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RESEARCH ARTICLE

# Why the present is not the key to past or future: moving beyond restricted relict habitat conditions to improve outcomes in mountain woodland restoration

Sarah H. Watts[1,2], Nadia Barsoum[3], Kirsty J. Park[1], Alistair S. Jump[1]

## Abstract

**Introduction:** Mountain woodland restoration can enhance upland biodiversity and contribute to nature-based solutions mitigating climate change impacts. However, high-altitude planting of trees and shrubs requires considerable commitment of time and practical effort and should be evidence-based to prioritize scarce resources for efficient restoration at scale. Many mountain woodlands have experienced substantial anthropogenic degradation into remnants that may not reflect past complexity and function.

**Objectives:** We examine where planting can deliver effective outcomes in mountain woodland restoration outside the constraints of using present-day distribution to indicate future potential. Following centuries of woodland clearance and overgrazing, Scotland has pioneered montane scrub restoration for over 30 years. This action offers the opportunity to study whether restoration replicating remaining habitat risks bias, or if outcomes can be improved through wider selection of planting locations.

**Methods:** Our research uses a long-term case study of *Salix lapponum* restoration planting in the Scottish Highlands to investigate the abiotic and biotic factors affecting treeline shrub health and productivity.

**Results:** Overall, only a small amount of variation in shrub growth and catkin presence was attributed to local environmental variables related to relict habitat conditions restricted to cliff ledges. There were positive associations with increasing soil fertility, vegetation height, soil depth, and tall herb cover and richness, but negative associations with increasing sedge and rush cover, soil wetness, and (contrary to expectations) soil pH.

**Conclusions:** Using present-day relict habitat as the basis for mountain woodland restoration planning constrains planting to only a subset of potential locations.

**Implications for Practice:** Restoration should encompass a broader range of suitable conditions that foster long-term ecosystem resilience and adaptive capacity for the future. *Salix lapponum* planting may take place in acidic to neutral soils, rather than concentrating only on the calcareous geologies of Scottish cliff-ledge refugia, but should avoid situations with evidence of poor outcomes, such as very wet habitats dominated by sedges and rushes. Indicator species of suitable or inappropriate conditions can help local planting site selection. Mountain woodland restoration must go beyond just re-creating remnant assemblages, toward a holistic approach to reestablish structural heterogeneity across the full range of opportunities available.

**Key words: arctic-alpine, conservation evidence, habitat restoration, montane scrub, mountain woodland, restoration practice**

## Introduction

Environmental degradation results in decreased ecological functionality and productivity, leading to substantial modifications in the distribution of species and habitats. For example, deforestation causes significant alterations in diversity, carbon sequestration, nutrient cycling, soil properties, and water regulation, with negative implications for the biological and socio-economic systems that depend on these characteristics and processes (Rocha-Santos et al. 2020; Faria et al. 2023; Mgelwa et al. 2024). Restoration must reestablish function, complexity, and resilience, particularly as extreme climatic events become more frequent and destructive under global change (Aerts & Honnay 2011; Bullock et al. 2022). However, action often occurs in heavily modified anthropogenic landscapes, compounded by interactions between land use legacies and contemporary plant biogeography (Vilà-Cabrera et al. 2023). Remnant habitats may not resemble the structure and composition of historical, fully functional conditions (Faria et al. 2023). Therefore, restoration seeking to replicate and expand existing relict patches using recent distributional records may risk bias from

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[1]Biological and Environmental Sciences, Faculty of Natural Sciences, University of Stirling, Stirling, U.K.
[2]Address correspondence to S. H. Watts, email s.h.watts@stir.ac.uk
[3]Forest Research, Alice Holt Lodge, Farnham, Surrey, U.K.


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past management and ecological loss (Willis et al. 2007; Monsarrat et al. 2019). To resolve this complication, we must better understand the performance of focal species across multiple ecological niches throughout the landscape. Such knowledge will help determine the full range of restoration potential in case remaining fragments are restricted to only a subset of habitats that might be occupied.

Informed restoration site selection is especially important for supporting the management of woody species, which typically require considerable investment in time and effort to enable their full ecological functioning to be reinstated. Interventions should be underpinned by research designed to improve future outputs and successfully deliver at scale. This evidence could be obtained from robust experimental studies (Christie et al. 2019), systematic monitoring and reporting of restoration outcomes, and exchange of knowledge on the most cost-effective techniques (Lindenmayer 2020). For example, woodland creation is more efficient following prior evaluations of the abiotic and biotic factors affecting tree growth, health, and fecundity (Brodersen et al. 2019; Löf et al. 2019).

This approach is particularly relevant to high-altitude planting of woody vegetation, which is a significant commitment due to access difficulties, remoteness, the slow growth rate of component species, and their vulnerability to herbivory. Ensuring appropriate micro-environmental conditions for tree and shrub growth is key to the successful restoration of the altitudinal treeline (Li & Yang 2004); the transition zone in mountain woodland between the timberline and the highest elevational limit of individual tree establishment (Dandan et al. 2022). Here, extreme differences in elevation and geomorphology often occur over short distances. Abiotic factors including temperature, wind, exposure, soil properties, and moisture availability can exert a dominant influence on mountain plant spatial patterns. This variability creates a heterogeneous treeline mosaic of increasing stand fragmentation and stuntedness between continuous cover woodland and higher altitude alpine plant communities, such as grasslands and heaths (Holtmeier 2009). Nevertheless, biotic factors (e.g. competition with neighboring vegetation) may also regulate the productivity of arctic-alpine shrubs (Boulanger-Lapointe et al. 2016).

Globally, montane scrub is a mountain woodland vegetation type containing species of high nature conservation concern that requires evidence for restoration effectiveness to improve project outcomes across wider regional landscape and national scales (Gilbert & Di Cosmo 2003; Watts 2024). Here, trees and shrubs are typically low-growing (<2 m tall), twisted, decurrent, and multi-branched, and are situated at the higher altitudes of mountain woodland vegetation mosaics. Common genera include *Eucalyptus*, *Nothofagus*, *Pinus*, *Podocarpus*, *Polylepis*, and *Rhododendron* in the southern hemisphere and tropics, and *Alnus*, *Betula*, *Juniperus*, *Pinus*, *Salix*, and *Sorbus* in temperate and northern regions (Holtmeier 2009; Ruiz et al. 2023).

Many mountain woodlands have experienced substantial anthropogenic degradation linked to overgrazing, agricultural expansion, fire, infrastructure development, and nutrient loading via atmospheric deposition (Holtmeier 2009; Bergmeier et al. 2010). These drivers can severely contract treeline habitats into restricted refugial fragments that may not reflect the complexity and character of their more extensive natural states in the past, or their potential to expand and recover in the future (Gilbert 2011; Watts 2024). Mountain woodland restoration offers an important array of biodiversity gains by supporting specialist arctic-alpine species, including range-restricted invertebrates and birds (Watts & Jump 2022). Furthermore, healthy and resilient treelines can provide effective nature-based solutions to mitigate climate change impacts, such as natural hazard protection, sheltering, slope stabilization, and downstream flood reduction (Holtmeier & Broll 2017; Gu et al. 2019; Monger et al. 2022).

Conservation efforts and habitat recovery have been initiated in Europe focusing on threatened montane willows (*Salix* spp.). Critically endangered species are being restored in Eastern Poland using reintroductions (Pogorzelec et al. 2020a, 2022) supported by studies of populations and their ecology in the Czech Republic and Poland (Pogorzelec 2008; Hroneš et al. 2019). For example, the habitat conditions and vegetation associations of isolated naturally-occurring *Salix lapponum* stands were investigated in the Krkonoše Mountains (Hroneš et al. 2018). In addition, montane willow survival, height and flowering has been assessed in relation to microhabitat and the cover of competing species 3–4 years after planting (Kamocki et al. 2022), and survival and condition monitored 12 months after transplantation (Pogorzelec et al. 2020b). However, research on restoration outputs tends to occur over very short time frames, is often concentrated in the early establishment phase, and does not account for the decades required for mountain woodland to develop into a functional and diverse vegetation mosaic (Mardon 2003).

Scotland presents an opportunity for longer-term study because this country has been pioneering montane scrub restoration for over 30 years, following severe population declines linked particularly to the introduction of domestic hill sheep (*Ovis aries*) in the eighteenth century and increased Red deer (*Cervus elaphus*) populations since the nineteenth century for recreational sport shooting (Hester 1995; Oosthoek 2013). The present-day montane willow communities of the Scottish Highlands are further described by Watts (2024), although these relict patches are now mostly confined to cliffs inaccessible to large herbivores (Stroh et al. 2023). Ongoing interventions to expand the total extent of montane willows in Scotland from 10 ha in the 1990s to circa 1000 ha by 2023 include planting, population reinforcement by genetic rescue, fencing, and landscape-scale management for low-density deer populations (Watts 2024).

While these actions demonstrate significant restoration progress, there are still relatively few assessments of the most appropriate locations for expanding montane willows beyond the refugia that past anthropogenic activity has constrained them to. Choosing suitable sites for reintroduction or supplementary planting is challenging when the full range of requirements for these rare species is not precisely understood and current habitat definitions are based on non-natural or ecologically degraded systems (Pogorzelec et al. 2020b; Arciszewski et al. 2023). Investigations into the factors affecting plant establishment and fecundity are, therefore, required to identify the most productive restoration sites for encouraging greater resilience and sustainability in the future.

Consequently, we sought to determine where planting can maximize efficiency and deliver effective outcomes in mountain woodland restoration outside the constraints of using present-day distribution to indicate future potential. Our research asks the following questions: (1) should relict habitat and refugial conditions be used as a focus for conservation and restoration planning? or (2) should we move beyond simply replicating the features and character of remaining habitat fragments to improve the likelihood of restoration success?

To address these issues we used data derived from more than 30 years of extensive tree and shrub planting at the foremost location for mountain woodland restoration in Scotland. Over 200 ha of treeline woodland and scrub have been reinstated at this site, featuring *Juniperus*, *Betula*, and arctic-alpine *Salix* species. Here, our study species is Downy willow (*S. lapponum*), which comprised most of the montane willow planting across a broad range of topographic conditions, exposure, soils, and associated plant communities. Such variability enabled us to resolve how the growth and productivity parameters of 1050 shrubs planted 16 years previously relates to local abiotic and biotic site variables, thereby studying situations representative of cliff-ledge constrained relict populations within a wider variety of planting locations. This research will improve understanding of the conditions that are favorable and unfavorable to mountain woodland establishment, examine the use of habitat indicator species for planting site selection, and challenge restoration practice to consider expanding into new sites that promote ecosystem function and resilience.

## Methods

### Study Species: *Salix lapponum*

*Salix lapponum* is a dioecious arctic-alpine shrub with a boreal-subarctic distribution across Northern Europe. It has a core range in Scandinavia and western Siberia, and extends into Poland, Belarus, and Scotland (Myklestad & Birks 1993; Hroneš et al. 2018). More isolated populations also exist in the mountains of central, southwestern, and southeastern Europe (Skvortsov 1999; Elven & Karlsson 2000). Globally, *S. lapponum* is threatened by agricultural expansion, eutrophication, tourism developments, changes in groundwater levels, large herbivore management, and competition or shading from lowland plant communities linked to climate change-enhanced succession (Pogorzelec 2010; Kołos et al. 2015; Hroneš et al. 2018). The species is considered vulnerable to extinction in Scotland (Cheffings et al. 2005), where montane willows form the highest altitude zone of shrubby mountain vegetation, usually at altitudes of 600–900 m. Relict patches are very small and fragmented, with current refugia typically sheltered by base-rich crags (with a mean pH range of circa 4.2–7.1) and restricted to thin soils (with a mean depth range of circa 4–20 cm) on rocky slopes and inaccessible cliff ledges alongside other grazing-sensitive tall herb vegetation (Gilbert 2011; Stroh et al. 2023).

### 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. The history and wider management of the site featuring mountain woodland restoration are described in Watts (2024). The main vegetation communities present at Ben Lawers are listed in Annex 1 European Union Habitat Directives (European Commission 2013). These include the priority habitats species-rich *Nardus* grasslands, alpine and subalpine calcareous grasslands, alpine and boreal heaths, and hydrophilous tall herbs (Watts et al. 2019, 2022). This location thus provides the opportunity to assess the growth and productivity of well-established *S. lapponum* scrub across a range of conditions. The Ben Lawers range is typical of much of upland Scotland in terms of its topography and variability of wet and dry habitats, and is within the country's core range of *S. lapponum*.

Sampling took place at Creag an Lochain (lat 56.520694, long −4.2845) on the mountain Meall nan Tarmachan at the western end of the Ben Lawers range, between an altitudinal range of 587–746 m above sea level (asl) (Fig. 1). During 2019–2023, a local weather station situated at 710 m asl (lat 56.506718, long −4.317989) recorded a mean annual precipitation of 1856 mm and a mean annual temperature of 4.35°C, ranging from a mean monthly minimum of −6.52°C in February to a mean monthly maximum of 10.62°C in July (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 (Mardon 2003). A large and complex crag system runs north to south across the site, comprising several tiers of cliffs and scattered, smaller outcrops and boulders. The exclosure is bounded to the east by a water body (Lochan na Lairige), but the fence does not prevent entry of Roe Deer (*Capreolus capreolus*) and Mountain Hare (*Lepus timidus*). Other common grazers include small mammals such as Field Vole (*Microtus agrestis*) and invertebrates. However, there was no notable evidence of herbivory recorded during this study.

A total of 45,303 montane willows were planted at Creag an Lochain during 2001–2017, including 34,602 *S. lapponum*, 10,440 *S. myrsinifolia*, and smaller numbers of *S. lanata* and *S. myrsinites* (Watts 2024). Planting occurred without fertilizer or ground preparation in clusters to create an open mosaic, but at semi-regular spacing within these clusters to an overall density of approximately 300 stems per hectare across the site. The stock was typically 2 years old at the time of planting, and 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 at Ben Lawers. Seed production is widespread across the study site.

The main quantity of planting took place in 2004–2006, including 18,285 *S. lapponum* from which the 1050 individual

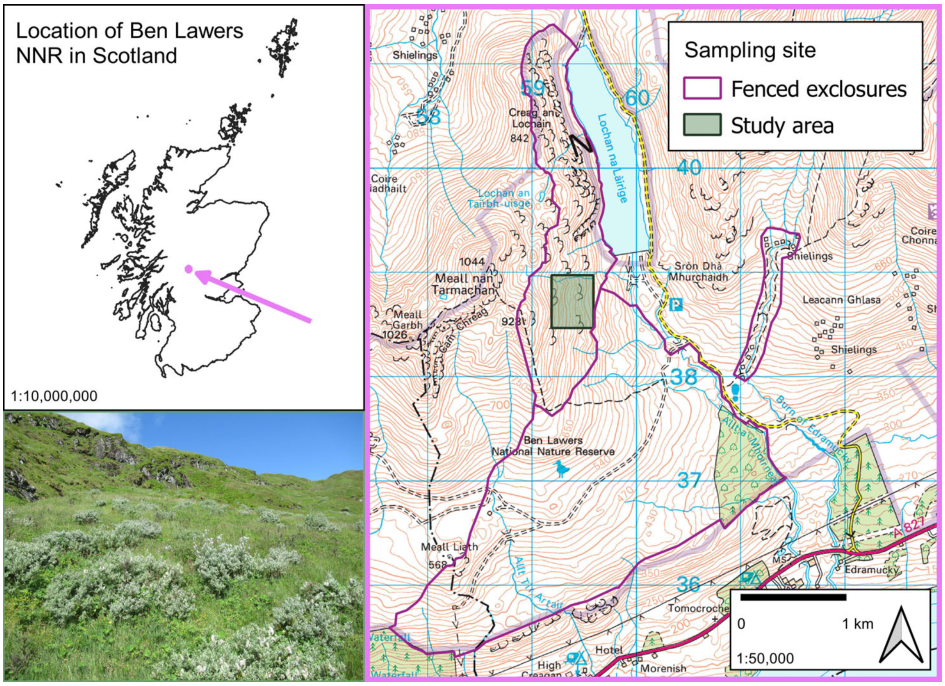


Figure 1. The location of the study site within Ben Lawers National Nature Reserve in Scotland. Planting of *Salix lapponum* was undertaken throughout the fenced exclosures, and the specific area (400 m by 515 m) used for this study is indicated in green. Background Ordnance Survey mapping source from 1:50,000 scale color raster, scale 1:50,000, Tiles: nn42, nn62, nn64, and nn44, Updated: 1 June 2023, Ordnance Survey (GB), using: EDINA Digimap Ordnance Survey Service, https://digimap.edina.ac.uk, Downloaded: 7 February 2024. © Crown copyright and database rights 2024 Ordnance Survey (AC0000851941).

shrubs measured in this study have been sampled. The study area is a smaller region within the wider Creag an Lochain planting site (400 m by 515 m; Fig. 1), and was selected for this research because it encompasses the full range of planting conditions used. These sites included situations resembling those where surviving relict montane willows are found in Scotland, for example in tall herb habitats (30% of planted willows in the study area) denoted by indicator species listed in Table S1, and areas directly below base-rich crags and cliffs (57% of willows) which offered shelter and mineral enrichment. However, planting also occurred across moderately sloping ground on the open hill (24%) or along streambanks (19%), as well as in other habitats including sedge-rich flushes and mires (31%), or upland grassland and heaths (39%). Although the microhabitats recorded during our survey may not exactly reflect past characteristics at the time of planting, some vegetation changes over time have been documented in detail. There has been an increase in tall herbs along with a reduction in bare ground, grazing-tolerant grasses, and low-growing herbs found at Creag an Lochain after large herbivores were excluded, while community composition has otherwise remained stable in flushes, mires, and heaths over the period since planting (Watts et al. 2019).

### Field Survey

Fieldwork was carried out during May to August 2021, with every measurement taken by the same surveyor and all *S. lapponum* sampled within the study area. Six growth and shrub health parameters (height, stem diameter, crown size, interannual growth, canopy density, and catkin presence) were recorded from 1050 *S. lapponum* bushes planted circa 16 years previously within an altitudinal range of 587–746 m (Table 1; Fig. 2). Interannual growth is a measure of plant performance in a particular year and can reliably be measured in this species using the distance between terminal bud scars up to at least 3 years previously (Munro 2013). Crown size and canopy density (i.e. the density of shoots, stems, and leaves) can vary significantly between individuals and have a substantial influence on plant biomass.

Abiotic and biotic predictor variables were also sampled at the level of the individual shrub, including slope angle, soil depth, shelter feature, surrounding vegetation height, tall herb species richness, percent cover of the five most abundant vascular plant species within the area of the shrub and its 30 cm perimeter, and overall cover of different functional plant groups. Further details of these methods of data collection are provided in Table 1, including those parameters especially relevant to relict conditions of montane willows in Scotland (soil depth and pH; sheltering by crags; tall herb richness and cover). A total of 49 measurements were recorded per shrub, giving a combined total of 51,450 raw data points for the 1050 *S. lapponum* sampled.

This fieldwork required two rounds of data collection. Firstly, all response variables and abiotic predictors as listed in Table 1 were recorded during May to August. Subsequently, the biotic variables were measured during four consecutive days in late August for comparability of vegetation measurements between

**Table 1.** The response and predictor variables measured from 1050 mature individual *Salix lapponum* shrubs at Creag an Lochain (Ben Lawers NNR) in 2021. Standard errors are given in brackets below the mean values. [a]These measurements together add up to a total of 100% vascular plant cover. [b]These variables are particularly relevant to relict cliff-ledge conditions of *S. lapponum* in Scotland. [c]species listed as indicators of upland tall herb habitat by the Joint Nature Conservation Committee (2009). "All summer" measurements were recorded during May to August 2021.

| *Measurement* | *Variable type* | *Range* | *Mean (SE)* | *Unit* | *Timing* | *Instrument* | *Protocol* |
|---|---|---|---|---|---|---|---|
| *Response variables* | | | | | | | |
| Height | Numerical | 9.0–148.8 | 54.2 (0.7) | cm | All summer | 1 m rule | Mean height of five random measurements across the canopy, each from ground level to the top of the tallest shoot touching the ruler |
| Stem diameter (mm) | Numerical | 5–62 | 15.2 (0.2) | mm | All summer | Calipers | Recorded at ground level from main stem; if multiple stems then largest is chosen |
| Crown size | Numerical | 0.07–17.2 | 2.7 (0.1) | $m^2$ | All summer | 1 m rule | (*a*) Measure across shrub canopy at widest point (*b*) Measure perpendicular across canopy Area calculated as $\pi \times (a) \times (b)$ |
| Interannual growth in 2020, 2019, and 2018 | Numerical | 0.9–30.0 | 7.4 (0.1) | cm | All summer | 30 cm rule | Mean length of three randomly selected shoots, tracked back in time using bud scars |
| Canopy density | Ordinal | | | % cover: low (<40%), medium (40–80%), or high (>80%) | All summer | Visual assessment | Assigning the density of canopy foliage when viewed from above into one of three categories |
| Catkin presence | Binary | | | Presence/absence | All summer | Visual assessment | Searching canopy and leaf litter below for any catkins |
| *Abiotic predictors* | | | | | | | |
| Altitude | Numerical | 587–746 | 681.5 (1.1) | m above sea level | All summer | Hand-held GPS | Record from the middle of each shrub |
| Northness | Circular | Between minus 1 and plus 1 | 0.03 (0.02) | Radians | All summer | Compass | Slope aspect recorded in the field in degrees; converted to a direction vector of northness using the formula cos(aspect) |
| Slope angle | Numerical | 2–62 | 27.2 (0.3) | Degrees | All summer | Rolling ball clinometer | Clinometer placed on top of meter rule positioned on the ground in the middle of shrub canopy |
| Soil depth[b] | Numerical | 10–50 | 31.4 (0.3) | cm | All summer | Metal depth probe | Mean of five random measurements around the shrub canopy, from the top of the soil surface (excluding leaf litter but including the fermentation layer) to the point when the metal probe reached impenetrable mineral material |
| Soil fertility | Numerical | 1.7–6.0 | 3.2 (0.02) | Ellenberg scale (*N*) | All summer | Visual assessment | Ellenberg values calculated using % cover values of the five most abundant vascular plant species within the area of the shrub and its 30 cm perimeter |
| Soil pH[b] | Numerical | 2.3–6.4 | 4.8 (0.02) | Ellenberg scale (*R*) | All summer | Visual assessment | Ellenberg values calculated as above |
| Soil wetness | Numerical | 4.6–7.9 | 6.5 (0.02) | Ellenberg scale (*F*) | All summer | Visual assessment | Ellenberg values calculated as above |

**Table 1.** Continued

| *Measurement* | *Variable type* | *Range* | *Mean (SE)* | *Unit* | *Timing* | *Instrument* | *Protocol* |
|---|---|---|---|---|---|---|---|
| Light | Numerical | 5.2–7.8 | 6.8 (0.01) | Ellenberg scale (*L*) | All summer | Visual assessment | Ellenberg values calculated as above |
| Shelter feature[b] | Categorical | | | Category | All summer | Measuring tape | Category assigning based on visual assessment and measurement from base of nearest crag directly uphill (if applicable).<br>C < 5: less than 5 m from base of a crag or cliff<br>C5-15: 5–15 m from base of crag or cliff<br>C15-25: between 15 and 25 m from base of crag or cliff<br>Stream: planted along a watercourse<br>Slope: open/none of the above |
| *Biotic predictors* | | | | | | | |
| Vegetation height | Numerical | 12.5–78.3 | 31.7 (0.3) | cm | End of August | 1 m rule | Mean of five random measurements taken within the 30 cm perimeter of the shrub, recorded as the highest touching point of vegetation |
| Tall herb richness[b] | Numerical | 0–10 | 4.3 (0.05) | Count | End of August | Visual assessment | Number of tall herb species[c] within the area of the shrub and its 30 cm perimeter |
| Tall herb cover[a,b] | Numerical | 0–80 | 32.1 (0.5) | % cover | End of August | Visual assessment | Recording cover of tall herb species within the area of the shrub and its 30 cm perimeter |
| Sedge/rush cover[a] | Numerical | 0–75 | 15.6 (0.5) | % cover | End of August | Visual assessment | Recording cover of sedges and rushes (*Carex* and *Juncus* spp.) within the area of the shrub and its 30 cm perimeter |
| Grass cover[a] | Numerical | 0–80 | 28.2 (0.5) | % cover | End of August | Visual assessment | Recording cover of grasses within the area of the shrub and its 30 cm perimeter |
| Dwarf-shrub cover[a] | Numerical | 0–65 | 4.2 (0.2) | % cover | End of August | Visual assessment | Recording cover of dwarf-shrubs within the area of the shrub and its 30 cm perimeter |
| Small herb cover[a] | Numerical | 5–50 | 17.9 (0.3) | % cover | End of August | Visual assessment | Recording cover of other forbs within the area of the shrub and its 30 cm perimeter |
| Pteridophyte cover[a] | Numerical | 0–50 | 2.0 (0.2) | % cover | End of August | Visual assessment | Recording cover of pteridophytes within the area of the shrub and its 30 cm perimeter |
| *Other variables* | | | | | | | |
| Shrub ID | Numerical | | | Count | All summer | N/A | Unique reference number for each individual in order of survey date and time |
| GPS coordinates | Numerical | | | 10 figure Ordnance Survey grid reference | All summer | Hand-held Global Positioning System unit | Record from the middle of each shrub |
| Plant sex | Categorical | | | Male/female/unknown | All summer | Visual assessment | Searching canopy and leaf litter below for any catkins |


Figure 2. (A) measuring *Salix lapponum* at Creag an Lochain, Ben Lawers NNR, (B) an example of tall herb vegetation present at the study site, featuring *Alchemilla glabra*, *Angelica sylvestris, Crepis paludosa*, *Filipendula ulmaria*, *Geranium sylvaticum*, *Geum rivale*, *Luzula sylvatica*, *Ranunculus acris*, *Solidago virgaurea*, and *Succcisa pratensis*, (C) *Carex nigra*, a sedge indicative of wet soil conditions. (D) An example of *S. lapponum* with a low canopy density (<40%). (E) An example of *S. lapponum* with a high canopy density (>40%).

plants, which would otherwise vary throughout the summer. Sketch maps, GPS (Global Positioning System) and photographs were used to accurately relocate each shrub to ensure that second-round measurements were attributed to the same individuals as previously. We did not measure *S. lapponum* belowground variables such as root growth and morphology, or directly sample soil conditions, to avoid disturbing a sensitive upland site protected by multiple conservation designations.

#### Data Analysis

All analyses were performed using R Statistical Software v4.1.2 (R Core Team 2021). Height, crown size, stem diameter, and interannual growth (calculated as a mean of the three preceding growing seasons) were all highly correlated (Supplement S1). These variables were combined into a single growth performance index measure using Principal Component Analysis (PCA). PCA axis 1 ("PCA growth") explained 75% of the variation in growth parameters. For a biological interpretation, a PCA growth value of 0 equates to a shrub height of approximately 50 cm, and a PCA growth value of 3 equates to a shrub height of approximately 100 cm (Supplement S1).

Cover-weighted Ellenberg scores for each *S. lapponum* sampled were calculated using MAVIS Plot Analyser v. 1.04 (Smart et al. 2016) from the Ellenberg values (Hill et al. 1999) of the five most abundant vascular plants species growing within 30 cm of the perimeter the shrub. Ellenberg values represent a nine-level ordinal classification of plants using expert-based rankings of species according to the position of their realized ecological niche along different environmental gradients (Ellenberg et al. 1991; Hill et al. 1999). These indicators provide a reliable assessment of local-scale conditions (such as nitrogen, moisture, and pH) without the need for direct measurements (Schaffers & Sýkora 2000; Diekmann 2003).

The association between PCA growth and all 17 abiotic and biotic site predictor variables listed in Table 1 was investigated using a linear model. Collinearity between predictor variables was tested using the Variance Inflation Factor (VIF), but did not affect model construction. Variables were centered and scaled during model fitting to standardize the coefficients. The stats::drop1 function was used for variable selection comparing the full model to a series of reduced models in which one predictor was removed. The full model was then compared to each of the reduced models using likelihood ratio tests, and predictor variables were dropped if they did not significantly decrease the likelihood relative to the full model. Two-way interactions were added thereafter to the resultant reduced models only if they were plausible and readily interpretable from prior knowledge of the study system, including interactions between soil depth, sheltering, Ellenberg values, and vegetation cover. However, no interactions were found to significantly improve the likelihood of the models. This model selection approach is suitable for statistical exploration to describe relationships in ecological data where there are many abiotic and biotic covariates and a lack of a priori knowledge (Tredennick et al. 2021).

Model assumptions of normality, linearity, and homogeneity were tested using a residuals versus fitted plot, normal *Q*-*Q* plot, scale-location plot, and Cook's distance. Spatial autocorrelation of PCA growth was also explored by fitting the simplified linear model again using the gls function (generalized least squares) from the nlme R package. A semivariogram was plotted representing half the average squared difference between the residuals at increasing distances from each other. The plot suggested that significant spatial clustering is not present in the residuals for the simplified linear model of PCA growth.

The association between interannual growth and the abiotic and biotic site predictors was examined using a linear mixed model incorporating the separate measurements for shoot growth in the three preceding growing seasons (2018–2020), and shrub ID as a random factor. Abiotic and biotic influences on canopy density and catkin presence were assessed using models derived from ordinal logistic regression and binary logistic regression. Similar to Kamocki et al. (2022) and Hroneš et al. (2018), catkin presence is used as a basic proxy for whether a shrub was investing in reproduction or not during the study season, incorporating both female and male shrubs. The influence of sex on plant size or environmental niche preferences was not tested due to a bias toward recording female shrubs. Although female catkins persist until at least August, male catkins usually fall off in early summer but can sometimes be found caught in the canopies of larger bushes for several weeks longer.

To test that the growth of large shrubs at the restoration site is still favorable in terms of catkin production, the presence of catkins was analyzed by binary logistic regression with "PCA growth" as the predictor variable in a separate model to ensure variable independence. The model selection and assumption testing approach used for PCA growth was also employed for the models of interannual growth, canopy density, and catkin presence.

The relationship between PCA growth and vegetation community composition (from the five most abundant vascular plants species growing within 30 cm of the perimeter of each shrub) was explored in ordination space with non-metric multi-dimensional scaling (NMDS) using a Jaccard distance matrix in four-dimensions in the vegan R package v.2.6.4. 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. Ellenberg fertility, pH, and wetness were fitted as environmental vectors using the envfit function.

## Results

The full range of measurements, mean values, and standard errors for each response and predictor variable are provided in Table 1. *Salix lapponum* height circa 16 years after planting ranged from 9 to 149 cm (mean = 54.2), and interannual growth ranged from 0.9 to 30.0 cm (mean = 7.4). The sex ratio of the shrubs sampled was 516 female:311 male: 223 unknown (i.e. no catkins present). Therefore, 79% had catkins and 21% did not have catkins, although it is anticipated that many shrubs of unknown sex may have been male because their catkins persist for a much shorter time than females. Ellenberg soil fertility at the site inferred from the surrounding vegetation ranged from 1.7 to 6.0 (mean = 3.2), and Ellenberg wetness ranged from 4.6 to 7.9 (mean = 6.5). Ellenberg pH spanned from 2.3 to 6.4 (mean = 4.8), which is a large range, although 97% of pH values were between 3.5 and 6. Tall herb cover within 30 cm of the perimeter of the shrubs ranged from 0 to 80% (mean = 32.1%), and the cover of sedges and rushes ranged from 0 to 75% (mean = 15.6%). The local weather recorded at 710 m asl relating to interannual growth measurement years was warmer and drier in 2018 than in 2019 or 2020, and wettest in 2019 (Supplement S2; Black & Watson 2024).

Table S2 provides the full results of modeling how *S. lapponum* growth and health parameters related to abiotic and biotic site variables. The simplified best-fitting linear model ($r^2 = 0.461$) and Figure 3 show that the size of *S. lapponum* circa 16 years after planting is positively associated with increasing soil fertility (coefficient = 0.567, $t = 7.119$), vegetation height (0.326, $t = 7.292$), soil depth (0.309, $t = 7.548$), tall herb richness (0.216, $t = 4.674$), and tall herb cover (0.292, $t = 4.668$), but negatively associated with increasing soil pH (−0.368, $t = -4.834$), cover of sedges and rushes (−0.267, $t = -3.506$), and soil wetness (−0.207, $t = -3.945$). However, interannual growth also varied significantly between years, with much longer shoot growth in 2018 than in 2019 or 2020 (Table S2; Supplement S2).

Ordinal logistic regression ($r^2 = 0.139$) and Figure 4 demonstrate that the probability of a shrub having a high canopy density is positively associated with increasing soil fertility (coefficient = 0.707, $t = 7.081$), tall herb cover (0.267, $t = 3.009$), and tall herb richness (0.195, $t = 2.872$), but negatively associated with increasing soil wetness (−0.368, $t = -4.933$) and pH (−0.653, $t = -7.577$). Binary logistic regression ($r^2 = 0.325$) and Figure 5 show that the probability of a shrub having catkins is strongly negatively related to the cover of sedges and rushes (coefficient = −1.310, $t = -10.220$), while vegetation height (0.267, $t = 2.444$), soil depth (0.251, $t = 2.904$), and tall herb richness (0.312, $t = 3.257$) had a positive association. When modeling catkin presence with PCA growth as the predictor variable, the odds ratio for PCA growth is 4.083 ($z = 13.23$, $p > 0.001$), and the probability of catkins being present is positively associated with increasing PCA growth (Fig. 5). Therefore, larger shrubs with a PCA growth value of 0 or greater (i.e. >50 cm in height) almost all produced catkins (a probability close to 1). Conversely, the smallest shrubs were significantly less likely to have catkins.

The NMDS plot (Fig. 6) of vascular plant community composition and PCA growth suggests that larger shrubs distributed to the top left of the plot (with greater NMDS2 values) are associated with increasing Ellenberg fertility and tall herbs including *Luzula sylvatica*, *Angelica sylvestris*, *Geranium sylvaticum*, *Ranunculus acris*, and *Rumex acetosa* (Fig. 2). Additional plant species with high Ellenberg fertility values and moderate wetness values recorded during the study are *Ranunculus repens*, *Tussilago farfara*, *Ajuga reptans*, and *Cirsium heterophyllum* (Table S1). In contrast, smaller shrubs with greater NMDS1 values are associated with increasing Ellenberg wetness and species of flushes and mires, including *Carex nigra* (Fig. 2), *Crepis paludosa*, *Equisetum pratense*, *Juncus conglomeratus*, and *Juncus articulatus* (Fig. 6). Additional plants with high Ellenberg wetness and low fertility values are *Narthecium ossifragum*, *Eriophorum angustifolium*, *Carex hostiana*, *Saxifraga aizoides*, *Carex panicea*, and *Carex viridula* (Table S1). With reference particularly to these indicator species, further detail on recommendations for practitioners working specifically with montane willows in Scotland based on our results is given in Supplement S3.

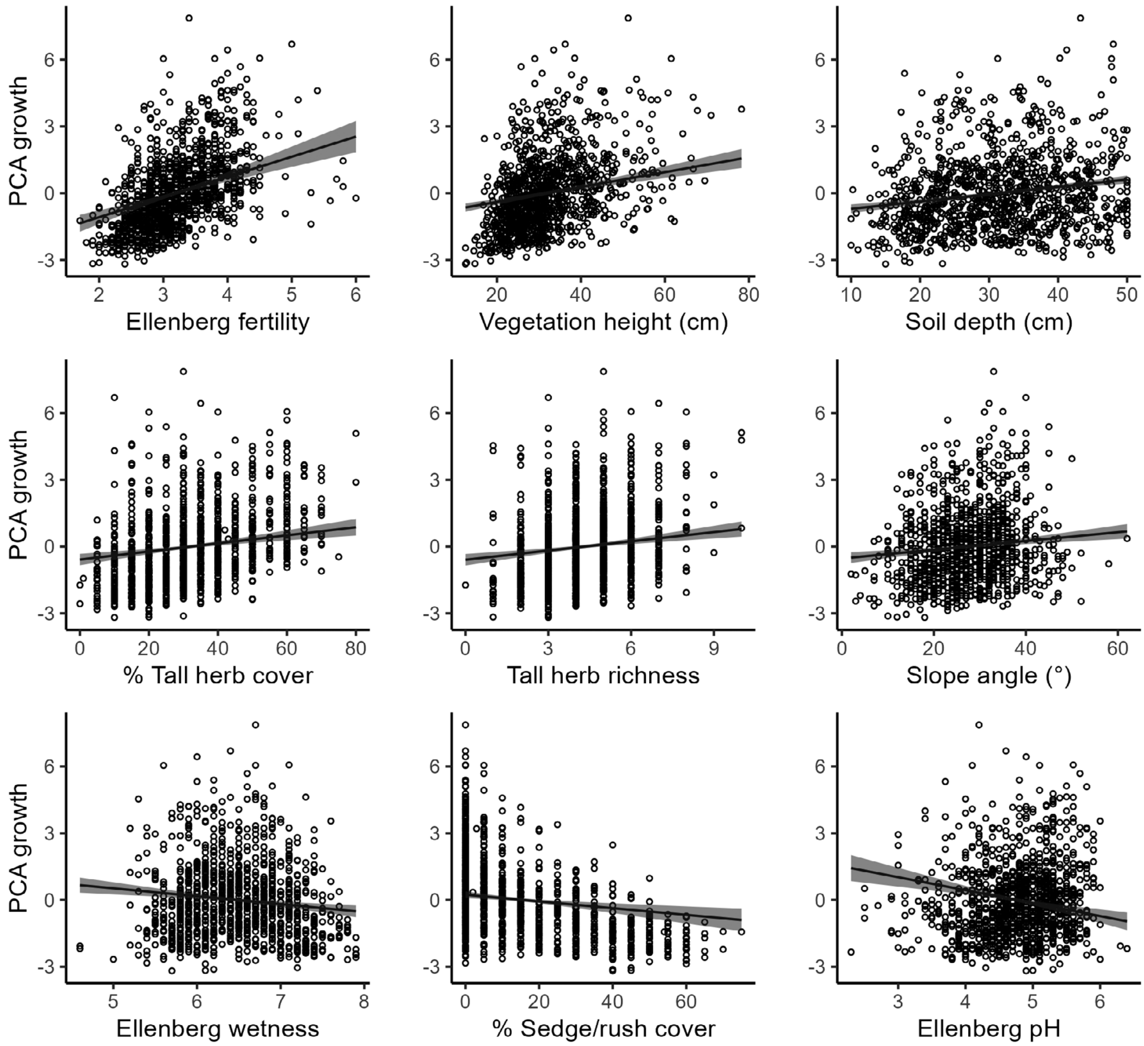


Figure 3. Model predictions of the linear model of Principal Component Analysis growth axis 1 (a combined variable of height, crown size, stem diameter, and interannual growth) from 1050 *Salix lapponum* planted at Ben Lawers. Generated by holding all other predictor variables at their mean value and selecting the shelter feature as C < 5 (less than 5 m from the base of a crag or cliff). Shaded areas represent 95% CI. Panels are ordered in descending order of model coefficient size from a positive to negative effect.

## Discussion

This study highlights a number of key abiotic and biotic variables influencing the health of restored montane willows which can help guide future restoration planting, with implications for management based on relict habitat conditions. The growth parameters of 1050 *Salix lapponum* individuals circa 16 years since planting were positively associated with higher levels of soil fertility, vegetation height, soil depth, and tall herb cover and richness; but negatively associated with increased levels of soil pH, cover of sedges and rushes, and soil wetness. There was no relationship with sheltering features including the distance from crags and cliffs. Similar results were presented for the separate models of PCA growth (a combined variable of height, crown size, stem diameter, and interannual growth), interannual growth accounting for variation between years, and canopy density; suggesting that those situations having a positive influence on annual, lateral, and vertical growth were also beneficial for overall aboveground biomass.

### Biotic Variables: Planting Guided by Vegetation Associated With Relict Sites

*Salix lapponum* growth and catkin presence were positively related to tall herb cover and richness, revealing that this functional vegetation group linked with montane willow refugial conditions in Scotland can be helpful to guide planting site selection. In terms of vascular plant composition there are similarities between productive locations for restoration and the present-day relict habitat. An indicator species approach thus has applications for promoting project efficiency and effectiveness. For example, *Luzula sylvatica* is a tall herb associate of *S. lapponum* cliff-ledge refugia but also has a far more

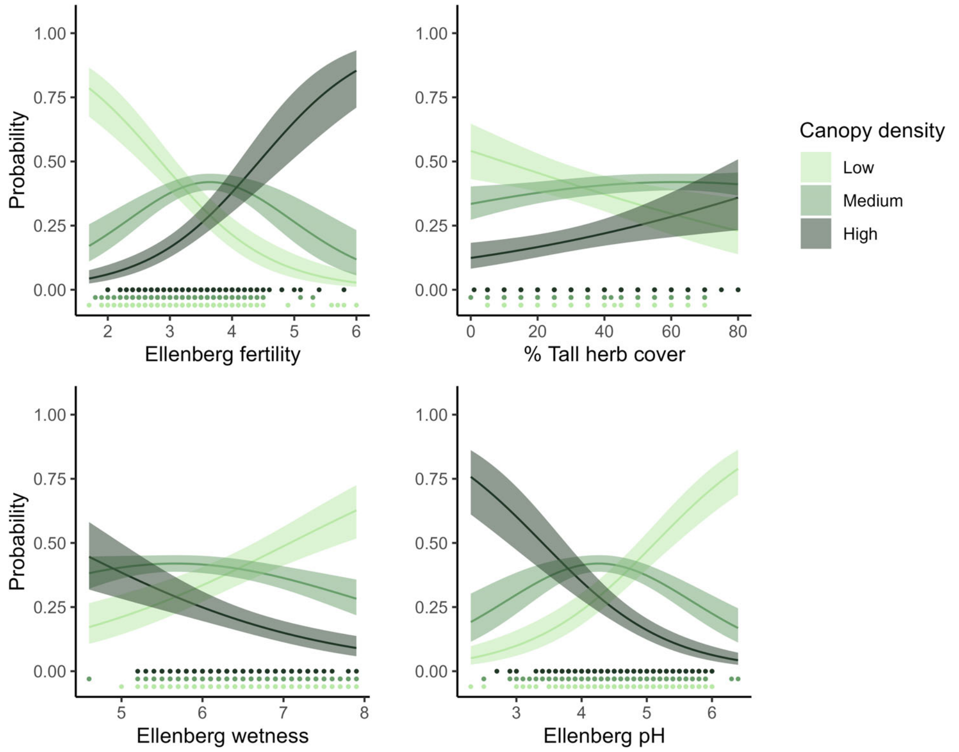


Figure 4. Ordinal logistic regression model predictions of the probability of shrubs with a canopy density in three ordered categories (low, medium, and high), derived from measurements on 1050 *Salix lapponum* planted at Ben Lawers. Predictions were generated by holding all other predictor variables at their mean value and selecting the shelter feature as C < 5 (less than 5 m from the base of a crag or cliff). Density of canopy foliage is defined as low (<40%), medium (40–80%), or high (>80%) when viewed from above. Shaded areas represent 95% CI. The distribution of raw data points for each *x*-axis measurement is provided by dots below the plot.

widespread distribution on open hillsides on a wide range of soils from calcareous to acidic pH (Hill et al. 1999; Stroh et al. 2023). Such indicator species can represent a suitably broad range of opportunities including conditions reflecting relict sites, rather than being overly restrictive only toward highly specialized refugia. The association between tall herbs and *S. lapponum* may also be used as a guide for planting in relation to wider restoration goals than simply fostering willow growth, for example through positive feedbacks and vegetation facilitation which can improve soil properties and sheltering effects over time (Bekker 2005; Dona & Galen 2007; Watts & Jump 2022). Although useful for choosing local restoration sites, indicator species should nevertheless be used with caution when generalizing beyond an individual study system. Where regional differences in species pools exist, it may be advantageous to focus on functional groups defined by life-history traits so that results have wider relevance and are more easily transposable to other areas (Verheyen et al. 2003; Hérault et al. 2005).

### Abiotic Variables: Association With Soil Characteristics and Sheltering

While our data show that planting montane willows alongside vegetation representative of present-day relict habitat conditions has aided restoration outcomes, applying other characteristics of refugial populations (crag sheltering and thin soils with higher pH) to assist site selection has not improved shrub growth and productivity. Soil fertility (inferred from the surrounding vegetation using Ellenberg values) had consistently the most strongly positive association with shrub growth parameters. There was also a positive association with soil depth, and negative associations with the wettest sedge-rich locations and increasing pH. The information on those species which represent poor conditions for restoration (e.g. *Carex*, *Eriophorum*, and *Juncus* spp.) could thus be used to maximize efficiency by ensuring future planting avoids such places.

Similar to our results, Hroneš et al. (2018) determined that *S. lapponum* in the Krkonoše Mts (Czech Republic) frequently occurred in nutrient-rich soils, although also in microhabitats perceived to be less optimal on the periphery of mires with fluctuating water levels. In contrast, Kamocki et al. (2022) reported that the survival rate of *S. lapponum* introduced into nutrient-poor habitats in northeast Poland was significantly higher than in more fertile conditions, but nevertheless noticeably lower in patches dominated by sedges. Very high soil fertility and eutrophication may even be a threat to montane willows (Seregin 2014), but those conditions are beyond the values recorded in this study. Our results were obtained from soils that overall have a low to medium fertility (Ellenberg value mean = 3.2), are moderately wet

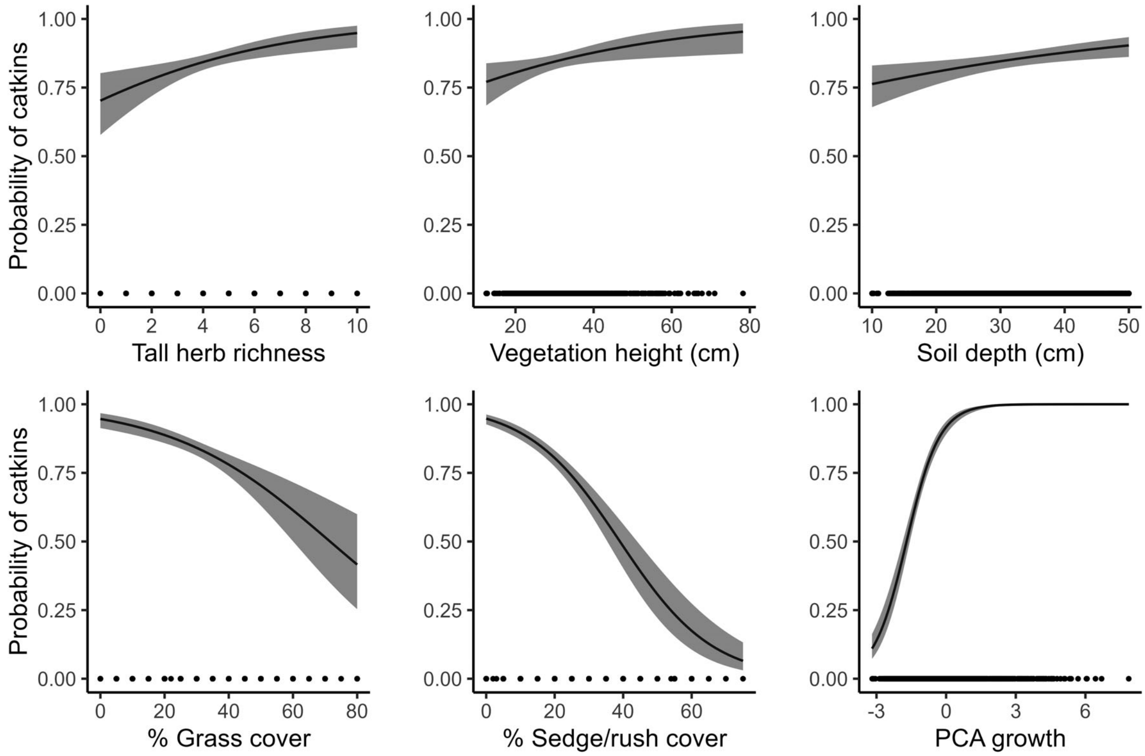


Figure 5. Model predictions of the binary logistic regression of catkin presence from 1050 *Salix lapponum* planted at Ben Lawers, generated by holding all other predictor variables at their mean value, and selecting the shelter feature as C < 5 (less than 5 m from the base of a crag or cliff). PCA growth in the bottom right panel was modeled separately to ensure variable independence from the abiotic and biotic predictors. Shaded areas represent 95% CI. The distribution of raw data points for each *x*-axis measurement is provided by dots below the plot.

throughout (Ellenberg value mean = 6.5), and with an acidic to neutral pH (Ellenberg value mean = 4.8). These data demonstrate variation within the typical environmental range for the study species in continental Europe, where *S. lapponum* is reported from acidic to neutral soils with pH ranging from approximately 4–6 (Pogorzelec 2008; Kołos et al. 2015; Hroneš et al. 2018).

In general, *S. lapponum* may have a broad tolerance to various ecological factors, particularly those related to groundwater, and does not have a special affinity for rocky slopes in systems outside Scotland (Pogorzelec 2008; Serafin et al. 2015; Arciszewski et al. 2023). Common habitats in Scandinavia and Russia include swamp edges, lake shorelines, forest tundra, and the "willow region" alongside other arctic-alpine *Salix* spp., *Betula* spp., herbaceous plants, and various dwarf-shrubs in the upper altitudinal reaches of the wider montane shrub zone (Skvortsov 1999; Totland & Esaete 2002). In Poland and the Czech Republic, *S. lapponum* grows on moist oligotrophic to mesotrophic soils, including bogs, wetlands, fens, and transitional mires (Elven & Karlsson 2000; Pogorzelec 2010; Kołos et al. 2015).

Yet in Scotland, *S. lapponum* is currently distributed on steep mountainsides and sheltered by cliffs with relatively base-rich and thin rocky soils often derived from calcareous schist or limestone, and only rarely on acidic substrates (Stroh et al. 2023). These relict stands occur outside of the present core range of the species in Europe, and are isolated and in decline, with their distribution strongly influenced by overgrazing largely restricting surviving populations to inaccessible cliff ledges (Watts 2024). Such marginal, disjunct populations are sometimes characterized by differentiation in genetics, ecological adaptations, performance, specific habitat requirements, and response to various abiotic and biotic interactions (Sexton et al. 2009; de Medeiros et al. 2018; Hroneš et al. 2018). The negative influence of increasing pH on the growth parameters presented here could also in part be related to the base-rich flush species inferring high Ellenberg values which concurrently have high wetness values. Nevertheless, our results indicate that using the relict conditions of higher pH, lower soil depths, and sheltering by crags as the basis for restoration planning constrains montane willow planting to only a subset of situations that might be occupied and could even omit those sites with the most productive outcomes.

### Future Considerations for Monitoring Restoration Project Effectiveness

To evaluate outcomes periodically in restoration schemes it is important to be able to rapidly and reliably record differences in plant size between locations, habitats, treatments, and years. Since our data included correlated growth parameters, fewer measurements could therefore be incorporated into studies of planting outputs in the future. For example, height provides an easily repeatable, simple assessment of overall growth over

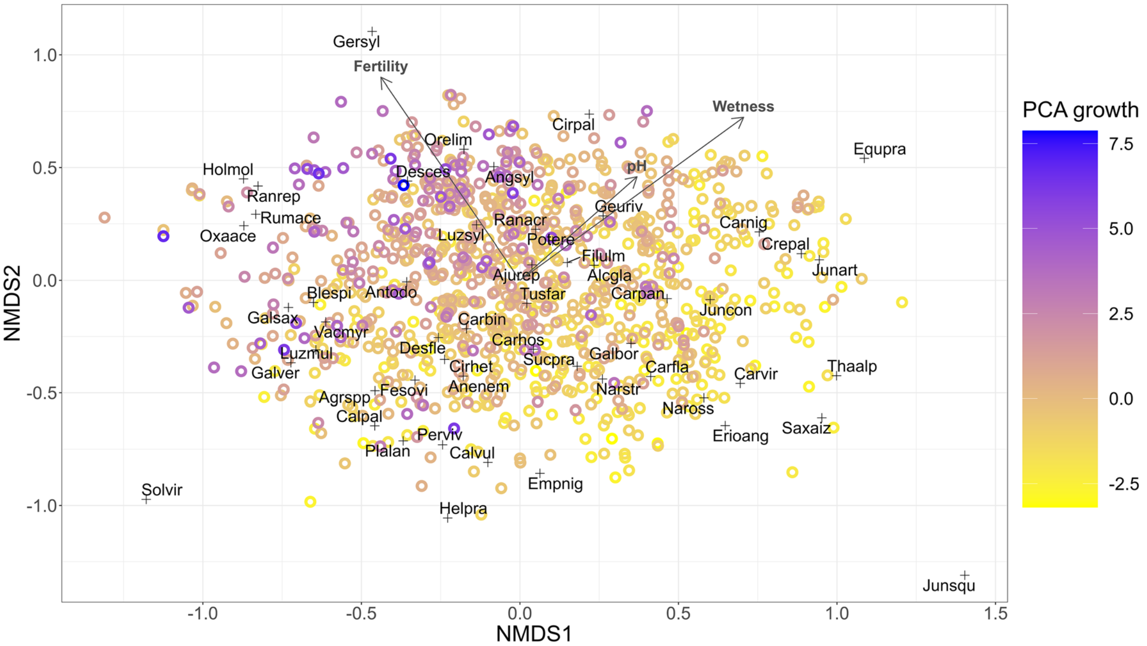


Figure 6. Non-metric multi-dimensional scaling (NMDS) plot exploring individual *Salix lapponum* shrub distribution (open circles; $n = 1050$) in ordination space in relation to vascular plant vegetation community composition. Species (crosses) are labeled with the first three letters of their genus and species names, with full names given in Table S2 in Supplement S3. Variation in shrub size is indicated by a color ramp of PCA growth (a combined variable of height, crown size, stem diameter, and interannual growth), with larger values representing larger shrubs. Ellenberg fertility, pH, and wetness are fitted as environmental vectors using the envfit function in the vegan R package v.2.6.4.

time, while interannual growth offers a finer evaluation of aboveground biomass production in an individual year. However, variation in annual weather should also be accounted for when assessing monitoring outputs because climate conditions in the year of planting and subsequent years may affect results. During our study, the drier, hotter conditions in 2018 could have contributed to a marked increase in *S. lapponum* shoot growth, while the reduced interannual growth in 2019 might be linked to cooler, wetter weather or compensation due to drought stress from the previous summer. As our data only allow a qualitative comparison between weather and interannual growth, further research is required to determine the influence of summer temperatures and precipitation on mountain woodland establishment and productivity, and thus the potential impacts of accelerated climate change.

Other factors that might affect shrub health and fecundity but were not measured in this study include snow cover, ectomycorrhizal fungi, invertebrate and small mammal herbivory, pathogens, soil texture, and planting distribution. The quality of out-planted material may be affected by underlying genetics (Głębocka & Pogorzelec 2017), prior external factors from the tree nursery environment, and propagation methods (Pogorzelec et al. 2020a; Arciszewski et al. 2023). The data provided here also do not account for causes of mortality and failure in earlier years of the project. Survival is a fundamental contributor to overall restoration outcomes and ideally would be analyzed along with growth, herbivory, and fecundity during annual monitoring of repeatedly measured individual plants from the project outset (Watts 2024).

Furthermore, the creation of viable, self-sustaining populations should be a fundamental goal of restoration. However, observations of the next generation establishing via seed generated from planted montane scrub are currently rare, and some limited new seedlings were only observed for the first time at our study site in 2021 despite years of widespread seed production (Watts 2023, 2024). Since adult occurrence and growth are not always precise indicators of the requirements for seeds and seedlings, characterizing and quantifying the recruitment niche would improve long-term restoration outcomes (Larson et al. 2023). Consequently, additional investigations are needed on the factors affecting and potentially constraining natural regeneration in mountain woodlands, including seed production, viability, dispersal, and the conditions for germination.

### Recommendations for Improving Restoration Practice

Existing restoration projects provide a useful reference for investigating the performance of target species across a range of ecological variation, thereby aiding management efficiency in the future by identifying conditions that promote effective restoration outcomes. In Scotland, planting *S. lapponum* in areas of higher fertility, deeper soils, and with tall herbs present could be beneficial for producing larger, healthier reproductive shrubs with dense canopies. Nevertheless, restoration projects aiming to deliver connectivity on a landscape scale should not become too restricted toward these very specific site attributes that only produce the biggest shrubs. Structural heterogeneity incorporating variation in plant size, growth form, and distribution is an important feature of the altitudinal treeline and its contribution to biodiversity. Open, shrub-less spaces could be facilitated by avoiding planting in areas of dense sedge cover and high soil wetness. Restoration encompassing an appropriately wide choice of suitable growing conditions for montane willows, together with broad genetic variability in planted stock, will also help build resilience and adaptations into future generations to buffer the impacts of climate change or outbreaks of pests and pathogens.

In fact, our results in relation to pH suggest that montane willow planting could also take place in acidic to neutral deeper soils, rather than concentrating only on the thinner calcareous soils indicative of their refugia. Overall, only a small amount of variation in growth and catkin presence was attributed to local environmental variables related to relict conditions. Therefore, restoration must achieve far more than simply re-creating the character and features of present-day remnant assemblages (Hobbs et al. 2009). This situation can be resolved by moving beyond just protecting and magnifying fragmented cliff-ledge restricted populations toward a holistic approach to reestablish mountain woodland across the full range of opportunities available that improve both habitat quality and quantity.

### Wider Relevance

Since the conservation of individual willow species does not on its own equate to restoration of an upper montane shrub zone, integrating a suitable variety of treeline taxa (e.g. *Salix*, *Juniperus*, *Pinus*, and *Betula* spp.) to create a mosaic of woody species and habitats will enable a more naturalistic, complex, and vibrant transitional ecotone (Watts 2024). Nevertheless, *S. lapponum* could act as a flagship species highlighting the value, methods, and outcomes of supplementary planting and translocating threatened plants to help tackle the nature and climate crises on a national scale. However, all efforts to reinstate the altitudinal treeline must be underpinned by action to combat the original causes of habitat loss and degradation, such as through removing the pressure of overgrazing by large herbivores. Examining more intact systems elsewhere in Europe, for example in Scandinavia, could also aid the selection of sites and species for mountain woodland reestablishment in Scotland.

Historical knowledge and references, paleoecology, and information on land use legacies are vital for understanding drivers of change involving the long-term distribution, composition, and function of ecosystems (Davies & Bunting 2010; Balaguer et al. 2014; Higgs et al. 2014). Although past and present-day relict conditions do not offer direct analogs for the future, they can guide restoration planning by providing an evidence base, as long as the concept of dynamic landscapes shaped by change is incorporated into decision-making (Harris et al. 2006; Wingard et al. 2017). We must be careful not to bias management toward narrow objectives involving suboptimal locations when there are greater prospects outside of these constraints (White & Walker 1997). Setting tight targets for achieving specific ecological results that are easily measured but inhibit variation and novelty may exacerbate biotic homogenization and vulnerability during rapid environmental change (Davies & Bunting 2010). Effective restoration interventions emerge from an awareness of intrinsic nature recovery potential and overcoming obstacles that limit this potential (Chazdon et al. 2024). Restoration practice should thus incorporate innovative approaches that foster long-term ecosystem health, diversity, flexibility, sustainability, and adaptive capacity for the future (Frietsch et al. 2023; Dudney et al. 2024).

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## Supporting Information

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

**Supplement S1.** Correlation of *Salix lapponum* growth parameters and a single measure of growth performance derived from Principal Component Analysis.
**Supplement S2**. *Salix lapponum* interannual growth at Creag an Lochain (Ben Lawers NNR) during 2018–2020, in comparison to local weather data.
**Supplement S3**. Site selection recommendations for practitioners planting montane willows in Scotland.
**Table S1**. A complete list of all vascular plant species recorded at Creag an Lochain, and their Ellenberg values.
**Table S2**. Full results and coefficients for the models of shrub growth response variables.

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