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REVIEW ARTICLE

Montane willow scrub restoration in Scotland: reviewing 30 years of progress to reestablish the altitudinal treeline

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Many mountain woodlands across the globe have undergone anthropogenic degradation with negative implications for the ecological and socioeconomic systems dependent on them. Montane willows are arctic-alpine species of high nature conservation concern within the altitudinal treeline. Scotland has been pioneering the restoration of montane willow scrub for three decades following widespread loss linked particularly to overgrazing by sheep and deer since the eighteenth century. In the 1990s, the total area of montane willows throughout the country was less than 10 ha, with most remaining populations highly fragmented, in rapid decline, and restricted to inaccessible cliffs. Subsequently, montane willow scrub restoration has been part of an overall 2659 ha area managed for the recovery of mountain woodlands in Scotland. By May 2023, 396,868 montane willows were planted in projects encompassing large-scale habitat creation, relict population reinforcement by genetic rescue, fencing, and landscape-scale management for low-density deer populations. This review summarizes restoration methods and outcomes with case study examples to promote conservation evidence and research on plant growth and survival, planting sites, associated biodiversity, molecular ecology, genomics, and long-term population sustainability. With the potential for montane scrub restoration to be widely expanded, improved connectivity to revive a treeline mosaic shaped by regeneration will tackle biodiversity loss and help mitigate climate change impacts on a national scale. However, caution must be applied to creating definitions of distinct habitats for restoration that are based on non-natural or ecologically degraded systems. These experiences are particularly relevant to montane and circumpolar regions with strongly modified landscape histories.

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

Implications for Practice

- Scotland has demonstrated significant capacity for severely degraded and critically endangered high-altitude vegetation to flourish under conservation management.
- Treeline reestablishment must be underpinned by long-term management for low-density large herbivore populations to reduce the risk of overgrazing.
- Restoration should aim to facilitate self-sustaining montane willow populations by natural regeneration, and optimize their genetic diversity.
- Further action will require reliable, repeatable long-term monitoring, opportunity mapping on a national scale to identify priority locations for restoration, landscape-scale collaboration, investment in rural jobs, and increasing the propagation of rare species.
- Restoration should move beyond simply magnifying the extent of remaining impoverished fragments, with montane willows becoming a common element integrated into a wider, biodiverse mountain woodland mosaic featuring other tree and shrub species.

Introduction

High-altitude areas can contain significant habitat heterogeneity and be disproportionately important for biodiversity (Greenwood & Jump 2014). The natural altitudinal treeline ecotone is a biological transition zone between closed-canopy forests and open vegetation, with a highly variable structure and overlapping distribution of many species (Dandan et al. 2022). However, mountain woodlands globally are vulnerable to perturbation (Holtmeier & Broll 2005; Wielgolaski et al. 2017) and

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often subject to considerable anthropogenic degradation and contraction, particularly during the last few hundred years. Driving factors include overgrazing by large herbivores, agricultural expansion, fire, outbreaks of pests and pathogens, infrastructure development, and nutrient loading via atmospheric deposition (Holtmeier 2009; Verheyen et al. 2009). Mountain woodlands are now fragmented and depleted in many areas, with negative repercussions for the ecosystem functions they once performed and thus the ecological and socioeconomic systems that depend on them.

Habitat restoration involving woody species is critical for tackling the dual biodiversity and climate crises (Chazdon & Brancalion 2019; Löf et al. 2019). The altitudinal treeline supports specialized communities of upland invertebrates, birds, mammals, fungi, and plants (Liston et al. 2012; Klaus et al. 2020; Warner et al. 2021). Mountain woodlands also provide a broad suite of benefits to people and wildlife, encompassing natural hazard protection, sheltering, slope stabilization, and reducing downstream flooding (Holtmeier & Broll 2017; Gu et al. 2019; Monger et al. 2022). These nature-based solutions are urgently needed to mitigate threats from escalating climate change, including soil erosion, warming temperatures, and extreme weather (Watts & Jump 2022).

Reporting management actions for ecological restoration is essential to meet targets and advance progress. Developing an accessible knowledge base of project outputs allows practitioners and policymakers to prioritize efforts that will deliver long-term gains. Yet, national syntheses on the restoration of mountain woodlands are lacking, even for those featuring species of high nature conservation concern. A notable example is montane scrub, which contains arctic-alpine willows (*Salix* spp.) listed on global World Conservation Union Red Lists (Schnittler & Günther 1999; Cheffings et al. 2005; Orsenigo et al. 2021).

In Europe, endangered sub-arctic willows are being reintroduced in Poland (Pogorzelec et al. 2020, 2022), informed by studies of their ecology and population structure across Eastern countries (Pogorzelec 2010; Serafin et al. 2015; Hroneš et al. 2018). Scotland has been pioneering montane willow restoration for over three decades, following extensive treeline eradication principally due to overgrazing by large herbivores since the eighteenth century. Ongoing interventions across this country demonstrate significant capacity for severely degraded vegetation to reestablish and flourish under conservation management.

The status of "montane willow scrub" as a habitat in Scotland was first reviewed by Mardon (1990) and Hester (1995), followed by initial restoration outlined by Gilbert and Di Cosmo (2003). Thereafter, the scale and breadth of activity expanded substantially, with a concurrent improvement in practitioner expertise and evidence-based knowledge. This review provides the first national assessment of montane scrub restoration toward returning highly restricted vegetation to more widespread distribution. Summaries of past and current threats, tree planting data, restoration techniques, and project outcomes enable discussion of the management and research required to reinstate a more contiguous altitudinal treeline mosaic. This material should promote further action to tackle the nature and climate emergency at scale, not only across Scotland but also in other geographical regions with potential for scrub communities to be regenerated in formerly degraded mountain systems.

Definition of Montane Scrub: Global Context

Montane scrub occurs at the upper altitudinal boundary of tree growth within the treeline; the transition zone (ecotone) between the timberline (below which trees can grow upright) and the tree species line (the highest elevational limit of individual tree establishment) (Dandan et al. 2022). The vegetation produces a mosaic of increasing stand fragmentation and stuntedness between continuous cover woodland and higher altitude alpine plant communities such as grasslands and heaths (Holtmeier 2009). Here, trees and shrubs are characteristically low-growing (<2 m tall), twisted, decurrent and multi-branched; a form often described using the German word "*Krummholz*." Woody growth is limited by low temperatures, strong winds, prolonged snow cover, and desiccation.

Temperate and northern montane scrub is commonly composed of various *Alnus*, *Betula*, *Juniperus*, *Pinus*, *Salix*, and *Sorbus* species, while analogous vegetation in the southern hemisphere and tropics features *Eucalyptus*, *Nothofagus*, *Pinus*, *Podocarpus*, *Polylepis*, and *Rhododendron* species (Holtmeier 2009; Hroneš et al. 2018; Ruiz et al. 2023). "Montane willow scrub" is listed as sub-arctic *Salix* spp. scrub in Annex 1 of the European Habitats Directive (H4080) and restricted in the European Atlantic Biogeographical Region to sub-arctic and boreo-alpine formations in the Alps, Pyrenees, Cantabrian Mountains, Carpathians, Iceland, and Scandinavia (European Commission 2013). In 2017, this habitat was present in only 881 10 × 10 km grid squares across the European Union, particularly in Sweden (300 10 × 10 km grid squares), and considered in favorable condition only in the Boreal region (Evans 2017).

Montane Willow Scrub in Scotland

Montane willows form the highest altitude zone of shrubby vegetation on Scottish mountains (Pakeman & Torvell 2008), typically at altitudes of 600–900 m, but down to 150 m in country's far North-West. Their precise altitudinal range varies in relation to latitude, topography, slope aspect, and oceanicity; generally occurring higher uphill in the more continental, drier climate of the Cairngorms (a mountain range in East Scotland).

There are seven key species (Table 1), including five specialist arctic-alpine willows: *Salix lanata*, *S. myrsinites*, *S. lapponum*, *S. arbuscula*, and *S. reticulata*, and two sub-montane willows more common at lower altitudes (*S. myrsinifolia* and *S. phylicifolia*). Other nationally frequent willows (*S. aurita*, *S. cinerea*, *S. caprea*, and *S. repens*) can also feature at high altitudes (Watts 2023a).

Montane willows produce a low canopy on a variety of upland soil types arising from acidic to highly base-rich geology, particularly over Moine or Dalradian schist. *Salix lapponum* is the most widely distributed of the arctic-alpine species, whereas the more calcareous-demanding *S. lanata* is far rarer and localized. Associated plants in Scotland presently include the dwarf shrubs *Calluna vulgaris* and *Vaccinium* spp.,

Table 1. Montane willow species in Scotland. World Conservation Union conservation status in Great Britain derived from Cheffings et al. (2005) and Botanical Society of Britain and Ireland (2021). Nationally Rare = occurring in 15 or fewer 10 × 10 km National Grid Ordnance Survey squares within Britain and Ireland; Nationally Scarce = occurring in 16–100 10 × 10 km National Grid Ordnance Survey squares within Britain and Ireland. 10 × 10 km OS (Ordnance Survey) grid squares = the number of 10 × 10 km Ordnance Survey grid squares in Scotland that each species has been recorded in post-1950, calculated using data by Watts (2023c). *for records above 400 m only. Sources for altitudinal data, growth form, and habitat requirement are: Montane Scrub Action Group (2016), Pearman and Corner (2022), Stroh et al. (2023), and Watts (2023a). European biogeography as listed in Stroh et al. (2023) according to the classification in Preston and Hill (1997). The arctic-alpine willow *Salix herbacea* grows as a prostrate mat on exposed mountain tops but is more typically a constituent of montane dwarf-shrub heath.

Species	*Common name*	*Conservation status in Great Britain*	*10 × 10 km OS grid squares containing relict populations*	*Altitude range (m)*	*Growth form*	*Current habitat*	*European biogeography*
Montane/arctic-alpine specialists							
Salix lanata	Woolly willow	Vulnerable; Nationally Rare	12	550–1044	Low growing to small bush (<1.5 m)	Highly base-rich soils; often on north-facing slopes on calcareous schist and limestone	Circumpolar Arctic-montane; absent from central Europe
S. myrsinites	Whortle-leaved willow	Endangered; Nationally Scarce	70	150–1020	Low-growing and spreading (<1 m)	Usually some base-enrichment and flushing; often in open vegetation and associated with limestone outcrops	European Arctic-montane; absent from central Europe
S. lapponum	Downy willow	Vulnerable; Nationally Scarce	90	140–1125	Low growing to erect bush (<2 m)	Wide range of soils, avoiding the most acid	Eurosiberian Boreo-arctic Montane
S. arbuscula	Mountain willow	Least Concern; Nationally Scarce	42	342–870	Procumbent to semi-erect (<1 m)	Base-rich soils, often within damp heath and grassland	European Arctic-montane; absent from central Europe
S. reticulata	Net-leaved willow	Least Concern; Nationally Scarce	23	430–1125	Prostrate (<0.2 m)	Base-rich rock ledges and moist cliffs	Circumpolar Arctic-montane
Secondary montane willow scrub species							
S. myrsinifolia	Dark-leaved willow	Least Concern	53*	0–940	Erect bush (<3 m)	Wide range of soils; damp mountain slopes	Eurosiberian boreal-montane
S. phylicifolia	Tea-leaved willow	Least Concern	73*	0–1020	Erect bush (<3 m)	Wide range of soils; often associated with water-body margins	Circumpolar boreo-arctic montane

and indicators of the hydrophilous tall herb fringe community, such as *Alchemilla glabra*, *Luzula sylvatica*, *Geranium sylvaticum*, *Geum rivale*, and *Trollius europaeus*. Montane willows found at the highest altitudes on base-rich outcrops can also co-occur with arctic-alpine and calcicolous forbs of calcareous grasslands, including *Dryas octopetala*, *Silene acualis*, *Saxifraga aizoides*, and *Thymus drucei*.

Supplement S1 summarizes the fauna recorded in association with montane willows in Scotland since the 1930s, as well as species of conservation interest, including examples of likely associates if restoration is upscaled in the future. The willows are ambophilous; pollen is transported between plants both by wind and by insects, primarily bumblebees (e.g. *Bombus monticola*; and Diptera), and they also support upland Lepidoptera, leaf-beetles, and host-specific willow-galling *Euura* sawflies, including a species endemic to Scotland. Montane willows can accommodate a biodiverse community of birds, small mammals, and their predators higher up the food chain, and facilitate the breeding of threatened birds that are declining elsewhere in Britain, e.g. Ring Ouzel (*Turdus torquatus*).

Past and Current Threats

The current population of montane trees in Scotland (e.g. *Salix*, *Betula*, *Juniperus*, *Populus*, and *Sorbus* spp.) may date back to colonization during a brief interglacial period (14,500–12,000 years ago) within the last ice age (Tipping 2003). Rising temperatures at the beginning of the current interglacial period (11–10,000 years ago) also facilitated the migration of larger tree species from southern refugia (e.g. *Betula*, *Pinus*, *Corylus*, and *Quercus* species), corresponding with an uphill movement of shrubs to create a discontinuous mosaic of treeline transition and montane scrub (Gilbert & Di Cosmo 2003; Smout et al. 2007). Animals, including humans, colonized Britain in parallel, and thus the extent and openness of woodland thereafter oscillated in response to climatic, biotic, and anthropogenic drivers (Oosthoek 2013; Gilbert 2016).

Widespread forest clearance began with the Neolithic period at least 3000 years ago, increasing substantially in the Iron Age (2500–2000 years ago) primarily due to agricultural activity (Ramsay & Dickson 1997; Smout et al. 2007; Woodbridge et al. 2014). Reductions in the populations of tall shrubs have occurred since the early Bronze Age (Tipping 1997), with wood originally collected for building materials, firewood, and charcoal. Further pressures in modern times have come from air pollution, wildfires, and muirburn (MacKenzie 2002; Gilbert 2016); a primary tool in grouse moor management for maintaining open hill habitats.

However, major loss of mountain woodland in Scotland has been 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; Smout et al. 2007; Oosthoek 2013). European sheep populations rose sharply in the twentieth century (Baldock et al. 1994), and more than doubled in Britain between 1960 and 1990 (Fuller & Gough 1999), reaching a peak of 31 million in 1998 (Bunce et al. 2018). Scotland has some of the highest red deer densities in Europe (Burbaitė & Csányi 2010), causing rapid upland vegetation change since at least the 1940s (Thompson & Horsfield 1997).

Overgrazing by large herbivores seriously impedes the development of slow-growing montane shrubs and significantly reduces their reproductive output through loss of flowering shoots and reserves available for catkin growth (Shaw et al. 2010a; Speed et al. 2013). Deer may preferentially choose to eat woody plants, especially in winter or early spring when food sources are scarce in the uplands and willow shoots offer high nutrition and palatability (Gilbert & Di Cosmo 2003; Gilbert 2016). Herbivory also indirectly influences pollen limitation when heavily grazed landscapes support fewer floral resources and pollinating insects (Shaw et al. 2021), while seedling establishment can be prevented by high levels of trampling, causing soil erosion and uprooting of plants (Miller et al. 1982).

There is now an almost complete absence of contiguous altitudinal treeline in Scotland (Armstrong et al. 2014). By the 1990s, the total area of relict montane willows throughout the country was unlikely to exceed 10 ha (Horsfield & Thompson 1997; Patterson et al. 2014). Only a few viable populations were left, with the majority in rapid decline. The largest remnant patch, located at Corrie Sharroch in the eastern Cairngorms, covered 0.5 ha on a steep, rocky slope.

Scotland's mountain woodlands are often contrasted to that of South-West Norway, owing to similar climates and land use histories until the late nineteenth century when socioeconomic pressures diverged (Armstrong et al. 2014; Halley 2017). Widespread reductions in grazing pressures have facilitated natural regeneration and recovery of Scandinavian montane scrub (Bryn 2008), demonstrating the potential for upland Scotland if there is a significant change in land management. In Norway, this opportunity is illustrated by the extensive mosaic habitat known colloquially as the "willow region," in which montane willows are common toward the upper altitudinal reaches of the wider shrub zone. Here, *Betula pubescens* is generally the most frequent woody species, and *B. nana*, *Vaccinium* spp., *Empetrum nigrum*, and *Arctostaphylos* spp. also feature often.

However, most surviving montane willow stands in Scotland are confined to inaccessible cliff ledges, ravines, and steep stream sides out of reach of large herbivores (Fig. 1). Such groups are defined as relict populations because they are restricted geographically by isolation into small islands of suitable habitat (Habel et al. 2010). These exposed, rocky locations inflict additional risks from rockfall and freeze–thaw, with little space or stability provided for regeneration and expansion. Although montane willows can spread vegetatively, asexual clonal reproduction is very limited within the Scottish context (Stamati et al. 2007). Fragmented populations are liable to pollination failure, low sexual recruitment, and hybridization between rare and more common species; exacerbated by the dioecious nature of willows (Shaw et al. 2010a).

In 2005, DNA-fingerprinting of 19 montane willow sites across Scotland showed little correlation between population size and their genetic diversity, which was relatively high (Scottish Montane Willow Research Group 2005). Given the longevity of

Figure 1. Left photo—*Salix lapponum* plants clinging to an inaccessible cliff-ledge in Lochaber, Western Scottish Highlands. Right photo—sub-arctic *S. lanata* scrub growing at over 1000 m on Geal Charn in the central Highlands. With more than 1000 plants, it is the largest relict population of this species in Scotland. This population is becoming increasingly vulnerable to reduced snow-lie and disturbance by large herbivores. Photos by S.H.W.

individual willows, those results suggested that the genetic structure of relict Scottish stands may currently reflect a time when the species were more abundant without major genetic bottlenecks and population differentiation. However, more recent research focusing on *Salix lapponum* and *S. myrsinites* in the Cairngorms found significant inbreeding, female biased sex-ratios, low seed set, and few surviving juveniles, indicating that reproductive limitation will be exacerbated in subsequent generations (Finger et al. 2022). Reduced genetic diversity through inbreeding depression might dilute the resilience and adaptive potential of Scottish montane willows during abiotic or biotic perturbations in the future, including extreme weather and epidemics of pathogens such as rust fungi (MacKenzie 2002; Milne et al. 2012; Kołos et al. 2015). Climate change is already causing a reduction in the extent and duration of snow cover in Scotland since the 1980s (Trivedi et al. 2007; Cameron et al. 2022), with negative implications for arctic-alpine plants in particular (Watts et al. 2022). Earlier spring snow melt leaves montane willows susceptible to browsing, reduced fruit set, and damage by erosion (Gilbert 2011). For example, the largest Scottish patch of *S. lanata* grows on relatively accessible ground on Geal Charn in the central Highlands (Fig. 1). This unique population persists alongside high deer densities but is becoming increasingly more trampled and disturbed as the duration of late winter snow-lie is curtailed; highlighting additional pressures imposed by the interaction between climate and land management (Marriott 2010; Marriott et al. 2015).

Restoration Beginnings in Scotland

Following early reviews of the status of montane scrub in Scotland (Mardon 1990; Hester 1995), interest in habitat restoration was stimulated by a major seminar "*A future for montane shrub communities*," held in 1996 as part of a Millennium Forest for Scotland project (Gilbert et al. 1997). Consequently, the Montane Scrub Action Group (now called the Mountain Woodland Action Group [MWAG]) was formed to share experience, identify conservation priorities, and improve national-level support for implementation. MacKenzie (2000) thereafter collated all the existing records for tall shrub species and high-altitude woodland remnants, justifying the inclusion of the treeline ecotone in landscape management strategic planning and financial incentive programs. A further conference in 2001 "*The challenge above the treeline*" reviewed progress and brought awareness to a range of stakeholders, policymakers, and practitioners (Gilbert 2002a). The first set of management guidance was produced by Gilbert (2002b) and updated into a handbook on mountain woodlands by Morris (2010). Most recently, a suite of five Best Practice Guidance Notes has disseminated information on methods for safeguarding and expanding woodland and scrub at higher altitudes (Montane Scrub Action Group 2016).

Restoration Extent and Tree Planting Data

Watts (2023b) mapped a gross area of 9377 ha covering restoration projects of all mountain woodland habitats in Scotland actioned by May 2023 (e.g. upland Caledonian pinewoods, mountain birchwoods, and montane scrub of *Salix* sp., *Betula nana*, and *Juniperus communis*), as well as 1466 ha approved for restoration management in the next few years. Of the current sites, montane willows featured within a gross project area of 2659 ha, of which 2238 ha were within fences excluding large herbivores, and 421 ha were unfenced. The actual delimited area where montane willows have been planted may be in the region of approximately 200–1000 ha. However, the true size of restored patches is difficult to estimate due to their discontinuous nature, which occurs within a larger mosaic of other upland vegetation communities including open ground. Not all planted seedlings will have established, and those that do survive also require at least 7–10 years before they grow to maturity.

As of May 2023, a total of 396,868 montane willows have been planted in Scotland (Table 2), distributed primarily in the Breadalbane region of the Central Highlands, the Cairngorms National Park, West Affric, and the Southern Uplands (Fig. 2A). Planting of *Salix lanata* and *S. myrsinites* has focused on the Cairngorms and West Affric (Fig. 2B & 2C), while *S. lapponum* is the most numerous species to be planted across the country (Fig. 2D). *Salix arbuscula* has been planted in only two projects so far within Breadalbane and Lochaber (Fig. 2E). The pioneering site for montane willow restoration in Scotland

Table 2. The total number of montane willows planted in Scotland for restoration projects as of May 2023, and the number of 10 × 10 km grid squares (defined by British National Grid Ordnance Survey) in which planting has occurred somewhere within the square. *These secondary montane willow species are counted if they were planted as part of a project featuring any of the montane/arctic-alpine specialist species listed above.

Species	*No. planted*	*10 × 10 km grid squares featuring planting*
Salix lanata	35,107	14
S. myrsinites	2657	8
S. lapponum	267,749	33
S. arbuscula	967	3
*S. myrsinifolia**	58,525	22
*S. phylicifolia**	31,863	14
Total	396,868	37

is Ben Lawers National Nature Reserve (Fig. 3), owned and managed by the National Trust for Scotland. No other restoration project in the country is comparable in scale and longevity; this work is described in more detail along with two other case study examples in Supplement S2.

Restoration Methods

Table S1 summaries the key "montane willow scrub" restoration projects undertaken in Scotland by May 2023, involving conservation charities, a government agency, and privately owned estates. There have been two main approaches:

- Large-scale planting/translocations where populations of arctic-alpine willows are not currently present but may have been historically, or are functionally extinct.
- Reinforcing/augmenting relict populations by supplementary planting for "genetic rescue."

Propagation sources of shrubs for these projects are generally provided by relict montane willows close to planting areas, preferably within a 10 km radius. Ideally, as many individuals as possible would be sampled from donor sites with greater than 50 plants, but relict populations in Scotland are often too small to meet this threshold. Nationwide biological recording by the Botanical Society of Britain and Ireland has been fundamental to identifying which locations to collect from (Botanical Society of Britain and Ireland 2022; Watts 2023c). Scattered and remote willows can be difficult to access within the limited window of opportunity to collect the short-lived seed of these species, and the proportion of viable seed is unreliable. A few catkins may still produce hundreds of progeny, but seed gathered from a low number of parents risks introducing and perpetuating poor genetic diversity into planting sites. Hybridization is also a threat if sources of rare species are from relict populations intermixed with other commoner willow taxa.

Seedlings grown in a tree nursery are usually ready for outplanting 1 or 2 years after seed collection. An alternative option is vegetative propagation from stem cuttings, for which willows have a particularly high success rate; maximized by collection in late spring before their leaf buds burst. As well as being grown for direct planting at a restoration site, cuttings can also be used to create a seed stand comprising individuals of known provenance and genetic identity, with at least 30–50 distinct clones and a mixed sex ratio. This approach is gaining popularity in Scotland, with the advantage of enhancing genetic diversity and producing large quantities of seedlings in a tree nursery without the need for any subsequent visits to relict populations. A minimum of 3–5 years is required between cutting collection and the production of their seedlings ready for out-planting. Wild seed is therefore often employed as a complementary source in the interim to allow restoration work to begin before a seed stand is fully operational.

Late spring planting allows young shrubs to establish before that year's winter dormancy. Mechanized ground preparation is impractical on steep and complex high-altitude terrain. Hand screefing instead removes the vegetation layer to form a shallow scrape for direct planting without the application of fertilizer, herbicides, or pesticides. Traditional tree spacing methods for woodland creation are also not suitable in the treeline context where scrub forms a discontinuous mosaic with other habitats. The density and pattern of planting can thus vary significantly depending on soil depth, slope angle, accessibility, sheltering, and topography. Maintaining large areas of unplanted open ground allows a naturalistic landscape to develop in the future.

Despite significant progress in propagation and planting, addressing the original causes of habitat degradation is critical to achieving montane scrub restoration. In Scotland, the primary focus is therefore eliminating the pressure of overgrazing by large herbivores, with most work to date involving fenced exclosures. This approach is required where livestock and deer reductions are not currently viable due to heritable grazing rights or wider land management practices. However, fences have a visual impact, restrict public access, cause bird collisions, promote dense ground flora growth, and are challenging to maintain in the mountain environment (Summers 1998; Tanentzap et al. 2013). Montane willows will never grow completely above browse height and are thus perpetually dependent on the upkeep of an exclosure if it is situated within a region of high herbivore densities.

Small-scale planting on cliffs and crags without fencing has occurred at several sites to augment relict populations, particularly for *Salix lanata*, e.g. Coire Garbhlach. However, the availability of suitable locations for population expansion by this method is limited, and working on such steep ground carries a significant health and safety risk. Instead, montane willow conservation alongside landscape-scale management for very low deer densities (<1/km^2 in targeted areas) is increasingly a preferential alternative to fencing for larger landholdings or neighboring estates working in collaboration, e.g. Cairngorms Connect, Mar Lodge, and Corrour (Supplement S2; Table S1).

Knowledge Gaps and Research Needs

Outcomes of Restoration Projects

Montane tree planting is a significant commitment due to the slow growth rate of component species, access difficulties, and

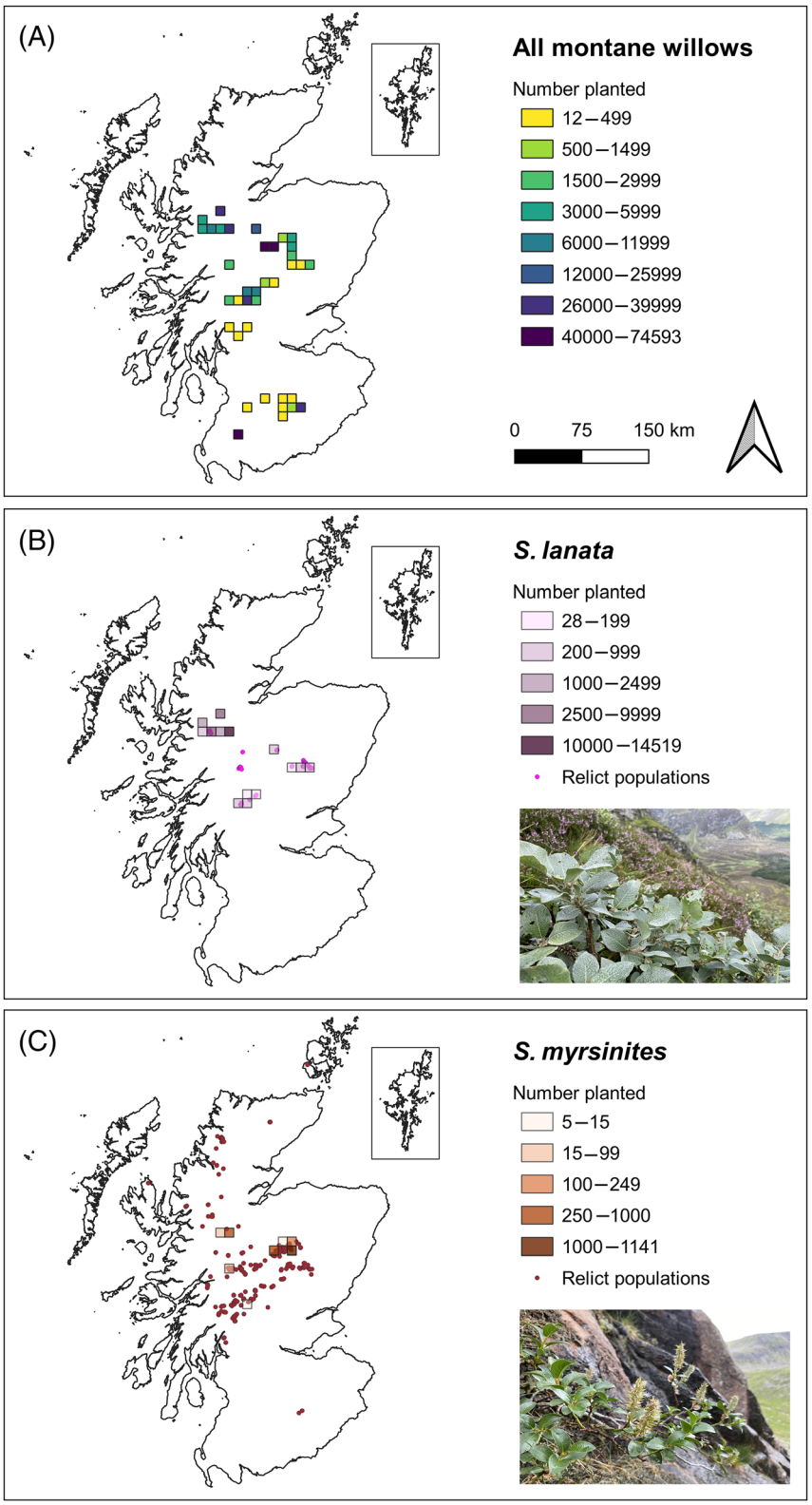

Figure 2. (A) The total number of montane willows planted in Scotland by May 2023 in 10 × 10 km British National Grid Ordnance Survey squares; combined for all species listed in Table 2. (B–E) The number of *Salix lanata*, *S. myrsinites*, *S. lapponum*, and *S. arbuscula* planted in Scotland by May 2023, also showing the distribution of remnant (unplanted) populations sourced from Botanical Society of Britain and Ireland (2022) and Watts (2023c). Planting data adapted from Watts (2023b). Photos by S.H.W.

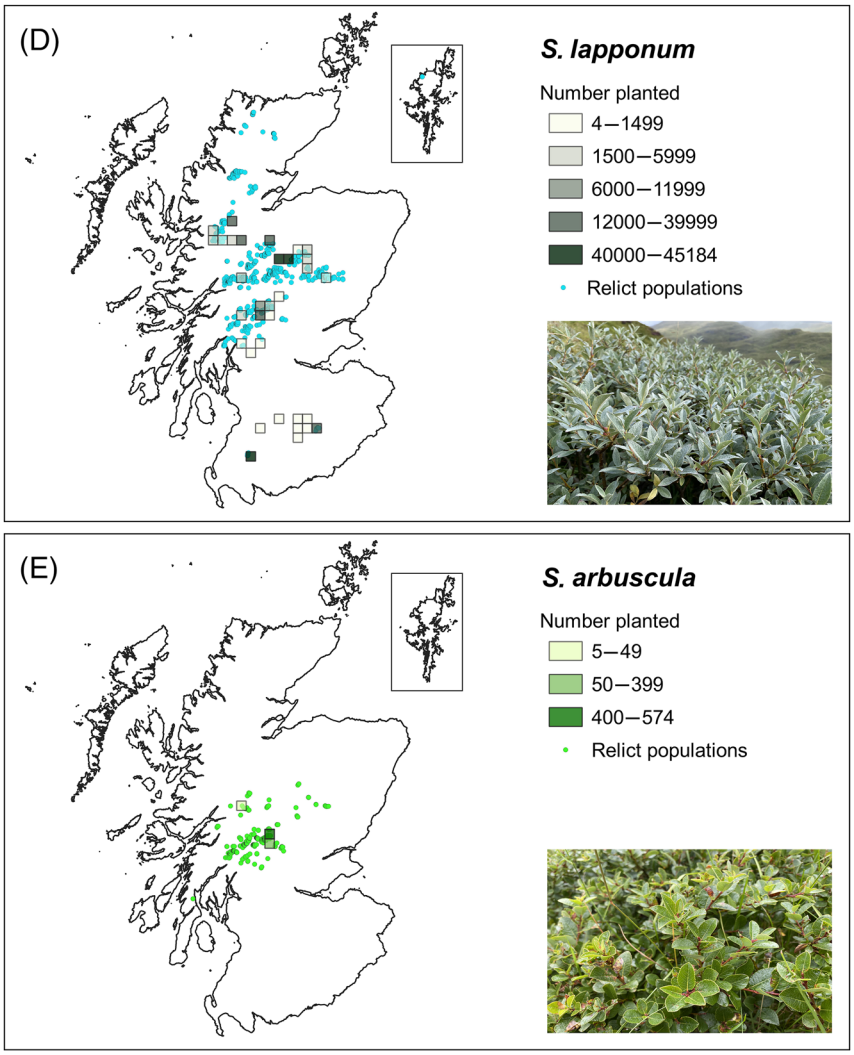

Figure 2 (Continued)

the long-term need to reduce overgrazing (Mardon 2003). Land managers must ensure that enough individuals survive to justify the expense and effort. However, resource-constrained environmental organizations must often focused on project delivery rather than rigorous scientific investigation during and post-restoration. The availability, breadth, precision, and longevity of monitoring data detailed in Table S1 is therefore inconsistent between projects. At various locations, montane willows have been planted in large numbers but with very limited follow-up reporting on their progress (Marriott et al. 2015). Some monitoring has comprised of a simple count of established plants in comparison to the numbers that were originally planted, even though this approach is likely to lead to a gross underestimate (Warwick 2016).

Restoration should avoid large-scale rapid planting in unsuitable or marginal sites, which could create unhealthy, structurally homogenous stands with negative implications for important open-ground habitats and soil carbon-nutrient dynamics. Such action may provide a reservoir for the spread of pests and pathogens, with the potential to damage nearby naturally occurring relict sites, particularly during the era of escalating climate change. Evaluations of the factors affecting plant establishment and fecundity are therefore required to identify the most productive restoration sites and encourage greater efficiency and resilience. This information is essential during high-risk planting (e.g. without fencing), or when trialing innovative management techniques.

Investigations must encompass a range of spatial–temporal scales, comprehensively studying the survival, growth, and browsing of repeatedly measured individual plants, and continuing for decades to follow wider development toward a cohesive and functional treeline. A standardized protocol for tracking restoration outcomes and providing conservation evidence could capitalize on highly accurate Global Positioning System (GPS)

Figure 3. Montane willow scrub restoration featuring planted *Salix lapponum* at Creag an Lochain, Ben Lawers National Nature Reserve owned and managed by the National Trust for Scotland. Photo by S.H.W.

technologies and the successful implementation of annual montane willow monitoring in recent years (e.g. at Mar Lodge and Corrour). Integrated biodiversity assessments will also reveal the response of associated species, colonization over time, and the unique assemblage that forms as a mature scrub matrix expands across Scotland's mountains.

Choice of Planting Sites, Species, and Habitat Definitions

While international studies can provide a helpful comparison for restoration potential, they do not account for the historical land use legacies distinct to Scotland. Consequently, there is still relatively little research characterizing the most appropriate locations for expanding montane willows beyond the refugia where they have been restricted to by past and present land management. Choosing suitable sites for reintroduction or supplementary planting can become difficult when the range of requirements for rare species are not precisely understood (Pogorzelec et al. 2020).

Salix lapponum is typically associated with calcareous outcrops in Scotland alongside grazing-sensitive tall herb communities, but across Europe it is generally considered an indicator of neutral to acidic conditions, including peat bogs, mires, stream banks, and swampy boreal forests (Pogorzelec 2008; Hroneš et al. 2018). Relict stands in Scotland do not represent the optimum naturally occurring habitats of montane willows and are distinct from the vegetation assemblages they would be ensconced within as a feature of a wider, more authentic montane scrub zone. Therefore, *S. lapponum* may thrive over a larger variety of planting situations and topographies (e.g. accessible ground, acidic soils, and flushed slopes), offering broader opportunities for restoration action among other shrub species. *Betula pubescens* forms adapted to the climate of the treeline ecotone in Scotland are nearly extinct, for the same reasons as the willows, and have been almost completely overlooked. Similarly, *B. nana*, a component of the "willow region" in Scandinavian, is wide-ranging in Northern Europe but primarily found in areas of blanket bog in Scotland (Dickson 1984; Rodwell 1998; Borrell et al. 2018). Populations may persist here as an escape from burning or overgrazing, and the Scottish range of *B. nana* is currently far more constrained than the area the species is adapted to (de Groot et al. 1997; Wang et al. 2014).

Mycorrhizal Fungi

Mycorrhizal fungi play a major role in vegetation dynamics by colonizing roots and providing nutrients derived from the soil in exchange for carbohydrates. The addition of compatible fungi during the nursery or planting stages can enhance the survival and growth of tree seedlings (Corkidi et al. 2008; Sebastiana et al. 2013). Therefore, coupling mountain woodland restoration with associated fungal communities may improve outputs, particularly where soils are low in inoculum and nutrients due to habitat loss and fragmentation (Milne et al. 2006). There are still very few studies of the fungi accompanying montane *Salix* in Scotland other than *Salix herbacea* or *S. repens* (Hesling 2013; Izumi 2020), and for arctic-alpine specialists, research is lacking globally. Using advances in environmental DNA (eDNA) metabarcoding techniques on soil samples collected at relict populations would provide new data on co-occurring fungi and is likely to uncover highly diverse ectomycorrhizas (ECMs), including species that are rare, endemic, or new to science. This information may help identify suitable fungi for culturing and developing montane willow inoculation trials.

Natural Regeneration

The creation of viable, self-sustaining populations must be a fundamental goal of montane willow conservation. Although this review has focused on planting projects, all woodland restoration should aim to facilitate natural regeneration as an essential foundation from the outset (Chazdon & Laestadius 2016). This goal will promote project efficiency, wider habitat connectivity, greater spatial heterogeneity, genetic adaptation, improved biodiversity, resilience, and long-term ecosystem stability (Chazdon & Guariguata 2016).

However, montane willow seeds have a very short viability period and require bare ground for germination (Shaw et al. 2010b). When large herbivores are excluded, as is common practice at Scottish restoration sites, soil disturbance is reduced and the ground flora can shift toward a community of taller species (Watts et al. 2019). Without enough exposed soil, willow recruitment might not occur even under a very large seed rain. There are still very few observations of new seedlings at montane willow planting sites in Scotland, despite adult plants having been established for years. Recruitment has only recently been identified 30 years after conservation work began at Ben Lawers (Supplement S2); restricted to very small areas of landslip. Identifying the factors limiting natural regeneration of montane willows will allow mitigation measures to be developed to overcome this barrier to long-term habitat recovery, potentially including ground disturbance, seed sowing, or changes in grazing practices. Additional information on seed dispersal and

germination rates will also assist conservation and tree nursery managers with seed collection, genetic rescue, and rare plant propagation.

Genetic Diversity

The adaptive potential of populations is underpinned by their provenances and genetic diversity, which should be measured, monitored, and reported to aid the planning of conservation actions (O'Brien et al. 2022). With translocations and supplementary tree planting on the increase, land managers may wish to source propagation material that optimizes genetic diversity and thus resilience and long-term project viability. Relict montane willows represent an opportunity for ex situ collections and expansion by regeneration, but inbreeding due to fragmentation and limited cross pollination may be perpetuated in the future without appropriate interventions (Finger et al. 2022). Molecular analysis is required to support restoration actions that aim to protect and utilize the local genetic diversity of relict populations and explore the potential advantages and implications of harnessing resources from a wider geographical area.

Compiling a comprehensive genetic inventory across the whole Scottish range of relict montane willows, and investigating contemporary gene flow using their seeds and seedlings would build upon valuable work undertaken in the Cairngorms and other selected locations (Scottish Montane Willow Research Group 2005; Stamati et al. 2007; Finger et al. 2022). This research will determine pathways for improved connectivity between relict populations and identify the most suitable sites from which to gather seed and cuttings, particularly in areas where conservation work is yet to commence. Concurrently studying genetic diversity within seed stands and planted populations will also provide a blueprint for assessing and mitigating inbreeding risks and reproductive failures in the restoration projects ahead.

Action for the Future

The distribution of relict sites and tree planting numbers in Figure 3 highlights gaps within the geographical range of Scotland's montane willows where conservation work is yet to be initiated, including in Lochaber, the Angus Glens, and the North-West Highlands. Opportunity mapping using national data on geology, soil type, topography, altitude, climate, and land use, in conjunction with the Scottish mountain woodland databases by Watts (2023b, 2023c), should be undertaken to identify priority locations for restoration. As well as focusing on sites of high nature conservation concern, future action should harness the capacity for nature recovery on land previously managed intensively for sport shooting (e.g. deer stalking and grouse moors), which often host relict populations of montane willows in need of rescue and enhancement.

The ecological prospects for much more of upland Scotland are evidenced by the extensive montane scrub reestablished over decades at Ben Lawers, and recent planting success in large-scale restoration projects in the Cairngorms and on private estates (e.g. Mar Lodge and Corrour; Supplement S2). Mountain woodland is rapidly gaining recognition for its importance to biodiversity and climate change mitigation (Watts & Jump 2022). To ensure these benefits are delivered, there must be sufficient support through national policy and funding to meet the needs of practitioners and investment in research spanning from the molecular to the landscape scales, as summarized in Table 3. A network of native tree nurseries and seed stands is also urgently needed across the country to be ready to meet rising demand for montane planting stock for the full range of local provenances.

Through the progression of wider collaboration fostering habitat connectivity, montane scrub restoration should help deliver a sustainable future by reducing impacts of the nature and climate emergencies on a national scale. Treeline reestablishment must be underpinned by management for low-density large herbivore populations to remove the pressure of overgrazing and enable a balance between sustainable numbers of animals and plant growth. This vision would require moving beyond relatively small-scale projects held behind fences toward action at landscape scales. Enhancing rural employment and retaining invaluable skills in deer management will be fundamental for meeting this goal.

Montane willow scrub restoration in Scotland should ultimately enable the revival of an altitudinal sequence and mosaic of vegetation shaped by natural regeneration, with arctic-alpine and sub-montane willows extending from within a flourishing herb-rich mountain woodland up toward their climatic limit, incorporated among other tree and shrub species. Therefore, the conservation care of threatened montane willows and their relict populations does not on its own equate to full restoration of the upper montane shrub zone in Scotland. Willows should become a common element of a larger, integrated mountain woodland matrix including open ground, rather than just a standalone habitat. It is not possible to succinctly divide up the natural altitudinal treeline into discrete components and vegetation types. But rather than being viewed as a problem for land managers and policymakers, this complexity is an attribute to be celebrated and embraced as a vibrant and enriching feature of upland biodiversity.

Broader Implications for Restoration Ecology

Montane willow scrub in Scotland is an informative and rare example of how restoration of vegetation on the brink of extinction has been tackled across an entire country. The work has applications for tree propagation, planting, and regeneration in other montane scrub zones in Europe, and demonstrates the role of large herbivores, conservation charities, government agencies, and private organizations in project delivery. However, this review also highlights wider research needs in restoration ecology (e.g. monitoring, site selection, biodiversity, and genetic diversity), and the challenges of transforming conservation actions specific to threatened species into a more holistic approach aiming to reestablish naturalistic transitional vegetation in mountains. Restoration simply magnifying the extent of the remaining species-impoverished fragments shaped by anthropogenic degradation would not reflect the character or biodiversity of more extensive altitudinal shrub zones in the past

Table 3. Key research and practice needs for montane willow restoration in Scotland, considering relict and restored populations, as well as action on the landscape and national scales.

	Relict populations	*Restored populations*	*Landscape and national scale*
Research needs	*Site requirements and outcomes of restoration projects*		
	Comprehensive descriptions of the complete range of site requirements of each montane willow scrub species in Scotland to enrich Best Practice Guidance for their conservation Long-term monitoring to assess temporal population dynamics in relation to climatic variables, herbivory, pathogen attack, and management actions	Evaluations of the abiotic and biotic factors affecting establishment, growth, and fecundity at planting sites Trial novel planting sites beyond the conditions of current cliff-ledge refugia, e.g. more acidic substrates, flushed soils, flatter ground, and mosaics of grasslands and heaths Long-term monitoring to assess temporal population dynamics and project outputs Trial short-term alternatives to fencing, e.g. browsing deterrents such as emulsified animal fat, brash, or sheep's wool	Synthesis of long-term outcomes of restoration projects across Scotland The effects of treeline advance (either via regeneration or artificially through planting) on soil carbon and nutrient cycling Opportunity mapping using national data on geology, soil type, topography, altitude, climate, land use, and montane willow distribution to identify locations where further restoration should be prioritized Potential for high-altitude birch forms of *Betula pubescens* to be integrated into a restored montane shrub zone mosaic featuring montane willows
	Associated biodiversity		
	Systematic surveys of understudied invertebrate taxon groups associated with montane *Salix*, including Coleoptera, Diptera, Hymenoptera, and Microlepidoptera Enhanced knowledge of host-specific gall-forming and leaf-mining taxa on montane willows; their distribution and life-history Co-occurring fungi and the microbiome of relict populations	Biodiversity assessments as restored habitat is colonized over time, including generalists and specialist invertebrates, true obligate species, and the microbiome Colonization of mycorrhizal fungi on planted willow Testing whether mycorrhizal fungi inoculation improves the outputs of out-planting programs	Characterize the unique bird assemblage colonizing montane willows in Scotland as they establish at large scale; both within core scrub and along its edges The effects of climate change and distributional range shifts on associated biodiversity and future colonization of the habitat
	Genetic diversity		
	Genetic diversity and gene flow in understudied areas of Scotland, e.g. North and West An analysis of contemporary gene flow (genetic study of seedlings and seeds) Implications of inbreeding and hybridization on population health, susceptibility to pathogen infection, and long-term viability	Genetic diversity, introgression, and frequency of hybridization in propagation material Genetic diversity of seed stands and planted populations for mitigating inbreeding risks and reproductive failures in the restoration projects of the future	A comprehensive genetic inventory across the whole Scottish range of montane willows
	Long-term management challenges		
	The impact of climate change (e.g. snow cover changes), and its interaction with large herbivore management Information on pollen flow, seed dispersal, and germination rates	Implications of large herbivore management on small mammal dynamics and their browsing Factors limiting natural regeneration Information on seed dispersal and germination rates	The impact of climate change on long-term restoration outcomes, habitat distribution, and the interaction with large herbivore management The socioeconomic factors limiting uptake and successful implementation of restoration projects at scale

Table 3. Continued

	Relict populations	*Restored populations*	*Landscape and national scale*
Practice needs	*Site requirements and monitoring*		
	Continue biological recording of all willow taxa (including hybrids) to identify previously unmapped populations, particularly in remote locations Regularly update distribution databases, e.g. Watts (2023c) and Botanical Society of Britain and Ireland (2022)	Refine and streamline methods for monitoring restoration outcomes, e.g. growth, survival and browsing using repeated measures of individual plants over time	Regularly update mapping data of restoration projects across Scotland (Watts 2023b) Move away from habitat definitions based on species-poor non-natural fragments, toward restoring willows as a common feature of a natural biodiverse treeline mosaic integrated with other tree and shrub species, such as *Betula* spp.
	Plant propagation		
	Identify suitable relict populations to provide new sources of propagation material from across Scotland Ensure seed and cutting collection encompasses sufficient genetic diversity rather than relying on few localized sources	Optimize genetic diversity and the number of distinct clones required in seed stands Mitigate the spread of pest and pathogens between tree nursery environment, planted and relict stands Screening for hybrids to avoid their unintentional transplantation to new sites	Map seed stands and tree nursery networks to identify sources of propagation material and potential gaps in supply
	Population health and resilience		
	Genetic rescue of small, fragmented populations Encourage expansion from relict stands via natural regeneration	Avoid large-scale rapid planting in unsuitable or marginal sites, which could create unhealthy, structurally homogenous stands Management to facilitate natural regeneration	Facilitate wider landscape connectivity and structural diversity of treeline mosaic habitats Build resilience and climate change adaptation into the restored habitat of the future
	People and policy		
	Promote citizen science for recording high-altitude trees and generating wider public interest in the restoration of mountain woodland habitats, e.g. Watts (2023a) Training in arctic-alpine and sub-montane *Salix* identification for entomologists, ecologists, and others engaged in upland biological recording Recognize relict populations as "priority woodland"; to increase their protection and potential for targeted conservation efforts	Foster community and volunteer engagement with montane scrub to generate personal connections that put people at the heart of habitat restoration Fully integrate montane scrub restoration into local management plans	Enhance rural employment and retain invaluable skills in deer stalking and the wider environmental sector Training and knowledge exchange to facilitate more specialist contractors capable of surveying and monitoring montane willows Landscape-scale regional nature restoration partnerships Sufficient support in national policy and funding frameworks
	Establishment at scale		
	Build and maintain a sufficient and genetically diverse supply of nursery stock from the full range of provenances to meet rising demand across Scotland	Move beyond small-scale projects held behind fences toward habitat restoration on the landscape-scale Balance large-scale planting with the conservation of other associated upland habitats, promoting a flourishing mosaic including open ground Develop the cross-over between montane scrub restoration along watercourses, and riparian woodland restoration in the upper catchments	Conservation action across the full geographical range of montane willows in Scotland, including in Lochaber, the Angus Glens, and the North-West Highlands Eliminate the pressure of overgrazing by large herbivores Utilize the potential for montane scrub restoration on deer sporting estates and grouse moors to support biodiversity and climate change mitigation in conjunction with land management diversification

or their possible natural states in the future. Caution must be applied to creating definitions of distinct habitats for restoration that are based on non-natural or ecologically degraded systems. These lessons are particularly relevant to montane and circumpolar regions with strongly modified landscape histories (e.g. Iceland) and other countries where arctic-alpine willows currently comprise a relict distribution, such as Central and Southern Europe.

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LITERATURE CITED

Armstrong H, Holl K, Halley D (2014) Restoring the Scottish uplands. Pages 25–34. In: Mccracken K (ed) Delivering multiple benefits from our land: sustainable development in practice. SRUC, Edinburgh, Scotland

Baldock D, Beaufoy G, Clark J (1994) The nature of farming: low intensity farming in nine European countries. Institute for European Environmental Policy, London, United Kingdom

Borrell JS, Wang N, Nichols RA, Buggs RJ (2018) Genetic diversity maintained among fragmented populations of a tree undergoing range contraction. Heredity 121:304–318. https://doi.org/10.1038/s41437-018-0132-8

Botanical Society of Britain and Ireland (2021) Updated vascular plant Red Data List for Great Britain. https://view.officeapps.live.com/op/view.aspx?src=https%3A%2F%2Fbsbi.org%2Fwp-content%2Fuploads%2Fdlm_uploads%2FVP-GBRL_19_02_2021-1.xlsx&wdOrigin=BROWSELINK (accessed 08 Jun 2023)

Botanical Society of Britain and Ireland (2022) BSBI distribution database. https://bsbi.org/taxon-lists (accessed 11 Mar 2023)

Bryn A (2008) Recent forest limit changes in south-east Norway: effects of climate change or regrowth after abandoned utilisation? Norsk Geografisk Tidsskrift-Norwegian Journal of Geography 62:251–270. https://doi.org/10.1080/00291950802517551

Bunce RG, Wood CM, Smart SM (2018) The ecology of British upland landscapes. I. Composition of landscapes, habitats, vegetation and species. Journal of Landscape Ecology 11:120–139. https://doi.org/10.2478/jlecol-2018-0015

Burbaitė L, Csányi S (2010) Red deer population and harvest changes in Europe. Acta Zoologica Lituanica 20:179–188. https://doi.org/10.2478/v10043-010-0038-z

Cameron I, Fyffe B, Kish A (2022) One Scottish snow patch survives until winter 2021/2022. Weather 77:143–145. https://doi.org/10.1002/wea.4157

Chazdon R, Brancalion P (2019) Restoring forests as a means to many ends. Science 365:24–25. https://doi.org/10.1126/science.aax9539

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

Chazdon RL, Laestadius L (2016) Forest and landscape restoration: toward a shared vision and vocabulary. American Journal of Botany 103:1869–1871. https://doi.org/10.3732/ajb.1600294

Cheffings CM, Farrell L, Dines TD, Jones RA, Leach SJ, McKean DR, Pearman DA, Preston CD, Rumsey FJ, Taylor I (2005) The vascular plant red list for Great Britain. Joint Nature Conservation Committee, Peterborough, United Kingdom

Corkidi L, Evans M, Bohn J (2008) An introduction to propagation of arbuscular mycorrhizal fungi in pot cultures for inoculation of native plant nursery stock. Native Plants Journal 9:29–38. https://doi.org/10.2979/NPJ.2008.9.1.29

Dandan X, Deshuai A, Jianqin Z (2022) Dynamics of the alpine treeline ecotone under global warming: a review. Journal of Resources and Ecology 13: 476–482. https://doi.org/10.5814/j.issn.1674-764x.2022.03.012

de Groot WJ, Thomas PA, Wein RW (1997) *Betula nana* L. and *Betula glandulosa* Michx. Journal of Ecology 85:241–264. https://doi.org/10.2307/2960655

Dickson JH (1984) Pleistocene history of *Betula* with special reference to the British Isles. Proceedings of the Royal Society of Edinburgh, Section B: Biological Sciences 85:1–11. https://doi.org/10.1017/S0269727000003845

European Commission (2013) Interpretation manual of European Union habitats – EUR28. European Commission, Brussels, Belgium

Evans D (2017) Mountain willow scrub in the European Union. Scrubbers' Bulletin 12:40–46

Finger A, Rao S, Cowie N, MacDonell T, Beck A, Denny B (2022) Conservation genetics of montane willow populations in Scotland-limited natural recovery despite long-distance gene flow and high genetic diversity. Environmental Research: Ecology 2:015001. http://doi.org/10.1088/2752-664X/ac9682

Fuller R, Gough S (1999) Changes in sheep numbers in Britain: implications for bird populations. Biological Conservation 91:73–89. https://doi.org/10.1016/S0006-3207(99)00039-7

Gilbert D (2002*a*) Montane scrub: the challenge above the treeline. Highland Birchwoods, Munlochy, Scotland

Gilbert D (2002*b*) Guidance for the restoration of montane scrub. Highland Birchwoods, Munlochy, Scotland

Gilbert D (2011) Interactions between climate and land use which drive dynamics in treeline ecotone scrub in Scotland. PhD thesis. University of Edinburgh, Edinburgh, United Kingdom.

Gilbert D (2016) Montane scrub: the missed opportunity of our ecologically impoverished uplands. Reforesting Scotland 54. https://www.reforestingscotland.org/wp-content/uploads/2016/09/160810-Montane-article-with-all-refs.pdf (accessed 03 Dec 2023)

Gilbert D, Di Cosmo L (2003) Towards restoration of treeline woodland and montane scrub. Botanical Journal of Scotland 55:177–187. https://doi.org/10.1080/03746600308685058

Gilbert D, Horsfield D, Thompson DBA (1997) The ecology and restoration of montane and subalpine scrub habitats in Scotland. Scottish Natural Heritage Review no. 83. Scottish Natural Heritage, Balleby, Scotland.

Greenwood S, Jump AS (2014) Consequences of treeline shifts for the diversity and function of high-altitude ecosystems. Arctic, Antarctic, and Alpine Research 46:829–840. https://doi.org/10.1657/1938-4246-46.4.829

Gu C, Mu X, Gao P, Zhao G, Sun W, Tatarko J, Tan X (2019) Influence of vegetation restoration on soil physical properties in the Loess Plateau, China. Journal of Soils and Sediments 19:716–728. https://doi.org/10.1007/s11368-018-2083-3

Habel JC, Assmann T, Schmitt T, Avise JC (2010) Relict species: from past to future. Pages 1–5. In: Habel JC, Assmann T (eds) Relict species. Springer, Berlin, Germany. https://doi.org/10.1007/978-3-540-92160-8_1

Halley DJ (2017) Woodland history in south west Norway – comparative insights from a parallel universe. Pages 42–53. In: Scottish Woodland History Conference 20.

Hesling E (2013) Arctic-alpine ectomycorrhizal fungi in Scotland: the ecology of unexplored fungal communities and threats to their survival. PhD thesis. University of Aberdeen, Aberdeen, United Kingdom.

Hester AJ (1995) Scrub in the Scottish uplands. Scottish Natural Heritage, Battleby, Scotland

Holtmeier F-K (2009) Mountain timberlines: ecology, patchiness, and dynamics. Springer Science & Business Media, Münster, Germany. https://doi.org/10.1007/978-1-4020-9705-8

Holtmeier FK, Broll G (2005) Sensitivity and response of northern hemisphere altitudinal and polar treelines to environmental change at landscape and local scales. Global Ecology and Biogeography 14:395–410. https://doi.org/10.1111/j.1466-822X.2005.00168.x

Holtmeier F-K, Broll G (2017) Feedback effects of clonal groups and tree clusters on site conditions at the treeline: implications for treeline dynamics. Climate Research 73:85–96. https://doi.org/10.3354/cr01431

Horsfield D, Thompson DBA (1997) Ecology and conservation of montane scrub. Pages 21–34. In: Gilbert D, Horsfield D, Thompson DBA (eds) The ecology and restoration of sub-arctic and subalpine scrub in Scotland. SNH review 83. Scottish Natural Heritage, Battleby, Scotland

Hroneš M, Hrachová Macurová S, Hradílek Z, Hekera P, Duchoslav M (2018) Habitat conditions, stage structure and vegetation associations of geographically isolated subalpine populations of *Salix lapponum* L. (Salicaceae) in the Krkonoše Mts (Czech Republic). Biologia 73:319–332. https://doi.org/10.2478/s11756-018-0051-4

Izumi H (2020) The proportions of ectomycorrhizal roots are varied depending on the different host plant compositions in Scottish arctic/alpine coastal relict vegetation. Mycoscience 61:151–154. https://doi.org/10.1016/j.myc.2020.04.001

Klaus NA, Rush SA, Weitzel SL, Holdrege MC (2020) Changes in tree canopy, groundcover, and avian community following restoration of a montane longleaf pine woodland. The American Midland Naturalist 184:163–176. https://doi.org/10.1674/0003-0031-184.2.163

Kołos A, Wołkowycki D, Banaszuk P, Kamocki A (2015) Protection of relic plant species at the limit of their geographical range: response of *Salix lapponum* to competitor removal. Annales Botanici Fennici 52:303–314. https://doi.org/10.5735/085.052.0505

Liston AD, Knight G, Heibo E, Bland K, Barstad T-E, Blank SM, Boevé J-L, Fiedler C, Grearson K, Halstead A (2012) On Scottish sawflies, with results of the 14th international sawfly workshop, in the southern highlands, 2010 (Hymenoptera, Symphyta). Beiträge zur Entomologie – Contributions to Entomology 62:1–68. https://doi.org/10.21248/contrib.entomol.62.1.1-68

Löf M, Madsen P, Metslaid M, Witzell J, Jacobs DF (2019) Restoring forests: regeneration and ecosystem function for the future. New Forests 50:139–151. https://doi.org/10.1007/s11056-019-09713-0

MacKenzie NA (2000) Low alpine, subalpine & coastal scrub communities in Scotland: a report to Highland Birchwoods. Highland Birchwoods, Munlochy, Scotland

MacKenzie NA (2002) Current status. In: Gilbert D (ed) Montane scrub: the challenge above the treeline. Highland Birchwoods, Munlochy, Scotland

Mardon DK (1990) Conservation of montane willow scrub in Scotland. Transactions of the Botanical Society of Edinburgh 45:427–436. https://doi.org/10.1080/03746609008684981

Mardon DK (2003) Conserving montane willow scrub on Ben Lawers NNR. Botanical Journal of Scotland 55:189–203. https://doi.org/10.1080/03746600308685059

Marriott RW (2010) Observations on woolly willow *Salix lanata* and the whorl snail *Vertigo modesta* at Coire Cheap on 6th to 7th July 2009. Report to Scottish Natural Heritage on behalf of the Woolly Willow BAP Steering group.

Marriott RW, McHaffie H, Mardon DK (2015) Woolly willow. Version 1.0. In: Gaywood MJ, Boon PJ, Thompson DBA, Strachan IM (eds) The species action framework handbook. Scottish Natural Heritage, Battleby, Scotland

Miller G, Kinnaird J, Cummins R (1982) Liability of saplings to browsing on a red deer range in the Scottish highlands. Journal of Applied Ecology 19:941–951. https://doi.org/10.2307/2403295

Milne J, Ennos R, Hollingsworth P (2006) Vegetation influence on ectomycorrhizal inoculum available to sub-arctic willow (*Salix lapponum* L.) planted in an upland site. Botanical Journal of Scotland 58:19–34. https://doi.org/10.1080/03746600608685104

Milne JM, Helfer S, Kirk C, Hollingsworth PM, Ennos RA (2012) Molecular evidence indicates that subarctic willow communities in Scotland support a diversity of host-associated *Melampsora* rust taxa. Fungal Biology 116:603–612. https://doi.org/10.1016/j.funbio.2012.02.008

Monger F, Spracklen DV, Kirkby MJ, Schofield L (2022) The impact of semi-natural broadleaf woodland and pasture on soil properties and flood discharge. Hydrological Processes 36:e14453. https://doi.org/10.1002/hyp.14453

Montane Scrub Action Group (2016) Best practice guides. Montane Scrub Action Group. https://www.msag.org.uk/best-practice-guides.html (accessed 08 Sep 2023)

Morris T (2010) Mountain woodlands best practice handbook. Highland Birchwoods, Munlochy, Scotland

O'Brien D, Laikre L, Hoban S, Bruford MW, Ekblom R, Fischer MC, Hall J, Hvilsom C, Hollingsworth PM, Kershaw F (2022) Bringing together approaches to reporting on within species genetic diversity. Journal of Applied Ecology 59:2227–2233. https://doi.org/10.1111/1365-2664.14225

Oosthoek J (2013) Conquering the highlands: a history of the afforestation of the Scottish uplands. Australian National University Press, Canberra, Australia. https://doi.org/10.22459/CH.02.2013

Orsenigo S, Fenu G, Gargano D, Montagnani C, Abeli T, Alessandrini A, Bacchetta G, Bartolucci F, Carta A, Castello M (2021) Red list of threatened vascular plants in Italy. Plant Biosystems – An International Journal Dealing with all Aspects of Plant Biology 155:310–335. https://doi.org/10.1080/11263504.2020.1739165

Pakeman RJ, Torvell L (2008) Identifying suitable restoration sites for a scarce subarctic willow (*Salix arbuscula*) using different information sources and methods. Plant Ecology & Diversity 1:105–114. https://doi.org/10.1080/17550870802236277

Patterson G, Nelson D, Robertson P, Tullis J (2014) Scotland's native woodlands results from the native woodland survey of Scotland. Forestry Commission Scotland. https://www.forestry.gov.scot/publications/74-scotland-s-native-woodlands-results-from-the-native-woodland-survey-of-scotland (accessed 08 Jan 2024)

Pearman DA, Corner RWM (2022) BSBI projects: altitudinal limits. http://bsbi.org/altitudes (accessed 08 Jun 2022)

Pogorzelec M (2008) Influence of chosen environmental abiotic factors on *Salix lapponum* L. populations in Polesie Lubelskie region. Polish Journal of Environmental Studies 17:581–586

Pogorzelec M (2010) *Salix lapponum* L. (Downy willow) in stands under anthropopressure in the Leczna-Wlodawa Lakeland. Acta Agrobotanica 63:47–53. https://doi.org/10.5586/aa.2010.006

Pogorzelec M, Bronowicka-Mielniczuk U, Serafin A, Parzymies M (2020) The importance of habitat selection for the reintroduction of the endangered *Salix lapponum* L. in eastern Poland. Journal for Nature Conservation 54:125785. https://doi.org/10.1016/j.jnc.2020.125785

Pogorzelec M, Hawrylak-Nowak B, Banach-Albińska B, Szczurowska A, Parzymies M, Spólna K (2022) From ex situ cultivation to stands in natural habitats: critical periods for plants during the reintroduction of *Salix lapponum* L. in eastern Poland. Journal for Nature Conservation 67:126172. https://doi.org/10.1016/j.jnc.2022.126172

Preston CD, Hill MO (1997) The geographical relationships of British and Irish vascular plants. Botanical Journal of the Linnean Society 124:1–120. https://doi.org/10.1111/j.1095-8339.1997.tb01785.x

Ramsay S, Dickson JH (1997) Vegetational history of central Scotland. Botanical Journal of Scotland 49:141–150. https://doi.org/10.1080/03746609708684862

Rodwell J (1998) British plant communities. Mires and heaths. Vol 2. Cambridge University Press, Cambridge, United Kingdom

Ruiz L, Carrión-Paladines V, Vega M, López F, Benítez Á (2023) Biological crust diversity related to elevation and soil properties at local scale in a montane scrub of Ecuador. Journal of Fungi 9:386. https://doi.org/10.3390/jof9030386

Schnittler M, Günther K-F (1999) Central European vascular plants requiring priority conservation measures – an analysis from national red lists and distribution maps. Biodiversity and Conservation 8:891–925. https://doi.org/10.1023/A:1008828704456

Scottish Montane Willow Research Group (2005) Biodiversity: taxonomy, genetics and ecology of sub-arctic willow scrub. Final report 2005. SEERAD Commission No. RBG/837/01. Royal Botanic Garden Edinburgh, Edinburgh, United Kingdom.

Sebastiana M, Pereira VT, Alcântara A, Pais MS, Silva AB (2013) Ectomycorrhizal inoculation with *Pisolithus tinctorius* increases the performance of *Quercus suber* L. (cork oak) nursery and field seedlings. New Forests 44: 937–949. https://doi.org/10.1007/s11056-013-9386-4

Serafin A, Pogorzelec M, Banach B, Mielniczuk J (2015) Habitat conditions of the endangered species *Salix myrtilloides* in eastern Poland. Dendrobiology 73:55–64. https://doi.org/10.12657/denbio.073.006

Shaw RF, Elston DA, Pakeman RJ, Young MR, Iason GR (2010*a*) The impacts of pollination mode, plant characteristics and local density on the reproductive success of a scarce plant species, *Salix arbuscula*. Plant Ecology 211: 367–377. https://doi.org/10.1007/s11258-010-9795-9

Shaw RF, Iason GR, Pakeman RJ, Young MR (2010*b*) Regeneration of *Salix arbuscula* and *Salix lapponum* within a large mammal exclosure: the impacts of microsite and herbivory. Restoration Ecology 18:1–9. https://doi.org/10.1111/j.1526-100X.2010.00720.x

Smout TC, MacDonald AR, Watson F (2007) History of the native woodlands of Scotland 1500–1920. Edinburgh University Press, Edinburgh, United Kingdom. https://doi.org/10.1515/9780748637560

Speed JD, Austrheim G, Hester AJ, Mysterud A (2013) The response of alpine *Salix* shrubs to long-term browsing varies with elevation and herbivore density. Arctic, Antarctic, and Alpine Research 45:584–593. https://doi.org/10.1657/1938-4246-45.4.584

Stamati K, Hollingsworth P, Russell J (2007) Patterns of clonal diversity in three species of sub-arctic willow (*Salix lanata*, *Salix lapponum* and *Salix herbacea*). Plant Systematics and Evolution 269:75–88. https://doi.org/10.1007/s00606-007-0578-2

Stroh PA, Walker KJ, Humphrey TA (2023) In: Pescott OL, Burkmar RJ (eds) Plant atlas 2020: mapping the distribution of the British and Irish flora (two volumes). Princeton University Press, Princeton, New Jersey. https://doi.org/10.2307/j.ctv2x6f08m

Summers R (1998) The lengths of fences in highland woods: the measure of a collision hazard to woodland birds. Forestry: An International Journal of Forest Research 71:73–76. https://doi.org/10.1093/forestry/71.1.73

Tanentzap AJ, Zou J, Coomes DA (2013) Getting the biggest birch for the bang: restoring and expanding upland birchwoods in the Scottish highlands by managing red deer. Ecology and Evolution 3:1890–1901. https://doi.org/10.1002/ece3.548

Thompson D, Horsfield D (1997) Upland habitat conservation in Scotland: a review of progress and some proposals for action. Botanical Journal of Scotland 49:501–516. https://doi.org/10.1080/03746609708684895

Tipping R (1997) The postglacial history of montane tall shrub communities in Scotland. Pages 11–20. In: Gilbert D, Horsfield D, Thompson DBA (eds) The ecology and restoration of montane and subalpine scrub habitats in Scotland. SNH Review 83. Scottish Natural Heritage, Battleby, Scotland

Tipping R (2003) Living in the past: woods and people in prehistory to 1000 BC. Pages 14–39. In: Smout TC (ed) People and woods in Scotland: a history. Edinburgh University Press, Edinburgh, United Kingdom. https://doi.org/10.1515/9781474472722-006

Trivedi MR, Browne MK, Berry PM, Dawson TP, Morecroft MD (2007) Projecting climate change impacts on mountain snow cover in central Scotland from historical patterns. Arctic, Antarctic, and Alpine Research 39:488–499. https://doi.org/10.1657/1523-0430(06-006)[TRIVEDI]2.0.CO;2

Verheyen K, Adriaenssens S, Gruwez R, Michalczyk IM, Ward LK, Rosseel Y, Van den Broeck A, Garcia D (2009) Juniperus communis: victim of the combined action of climate warming and nitrogen deposition? Plant Biology 11:49–59. https://doi.org/10.1111/j.1438-8677.2009.00214.x

Wang N, Borrell JS, Bodles WJ, Kuttapitiya A, Nichols RA, Buggs RJ (2014) Molecular footprints of the Holocene retreat of dwarf birch in Britain. Molecular Ecology 23:2771–2782. https://doi.org/10.1111/mec.12768

Warner E, Hector A, Brown N, Green R, Savory A, Gilbert D, McDonnell A, Lewis OT (2021) The response of plants, carabid beetles and birds to 30 years of native reforestation in the Scottish highlands. Journal of Applied Ecology 58:2185–2194. https://doi.org/10.1111/1365-2664.13944

Warwick A (2016) Ben Lawers NNR, Creag an Lochain montane scrub project: evaluation of montane willow restoration project from 2001–12. National Trust for Scotland, Perthshire, United Kingdom

Watts SH (2023*a*) High mountain trees: altitudinal records recently broken for eleven different tree species in Britain. British & Irish Botany 5:167–179. https://doi.org/10.33928/bib.2023.05.167

Watts SH (2023*b*) HabMoS – mountain woodland – restoration projects. NatureScot. https://spatialdata.gov.scot/geonetwork/srv/eng/catalog.search#/metadata/f72339e7-9e8c-478b-a688-665e66e68397 (accessed 30 Dec 2023)

Watts SH (2023*c*) HabMoS – mountain woodland – wild relict remnant points. NatureScot. https://spatialdata.gov.scot/geonetwork/srv/eng/catalog.search#/metadata/3c165034-238b-4d01-94b3-79802c874e98 (accessed 30 Dec 2023)

Watts SH, Griffith A, Mackinlay L (2019) Grazing exclusion and vegetation change in an upland grassland with patches of tall herbs. Applied Vegetation Science 22:383–393. https://doi.org/10.1111/avsc.12438

Watts SH, Jump AS (2022) The benefits of mountain woodland restoration. Restoration Ecology 30:e13701. https://doi.org/10.1111/rec.13701

Watts SH, Mardon DK, Mercer C, Watson D, Cole H, Shaw RF, Jump AS (2022) Riding the elevator to extinction: disjunct arctic-alpine plants of open habitats decline as their more competitive neighbours expand. Biological Conservation 272:109620. https://doi.org/10.1016/j.biocon.2022.109620

Wielgolaski FE, Hofgaard A, Holtmeier F-K (2017) Sensitivity to environmental change of the treeline ecotone and its associated biodiversity in European mountains. Climate Research 73:151–166. https://doi.org/10.3354/cr01474

Woodbridge J, Fyfe RM, Roberts N, Downey S, Edinborough K, Shennan S (2014) The impact of the Neolithic agricultural transition in Britain: a comparison of pollen-based land-cover and archaeological 14C date-inferred population change. Journal of Archaeological Science 51:216–224. https://doi.org/10.1016/j.jas.2012.10.025

Supporting Information

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

Supplement S1. Notable insects, mammals, and birds recorded in montane willow scrub in Scotland since the 1930s, as well as birds that may colonize as restoration work expands.

Supplement S2. Case study examples of montane willow scrub restoration projects in Scotland: Ben Lawers NNR, Mar Lodge Estate, and Corrour Estate.

Table S1. Montane willow scrub restoration projects in Scotland where more than 1000 willows have been planted.

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