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RESEARCH ARTICLE

Room to regenerate: microhabitats and the recruitment niche as drivers of mountain woodland restoration

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Abstract

Introduction: Natural regeneration is an efficient, minimal-intervention approach essential for facilitating resilient, self-sustaining ecosystems during woodland restoration. However, recruitment can be slow, uncertain, or highly restricted, particularly in mountain woodland systems where tree planting and large herbivore management are necessary to reverse habitat fragmentation.

Objectives: We sought to determine the factors limiting natural regeneration from planted montane willow scrub by investigating the recruitment niche of Downy willow (*Salix lapponum*), an arctic-alpine species requiring restoration across Europe. We studied seed dispersal phenology, germinability, and the effect of microhabitat on seedling establishment to aid seed collection, restoration site selection, and management for self-sustaining populations.

Methods: Using a long-term landscape-scale restoration project in Scotland featuring a large herbivore exclosure containing abundant planted individuals, we quantified catkin maturation and seed viability across multiple years and integrated field surveys of natural regeneration with a direct seed sowing experiment.

Results: Seed dispersal occurred from mid-June to early July, with an average seed viability of 60%, but 8% of female plants experienced total catkin development failure. Bryophyte-dominated microhabitats in landslips had greater seedling frequency and survival compared to bare soil or dense vegetation.

Conclusions: Seed production and viability are not limiting *S. lapponum* regeneration from large numbers of planted individuals, but may be affected by weather fluctuations and plant-specific genetic factors. In contrast to the common assumption that bare soil is essential for *Salix* establishment, we show that wet bryophytes are prime regeneration substrates for *S. lapponum*, revealing a complex recruitment niche influenced by disturbance and microclimate.

Implications for Practice: Within fenced areas that protect adult plants from browsing, montane willow regeneration is limited by ground flora growth and restricted to rare microsites of bryophyte mats. These moss-dominated microhabitats require greater conservation focus due to potential threats from climate change impacts and vegetation encroachment. Rather than relying on enclosures, mountain woodland restoration should address overgrazing through wider management for low-density large herbivore populations. Studying the recruitment niche is therefore important for disentangling how restoration is shaped by trade-offs across life-history stages, and understanding the constraints and opportunities for sustainability across multiple scales from microsites to landscape-scale processes.

Key words: arctic-alpine, bryophytes, conservation management, habitat restoration *Salix lapponum*, montane scrub, natural colonization, regeneration

Introduction

Habitat restoration involving woody species is critical for tackling the dual biodiversity and climate crises by enhancing ecosystem function and carbon storage (Chazdon & Brancalion 2019; Löf et al. 2019). However, delivery at scale presents significant challenges regarding management efficacy and resource allocation to support biological and socioeconomic objectives. Tree planting can rapidly create woodland over large areas, but is often expensive, prone to high mortality and biosecurity risks, with soil disturbance potentially affecting belowground carbon stocks (Fleischman et al. 2020; Friggens et al. 2020; Friis et al. 2025). In contrast, natural regeneration offers a cost-effective minimal-intervention approach that promotes woodland resilience, complexity, and diversity (Chazdon & Guariguata 2016; Löf et al. 2021; Fleiss et al. 2025) while preserving locally adapted genotypes and heterogeneous stand structures (Murcia 1997; Borghetti & Giannini 2001; Bauld et al. 2023). Nevertheless, regeneration and natural colonization can be slow or uncertain, particularly in temperate regions and where seed sources are distant, and hybrid methods may provide

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a balance depending on the intended objectives (Fleiss et al. 2025; Hughes et al. 2026).

Tree planting is thus a step along the trajectory toward restoration rather than an end point, with long-term success depending on the recovery of self-sustaining, adaptable ecosystems. Achieving this fundamental goal at scale requires knowledge of the circumstances which enable the essential processes for natural regeneration throughout various life-history stages (Behrend et al. 2025). Focusing only on the environmental needs of mature plants overlooks establishment barriers, since adult occurrence may not necessarily be a reliable indicator of recruitment potential (Bell et al. 2014). To address this gap, the "recruitment niche" describes the abiotic and biotic conditions required for germination, emergence, and seedling survival (Grubb 1977; Larson et al. 2023). For example, regeneration may fail despite abundant seed production if there are constraints on dispersal, viability, or suitable sites for germination and seedling growth. This scenario is especially relevant to early successional species, for which disturbed environments may be key to colonization (Barsoum 2001).

The recruitment niche is shaped by interacting factors, including microclimate, microhabitat, soil properties, herbivory, and competition, which can be difficult to disentangle using a single approach. Observational studies capture natural variation in real-world situations (Chen et al. 2025), whereas experiments test specific causal mechanisms (Häggström et al. 2024). Combining these methods provides a more comprehensive understanding of how and where regeneration might occur, and is particularly helpful for examining heterogeneous woodlands with strong environmental gradients. For example, mountain woodlands occur in the transition zone between the timberline and the upper elevational limit of tree establishment (Dandan et al. 2022). Seed dispersal and the availability of microhabitats for seedling recruitment at these climatically stressful sites can depend on weather fluctuations, topography, soil moisture, nutrient content, or the surrounding vegetation (Resler et al. 2005; Catorci et al. 2012).

Globally, many mountain woodlands have significantly declined due to overgrazing, agricultural expansion, fire, infrastructure development, and pollution (Holtmeier 2009; Bergmeier et al. 2010; Speed et al. 2011). Their restoration can benefit biodiversity by supporting specialist arctic-alpine species including range-restricted invertebrates and birds, and deliver nature-based solutions to mitigate climate change impacts (Watts & Jump 2022). Where seed sources remain, reducing pressures such as overgrazing may reestablish mountain woodlands via natural regeneration, as successfully demonstrated by mountain birch expansion in Scandinavia and Iceland (Bryn 2008; Snorrason et al. 2016; Óskarsson & Traustason 2023). However, supplementary planting or reintroduction is typically used to conserve arctic-alpine willows and montane scrub with severe range contraction and population fragmentation (Pogorzelec et al. 2020, 2022). Nevertheless, mountain woodland restoration driven by such planting must aim to foster the long-term sustainability of high-altitude tree and shrub communities by striving to revive natural regeneration from the outset.

In Scotland, despite decades of montane willow planting across the country to reinstate altitudinal treelines, observations of new seedlings remain very sparse at relict populations and restoration sites (Stamati et al. 2007; Watts 2024; Watts et al. 2025), with similar restrictions noted elsewhere in Europe (Pogorzelec et al. 2014; Kołos et al. 2025). Whether these recruitment failures arise from poor reproductive output, a lack of suitable microhabitat, post-germination mortality, or a combination of these factors, remains unresolved. Regeneration may equally be affected by insufficient mature trees for impactful seed production, a short seed viability period, climate fluctuations, or the requirement of willows for exposed soil for germination (Shaw et al. 2010). For example, complete exclusion of large herbivores to prevent overgrazing, which is common practice during these restoration projects, can allow tall, vigorous ground flora to proliferate at the expense of bare ground (Watts et al. 2019). Therefore, in such situations, willow seedling establishment may rely on dynamic natural erosive processes such as landslip and rockfall (Mardon 2003).

Consequently, we sought to determine the factors limiting natural regeneration from planted montane willow scrub by asking:

- What is the timing and length of the catkin maturation and seed dispersal period for mature planted montane willows?
- What is the germination rate of their seed?
- Which microhabitat types are naturally regenerated seedlings associated with?
- How does microhabitat type influence seedling establishment and survival?

To address these questions, we investigated the recruitment niche of Downy willow (*Salix lapponum*), the most widely planted montane willow species in Scotland and the focus of significant conservation efforts elsewhere in Europe (Kołos et al. 2015; Pogorzelec et al. 2022; Watts 2024). Our study utilized a 30-year landscape-scale restoration project featuring a large herbivore exclosure containing abundant reproductively mature individuals (Mardon 2003; Mardon & Cole 2022; Watts et al. 2025). We quantified seed dispersal phenology and viability across multiple years to directly inform seed collection and propagation approaches that account for both seasonal and interannual variability. Integrating observational field surveys of natural regeneration with a direct seed sowing experiment enabled us to examine how recruitment patterns manifest across microsites, and between habitat-type treatments (bare soil, open mats of bryophytes, or vegetated sward) under more controlled circumstances. By identifying the underlying mechanisms and conditions that restrict or facilitate seedling establishment and early survival, this research will guide restoration site selection, planting design, and grazing strategies to support self-sustaining populations and long-term mountain woodland recovery.

Methods

Study Species

Salix lapponum is a dioecious arctic-alpine shrub with a boreal-subarctic distribution across northern Europe, including

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Scandinavia, western Siberia, and Scotland (Myklestad & Birks 1993; Skvortsov 1999). More isolated, critically endangered populations are also found in the mountains of central, southwestern, and southeastern Europe, for example the Alps and the Sudetes (Mirek et al. 2006; Grulich 2012; Hroneš et al. 2018). Flowering is marked by the production of catkins in spring to early summer, with pollination by both insects and wind (Peeters & Totland 1999). Each catkin may release hundreds to thousands of tiny seeds adapted for wind dispersal. Vegetative reproduction rarely occurs in Scotland and does not play a significant role in population structure (Stamati et al. 2007), but may be more common in central European populations (Kołos et al. 2015). In Scotland, most surviving relict patches of this species are now confined to inaccessible cliffs, gullies, and rocky slopes due to centuries of overgrazing by large herbivores. Action to expand the total extent of montane willow scrub in this country from 10 ha in the 1990s to approximately 1000 ha by 2023 has incorporated planting of over 265,000 *S. lapponum* (Watts 2024).

Study Site

The research was conducted on the Ben Lawers mountain range in the central Southern Highlands of Scotland, within a National Nature Reserve (NNR) owned and managed by The National Trust for Scotland (NTS) for the primary purpose of nature conservation. Sampling took place at Creag an Lochain (lat 56.520694, long −4.2845) specifically on the mountain Meall nan Tarmachan at the western end of the Ben Lawers range (Fig. 1), between an altitudinal range of 587–761 m above sea level (asl). A local weather station installed in 2018 (lat 56.506718, long −4.317989; 710 m asl) recorded a mean annual precipitation of 1856 mm and a mean annual temperature of 4.35°C during 2019–2023, with monthly minimum and maximum means of −6.52°C (February) and 10.62°C (July), respectively (Black & Watson 2024).

A double electric deer fence was erected around Creag an Lochain in 2000 to exclude large herbivores from 180 ha between the altitudes of 525–923 m. As well as providing a suitable area for widespread planting in the absence of grazing by sheep and red deer, this location was chosen because it was anticipated that the dynamic processes of landslip and rockfall around the large complex of cliffs running across the site might potentially create niches for future seedling establishment (Mardon 2003). The main quantity of montane willow planting took place here in 2004–2006, including 18,285 *S. lapponum*, of which 1050 were sampled in a concurrent study on growth rates in relation to planting location and microhabitat in 2021 by Watts et al. (2025).

Planting occurred without fertilizer or ground preparation, to a density of approximately 300 stems per hectare. All stock was of local origin produced by the NTS tree nursery through propagation sources (seed and cuttings) collected from the Ben Lawers range and populations on three nearby mountains within 20 km. The seed source for Creag an Lochain planting was "2nd generation"; gathered from plants established through previous restoration projects elsewhere at Ben Lawers.

Timing of Catkin Dehiscence

The timing of seed dispersal via catkin dehiscence was studied using a method similar to Guilloy-Froget et al. (2002). Five female shrubs were randomly chosen in 2021 from the 2004–2006 *S. lapponum* planting cohort, each spaced approximately 50 m apart along a transect that ran uphill from 663–706 m asl. Branches at different orientations within the canopy were marked to have a combined total of 100 catkins to assess. The number of catkins in each of the following categories was recorded every 3–4 days throughout June to early July:

- Not ripe (no capsules open).
- Less than 50% of capsules open.
- Greater than 50% of capsules open.
- Fallen (all seed dispersed from all capsules).

This survey was repeated annually from 2021–2023 following the same individual shrubs each year. Complete datasets were gathered for four of the chosen plants (B–E). The fifth plant (A) did not produce any seed, with catkins failing to develop and mature in three successive years. A random subsample of 100 of the 516 female shrubs concurrently studied at the site by Watts et al. (2025) was also surveyed annually in 2021–2023 to determine the proportion of individuals producing seed or experiencing total catkin development failure similar to Shrub A. There were no visible differences in leaf morphology or growth form to suggest that any of the sampled shrubs had been affected by hybridization.

Germinability and Duration of Seed Viability

In 2022, seed was collected from the four marked shrubs B–E during their period of maximum dispersal and assessed for viability by testing germination rates. A total of 100 seeds from each individual were sown immediately after collection on wet filter paper in Petri dishes kept moist with distilled water. A seed was considered to have germinated with the appearance of two healthy cotyledons.

In 2023, a larger quantity of seed was also gathered from across the study site using a random subsample of 30 female shrubs studied by Watts et al. (2025). This seed was pooled into one composite sample. Batches of 100 seeds were sown in trays of peat-free compost at 3-day intervals for up to 3 weeks after collection to determine the duration of viability using germination tests as above. Subsamples of the composite seed were also stored in both a domestic fridge (4°) and freezer (−18°), and sown in separate batches of 100 at 14 days after collection, to trial different approaches that restoration practitioners might use to prolong viability.

Natural Regeneration Surveys

Natural regeneration from the restored *S. lapponum* population at Creag an Lochain was observed for the first time in 2021, and has only been observed within landslip areas (Watts 2023; Watts et al. 2025). A systematic field survey was conducted in 2022 to assess microhabitat frequency within these landslips. Transects were evenly spaced at 1 m intervals positioned

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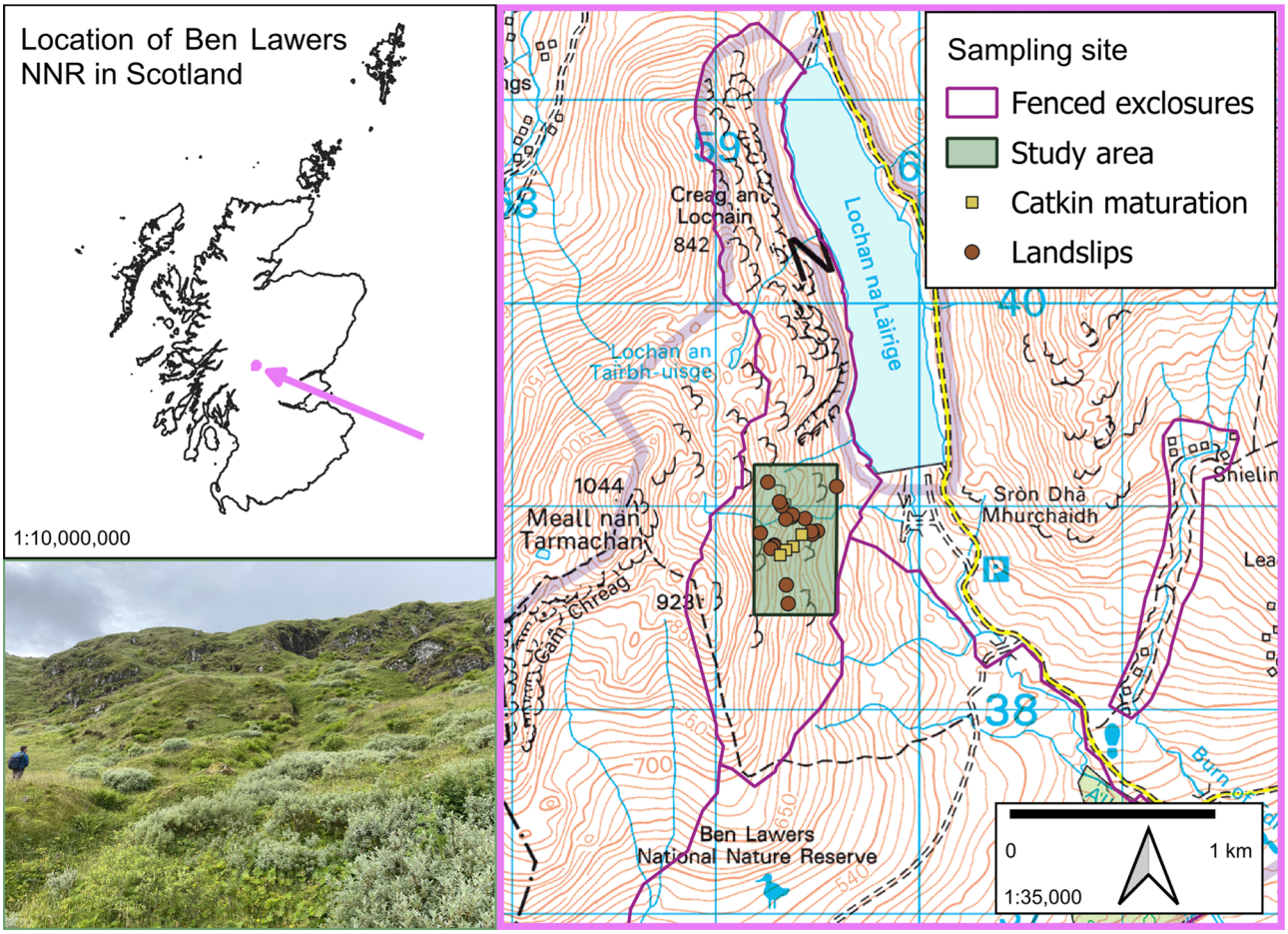

Figure 1. The location of the study site within Ben Lawers National Nature Reserve in Scotland. Planting of *Salix lapponum* was undertaken throughout the fenced exclosures, and the specific area used for this study, and also by Watts et al. (2025), is indicated in green. The location of the four shrubs studied for catkin maturation is given along with distribution of landslips. Background Ordnance Survey mapping source from 1:50,000 scale color raster (Tagged Image File Format geospatial data). Tiles: nn42, nn62, nn64, nn44 updated: 1 June 2023, Ordnance Survey (Great Britain), using: EDINA Digimap Ordnance Survey Service, <https://digimap.edina.ac.uk>, downloaded: 7 February 2024. © Crown copyright and database rights 2024 Ordnance Survey (AC0000851941).

horizontally across the slope of each landslip to cover the range of microclimatic conditions present from top to bottom. Microhabitat type was recorded using point sampling every 50 cm along the transects (Fig. 2), classified as either:

- Soil (bare; no vegetation).
- Fine Scree (small rock fragments; gravel to small pebbles less than 5 cm in diameter).
- Consolidated Aggregate (larger rocks greater than 5 cm in diameter forming a relatively stable substrate).
- Dry Bryophyte crust with scattered grasses/herbs.
- Wet Bryophyte mat with scattered grasses/herbs.
- Sward dominated by herbs and graminoids.

Dry and Wet Bryophyte microhabitats were defined by soil moisture differentiated by contrasting moss taxa (Supplement S2) generally representing lower and higher Ellenberg values (Hill et al. 2007) for moisture, respectively.

The microhabitat surrounding a total of 237 individual seedlings of approaximately 1–3 years in age was also surveyed within the landslips. A 15 cm diameter circular sampling plot was temporarily positioned around each seedling, and the predominant microhabitat type in every plot was assigned to one of the categories listed above. Quantitative data on the cover of associated vascular plant and bryophyte species were additionally collected from within the plots using a point count method. A metal pin of 1.5 mm diameter was inserted into the plot 20 times at random positions, and the number of touches by every plant species on the pin was recorded, as well as any touches on bare soil or rock not covered by vegetation.

Direct Seed Sowing Experiment

Seed collected from the four marked shrubs B–E during their period of maximum dispersal in 2022 was also used for direct sowing. In landslip sites not currently containing any naturally regenerated seedlings across an altitudinal range of 570–761 m asl, ten 25 cm × 25 cm experimental plots were marked out in each of:

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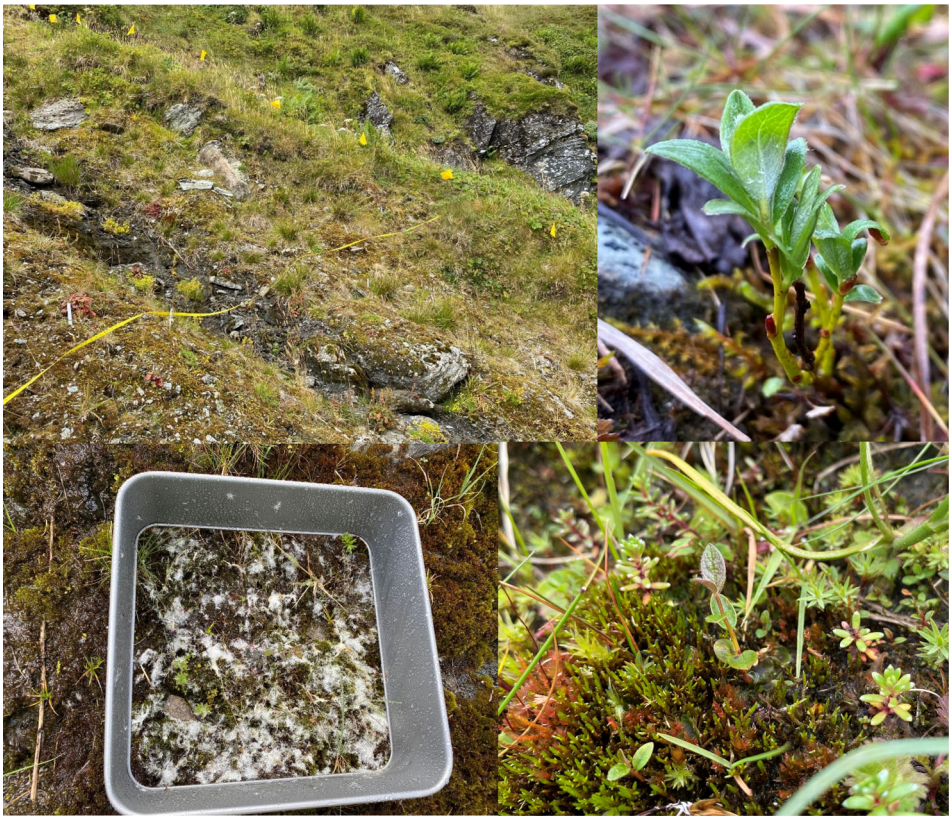

Figure 2. Top: A landslip site at Ben Lawers NNR (left), surveyed for *Salix lapponum* seedlings (right) that had naturally regenerated. Bottom left: An example of a *S. lapponum* seed sowing plot in the Wet Bryophyte microhabitat, of 25 × 25 cm size made from a removable bottom cake tin. Four hundred milliliters of seed fluff has been sown and damped to the vegetation surface using a spray bottle. Bottom right: A seedling from the seed sowing experiment growing in Wet Bryophyte habitat during July 2023 (year 2) among *Anomobryum julaceum*, *Bryum pallens*, *Dichodontium palustre*, *Pellia* spp., and *Saxifraga aizoides*.

- Soil (bare; no vegetation).
- Dry Bryophyte crust with scattered grasses/herbs.
- Wet Bryophyte mat with scattered grasses/herbs.
- Sward dominated by herbs and graminoids.

Sowing occurred within 3 days since seed collection. With a removable bottom cake tin functioning as a high-sided quadrat, 300 mL of *S. lapponum* seed fluff was spread across each plot and dampened down using a spray bottle to mimic rain and allow the seed to stick to the substrate (Fig. 2). Two cohorts of 20 plots (five in each habitat type) were sown 5 days apart to mitigate against any external stochastic events (e.g. extreme weather) that might have unexpectedly caused widespread germination failure. The plots were revisited regularly to count the number of seedlings present; every 5 days while the seed germinated, and then every 2 weeks until the end of the summer. This monitoring also continued once a month during May–September 2023.

Data Analysis

All analyses were performed using R Statistical Software v4.5.1 (R Core Team 2021). The number of growing degree days from May to July in 2021–2023 was calculated from the average of daily maximum and minimum temperatures using the local weather station data, with a growing threshold set at 10°C. Linear regression was used to assess the relationship between seed germination and days since seed collection under room temperature storage conditions.

A Chi-squared goodness-of-fit test determined if naturally regenerating seedlings were more frequently associated with any of the landslip microhabitat types than expected if they were distributed randomly. The point count data on bryophytes, vascular plants, bare soil, and rock within the naturally regenerated seedling plots were converted to values for percent cover using the formula $x/20 \times 100$ (where x is the number of touches for an individual species). Community composition of Wet Bryophyte, Dry Bryophyte, and Sward microhabitats was explored in ordination space with non-metric multi-dimensional scaling (NMDS) using a Bray–Curtis distance matrix in three dimensions in the vegan R package v.2.7.1. Rare species were down-weighted to reduce their influence on the analysis by assigning lower weights to those species occurring in less than 5% of samples. The other three microhabitat types (Soil, Fine Scree, and Consolidated Aggregate) were not included in the ordination due to an absence of vegetation cover in those plots. Indicator species analysis incorporating the Indicator Value (IndVal) index measured the association between different bryophyte and vascular plant taxa and each microhabitat type.

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A generalized linear mixed model (GLMM) tested the influence of microhabitat type on seedling germination in the seed sowing experiment, with the maximum number of seedlings recorded in each plot as the response variable, and cohort included as a random intercept effect. Repeated measures GLMMs also assessed the variation in seedling survival over time between the microhabitats, with the number of seedlings per plot as the response variable, and Plot ID nested within cohort included as a random intercept effect. Separate models were run for data gathered throughout year 1 (year of sowing) and year 2 (the subsequent growing season) of the experiment. A further GLMM also tested the influence of microhabitat type on the final number of seedlings recorded in year 2 (i.e. last data point gathered from each plot in September 2023).

GLMMs were fitted with a negative binomial distribution to correct for over-dispersion using the glmmTMB package with a zero-inflation component also included in the models from year 2. Assessments of model fit, over-dispersion, heteroscedasticity, and zero-inflation were conducted using the DHARMa package. A test of collinearity between fixed effects was undertaken using the variance inflation factor, and the fixed effect of time was scaled to improve interpretability of the model estimates. Model performance was quantified using the marginal and conditional r^2.

Results

Timing of Catkin Dehiscence

The *Salix lapponum* catkin dehiscence period at Ben Lawers occurred in each year of study from the middle of June until early July, with some variation in dehiscence phenology between years. The peak period of seed release in 2021 and 2022 was around the 24th of June, but in 2023 seed was released approximately 2 weeks earlier (Fig. 3). Overall, the weather was warmer and drier in 2023 than both 2021 and 2022, with higher minimum, maximum, and mean temperatures. There was also a greater number of cumulative growing degree days (days with an average of daily maximum and minimum temperatures over a threshold set at 10°C) particularly in mid-May to early June 2023 (Supplement S1). Of the 100 female shrubs surveyed for seed set during peak catkin dehiscence, eight individual plants (8%) experienced total catkin development failure every year during 2021–2023.

Germinability and the Duration of Seed Viability

Seed viability across 2021–2023 ranged from 36 to 82%, with an overall mean of 60% ± 4.31 SE, although germination rates were higher in 2023 (Table S1). For seed stored at room temperature that was not sown immediately after collection, the viability declined steadily over time by approximately 5.5% per day ($r^2 = 0.98$, $F_{[1,4]} = 219.4$, $p < 0.001$), with no germination occurring beyond 14 days (Fig. 4). However, cold storage improved germination rates at 14 days after collection, whereby seed stored in the fridge had similar germination to those kept at room temperature 8 days after collection, and seed stored in the freezer had similar germination to seeds sown immediately after collection.

Natural Regeneration Surveys

Of the 237 naturally regenerated seedlings studied in landslip areas, 34.6% were found in the Dry Bryophyte microhabitat,

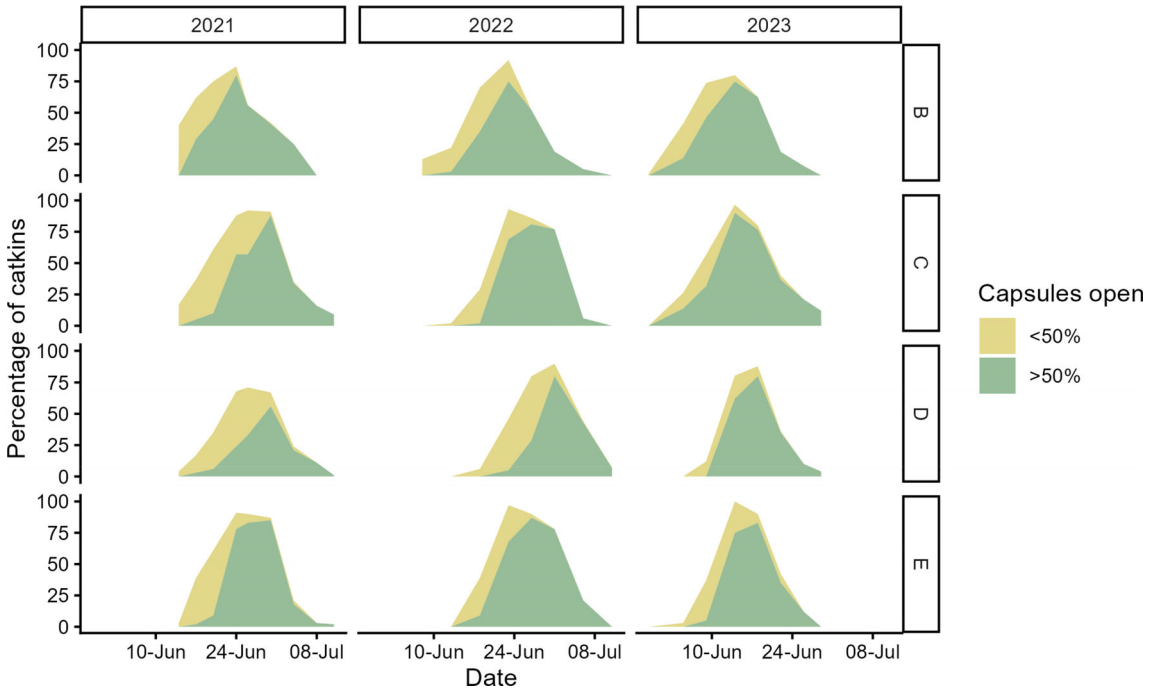

Figure 3. The catkin dehiscence period of four *Salix lapponum* shrubs observed at Ben Lawers NNR during 2021–2023. One hundred catkins were followed per bush per year, recording the number that had greater or less than 50% of their seed capsules open.

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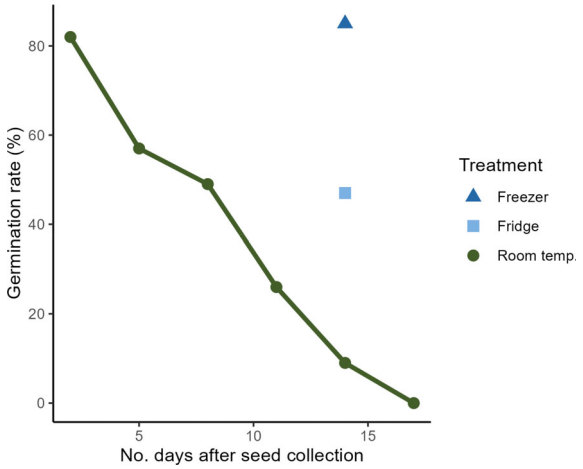

Figure 4. The percentage germination rate of *Salix lapponum* seed collected from across the montane scrub restoration site at Ben Lawers NNR, sown at intervals of 3 days. Linear regression of room temperature germination: $r^2 = 0.98$, $F_{[1,4]} = 219.4$, $p < 0.001$. Seed stored in a fridge and freezer was also tested at 14 days since collection.

31.6% in the Wet Bryophyte microhabitat, 29.1% in the Sward, and 1.7% on Soil. Considering microhabitat frequency, these seedlings were more often associated with microhabitat types predominantly containing bryophytes (Table S2; goodness-of-fit test $\chi^2 = 101.89$, $p < 0.001$), while there were proportionally fewer seedings growing on bare soil or in a dense sward. The Wet Bryophyte, Dry Bryophyte, and Sward microhabitats differed in their bryophyte and vascular plant species community composition (Fig. 5). Indicator species analysis found that those strongly associated with the Wet Bryophyte habitat were *Anomobryum julaceum*, *Blindia acuta*, *Ctenidium molluscum*, *Dichodontium palustre*, *Pellia* spp., and *Philonotis fontana*, while the Dry Bryophyte habitat was associated with *Atrichum undulatum*, *Pogonatum urnigerum*, *Nardia scalaris*, and *Scapania undulata*.

Direct Seed Sowing Experiment

Germination occurred in all 40 seed sowing plots, although there was considerable variation in the number of germinated seedlings between plots, ranging from a minimum of 13 (Sward microhabitat) to a maximum of 452 (Wet Bryophyte microhabitat). Germination was greatest in both the Soil (mean = 300.9 ± 24.1 SE) and Wet Bryophyte (mean = 266.0 ± 36.9 SE) plots, but significantly less in the Dry Bryophyte (mean = 101.6 ± 17.9 SE) and Sward (mean = 31.9 ± 5.04 SE) plots (Table 1).

The number of seedlings declined over time during both year 1 (Fig. 6) and year 2 (Fig. 7) of the experiment. Over year 1, the number of seedlings was similar for Soil and Wet Bryophytes, but significantly lower in Dry Bryophyte and Sward, with an interaction between time and microhabitat type (Table 1). However, during year 2, there was no significant difference between Soil, Wet or Dry Bryophyte habitats. By the end of the experiment, the number of surviving seedlings was greatest in Wet Bryophytes (max = 111, mean = 28.4 ± 10.9 SE), but with no statistically significant difference between Soil (max = 44, mean = 17.2 ± 4.8 SE) or Dry Bryophyte (max = 51, mean = 15.6 ± 6.3 SE) plots (Table 1). The number of

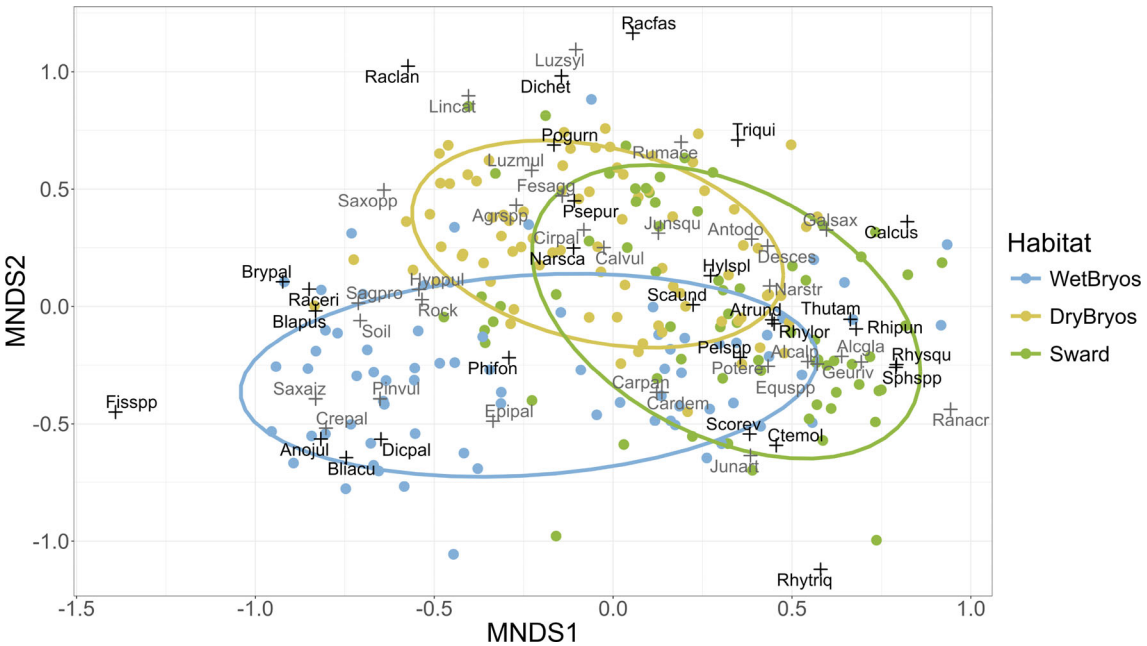

Figure 5. Non-metric multi-dimensional scaling (NMDS) plot exploring the distribution of naturally regenerated *Salix lapponum* seedlings (colored circles; $n = 237$) in ordination space in relation to the community composition of associated bryophytes (black text) and vascular plants (gray text). Species (crosses) are labeled with the first three letters of their genus and species names, with full names given in Supplement S2. These species were recorded at landslip sites within a circular sample plot of 15 cm diameter, with each individual seedling positioned at the center.

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Table 1. Negative binomial GLMM coefficients for data collected on *Salix lapponum* seed germination and subsequent seedling survival in the seed sowing experiment undertaken at Ben Lawers in four different microhabitats: Soil, Wet Bryophytes, Dry Bryophytes, and Sward. All habitat comparisons are with the Soil microhabitat. Germination: model of the maximum number of seedlings recorded in each plot ($n = 40$). Year 1 and year 2: repeated measures models for the number of seedlings in each plot recorded over time throughout the experiment at fortnightly intervals in year 1 and monthly intervals in year 2, including the interaction of time and microhabitat. Final Survival: model of the final number of seedlings recorded in each plot in September 2023. Cohort was included as a random intercept effect in the models of Germination and Final Survival, and Plot ID nested within cohort was included as a random intercept effect in the models of year 1 and year 2. Numbers in brackets are SEs. *p* Value significance levels: * less than 0.05; ** less than 0.01; *** less than 0.001.

	Germination	*Year 1*	*Year 2*	*Final Survival (end of year 2)*
Time (days since sowing)		−0.14*** (0.03)	−0.34*** (0.04)	
Habitat Wet Bryos	−0.12 (1.77)	−0.40 (0.30)	0.71 (0.84)	0.60 (0.48)
Habitat Dry Bryos	−1.13*** (0.18)	−1.57*** (0.31)	−1.01 (0.87)	−0.20 (0.47)
Habitat Sward	−2.27*** (1.18)	−2.90*** (0.31)	−2.62** (0.94)	−5.15*** (1.12)
Wet Bryos: time		−0.12** (0.04)	−0.01 (0.05)	
Dry Bryos: time		−0.11* (0.05)	−0.18** (0.06)	
Sward: time		−0.25*** (0.05)	−0.46** (0.14)	
Zero-inflation			−3.75*** (0.62)	−1.59*** (0.54)
Marginal r^2	0.81	0.69	0.51	0.85
Conditional r^2	0.83	0.96	0.99	0.85

surviving seedlings was significantly lower in the Sward (mean- $= 0.1 \pm 0.1$ SE), since 9 out of the 10 plots of that microhabitat type had no seedlings remaining. However, two plots in Soil, three in Wet Bryophytes and one in Dry Bryophytes also had no seedlings left by the end of the experiment. Those two Soil plots had been completely buried by ongoing erosion, while a further two plots of the same microhabitat type had also been subjected to some erosion and burial with a low number of seedlings still remaining. Throughout the experiment, there was no disturbance observed in plots of the other three habitat types, and no evidence of damage on seedlings due to herbivory by small mammals (e.g. voles or hares) or invertebrates (e.g. slugs) in any of the 40 plots.

Discussion

Our investigation of *Salix lapponum* recruitment within a long-term mountain woodland restoration project identified that seed

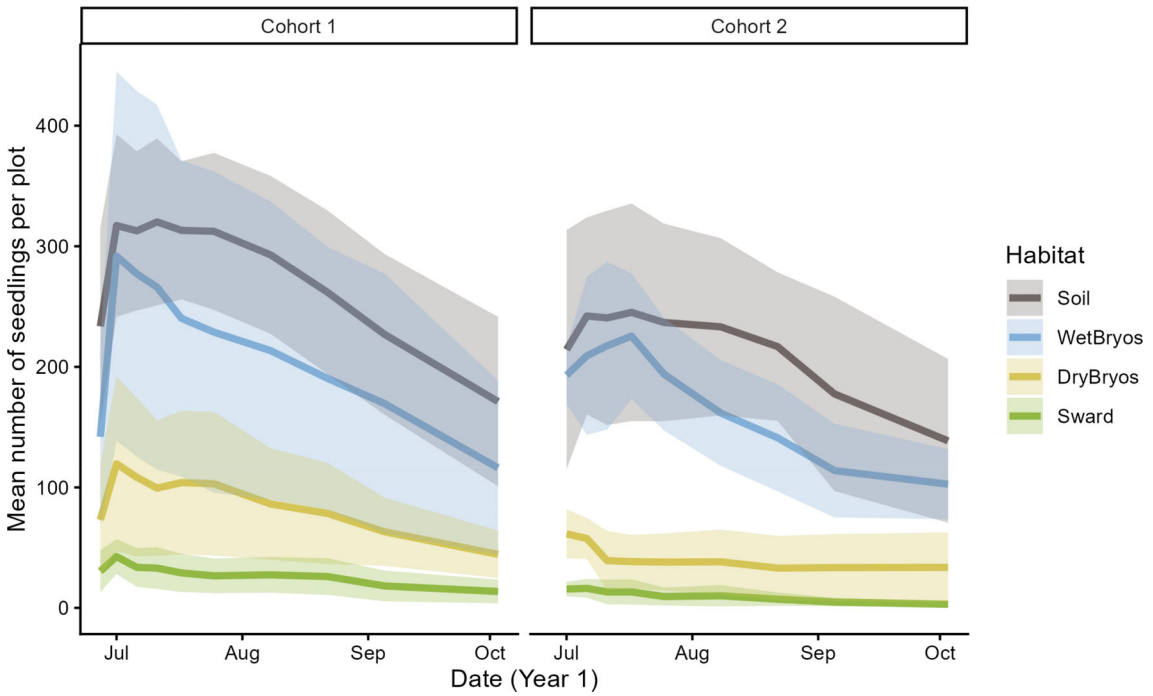

Figure 6. The mean number of seedlings surviving per 25 × 25 cm plot in each of the four microhabitat types of landslips at the *Salix lapponum* restoration site at Ben Lawers. Data are from year 1 of the experiment (i.e. the year the seed was sown). Two cohorts of 400 mL seed fluff per plot were sown in different plots 5 days apart as a buffer for any stochastic event which may have dramatically reduced germination (e.g. high precipitation or drought). $n = 5$ per habitat type per cohort; shaded areas = 95% CIs.

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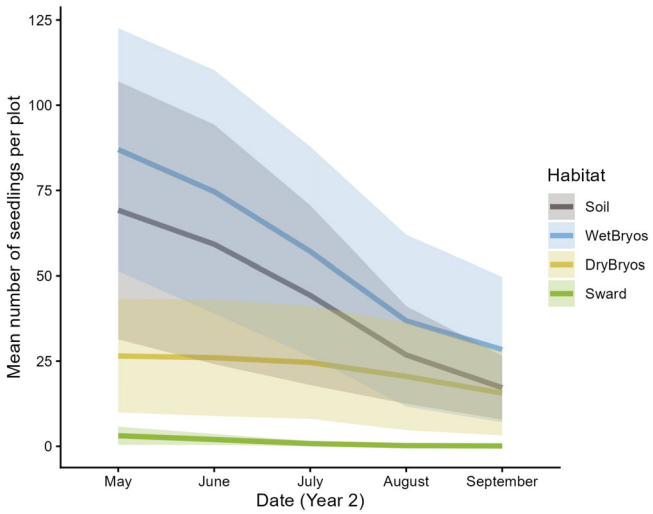

Figure 7. The mean number of seedlings surviving per 25 × 25 cm plot in each of the four microhabitat types of landslips at the *Salix lapponum* restoration site at Ben Lawers, in the summer growing season during the year following the direct seeding experiment (year 2). $n = 10$ per habitat type; both cohorts from Figure 6 have been combined. Shaded areas = 95% CIs.

dispersal occurred from mid-June to early July, with an average seed viability of 60%. Total catkin development failure was experienced each year by 8% of female plants in the study area. Natural regeneration surveys found that seedlings were most frequently associated with bryophyte-dominated microhabitats in landslip areas, particularly Wet Bryophyte communities, and were relatively rare on bare soil or in dense sward. Germination of experimentally sown seed was highest in Soil and Wet Bryophyte microhabitats and lowest in Sward, while long-term survival was greatest in Wet Bryophyte plots and almost absent from the Sward.

Catkin Dehiscence and Seed Viability

Examination of catkin dehiscence showed abundant seed release from 92% of female shrubs. Weather is likely to influence the dispersal of this seed, with catkin maturation occurring earlier during sustained hot, dry periods in spring and early summer. This timing could have implications for recruitment if warming accelerates seed release when soil moisture is concurrently limiting. Alternatively, heavy rainfall events can inhibit dispersal when the silky willow seed hairs that facilitate wind transport become waterlogged and remain attached to the parent shrub (Scottish Montane Willow Research Group 2005). Consequently, variation in temperature and precipitation through climate change may generate less predictable phenological patterns in *Salix* spp., potentially disrupting the synchrony between population-level seed dispersal processes and favorable establishment conditions (Cooper et al. 2006; Perry et al. 2020; Díaz-Alba et al. 2023).

Individual-level reproductive variation was evident through total catkin development failure recorded in 8% of female shrubs each year. This outcome consistently affected the same plants despite their neighbors producing seed normally, and the existence of an abundance of males distributed throughout the site at a relatively balanced sex ratio (Watts et al. 2025). These repeated observations suggest that plant-specific genetic factors may be responsible rather than site-wide environmental conditions, possibly arising from the local *S. lapponum* population used as source material during restoration. Such isolated, peripheral, or fragmented remnant populations are often associated with reduced reproductive function (Angeloni et al. 2011; Aguilar et al. 2019; Carbognani et al. 2019). If a limited number of relict parent plants are used to propagate seed and cuttings, reduced genetic diversity and inbreeding could manifest as poor fruit development or genetic incompatibility between individuals, leading to fertilization failure (Broadhurst et al. 2008; Nagamitsu & Futamura 2014).

Although only approximately 10% of female individuals in our study exhibited total catkin development failure, these plants will not contribute to any recruitment. Genotyping of planted stock and regenerated seedlings will help to identify the underlying cause and ascertain if this effect could be exacerbated over time through further inbreeding. Supplementary planting and "genetic rescue" involving unrelated individuals is advised for population reinforcement and connectivity, and may be essential at restoration sites where severe reproductive failures are evident in the next generations (Finger et al. 2022).

Aside from reproductive constraints recorded on a small subset of individuals, a mean seed viability of 60% suggests that the planted population we studied otherwise retains sufficient capacity for successful regeneration. This value is comparable to other studies on *S. lapponum*, including 65% germination from relict populations local to Ben Lawers (Shaw et al. 2010), and 71% germination from endangered populations in eastern Poland (Pogorzelec et al. 2014). Our mean seed viability also falls within the range reported for arctic-alpine *Salix* spp. more generally (Müller et al. 2011; Boulanger-Lapointe et al. 2016; Angers-Blondin et al. 2018). Together, our data on catkin dehiscence and seed germinability therefore emphasize that seed production is not limiting *S. lapponum* recruitment at restoration sites where large numbers of individuals have been planted in close proximity.

Microhabitat Type and the Recruitment Niche

Naturally regenerated *S. lapponum* seedlings in landslip areas were more frequently associated with microhabitats predominantly containing bryophytes, rather than dense sward or unvegetated soil. This observation contrasts with a common generalization concerning the importance of bare soil for seedling establishment in *Salix* spp. (Gage & Cooper 2005; Díaz-Alba et al. 2023). During a field experiment by Shaw et al. (2010), very few *S. lapponum* and *S. arbuscula* seedlings survived in vegetated or mown microsites after one summer (≤0.3%), compared to open disturbed soil (19.4%). That study concluded both species require bare ground for early survival, at least during the first year of growth and preferably longer. The small willow seeds are very short-lived, and tall vegetation may prevent them from reaching the substrate, or outcompete

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any resulting seedlings. However, Shaw et al. (2010) did not measure regeneration in bryophyte-dominated microhabitats.

Our research thus provides a more nuanced insight into the recruitment niche of *S. lapponum*. Plant establishment in arctic-alpine systems often relies on microtopography or vegetation cover to buffer harsh climatic conditions. Bryophytes may improve the nutrient content of thin soils, retain moisture, and moderate temperature extremes, thereby reducing desiccation and frost risk in their immediate surroundings and acting as local-scale ecosystem engineers which facilitate seedling establishment (Wheeler et al. 2011; Sand-Jensen et al. 2015; Lett et al. 2017). Accordingly, our seed sowing experiment showed that survival was greatest within wet bryophyte mats. This result rules out the possibility that the association between naturally regenerated seedlings and mosses arose solely from vegetation succession onto landslip patches that were previously bare soil when the seed germinated. Bryophyte seedbeds featuring acrocarp mosses adapted to flushing represent key microsites for *Salix* regeneration, particularly where water limitation might constrain establishment in exposed alpine environments (Angers-Blondin et al. 2018). Similarly, Behrend et al. (2025) found that natural colonization of Icelandic mountain birch (*Betula pubescens* ssp. *tortuosa*) was highest in a thin bryophyte layer including mosses less than 2 cm tall.

Landslips remain important for creating open microsites for germination, as no seedlings were observed outside of these areas. However, the bare soil present here may experience continued erosion which decreases survival over time. The recruitment niche of *S. lapponum* is therefore more complex than previously assumed, reflecting a balance between disturbance processes, substrate stability, and the microclimatic conditions that support early seedling persistence in montane environments. Future research should explore the interactions between seed source proximity, large herbivore densities, soil conditions (e.g. pH and nutrient content), and snow-lie, and whether willow establishment and vegetation succession might have a negative feedback effect on moss cover. Since pioneer arctic-alpine plants are particularly vulnerable to climate change impacts, including reduced snow cover and competitive exclusion from more generalist species, vital bryophyte microhabitats and the montane *Salix* regeneration they support could be threatened by increasingly warmer summers (Alatalo et al. 2020; Watts et al. 2022). Bryophyte mats may consequently require greater conservation recognition and focus both for the species they are composed of, and those that rely on such critical recruitment niches.

Guidance for Practitioners: Seed Collection

We demonstrate that the peak of *S. lapponum* seed dispersal at our study site typically occurs during the fourth week in June, although sustained hot, dry weather in early summer can bring catkin dehiscence forward by 2 weeks. This result is contrary to existing guidance for practitioners in Scotland that seed collection in montane willow restoration projects should take place from late June to August (Montane Scrub Action Group 2016). Instead, it would be more effective to gather seed during early to mid-June as catkins mature before their peak release, and account for variations in timing due to the weather, to avoid missing the short window of opportunity to achieve propagation. Cold storage provides an additional flexible option for increasing the seed viability period when weather conditions are unstable, prior to sowing at a tree nursery or directly in the field. These shifting recommendations reflect the potential for climate change to affect the delivery and outcomes of restoration projects in mountain systems, and the need for management to adapt accordingly.

Guidance for Practitioners: Large Herbivore Management

Poor seedling establishment in dense vegetation could indicate that large herbivore exclusion may hinder regeneration at mountain woodland restoration sites. Fencing is an effective tool for facilitating tree growth in woodland systems impacted by overgrazing because it simultaneously reduces browsing, trampling, and understory degradation (Lorite et al. 2021; Murphy et al. 2022; Abe et al. 2024). However, these changes also encourage competitive ground flora growth and can decrease the availability of suitable niches for germination and seedling survival (Perrin et al. 2006; Löf et al. 2021). In our study, montane willow regeneration within fences is restricted to rare, unstable landslip microsites, suggesting that relying only on natural disturbance processes in the absence of large herbivores might constrain reproductive success.

Remedial measures to overcome this recruitment barrier could involve manually clearing vegetation, including root systems in more stable patches near adult plants, and supplementing the natural seed rain if required with interventional sowing as trialed in our experiment (Willoughby & Jinks 2009; Shaw et al. 2010). These actions might enable colonization of small patches of bare soil, although direct seeding generally produces highly variable and unreliable outcomes depending on the tree species, site conditions, climate, and management (Doust et al. 2006; Grossnickle & Ivetić 2017). The techniques required to specifically promote the prime regeneration microhabitats of wet acrocarpous mosses are also expected to be more complicated and have not yet been explored in this context. Furthermore, such short-term interventions are too localized and impractical to apply over large areas and do not achieve the aim of enabling self-sustaining populations.

Instead, restoration should focus on addressing overgrazing without the use of fences through landscape-scale deer and livestock management for low-density large herbivore populations (Newman et al. 2014). For example, reducing red deer populations to below 3/km^2 is key to facilitating mountain woodland establishment outside of refugial sites in the Scottish Highlands (Watts et al. 2026), supporting the survival and regeneration of a range of upland tree species including *Betula nana*, *B. pubescens*, *Pinus sylvestris*, and *Salix* spp. (Rao 2017; Painting & Rao 2020; Watts 2024). This holistic approach can be augmented by regional collaboration across multiple landholdings (Gullett et al. 2023), and will foster wider habitat connectivity, diversity, structural heterogeneity, and complexity by promoting a healthy montane mosaic of trees, shrubs, and open ground (Newman et al. 2014).

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Wider Relevance for Restoration

Through investigating the limitations on regeneration in restored montane willow scrub, we identified management outcomes and recommendations contrary to expectations and previous guidance on seed collection, seedling establishment microhabitat, and large herbivore exclusion. Furthermore, practices that enhance adult survival and growth, such as removing disturbance or grazing, may inadvertently constrain recruitment. Studying the recruitment niche is therefore important for disentangling how restoration is shaped by trade-offs across life-history stages, and exploring how such processes can be balanced to support long-term population persistence (Löf et al. 2019; Larson et al. 2023).

These trade-offs are particularly relevant when considering entire plant communities, as different species often display contrasting responses to the same environmental or biotic factors. Mountain woodland restoration, which should move beyond single-species conservation toward a mosaic of treeline species and habitats (Watts 2024), highlights the need for flexible approaches that accommodate diverse ecological requirements for natural regeneration rather than a one-size-fits-all model (Suding 2011). By recognizing the key role of bryophyte niches in the context of wider population dynamics and regional management interventions, our research emphasizes that restoration success depends on understanding constraints and opportunities across multiple scales, from microsites to landscape-level processes, that shape the structural and spatial conditions for long-term sustainability.

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Supporting Information

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

Supplement S1. Summary of weather data from the study period during 2021–2023.
Supplement S2. List of vascular plants and bryophytes associated with natural regeneration of *Salix lapponum* in surveyed landslip sites at the Ben Lawers montane willow scrub restoration site.
Table S1. The percentage germination rates of *Salix lapponum* seed from four selected shrubs at Ben Lawers NNR during 2021–2023.
Table S2. The frequency and proportion of microhabitat types found in landslips at the *Salix lapponum* restoration site at Ben Lawers NNR.

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