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BRITISH ECOLOGICAL SOCIETY Ecological Solutions and Evidence

PRACTICE INSIGHTS

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

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Abstract

1. Creating 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 in Great Britain. 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 the 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. *Solutions*. 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

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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.

KEYWORDS
forest restoration, knowledge exchange, native woodland, natural colonisation, natural regeneration, practitioner knowledge, tree planting, woodland creation

1 | BACKGROUND

Efforts are underway globally to expand tree cover to respond to the combined climate and biodiversity crises. Abandoned agricultural land has provided the opportunity for woodland colonisation at scale in many locations globally, although some of these areas are recultivated within a few decades as croplands continue to expand (Crawford et al., 2022; Potapov et al., 2022). In many temperate regions, active tree planting has been the primary method of woodland establishment, but its environmental benefits are sometimes overestimated (Holl & Brancalion, 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; Figure 1). In Great Britain, woodland cover has increased by nearly 10% since 2005 (Forest Research, 2025), and each nation has ambitious targets for ongoing woodland creation, primarily through woodland expansion on existing agricultural land. Whilst historically, woodland expansion in Britain has been achieved mainly through tree planting schemes, natural colonisation is now also being promoted and offered financial incentives. Understanding the process and benefits of natural colonisation will help inform land management and policy to support biodiversity in the long term.

In a typical tree planting programme in Britain, 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-Montemayork et al., 2022; Figure 2). Natural colonisation is considered to result in more locally adapted and natural woodland than tree planting, requiring fewer resources (Fleiss & TreE PlaNat Knowledge User Board, 2025, as supplied in Supporting Information S1; Figure 2). 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

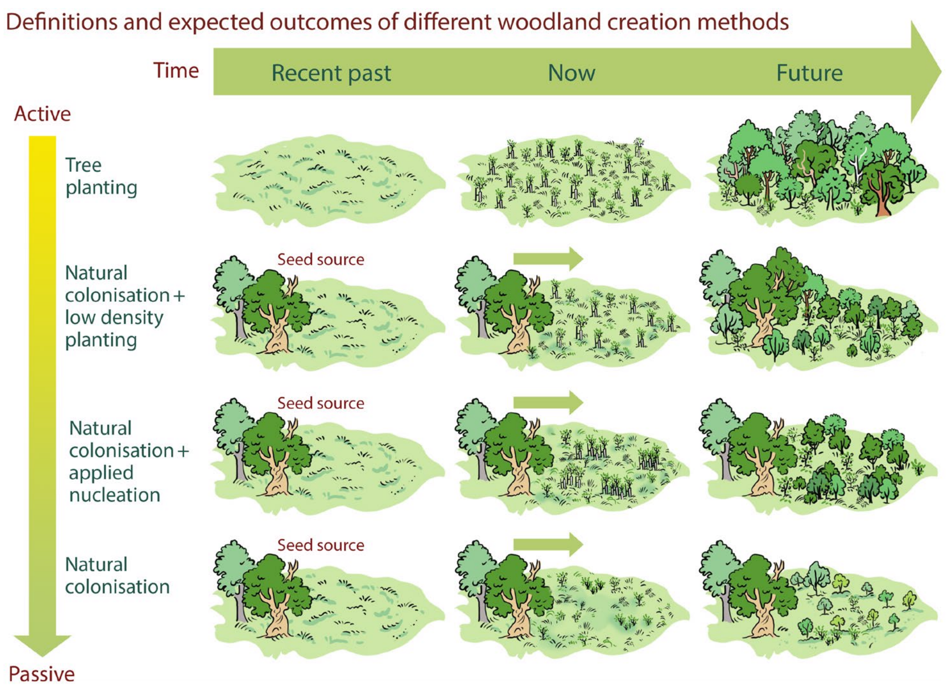

FIGURE 1 Comparison of tree planting, natural colonisation and hybrid methods (low-density planting and 'applied nucleation', where small clusters of trees are planted) in a lowland context (The Woodland Trust et al., 2025).

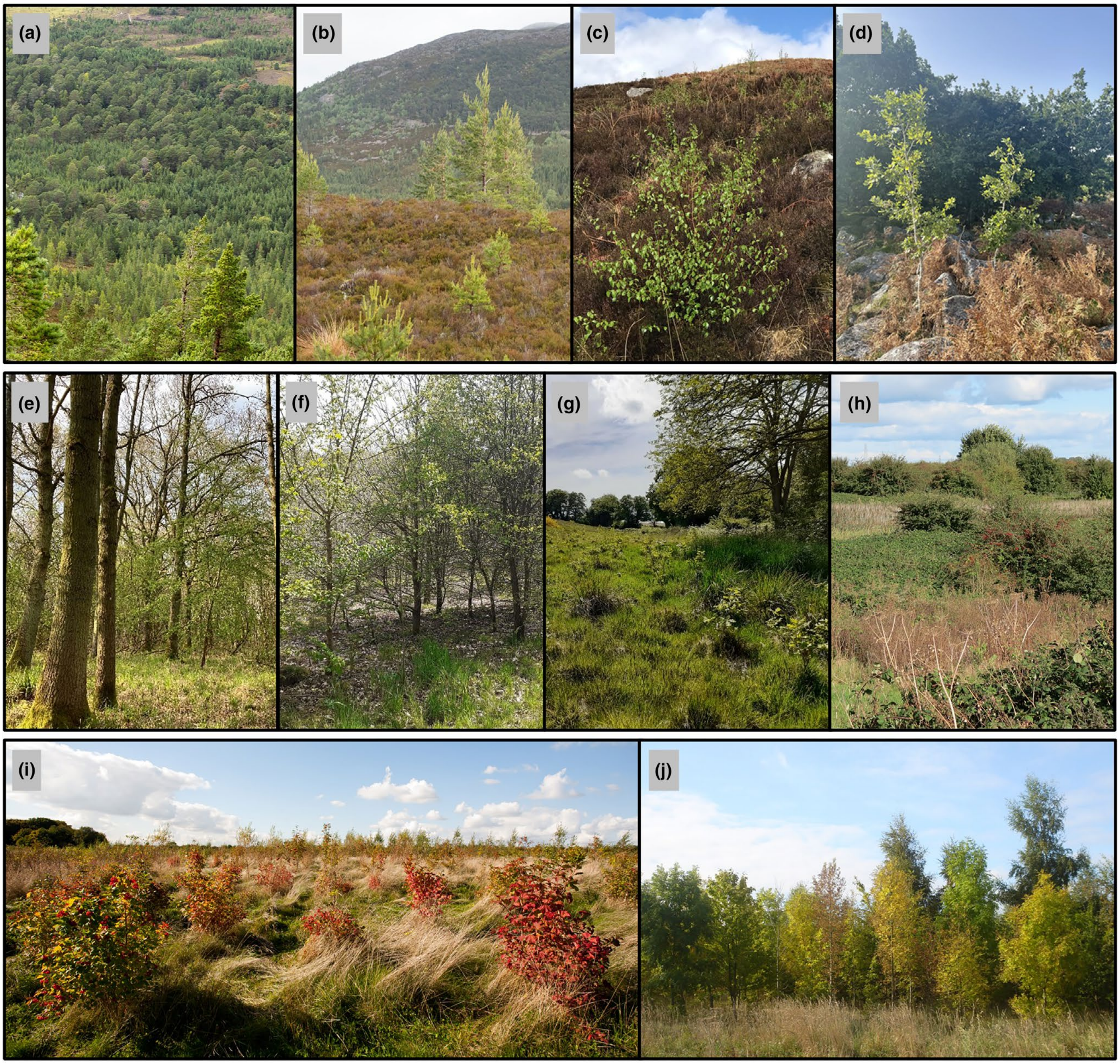

FIGURE 2 Photos of woodland creation. Natural colonisation in the uplands: (a) ~40 years and (b) ~20 years of pinewood expansion in the Cairngorms (NatureScot); (c) young birch in the Highlands following 3 years' deer fence protection (John Sutherland); (d) young oak at Sampford Spiney, Merrivale, natural colonisation site on Dartmoor (Thomas Murphy). Natural colonisation in lowland England: (e) following 62 years at Monks Wood, Cambridgeshire (Richard Broughton), following (f) 20 years and (g) 5 years at Hucking, Kent (Clive Steward), (h) following 30 years at Noddle Hill, Hull (still at the scrub stage, Richard Broughton). Tree planting: (i) Heartwood Forest, Hertfordshire, ~15 years old and (j) Londonthorpe Wood, Lincolnshire, ~6 years old (Katherine Jaiteh and Judith Parry, Woodland Trust Media Library).

establishment. Similarly, hybrid approaches combining planting and natural colonisation simultaneously (e.g. low-density planting and 'applied nucleation' or cluster planting; Figure 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; Broughton et al., 2022; Murphy et al., 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

TABLE 1 Outcomes of natural colonisation at various sites: Dispersal distances and time taken for woodland establishment (partial information available for some sites only). NB that we cite CS1 for Case Study 1, CS2 for Case Study 2 etc., as provided in Supporting Information S1.

Site and habitat	Dispersal distances, tree density and time taken	Tree species (see Table S2 for botanical names)	Use of tree planting	Source
Lowland				
Multiple sites across England: arable and improved grassland (lowland) and heath and acid grassland (upland)	After 20 years of natural colonisation, tree densities of 100 stems/ha were achieved at 70 m from the adjacent 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	Not identified (remote sensing study)	None	Bauld et al. (2023)
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 4 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) 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	Mostly oak, ash, field maple, hawthorn, blackthorn colonising. Adjacent to oak-ash woodland	None	CS14; Broughton et al. (2021)
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 et al. (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)

TABLE 1 (Continued)

Site and habitat	Dispersal distances, tree density and time taken	Tree species (see Table S2 for botanical names)	Use of tree planting	Source
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 and glacial till). Closed canopy not achieved after 40 years (possibly slowed by ash dieback)	Predominantly ash, with hawthorn, hazel, juniper and rowan	Extensive planting of a diverse range of tree species. Predominantly in areas away from seed sources to accelerate woodland creation	CS2; Porton et al. (2024)
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 4 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

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 their benefits and the uncertainty of their 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 (some 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 and 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 the inter-disciplinary 'TreE PlaNat' project (Fuentes-Montemayor et al., 2025). As well as highlighting knowledge needs amongst 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; Fleiss & TreE PlaNat Knowledge User Board, 2025, as supplied in Supporting Information S1).

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 Supporting Information S1, and botanical names of species referred to in the case studies in Table S2. 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 amongst 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; Supporting Information S1; 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 (Figure 2h) has high biodiversity value, with complex, mixed vegetation providing multiple niches, such as for pollinators (CS14; Broughton et al., 2021; Mortimer et al., 2000). 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 et al., 2022). In upland environments, natural colonisation can help the 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, 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 (Figure 2a–h; CS4, CS14; Broughton et al., 2021; Forest Research, 2020; Spracklen et al., 2013). 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, Kunin, Watts, & Ziv, 2023, Hughes, Kunin, Ziv, & Watts, 2023).

3 | ECOLOGICAL FACTORS LIMITING 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 12 years (CS11) or take many decades (CS15). Progress is often slower across the British uplands, constrained by diminished available seed sources, 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 (Figure 3; Supporting Information S1). 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

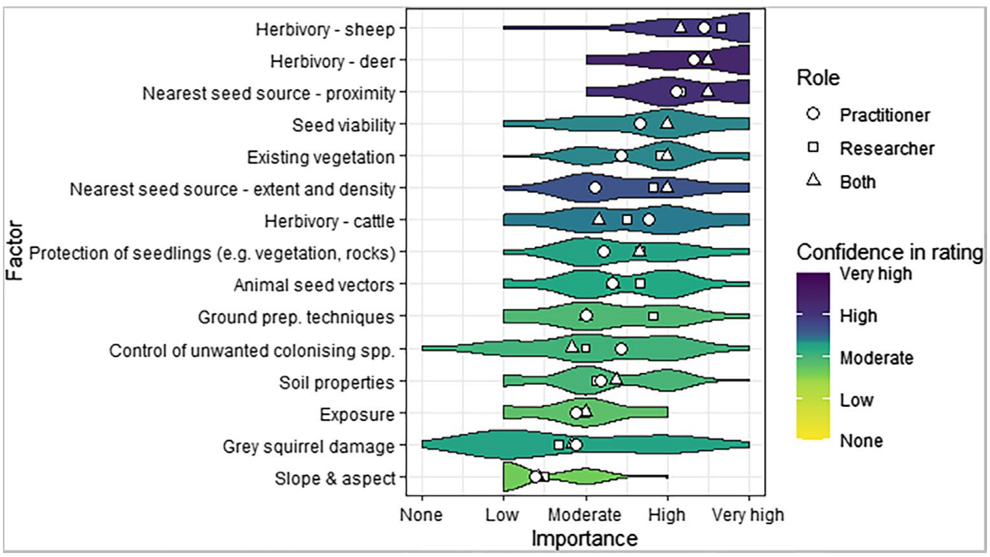

FIGURE 3 Kite diagrams of the perceived importance of key ecological factors influencing natural colonisation, from the survey of 21 experts (practitioners, researchers and individuals who are both practitioners and researchers). Factors are ranked according to mean importance rating, points show mean 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 the full suite of factors included in the survey, and comparison of ratings between upland and lowland habitats, see Figure S1.

case studies and existing literature to summarise current knowledge on these factors (seed source and dispersal, herbivory, competing vegetation and ground disturbance and site characteristics) below.

3.1 | 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 the nearest seed source for seedling establishment (Figure 3; CS1–15; Bauld et al., 2023; Broughton et al., 2021; Gullett et al., 2023; Murphy et al., 2022; Porton et al., 2024; Spracklen et al., 2013; Thompson, 2004). Actual seed dispersal distance varies considerably and appears to be shorter on average in the uplands than in the 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 (Figure S1). However, the 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 the presence of jays *Garrulus glandarius*, and acorns only travel very short distances in the absence of jays (CS1, CS15; Broughton et al., 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.

3.2 | Herbivory

Herbivore pressure, particularly by deer and sheep, is highly limiting to seedling establishment and survival (Figure 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; Murphy et al., 2022; Porton et al., 2024).

3.3 | 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 (Figure S1). 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 the 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 (Figure 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. The potential influence of soil disturbance on the composition of colonising species also remains unknown.

3.4 | 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 in the lowlands (Figure S1). 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

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

Graphics were created using keyword prompts on Microsoft Copilot. The prompts for each graphic included using the titles for the main identified knowledge gaps on natural colonisation.

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?

(Continues)

BOX 2 (Continued)

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?

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.

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.

5.1 | Adaptive land management

Whilst 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).
- Consider 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 after some years of natural colonisation could mitigate the absence of certain species or lower stem densities than desired (which may be a requirement of some funding offers).
- Consider 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).

5.2 | 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.

5.3 | 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.

6 | CONCLUSIONS

There are a limited number of examples of woodland creation through natural colonisation in Great Britain, and as it is a highly variable process, many knowledge gaps remain. Nevertheless, the knowledge that we have collated from practitioners and researchers shows that the availability of seed sources and herbivory levels are the most important ecological determinants of the success of natural colonisation. By combining natural colonisation with tree planting, land managers can meet a broader range of woodland creation site objectives, but there are few tested examples of these hybrid approaches. The combination of inherent variability in the process of natural colonisation and a large number of associated knowledge gaps means that land managers and advisors face considerable uncertainty in designing and implementing woodland creation through natural colonisation and hybrid approaches. Site monitoring and adaptive management in response to progress can help meet site objectives, and it is essential that policies on natural colonisation support adaptive land management. Ongoing collaboration between land managers and researchers to monitor woodland creation and implement long-term and/or large-scale experiments will help further understanding of natural colonisation and support best practices for woodland creation in the long term.

AUTHOR CONTRIBUTIONS

Susannah Fleiss, Marc J. Metzger, Vanessa Burton, Elisa Fuentes-Montemayor, Rachel Orchard, Heather Gilbert, Kevin Watts, Bianca Ambrose-Oji, Laura Braunholtz, Julia Koricheva, Matt Guy and Kirsty J. Park conceived and facilitated the knowledge exchange activities leading to the collation of information presented in this article; all other authors, Vanessa Burton and Laura Braunholtz, contributed case studies and/or land management experiences as primary information for the article; Susannah Fleiss, Marc J. Metzger, Vanessa Burton, Kevin Watts and Elisa Fuentes-Montemayor led the writing of the manuscript. All authors have read and approved the final version of the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

The case studies of natural colonisation are available in Supporting Information S1 and at the Edinburgh Research Archive https://doi.org/10.7488/era/3766.

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SUPPORTING INFORMATION

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

Supporting Information S1. 15 case studies of woodland creation through natural colonisation in Great Britain.

Table S1. Summary of the eight Knowledge User Board meetings held throughout the inter-disciplinary TreE PlaNat project (socio-ecological consequences of Treescape Expansion through Planting and Natural colonisation).

Table S2. Common and botanical names of tree and shrub species referred to in the case studies of natural colonisation (Supplementary Information 1).

Figure S1. Kite diagrams of the perceived importance of ecological factors influencing the process of natural colonisation (full suite of factors included in survey), from the results of a survey of 21 experts (practitioners, researchers and individuals who are both practitioners and researchers). As for main article Figure 3, factors are ranked according to overall mean importance rating, and shading corresponds to overall mean rating in respondents' confidence in their answers, but here points show mean rating by respondent study system. Both importance and confidence were rated on a five-point scale as labelled.

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