Creating woodland through natural processes: Current understanding and knowledge gaps in Great Britain

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Abstract

1. Creating new woodlands through natural processes, as opposed to traditional tree planting, is expected to result in more structurally diverse, locally-adapted woodlands that enhance the resilience of existing treescapes. However, the outcomes of natural colonisation can be variable, and there is still considerable uncertainty around the ecological processes involved.
2. To address knowledge gaps and guide a future research and policy agenda, we synthesise current knowledge of the ecology of natural colonisation. We combine expertise from 31 practitioners and researchers spanning varied British contexts, including insights from 15 case studies and an expert survey on the relative importance of ecological factors influencing natural colonisation.
3. The most important determinants of successful natural colonisation, identified by practitioners and researchers, were availability of seed sources and low levels of herbivory. However, key knowledge gaps remain around the timeframe and trajectory of woodland development, and appropriate management practices. Natural colonisation and tree planting can be combined to meet diverse woodland objectives, but this has been little explored to date.
4. *Synthesis and applications* Land managers and advisors face uncertainty and many knowledge gaps when creating woodland through natural processes. Site monitoring and adaptive management can help meet site objectives that, in turn, can be supported by policies reflecting uncertainties in the process. Collaboration between researchers and land managers to monitor woodland development, use experimental approaches, and share knowledge, will help further applied ecological understanding, supporting informed decision-making by land managers.

1. Background

Efforts are underway globally to expand tree cover to respond to the combined climate and biodiversity crises. In Great Britain, there are ambitious targets to increase woodland cover from 13% of total land area to 17% by 2050. In many temperate regions, active tree planting has been the primary method of woodland establishment, but its environmental benefits are sometimes overestimated (Holl, 2020); there is growing interest in using more passive restoration approaches that make use of natural processes, such as natural colonisation (where trees colonise and establish new woodlands from nearby seed sources, on previously unwooded land) (Crouzeilles et al., 2017; Fig. 1). In a typical tree planting programme, closed-canopy woodland is established quickly through dense, evenly-spaced planting of a small number of species, which are very rarely of local provenance, as locally-sourced tree whips for planting are not available in many British provenances (Fuentes-Montemayor et al., 2022). Natural colonisation is considered to result in more locally-adapted and natural woodland than tree planting, requiring fewer resources (Supplementary Information 1). However, there is a limited understanding of how best to target, initiate and manage natural colonisation, particularly given the highly variable timeframe, trajectory and success of woodland establishment. Similarly, hybrid approaches combining planting and natural colonisation simultaneously (e.g. low-density planting and 'applied nucleation' or cluster planting; Fig. 1), or in succession (e.g. supplementary planting to complement or support ongoing natural colonisation), have been little explored in a temperate context. Hybrid approaches might allow land managers to speed up the woodland creation process in comparison to natural colonisation alone, and help establish trees far from available seed sources, increasing the tree species diversity (Table 1). Evidence suggests that woodland creation through natural colonisation is often spatially restricted to a fringe around existing seed sources, that tree cover can take several decades to develop, and that the resulting tree species mix is difficult to predict (Bauld et al., 2023, Murphy et al., 2022, Broughton, 2022). 'Success' of woodland creation through natural colonisation is often initially qualified by stem density, indicating succession to woodland (e.g. current England Woodland Creation Offer grant requires 100 tree and shrub stems per ha and 60% woody cover after 10 years (Forestry Commission, 2024)), although natural colonisation can also create more open or mosaic habitats (e.g. shrubland, wood-pasture). To expand the use of natural colonisation in temperate, agriculturally-dominated landscapes, such as in Great Britain, land managers and ecologists need an improved understanding of the processes and its benefits, and the uncertainty of its outcomes.

In response to the limited empirical knowledge on the use of natural colonisation, especially within temperate landscapes, in this paper we:

(1) Synthesise knowledge and experiences from researchers and practitioners, across Great Britain, on the outcomes of natural colonisation through existing research and case studies;
(2) Identify limiting factors of natural colonisation through a survey of 21 experts (co-authors of this paper and Knowledge User Board members) to understand the perceived relative importance of different ecological factors for the process of natural colonisation;
(3) Examine the collected case studies and existing literature to assess the extent to which the perceived limiting factors identified in (2) are supported by empirical or case study evidence;
(4) Identify remaining knowledge gaps, suggest future research priorities and make recommendations for policy & practice.

Our insights draw upon several sources, including discussions held as part of a 'Knowledge User Board' of 20 practitioners (land managers, policymakers and other roles within governmental, non-governmental environmental and private forestry and farming organisations), who met on a quarterly basis between March 2023 and December 2024, as part of an inter-disciplinary project. As well as highlighting knowledge needs among diverse practitioners, these discussions revealed a wealth of experience and highlighted the need for ongoing knowledge sharing between research, policy and practice. To this end, we also organised a webinar where 10 experts (project members and invited researchers and practitioners) shared their insights on the ecology of natural colonisation, and compiled 15 case studies of woodland creation through natural colonisation (Box 1; Supplementary Information 1).

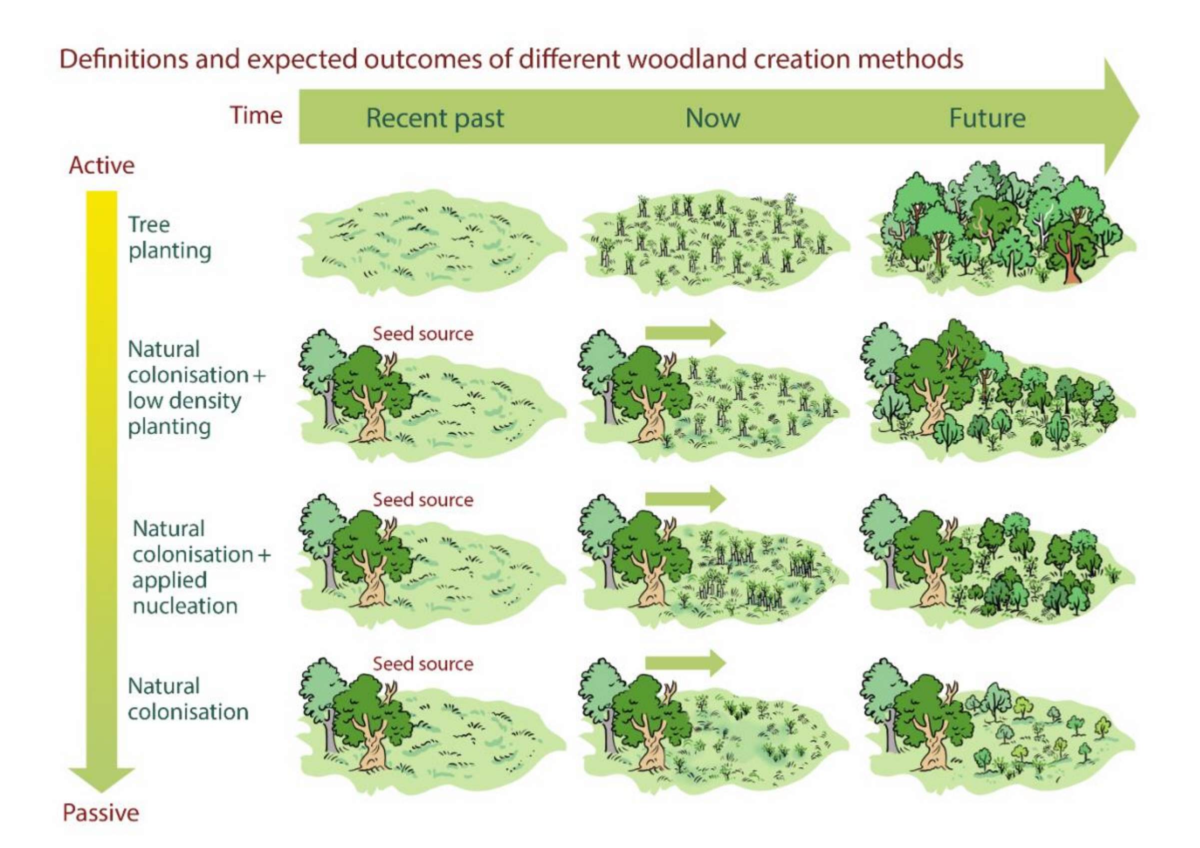

Figure 1. Comparison of tree planting, natural colonisation and hybrid methods (low density planting and 'applied nucleation', where small clusters of trees are planted), in a lowland context.

Box 1: Summary of case studies informing the synthesis

We have collated 15 case studies of woodland creation through natural colonisation across Great Britain (nine in the uplands and six in the lowlands), to address a key knowledge need highlighted by discussions with the Knowledge User Board. Case studies were provided by Knowledge User Board members, and contacts from the project's extended network (e.g. invited webinar speakers, Knowledge User Board members' colleagues, mailing list subscribers). We provide the full descriptions of these case studies in Supplementary Information 1, and botanical names of species referred to in the case studies in Supplementary Table 2. Natural colonisation at the case study sites spans 0.5 – 1000+ ha and 2 – 70+ years. Natural colonisation was chosen as an approach to woodland establishment in most case studies to restore biodiversity, often as part of a wider initiative, often combined with tree planting. Many case studies highlight the importance of a nearby seed source and low levels of herbivory (particularly by deer) for successful seedling establishment. However, outcomes were highly variable, both among and within sites, with a broad range of lessons learned and knowledge gaps highlighted. We refer to the case studies throughout this paper, to synthesise knowledge and insights from both practitioners and researchers. We cite CS1 for Case Study 1, CS2 for Case Study 2 etc.

2. Outcomes and perceived benefits of natural colonisation

Our case studies illustrate that natural colonisation can provide numerous environmental and societal benefits, both during woodland establishment, and for the developing woodland (Box 1; Supplementary Information 1; Table 1). Current research evidence supports these benefits highlighted in the case studies to varying degrees, which we highlight throughout this section, by referencing both case studies and academic literature. Natural colonisation does not always require the labour and resources (e.g. nursery stock, tree guards) associated with tree planting, which reduces establishment costs, and removes risks associated with nursery stock shortages and plant pathogen transport (CS8, CS11, CS13). Compared to planting, soil disturbance onsite is minimal (unless using intensive ground preparation techniques, such as scarification, which have been trialled in some instances as a method of reducing competing vegetation and supporting tree seedling establishment), reducing potential soil carbon losses. Under favourable conditions, natural colonisation can enable landscape-scale restoration where planting is not practical (CS2, CS4, CS7, CS8, CS9), such as in mountainous areas like the Cairngorms, where natural colonisation is restoring woodland biodiversity and providing social and wellbeing benefits (CS7; Gullett et al., 2023).

The transitional scrub phase during natural colonisation in lowland areas (Fig. 2h) has high biodiversity value, with complex, mixed vegetation providing multiple niches, such as for pollinators (CS14; Mortimer et al., 2000, Broughton et al., 2021). These early successional habitats continue to provide such biodiversity value where establishment of tree cover is slow (which may otherwise be perceived as ‘unsuccessful’ in rapidly achieving closed-canopy woodland), and can also support recreation (CS13, CS15; Broughton, 2022). In upland environments, natural colonisation can help expansion of globally rare and biodiverse temperate rainforest fragments where planting is difficult to achieve, support climate refugia, and often remnant woodland ground flora (CS1-9; Table 1; Ellis, 2020, Murphy et al., 2022, Murphy et al., 2024, Porton et al., 2024). Due to climate, landscape and herbivore constraints, natural colonisation in the uplands can produce spatially variable and diverse outcomes, with scrub-herbivory dynamics potentially supporting both mosaic habitats and closed-canopy woodland development, connecting existing woodland biodiversity, and restoring hydrological functioning (CS1-9; Murphy et al 2021). Overall, woodlands established through natural colonisation appear structurally complex (vertically and horizontally), with a diverse age profile, varying distances between trees, and a patchy canopy structure with varying light penetration: factors important for woodland habitat quality (Fig. 2a-h; CS4, CS14; Spracklen et al., 2013, Broughton et al., 2021, Forest Research, 2020). Woodlands established through natural colonisation also appear to have the potential to support greater biodiversity more quickly than through conventional planting, including priority species in the uplands, such as black grouse and beaver (CS7).

The establishment of trees from local seed sources is expected to conserve the genetic diversity of local tree populations, and allow them to adapt to new site conditions, pathogens and environmental change by natural selection, enhancing the resilience of both new and existing woodlands. Natural colonisation most readily takes place adjacent to existing woodland, or mature hedgerows, enhancing woody habitat connectivity, the potential for the expansion of ground flora and other woodland specialists, and buffering the existing woodland from surrounding land-use impacts and climatic extremes (CS1, CS3, CS10; Bauld et al., 2023, Hughes et al., 2023a, Hughes et al., 2023b).

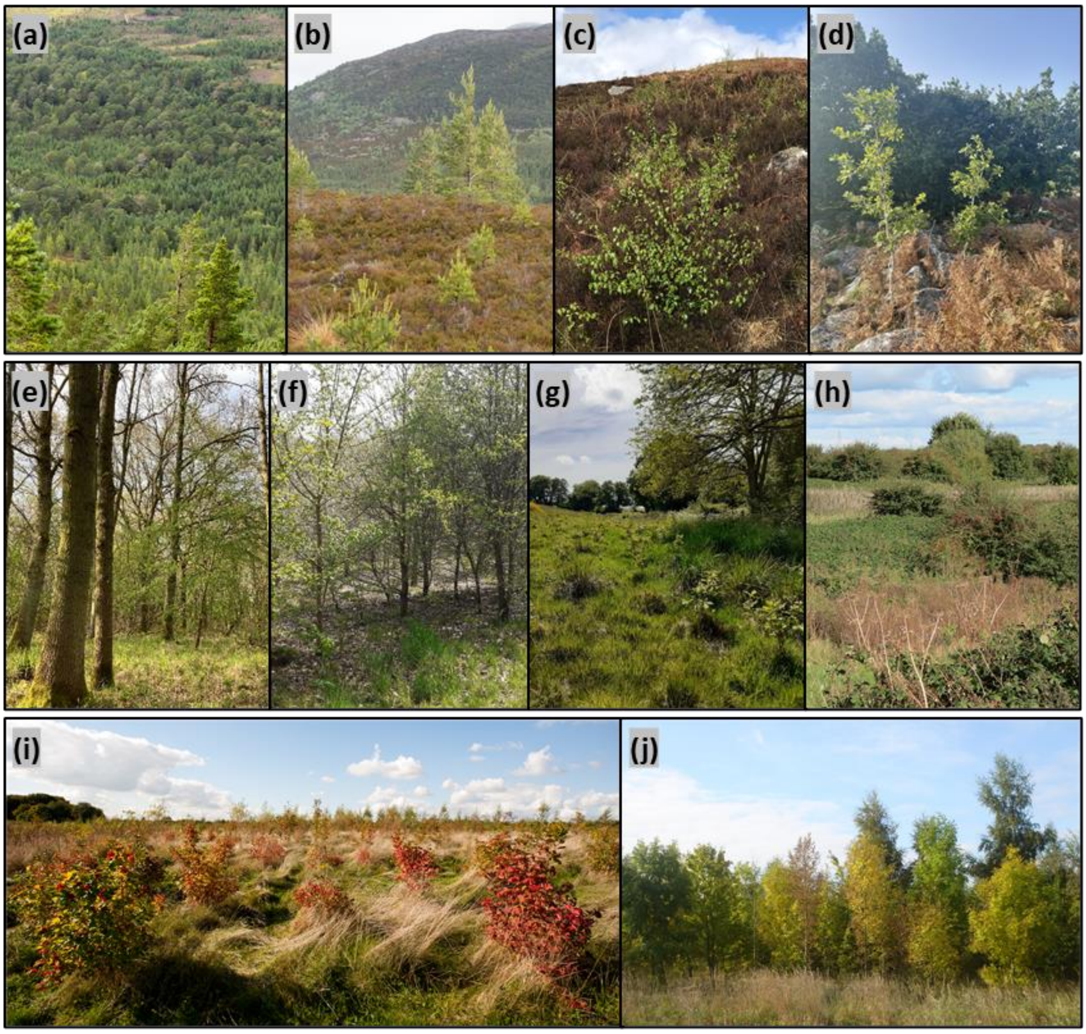

Figure 2. Photos of woodland creation. Natural colonisation in the uplands: (a) ~40 years and **(b)** ~20 years of pinewood expansion in the Cairngorms; **(c)** young birch in the Highlands following 3 years' deer fence protection; **(d)** young oak at Sampford Spiney, Merrivale, natural colonisation site on Dartmoor. **Natural colonisation in lowland England: (e)** following 62 years at Monks Wood, Cambridgeshire, following **(f)** 20 years and **(g)** 5 years at Hucking, Kent, **(h)** following 30 years at Noddle Hill, Hull (still at the scrub stage, credit xx). **Tree planting: (i)** Heartwood Forest, Hertfordshire, ~15 years old, and **(j)** Londonthorpe Wood, Lincolnshire, ~6 years old.

3. Ecological factors influencing natural colonisation

Both case studies and existing literature highlight the high degree of variability in the process of natural colonisation, both in the distance over which trees and shrubs establish from the nearest seed source, and the time taken (Table 1). For example, in lowland England, canopy closure can occur within twelve years (CS11) or take many decades (CS15). Progress is often slower across the British uplands, constrained by diminished available seed source, lower temperatures, poorer (and wetter) soils, and herbivores (deer and livestock) (Table 1), although colonising birch can close canopy after a decade in favourable conditions in the Highlands (CS6). Our case studies highlight that the process and outcomes of natural colonisation can vary substantially within sites, often due to factors that are not understood (CS4, CS7, CS8, CS15). We conducted a survey of 21 experts (practitioners and researchers), to rate the perceived relative importance of ecological factors influencing natural colonisation, and provide confidence in these ratings. Overall, practitioners and researchers agree that proximity to seed sources and low herbivory (particularly by sheep and deer) are the most important factors for the success of natural colonisation (Fig. 3; Supplementary Information 1). However, many other interacting factors also determine the speed and trajectory of colonisation, making the process highly context-specific (depending on local site, tree species, climate, season, stage of woodland development, etc.) and complex to predict. The perceived importance of different factors also depends on the objectives for woodland creation: for example, wind-dispersed willow and birch can colonise some sites quickly, but may not meet land managers' biodiversity objectives (CS6). We use our case studies and existing literature to summarise current knowledge on these factors below.

Table 1. Outcomes of natural colonisation at various sites: dispersal distances and time taken for woodland establishment (partial information available for some sites only).

Site and habitat	**Dispersal distances, tree density and time taken**	**Tree species** (see Supplementary Table 2 for botanical names)	**Use of tree planting**	**Source**
Lowland				
Multiple sites across England: arable and improved	After **20 years** of natural colonisation, tree densities of 100 stems/ha were achieved at 70 m from the adjacent	Not identified (remote sensing study)	None	Bauld et al. (2023)

grassland (lowland), and heath and acid grassland (upland)	woodland edge in upland sites, and 140 m in lowland sites on average, although there was considerable variability around these figures. Densities peaked at 20 m from the adjacent woodland edge, where there were 170 trees/ha in upland sites and 400 trees/ha in lowland sites on average.			
Multiple sites across lowland England – 9 natural colonisation & 12 hybrid	After **14-43 years** of natural colonisation at ex-farmland sites adjacent to existing woodland, there were ~720-2300 stems/ha. At hybrid sites (13-28 years old), there were ~400-2200 stems/ha.	Variable across sites. Predominantly willow, hawthorn, oak, silver birch, blackthorn and ash	Some tree planting in 12 hybrid approach sites (spatially mixed at four sites, discrete areas at eight sites),	Braunholtz et al. *In prep*.
Rickstaddle Farm, East Sussex	Scrub formed within four years and had a closed-canopy woodland in **12 years** from the start of natural colonisation	Willow (goat, grey & crack), hornbeam, oak, ash, aspen, blackthorn, downy birch, hawthorn, field maple sycamore, crab apple	None	CS11
Monks Wood, Cambridgeshire	Closed canopy oak-ash woodland developed through natural colonisation in **40-50 years**, with densities of 390 trees/ha after 59 years, at a field surrounded by ancient woodland on three sides (maximum distance to woodland edge 112 m).	Mostly oak, ash, field maple, hawthorn, blackthorn colonising. Adjacent to oak-ash woodland	None	CS14; Broughton et al. (2021)

	There were 132 trees/ha following **25 years** of natural colonisation on a younger grassland, all of which was within 122 m of the nearest ancient woodland edge.			
Noddle Hill, East Yorkshire	After **33 years** of natural colonisation, only 53% of the site was covered by thorny scrub (average woody vegetation height 2.1 m), but the nearest mature woodland is at a distance of 1.5 km (there are, however, hawthorn-dominated hedgerows at the site).	Hawthorn, with some elder, willows, ash, oak, silver birch, blackthorn. Bramble forms the dominant scrub cover.	None	CS15; Broughton (2022)
Upland				
Multiple sites on Dartmoor	After ~**10 years** of natural colonisation, oak largely dispersed within 10-20 m of nearest seed source, at densities up to 1900 saplings/ha, although this varied substantially by site. Maximum dispersal distance was 75 m. This was primarily by mammal and wind dispersal, with principal animal dispersers (jays) diminished or absent. Hawthorn, rowan and holly had greater dispersal distances of up to 50-100 m.	Oak, hawthorn, holly, rowan	None	CS1; Murphy et al. (2022)
Wild Ingleborough, Yorkshire Dales	On limestone soils, 100 trees/ha after 10 years of natural colonisation attained at a distance of 113 m from the nearest woodland edge. Natural colonisation progressed more slowly on other soil types (peat	Predominantly ash, with hawthorn, hazel, juniper and rowan	Extensive planting of a diverse range of tree species. Predominantly in areas away from seed	CS2; Porton et al. (2024)

	and glacial till). Closed canopy not achieved after **40 years** (possibly slowed by ash dieback).		sources to accelerate woodland creation.	
Hardknott Forest, Cumbria	Natural colonisation following clearfell of conifer plantations gave rise to closed canopy (predominantly birch) after 15 years, and tree densities of 3000 stems/ha after **25 years**. Colonisation occurred up to 2 km from the nearest seed source, with no relationship between establishment of animal-dispersed species (oak and rowan) and distance to seed source. Birch colonised most densely within 20 m of a stand of mature trees.	Predominantly birch, rowan and willow	None	CS4; Spracklen et al. (2013)
Multiple sites across Scottish Highlands	In general, 90% of seed falls within 60 m of nearest canopy edge, and very little beyond 150 m. Colonising birch can close canopy after 10 years in favourable conditions. At Tomnavoulin, Banffshire, young woodland formed 120-150 m from the existing woodland edge in **35 years**, but tree dispersal distances appeared further than average. On deer removal or substantial reduction, there often is an initial ‘pulse’ of colonisation (probably largely ‘advanced’ regeneration: previously germinated but low-growing seedlings) followed by a slow rate of ongoing recruitment.	Scots pine, birch	None	CS6; Thompson (2004)

Cairngorms Connect	Scots pine, birch and willows mainly establishing within ~50 m of seed source, but some individual trees several km away. Rowans establishing further from seed sources in some areas due to bird dispersal. Sapling densities highly spatially variable, reaching >1100 stems per ha in some areas but more commonly ~100-400 stems per ha, after 20-35 years of intensive deer culling.	Predominantly Scots pine, also birch, eared willow, rowan	Small areas of planting in locations remote from existing seed sources	CS7; Gullett et al. (2023)
Corrour, Scottish Highlands	Most seedlings are within 50 – 100 m of the seed source, but some establish 500 m and up to 1000 m away (like other sites in the Highlands, probably largely 'advanced' regeneration). After **four years** of deer exclusion, vegetation has a mean density of 800 seedlings/ha and some trees are nearly 2 m tall.	Downy birch, rowan, willow (eared, goat, grey) and alder	Some native woodland planting in areas without nearby seed sources, and because some key species are not present (e.g. Scots pine and sessile oak).	CS9

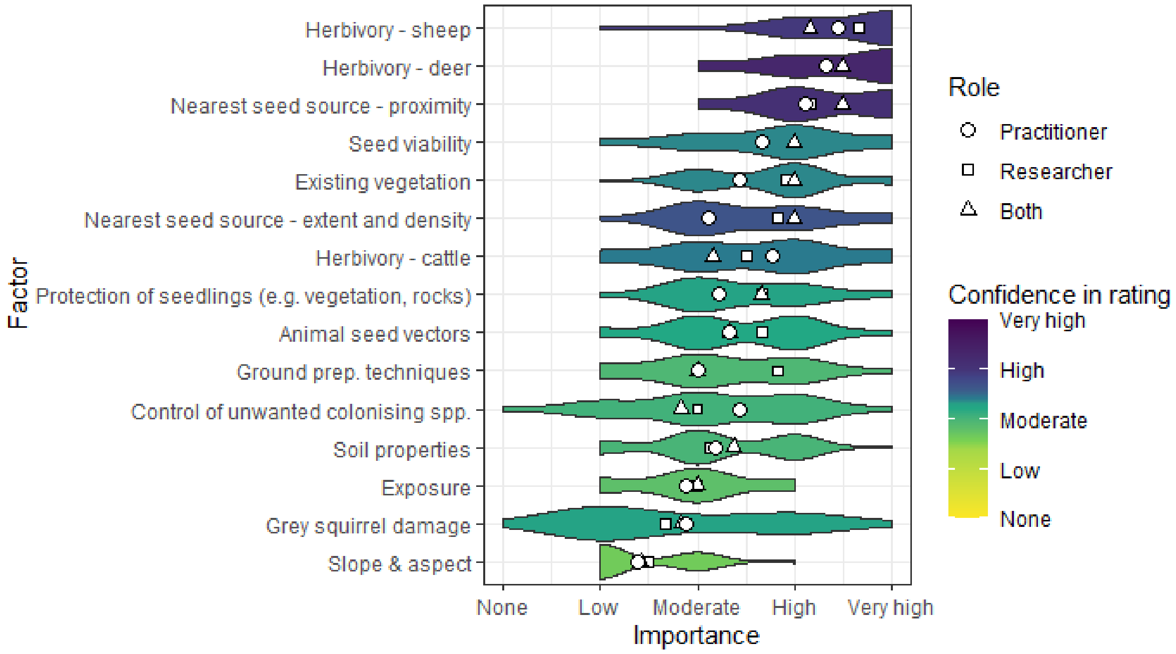

Figure 3. Kite diagrams of the perceived importance of key ecological factors influencing natural colonisation, from the survey of 21 experts (practitioners, researchers, and individuals who are both practitioners and researchers). Factors are ranked according to mean importance rating, points show mean rating by respondent role, and shading corresponds to mean rating in respondents' confidence in their answers. Both importance and confidence were rated on a five-point scale as labelled. For full suite of factors included in the survey, and comparison of ratings between upland and lowland habitats, see Supplementary Fig. 1.

Seed source and dispersal

Trees generally colonise most densely adjacent to a seed source (e.g. existing woodland), gradually expanding the existing woody habitat. Numerous existing studies, all of our case studies, and survey results have identified the importance of distance to nearest seed source for seedling establishment (Fig. 3; CS1-15; Porton et al., 2024, Spracklen et al., 2013, Bauld et al., 2023, Thompson, 2004, Gullett et al., 2023, Murphy et al., 2022, Broughton et al., 2021). Actual seed dispersal distance varies considerably, and appears to be shorter on average in the uplands than lowlands (Table 1; Bauld et al., 2023).

Broadly, British lowland woodlands are more dominated by animal-dispersed tree species (e.g. oak, beech, hazel, hawthorn, blackthorn) than upland woodlands, reflected in the greater perceived importance of the presence, abundance and behaviour of animal seed vectors for colonisation in the lowlands (Supplementary Fig. 1). However, lack of animal-dispersed species in upland sites may reflect deer pressure, as wind-dispersed species (particularly birch and Scots pine) are often less palatable to deer (CS6-8). Oak dispersal in both lowland and upland sites can depend on presence of jays *Garrulus glandarius* and acorns only travel very short distances in the absence of jays (CS1, CS15; Broughton, 2022, Murphy et al., 2022). However, exceptionally long dispersal distances of rowan (hundreds of metres or more) have been noted in the Scottish Highlands, presumably by birds (CS7, CS9). Prevailing wind direction can also drive seed dispersal (CS6, CS7), although its importance in different contexts is not yet understood.

Herbivory

Herbivore pressure, particularly by deer and sheep, is highly limiting to seedling establishment and survival (Fig. 3); indeed, most (but not all) case studies included herbivore exclusion/control (CS1-15). Herbivore control is generally most costly in the uplands, where red deer (heavy browsers with a strong preference for young broadleaves) are abundant and land parcels often unfenced. Several case studies suggest that establishing woodlands through natural colonisation can be much cheaper than planting, including in the long-term and at landscape-scale (CS1-11, CS13, CS14). Seedlings can establish in the presence of herbivores when protected (e.g. by rocky areas, steep terrain, and 'nurse' vegetation species which are generally dense, unpalatable or thorny), although browsing may influence the distribution of established seedlings (CS1, CS2, CS11, CS14; Broughton et al., 2021; Murphy et al., 2022; Porton et al., 2024). Low densities of cattle, and sometimes deer, do not appear to limit colonisation, but may encourage a habitat mosaic with some open areas, supporting greater diversity overall (CS2-4; Porton et al., 2024; Murphy et al., 2022).

Competing vegetation and ground disturbance

Availability of niches and competition from existing vegetation are considered important for the process of natural colonisation, but given a moderate confidence rating in survey responses (Supplementary Fig. 1). Removal of highly competitive vegetation can aid colonisation (e.g. removal of unwanted regenerating conifers at ex-plantation sites; CS4). However, one land manager reported that planted trees survive drought best when surrounded by a tall sward, possibly through improved soil moisture retention, in addition to potential 'nurse' benefits of shrubs, bracken, and brambles to tree seedlings (CS1, CS2, CS11, CS14; Murphy et al., 2024, Porton et al., 2024). Tree species vary in their ability to colonise and persist in different conditions (e.g. grass sward vs bare ground); oaks can grow quickly from 'advanced regeneration' (previously established but stunted seedlings) when herbivore pressure is reduced (CS6, CS9; Thompson, 2004).

The impacts of ground preparation on seedling establishment are not well understood, but several case studies document rapid colonisation of disturbed soil: on a clear-felled conifer plantation (CS4), on bare ground intended for scrapes (CS13), and following an intense fire (CS6). Light poaching and/or trampling of dominant vegetation (e.g. bracken) by large fauna such as cattle, ponies, and pigs may help facilitate natural colonisation, by opening up the sward at early stages of establishment (CS2, CS3; Murphy et al., 2022). Practitioners perceive ground preparation as being less important than researchers do (Fig. 3), perhaps because of doubts that its usefulness would outweigh additional labour and costs; understanding the site conditions and objectives under which its potential to speed up colonisation remains a key knowledge gap (Box 2). The potential influence of soil disturbance on the composition of colonising species also remains unknown.

Site characteristics

Soil properties, site elevation, exposure, slope, aspect and other physical characteristics influence natural colonisation to varying degrees at different sites, depending on the limitations imposed by other factors (e.g. herbivory). Survey results suggest that soil properties are perceived as more important for determining natural colonisation in the uplands than lowlands (Supplementary Fig. 1).

Seedlings can struggle to establish in carbon-rich peat and waterlogged soils, which are extensive across British uplands, but these areas may provide greater carbon and biodiversity benefits as open peatland habitats (as an Environmental Impact Assessment in the UK should determine; CS2, CS4, CS6; Murphy et al., 2024, Thompson, 2004). Site exposure, particularly low temperatures and high wind speeds, hinders seedling establishment and growth, but existing vegetation can alleviate this (e.g. shrubs, bracken; CS1).

4. Knowledge gaps

We identified many knowledge gaps on factors influencing natural colonisation, its outcomes and benefits, and how best to achieve aims of woodland expansion through combining it with other woodland creation methods (Box 2). Our understanding of natural colonisation is limited by its variability, the importance of individual site context, limited British examples to date (particularly with long-term records, e.g. CS8, CS14), and an apparent bias in reporting woodland creation successes rather than 'failures', where woodland does not establish in a certain timeframe (e.g. CS15). Broadly, land managers currently using natural colonisation are 'early adopters', and have often needed to apply their own knowledge to achieve desired outcomes, with limited support from evidenced-based guidance. As well as guiding a future research agenda, we intend our list of knowledge gaps to help inform land managers' decision-making, by highlighting uncertainties, although the importance of these will depend on site context and the desired timeframe for woodland creation.

Box 2. Knowledge gaps on natural colonisation, identified by practitioners and researchers

Driving factors: seed source and dispersal

- How do local ecological conditions determine the dispersal and establishment abilities of different tree species?
- How do dispersal distances vary by seed source type (e.g. well-wooded landscapes compared to isolated stands of mature trees)?
- What are the relative contributions of different mammals and birds to seed dispersal, including their impacts on seed viability and seed predation (e.g. jays and other corvids, thrushes and other passerines, small rodents, grey squirrels)?
- What are the key determinants (moisture, nutrients, vegetation communities, weather) of the movement and behaviour of animal dispersers in a landscape, and how do these affect natural colonisation?
- How does the configuration of existing trees in a landscape affect the potential for natural colonisation?

Driving factors: herbivory

- How do different grazing species and the intensity and timing/seasonality of herbivory affect natural colonisation and ongoing development to a closed-canopy woodland?
- How can grazing by cattle assist natural colonisation in upland open and scrub habitats?
- Do grey squirrels reduce tree establishment or survival?

Driving factors: competing vegetation, ground disturbance and soil properties

- How do soil type, hydrology and existing ground vegetation affect natural colonisation?
- When is surrounding ground cover beneficial for establishing trees (e.g. regulating soil moisture through drought), and when is it hindering (e.g. competition for resources)?
- What are the interactions of soil factors with grazing?
- What are the effects of ground preparation/disturbance on natural colonisation? Does it help or hinder the process, or do impacts such as soil disturbance outweigh potential benefits (e.g. from soil carbon emissions)? When is intervention necessary to help facilitate colonisation?
- When does disturbance by large fauna (e.g. cattle, pigs) assist or hinder seedling establishment?
- What is the role of mycorrhizal communities and other soil biota, particularly if these are lacking in long-deforested areas?

Driving factors: local ecology and microclimate

- What are the effects of slope, aspect and microclimate on natural colonisation? How do these and other factors act in different contexts across Great Britain?
- How do other ecological factors influence new and existing (potential seed source) woodlands? E.g. pollinator decline, climate change

Outcomes of natural colonisation

- What is the potential tree density achievable through natural colonisation under different conditions?
- Can we predict the outcomes of natural colonisation? How can we assess a site for its potential?
- How can we assess the progress of a site undergoing natural colonisation?

- How can we use natural colonisation to maintain favourable conditions for woodland development in the long-term, and facilitate a long-term ecological recovery of long-deforested woodlands, to full species assemblage of flora and fauna?
- What are the opportunities for production from naturally colonised woodlands (e.g. timber, coppice products; also carbon credits)? How can management best support these?
- How can natural colonisation support wood-pasture creation, that includes open grazed areas as well as woodland patches?
- Do naturally colonised tree populations show genetic adaptation to environmental change, and over what timescale? How does this potential genetic resilience relate to seed source and other landscape factors?
- What is the carbon balance of natural colonisation through time, including impacts on soil carbon?
- What are the relative costs of woodland establishment through natural colonisation and tree planting over time, in relation to different site objectives?
- How should weeds be managed in the early stages of natural colonisation, particularly on lowland arable sites?

Combining natural colonisation with other woodland creation methods

- When and how should tree planting and natural colonisation be combined? Can this result in more diverse and resilient woodlands than through a single method alone? How does this change over time? How can we assess the landscape context to decide on the most appropriate woodland creation methods?
- Is the genetic diversity of native woodlands sufficient for tree populations to adapt to environmental change? When might planting for adaptation to future environmental conditions be beneficial?
- How can planted trees and woodlands support natural colonisation far from an established seed source, across a range of landscapes and contexts?
- When is direct seeding most effective, and for which tree species? When and how should direct seeding be combined with natural colonisation and/or tree planting?

Perceptions and social benefits of natural colonisation

- What are the social and other societal benefits of natural colonisation, and how can sites be designed and managed to best support these?
- How are different stages of natural colonisation perceived by local communities and site visitors and how does this compare to tree planting?
- How can natural colonisation benefit people and nature in challenging contexts for restoration, such as peri-urban areas or alongside infrastructure (e.g. road and rail)?

- What level and format of information should be provided to the general public, to showcase the process and objectives of natural colonisation at a site, and avoid misunderstandings such as perceived land abandonment?

5. Implications and recommendations for management, policy and research

Although our focus is on Great Britain, many of the knowledge gaps and implications are applicable to other contexts, since the establishment of woodland is underpinned by fundamental ecological processes. The process and outcomes of natural colonisation are highly variable, but combining natural colonisation with tree planting substantially broadens the range of contexts in which it might be used to successfully create woodland. Based on the evidence synthesised here, in this section we outline key ways in which land management, policies, and research can support woodland creation through natural colonisation and hybrid approaches.

Adaptive land management

While allowing natural processes to take their course without intervention can be a site objective itself (CS9, CS11, CS14, CS15), sites with specific target objectives for woodland creation will often require adaptive management approaches in the long-term. By monitoring and reviewing site progress and responding to changes accordingly, site managers can enable the dynamic process of natural colonisation to lead to desired management outcomes.

We recommend that land managers and their advisors:

- Acknowledge the inherent variability and dynamism of natural colonisation in woodland creation plans, setting appropriate objectives (e.g. allowing for more time to canopy closure than through tree planting).
- Considerer planting alongside natural colonisation, to help increase stem density and canopy cover and/or introduce desired species (e.g. for timber, or to help restore tree species that are rare or absent in a landscape), if natural colonisation alone cannot meet site objectives

(e.g. CS7, CS9; Gullett et al., 2023). Planting and natural colonisation could be simultaneous, or supplementary planting could mitigate absence of certain species or lower stem densities than desired (which may be a requirement of some funding offers).

- Considerer collaboration with neighbouring land managers for landscape-scale projects (e.g. coordinated deer control), which require clear communication and agreed shared visions for management and goals (CS7; Gullett et al., 2023).

Policy and professional advice

Since post-war policy efforts to increase tree cover across Great Britain, most woodland creation has been through tree planting. To increase the use of natural colonisation for woodland expansion, we recommend that policymakers:

- Include natural colonisation in national/regional strategies and targets for woodland expansion, prioritising areas most likely to colonise successfully and/or benefit existing habitats (e.g. near existing woodland).
- Support training of land managers and advisors on natural colonisation and hybrid approaches.
- Support further development of financial incentives for natural colonisation and hybrid approaches, acknowledging the inherent variability of the process by incorporating flexibility, support, and advice during the application process, and supporting adaptive management.
- Continue financial and capital support for applied research to address key knowledge gaps, in line with our suggestions below.

Collaborative research and knowledge exchange with and for land managers

Land managers and advisors face many uncertainties when facilitating natural colonisation, reflected by numerous knowledge gaps (Box 2). There is a strong need for collaborative research and monitoring with and for land managers, to help informed decision-making and effective adaptive management.

We recommend that researchers:

- Prioritise management intervention options in future research questions (e.g. grazing and herbivore presence/densities, ground preparation, supplementary planting or seeding, and thinning of established seedlings).
- Develop pragmatic trial designs that can be implemented in operational management systems, to test interventions under replicated, controlled, long-term experiments (e.g. ground preparation trials at Fairfield Forest in Worcestershire (CS12)).
- Establish collaborations with land managers and advisors to undertake long-term monitoring and recording of individual sites, share and report failures and successes, and establish good practice for woodland creation using natural processes.
- Collaborate with land managers and advisors to develop operational indicators and monitoring protocols to understand the process of natural colonisation, and identify when and how to intervene, depending on site goals and context.

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Author contributions

SF, MJM, VB, EFM, RO, HG, KW, BAO, LB, JK, MG and KJP conceived and facilitated the knowledge exchange activities leading to the collation of information presented in this article; all other authors, VB and LB contributed case studies and/or land management experiences as primary information for the article; SF, MJM, VB, KW and EFM led the writing of the manuscript. All authors have read and approved the final version of the manuscript.

Acknowledgements

Many thanks to Sian Atkinson, Mel Meaden, Chris Tucker, Neil Strong, Fran Graham, Rob Cleaver, Jon Lewney, Hazel Earnshaw, Jonathan Callis, Robin Truslove, Georgie Pelly, Phil Knott, Sophie Bray, Eleanor Marks and Alex Pearson for their contributions through the Knowledge User Board discussions, to Maddy Pearson for her role in setting up the Knowledge User Board, to Jim Turner for information on Gait Barrows case study, and to Thiago Silva, Sam Hughes, Mel Meaden and Neil Strong for comments on the research and/or manuscript. This work was part of the TreE PlaNat project funded by the UKRI 'Future of UK Treescapes' Programme, grant number NE/X004619/1.

Data availability

The case studies of natural colonisation are available in Supplementary Information 1.

Conflict of interests

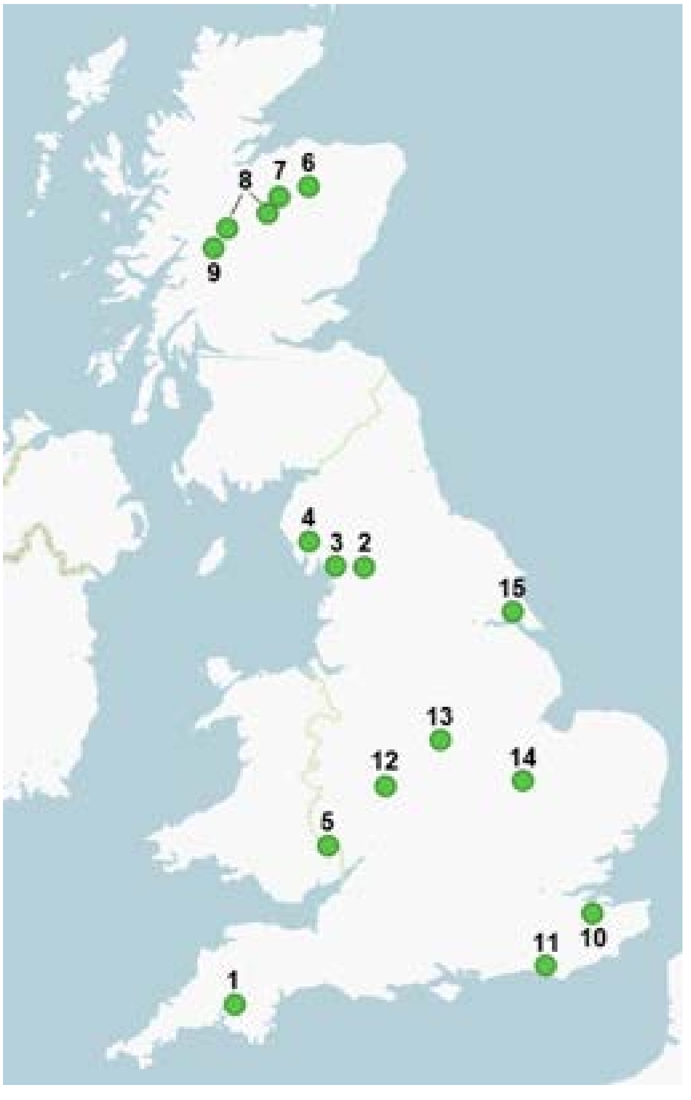
The authors have no conflicts of interest to declare.

Factsheet: Case studies of woodland creation through natural colonisation

Natural colonisation: what to expect?

Natural colonisation has the potential to create biodiverse, locally-adapted woodlands, and help expand tree and woodland cover across the UK, but the outcomes of the resulting habitat are uncertain. These fifteen case studies provide an overview of some of the timescales and outcomes of creating woodland through natural colonisation in a range of habitats across Britain. The natural colonisation across the case studies spans 0.5 – 1000+ ha and 2 – 70 years, and cover both upland areas (Case Studies 1 – 9) and lowland areas (Case Studies 10-15). In lowland England, the timeframe for naturally-colonised woodland to resemble mature woodland varies from within 50 years (Monks Wood, Case Study 14) to much longer (e.g. very low tree cover after 30 years at Noddle Hill, Case Study 15). In the Scottish Highlands, young woodland can form within 30-40 years under intense deer management, but this is also highly variable (Case Studies 6,7,8).

As the case studies were collected from different sources, it was not possible to provide the same level of detail for every site. Some case studies are too recent to provide information on tree establishment, but are included to show the breadth of examples where natural colonisation is being used across Britain.



Map of case studies

Why use natural colonisation?

Biodiversity restoration is a key aim in the vast majority of the case studies. Many site managers view the longer time taken to form a structurally diverse woodland, with locally-adapted seedlings, as strong benefits of using natural processes over tree planting. However, **half of the case studies also had areas of tree planting**, to help meet site goals such as habitat restoration, through planting of species that were not present in mature form as seed source, or to ensure the development of some closed-canopy woodland within a shorter timeframe.

Some key lessons learned

Deer management is key to success in the uplands, but exactly what density of deer young woodland can support is still uncertain.

Proximity to a seed source is also crucial for colonisation of diverse seedling species. All case studies had some mature native trees or woodland nearby as seed sources.

There are many remaining key knowledge gaps, such as whether to intervene when young woodland is dominated by a small number of colonising species, how best to manage the variable outcomes of natural processes, and understanding the roles of soils and mycorrhizae.

Uplands - Case study 1

Dartmoor Atlantic Oak Woodlands (Merrivale)

Case study provided by Thomas Murphy, University of Plymouth

Publicly accessible
Grid ref. SX551741

Aims of the natural colonisation: The natural colonisation is unplanned with no dedicated planning, however, lower density and mixed growth forms of seedlings might support movement/ expansion of epiphyte lichen species from adjacent ancient oak woodland habitat.

Site description: Upland landscape of west Dartmoor, dominated by grassland and scrub habitat, bordering Sampford Spiney SSSI. The dominant land uses are grazing livestock (sheep and cattle) with some existing oak woodland. There are large granite boulders and the soils are podsols.

Area set aside for natural colonisation: ~1 ha

Year that natural colonisation began: 2010 – 2015

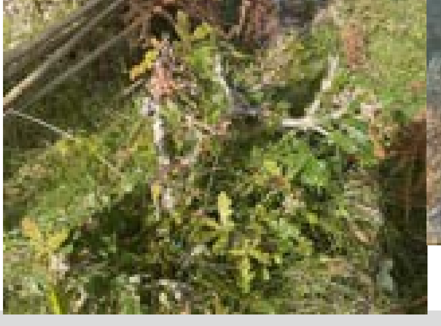
Seed sources for natural colonisation: Nearby oak woodland

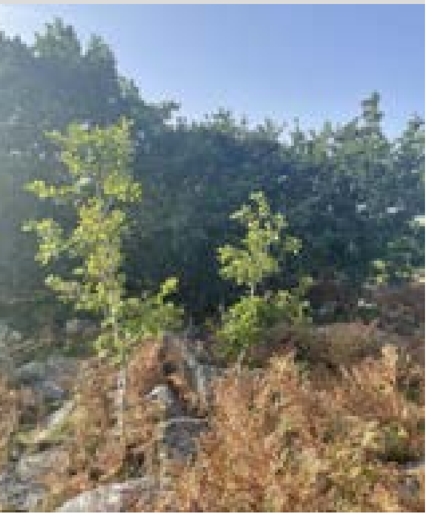
Preparation actions prior to the natural colonisation: None

Maintenance during establishment of natural colonisation: None

"Both natural colonisation and tree planting have a role to play in creating resilient woodlands – the choice depends on the context.

Natural colonisation does not always create better woodlands – some natural colonisation is species poor and will be for a long time."





Young oaks (Thomas Murphy)

Which species have successfully colonised, and where? What is the resulting woodland structure? Relatively low species diversity and slow colonisation: oak has colonised up to 10m from the existing woodland edge, with rowan, holly and hawthorn 50 to 100m away. The site is a long way from closed-canopy woodland. Some saplings old and very small, others tall – site has high vertical diversity.

Dominant drivers of natural colonisation: Both granite clitter and bracken can protect seedlings from grazing livestock and provide shelter. Acorns are mostly wind-dispersed here, so oaks only establish 10m from the seed source. Sheep browsing, exposure and competition from the grass sward limit seedling establishment.

Lessons learned: Natural colonisation is complicated - in particular areas, it's not simply a matter of removing animal grazers – expansion site might need a helping hand to kick start the process.

Key challenges: Particularly in upland landscapes, lack of existing trees as a seed source nearby and dispersal agents means it is not always true that natural colonisation produces species diverse woodlands. The species mix and speed of natural colonisation are unpredictable, which puts us at risk of failing to achieve desired outcomes. This also makes planning very difficult as management of naturally colonised sites will look different in each location.

Advice for others: Supporting natural colonisation will involve different approaches at different sites, depending on the context and landscape. Consider the woodland objectives. Natural colonisation alone won't always provide all of these. Think about the suitability of conditions for trees through time and adapt management accordingly.

Knowledge gaps:
Role of natural colonisation in supporting movement of key taxa from upland refugia sites? Landscape constraints to natural colonisation and role of natural colonisation in supporting wider resilience and functioning compared to planting approaches? How might planting support improved natural colonisation outcomes? Influence of herbivore behaviour on natural colonisation processes?

Also see Murphy *et al.* 2022 https://doi.org/10.1002/2688-8319.12126 and 2024 https://doi.org/10.1016/j.foreco.2024.121895

Uplands - Case study 2

Wild Ingleborough, Yorkshire Dales

Case study provided by George Porton, University of Leeds

Publicly accessible

Grid ref. SD742758

Aims of the natural colonisation: Nature restoration and conservation

Site description: Upland limestone pavement landscape in the Yorkshire Dales. Entire site area is 1195 ha, covering approx. 300-650m elevation, with habitats of limestone grassland, acid grassland, blanket bog and fragments of remaining woodland. In the past the entire area was grazed by sheep. Over the years different areas of land have switched to no grazing or cattle grazing, following the removal of sheep.

Area set aside for natural colonisation: Sheep are slowly being removed from site although this process is not yet complete. Extensive cattle grazing and livestock exclusion used to promote colonisation. Total site area is 1195 ha, with a 31 ha area forming the most successful colonisation site, and saplings establishing at a lower density across a much wider area.

New woodland on limestone pavement after 40 years of natural colonisation (Dominick Spracklen)

Year that natural colonisation began: 1977 onwards, varying across the site.

Other methods of woodland creation: None

"A closed canopy woodland has not developed after 40+ years. However, that may be due to the limestone pavement creating open areas, slow growth in uplands , limited seed source and the main canopy tree of Ash suffering from die back"

Seed sources for natural colonisation: Existing woodland fragments that make up less than 3% of the habitat at the site (distance from these to our survey plots ranges 0 – 2000 m)

Which species have successfully colonised? Mainly ash, rowan, hawthorn, juniper and hazel. Trees such as Oak and Birch uncommon in colonising trees, suggesting planting needed for diverse woodlands.

Timeframe for natural colonisation: From modelling the process based on recent patterns of tree establishment, we predict a density of 1000 stems per hectare 90 m from woodland, 30 years after sheep are removed. There is a lot of uncertainty around this estimate currently, but we hope to improve our understanding of this through further data collection. Cattle grazing across the site means that trees are establishing slowly, but mostly still a long way from forming a closed-canopy woodland.

Dominant drivers of natural colonisation: Grazing by sheep significantly hindered natural colonisation. Natural colonisation also more effective closer to existing woodland and on areas of limestone soil (possibly because the limestone pavement protects seedlings), rather than peat. Natural colonisation was possible on areas extensively grazed by cattle and areas where livestock were excluded altogether.

Key challenges: Lack of existing seed sources and land ownership/influence over grazing management.

Key knowledge gaps: How different grazing regimes affects natural colonisation (e.g. species, intensity, timing); the dispersal/colonisation abilities of different tree species; how soil type and existing ground vegetation affects natural colonisation. and how those interact with grazing type. How does natural colonisation affect soil carbon?

See Porton *et al.* (2024) Ecological Solutions and Evidence 5(2): https://doi.org/10.1002/2688-8319.12338

Uplands – Case study 3

Publicly accessible
Grid ref. SD478768

Gait Barrows NNR, North Lancashire

Case study provided by Jim Turner, Natural England and Bill Grayson, Morecambe Bay Grazing Company

Aims of the natural colonisation: Woodland creation is not a primary objective of the management of the site, but blurring ecotones (supporting transitional areas between habitats) to positively impact biodiversity is a part of the management plan. This has led to natural regeneration of scrub and some woodland species in areas of semi-improved grassland.

Site description: 122 ha nature reserve, predominantly calcareous grassland, with alkaline fen, woodland, and limestone pavements.

Year that natural colonisation began: 2020

Other methods of woodland creation: None

"There is a risk in the form of reducing the diversity of vascular plants in the meadows due to the shift in grazing, scrub colonisation and ranker sward."

Seed sources for natural colonisation: Nearby established woodland of hawthorn, blackthorn, hazel, ash, oak, sycamore, yew and other species. The site includes ancient woodland and mature hedgerows.

Preparation actions prior to the natural colonisation: None

Maintenance during establishment of natural colonisation: Deer management across the site, and winter cattle grazing.

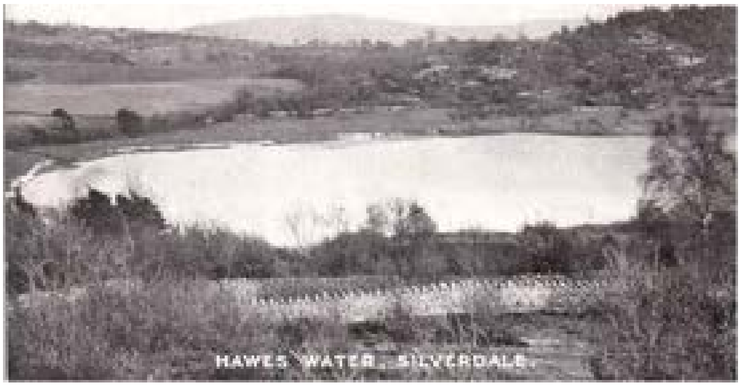
Which species have successfully colonised? Blackthorn and hawthorn are frequent pioneers with seedlings/saplings of oak and hazel also often found

Is natural colonisation proceeding in line with expectations? Scrub colonisation has occurred faster than anticipated but is broadly in line with expectations.

Dominant drivers of natural colonisation: The grazing pattern of the cattle are the dominant pressures. The natural colonisation is largely due to shifting from late summer grazing to winter grazing and has enabled the blurred ecotones and scrubby regeneration.

Successes and reasons behind them: Given the close seed sources and switch to winter grazing, scrub establishes easily, starting the process of transition to woodland.

Failures and reasons behind them: For this site it may be that we are losing too much of the species rich grassland habitat to scrub and may need to revise grazing patterns/management to take this into account.



Images - Top: Gait Barrows at around 1900, looking Southwest from an area that has now formed closed-canopy woodland through natural colonisation; middle: view of scrub/pasture looking North to South (Bill Grayson); bottom: reverse view looking South to North, showing mature woodland following ~100 years of natural colonisation (background) and pastures kept open prior to the switch to winter grazing in 2020 (foreground; Jim Turner).

Uplands - Case study 4

Hardknott Forest, Cumbria

Case study provided by Dominick Spracklen, University of Leeds

Publicly accessible
Grid ref. SD235995

Aims of the natural colonisation: Nature restoration

Site description: Upland site of 630 ha, spanning ~100-500 m above sea-level. Habitats are primarily ex-conifer plantation (previously moorland or improved farmland), unplanted moorland, and unimproved farmland, and some native woodland.

Area set aside for natural colonisation: 300 ha

Year that natural colonisation began: Around 1998

Other methods of woodland creation: None

"Natural colonisation provides a varied mosaic of sapling densities, but there is anecdotal evidence that sapling density is lower in wet peaty soils."

Seed sources for natural colonisation: Fragments of mixed native woodland, including oaks, birches, rowan, holly and willows

Preparation actions prior to the natural colonisation: Clear felling of conifer forestry close to native woodland, which facilitated natural colonisation in those areas. Some natural colonisation has also taken place on unplanted moorland and unimproved farmland.

20 years of natural colonisation (D. Spracklen)

Maintenance during establishment of natural colonisation: Removal of non-native conifers, deer culling, maintenance of stock-proof boundary fence and exclusion of sheep.

Which species have successfully colonised? 13 species dominated by birch, rowan and willow, at an average density of 3000 saplings/ha. Rowan was the initial coloniser in the first 2-3 years after clear felling, after which the other species increasingly colonised.

Colonisation distance and timeframe: Closed-canopy woodland has developed in 15 years in some areas. Saplings have established up to 2000 m from the nearest seed source, but the vast majority are within 100 m

Successes and reasons behind them: Near to native woodland remnants, clear felling conifer plantation results in conditions favourable for natural colonisation – the soil disturbance enhances the density of native saplings. However, controlling conifer regeneration is crucial for the development of native broadleaf woodland, as are removing sheep and managing deer, and maintaining the boundary fence. Colonisation is generally most effective in free-draining areas rather than wet, peaty soils.

Also see Spracklen *et al.* (2013) 'Regeneration of native broadleaved species on clearfelled conifer plantations in upland Britain' https://doi.org/10.1016/j.foreco.2013.08.001

Uplands - Case study 5

Dunkard, Cross Ash, Monmouthshire

Case study provided by Jenny Knight and Kate Beavan, Stump up for Trees

Not publicly accessible

Monitoring young planted trees (Jenny Knight)

"We are examining whether including seed source of a wider variety of native species will encourage further development, as part of a 12-year monitoring programme that we have just started"

Aims of the natural colonisation: Restoring a previous woodland site (pre 1970s), water management, creation of biodiversity corridors, ecological restoration, stock improvements.

Site description: Pasture to natural colonisation. The surrounding landscape is also mostly permanent pasture. Site area: 4.05 ha

Area set aside for natural colonisation: 0.5 ha

Year that natural colonisation began: 2022

Other methods of woodland creation: Various woody habitat created by planting (various densities and species mixes): dispersed scrub woodland, 5m wide hedgerow, wood pasture, medium density native broadleaf, wet woodland

Planting with volunteers (Jenny Knight)

Seed sources for natural colonisation: Adjacent woodland and hedgerows

Preparation actions prior to the natural colonisation: The site is enclosed by stock fencing (not deer-proof).

Maintenance during establishment of natural colonisation: We are currently reviewing the need for fencing/tree guards as protection from livestock. So far, we haven't used any plastic guards at this site, and will continue to do so as long as survival rates remain high. Planted trees are now fairly tall, which helps withstand browsing damage.

Which species have successfully colonised? Mostly goat willow so far – but very little time has lapsed since the area was set-aside for natural colonisation. So far, planted saplings are establishing much faster than natural colonisation.

Is natural colonisation proceeding in line with expectations? In summer 2024, monitoring revealed increased prevalence of deer in the area, evident in losses in the corner nearest to the old woodland. This may also explain a lack of diversity in the natural colonisation at this early stage. Survival rates in planted trees across the site are otherwise good at a live rate average of 77 per 100.

Uplands - Case study 6

Tomnavoulin and other woodland grant scheme sites, Scottish Highlands

Case study provided by Richard Thompson, Forestry and Land Scotland (at Forest Research when this privately owned site was studied)

Aims of the natural colonisation: Native woodland restoration

Site description: Upland dry heath with 20 ha of mature upland birchwood at the base of the hill

Area of natural colonisation: 6 ha now established

Year that natural colonisation began: 1987, after a large, intense fire

Other methods of woodland creation: None

Tomnavoulin in 2001 (Richard Thompson)

Tomnavoulin in 2021, with distances of newly colonised woodland from the seed source (Richard Thompson)

"A disturbance event can deliver lots of naturally colonised trees if seedlings are then protected. However, fire in particular causes considerable loss of biological diversity."

Seed sources for natural colonisation: Existing birchwood

Preparation actions prior to the natural colonisation: Intense fire in mid 1980s.

Maintenance during establishment of natural colonisation: Ongoing deer management.

Which species have successfully colonised? Very limited diversity – almost entirely birch.

Colonisation distance and timeframe: At Tomnavoulin, young woodland has formed up to 120-150 m from the existing woodland edge in ~35 years, with some saplings at a distance of 600 m. In general in the Highlands, 90% of seed falls within 60 m of the nearest canopy edge; and colonising birch can close canopy after 10 years in favourable conditions.

Successes and reasons behind them: At Tomnavoulin, the lack of vegetation competition after the fire and infertile, free draining podsolic soils have supported natural colonisation of windblown birch seeds. The colonised area is also downwind of the existing woodland.

Dominant drivers of natural colonisation: From multiple sites in the Highlands, we know that removal of deer or sheep facilitates rapid colonisation and/or growth of existing but heavily browsed seedlings. Seed source (extent and proximity) and competing vegetation (particularly for small-seeded species) are also key. In general, drier, infertile sites appear best suited to forming closed-canopy woodland. Colonisation is most likely to fail where burning or sheep grazing recommence, or deer culling is reduced. Selective browsing by deer can greatly reduce the species diversity of established woodland: animal dispersed species such as rowan, holly, oak and hazel are all very palatable to deer and these rarely get chance to successfully establish, even in suitable sites with a seed source nearby.

What are the main knowledge gaps? What is the role of mycorrhizae? What is the full mechanism of background seed rain – e.g. dispersal distances in well-wooded landscapes compared to against isolated stands? Low-density grazing with cattle to support colonisation appears to be a black art, as they can still preferentially browse palatable species. How to avoid unwanted colonisation of priority habitats (e.g. calcareous grassland).

Also see Thompson (2004) 'Predicting Site Suitability for Natural Colonisation: Upland Birchwoods and Native Pinewoods in Northern Scotland' https://cdn.forestresearch.gov.uk/2022/02/fcin054-1.pdf

Uplands - Case study 7

Cairngorms Connect, Scottish Highlands

Case study provided by Pip Gullett, RSPB

Publicly accessible
Grid ref. NH960163

Aims of the natural colonisation: Landscape-scale nature restoration.

Site description: 60,000 ha mixed upland site: heath, bog, wetlands, montane areas, Caledonian pinewood, and some upland birchwood. Much of the area was historically cleared and heavily grazed.

Area set aside for natural colonisation: ~164 ha establishing annually, over a 6,300 ha regeneration zone.

Year that natural colonisation began: Early – mid 1980s, in line with increased deer culling.

Other methods of woodland creation: There were small areas of planting in locations remote from existing seed sources, to develop seed sources for future natural colonisation.

"Monitoring of comparable areas in SW Norway suggests that natural colonisation supports a fuller suite of species, including habitat for priority species such as black grouse and beaver."

Caledonian pinewood colonisation in the Cairngorms: 1973 (above); 2023 (below) (NatureScot)

Seed sources for natural colonisation: Existing established mature trees and woodland – mostly birch and pine, with some other broadleaves.

Preparation actions prior to the natural colonisation: Coordinated deer culling across the entire site, with small areas of shrub cutting to increase the niches available for colonisation.

Maintenance during establishment of natural colonisation: Ongoing deer management

Which species have successfully colonised? Mostly Scots pine and some birch, usually within 50m from the nearest seed source, but occasionally several kilometres away. Rowan occasionally colonises remote areas by bird dispersal. On open the open hill, seedlings sometimes colonise downwind of a mature tree, demonstrating that prevailing wind affects dispersal.

"There are some surprises, such as successful natural colonisation on one side of a valley but not the other. We don't fully understand the effects of aspect, soils, microclimate etc. in this context."

Successes and reasons behind them: Deer control was key, which led to a sudden 'pulse' of colonisation. Some shrub clearing also reduced competing vegetation. There are also social and wellbeing benefits in restoring woodland to parts of the uplands.

Failures and reasons behind them: Few broadleaves colonise with success, but these are highly palatable, with limited seed sources. Montane willows, dwarf birch and high altitude downy birch are too scarce to provide sufficient seed (and genetic variation) for natural colonisation, making some planting necessary.

Key knowledge gaps: What is the influence of soil and mycorrhizae, especially in long-deforested areas? How can these woodlands make a long-term recovery to a full species assemblage? What are the impacts of climate change and pollinator decline?

Key challenges: There are some conflicting visions for the land, such as preferences for no interventions versus some planting. Similarly, effective reduction of deer numbers in the landscape depends partly on visions and management by neighbouring estates. Demonstrating the link between reduced deer numbers and colonisation has been difficult, because of a lack of coordinated monitoring of deer browsing, but this has now been unified.

Also see Gullett *et al.* 2023 https://doi.org/10.1111/1365-2664.14501

Uplands - Case study 8

Creag Meagaidh (CM) National Nature Reserve, Badenoch, and Invereshie and Inshriach (I&I) National Nature Reserve, Strathspey, Scottish Highlands*

Case study provided by NatureScot

Publicly accessible

Grid refs. NN482872 and NH852012

Aims of the natural colonisation: Landscape-scale nature restoration and conservation

Site description: Mosaic of habitats, mostly dry, wet and montane heaths, with some blanket bog, upland rough grassland and ancient woodland. Site areas: ~4,000 ha (CM) and ~3,500 ha (I&I)

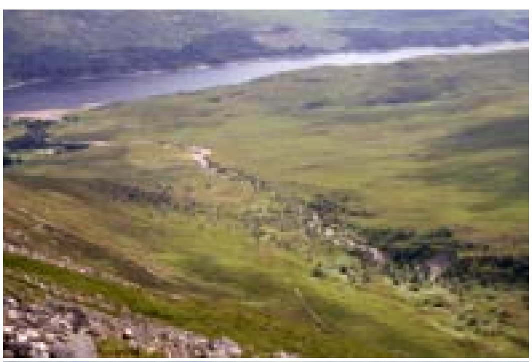
Area set aside for natural colonisation: Over 50 ha (CM) and over 100 ha (I&I) and increasing.

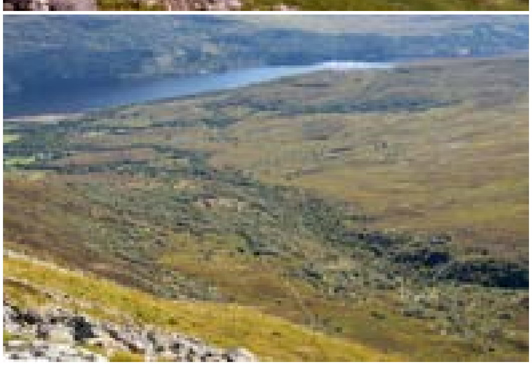
Year that natural colonisation began: Deer management increased in the late 1990s and early 2000s (I&I) and late 1980s (CM).

Other methods of woodland creation: At I&I, some planting of native Scots pine (~40ha total) in the 1960s/70s.

"Through low-intervention management, we can restore habitats at scale by promoting the conditions for woodlands to expand naturally. This requires low capital cost, gives more flexibility (not tied to any grant payments) and potentially offers greater ecosystem benefits."

Invereshie and Inshriach in 1994 (above) and in 2023 (below) (NatureScot)





Creag Meagaidh in 1994 (above) and 2023 (below) (NatureScot)

"Wild deer are part of our native ecosystems, so we accept a certain level of loss of young trees, adding to the structural complexity of the site. Monitoring is essential to ensure that browsing does not reduce tree diversity."

Seed sources for natural colonisation: Nearby ancient woodland: mostly birch, with rowan, willow, alder and some other species (CM); mostly Scots pine (some 'granny pines' in open areas), juniper and birch, with some rowan, willow and aspen (I&I).

Preparation actions prior to the natural colonisation: Sustained wild deer management (no ground preparation).

Maintenance during establishment of natural colonisation: Ongoing deer management. Cattle grazing has also started to encourage natural colonisation at CM.

Which species have successfully colonised? Following seed sources: mostly Scots pine (I&I), birch and alder (CM).

Colonisation distance and timeframe: Seedling numbers initially increased rapidly, then steadily (by 25% between 2017 and 2023, in a survey at I&I). At I&I, Scots pine, juniper and a few broadleaves are colonising sparsely uphill, at 600-800 masl.

Successes and reasons behind them: Significant and sustained efforts in deer management are key, as are good seed sources.

Failures and reasons behind them: The more palatable broadleaves continue to be browsed, in spite of deer control.

Key knowledge gaps: Some areas of ancient woodland that were felled in WWII have not colonised, despite having mature woodland nearby, and trials of cutting and burning. This is not necessarily a 'failure' as the result is a biodiverse habitat mosaic: an advantage of natural colonisation over planting. There is still a lot we don't understand about the process.

See https://storymaps.arcgis.com/stories/6b645896d1d84e45a59adbcea693c994 for additional fixed-point photos

*Invereshie and Inshriach are also part of the wider Cairngorms Connect landscape – see Case Study 7

Uplands - Case study 9

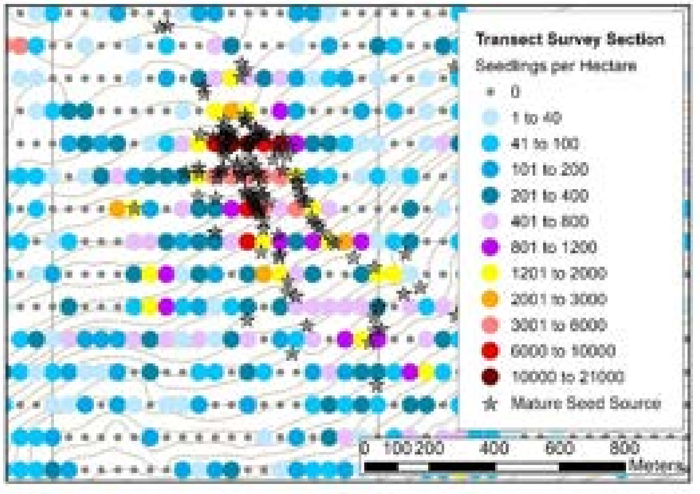
Corrour, Lochaber, Scottish Highlands

Case study provided by John Sutherland, Corrour Estate

Publicly accessible, but remote and without road access
Grid ref. NN356692

Aims of the natural colonisation: Nature restoration using self-willed natural processes as far as possible. 1,140 ha have been identified as suitable for natural colonisation across the estate to date, which are being developed first. Overall, there are 11,000 ha with the potential for increased tree cover.

Site description: West Highland estate, spanning 260 – 600 m elevation. Mostly wet and dry heath and acid grassland, with a scatter of mature native woodland trees. Typical glacial landscape of the region - lochs and rivers at the bottom of glens, surrounded by hills up to 1000 m. Sheep grazing ceased in the 1990s, and the only significant browsing pressure is now from deer (mainly red).



Seedling survey results (John Sutherland)

"The hypothesis is that cumulatively, over time, a small proportion of seed can travel great distances."

Area set aside for natural colonisation: Currently 1,140 ha

Year that natural colonisation began: Seedlings were first recorded 2006, but they could be decades old, growing slowly, or failing to establish due to browsing.

Other methods of woodland creation: Some native woodland planting in areas without nearby seed sources, and because some key species are not present (e.g. Scots pine and sessile oak).

Seed sources for natural colonisation: Individuals and small groups of mature native broadleaves are scattered throughout the estate, with a linear woodland following the West Highland railway line.

Preparation actions prior to the natural colonisation: None.

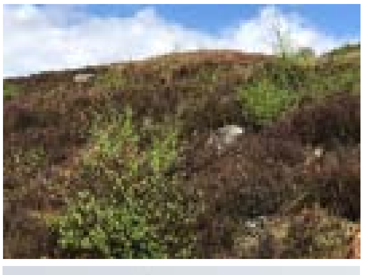
Maintenance during establishment of natural colonisation: Deer management. 180 ha were fenced in 2020, but now plan to increase deer control in target areas to allow seedling establishment.

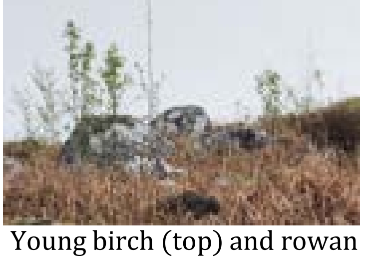
Which species have successfully colonised? In line with seed sources: downy birch, rowan, willow (eared, goat, grey) and alder are all colonising.

Is natural colonisation proceeding in line with expectations? Birch woodland is establishing as expected. There is potential for pine woodland in some locations but no pine seed sources, so we are considering planting.

Colonisation distance and timeframe: Most seedlings are within 50 - 100m of the seed source, but seedlings do establish at a distance of 500m and up to 1000m. After four years of deer exclusion, vegetation in the 2020 fenced area has a mean density of 800 seedlings per ha and some trees are nearly 2m tall.

"Deer control is fundamental to successful natural colonisation"





Young birch (top) and rowan (bottom) (John Sutherland)

Successes and reasons behind them: Ecological surveys confirmed the potential for natural colonisation and the need for deer control. Seedlings are now establishing and can compete with existing vegetation.

Failures and the reasons behind them: So far, deer control has reduced browsing but not sufficiently to allow new seedling establishment. Lower deer numbers than anticipated are required, so we will focus future increased culling efforts on specific areas to allow seedling establishment.

What are the key knowledge gaps? Assessing natural colonisation potential where there is little or no sign of advance natural regeneration, vegetation management, and timescales required.

Lowlands - Case study 10

Hucking Estate, Hucking, Kent

Case study provided by Clive Steward, Woodland Trust

Publicly accessible
Grid ref. TQ843574

Area of natural colonisation left since 2004, in 2023 (Clive Steward)

Aims of the natural colonisation: Woodland habitat creation as part of a wider nature recovery project across the whole site, including improving habitat connectivity and sequestering carbon.

Site description: Improved grassland and arable prior to natural colonisation, although some areas (including some naturally colonised) were woodland until the mid 20th century. The surrounding landscape is mostly arable farming, with isolated patches of woodland and chalk grassland. Site area: 305 ha

Area set aside for natural colonisation: Approx. 40 ha

Other methods of woodland creation: Tree planting in nearby areas to the natural colonisation

Year that natural colonisation began: Approx. 5 ha set aside in 2004 and 35 ha in 2017

"So far no failures. You have to be patient. You end up with woodland composed of trees which are nearby. If there are species not present which you need then these would need to be introduced through planting or direct seeding if you are brave enough!"

Seed sources for natural colonisation: Nearby woodland of oak, ash, hornbeam and field maple (2004 area); nearby mature individual English oak trees (2017 area)

Preparation actions prior to the natural colonisation: None

Maintenance during establishment of natural colonisation: None

Which species have successfully colonised? Oak, hawthorn, willow, blackthorn, field maple, hazel

Successes and reasons behind them: There are no deer in the area (fallow deer 15 miles away), which has been key to success. Would have used deer control measures if there had been deer present.

Failures and reasons behind them: None so far

Area of natural colonisation left since 2017, in 2022 (Clive Steward)

Also see www.woodlandtrust.org.uk/visiting-woods/woods/hucking-estate

Lowlands - Case study 11

Rickstaddle Farm, Lewes, East Sussex

Not publicly accessible

Case study provided by Robin Williams, Namayasai LLP

Field in 2008, prior to natural colonisation (Robin Williams).

"Natural colonisation is the simplest, cheapest and quickest way to create woodland."

Site description: Rough pasture prior to natural colonisation. The site is adjacent to existing woodland on one side, with arable and horticultural land on the other sides. Many wild deer, hare and rabbits.

Area set aside for natural colonisation: 9 ha

Other methods of woodland creation: Planting ~0.1% of the area with Scots pine and larch (mixed success).

Year that natural colonisation began: 2008

Seed sources for natural colonisation: Nearby semi-ancient woodland and one individual mature oak. In descending order of number of trees: willow (goat, grey & crack), hornbeam, oak, ash, aspen, blackthorn, hawthorn, sycamore, crab apple.

Preparation actions prior to natural colonisation: None.

Maintenance during establishment of natural colonisation: Access around the perimeter maintained by topping a 2-metre wide strip twice a year. Annual cutting of adjacent hedgerows was reduced to a three-year cycle, which may have supported field maple, hawthorn and blackthorn colonisation.

Which species have successfully colonised? In descending order of number of trees: willow (goat, grey & crack), hornbeam, oak, ash, aspen, blackthorn, white birch, hawthorn, field maple, sycamore, crab apple.

Colonisation distance and timeframe: The area had formed scrub by 2012 and had a closed canopy in 2020, up to 150 m from the seed source. Canopy height is around 12 m, and the largest trees have ~50-70 cm girth at a height of 60 cm (willow and birch).

Dominant drivers of natural colonisation: A natural process, driven by the pressures for survival of species. Dense willow scrub provided the main initial protection for young oaks and hornbeams, also aided by brambles. Some browsing by deer and hares.

Successes and reasons behind them: Deliberate tree planting totally un-necessary for native woodland and a waste of resources.

Failures and reasons behind them: A small group of Scots pine deliberately planted, also in 2024 hybrid larch. Work in progress.

Key challenges: No/limited funding available for natural colonisation (especially at the time).

Key knowledge gaps: Learning what flora and fauna are present and what else is going on out of sight; how do seeds of different species disperse over different distances and timescales?

Right: naturally colonised woodland in 2024 (Robin Williams).

Lowlands - Case study 12

Fairfield Forest, Worcestershire

Case study provided by Vanessa Burton, Woodland Trust

Publicly accessible
Grid ref. SO938744

Aims of the natural colonisation: Experimental site to examine the impacts of different techniques for ground preparation – does it help or hinder natural colonisation; do any negative impacts (e.g. soil disturbance) outweigh any potential benefits? Soil sampling is also taking place across the site, to understand the impacts of ground preparation and natural colonisation on soils.

Site description: 51 ha lowland site woodland creation site on former agricultural land (Fairfield Forest) adjacent to an existing ancient woodland, Pepper Wood,

Area set aside for natural colonisation: 6.3 ha

Other methods of woodland creation: Tree planting (native broadleaves)

Experimental design of the natural colonisation area (Woodland Trust)

Year that natural colonisation began: Following ground preparation in Autumn 2023.

Seed sources for natural colonisation: Adjacent ancient woodland (Pepper Wood).

Preparation actions prior to the natural colonisation: Experimental ground preparation techniques for the natural colonisation took place in Autumn 2023 (chain harrowing, mob grazing with sheep, turf stripping, and a control without any intervention).

Maintenance during establishment of natural colonisation: There are deer in the area but deer management is ongoing.

Success, failures and lessons learned: Integrating experiments into conservation action is tricky - the 'ideal' experiment design wasn't possible, so concessions were made to ensure that plots lined up with management units to ensure longevity of plots. The main success is a large and varied creation site which combines planting, natural colonisation and direct seeding, alongside a collaborative monitoring project.

"Key challenges around creating woodland through natural colonisation include ensuring competitive & long term funding to make it an attractive option, and managing herbivores at scale. Also, communicating the benefits to the public is important, so they understand successional stages and the benefits of scrubby open woodland."

Lowlands - Case study 13

Swannymote Wood, Whitwick, Leicestershire

Case study provided by Simon Greenhouse, National Forest Company

Publicly accessible
Grid ref. SK443168

Image to left: Time-series 1, from top to bottom: 2008, 2012, 2013, 2020 (Simon Greenhouse)

Aims of the natural colonisation: Capitalising on circumstances to create woodland, as natural colonisation was already taking place in certain areas. Also enhancing biodiversity, providing recreation and increasing landscape forest cover

Site description: Pasture to natural colonisation. The surrounding landscape is mostly pasture with some woodland. Site area: 22.7 ha

Area set aside for natural colonisation: 2.5 ha

Year that natural colonisation began: 2007

Other methods of woodland creation: Tree planting in other areas of site

Seed sources for natural colonisation: Adjacent oak/birch SSSI woodland

"We saw evidence of natural colonisation during the woodland creation planning, and assessed which areas might be most suitable, to capitalise on circumstances."

Preparation actions prior to the natural colonisation: Initial site design included a number of shallow scrapes to create wetter habitat patches. However, these colonised with tree seedlings, inspiring the use of that part of the site for further natural colonisation. Grass was mown to create the coupe boundary.

Maintenance during establishment of natural colonisation: Small amount of respacing in year 5

Which species have successfully colonised? Silver and downy birch, willow, oak, Scots pine

Successes and reasons behind them: We chose areas where there was already evidence of natural colonisation during woodland planning

Failures and reasons behind them: Oak seedlings were numerous, but then out-competed by faster growing species. Squirrel damage heavily impacted willow and birch, seemingly more in areas of natural colonisation than planting, possibly due to the difference in species mixture.

Time-series 2, from top to bottom: 2007, 2008 showing mown coupe boundary, 2012, 2016, 2020 (Simon Greenhouse)

Publicly accessible
(1961 area of colonisation)
Grid ref. TL201796

Lowlands - Case study 14

Monks Wood, Woodwalton, Cambridgeshire

Case study provided by Emma Dear, Natural England and Richard Broughton, UK Centre for Ecology & Hydrology

Aims of the natural colonisation: Restore biodiversity, and scientific research into the process of natural colonisation

Site description: Monks Wood NNR is an ancient woodland, with species-rich rides. Surrounding landscape is mixed farmland (pasture and arable) with woodland pockets.

Area set aside for natural colonisation: Two fields adjacent to the ancient woodland were set aside: a 4 ha barley field (abandoned after a final harvest & ploughing), and 2 ha of unimproved grassland (6 ha in total).

Year that natural colonisation began: 1961 (4 ha barley field) and 1996 (2 ha grassland)

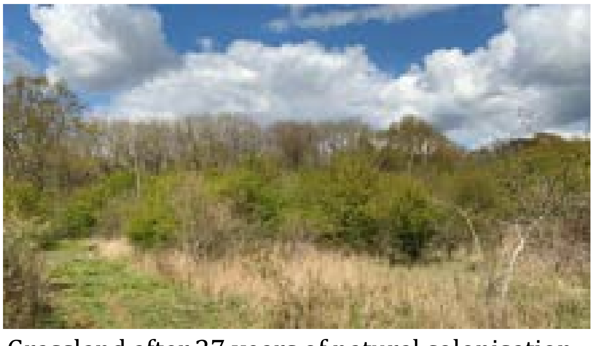
Other methods of woodland creation: None

Seed sources for natural colonisation: Adjacent ancient woodland, dominated by oak, ash and field maple, with hawthorn and hazel understory (some. wild service and birch in the interior). The barley field is surrounded on 3 sides by woodland, and the grassland on one side only, but is bounded by hedges with some hedgerow trees.

Preparation actions prior to the natural colonisation: The barley field was abandoned after ploughing, and the grassland after mowing.

Maintenance during establishment of natural colonisation: Some deer management in adjacent ancient woodland from late 1990s but none in the areas of natural colonisation

Aerial view of shrubland in blossom, after 24 years of natural colonisation in the grassland (Richard Broughton, 2020)



Grassland after 27 years of natural colonisation (Emma Dear, 2023)

"Natural colonisation establishes slowly. Ecologically and in biodiversity terms this should be viewed as a positive. This is a low cost way of establishing semi-natural woodland."

62 years of natural colonisation of the barley field (Richard Broughton, 2023)

Which species have successfully colonised? Mostly oak, ash, field maple, hawthorn and blackthorn. Animal-dispersed species are more abundant than in the adjacent ancient woodland, particularly in the more recently colonised site (2 ha grassland). Wind-dispersed and suckering species (ash, elm, willow, field maple) are near seed sources.

Resulting woodland structure: The older (barley field) site became wildlife-rich shrubland after 10-15 years and closed-canopy broadleaved woodland after 40-50 years, with densities of 390 trees/ha after 59 years (132/ha after 25 years in grassland).

Successes and reasons behind them: The transitional shrubland (scrub) habitat has high biodiversity value, particularly for invertebrates, and the woodland that followed is structurally diverse, created at low cost. The young woodland was resilient to drought periods. Protective thicket of thorn scrub meant that herbivory was not an issue for larger trees to colonise, in spite of presence of brown hares, rabbits, grey squirrels, roe and muntjac deer.

Also see Broughton *et al.* 2021 https://doi.org/10.1371/journal.pone.0252466 **and** www.ceh.ac.uk/press/passive-rewilding-can-rapidly-expand-uk-woodland-no-cost

Lowlands - Case study 15

Noddle Hill, Bransholme, Hull

Case study provided by Richard Broughton, UK Centre for Ecology & Hydrology

Publicly accessible
Grid ref. TA108348

"Although closed-canopy woodland remained a distant prospect even after 33 years, the habitat mosaic of shrubland, grassland and wetland could be considered a valuable outcome."

33 years of natural colonisation: shrusbland and grassland mosaic (above); reedbed wetland (below) (Richard Broughton, 2022)

Aims of the natural colonisation: Expanding woodland cover and restoring biodiversity

Site description: Noddle Hill Nature Reserve is a 48 ha estuarine floodplain site, with 'rewilded' areas, a recreational fishing pond, tree planting, and permitted pony grazing. The site was previously farmland, and is currently surrounded by arable farming, pasture, amenity sports fields and residential housing. Low-lying land, with high groundwater and shallow seasonal flooding.

Area set aside for natural colonisation: 25 ha left to 'rewild passively' across seven contiguous fields

Year that natural colonisation began: 1988

"Blossom- and berry-rich thorny shrubs could provide important ecosystem services of enhanced biodiversity, pollinator resources and cultural services for many decades before any closed-canopy woodland develops."

Other methods of woodland creation: None within the 25 ha, although adjacent fields were planted with trees in 2000

Seed sources for natural colonisation: Far: the nearest mature woodland is 1.5 km away. In 1988, the site included 2.7km of hawthorn-dominated hedgerow, one mature crack willow, and only 1% mature woodland cover with a 1 km radius of the site. Trees planted in adjacent fields in 2000 have not yet matured.

Preparation actions prior to the natural colonisation: In 1988, clayey soils were imported and spread over 70% of the site at a depth of ~1m, intended for future development. The initial ground surface was a patchwork of bare soil, seasonally wet grassland/ex-arable, and existing hedges and ditches.

Maintenance during establishment of natural colonisation: None (herbivores generally scarce)

Which species have successfully colonised? Predominantly bramble, with hawthorn and dog/field roses, followed by elder, crack willow, ash, oak, some silver birch, grey willow and blackthorn.

Successes and failures: After 33 years, trees remained scarce! Thorny scrub thickets covered 53% of the site (average woody vegetation height 2.1 m). This has supported high diversity and abundance of songbirds but is not woodland creation as such (yet). The lack of tree colonisation is in spite of large areas of bare soil available for colonisation, and probably due to combined lack of seed sources and animal dispersers.

Also see Broughton *et al.* (2022) PLOS ONE 17(11): [e0277545]