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Thinking outside the bog: Planting dwarf birch (*Betula nana*) for mountain woodland restoration beyond habitat refugia constrained by overgrazing

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ABSTRACT

The contemporary distribution of threatened species may not be in equilibrium with their full ecological niche. Understanding range contraction due to anthropogenic land-use pressures will reduce bias in management aimed at expanding present-day forests. Many mountain woodlands currently occur as fragments, with uncertainty regarding their optimal distribution and restoration potential, particularly in landscapes shaped by large herbivore management. Our high-altitude planting experiment replicated at three sites in Scotland investigates the influence of browsing on the extent and condition of mountain woodland. Planting of dwarf birch (*Betula nana*) in three different habitats monitored for up to six consecutive years tested whether this upland tree species may currently be confined to blanket bog because of historical and contemporary overgrazing. At red deer (*Cervus elaphus*) densities managed at 3–6 per km^2, browsing of planted *B. nana* and mortality linked to browsing were much greater in grass and heath vegetation than in blanket bog. In contrast, survival was similar for all three habitats when large herbivores were excluded, while growth outputs were not more productive in blanket bog at any of the three sites, and at one location interannual growth was significantly greater in the grass and heath. Therefore, blanket bog is not more favourable for *B. nana* establishment in Scotland compared to potential alternatives based on distributions elsewhere in northern Europe, and may instead represent a refugium where relict populations escape overgrazing. Our results suggest that active management to reduce deer densities to approximately 3 per km^2 or below is currently pivotal for mountain woodland restoration outside of such refugial sites in Scotland. This research illustrates the value of a “thinking outside the box” approach in applied forest ecology whereby restoration management moves beyond simply reproducing the features of constrained present-day fragments and accounts for land-use legacies while addressing the original causes of habitat loss at scale.

1. Introduction

Anthropogenic pressures and land management can transform the distribution and performance of threatened species and habitats. Knowledge of drivers of change and their interactions with local habitat conditions and species is important in applied ecology for supporting policy and action for ecosystem restoration. For example, plant biogeography and demography are significantly modified by anthropogenic land-use legacies: the persistent impacts of human land-use on ecosystem properties (Vilà-Cabrera et al., 2023). Woody species (e.g. trees and shrubs) have been particularly affected globally by widespread deforestation, harvesting, and intensively managed plantations. Such land-use legacies can substantially alter woodland ecosystem stability, resilience, genetics, functional composition, adaptive potential, and responses to further changes in management and climate (Hereş et al. 2021; Rhoades et al., 2024).

Consequently, the contemporary distribution of trees and shrubs may not be in equilibrium with the environmental conditions they are able to exploit and thrive in (Goring and Williams, 2017; Vilà-Cabrera et al., 2019). This discrepancy has implications for restoration practice, which typically focuses on reestablishing and regenerating ecosystems in landscapes that have been heavily modified and degraded by anthropogenic activity. Fragmented, remnant woodland patches are unlikely to resemble the character and structure of historical, fully functional systems (Faria et al., 2023). Restoration efforts seeking to replicate and expand existing habitat without enough knowledge of

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current and past pressures risk bias towards present-day refugial locations that do not represent the full range of opportunities available (Braunisch et al., 2008). Understanding the management practices that may have created land-use legacies and continue to constrain the distribution of threatened trees and shrubs will foster improved restoration outcomes.

This approach is especially relevant to the recovery of mountain woodlands within the altitudinal treeline; the transition zone between the timberline and the highest elevational limit of individual tree establishment (Dandan et al., 2022). These systems have experienced substantial anthropogenic degradation due to agricultural expansion, fire, infrastructure development, overgrazing, and nutrient loading via atmospheric deposition (Holtmeier, 2009; Bergmeier et al., 2010). Mountain woodland restoration offers potential for a broad array of biodiversity gains and can support specialist high-altitude or arctic-alpine species including range-restricted invertebrates and birds (Watts and Jump, 2022). Robust and resilient treelines also provide nature-based solutions to mitigate climate change impacts including natural hazard protection, sheltering, slope stabilization, and downstream flood reduction (Holtmeier and Broll, 2017; Gu et al., 2019; Monger et al., 2022). However, restoration site selection is difficult when the optimum requirements of scarce high-altitude trees and shrubs are poorly understood (Pogorzelec et al., 2020). Any planting in novel locations must be justified by evidence that such management is appropriate and worthwhile. Otherwise, large-scale action in unsuitable or marginal sites could fail entirely, or create unhealthy populations with negative implications for soil carbon-nutrient dynamics, open ground species, and the spread of pests and pathogens (Watts, 2024).

Scotland has been practicing mountain woodland restoration for over thirty years, following widespread loss often linked 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 hunting (Hester, 1995; Oosthoek, 2013; Bunce et al., 2014; Watts, 2024). Additional pressures have come from pollution, muirburn (the controlled burning of moorland vegetation), and wildfires (Gilbert, 2016). But there is still some uncertainty over the relative importance of natural climatic or human drivers in determining the present extent of Scottish mountain woodlands, and the scope for practitioners to facilitate effective restoration in such landscapes shaped by large herbivore dynamics.

We therefore examined the effects of large herbivore management and overgrazing both as a land-use legacy and ongoing influence on the distribution and condition of mountain woodland by asking the following questions: (i) are remnant populations constrained to a narrower range of habitat than they might occupy? (ii) does overbrowsing restrict high-altitude trees to these refugial habitat niches? and (iii) can restoration outcomes (tree survival and growth) be improved by planting outside the limitations of such refugial habitat?

To investigate these questions, we undertook a high-altitude planting experiment at three sites in Scotland. We assessed growth, survival, and browsing rates over six consecutive years to study montane tree establishment, performance, and restoration outcomes across a range of potentially suitable habitats and contrasting red deer management practices. Our focal species, *Betula nana* L. (dwarf birch), has declined significantly in Britain over recent centuries, with range contraction and fragmentation continuing since the 1990s (Borrell et al., 2018). *Betula nana* provides a useful case study example because it is wide-ranging in northern Europe, but in Scotland is mostly associated with a narrow range of primarily blanket bog habitats (Dickson, 1984; Rodwell, 1998; Stroh et al., 2023). We hypothesise that populations might persist here as a refuge from burning or overgrazing by large herbivores. Upland grassland and dwarf shrub heath habitats may provide wider opportunities for range expansion because these vegetation types are similar to Scandinavian counterparts where the species does occur (Gilbert, 2011). Conducting the experiment at three locations enabled *B. nana* performance to be tested in diverse situations with relevance to restoration across a broad range of habitat conditions and topography currently typical of much of upland Scotland. Our research thus links upland ecology and forest management to provide clear applications to decisions concerning tree planting, deer management, and woodland biodiversity.

2. Methods

2.1. Study species: Betula nana

Betula nana is a monoecious, wind-pollinated deciduous shrub with a circumpolar distribution across the boreo-arctic region of the Northern Hemisphere, and a core range in northern Europe and western Asia (de Groot et al., 1997). Globally, the species is threatened by atmospheric nutrient depositions, changes in hydrology, commercial forest expansion, and climate change (Gostynska-Jakuszewska and Lekavicius, 1989; Schwarz and Poschlod, 2015). *Betula nana* is a component of the transitional shrub zone in mountain woodland between forests and higher-altitude heathlands and also features in exposed sub-arctic tundra, dwarf-shrub dry heaths, and wet, acidic, nutrient-poor montane habitats (Fredskild, 1991; Virtanen et al., 1999). However, *B. nana* is not currently a predominant component of any upland National Vegetation Classification in Britian (Averis et al., 2004). Typical locations for this species throughout Scotland are blanket bogs and mires on flat or gently sloping waterlogged ground where peat occurs at depths greater than 2 m, and up to an altitude of 860 m. However, rare populations are also found on better drained, shallower or gravelly mineral soils amongst scree and rock crevices on steeper ground at a few sites in the Cairngorms National Park (Gilbert, 2011; Stroh et al., 2023). *Betula nana* can grow to over 1.5 m in height, but in Scotland it is generally restricted to below 1 m as a multi-stemmed, prostrate bush. The species is listed as Nationally Scarce in Britain and Critically Endangered in England (Stroh et al., 2023).

2.2. Experimental design

The field experiment was undertaken at three sites across Scotland – Ben Lawers, Corrour, and Glen Finglas (Fig. 1; Table 1). The sites are similar in their general topography and variety of wet and dry upland habitats including grassland, heaths, bogs, and mires. Montane tree planting and large herbivore management is ongoing as part of wider landscape-scale ecosystem recovery at these locations (Watts, 2024). The study sites have had contrasting deer management measures in place, facilitating experimental planting across a gradient of browsing intensity ranging from large herbivore exclusion using fences (all sites), to open hill red deer (*Cervus elaphus*) densities of 3 per km^2 (Corrour) and 6 per km^2 (Glen Finglas). Owing to the distribution of planting habitats and existing infrastructure at each site which is difficult to install in upland environments, fenced planting groups were all contained within one large exclosure at both Ben Lawers and Glen Finglas, while at Corrour the experiment used six small exclosures of approximately 200 m^2. At Ben Lawers there was no unfenced treatment due to the additional presence of sheep (*Ovis aries*) in the surrounding landscape. At Corrour and Glen Finglas planting also occurred in equivalent habitats outside of the exclosures where densities of red deer were consistent during the experiment. The fencing at Glen Finglas was slightly damaged due to age and exposure, and thus did not provide total exclusion of red deer during the experiment. Herbivore densities within this ‘fenced’ treatment at Glen Finglas were consistently lower than the unfenced treatment at that site, but at 3–6 per km^2 were nevertheless higher than the unfenced treatment at Corrour (Table 1), offering the opportunity to include an intermediate level of browsing within the experimental design.

Red deer populations were regularly evaluated during the study period by helicopter and foot counts, and herbivore impact assessment using observations of dunging, trampling, and browsing of surrounding

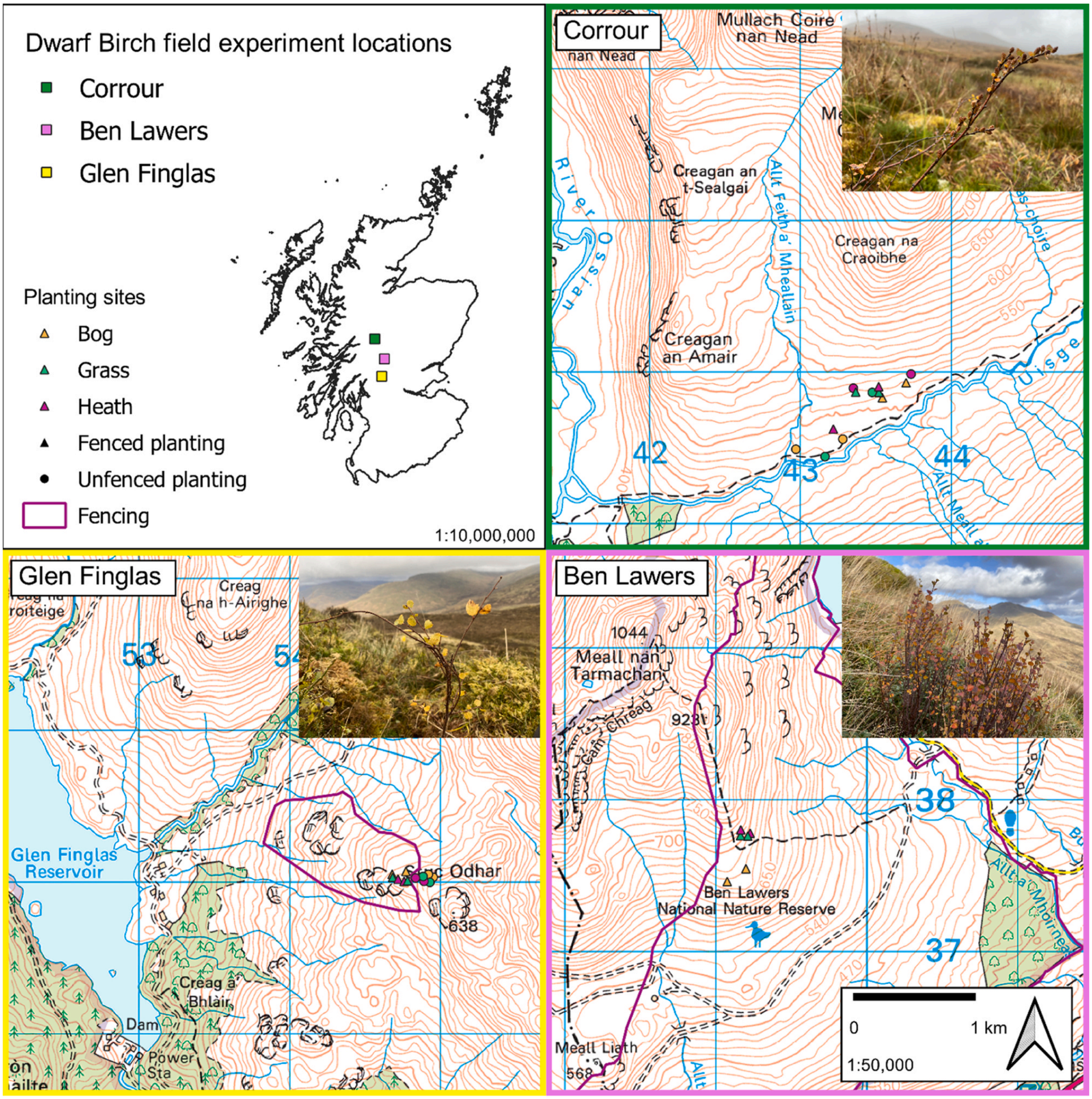

Fig. 1. The location of the *Betula nana* planting experiment sites in Scotland. Fenced planting sites at Corrour were within individual large herbivore exclosures too small to map at this scale. Background Ordnance Survey mapping source from 1:50 000 Scale Colour Raster [TIFF geospatial data], Scale 1:50000, Tiles: nn47, nn50, nn53. Updated: 1 June 2023, Ordnance Survey (GB), Using: EDINA Digimap Ordnance Survey Service, <https://digimap.edina.ac.uk>, Downloaded: 2024–11–18. © Crown copyright and database rights 2024 Ordnance Survey (AC0000851941).

vegetation. The exclosure systems used were not designed to inhibit the movement of small mammals through fences. Some field signs (droppings and vegetation clipping) were observed for field vole (*Microtus agrestis*) and mountain hare (*Lepus timidus*) in the planting habitats at Ben Lawers and Corrour, with field vole signs only at Glen Finglas. No field signs for water vole (*Arvicola amphibius*) were present at any locations used for the experiment.

Across the three trial sites, a total of 750 *B. nana* seedlings were planted in three different habitat types as defined by the National Vegetation Classification (NVC) given in Averis et al. (2004):

- “Bog”: NVC type *Calluna vulgaris* – *Eriophorum vaginatum* blanket mire M19
- “Grass”: NVC type U4 *Festuca ovina-Agrostis capillaris-Galium saxatile* grassland or U5 *Nardus stricta-Galium saxatile* grassland
- “Heath”: NVC type *Calluna vulgaris-Erica cinerea* heath H10 or H18 *Vaccinium myrtillus-Avenella flexuosa* heath

All three habitats have been affected by centuries of upland land management in Scotland, and are thus of semi-natural origin shaped by anthropogenic influence.

Seedlings were of two years in age and local provenance to each site (Table 1), propagated in containers (root trainers) by a commercial tree nursery to the same specification for all three experimental sites. Planting was arranged within two groups of 25 individuals per treatment type, giving a total of 50 replicate trees in each habitat and grazing management treatment combination per site. Planting groups were

Table 1
Attributes of the three *Betula nana* planting experiment sites.

	Ben Lawers	Corrour	Glen Finglas
Location	Perthshire, Central Highlands	Lochaber, Western Highlands	Stirling, The Trossachs
Lat/Long	56.509764 °N, −4.289927 °W	56.802506 °N, −4.565268 °W	56.251402 °N, −4.344937 °W
British National Grid coordinates	259177 737650	243456 770822	254812 709016
Total no. trees planted	150	300	300
Planting date	September 2018	September 2020	October 2021
GB seed zone provenance	202	201	202
Altitude range	675–730 m	480–530 m	525–565 m
Site aspect	south-east	south-west	north-west
Unfenced treatment	None	150 trees with an open hill deer density of c.1–3 per km^2	150 trees with an open hill deer density of c.6 per km^2
Fenced treatment	All 150 planted trees within a large herbivore exclosure erected in 2000	150 planted trees inside six small fenced exclosures (2 per habitat type) built immediately prior to planting in 2020	150 planted trees inside a fence erected in 1998. Incursion of red deer and sheep was frequent during experiment, at a slightly lower deer density than outside the fence (3–6 per km^2)
Habitat NVC treatment types (Averis et al. 2004)	Bog: M19 Grass: U4 Heath: H18	Bog: M19 Grass: U5 Heath: H10	Bog: M19 Grass: U4 Heath: H18
Typical bog species	*Avenella flexuosa*, *Calluna vulgaris*, *Eriophorum vaginatum*, *Vaccinium myrtillus*, *Pleurozium schreberi*, *Sphagnum* spp.	*Calluna vulgaris*, *Erica tetralix* *Eriophorum vaginatum*, *Narthecium ossifragum*, *Pleurozium schreberi*, *Sphagnum* spp.	*Calluna vulgaris*, *Eriophorum angustifolium* *Eriophorum vaginatum*, *Vaccinium myrtillus*, *Pleurozium schreberi*, *Sphagnum* spp.
Typical grass species	*Agrostis* spp., *Avenella flexuosa*, *Festuca ovina/vivipara*, *Galium saxatile*, *Hylocomium splendens*, *Rhytidiadelphus squarrosus*	*Agrostis* spp., *Galium saxatile*, *Molinia caerulea*, *Nardus stricta*, *Hylocomium splendens*, *Rhytidiadelphus squarrosus*	*Agrostis* spp., *Anthoxanthum odoratum*, *Festuca ovina/vivipara*, *Galium saxatile*, *Hylocomium splendens*, *Rhytidiadelphus squarrosus*
Typical heath species	*Avenella flexuosa*, *Galium saxatile*, *Vaccinium myrtillus*, *Hylocomium splendens*, *Polytrichum commune*	*Calluna vulgaris*, *Erica cinerea*, *Molinia caerulea*, *Hypnum jutlandicum*, *Pleurozium schreberi*, *Racomitrium lanuginosum*	*Avenella flexuosa*, *Galium saxatile*, *Vaccinium myrtillus*, *Hylocomium splendens*, *Polytrichum commune*
Landowner	National Trust for Scotland	Private Estate	Woodland Trust
Conservation designations	Planting within National Nature Reserve (NNR), and near to a Site of Special Scientific Interest (SSSI) and Special Area of Conservation (SAC)	None	Loch Lomond and the Trossachs National Park, The Great Trossachs Forest National Nature Reserve (NNR)

positioned in independent habitat patches at least approximately 100 m apart. All trees were labelled with metal tree tags providing a unique identification number loosely tied at the base of the main stem using plastic-coated zinc wire.

Within each of the three study sites, the date of planting, altitude, aspect, and species composition of the habitats was consistent for all planting replications. However, there was some variation between sites (Fig. 1; Table 1). At Corrour, planting in the heath took place in vegetation predominantly featuring *Calluna vulgaris* on thinner soils with more climatic exposure, whereas *Vaccinium myrtillus* was the most common dwarf-shrub in the planted heaths at Ben Lawers and Glen Finglas.

2.3. Field measurements

Baseline measurements of height, leading stem length, crown size, and stem diameter were recorded from each tree immediately after planting (see Table 2 for methods). These measurements were subsequently repeated during annual monitoring in October to coincide with the end of each growing season, with the addition of survival, mode of mortality, browsing, and interannual growth (Table 2; Fig. 2). An interim visit was also made to each site in March to assess survival, mode of mortality, and browsing over the winter. Trees identified as newly dead during each survey were assessed as browsed or not, and then subsequently removed from the dataset. All measurements were taken by a single surveyor thereby creating a dataset free of inter-observer bias. Measurements continued until October 2024, giving six years of data collection at Ben Lawers, four at Corrour, and three at Glen Finglas.

2.4. Data analysis

To investigate variation in growth and thus tree performance between different habitat types and grazing management treatments, four plant size measurements (height, length, crown size, and stem diameter) were combined into a single growth performance measure using Principal Component Analysis (PCA) because they were all highly correlated (Supplement S1). PCA is a commonly used tool for reducing the complexity and dimensionality of multiple variables (Carrer et al., 2007; Dupire et al., 2016; Wang et al., 2022), and has previously been applied to analyse the size montane shrubs (Watts et al., 2025). This approach overcomes challenges with representing size by single measures of plant height or area for species which often have complex canopies of multi-stemmed, lateral growth rather than routinely producing a single upright, leading shoot. PCA axis 1 ("PCA Size") explained 64 % of the variation in growth parameters and comprised values ranging from −3.94 (small trees) to 11.44 (larger trees). For a biological interpretation, a PCA Size value of 0 equates to a height of approximately 40 cm, a length of 55 cm, and a stem diameter of 7 mm.

Table 2
Annual and biannual measurements recorded on all trees during the experiment. *also recorded as baseline measurements immediately after planting.

Measurement	Variable type (unit)	Timing	Protocol
Height*	Numerical (cm)	October	From the ground to the tallest part of the plant *in situ*, discounting leaves
Leading stem length*	Numerical (cm)	October	From the ground to the tallest part of the plant pulled to its maximum length, discounting leaves
Crown size*	Numerical (cm)	October	(a): Measure across shrub canopy at widest point (b): Measure perpendicular across canopy Area calculated as π * (a) * (b)
Stem diameter*	Numerical (mm)	October	Recorded at ground level from main stem
Interannual growth	Numerical (cm)	October	Mean length of three random new unbrowsed shoots from the current growing season
Survival	Binary	October and March	Indicating if a tree had survived the current growth season or not
Browsing	Binary	October and March	Indicating whether a tree was browsed or not during the current growing season, attributed to species as: • red deer: shoots with a ragged cut or stripped bark • mountain hare: leader shoot cut by a clean cut • vole: irregular spaced gnaw marks
Mortality	Categorical	October and March	Mode of mortality classified as either: • severe browsing by red deer: the leader shoot cut down to its base with a ragged cut or stripped bark • uprooting by red deer: the tree and its root plug lying unearthed outside the planting hole with evidence of severe browsing by deer • severe browsing by mountain hare: the leader shoot cut down to its base by a clean cut • severe browsing by voles: the leader shoot cut down to its base by irregular spaced gnaw marks • unknown: tree dead in situ with no signs of severe browsing or other causes

Since grazing management and other attributes were not directly comparable between sites, the following analyses were run separately for each site. Variation in survival between different planting habitats and grazing managements over time was tested using a repeated measures binary logistic regression Generalized Linear Mixed-effects Model (GLMM). Red deer browsing occurrence where these large herbivores were present (unfenced situations at Corrour, and both unfenced and fenced at Glen Finglas) was also tested using a repeated measures binary logistic regression GLMM. Interannual growth was square-root transformed to ensure a normal distribution. Variation in PCA Size, height, stem diameter, and square-root transformed interannual growth was tested using repeated measures Linear Mixed-effects Models (LMM).

We used a model selection and simplification process whereby variables were dropped if they did not significantly improve model fit. All six models (survival, deer browsing, interannual growth, PCA Size, height, and stem diameter) were run using the predictor variables of year since planting, habitat type, grazing management, and their interactions, with the baseline size (i.e. the size of each plant at the time of its planting in Year 0) included as a model covariate to account for initial size differences between individuals. Baseline size was represented by initial PCA Size in all models apart from those of height and stem diameter, in which each of those respective baseline initial measurements were used. The models also incorporated the random intercepts of individual Tree ID nested within Planting Group. Using likelihood tests, these full models were compared to reduced models in which non-significant interactions were removed. Interactions and covariates were only retained during this model selection process if they significantly improved model fit. Therefore, the covariant of baseline size was kept in the final models of PCA Size, height, and stem diameter. Model assumptions of normality, linearity, and homogeneity were tested using a Residuals vs fitted plot, Normal Q-Q plot, Scale-location plot, and Cook's distance. Analyses were performed using R Statistical Software v4.1.2 (R Core Team, 2021).

3. Results

3.1. Survival and browsing damage

Within the fence at Ben Lawers, *B. nana* survival remained similarly high in all three habitats, even after six years since planting (Fig. 3; Table 3). Damage by small mammals (field vole and mountain hare) resulted in the mortality of 4 % of Ben Lawers plants in both the bog and heath, and 10 % in the grass. An additional 13 % and 6 % of plants in the bog and grass habitats respectively died due to an unknown mode of mortality not attributed to herbivory.

Four years after planting at Corrour, survival was still at least 88 % for all treatments (remaining at 100 % for fenced bog and grass), except for the unfenced heath which dropped to 52 % (Fig. 3). Survival was significantly lower outside the fences and in the heath (Table 3). All mortality at Corrour was caused by heavy browsing and uprooting by red deer, apart from one plant in each of the three habitat types which all died of unknown causes, while no mortality was attributed to small mammal damage. Outside the fence at Corrour, the percentage of trees that were browsed by red deer was significantly greater in the grass and heath compared to the bog (Table 3, Fig. 4). Throughout the four years of the experiment the deer browsing rate of trees varied between 20 % and 43 % in heath, peaked at 45 % in the grass, and varied between 2 % and 12 % in the bog (Fig. 4).

Planted *B. nana* at Glen Finglas experienced substantially more mortality than the other two study sites, most notably in the unfenced grass which had fallen to just 2 % survival after one year, with only a single tree out of 50 remaining (Fig. 3). Survival was lower outside the fence than inside it (where there was some incursion by red deer and sheep), and significantly higher in the bog compared to heath or grass. There was also a negative interaction between treatments with survival being even lower in unfenced grass and unfenced heath (Table 3). All mortality both inside and outside the fence at Glen Finglas was due to heavy browsing and uprooting by large herbivores, and no mortality or browsing was associated with small mammal damage.

The deer browsing rate at Glen Finglas was also significantly greater on trees in the grass and heath habitats compared to the bog, and there was an interaction between fencing and habitat treatments in the browsing model; analogous to the results for mortality (Table 3). Outside the fence 100 % of all trees planted in the grass were browsed, and browsing on those in the heath varied between 30 % and 72 % throughout the experiment (Fig. 4). Deer browsing rates were similar for trees in the heath and grass inside the fence where there was frequent incursion by red deer, while in the bog, browsing was low in years two and three of the experiment (varying between 6 % and 10 %), after a peak of 65 % in the first year.

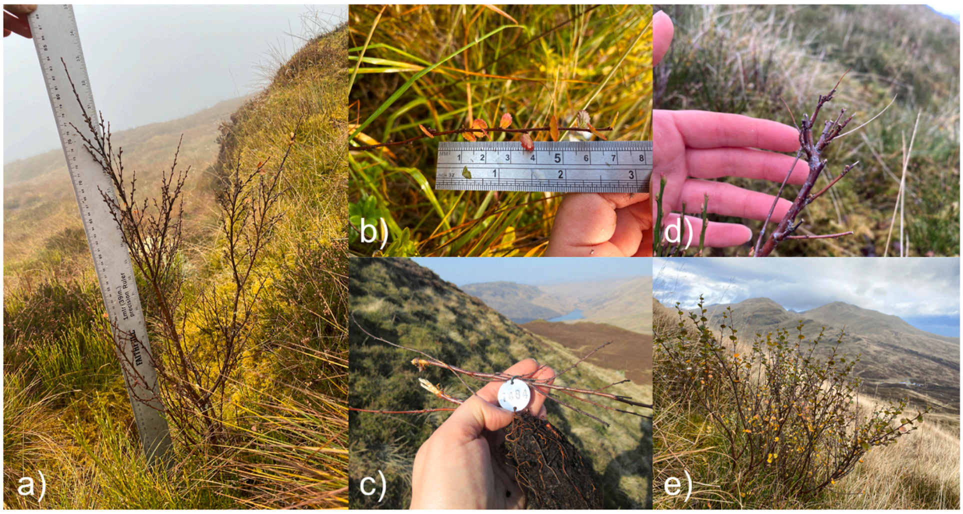

Fig. 2. Photos of *Betula nana* measurements in the field: a) height b) interannual growth c) tagged tree uprooted by severe large herbivore browsing d) browsing damage by red deer e) healthy tree at Ben Lawers six years after planting.

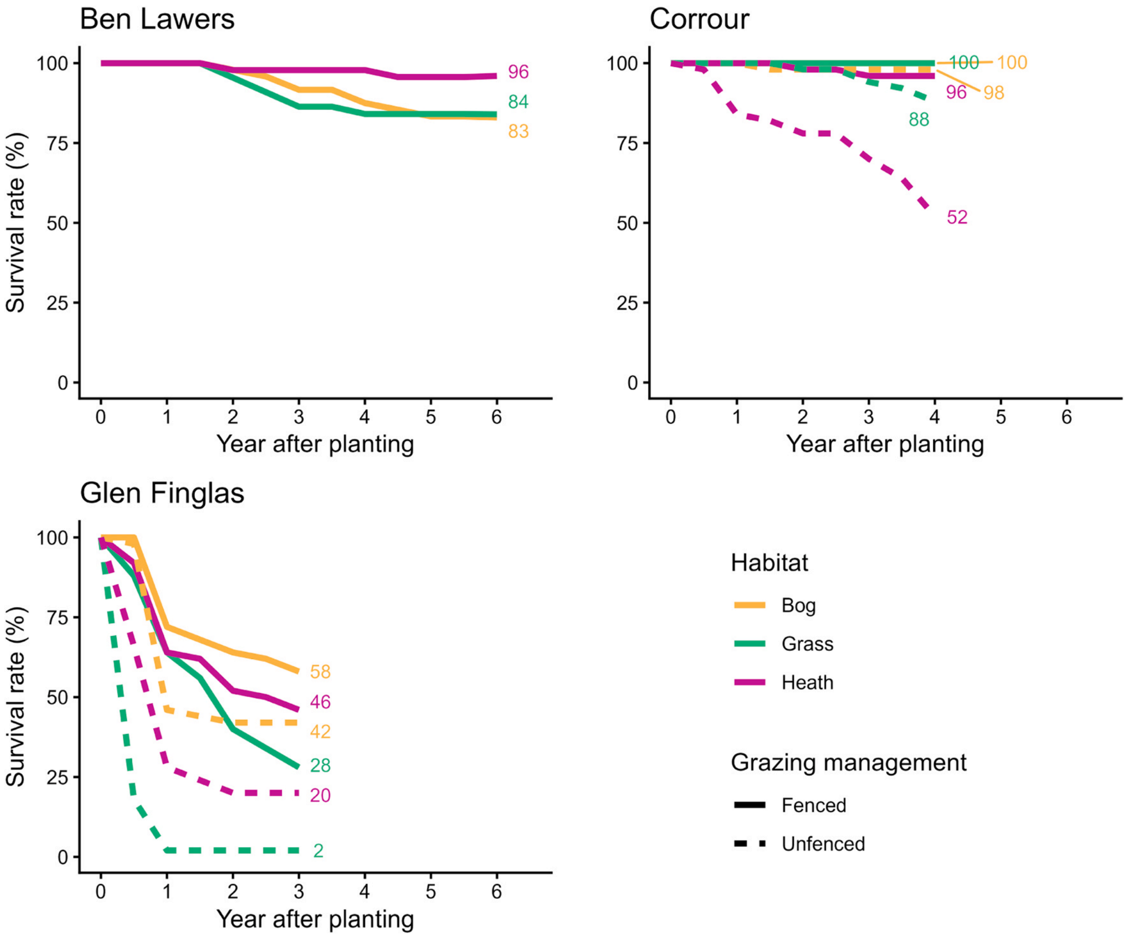

Fig. 3. Survival rates over time of *Betula nana* planted at three sites in contrasting habitat types, and inside and outside fences. Planting dates: 2018 for Ben Lawers, 2020 for Corrour, and 2021 for Glen Finglas. $n = 50$ per treatment per site. Coloured text gives the final survival rates of the experiment.

3.2. *Interannual growth and plant size*

At both Ben Lawers and Glen Finglas, interannual growth increased over time (Table 3). While there was no variation in inter-annual growth increments between habitats at Ben Lawers, interannual growth at Glen Finglas was significantly greater on trees in the grass and heath than in the bog (Fig. 5; Table 3). At Corrour, interannual growth decreased over time in all habitat types and was significantly lower in the bog compared with the grass from 2 years after planting onwards.

PCA Size increased over time at Ben Lawers, particularly from 4 years after planting (Fig. 6), and did not differ between habitats at both Ben Lawers and Glen Finglas (Table 3). At Corrour, PCA Size decreased

Table 3
Regression model coefficients for analyses of *Betula nana* data collected across the duration of the planting experiment at three study sites in three different planting habitats (bog, grass, and heath) and two grazing management treatments (fenced and unfenced, although all trees at Ben Lawers were fenced). Survival: a GLMM repeated measures binary logistic regression. Deer browsing: a GLMM repeated measures binary logistic regression testing the effects of deer densities outside fences at Corrour (1–3 per km^2) and Glen Finglas (6 per km^2), as well as inside the fence at Glen Finglas where incursion by deer was frequent (3–6 per km^2). IA growth: repeated measures linear regression (LMM) of square-root transformed interannual growth. PCA Size: repeated measures linear regression (LMM) of PCA Size (a combined variable of plant height, length, crown size, and stem diameter, derived from Principal Component Analysis). The covariant baseline PCA Size is the size of each individual plant at the time of planting. The models included the random intercepts of Tree ID nested with Planting Group, and interactions were retained only if they significantly improved model fit. Numbers in brackets are standard errors. P-value significance levels: *< 0.05; **< 0.01; ***< 0.001.

Coefficient	Survival: Ben Lawers	Survival: Corrour	Survival: Glen Finglas	Deer browsing: Corrour	Deer browsing: Glen Finglas	IA growth: Ben Lawers	IA growth: Corrour	IA growth: Glen Finglas	PCA Size: Ben Lawers	PCA Size: Corrour	PCA Size: Glen Finglas
Year	**-0.51***** (0.07)	**-0.72***** (0.10)	**-0.80***** (0.07)	0.02 (0.08)	-0.07 (0.09)	**0.18***** (0.01)	**-0.21***** (0.01)	**0.10*** (0.04)	**0.97***** (0.02)	**-0.36***** (0.02)	**0.08*** (0.03)
Baseline PCA Size									**0.52*** (0.20)	**0.61***** (0.06)	**0.67***** (0.12)
Habitat Grass	2.77 (2.31)	-0.99 (0.68)	**-0.90***** (0.21)	**1.28*** (0.62)	**1.94***** (0.25)	0.16 (0.24)	**0.24*** (0.07)	**0.42*** (0.17)	-0.25 (0.48)	**0.78*** (0.21)	0.18 (0.30)
Habitat Heath	-0.46 (2.29)	**-3.45***** (0.67)	**-0.48*** (0.22)	**2.29***** (0.62)	**1.71***** (0.25)	0.19 (0.24)	-0.11 (0.07)	**0.64**** (0.14)	-0.14 (0.47)	-0.42 (0.22)	0.02 (0.25)
Grazing Unfenced	N/A	**-3.30***** (0.68)	**-0.90***** (0.22)	N/A	**0.91***** (0.26)	N/A	0.08 (0.06)	0.30 (0.14)	N/A	-0.05 (0.21)	0.46 (0.24)
Habitat Grass: Grazing Unfenced			**-2.43***** (0.40)		**0.83*** (0.47)					-0.48 (0.30)	
Habitat Heath: Grazing Unfenced			**-0.59*** (0.31)		-0.55 (0.35)					0.07 (0.30)	
Marginal R^2	0.22	0.61	0.42	0.15	0.23	0.18	0.18	0.17	0.57	0.38	0.22
Conditional R^2	0.74	0.63	0.42	0.43	0.23	0.51	0.37	0.39	0.77	0.59	0.63

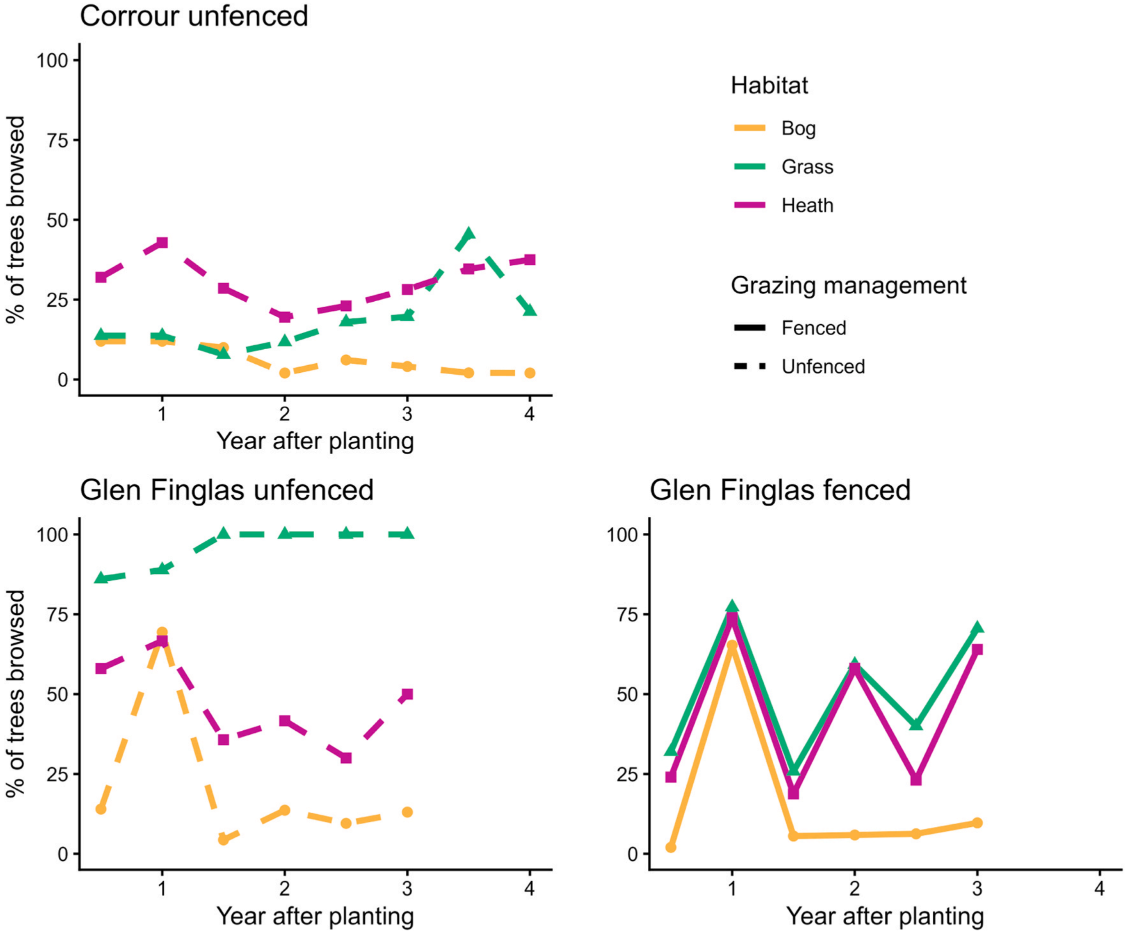

Fig. 4. The percentage of planted *Betula nana* trees browsed by red deer in contrasting habitat types outside fences at Corrour (deer density: 1–3 per km^2) and Glen Finglas (deer density: 6 per km^2), as well as inside the fence at Glen Finglas where incursion by large herbivores was frequent (deer density: 3–6 per km^2). Planting dates: 2020 for Corrour and 2021 for Glen Finglas. $n = 50$ per treatment per site.

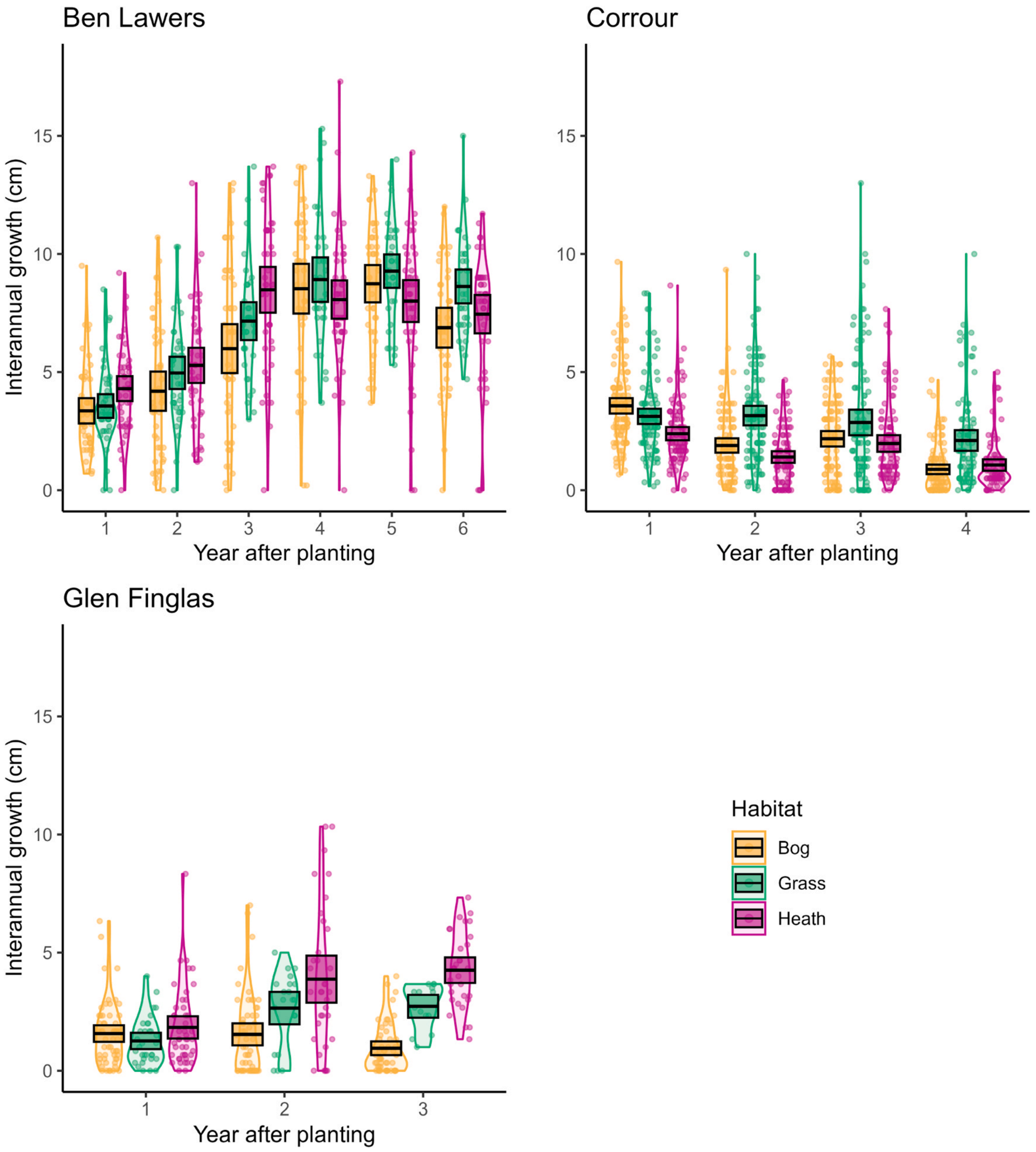

Fig. 5. Pirate plot of interannual growth over time of the *Betula nana* planted at three sites in contrasting habitat types. Data are combined for plantings inside and outside fences because this treatment had no significant effect on interannual growth. The solid bar shows the mean, the box indicates 95 % Confidence Intervals, and the "bean" and scattered points provide the distribution of the raw data. Planting dates: 2018 for Ben Lawers, 2020 for Corrour, and 2021 for Glen Finglas. $n = 50$ per treatment per site.

slightly over time, and was significantly greater in the grass compared to the bog in years 3 and 4 after planting. Baseline size at time of planting had a significantly positive effect on plant size throughout the duration of the experiment at all three sites. These results for PCA Size correspond with those for height, while stem diameter also had comparable trends, except for the results at Corrour which showed an increase in stem diameter over time and no difference between habitat treatments (Supplement S2).

4. Discussion

Using a field experiment at three upland sites in Scotland, we show that there are important interactions between habitat type (grass, bog, and heath) and levels of browsing by large herbivores that influence survival and growth of *Betula nana*. Where red deer densities are c.3–6 per km^2, browsing of planted *B. nana* and mortality linked to this browsing was much greater in grass and heath habitats than in blanket bog. In particular, the high mortality across the experiment at Glen Finglas (which had the greatest red deer density of the three study sites) was explained by higher browsing rates. Where large herbivores were excluded, tree survival rates were similar in all three habitats, highlighting the browsing habitat preferences of red deer. Nevertheless, trees planted in blanket bog did not exhibit greater growth rates or plant size at any of the three sites. In fact, interannual growth was significantly greater for the trees in the grass habitat than in the bog at two of the three study sites (Corrour and Glen Finglas), and was also greater in the heath than in the bog at Glen Finglas. Thus, the outcome of planting *B. nana* in blanket bog was only more successful in comparison to the grass or heath when these two habitats experienced greater mortality due to overbrowsing by large herbivores.

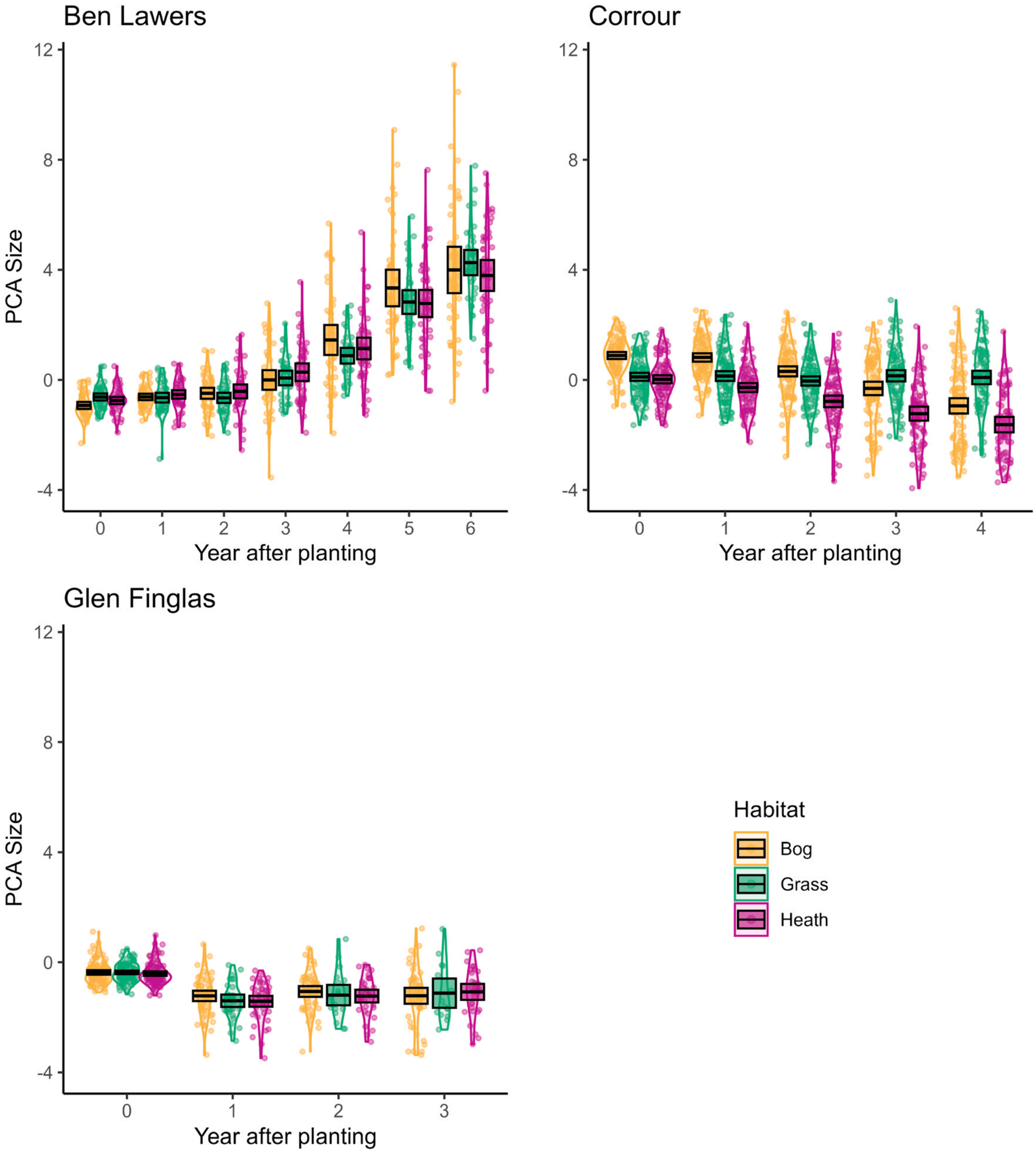

Fig. 6. Pirate plot of the overall size of *Betula nana* planted at three sites in contrasting habitat types. PCA Size = a combined variable of plant height, length, crown size, and stem diameter, derived from Principal Component Analysis. Data are combined for plantings inside and outside fences because this treatment had no significant effect on PCA Size. The solid bar shows the mean, the box indicates 95 % Confidence Intervals, and the "bean" and scattered points provide the distribution of the raw data. Planting dates: 2018 for Ben Lawers, 2020 for Corrour, and 2021 for Glen Finglas. $n = 50$ per treatment per site.

4.1. *A constrained habitat range*

We sought to determine if remnant populations of montane trees are restricted to a narrower range of habitats than they might optimally occupy. Wang et al. (2014) used pollen analysis to show that *B. nana* was formerly widespread in Scotland, with a larger and more southerly distribution. While those authors found that Holocene climate warming and genetic introgression with *B. pubescens* influenced these historical declines, their ecological niche modelling also suggested that the Scottish range of *B. nana* is currently far more limited than the area it might potentially occur in. Our results provide evidence that the present-day primary habitat of *B. nana* in Scotland (blanket bog) is not more favourable for establishment and growth of the species, in comparison to potential alternatives (grasslands and heathlands) based on the distribution of this montane boreo-arctic shrub elsewhere in northern Europe.

Correspondingly, research on *B. nana* in bogs and mires in central Europe and Finland demonstrated that raised water tables decreased vegetative growth, reproduction, and survival, while drainage facilitated an increase in cover (Jukaine et al., 1995; Ejankowski, 2008; Ejankowski, 2010). Other arctic-alpine shrub species are also likely to be persisting in sub-optimal locations which do not reflect the character or productivity of more widespread altitudinal treeline zones in the past (Watts et al., 2025). For example, montane willows in Scotland currently occur in very small fragments on inaccessible cliffs and ravines, while refugia populations in Poland and the Czech Republic grow in bogs, fens, and mires (Pogorzelec, 2010; Watts, 2024). These findings indicate that relict populations of montane trees which were formerly more extensive are enduring in marginal habitat more constrained than the full range of conditions that might support them.

4.2. Overgrazing as a land-use legacy and ongoing pressure

Our results demonstrate that blanket bog does provide *B. nana* a refuge from overgrazing, compared to grass and heath habitats where the trees were more prone to mortality linked to browsing by red deer. This outcome could have contributed to the declining and currently restricted distribution of the species in Scotland due to historical legacies and ongoing land management for high densities of large herbivores. In general, high ungulate density has significant effects on browsing intensity, forage selection, sapling height, and recruitment, and may thus alter tree species composition (Ramirez et al., 2018; Borowski et al., 2021; Candaele et al., 2023). At greater elevations, palatable mountain tree seedlings are more likely to be browsed due to low primary productivity and forage availability (Bernard et al., 2024). Upland tree species are also particularly susceptible to damage at high-altitude due to their slow-growth rates and lack of tall stems to reach above browse height (Watts, 2024). Additionally, waterlogged habitats such as bogs could be less favourable for large herbivores to forage in compared to better drained slopes of grass and heath vegetation where *B. nana* will grow well if not inhibited by overbrowsing. However, blanket bogs are not entirely immune to herbivore impacts, being vulnerable to trampling contributing to erosion and peatland degradation (Watts, 2020).

Scottish mountain woodlands are often compared to those of southwest Norway, owing to similar climates and land use histories until the late nineteenth century when reductions in grazing pressures due to land-use abandonment facilitated a recovery of Scandinavian montane scrub (Bryn, 2008; Halley, 2017). Here, an extensive, complex mountain woodland mosaic has reformed commonly featuring integrated *Salix* and *Betula* species. A close relationship between treeline re-growth and the decline in alpine farming (including grazing livestock in woodland pastures) has also been identified in the European Alps (Gehrig-Fasel et al., 2007; Garbarino et al., 2013).

In contrast, Scotland has one of the highest densities of red deer in Europe (Burbaitė and Csányi, 2010). Numbers have doubled since the 1990s, aligning with a recent range contraction of *B. nana* (Borrell et al., 2018). Red deer densities are currently sitting at an average of approximately 10 per km^2 across the Highlands, but more locally ranging widely from below 1 to over 64 per km^2 (Albon et al., 2019). These national figures are too high for widespread restoration of mountain woodland to occur, since the *B. nana* planted in our experiment struggled to thrive even at 6 per km^2.

Further potential causes of mountain woodland contraction and loss involve frequent moorland burning, hybridisation, genetic introgression, and climate change (Gilbert and Di Cosmo, 2003; Wang et al., 2014; Zohren et al., 2016). Other factors that can influence upland tree growth, survival, and establishment not measured in our study include snow cover, soil depth and nutrient content, small mammal herbivory, ectomycorrhizal fungi, and pathogens (Heroldová et al. 2012; Martius et al., 2024; Haupt et al., 2025; Watts et al., 2025). Patterns in browsing intensity may also be affected by surrounding vegetation height and cover, variation in tree height, the broader red deer habitat structure, and foraging behaviour (Borowski et al., 2021; Schwegmann et al., 2023; Cacciatori et al., 2025). In our research, there could have been potential confounding effects arising from plantings occurring in different years and variability in experimental design between sites. Since the analyses were performed separately for each site, our study locations are thus not true statistical replicates.

4.3. Improving mountain woodland restoration outcomes: planting, deer management, and regeneration

For *B. nana*, environmental niche modelling predicts that declining trends will continue and become increasingly severe without management interventions such as transplanting and assisted gene flow (Borrell et al., 2018, 2019). Without the pressure of overbrowsing, our experiment demonstrates that *B. nana* could be planted into upland grasslands and heaths to improve and expand this mountain woodland species outside the limitations of blanket bog. Such action incorporates vegetation communities analogous to those elsewhere in the European range of *B. nana*, thereby increasing the distribution of potential opportunities as well as the complexity and productivity of restored habitat. However, any planting into novel habitats beyond those specifically explored in our experiment should be closely monitored with trials before wider implementation is adopted, to avoid high tree mortality and negative impacts on sensitive montane vegetation and soils (Watts, 2024).

Accounting for land-use legacies and the influence of large herbivores will enhance both the quality and quantity of mountain woodland and embed vital habitat connectivity through planting targeted areas, especially where local seed sources are no longer present. Therefore, efforts to reestablish altitudinal treeline mosaics must be underpinned by action to address the original causes of loss. Our results show that active management to reduce deer densities to approximately 3 per km^2 or below is currently pivotal for mountain woodland establishment outside of refugial sites in Scotland, although herbivore impact is ultimately a more important measure of outcomes than animal numbers alone (Putman et al., 2011).

This broad recommendation is in line with other studies across the country on upland tree regeneration, survival, and growth for a range of species which are affected by deer population density and browsing pressure in both woodland and more open ecosystems. Scott (2001) recorded a reduction in browsing, and concurrent increase in both stem density and annual growth of *B. nana* inside a Caledonian Pinewood (*Pinus sylvestris* forest) after the red deer density was lowered to 3–4 per km^2. Red deer reduction to below 3 per km^2 has also promoted the density and height of *Betula pubescens* and *Pinus sylvestris* both within forest and in open habitats in the Cairngorm mountains (Rao, 2017; Painting and Rao, 2020; Gullett et al., 2023), while corresponding results have been determined by simulation modelling of open hill regeneration of *Betula pubescens* in the central Highlands (Tanentzap et al., 2013). Furthermore, deer densities of below 3 per km^2 have been key to facilitating high survival rates (exceeding 98 %) of arctic-alpine *Salix* spp. planted without fencing at various sites in the Scottish Highlands (Watts, 2024).

Our experiment also highlights the long-term challenges of using fences to control grazing. Incursion of sheep and deer within the Glen Finglas exclosure caused greater browsing and mortality rates than on the open hill at Corrour where deer are managed for a low density across the whole estate. In addition, fences are costly, difficult to install and maintain in high-altitude locations, can limit ground disturbance, restrict human access, and negatively impact some bird species (Summers, 1998; Tanentzap et al., 2013). Mountain woodland restoration should thus progress outside of relatively small, disconnected projects contained within exclosures, towards action at the landscape scale aiming for a synergy between sustainable large herbivore populations and native woodland recovery without reliance on the use of fencing. This vision can be achieved by collaborative deer management across multiple adjoining landholdings (Gullett et al., 2023). Furthermore, robust natural regeneration of *B. nana* is now beginning to occur in heathland (Fig. 7) as a consequence of widespread reductions in herbivore impact in the Cairngorms (Painting and Rao, 2024). Together with the results of our study, this outcome demonstrates opportunities for ecological restoration across much more of upland Scotland through reestablishment of an open assemblage of montane trees and dwarf-shrubs by planting or regeneration, depending on the availability of local seed sources.

4.4. Broader implications and conclusions

A key objective of mountain woodland restoration should be the revival of naturalistic, transitional heterogeneous vegetation which

Fig. 7. Natural regeneration of robust *Betula nana* taller than 1.5 m in heathland at Mar Lodge Estate, Cairngorms, in response to a landscape-scale reduction in large herbivores.

incorporates a mix of tree and shrubs (e.g. *Salix*, *Juniperus*, *Pinus,* and *Betula* spp.) with open ground habitats including heathlands and grasslands (Watts, 2024). However, these mosaics do not fit discrete, conventional habitat types accounted for in the National Vegetation Classification for Britain (Rodwell, 1998; Averis et al., 2004). Such definitions of plant groups often encompass communities that have been shaped by landscape history and land-use, and can even omit near extinct assemblages such as those principally featuring mountain *Betula* species. Rigid homogenous categorisations should not represent instructions or precise prescriptions for environmental management that are static in time, especially during an era of accelerating global change (Hearn et al., 2011). Restoration seeking primarily to reinstate pre-existing, historical biotic integrity in terms of species composition and structure (Cowie et al., 2018) prioritises delineated human expectations over ecological complexity, variability, function, and legacies (Higgs et al., 2018; Rohwer and Marris, 2021). Rather than being firmly guided by circumstances rooted in the present-day, decision-making aimed at long-term resilience should balance the consequences of past and future pressures together with an evolving scientific understanding and appreciation of ecosystem dynamics. This reasoning also challenges an over-reliance on conservation designations and protected areas which safeguard the status-quo, negating a more holistic and landscape-level outlook in environmental policy (Selman, 2009).

While anthropogenic pressures may continue to place limits on local population expansion, extensive suitable areas with opportunities for reestablishment can exist outside the currently restricted range of vulnerable species (Kont et al., 2023; Watts et al., 2025). Effective interventions emerge from an awareness of intrinsic nature recovery potential that enhances ecosystem health, sustainability, and adaptive capacity for the future through flexibility (Higgs et al., 2018; Chazdon et al., 2024; Dudney et al., 2024). Restoration should aim to surpass the constraints of sub-optimal refugia, physical barriers such as fencing, and static classifications of anthropogenically modified vegetation. Therefore, this study demonstrates the value and application of a “thinking outside the box” approach that moves beyond simply replicating the features of contemporary habitat fragments and accounts for historical land-use legacies.

CRediT authorship contribution statement

Sarah Watts: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Visualization, Writing – original draft, Writing – review and editing. **Andrew Warwick:** Conceptualization, Investigation, Methodology, Writing – review and editing. **Kirsty Park:** Supervision, Writing – review and editing. **Nadia Barsoum:** Supervision, Writing – review and editing. **Alistair Jump:** Methodology, Funding acquisition, Supervision, Writing – review and editing.

Declaration of Competing Interest

The authors declare no conflict of interest to declare.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.123430.

Data availability

Data will be made available on request.

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