Woodland expansion in the presence of deer: 30 years of evidence from the Cairngorms Connect landscape restoration partnership

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Abstract
1. Restoring native woodlands to areas where they have been lost is a key element for tackling the nature and climate crises. Natural regeneration offers the potential to achieve this cheaply and at scale, but browsing ungulates like deer can inhibit this or alter the pattern of regeneration. This issue is particularly pronounced in the Scottish Highlands, a heavily deforested region with high deer numbers.

2. We describe the work of the 60,000 ha landscape restoration partnership, Cairngorms Connect, in speeding up natural woodland expansion. We use 30 years of regeneration monitoring to show a consistent, large-scale expansion of native woodland, largely through natural regeneration alongside deer culling, without the use of fences. This was achieved across the partnership, despite differing management histories and land-managing organisations (comprising two statutory agencies, one private landowner and one non-governmental organisation).

3. During peak periods of woodland expansion, the area of new woodland (i.e. exceeding 100 trees per hectare) increased by 1.2%, 1.7%, 2.7% and 6.0% annually in the four landholdings' regeneration zones, equating to a total of approximately 164 ha annually of new woodland.

4. Natural regeneration is however patchy and hard to predict. Higher levels of management intervention may be needed to increase species that are rarer, more palatable or further from seed sources; we recommend long-term field trials to inform this, such as those underway in Cairngorms Connect. Further research
should develop techniques for remote sensing of woodland expansion, verified against field data and combined with the development of process-based models to enable us to predict the outcomes of different management scenarios.

5. Synthesis and applications. We show that collaborative deer management across multiple adjoining landholdings can achieve rapid landscape-scale native woodland expansion with minimal need for planting or fencing. Our results show the power of monitoring regeneration directly, to inform deer management for an area. We demonstrate that by uniting over a shared vision, organisations with differing management approaches and histories can build understanding alongside landscape-scale ecological restoration.

KEYWORDS
fencing, forests, herbivores, landscape scale, native woodland, regeneration, restoration, Scotland

1 | BACKGROUND

Restoring and expanding forests across the world is an urgent priority for human societies as a key means to mitigate the crises of climate change and biodiversity loss (Chazdon & Brancalion, 2019). In many parts of the world, wild deer play a critical role in determining the structure, composition and functioning of forests (Côté et al., 2004; Ramirez et al., 2018), alongside numerous bottom-up abiotic factors that influence patterns of tree regeneration, often interacting with top-down effects of large mammalian herbivores (Kuijper et al., 2010; Ramirez et al., 2021). Despite exerting crucial positive effects on ecosystems (such as creating regeneration niches in dense understorey vegetation), deer can also limit tree regeneration and high deer densities can inhibit woodland expansion (Miller et al., 1998; Ramirez et al., 2018). Deer culling is widely used to enable trees to grow where this is the management target (Côté et al., 2004; Thomas et al., 2015), but evidence showing that deer reduction can promote landscape-scale woodland expansion is lacking (Agra et al., 2016).

In the UK, ancient native pinewood is now an extremely localised habitat, largely restricted to the Highlands of Scotland and covering approximately 1% of its former range (Salmela et al., 2010). These native pinewoods (dominated by Scots pine [Pinus sylvestris] alongside several broadleaved tree species) in Scotland provide crucial habitat for numerous species of conservation concern and deliver important ecosystem services including climate regulation (Thomas et al., 2015 and references therein); expanding their area is therefore a major conservation and governmental objective (see https://www.gov.scot/publications/scotlands-forestry-strategy-20192029/pages/6/). The main factor limiting the widespread natural expansion of these pinewoods in Scotland is considered to be browsing by red deer (Cervus elaphus), with other critical limiting factors being the availability of seed sources and regeneration niches—the latter due to the prevalence of a dense shrub layer throughout much of the woodland expansion zone (Miller et al., 1998; Rao, 2017). In Britain as in many parts of the world, deer culling is a key element of current land management practice; nevertheless, Scotland has one of the highest red deer densities in Europe (Burbaïté & Csányi, 2010). In recent years, there has been a gradual shift in management philosophy in Scotland, with increasing numbers of land managers wishing to re-establish woodland on areas formerly managed as open habitats (Thomas et al., 2015).

In the west of the Cairngorms National Park in the Scottish Highlands, from the 1990s a shared vision for land management evolved among four neighbouring public and private landowners. In 2014, this partnership was formally established as Cairngorms Connect (http://cairngormsconnect.org.uk), with a vision to restore natural processes and ecosystems across ~60,000 ha of forest, floodplain and montane habitats managed by four organisations (Figure 1): Forestry and Land Scotland (FLS) and NatureScot (both statutory agencies), the Royal Society for the Protection of Birds (RSPB, an environmental NGO) and Wildland Ltd (WLL, a private enterprise). Expanding the area of native woodland is a core target and to this end, several management practices have been used over the past three decades: (a) deer culling effort has been increased, (b) targeted vegetation management has been used to create regeneration niches, and (c) planting/sowing of trees has been used in some areas, particularly where seed sources are lacking (e.g. see Beaumont et al., 2005; Finger et al., 2023; Jardine et al., 2010; Scottish Natural Heritage, 2009). Alongside these management actions, a tree regeneration monitoring programme was established within each partner’s landholding.

Here, we report on 30 years of regeneration monitoring from across the Cairngorms Connect partnership. In four sections, practitioner leads for each of the four partners describe how woodland expansion has progressed in each landholding and present supporting evidence. We then review the overall picture in the Discussion. For the first time (to our knowledge: Agra et al., 2016), we provide extensive evidence supporting the successful use of deer culling to enable woodland expansion at a landscape scale.

Fieldwork and data collection were carried out with appropriate landowner permissions (no licences required). In terms of the habitat restoration work to which the research refers, deer culling was carried out with appropriate ‘Authorisations’ from NatureScot, when required. Ethics approval was not required. Consents for forest...
expansion were secured through Environmental Impact Assessments (informed by Habitats Regulations Assessments) and approval given by NatureScot, as Operations Requiring Consent.

2 | FORESTRY AND LAND SCOTLAND

FLS manages ~9200 ha of land within the partnership area, comprising Glenmore and Inshriach Forests (predominantly plantation Scots pine, with small areas of non-native conifer plantation) and upper Rothiemurchus Pinewoods (one of the largest remnant native pine-woods in Scotland). Further detail on historical context is given in Jardine et al. (2010). Here, we focus on recent woodland expansion in the Glenmore and adjacent Rothiemurchus areas.

When FLS (Forestry Commission at the time) acquired the land in 1923, most of the original forest had been felled, and FLS began a significant phase of replanting Scots pine, including experimental regeneration plots. Non-native conifers Sitka and Norway spruce (*Picea sitchensis* and *P. abies*) were planted later and a deer fence was erected, enclosing the forest. In 1992, there was growing recognition of the importance of native woodland and protecting the last remnants of ancient native pinewood. A Caledonian Forest Reserve was created, with environmental conservation as the primary objective, and by 2001, all fences had been removed from the Glenmore estate. The removal of non-native trees began in earnest, and the majority had been cleared by 2004. Culling of both red and roe deer was increased (Figure S2), with populations reduced from approx. 34 deer km$^{-2}$ in 2001 to around 6 km$^{-2}$ by 2008 (Jardine...
et al., 2010); numbers have since fluctuated around 6–10 deer km$^{-2}$, estimated at 7.5 deer km$^{-2}$ in the latest survey in 2019 (unpublished data). Following the initial reduction in deer numbers in the early 2000s, managers observed profuse regeneration on previously open ground, including at higher altitudes (e.g. 71 ha of newly establishing woodland was recorded above 650 m in 2008: Jardine et al., 2010). Scots pine was the most abundant regenerating species, but with several broadleaved species (common alder [Alnus glutinosa], birch [Betula pubescens, B. pendula] and eared willow [Salix aurita]) also recolonising where seed sources existed. This natural regeneration was supplemented with small-scale planting of species without a seed source, specifically bird cherry (Prunus padus) and aspen (Populus tremula), on slopes with drier soils above the existing tree line.

In 2016–17, a detailed survey to assess woodland expansion was carried out across 2026 ha of the FLS regeneration zone, showing extensive regeneration, albeit often at low densities (Figure 2; Figure S1). Individual Scots pine saplings were aged using whorl counts, to determine the pattern of regeneration over time. This showed that the rate of woodland expansion onto previously open ground peaked in 2006–2010 following the removal of deer fences and the increase in deer culling (Figure 2); during this period, ~34 ha (1.7% of the survey area) was added each year to the category having >100 trees per ha. In more recent years (2011–2016), the recorded rate of expansion has declined; this may partly reflect the fact that small saplings (commonly under 4–5 years old) are not picked up with these survey methods, so regeneration from 2011 to 2012 onwards will not be recorded in the 2016–2017 surveys reported here; however, see Section 6 for further discussion of these patterns. Overall, with the sustained effort to keep both roe and red deer numbers low, the survey area has achieved significant establishment of new woodland, with an overall mean regeneration density of 83 stems ha$^{-1}$ (s.e. 6.1) in 2016/17.

### 3 | NatureScot

NatureScot’s land at Invereshie and Inshriach covers over 3000 ha of varied habitats, from ancient native pinewood to the montane plant communities of the high mountain plateau. The site includes Creag Fhiaclach (‘The Toothed Crag’), thought to be Britain’s highest natural tree line at >600 m altitude, where twisted and stunted forms of Scots pine grow alongside juniper (Juniperus communis) scrub. Invereshie and Inshriach were originally separate landholdings, acquired in 1954–56 by FLS (Forestry Commission at the time) and NatureScot (Nature Conservancy Council at the time); these two statutory agencies continue to share management of these areas. The NatureScot land has been managed as a National Nature Reserve (NNR) since 1954.

In 1976, the emphasis for deer control at Invereshie and Inshriach changed. NatureScot was determined to reduce deer numbers to levels that would allow widespread natural regeneration of the forest, and deer culling effort was increased accordingly (Scottish Natural Heritage, 2009), with annual deer population monitoring based on habitat impacts (rather than direct counts of deer). In addition, strategic deer fencing was used in the 1980s and 1990s to restrict access of red deer into the woodland. To monitor the success of natural regeneration following the increase in culling effort and erection of the fence, three 1-km-long transects were established in 1983 in areas close to mature woodland, with surveys repeated several times over the next 12 years. Surveys comprised recording every tree visible above the field layer across a 2-m-wide strip, separated by species (see Figure S1 for transect locations and Supplementary Information 3 for methods). This allowed the evaluation of changes in regeneration density over time, following the initial increase in deer culling effort. These transects were discontinued after 1995, as the density of trees made surveying impractical, and in 2007, a new tree transect was established, on more open ground; this was monitored during 2007–2018. These transect surveys show that considerable regeneration has occurred in all four locations since 1985 (Figure S4). The most abundant recolonising species has been Scots pine, due to the dominance of this species in adjacent woodlands, with Scots pine densities doubling every ~6.5 years on average across the transects. There has also been some regeneration of juniper and broadleaved trees (mostly rowan [Sorbus aucuparia] and birches), but there is evidence that herbivores have selectively browsed broadleaved tree seedlings and saplings, which is likely to have restricted their establishment.

By the mid-1990s, deer browsing impacts had reduced to levels that allowed natural regeneration, due to the fence protection and continued culling. However, concerns over fence strikes by capercaillie

**FIGURE 2** Estimated temporal pattern of woodland regeneration, following deer reduction, of the regeneration zone in Forestry and Land Scotland’s Cairngorms Connect properties at Glenmore and Rothiemurchus. Data from surveys conducted in 2016–2017 are displayed, covering 2026 plots of 0.01 ha each on a 100 m grid within the regeneration zone adjoining mature woodland (see Supplementary Information 2 for more detail on survey methods). Of these plots, 369 had regeneration present in 2016–2017; for these plots, the main establishment date of regeneration was estimated using pine whorl counts. Major management changes are indicated in blue. See Figure S3 for the characteristics of this regeneration by age class (modal height,stem density, altitude and species composition).
led to the removal of all deer fencing by 1999, including the boundary fence between the FLS and NatureScot-owned land, and the two organisations formally adopted the joint vision of establishing a regenerating native woodland in the presence of deer without the use of fencing. To this end, deer culls were increased in the early 2000s (from an average annual cull of 20 deer in 1971–1998, to an average annual of 42 deer in 1999–2004; Figure S5); deer numbers on site are now very low, with dung surveys in 2015 and 2019 suggesting just three and one deer km\(^{-2}\), respectively (unpublished data). A detailed survey of open habitats at points across 489 ha of the regeneration zone was completed in 2017 (Figure 3; see Figure S1 for area covered), following the same methods as the FLS regeneration surveys. This showed that the early 2000s culls had resulted in further natural regeneration, especially of Scots pine; as in FLS ground, an initial burst of regeneration was followed by an apparent slowdown (see Section 6). Median altitude of regeneration rose markedly after 2000, from ~300 to ~400–500 m (Figure S6). In the period of most rapid woodland development (2000–2012), an average of 13 ha (2.6% of the survey area) crossed the 100 trees ha\(^{-1}\) threshold, every year. Fixed-point photographs help to visualise these changes (Figure 4; Figure S7).

*RSPB*

RSPB’s Abernethy Reserve covers approx. 13,600 ha at the northern end of the Cairngorms Connect area, rising from the Spey valley floor to the Arctic-alpine plateau of the Cairngorms at over 1300 m altitude. The majority of the area has been owned and managed by RSPB since 1989 and includes >2000 ha of ancient native pinewood, 1600 ha of Scots pine plantation, a few ha of upland birchwood and >1000 ha of young and regenerating forest. Since purchase in 1989, RSPB has sought to restore woodland to its natural altitudinal limit (Beaumont et al., 2005). Since 2005, the goal has been to double the woodland area over the next 200 years. This is being achieved through a combination of increased deer control to enable natural regeneration, supplemented by targeted planting of broadleaves (to provide seed sources in more remote areas), and field layer management (where it may benefit natural regeneration).

During 1989–2004, the increased deer culling effort (370 deer per year on average) brought about a dramatic reduction in red deer densities, from ~11 km\(^{-2}\) in 1989 to ~2 km\(^{-2}\) in 2004 (Beaumont et al., 2005); the latest dung survey in 2018 estimated red deer densities at 3.4 km\(^{-2}\) in the forested area and 6.2 km\(^{-2}\) in the open ground of the woodland expansion zone (unpublished data). Culling effort has been further increased in recent years, with an average cull of over 600 per year during 2019–2021. The culling operation has evolved over the decades. Initially, a cull target was sought, with most culling across the upper forest and open ground, focussing on red deer. From 2007, the focus changed to cull primarily within the ‘expansion zone’ on the forest edge to encourage natural regeneration and (from 2012) protect planted broadleaved trees. From 2020, deer management has sought to reduce deer density across the whole site, including remote open ground and plantation forests on low ground. With roe deer increasing locally, culling at Abernethy now focusses on both deer species.

To assess woodland expansion in response to deer reductions, three rounds of regeneration surveys were conducted, in 2000–2003, 2010–2011 and 2019 (Figure 5; see Supplementary Information 4 for methods). Between 2000 and 2019, regenerating Scots pine more than doubled in density, from ~100 to ~230 stems ha\(^{-1}\) (Figure 5). Using these data, we estimate that pine densities doubled in a ~15-year period (~2004 to 2019). We also saw a response from broadleaved species between 2010 and 2019, with increases in rowan, birches, common alder and aspen, as well as increases in non-native spruces despite ongoing management to remove these (Figure 5). In contrast, willows declined between 2000 and 2019; this concerning trend will be investigated further. During the most rapid period of increase in the early 2000s, an estimated 28 ha (1.2% of the regeneration survey area) annually changed from being very open to lightly wooded (i.e. >100 stems ha\(^{-1}\)). Overall, our regeneration surveys show that between 2005 and 2019, >500 ha of ‘young woodland’ (i.e. >400 stems ha\(^{-1}\)) has been established, with a further 500 ha expected to establish as woodland by 2030 (i.e. >200 stems ha\(^{-1}\)). Fixed-point photographs help to illustrate the dramatic habitat changes taking place (Figure 4; Figure S8).

It is important to note that some of the recent observed increases at RSPB Abernethy in broadleaved species have been a result of the planting of ~50,000 broadleaved saplings; these have been planted strategically to create new patches of seed source to enable natural regeneration in the long-term. Without this planting, we suspect that the increase in birch would have been less...
marked and there would likely have been no increase in alder or aspen. In contrast, no rowan has been planted and its recent increase appears to be due to ongoing seed dispersal through bird faeces, in combination with the declining deer density (driven by culling) that is allowing formerly suppressed saplings to grow. We hope that as deer density reduces further, we may observe similar expansion of other, rarer animal-dispersed species such as holly (*Ilex aquifolium*) and bird cherry. Going forward, we plan to expand our work to create further new broadleaved seed sources in areas more distant from the existing forest, including montane shrub species on higher ground, and trials and monitoring have been set up to support this.

5 | WILDLAND LIMITED

Wildland Ltd’s holdings make up >31,500 ha in the southern half of the Cairngorms Connect area. The landholding includes the glens of Feshie and Tromie, which are potentially biologically rich glacial valleys supporting remnants of seminatural woodland, rare Arctic willow scrub and near-natural montane vegetation. When Wildland Ltd acquired Glenfeshie Estate in 2006, the area had been managed as a grazing resource for livestock and red deer for many centuries, with native woodlands continuing to decline in quality and virtually no tree regeneration surviving above the field layer.

In Glen Feshie, culling effort was dramatically increased from the early 2000s, with red deer numbers being reduced from >35 deer km\(^{-2}\) in 2000 to between 2 and 5 deer km\(^{-2}\) in 2021. To assess the effects of this increased culling effort, regular monitoring of deer occupancy and tree seedling browsing damage and seedling emergence (i.e. seedlings emerging above the surrounding vegetation) was carried out at 22 transects, including a total of 176 sample plots, between 2001 and 2014 (Figure 6; see Supplementary Information 5 for detailed methods). These surveys showed a reduction in damage and an increase in seedling emergence that coincided with the reductions in deer numbers (Figure 6). For instance, the proportion of tree seedlings emerging above field layer vegetation increased from zero in 2004 (when deer occupancy
NatureScot land, an initial burst of regeneration appeared to be followed by a slowdown (2010–2012, Figure 6; see Section 6).

Alongside these positive changes, regeneration surveys across 723 ha of mature woodland and 1487 ha of unforested ground in Glen Feshie indicated a significant increase in the extent and density of natural regeneration during 2007–2020 (Figure S10). Over the entire 2210 ha survey area, fully established woodland (here, classed as >1100 stems ha⁻¹) increased from 1.3% in 2007 to 8.7% in 2020, whilst regenerating woodland (here, classed as 100–1100 stems ha⁻¹) increased from 10% to 55% over the same period (Figure S10). When considering only the unforested portion of the survey area (1487 ha), we observed a total of 1151 ha (i.e. 77% of the area) moving above 100 stems ha⁻¹ during 2007–2020, equating to an average of 89 ha (6.0%) of the formerly open area transitioning to regenerating woodland annually. Over the same time period, we have observed signs of recovery among other species groups; for example, capercaillie have returned to the glen. Similarly, there are positive changes at high altitudes, with the evidence of recovery of montane willow populations (Supplementary Information 6). Fixed-point photographs help to illustrate the dramatic habitat changes taking place (Figure 4; Figure S9).

In the neighbouring Glen Tromie, restoration is at an earlier point. Culling effort was increased in 2015, and the density of red deer was subsequently reduced from an estimated 45 deer km⁻² in 2003 to approximately 9.0 deer km⁻² in 2017 and just 1.9 deer km⁻² in 2020. Tree seedling damage and emergence were monitored in 2019 and 2020. Damage to tree seedlings above the field layer vegetation roughly halved in just 1 year, from 7% in 2019 to 4% in 2020. Baseline regeneration surveys (equivalent to those conducted in Glen Feshie) were undertaken in 2017 and will be repeated in due course to assess the extent of regeneration in response to the reduced deer numbers; however, early signs are promising and we anticipate a similar response to that observed in Glen Feshie following significant culling (see also Supplementary Information 7).

In the vision for Wildland holdings in Cairngorms Connect, red deer will remain as a key species, effective in sculpting the shrub and herb layers and maintaining open spaces. Periodic influxes of deer will continue to impact the forest, but appropriate densities will be maintained to safeguard the woodland resource and, secondarily, to maintain the potential for commercial income from the deer.

6 | DISCUSSION

We show that over the past 30 years, natural regeneration has led to rapid woodland expansion across much of the Cairngorms Connect area. Our results suggest that over recent years, in core surveyed regeneration areas totalling 6315 ha, approximately 164 ha of new woodland (>100 stems ha⁻¹) has been established annually. If this rate was maintained, it would equate to 820 ha over a 5-year period. This expansion has occurred alongside the removal of most deer fences in the 1990s, combined with a major increase in deer culling that has markedly decreased deer abundance; many parts of...
the Cairngorms Connect area are now believed to have less than the 4deerkm\(^{-2}\) threshold at which natural regeneration generally increases (Beaumont et al., 2005; Putman et al., 2011). The large-scale patterns shown in this study add to earlier work suggesting a strong causal link between deer numbers and pine regeneration in the Cairngorms (Beaumont et al., 2005; Rao, 2017). Therefore, we believe woodland expansion across Cairngorms Connect has occurred as a direct result of the increased collaborative deer cull over the past 30 years. To our knowledge, this study offers the first published evidence (Agra et al., 2016) supporting the use of deer culling to enable woodland expansion across many thousands of hectares. Importantly, we show that some level of deer presence is compatible with woodland regeneration and expansion, supporting the idea that retaining native deer in woodland can deliver better nature conservation outcomes than complete exclusion (Newman et al., 2014). Our work supports previous studies suggesting that tree regeneration can occur freely at red deer densities below 4km\(^{-2}\) in Scottish forests (Putman et al., 2011) or 2.3km\(^{-2}\) in temperate forests more generally (Ramirez et al., 2018), although our experience suggests that the most palatable tree species (e.g. rowan and aspen) may require periods with lower deer densities. The specific deer density that an area can sustain, whilst still allowing tree regeneration, will also be influenced by factors such as ground conditions, climate and altitude, due to potential interactions between abiotic and biotic factors influencing regeneration (Kuijper et al., 2010; Ramirez et al., 2018, 2021; see below). Given that established woodlands can sustain higher ungulate densities without detrimental impact (Ramirez et al., 2018), it may be that intensive deer control could take place in pulses of a few years/decades in each area, enabling phases of extensive woodland renewal and enlargement. The length of higher-intensity control periods would need to be tailored to the growing conditions in specific areas, to allow sufficient time for saplings to establish and grow above browse height for example in temperate regions at lower altitudes and better soils, pulses of 10–20 years could perhaps be sufficient, whilst at higher altitudes a few decades may be required.

6.1 | Caveats and further work

Scaling up nature conservation presents challenges, and Cairngorms Connect is a good example of this, illustrating the sorts of challenges that may arise and approaches to resolve them. Although the 60,000ha area now forms a single partnership with shared vision and goals, each of the four landowning partners manages various parcels of land, each with different histories, leading to a complex patchwork of management and monitoring. This presents challenges for interpreting the picture across the entire partnership in a unified way and leads to some limitations with the current study. For instance, browsing damage was recorded systematically only on Wildland’s landholdings, limiting our ability to show a mechanistic link between reduced deer numbers and increased tree regeneration across the partnership area; future surveys should include an assessment of browsing damage and seek to identify patterns in browsing related to tree species and spatiotemporal factors. Moving forward as a partnership, we plan to align the methodologies and timing of our field-based regeneration surveys as far as possible, with this paper being a key step in doing so. To enable unified assessment across the full partnership area, we aim to increase our usage of remote sensing methods (alongside ensuring that our future field surveys are designed with this in mind) and have been piloting suitable methods.

It is crucial to emphasise that woodland expansion is controlled by numerous factors alongside deer browsing (e.g. Kuijper et al., 2010; Ramirez et al., 2021), and as deer numbers decline, these other factors will increasingly come to the fore. Indeed, the temporal pattern of regeneration following reduced deer numbers observed in this study (initial burst, followed by a slowdown in regeneration rate) could be evidence of this shift in limiting factors as deer numbers decline. For instance, the initial burst of regeneration may have led to all existing regeneration niches being filled, with few new niches being opened up subsequently due to reduced disturbance by red deer. It is also possible that some of the initial burst of regeneration originated from the release of a pre-existing bank of small seedlings that germinated whilst deer numbers were still high, but had been kept small by browsing (Kuijper et al., 2010; Miller et al., 1998), since our FLS, NatureScot and RSPB survey methods do not record seedlings below the height of surrounding vegetation. Further work should seek to better understand how other factors interact with deer numbers and to identify the spatial and mechanistic dependencies of tree demography across long-deforested areas, including proximity to seed sources, altitude, aspect, soil type, vegetation type and topography. Such studies should be used to develop predictive models to feed into an adaptive management framework by enabling managers to determine the deer density and patterns of habitat use that a specific area may sustain, whilst still enabling tree regeneration (Ramirez et al., 2018). Future surveys across Cairngorms Connect (and other similar restoration projects) should also include quantitative, repeatable monitoring of tree browsing damage, which was missing from much of the area in the current study.

Our work informs discussions around the relative merits of planting, natural regeneration and intermediate approaches. An important finding was the difference in regeneration success between tree species: Scots pine showed the greatest expansion, whilst the rarer broadleaves showed limited expansion. This may partly reflect preferential browsing of broadleaves by deer (Ramirez et al., 2023), but is likely to be also a reflection of the lack of seed sources for rarer species and the requirement of some species for more open ground conditions to germinate successfully; future work as outlined above should help to elucidate this. Several authors have highlighted the merits of a spectrum of approaches to achieve woodland expansion (e.g. Reid et al., 2018), including ground preparation to aid regeneration from natural seed rain (Wijedasa et al., 2019), and ‘assisted regeneration’ (Chazdon et al., 2020), whereby small pockets of trees are planted or sown in areas remote from seed sources, to then expand...
managed the regeneration surveys at Wildland. All authors reviewed the manuscript.

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CONFLICT OF INTEREST STATEMENT
The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT
Data are available via the Dryad Digital Repository: https://doi.org/10.5061/dryad.8ght76vh (Gullett et al., 2023).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Supplementary Information 1. Details of methods used to create the woodland maps in Figure 1.

Supplementary Information 2. Details of FLS regeneration survey methods.

Supplementary Information 3. Details of NatureScot tree transect methods.

Supplementary Information 4. Details of RSPB regeneration survey methods.

Supplementary Information 5. Details of WLL deer and regeneration survey methods.

Supplementary Information 6. Montane willows results from WLL.

Supplementary Information 7. Glen Tromie results from WLL.

Supplementary Information 8. Further acknowledgements.

Figure S1. As Figure 1c (existing woodland) but also showing the regeneration survey areas from which data are reported in this paper.

Figure S2. Deer cull figures for FLS Glenmore, during 2000–2020.

Figure S3. Characteristics of woodland regeneration on FLS ground (Glenmore, Rothiemurchus): (a) Modal height; (b) stem density; (c) altitude; (d) species composition.

Figure S4. Tree transect survey results at NatureScot Invereshie & Inshriach, 1983–2018.

Figure S5. Deer cull figures for NatureScot Invereshie & Inshriach, during 1971-2022.

Figure S6. Characteristics of woodland regeneration on NatureScot ground (Invereshie and Inshriach): (a) Modal height; (b) stem density; (c) altitude; (d) species composition.

Figure S7. Further fixed-point photographs, NatureScot ground.

Figure S8. Further fixed-point photographs, RSPB ground.

Figure S9. Further fixed-point photographs, Wildland ground.

Figure S10. Map showing natural tree regeneration in Glen Feshie in 2007 and 2020.