.org/10.3375/043.035.0116

Hannak, N., & Eggertsson, Ó. (2020). The long-term effects of climatic factors on radial growth of downy birch (*Betula pubescens*) and rowan (*Sorbus aucuparia*) in East Iceland. *Icelandic Agricultural Sciences*, *33*, 73–87. https://doi.org/10.16886/IAS.2020.07

Hartig, F. (2022). DHARMa: residual diagnostics for hierarchical (multi-level / mixed) regression models. R package version 0.4.6

Hernández, J. A., & Pérez, D. R. (2024). Performance of five arid land shrub species in direct seeding: Implications for seed-based restoration. *Restoration Ecology*, *32*(2), e14022. https://doi.org/10.1111/rec.14022

Holl, K. D., & Aide, T. M. (2011). When and where to actively restore ecosystems? *Forest Ecology and Management*, *261*(10), 1558–1563. https://doi.org/10.1016/j.foreco.2010.07.004

Holmgren, M., Scheffer, M., & Huston, M. A. (1997). The interplay of facilitation and competition in plant communities. *Ecology* *78*(7), 1966–1975. https://doi.org/10.2307/2265937

International Union for Conservation of Nature (IUCN) (2020). The Bonn challenge. https://www.bonnchallenge.org/ (accessed 4th of September 2024)

Johnson, E. A., & Fryer, G. I. (1992). Physical characterization of seed microsites—Movement on the ground. *The Journal of Ecology*, *80*(4), 823. https://doi.org/10.2307/2260869

Jones, C. C., & 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. http://www.jstor.org/stable/4096692

Jørgensen, M. H., Elameen, A., Hofman, N., Klemsdal, S., Malaval, S., & Fjellheim, S. (2016). What's the meaning of local? Using molecular markers to define seed transfer zones for ecological restoration in Norway. *Evolutionary Applications*, *9*(5), 673–684. https://doi.org/10.1111/eva.12378

Jutila, H. M., & Grace, J. B. (2002). Effects of disturbance on germination and seedling establishment in a coastal prairie grassland: A test of the competitive release hypothesis. *Journal of Ecology*, *90*(2), 291–302. http://www.jstor.org/stable/3072133.

Kim, M., Lee, S., Lee, S., Yi, K., Kim, H.-S., Chung, S., Chung, J., Kim, H. S., & Yoon, T. K. (2022). Seed dispersal models for natural regeneration: A review and prospects. *Forests*, *13*(5), 659. https://doi.org/10.3390/f13050659

Kimball, S., Lulow, M., Sorenson, Q., Balazs, K., Fang, Y.-C., Davis, S. J., O'Connell, M., & Huxman, T. E. (2015). Cost-effective ecological restoration. *Restoration Ecology*, *23*(6), 800–810. https://doi.org/10.1111/rec.12261

Lamarre, J. J., Dhar, A., & Naeth, M. A. (2023). Arctic ecosystem restoration with native tundra bryophytes. *Arctic, Antarctic, and Alpine Research*, *55*(1), 2209394. https://doi.org/10.1080/15230430.2023.2209394

Larson, J. E., Agneray, A. C., Boyd, C. S., Bradford, J. B., Kildisheva, O. A., Suding, K. N., & Copeland, S. M. (2023). A recruitment niche framework for improving seed-based restoration. *Restoration Ecology*, e13959. https://doi.org/10.1111/rec.13959

Lidman, F. D., Karlsson, M., Lundmark, T., Sängstuvall, L., & Holmström, E. (2023). Birch establishes anywhere! So, what is there to know about natural regeneration and direct seeding of birch? *New Forests*. https://doi.org/10.1007/s11056-023-09971-z

Liu, Z., & Evans, M. (2021). Effect of tree density on seed production and dispersal of birch (*Betula pendula* Roth and *Betula pubescens* Ehrhs). *Forests*, *12*(7), 929. https://doi.org/10.3390/f12070929

Magnusson, S. H., Magnusson, B. (1990). Birkisáningar til landgræðslu og skógræktar [Seeding of birch for land reclamation and woodland establishment]. *Ársrit Skogræktarfélags Íslands 1990*, 9 - 18. Summary in English.

Meli, P., Holl, K. D., Rey Benayas, J. M., Jones, H. P., Jones, P. C., Montoya, D., & Moreno Mateos, D. (2017). A global review of past land use, climate, and active vs. Passive restoration effects on forest recovery. *PLOS ONE*, *12*(2), e0171368. https://doi.org/10.1371/journal.pone.0171368

Mori, A. S., Lertzman, K. P., & Gustafsson, L. (2017). Biodiversity and ecosystem services in forest ecosystems: A research agenda for applied forest ecology. *Journal of Applied Ecology, 54,* 12-27. https://doi.org/10.1111/1365-2664.12669

Myers-Smith, I. H., Forbes, B. C., Wilmking, M., Hallinger, M., Lantz, T., Blok, D., Tape, K. D., Macias-Fauria, M., Sass-Klaassen, U., Lévesque, E., Boudreau, S., Ropars, P., Hermanutz, L., Trant, A., Collier, L. S., Weijers, S., Rozema, J., Rayback, S. A., Schmidt, N. M., … Hik, D. S. (2011). Shrub expansion in tundra ecosystems: Dynamics, impacts and research priorities. *Environmental Research Letters*, *6*(4), 045509. https://doi.org/10.1088/1748-9326/6/4/045509

Óskarsdóttir, G., Svavarsdóttir, K., Speed J.D.M, & Thórhallsdóttir, T.E. (2025). The recruitment niche of mountain birch (*Betula pubescens* spp. *tortuosa*) and implications for woodland restoration. *Ecological Applications*, in print.

Ottósson, J. G., Sveinsdóttir, A. & Harðardóttir, M. (2016). Vistgerðir á Íslandi [Habitat types in Iceland]. *Fjölrit Náttúrufræðistofnunar* 54. 299 pp. Abstract in English.

Pálsdóttir, A. E., Gill, J. A., Alves, J. A., Pálsson, S., Méndez, V., Ewing, H., & Gunnarsson,

T. G. (2022). Subarctic afforestation: Effects of forest plantations on ground-nesting birds in lowland Iceland. *Journal of Applied Ecology*, *59*(10), 2456–2467. https://doi.org/10.1111/1365-2664.14238

Pálsson, S., Wasowicz, P., Heiðmarsson, S., & Magnússon, K. P. (2023). Population structure and genetic variation of fragmented mountain birch forests in Iceland. *Journal of Heredity*, *114*(2), 165–174. https://doi.org/10.1093/jhered/esac062

R Core Team (2023). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Renison, D., Cingolani, A. M., Suarez, R., Menoyo, E., Coutsiers, C., Sobral, A., & Hensen, I. (2005). The restoration of degraded mountain woodlands: Effects of seed provenance and microsite characteristics on *Polylepis australis* seedling survival and growth in central Argentina. *Restoration Ecology*, *13*(1), 129–137. https://doi.org/10.1111/j.1526-100X.2005.00015.x

Shono, K., Cadaweng, E. A., & Durst, P. B. (2007). Application of assisted natural regeneration to restore degraded tropical forestlands. *Restoration Ecology*, *15*(4), 620–626. https://doi.org/10.1111/j.1526-100X.2007.00274.x

Snorrason, A., Traustason, B., Kjartansson, B. Þ., & 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

Strassburg, B. B. N., Beyer, H. L., Crouzeilles, R., Iribarrem, A., Barros, F., De Siqueira, M. F., Sánchez-Tapia, A., Balmford, A., Sansevero, J. B. B., Brancalion, P. H. S., Broadbent, E. N., Chazdon, R. L., Filho, A. O., Gardner, T. A., Gordon, A., Latawiec, A., Loyola, R., Metzger, J. P., Mills, M., … Uriarte, M. (2018). Strategic approaches to restoring ecosystems can triple conservation gains and halve costs. *Nature Ecology & Evolution*, *3*(1), 62–70. https://doi.org/10.1038/s41559-018-0743-8

Svejcar, L. N., Kerby, J. D., Svejcar, T. J., Mackey, B., Boyd, C. S., Baughman, O. W., Madsen, M. D., & Davies, K. W. (2023). Plant recruitment in drylands varies by site, year, and seeding technique. *Restoration Ecology*, *31*(2), e13750. https://doi.org/10.1111/rec.13750

Valdez, J. W., Hartig, F., Fennel, S., & Poschlod, P. (2019). The recruitment niche predicts plant community assembly across a hydrological gradient along plowed and undisturbed transects in a former agricultural wetland. *Frontiers in Plant Science*, *10*, 88. https://doi.org/10.3389/fpls.2019.00088

Vander Mijnsbrugge, K., Bischoff, A., & Smith, B. (2010). A question of origin: Where and how to collect seed for ecological restoration. *Basic and Applied Ecology*, *11*(4), 300–311. https://doi.org/10.1016/j.baae.2009.09.002

Wandrag, E. M., Catford, J. A., & Duncan, R. P. (2019). Quantifying niche availability, niche overlap and competition for recruitment sites in plant populations without explicit knowledge of niche axes. *Journal of Ecology*, *107*(4), 1791–1803. https://doi.org/10.1111/1365-2745.13137

Wickham, H. (2016). ggplot2: Elegant graphics for data analysis. Springer-Verlag New York.

Willis, J. L., Walters, M. B., & Gottschalk, K. W. (2015). Scarification and gap size have interacting effects on northern temperate seedling establishment. *Forest Ecology and Management*, *347*, 237–247. https://doi.org/10.1016/j.foreco.2015.02.026

Young, T. P., Petersen, D. A., & Clary, J. J. (2005). The ecology of restoration: Historical links, emerging issues and unexplored realms: Ecology of restoration. *Ecology Letters*, *8*(6), 662–673. https://doi.org/10.1111/j.1461-0248.2005.00764.x

Yuen, B., Stuart, C. E., Pittman, S. J., Green, S. J., Henderson, L. M., & Wedding, L. M. (2023). Habitat suitability models of elkhorn coral provide ecological insight to support coral reef restoration. *Restoration Ecology*, *31*(5), e13953. https://doi.org/10.1111/rec.13953

Zeileis, A., & Hothorn, T. (2002). Diagnostic checking in regression relationships. *R News, 2*, 7–10.

Supplementary materials

Behrend, A. M., Thórhallsdóttir, T. E., Svavarsdóttir, K. & Aradóttir, Á. L. (2025). Assessing safe-site limitations to support recruitment niche-based restoration frameworks. [manuscript]

Table S1. Overview of the different seed sources, their germination rates and how they were distributed over the three different experimental sites. The amount of bulk distributed per plot corresponded to 1.500 viable seeds, which was calculated based on the amount of bulk available from the Thórsmörk seed source.

Seed source	Germination rate (%)	Viable seeds per 1 gram	Number of viable seeds per subplot	Amount of bulk distributed per subplot (g)
Búrfellsskógur	6.3	674	1 500	3
Neðri Dalur	1.7	158	1 500	9.5
Hafnarskógur	22.9	3 962	1 500	0.5
Thórsmörk	10	1 060	1 500	1.4

Table S2. Results from the best fitting generalized linear mixed model (GLMM) on the effect of disturbance and habitat type on average seedling emergence. Model structure: glmer(sum ~ Disturbance * Habitat type + Seed source (1 | Study area/Plot ID), family = poisson).

	Estimate	**Std. Error**	**z-value**	***p***
Intercept	0.59	0.94	0.62	0.54
Disturbance				
Undisturbed	-1.43	0.05	-11.55	**<0.001**
Seed source				
Standard seeds	-0.56	0.1	-5.82	**<0.001**
Habitat type				
5.3	1.36	0.58	2.37	**<0.05**
10.4	1.33	0.56	2.37	**<0.05**
10.8	2.19	0.56	3.92	**<0.001**
Disturbance:habitat type				
Undisturbed:5.3	0.14	0.39	0.35	0.72
Undisturbed:10.4	-13.3	0.81	-1.13	0.89
Undisturbed:10.8	3.07	0.36	8.48	**<0.001**

Table S3. Results from the best fitting GLMM on the effect of disturbance, habitat type and seed source on emergence (as a binomial variable) in every experimental plot. Model structure: glmer(Emergence ~ Disturbance + Habitat type + Seed source + (1 | Study area/Plot ID), family = binomial).

	Estimate	**Std. Error**	**z-value**	***p***
Intercept	1.38	0.92	1.51	0.13
Disturbance				
Undisturbed	-4.02	0.83	-4.85	**<0.001**
Seed source				
Standard seeds	0.03	0.49	0.06	0.95
Habitat type				
5.3	0.82	0.87	0.94	0.35
10.4	-0.09	0.86	-0.11	0.91
10.8	2.63	0.99	2.67	**<0.01**

Table S4. Results from the best fitting GLMM on the effect of disturbance, habitat type and seed source on survival (as a binomial variable) in every experimental plot. Model structure: glmer(Survival ~ Disturbance + Habitat type + Seed source + (1 | Study area/Plot ID), family = binomial).

	Estimate	**Std. Error**	**z-value**	***p***
Intercept	-0.69	1.08	-0.64	0.53
Disturbance				
Undisturbed	-3.11	0.72	-4.34	**<0.001**
Seed source				
Standard seeds	-0.46	0.54	-0.86	0.39
Habitat type				
5.3	1.09	0.96	1.14	0.25
10.4	1.27	0.98	1.29	0.2
10.8	3.17	1.11	2.88	**<0.01**

Table S5. Model outputs for the generalized linear mixed-effect model testing for the association between microsites and seedling emergence of the first cohort in undisturbed habitats. Full model code: glmmTMB(Emergence ~ Microsite + (1 | Study area/Plot ID) + (1 | Habitat type), family = poisson(link = "log")).

	Estimate	**Std. Error**	**z-value**	***p***
Intercept	-11.32	1.61	-7.05	**<0.001**
Microsite				
Soil	0.8	0.97	0.82	0.41
Gravel	1.06	0.96	1.1	0.27
Pebbles	0.91	0.93	0.98	0.33
Rocks	-0.1	1.11	-0.09	0.93
Biocrust	1.93	0.94	2.85	**<0.01**
Moss <1cm	2.01	0.95	2.12	**<0.05**
Moss 1-2 cm	1.72	1.05	1.64	0.1
Lichens	-0.33	1.03	-0.32	0.74
Grasses	0.26	1.09	0.2	0.81
Sedges and rushes	-1.59	1.24	-1.29	0.19
Forbs	-1.74	1.27	-1.37	0.17
Dwarf shrubs	0.39	0.96	0.41	0.68
Ferns and horsetails	-4.49	43.71	-0.05	0.99
Dead moss and grass	3.14	0.99	3.19	**<0.01**

Table S6. Model outputs for the generalized linear mixed-effect model testing for the association between microsites and emergence of the first cohort in disturbed habitats. Full model code: glmmTMB(Emergence ~ Microsite + (1 | Study area/Plot ID) + (1 | Habitat type), family = poisson(link = "log")).

	Estimate	**Std. Error**	**z-value**	***p***
Intercept	-4.4	1.52	-2.9	**<0.01**
Microsite				
Soil	4.07	0.71	5.71	**<0.001**
Gravel	0.53	0.76	0.7	0.48
Pebbles	0.14	0.79	0.18	0.86
Rocks	-0.5	0.92	-0.55	0.58
Biocrust	2.89	0.83	4.52	**<0.001**
Moss <1cm	3.59	0.74	4.99	**<0.001**
Moss 1-2 cm	2.29	0.75	3.07	**<0.01**
Lichens	-0.01	0.83	-0.01	0.99
Grasses	3.69	0.74	4.99	**<0.001**
Sedges and rushes	0.87	0.86	1.01	0.31
Forbs	2.5	0.73	3.41	**<0.001**
Dwarf shrubs	1.85	0.81	2.29	**<0.05**
Ferns and horsetails	1.82	0.76	2.4	**<0.05**
Dead moss and grass	5.62	0.73	7.72	**<0.001**

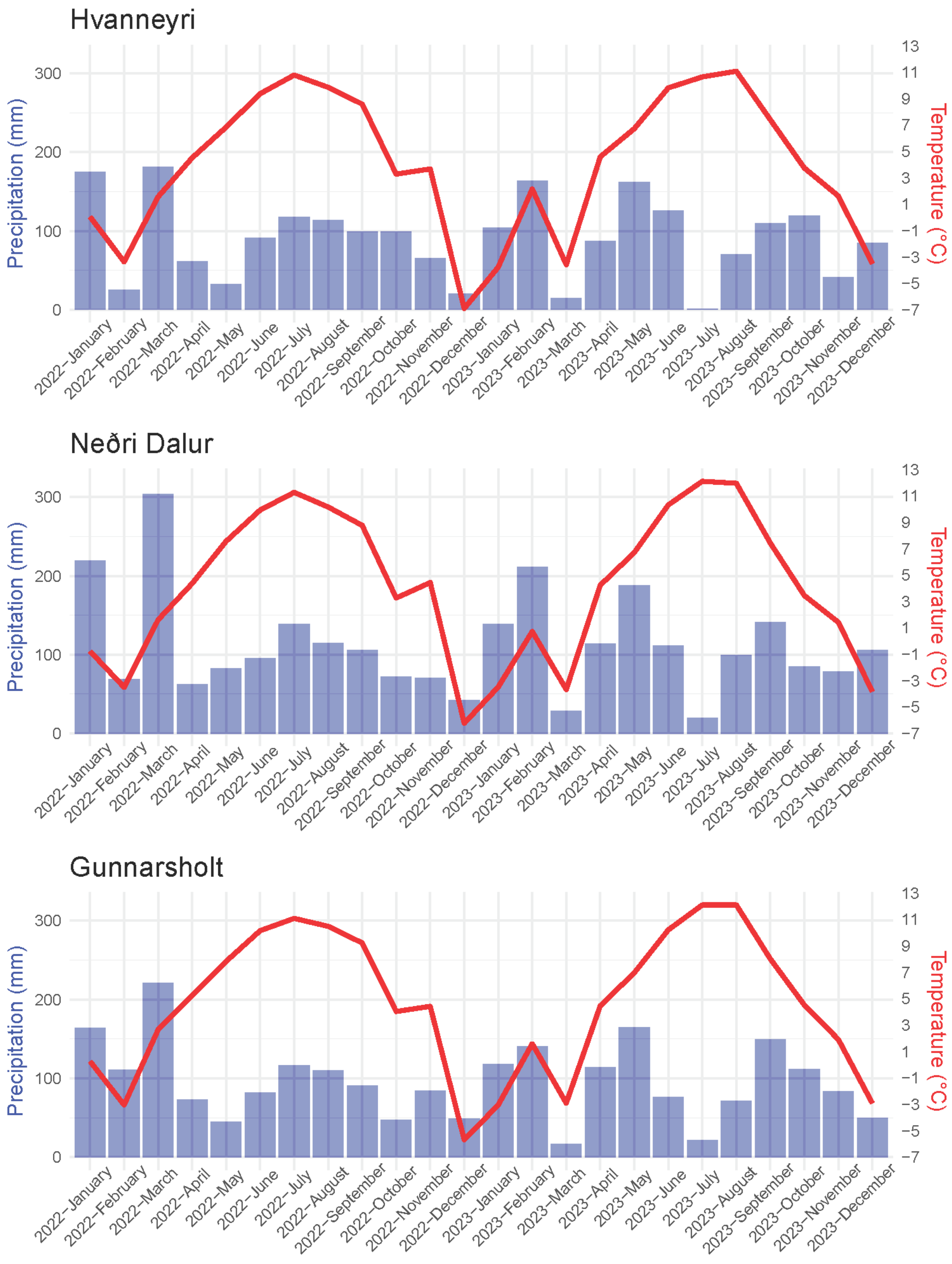


Figure S1. Montlhy precipitation and average temperature from the time between seeding (December 2021) and until the final survey (October 2023) for weather stations closest to the study areas (at distances no more than 8 km). Data was obtained from the following weather stations: Hvanneyri, Hjarðarland (for Neðri Dalur) and Hella (for Gunnarsholt).

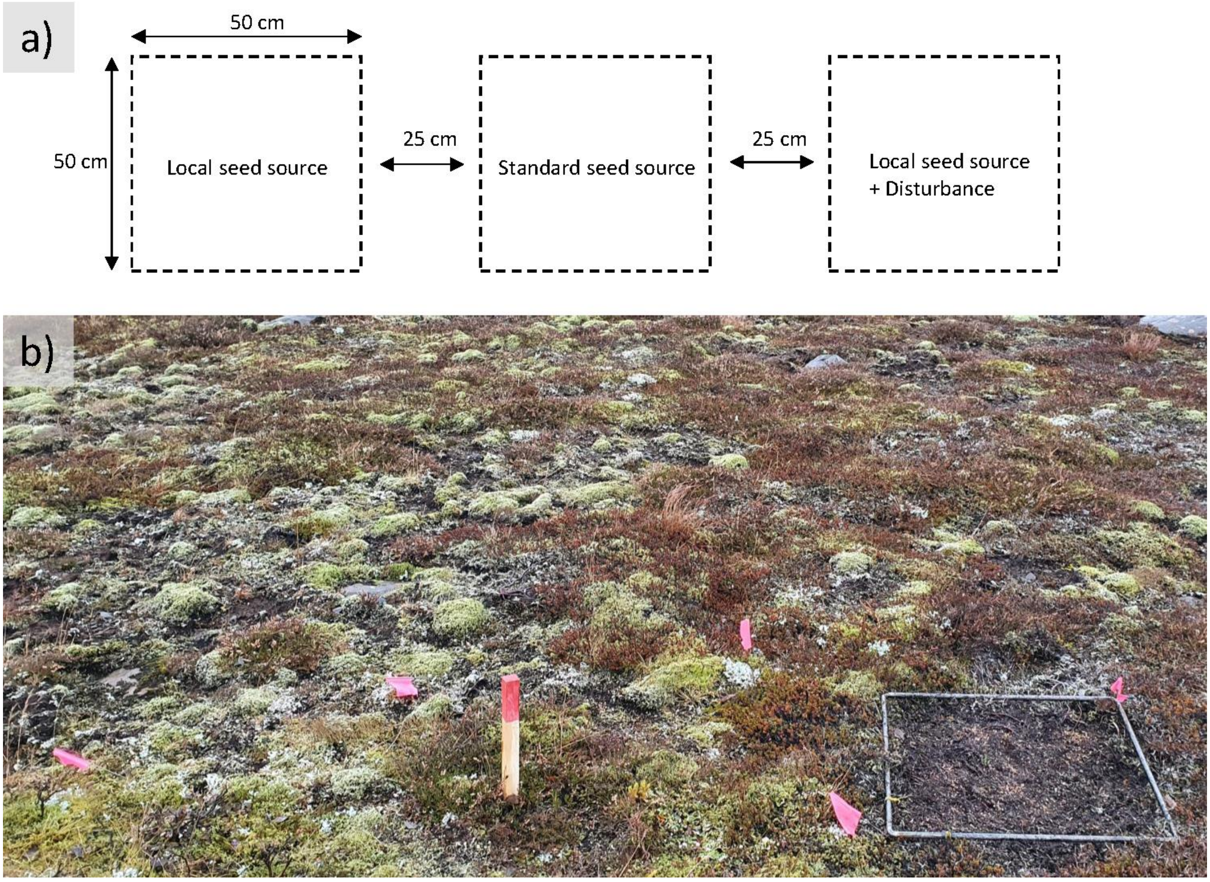


Figure S2. Experimental design of the seeding experiments. **a)** conceptual figure of an experimental block consisting of three randomly generated plots with different treatments; **b)** a photograph of an experimental block in Gunnarsholt, habitat type 1.3. The flags/poles mark the lower left and upper right corner of the 0.5 x 0.5 m plots respectively. Here, the disturbed plot is to the far right (within the quadrant). In Neðri Dalur, the standard seed source was used in the disturbed plots, as there was not enough of the local seed source for both the disturbed and undisturbed plots.