Drivers of natural colonisation and regeneration within planted woodlands in England: towards an integrated approach to increase resilience

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ABSTRACT

Increasing woodland cover is at the heart of global and national strategies to combat climate change. While tree planting is a rapid and scalable means of woodland creation, it remains expensive and prone to high mortality, highlighting the need for additional more cost-effective methods including natural colonisation and regeneration. A key question is whether trade-offs between the advantages of rapid planting and natural colonisation can be avoided by using a combined approach. Yet few studies have quantified ongoing colonisation and regeneration within planted woodlands and the habitat and management drivers influencing these processes. This study explores the relative importance of seed source (parent candidate) trees, woodland habitat, management, browsing, and scrub variables in influencing natural colonisation and regeneration within 57 planted woodlands across East Anglia, UK. We test for these effects on three species of colonising tree sapling, and the total number and species richness of all tree saplings (colonising and regenerating). *Fraxinus excelsior* and *Acer campestre*, showed parent candidate (PC) variables to have greater influence on colonising sapling abundance than woodland or management variables, while effects were much weaker for *Quercus robur*. Woodland age was a positive predictor for *A. campestre* saplings, more equivocal for *F. excelsior*, and had no influence on *Q. robur*. However, woodland age had a strong positive influence on species richness of tree saplings and on percentage cover and species richness of scrub. Canopy cover was the strongest predictor of total tree sapling abundance. Management had negative effects on *Q. robur*, total number of saplings and scrub coverage. Species compositional analyses showed most sapling taxa were associated with older, unmanaged, more diverse plantations, with greater canopy cover and scrub species richness. We conclude that substantial natural colonisation occurs within planted woodlands, complementing regeneration and tree planting in enhancing woodland creation. Further research on the potential benefits of combining active and passive methods of afforestation is needed to ensure woodland creation and management is optimised for biodiversity and ecosystem services.

1. Introduction

1.1. Background

The importance of planting more trees and of woodland creation for carbon sequestration, climate regulation, water supply, fuel provision and human wellbeing is widely acknowledged in international schemes including the United Nations Sustainable Development Goals and the Bonn Challenge (Dave et al., 2019). In the UK, the government's "England Trees Action Plan" has allocated over £500 million towards woodlands between 2020 and 2025. As a method of afforestation, tree planting is relatively quick and predictable and allows for spacing and species composition to be predetermined facilitating long-term

management such as selective thinning and timber extraction. Planting trees also enables the introduction of genetic varieties and species with potentially greater timber yields, climate change resilience, and disease resistance. An alternative approach is that of natural colonisation or passive rewilding in which areas of land afforest through natural pathways of succession (Corbin and Holl, 2012; 1995; Harmer, 1999; Olrik et al., 2012). This process occurs through vegetative spread (i.e., suckering) and through wind, gravity or animal dispersed seed (Hodge and Harmer, 1996). Natural colonisation confers many advantages over tree planting including reductions in labour, transportation costs and carbon emissions (Broughton et al., 2021), and biosecurity risks via use of local seed sources (Forestry Commission, 2021), while maintaining locally adapted genotypes (Bauld et al., 2023). Although natural colonisation

can be a much slower and less predictable method of afforestation than tree planting (Rodwell and Patterson, 1994), the heterogeneous intermediary successional stages including scrub have intrinsic biodiversity value (Mortimer et al., 2000; Cordingley et al., 2016).

Meta-analyses have indicated either no difference in the rate or outcome of active versus passive methods (Jones et al., 2018; Meli et al., 2017), or that passive methods tend to perform better than active restoration (Huang et al., 2019; Ren et al., 2017; Wei et al., 2023). Despite the ongoing debate, natural colonisation and tree planting need not be viewed as mutually exclusive approaches (Fuentes-Montemayor et al., 2022). The theory of applied nucleation whereby clumps of trees or vegetation (planted or naturally occurring) act as focal points around which colonisation occurs, is well documented (Rey Benayas et al., 2008; Corbin and Holl, 2012). Biotic and abiotic limitations on sapling colonisation may be mitigated within nuclei (Corbin and Holl, 2012), with abundance and species richness of colonising seedlings being reported to be higher than in comparatively open habitats (Corbin et al., 2016). Colonisation within planted woodlands may similarly be facilitated with planted trees providing shelter from wind and sun, restricting growth of outcompeting ruderal vegetation (Harmer, 1999), facilitating seed dispersal by trapping wind-blown seed and by providing habitat and perches for seed dispersers including small mammals and frugivorous birds (Harmer and Kerr, 1995).

1.2. Hypothesised predictors of colonisation within woodlands

Most plants exhibit a seed dispersal curve in which dispersal is highest close to the parent tree (Cain et al., 2000). Distance to the nearest seed source or parent candidate (PC) tree has been found to be significant in numerous studies of colonisation (e.g. Clark et al., 2004; Wang et al., 2020) and interacts with dispersal mechanisms although not always predictably (Wang et al., 2020). Size of the seed source is also considered important and is frequently estimated using basal area, diameter at breast height (DBH) and/or height of PC trees. Larger plants produce greater seed crops (Bogdziewicz et al., 2020; Greene and Johnson, 1994), indicating an overall size:fecundity relationship. However, whether this is really driven by plant mass, width or height is still debated (Thomson et al., 2011; Wang et al., 2020). Furthermore, seeding patterns can be highly stochastic and ultimately driven by individual variation (Clark et al., 2004).

Canopy cover influences colonisation and regeneration as light demands of tree species vary, with pioneers typically colonising more open ground (Vera, 2000). Nevertheless, the pioneer vs climax distinction is not absolute with late successional species such as oak (*Quercus robur*) also being light demanding (Rackham, 2006; Vera, 2000). Natural colonisation within planted woodlands is likely to involve sapling species with variable light requirements. The practice of using "nurse trees" to shelter saplings is common in commercial forestry (Meinzer et al., 2011) highlighting the potential benefits of an overstorey on sapling colonisation and regeneration

Management of woodland, which in this study is defined as vegetation removal, can vary substantially among plantation woodlands, with potentially significant impacts on colonisation and regeneration. For the initial establishment phase of a plantation (0–3 years), it is recommended that vegetation growing around the trees is suppressed either with herbicide application or by manual/mechanical weeding partly to reduce competition for light and nutrients (Woodland Trust, 2022). Targeted removal of vegetation within planted woodlands may disproportionately affect less "desirable" species (Harmer et al., 2017), whereas mechanical methods are indiscriminate, leaving sapling responses dependent on life history traits especially in relation to sensitivity to coppicing (Rackham, 2006).

Herbivore browsing can alter the species abundance, richness and composition of a mature woodland understory (Knight et al., 2009; Goetsch et al., 2011). Plantation woodlands may similarly be affected, with saplings under more open canopy being more palatable due to

increased sucrose levels (Tixier et al., 1997). Deer can preferentially browse on scrub species and notably on bramble over tree saplings (Harmer et al., 2010). With UK deer populations increasing (Putman et al., 2011), browsing pressure is likely to play a significant role in sapling colonisation and regeneration (Fuentes-Montemayor et al., 2022).

The positive influence of scrub on sapling colonisation and regeneration is widely reported (Vera, 2000). Bramble (*Rubus fructicosus*) has been found to benefit ash (Van Uytvanck et al., 2008) and oak (Kuiters and Slim, 2003) sapling establishment, and both birch (*Betula pendula*) and willow (*Salix spp.*) regeneration (Harmer et al., 2010) by providing protection against herbivores and/or an alternative food source. Scrub has high intrinsic value especially for the declining populations of ground-nesting birds and small mammals (Mortimer et al., 2000), however, its role in facilitating sapling colonisation of planted woodlands needs further exploration.

1.3. Aims

A key aim of this study is to build on existing research that quantifies the influence of seed source characteristics and surrounding environmental conditions upon natural colonisation within planted woodland, as distinct from colonisation of more open ground outside woodland. Specifically, using data on three of the most abundant tree sapling species deemed to be colonisers in our study (*Fraxinus excelsior*, *Acer campestre*, and *Quercus robur*), we test the prediction that size, quantity and proximity of seed source trees will positively influence colonisation. We further predict that older, unmanaged, less intensively browsed woodlands, with higher scrub species coverage, will have higher levels of natural colonisation of the same three sapling species. We test the same predictions for both the total number and species richness of all tree saplings, including regenerating as well as colonising species. We further test woodland habitat variables as predictors of scrub coverage and species richness. Finally, we explore environmental correlates of overall sapling community composition. The study findings are used to evaluate the relative importance of seed source, woodland habitat, management and browsing variables for woodland creation strategies. We adopt a large-scale, multi-site approach to maximise the generality of findings concerning drivers of colonisation.

2. Materials and methods

2.1. Study sites

The study focused on woodland sites within East Anglia, UK (Fig. 1). Exploratory site visits indicated that planted woodlands between 4 and 18 years old represented an ideal age range to test the hypothesised drivers of colonisation. Sites < 4 years old were still being managed for plantation establishment and thus colonisation was virtually absent, whereas sites > 18 years old were either closed canopy or being managed through selective thinning and coppicing. Under the guidance for UK government woodland creation grants awarded from 2004 to 2018, woodlands were required to have a minimum of 80 % native/naturalised broadleaf, spacing of 1100–1600 stems per ha and to protect against browsing damage. By selecting woodlands falling under grant schemes, a significant amount of potential site idiosyncrasy was eliminated. In total, 57 sites belonging to 16 different landowners (Fig. 1) were selected of which 10 were private landowners, and six were classed as community woodlands. Sites occur on soils ranging from fine-loam to clay-loam to clay, close to temperate "Histisols" (organic soil), with pH ranging from 6.8 to 7.6; climate is continental temperate-type with wet and cold winters and relatively dry and mild summers.

2.2. Data collection

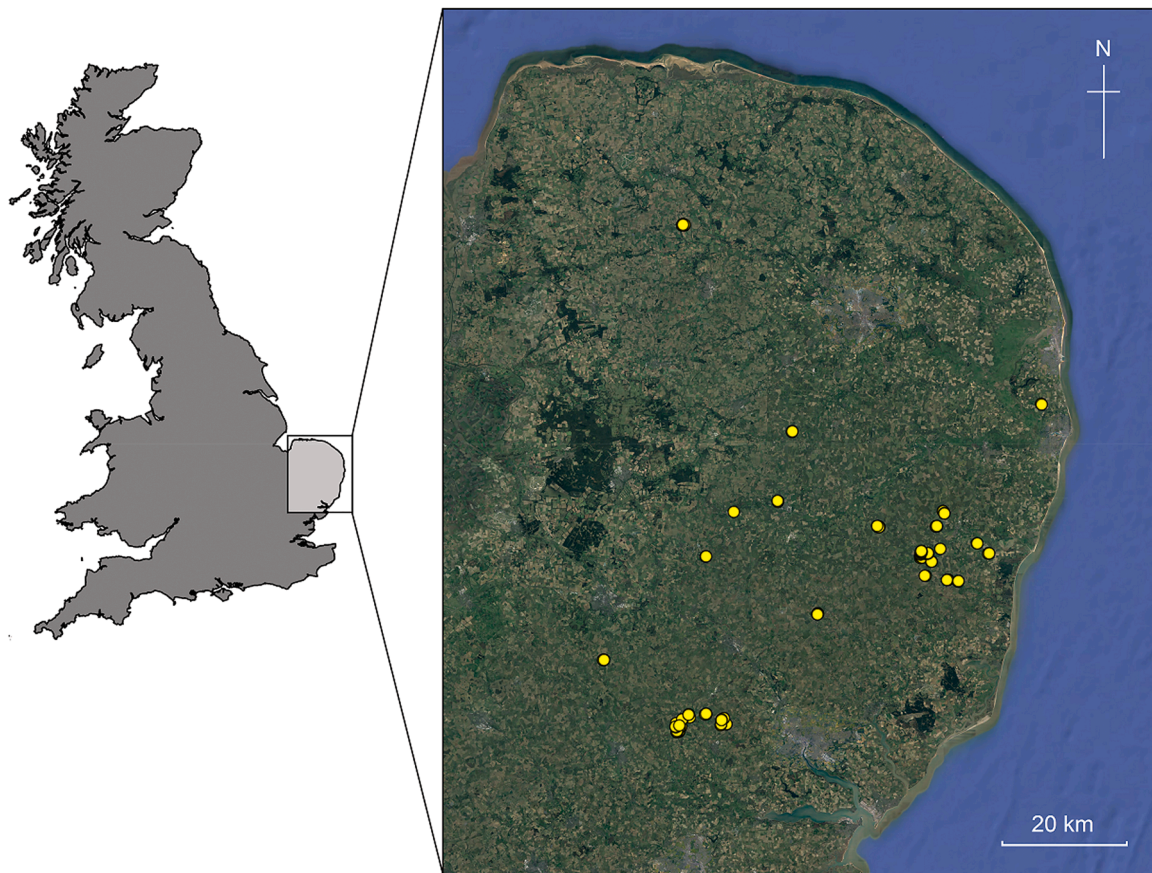To avoid any sample bias towards early-germinating species, the

Fig. 1. Fifty-seven plantation woodlands (yellow circles) from 16 different landowners across East Anglia, UK, were surveyed for natural colonisation between May and July, 2022.

main field data were collected between 15th May and 20th July 2022 (with some additional environmental data collection in Nov 2022). Within selected woodlands, 5 × 5 m quadrats were positioned randomly while avoiding placement < 50 m away from another quadrat or within open areas (e.g., glades or rides) where no trees were planted. Numbers of quadrats per woodland site increased in number roughly in proportion with woodland area, from one quadrat up to a maximum of 10 quadrats per site, to balance sampling effort with a sufficient variety of sites. Woodlands sampled ranged in size between 0.3 ha and 12.46 ha. Quadrat densities varied from an average of 2.1 per hectare for woodlands <1 ha, decreasing to densities averaging 0.8 per hectare for woodlands of 4 ha or more (Table S1).

2.2.1. Tree sapling species and scrub data

The species assignment to tree saplings versus scrub used in this study was as follows: hawthorn (*Craetagus monogyna*), blackthorn (*Prunus spinosa*), bramble (*Rubus fructicosus*) and rose (*Rosa spp.*) were considered "thorny scrub" species; dogwood (*Cornus sanguinea*), spindle (*Euonymus europaeus*), wild privet (*Ligustrum vulgare)*, broom (*Cytisus scoparius*), guelder rose (*Viburnum opulus*), and old man's beard (*Clematis vitalba*) were deemed "non-thorny scrub" species; all other woody species comprised "tree sapling" species. Within each 5 × 5 m quadrat, tree sapling abundances were recorded at the species level except for counts aggregated within *Salix* spp. Although identification of the different oak species can be problematic for small saplings, diagnostic features for separating these were checked against reliably identified local tree nursery samples. All scrub species were quantified using a visual assessment of percentage cover per quadrat.

Assignment of saplings as either "colonising" or "regenerating" taxa, was determined, respectively, by whether they did not or did have seed-

bearing PCs within the plantations in which they were found (see results). Confirmation of the distinction between regenerating and colonising species requires genetic testing of saplings and PC trees, hence was beyond the scope of the study. However, none of the species classified as regenerating were found in samples where there were no potential PCs amongst the planted trees, either within the quadrat itself or within a few metres.

2.2.2. Colonising species and parent candidate (PC) predictor variables

Seed source variable data were collected for the PCs (the nearest seed-bearing conspecific tree – see details in Table S2) for ash (*Fraxinus excelsior*), pedunculate oak (*Quercus robur*), and field maple (*Acer campestre*), for use in individual species analyses. Ash and pedunculate oak were chosen because of their long maturation times, ensuring that colonisation was by far the most likely mechanism operating within woodlands of this age (4 –18 years). Field maple was chosen because it is known to have been widely planted in hedgerows in E. Anglia, a seed source external to plantation, and tends to spontaneously establish, being also a subdominant lower canopy species (Wahlsteen et al., 2023). However, field maple was also widely planted in plantations and has a minimum age to seed set of *circa* 10 years, much less than ash and pedunculate oak. Nevertheless, a 10–18 year-old tree would be expected to produce much less seed than a more mature tree, increasing the likelihood that field maple sapling presence is an outcome of colonisation. Additionally, these three sapling species showed the highest numbers of quadrats occupied, hence sample sizes.

Parent candidate (PC) variables used in the individual species analyses of colonisation by ash, field maple and pedunculate oak included: Diameter at breast height (DBH) of nearest PC; Height of nearest PC (m); Distance to the nearest PC (m) measured as ground distance from the

centre of the quadrat to the nearest edge of the PC canopy; Number of PCs within 100 m radius from the centre of quadrats – chosen as a maximum dispersal distance following Olrik et al. (2012), Broughton et al., (2021) (see Table S2 for detailed methodology). Data on PCs of other sapling species were not collected.

2.2.3. Woodland habitat, management and browsing, and scrub variables

Further environmental predictor variables measured for each quadrat sample were grouped as "woodland habitat", "management and browsing", and "scrub" variables. Woodland habitat variables included: Age of plantation; Canopy Cover percentage cover; Distance to nearest hedgerow (m) – used as a proxy for seed source proximity for potential scrub colonisation; Distance to the nearest ride (m) defined as unplanted strips of land ≥ 2 m in width (see Table S3 for detailed methodology). Three additional woodland variables were measured only for use in the canonical correspondence analysis (CCA) (see below) to avoid model over-parameterisation, including: Number of planted trees per quadrat – visual count; Plantation composition (mixed; diverse) – a plantation-wide categorical estimate dividing samples between Mixed (2–7 species) and Diverse (≥ 8 species) - a minimum of 2 species and a maximum of 18 was recorded at any one site; species richness of the planted trees per quadrat – visual count (Table S3).

Management and browsing variables relating to vegetation manipulation within the planted woodlands included: Management (managed; unmanaged) defining all woodlands in which there had been (managed) and had not been (unmanaged) manipulation of the vegetation between planted trees beyond the initial three years after planting recommend by the Woodland Trust (2022); Browsing intensity by deer and rabbit (quantified separately) – six-minute timed visual counts (see Table S4 for details).

Scrub variables collected within each quadrat included percentage cover of: hawthorn; bramble; blackthorn; rose; and non-thorny scrub. The first four variables were used as predictors of tree colonisation, and in separate analyses, were combined with the non-thorny scrub to form the response variables: percentage cover of all scrub; and species richness of scrub (see Table S5).

2.3. Statistical analysis

2.3.1. Sapling colonisation and regeneration

Drivers of tree colonisation were analysed using generalised linear mixed models (GLMMs) with a negative binomial distribution since Poisson models were highly overdispersed (assessed by calculating *Residual deviance / Residual degrees of freedom* and by using the *testdispersion* function in the package DHARMa version 0.4.7 (Hartig, 2019). Individual species GLMMs were performed on the most commonly occurring species deemed to be colonising (see above): ash, field maple and pedunculate oak sapling counts. Further GLMMs were performed on total counts and species richness of all tree saplings (including colonising and regenerating species). All GLMMs used woodland habitat, management and browsing, and scrub predictor variables, while those for individual species additionally tested seed source (parent candidate) variables (see Table S5).

2.3.2. Scrub colonisation

Percentage cover of scrub was computed as the sum of percent coverages of individual species (hawthorn, blackthorn, bramble, rose and non-woody scrub) and exceeds 100 % in certain quadrats with overlapping areal coverage between scrub taxa. Hence, as a response variable it was $\log_{10}$ transformed and analysed using a linear mixed model (LMM). Species richness of scrub was calculated by counting the individual scrub species within each quadrat, with *Rosa* spp and *Rubus* spp aggregated. Both percentage cover and species richness of scrub analyses used the woodland habitat and management / browsing variables as predictors (Table S5).

2.3.3. Model selection

Statistical analyses and graph generation were performed in RStudio (version 2022.07.0). All pairwise combinations of predictor variables were tested for collinearity using Pearson correlation coefficients (see Table S6 in Supplementary Material). Since no pairs of predictors simultaneously fitted in models shared values of Pearson $r \geq 0.7$, collinearity was not considered problematic (Dormann et al., 2013). Site was classified by woodland ownership and tested as a random effect to account for any non-independence arising from common management regime and/or spatial proximity. Where site improved AIC scores by ≥ 2, it was retained. To prevent over-fitting of final models, each of the four predictor variable groups (seed source (parent candidate), woodland habitat, management / browsing, and scrub variables, Table S5) was first subjected to a predictor filtering procedure. All variables that were included in the best model (lowest AIC) arising using a dredge function (MuMIn package – Barton, 2022) and/or were significant (p < 0.05) in a full model (fitting all predictors in the group), were selected as candidates to be tested in the final model run. The latter, starting with all candidate predictors fitted in a full model, used a backwards removal procedure until all remaining variables were significant (p < 0.05), hence a minimum adequate model (MAM) was found.

We tested for spatial autocorrelation in residuals of all final MAMs by plotting correlograms of these using the plot.correlog function in the *ncf (version 1.3–2)* package in R. In all cases, no significant spatial autocorrelation was found, hence all final MAMs were retained.

2.3.4. Canonical ordination

Canonical ordination using CANOCO software (version 4.5) was performed to determine the relative importance of woodland habitat variables, management and browsing intensity, and scrub species in influencing major gradients of variation in species composition and relative abundance of tree sapling taxa across woodland quadrats. The influence on taxa deemed to be colonising or regenerating (see Table 1) was explored. A preliminary detrended correspondence analysis (DCA) of tree sapling species data found intermediate gradient lengths of 3.15 (Axis 1) and 2.81 (Axis 2). Given the heterogeneity of sapling species distribution, we opted for a unimodal approach, hence canonical correspondence analysis (CCA), with down-weighting of rare species to minimise their disproportionate influence. Dummy variables were included for the binary categorical "Management" and "Plantation composition" variables.

3. Results

3.1. Summary of colonisation and regeneration

Tree saplings were found in 122 of 133 quadrats (97.7 %), comprising 3405 in total across 20 species. Nine tree sapling species were deemed "colonising" i.e. those without seed-bearing PCs within the plantation (Table 1). Although these included species that had been planted (e.g. oak, ash, field maple, sycamore, small-leafed lime, and sweet chestnut), their ages of maturation and the youth of the plantations indicated these sapling species to be colonisers. Eleven sapling taxa were found to have seed-bearing PCs present within plantation woodland, hence were deemed to be "regenerating" (Table 1). Pedunculate oak, ash and field maple were the most widespread putatively colonising species (lacking seed-bearing PCs within the plantation) being found in 80, 72 and 72 quadrats, respectively (Table 1). Ash was by far the most abundant colonising species in terms of total sapling counts, followed by field maple and pedunculate oak. In descending order of total sapling counts, silver birch, hornbeam and wild cherry were the three most important regenerating species (parents among the planted trees, Table 1).

Table 1

Summary of tree sapling data from 20 taxa occurring among 122 of 133 5 × 5-m quadrats across 57 plantation woodland sites in East Anglia, sampled between May and July 2022. Classification of taxa as colonising or regenerating was dependent on, respectively, absence or presence of seed-bearing parent candidate trees within each woodland in which the tree sapling taxon occurred. Additional data: number of quadrats (percentage of total in brackets); total number of saplings; mean saplings per quadrat +/- standard error (S.E.) in brackets. All species = similar statistics for counts of saplings pooled across all taxa. Species are ranked by number of quadrats (frequency).

Scientific name	Common name	Colonising / Regenerating	Number of quadrats (percentage of total)	Total saplings	Mean (±S.E.) per quadrat
Quercus robur	Pedunculate oak	Colonising	80 (60.2 %)	368	2.77 (±0.36)
Fraxinus excelsior	Ash	Colonising	72 (54.1 %)	1445	10.87 (±2.91)
Acer campestre	Field maple	Colonising	72 (54.1 %)	559	4.20 (±0.77)
Betula pendula	Silver birch	Regenerating	32 (24.1 %)	414	3.11 (±1.11)
Carpinus betulus	Hornbeam	Regenerating	30 (22.6 %)	241	1.81 (±0.61)
Corylus avellana	Hazel	Regenerating	30 (22.6 %)	103	0.77 (±0.38)
Salix spp.	Willow	Regenerating	26 (19.5 %)	63	0.47 (±0.16)
Prunus avium	Wild cherry	Regenerating	17 (12.8 %)	140	1.05 (±0.57)
Acer pseudoplatanus	Sycamore	Colonising	11 (8.3 %)	23	0.17 (±0.07)
Quercus cerris	Turkey oak	Colonising	5 (3.8 %)	14	0.11 (±0.07)
Prunus cerasifera	Myrobalan plum	Colonising	3 (2.3 %)	9	0.07 (±0.05)
Tilia cordata	Small-leafed lime	Colonising	3 (2.3 %)	6	0.045 (±0.03)
Alnus glutinosa	Alder	Regenerating	2 (1.5 %)	9	0.07 (±0.06)
Castanea sativa	Sweet chestnut	Colonising	2 (1.5 %)	2	0.015 (±0.011)
Ilex aquifolium	Holly	Regenerating	2 (1.5 %)	2	0.015 (±0.01)
Populus tremula	Aspen	Regenerating	1 (0.8 %)	2	0.015 (±0.015)
Ulmus glabra	Wych elm	Colonising	1 (0.8 %)	2	0.015 (±0.015)
Pinus sylvestris	Scots pine	Regenerating	1 (0.8 %)	1	0.008 (±0.01)
Prunus laurocerasus	Cherry laurel	Regenerating	1 (0.8 %)	1	0.008 (±0.008)
Quercus ilex	Holm oak	Regenerating	1 (0.8 %)	1	0.008 (±0.008)
All Species	———	———	122 (91.7 %)	3405	25.6 (±3.60)

3.2. Factors promoting tree sapling colonisation

The GLMM for ash showed a positive relationship between the number of ash saplings and height of the nearest PC, and a negative relationship with distance to PC, rabbit browsing intensity and percentage cover of *Rosa* spp. Older woodlands had higher levels of ash colonisation and no other variables had a significant relationship with ash (Table 2).

The GLMM for field maple showed that significant positive predictors of colonisation were DBH of the nearest mature maple, number of maples within 100 m, and age of the woodland. Distance to the nearest hedgerow had a negative effect on field maple colonisation while the management, browsing and scrub variables had no significant effect (Table 2).

Of the quadrats where pedunculate oak was found, 82.5 % had a PC within 100 m. However, the GLMM showed distance to PC was borderline significant (p = 0.05), therefore it was retained in the MAM (Table 2). Managed sites averaged slightly less colonisation as did

Table 2

Minimum adequate models (MAMs) of tree colonisation and regeneration within planted woodlands showing slope (estimate) values, standard errors (SE) and associated significance levels: P values = 0.0501(*), < 0.05 = *, < 0.01 = **, and < 0.001 = ***, < 0.0001 = ****. Independent variables were standardised. Measures of explanatory power included the *pseudo r²* statistics, R^2m (variation explained by fixed effects), R^2c (variation explained by both fixed and random effects), *Deviance explained* as an index of explanatory power in Poisson GLM. ——— = when seed source variables were not tested.

Response variable:	Ash saplings Estimate	± SE	Maple saplings Estimate	± SE	Oak saplings Estimate	± SE	All saplings Estimate	± SE	Sapling species richness Estimate	± SE
Intercept	2.787	(± 0.221) ****	1.575	(± 0.115) ****	0.034	(± 0.472)	1.774	(± 0.442) ****	1.049	(± 0.052) ****
Distance to nearest PC	−0.908	(± 0.160) ****			−0.199	(± 0.102) (*)	———	———	———	———
Height of nearest PC	0.809	(± 0.158) ****					———	———	———	———
DBH of nearest PC			0.473	(± 0.112) ****			———	———	———	———
Number of PCs within 100 m			0.372	(± 0.115)**			———	———	———	———
Age of plantation	0.569	(± 0.156)***	0.352	(± 0.118)**					0.255	(± 0.052) ****
Canopy cover							0.482	(± 0.139)***		
Distance to hedgerow			−0.372	(± 0.159)*						
Distance to ride					0.181	(± 0.085)*				
Management					−1.137	(± 0.554)*	−1.839	(± 0.571)**		
Rabbit browsing intensity	−0.042	(± 0.012)***								
Deer browsing intensity										
Scrub – Rose spp.	−0.325	(± 0.160)*								
Site as random effect	No		No		Yes		Yes		No	
Deviance explained	0.473		0.409							
R^2m	0.556		0.447		0.203		0.334		0.161	
R^2c	0.556		0.447		0.552		0.567		0.161	
AIC	541.5		449.3		433.6		1089.2		505.5	

samples that were closer to rides, although significance was weak in both cases (p = 0.04; p = 0.03, respectively). None of the other predictors showed significant relationships with pedunculate oak saplings (Table 2).

The GLMM of total saplings (regenerating and colonising) showed that plantations that were unmanaged or had higher canopy cover had significantly greater colonisation and regeneration (Table 2, Fig. 2a). Contrary to expectations, there was no significant effect of scrub species, browsing or the age of the plantation. In contrast, plantation age was shown to be the most important driver of sapling species richness with no other predictors retained in the MAM (Table 2).

Overall, the explanatory power of the final MAMs for ash and field maple was considerable (pseudo R^2m = 56 % and 45 %, respectively), while that for oak colonisation was relatively poor (20 %), with the all-saplings model being intermediate (33 %, Table 2).

3.3. Factors promoting scrub colonisation

Scrub species were found in 111 of 133 quadrats (83.5 %) and a total of 10 species of woody scrub were identified including: hawthorn, blackthorn, bramble, *Rosa* spp., dogwood, wild privet (*Ligustrum vulgare*), spindle, broom (*Cytisus scoparius*), guelder rose *(Viburnum opulus)*, and old man's beard (*Clematis vitalba*). The mean richness across quadrat samples was 2.71 species (median=2) while the most diverse sample had 8 scrub species. Both scrub species richness and scrub percentage cover were higher in older plantations, and percentage cover was also higher in unmanaged plantations (Table 3). Neither proximity to established hedgerow nor canopy cover were retained in MAMs for either the species richness or percentage cover of scrub (Table 3). Scrub coverage was also higher in plantations browsed more heavily by deer (Table 3).

3.4. Environmental correlates of tree sapling species composition

For the canonical correspondence analysis (CCA), 12 of the 17 environmental variables showed marginal significance (P < 0.05) using Monte Carlo tests, with 999 random permutations (Table 4), and were retained in the final CCA bi-plot (Fig. 3). Marginal effects (where each variable is tested on its own) were preferred over conditional effects to allow a range of candidate explanatory variables to be visualised in relation to tree sapling species composition.

Table 3

Minimum adequate models (MAMs) of scrub colonisation (percentage cover and species richness) within planted woodlands showing slope (estimate) values, standard errors (SE) and associated significance level: P values < 0.05 = *, < 0.01 = ** , and < 0.001 = ***, < 0.0001 = ****. Independent variables were standardised. Measures of explanatory power include the *pseudo r²* statistics, R^2m (variation explained by fixed effects), R^2c (variation explained by both fixed and random effects).

Response variable:	Scrub percent cover		Scrub species richness	
	Estimate	± SE	Estimate	± SE
Intercept	−1.331	(± 0.699)	−0.324	(± 0.032)*
Age of plantation	0.207	(± 0.051) ****	0.102	(± 0.019) ****
Canopy cover				
Distance to hedgerow				
Distance to ride				
Management	−1.021	(± 0.435)*		
Rabbit browsing intensity				
Deer browsing intensity	0.023	(± 0.010)*		
Site as random effect	Yes		Yes	
R^2m	0.334		0.259	
R^2c	0.408		0.406	
AIC	829.1		476.5	

Axis 1 of the ordination bi-plot (Fig. 3) represents a gradient of sapling community variation associated with quadrat-level species richness of scrub and deer browsing, allied with age and tree species composition (mixed vs diverse) of the woodland plantation. Axis 2 corresponds to community variation associated mainly with the amount of hawthorn in quadrats, and to a lesser extent *Rosa* species, both taxa being negatively correlated with distance to the nearest ride which has a weakly positive Axis 2 association (Fig. 3, Table 4). Management (and the lack of) is split in its association between both Axis 1 and Axis 2, with management having negative scores for both axes. It is notable that nine of eleven sapling taxa deemed to be regenerating have positive Axis 1 scores, hence tend to be associated with older, unmanaged and more diverse plantations and higher scrub richness. Additionally, a cluster of sapling species mostly deemed to be colonising (including ash and oak species) are somewhat (albeit weakly) more associated with managed and less diverse plantations, with fewer scrub taxa and less deer browsing. Both *Acer* species (and the less common *Ulmus glabra*) are distinct in being deemed to be colonising and yet associated with older
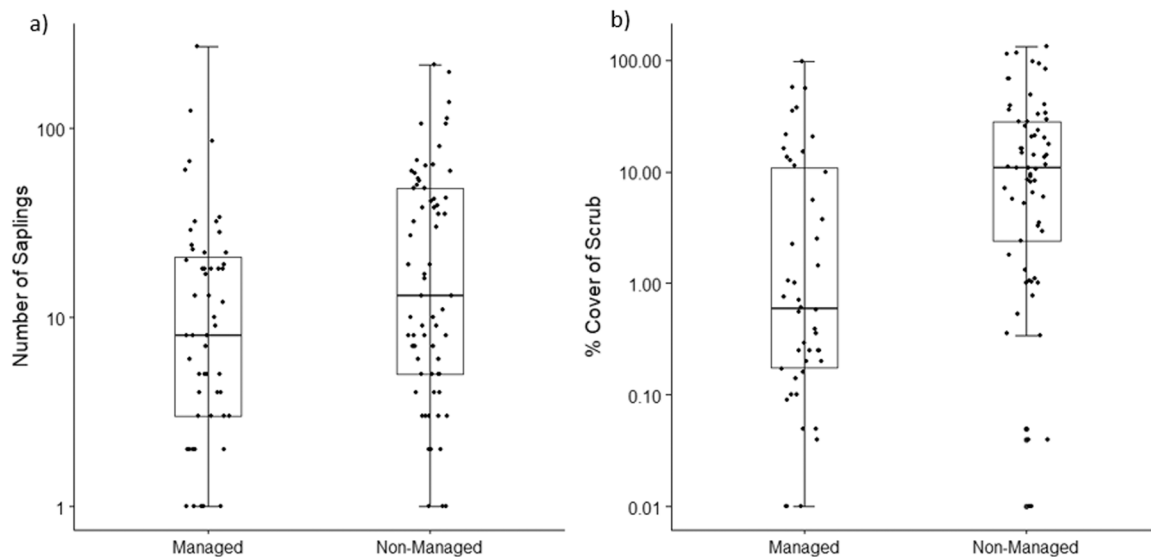

Fig. 2. The relationship between management and (a): number of all saplings found, (b), percentage cover of scrub. Management had a significant negative effect on the number of saplings and the percentage cover of scrub – see model estimates and tests of significance in Tables 2 and 3 respectively. Boxplot uses the summary statistics: median, hinges (interquartile range = IQR), and whiskers + /-1.5 * IQR.

Table 4

Results of Canonical Correspondence Analysis (CCA) testing the association between woodland habitat variables, management / browsing, and scrub variables and tree sapling species colonisation and regeneration in 122 quadrat samples containing ≥ 1 sapling. Significance (p < 0.05) of each environmental variable was calculated individually (marginal effects) using Monte Carlo tests with 999 random permutations. The lambda (λ) value corresponds to the amount of variation explained by a variable and the p-value the associated significance.

Environmental variable	λ	P
Scrub species richness	0.44	0.001
Plantation age	0.20	0.001
Mixed plantation	0.18	0.001
Diverse plantation	0.18	0.001
Deer	0.17	0.001
C. monogyna	0.13	0.001
Managed	0.12	0.001
Unmanaged	0.12	0.001
Rosa spp.	0.11	0.023
Canopy cover	0.09	0.005
P. spinosa	0.08	0.047
Plantation tree species richness	0.07	0.028
R. fructicosus	0.06	0.029
Distance to ride	0.06	0.033

plantations with higher canopy cover and high coverage of scrub species.

4. Discussion

Natural colonisation within planted woodland, distinct from natural regeneration, is a largely overlooked process of benefit to woodland biodiversity and resilience. This study found evidence from three tree sapling species indicating that colonisation can occur extensively within planted woodlands, primarily driven by size-associated traits, proximity and frequency of parent candidate trees outside the plantation. Woodland habitat variables were also influential including the age of the woodland and to a lesser extent management and canopy cover. The rate of tree colonisation was more rapid than has been observed for other taxa e.g. woodland ground flora or woodland birds, which can take decades to centuries (Matlack, 1994). As expected, colonisation of tree and scrub species was significantly lower in sites where removal of vegetation between the planted trees was practiced. While no individual scrub species was associated with colonisation by a particular tree sapling species, an association between scrub species richness and species composition of tree saplings, especially those deemed to be regenerating, indicates that further research into the role of scrub colonisation within planted woodland is needed.

4.1. Tree sapling colonisation and regeneration

In this study, ash was the most abundant sapling species and its colonisation success determined more by PC (seed source) variables than was the case for either pedunculate oak or field maple. As hypothesised, and consistent with other studies on seed dispersal, both proximity (c.f. Cain et al., 2000; Clark et al., 2004; Wang et al., 2020) and height (Thomson et al., 2011) of the PC were important. The univariate fit of woodland age with ash saplings is weakly negative (Table S7), visualised also in the CCA, and consistent with the reputation of ash as a pioneer (Kerr and Cahalan, 2004). However, once PC variables are accounted for in the GLMM, the slope for age of woodland reverts to positive – likely due to an observed increase in distance to nearest PC with age of woodland across our sites. The negative effect of rabbit browsing on ash colonisation may be explained by ash being highly palatable (Rackham, 2006). Anecdotal evidence supporting this comes from Wytham Woods where ash regeneration increased considerably in the 1950s following the arrival of myxomatosis (Kirby, 2020).
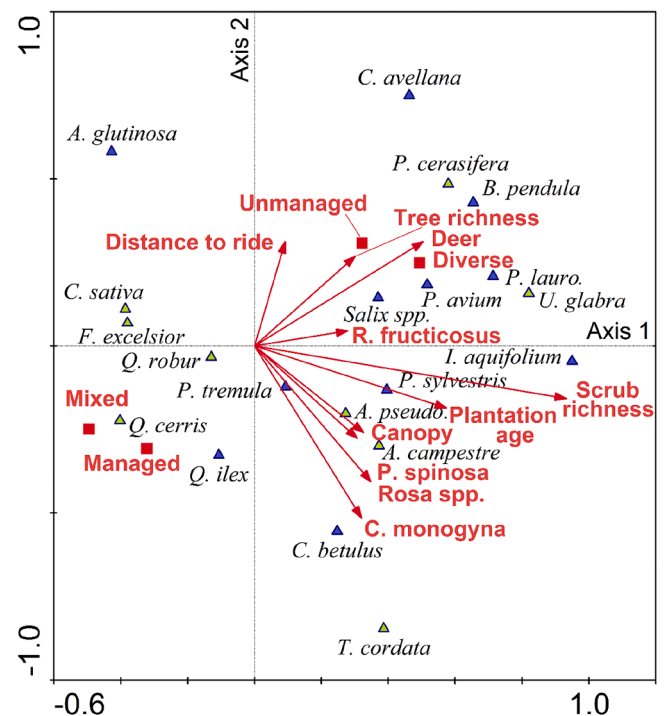

Fig. 3. Ordination bi-plot of canonical correspondence analysis (CCA) of composition of 20 tree sapling species (nine coloniser species centroids = green triangles; 11 regenerating species centroids = blue triangles) and marginally significant environmental variables (continuous = red arrows; categorical = red squares) in 122 quadrat samples containing ≥ 1 sapling. Quadrats were sampled across 57 sites in East Anglia between May-July, 2022. Rare sapling species (occurring in fewer than 5 % of quadrats) were downweighted in the CCA. Abbreviated sapling species names are as follows: *A. campestre, Acer campestre*; *A. pseudo., Acer pseudoplatanus*; *A. glutinosa, Alnus glutinosa*; *B. pendula, Betula pendula*; *C. betulus, Carpinus betulus*; *C. sativa, Castanea sativa*; *C. avellana, Corylus avellana*; *F. excelsior, Fraxinus excelsior*; *I. aquifolium, Ilex aquifolium*; *P. sylvestris, Pinus sylvestris*; *P. tremula, Populus tremula*; *P. avium, Prunus avium*; *P. cerasifera, Prunus cerasifera*; *P. lauro., Prunus laurocerasus*; *Q. cerris, Quercus cerris*; *Q. ilex, Quercus ilex*; *Q. robur, Quercus robur*; *Salix spp., Salix* species; *T. cordata, Tilia cordata*; *U. glabra, Ulmus glabra*. Categorical environmental variables are presented as centroids (red squares) and continuous variables as red arrows. Abbreviations of woodland environmental variable names: Canopy, canopy cover; C. monogyna, *Crataegus monogyna*; Deer, deer browsing intensity; Diverse, plantation composition ≥ 8 species; Managed, managed plantation; Mixed, plantation composition of 2–7 species; P. spinosa, *Prunus spinosa*; R. fructicosus, *Rubus fructicosus*; Rosa spp., *Rosa* species; Tree richness, plantation tree species richness; Scrub richness, scrub species richness; Unmanaged, unmanaged plantation.

Based on quadrats in which ash, maple and oak saplings were present, ash had by far the highest sapling:PC ratio (1.58 as opposed to 0.35 and 0.42 for maple and oak, respectively), highlighting its colonisation superiority. Ash is an aggressive competitor of other tree species (Kerr and Cahalan, 2004) and is tolerant of drought (Marigo et al., 2000). Furthermore, the ability of ash to regenerate post-coppicing (Evans, 1992) will likely have conferred some resistance to mowing/strimming as indicated by ash colonisation being relatively tolerant of management in our analyses.

While ash has not been widely planted in the UK since the outbreak of dieback in 2012, genetically resistant individuals have been identified and mortality predictions moderated (Coker et al., 2019; Carroll and Boa, 2024). The finding in this study, of ready colonisation by ash in planted woodlands, when PCs are in the vicinity, therefore indicates an opportunity for ash recovery with future potential to increase population resistance to dieback.

Field maple had the highest number of PCs (average = 23.3) in the

landscape surrounding each woodland in which saplings were found and had a significant positive influence on colonisation. Maples were extensively planted in hedgerows in East Anglia from the 1800s and were mainly managed through coppicing or pollarding (Barnes and Williamson, 2011), which may explain why DBH rather than height was a better colonisation predictor. DBH and height are also proxies for tree age which is positively associated with fecundity in many plant species (Mencuccini et al., 2005). The age beyond which tree fecundity declines (Qiu et al., 2021) is unlikely to have been a factor in this study as mean DBH of field maple was 0.5 m. Importance of proximity of hedgerows for field maple colonisation is likely explained by the role of hedges as a seed source but could also relate to wider ecological benefits such as increased pollination (field maples are allogamous), better soil structure and reduced water run-off. Hedgerows may also benefit colonisation by acting as vertical structures to trap/slow wind-dispersed seed (Corbin et al., 2016).

In this study, all but one landowner reported that planting was done on areas that had been cleared of all vegetation. Age of woodland here represents time since colonisation could occur, likely explaining the positive correlation with field maple colonisation. Interestingly, woodland age was not observed to be important in the pedunculate oak or all-saplings analyses but was important for total sapling species richness.

Pedunculate oak was the most widely occurring tree sapling species but only weakly predicted by proximity to a PC, distance to nearest ride and management. None of the scrub species in this study predicted oak colonisation, in contrast both to evidence suggesting scrub facilitates it in more open ground (Kuiters and Slim, 2003; Harmer et al., 2010), and conversely that bramble cover is a negative predictor of $Q.\ robur$ seedling survival in mature stands (Harmer and Morgan, 2007). Pedunculate oak may also rely more heavily on scrub in open ground for protection from climatic stress; within woodlands, planted trees may provide this protection, weakening the role of scrub.

Acorns dispersed by gravity alone tend to fall within or close to the boundary of the canopy. Across the samples, the nearest oak canopy edge to a quadrat was 7.1 m which is a considerable distance suggesting that most oak saplings were likely dispersed by either small rodents (Ouden et al., 2005; Soné and Kohno, 1996), squirrels (Steele and Yi, 2020) and/or corvids (e.g. Pesendorfer et al., 2016). Individual jays are estimated to bury up to 10,000 acorns per autumn (Schuster, 1950, reported in Vera, 2000) with dispersal distances ranging from a few meters to several kilometres (Pons and Pausas, 2007). In this study, acorn bearing trees were identified within the plantation in ten samples where pedunculate oak saplings were abundant, suggesting potential regeneration. However, given the age of woodland sites (4 –18 years), that oaks tend to reach sexual maturity after $circa$ 50 years (Forestry Commission, 2022), and that there were no ready means to test acorn viability, we assumed colonisation, hence discounted these trees as PCs in our analyses. Nevertheless, rapid climate change and elevated CO_2 levels have been linked to earlier maturation of many species (Brienen et al., 2020).

Total counts and species richness of all saplings combined, was positively associated with canopy cover and woodland age, respectively. The CCA showed centroids for regenerating sapling species largely to be associated with older woodlands, with high scrub species richness and canopy cover (Fig. 3). Although not tested in GLMMs, sapling species richness was clearly not a function of planted tree species richness (Pearson r = -0.008), consistent with the majority of recorded saplings being judged to be colonisation not regeneration (2428/3405 = 71.31 %). Given that many heavily browsed saplings were either dead or unidentifiable in the field, thus counted as deer browsing rather than saplings, the relationship revealed between deer browsing and saplings in this study should be treated cautiously.

Available light penetrating woodland canopies is known to enhance sapling colonisation (Evans, 1984; Harmer, 2001). However, the positive associations between canopy cover and sapling survival observed here, may reflect shading protection against increasing intensity of warming climate events (drought, ground desiccation, sun scorch) and other abiotic effects (e.g. Rey Benayas et al., 2015). This has implications for the creation of woodlands using natural colonisation of open ground – sapling mortality could be high in conditions of extreme heat and drought without protection from an overstorey.

The negative effect of management on numbers of unplanted saplings (both colonising and regenerating) confirms the impact of vegetation removal. Where selective removal of vegetation was reported, it was often focused on "less desirable" species such as bramble and $Salix$. In sites with indiscriminate vegetation management between trees, species better adapted to coppicing, such as ash and field maple, were less affected.

4.2. Scrub colonisation

The positive effect of plantation age on scrub percentage cover and species richness is consistent with metacommunity theory, with rapid increases in species richness predicted in the early and mid-successional stages (Mouquet and Loreau, 2003; Sferra et al., 2017). Nevertheless, scrub percentage cover was consistently low across sites with the most abundant species being bramble averaging 10 % coverage per quadrat, followed by hawthorn (2 %). Scrub is associated with early successional stages that may be effectively bypassed within plantation habitats where overstorey vegetation is already present (Corbin and Holl, 2012). Low scrub cover was also due to widespread scrub removal despite more recent research on benefits of scrub for ground-nesting birds and small mammals. Woody scrub was deliberately allowed to flourish in only four of the 57 woodland sites that were surveyed. At other sites, either scrub removal was practiced, or the site had been neglected since planting, hence scrub coverage was mostly the outcome of chance than design. Management being a significant negative predictor of scrub coverage is not only about the unpopularity of bramble (which averages 36.5 % of scrub found), since the negative effects extend also to scrub species richness. Furthermore, management was largely synonymous with mowing/strimming which boosts the growth of grass species whilst discouraging woody scrub species (Harmer, 2003).

The hypothesis that hedgerows, as a primary seed source of scrub species, would be positively associated with scrub coverage, was not supported. As with oak saplings, rides that border plantations may disrupt gravitational dispersal and vegetative spread from the seed source. All scrub species found in this study (except for broom) are edible to birds, therefore seed may be dispersed over relatively large distances exceeding the range analysed within this study (100 m).

Although a negative effect of deer browsing on scrub coverage might be expected, the positive association in this study may reflect deer activity being highest where scrub forage is more abundant. Additionally, deer may simply feel safer in scrubbier habitat; of the privately owned woodlands surveyed, over 80 % reported some level of management of deer populations.

While plantation age is the main driver of both scrub and sapling species richness (Table 2 and 7), the potential influence of scrub on saplings cannot be ruled out in this study. In the CCA, species richness of scrub was the independent variable most strongly correlated with variation in sapling species composition, being positively associated with counts of sapling species deemed to be regenerating. Furthermore, the coverage of no single scrub species showed a positive effect on colonisation of tree saplings suggesting the anthropogenic nature of planted woodlands may result in successional pathways and communities atypical to those of open ground.

Patterns of colonisation will be influenced by various temporal factors: germination periods can vary across species and sites; browsing patterns can vary throughout the seasons with broadleaves grazed preferentially in summer and conifers in winter (Pfeffer et al., 2021); and there is interannual variation in seed abundance e.g. mast years. To avoid temporal bias, sampling in summer and winter over successive years is recommended for future research.

5. Conclusions

This study found evidence that colonisation and regeneration can co-occur extensively within planted woodlands, primarily driven by parent candidate characteristics, the age of the woodland and to a lesser extent management and canopy cover. While the net effect of management in the form of vegetation removal was weak in relation to colonisation, its strong negative impact on overall sapling counts suggests a trade-off dynamic with passive components (colonisation and regeneration) of woodland creation. The more uncertain successional trajectory of natural colonisation has been perceived as less favourable for use with more specific woodland creation objectives such as timber production (Bauld et al., 2023). However, timber as a primary aim makes up a minority of new broadleaf woodland creation, with biodiversity, landscape, carbon sequestration, flood mitigation and recreation all being more common objectives (Lawrence, Dandy and Urquhart, 2010) that are potentially enhanced by combining passive and active afforestation.

Promoting natural colonisation and natural regeneration within planted woodlands has potential as an integrated woodland creation approach to increase biodiversity and ecological resilience. Natural colonisation enhances structural and ecological heterogeneity of planted woodlands, while also offering reduced risks of importing disease or pests, and greater local ecological suitability, and/or potential for genetic admixing of local trees with imported stock better adapted to warmer climates. Promotion of colonisation friendly practice within plantations could be incentivised at relatively much lower cost than the cost of planting itself (MacMillan et al., 1998). However, a more intentional or facilitatory approach to natural colonisation will depend also on sufficient availability of seed source trees, as well as ecological connectivity, including dispersal opportunities (e.g. habitat corridors), within the landscape.

Given the scale of recent and proposed UK and global tree planting initiatives, if colonisation can be promoted within planted woodlands (or portions of them) then potentially large tracts of land could be better managed both economically and environmentally. This study suggests that tree planting and colonisation are compatible within temperate broadleaf woodlands but further confirmatory research is needed to assess how they interact, especially with management practices and as plantations age.

CRediT authorship contribution statement

Feadora Morris: Conceptualization, Methodology, Fieldwork – planning, management and execution, Writing – original draft, Data analysis, Funding acquisition. **Richard G. Davies:** Conceptualization (supporting), Methodology (supporting), Data analysis (supporting), Writing – review & editing, Supervision, Funding acquisition, Project administration.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2024.122492.

Data availability

Data will be made available on request.

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