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RESEARCH ARTICLE

Larger and structurally complex woodland creation sites provide greater benefits for woodland plants

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Abstract

1. Reforestation initiatives are underway across the world. However, we know relatively little about the ecological consequences of creating and restoring forest ecosystems, and there is a lack of studies examining the drivers of species colonisation and establishment across appropriate temporal and spatial scales to inform conservation practice.
2. Using data from a long-term natural experiment (the WrEN project), we explore ground plant species occurrence and community composition in 102 woodland creation sites (10–160 years since planting), and 27 old growth woodlands (>250 years). We conducted field surveys to collect data on occurrence of plant species (classified into woodland specialist, woodland generalist, or non-woodland) and used Structural Equation Modelling to investigate the influence of local (age, size, woodland structure) and landscape-level (amount of surrounding woodland) attributes on species richness.
3. Woodland generalists are readily colonising woodland creation sites to similar levels found in old growth woodlands. However, there were fewer woodland specialist and more non-woodland plants in creation sites than in old growth. Specialists and generalists were more likely to be present in larger woodlands and those with higher variation in tree size (which was higher in older woodlands) and did not appear to be influenced by features of the surrounding landscape. Some plant communities in older creation sites (80–160 years) were similar to old growth, suggesting colonisation of a typical old growth flora over time; however, some sites were shifting away from this trajectory.
4. Specialists are slow to colonise woodland creation sites and their occurrence was low relative to old growth woodlands even after >80 years. However, woodland management to increase structural complexity may enhance the establishment of woodland plants. The lack of influence of the surrounding landscape on species occurrence is likely due to most of the study sites being relatively isolated resulting in limited colonisation. This suggests that new woodlands need to be adjacent or very near to existing woodland to receive the benefits of increased

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colonisation. Our results highlight the importance of creating large and structurally complex woodlands, close to existing woodlands to facilitate the colonisation and establishment of woodland plants.

KEYWORDS
biodiversity, colonisation, reforestation, restoration, tree planting, woodland creation, woodland plants, WrEN project

1 | INTRODUCTION

There are many global initiatives underway to increase tree cover to combat climate change (Canadell & Raupach, 2008; Leclère et al., 2020) and protect and restore biodiversity (Leclère et al., 2020; Newmark et al., 2017; Wang et al., 2022). Examples include the 2008 United Nation's REDD+ initiative to reduce emissions from deforestation and forest degradation, the 2011 Bonn Challenge to restore 350 million hectares of degraded and deforested lands by 2030, and the UN Decade on Ecosystem Restoration (2021–2030). Predicting the benefits of increased tree cover is arguably more straightforward for carbon storage and climate change mitigation than it is for biodiversity (Bastin et al., 2019; Cook-Patton et al., 2020; Soto-Navarro et al., 2020). This is partly due to the significant temporal lags between restoration actions, such as woodland creation, and species' responses (Jackson & Sax, 2010). These temporal lags, or colonisation credits, have been observed in a wide range of species and ecosystems and found to operate over a broad range of spatial and temporal scales (Lira et al., 2019). Woodland plants are exceptionally slow colonisers as they struggle to reach new isolated patches, with colonisation credits existing for more than a century (Brunet et al., 2021; Honnay et al., 2002; Hughes et al., 2023; Naaf & Kolk, 2015; Vellend et al., 2006). However, attributes of the local site and surrounding landscape may also directly influence plant colonisation and establishment within newly created woodlands. Understanding which attributes are most important, and over what spatial and temporal scales, could help to maximise the biodiversity benefits of future woodland creation.

It has been well reported that woodland plant species richness is higher in older (Brunet, 2007; Brunet et al., 2021; Pierik et al., 2010) and larger woodland creations sites (Petit et al., 2004; Pierik et al., 2010; Usher et al., 1992), as colonisation events accumulate over time and the establishment of self-sustaining populations is aided by more suitable available habitat (MacArthur & Wilson, 1967; McGuinness, 1984). In addition, as recently created woodlands age, woodland structure (e.g. variation in tree size) and environmental factors (e.g. light availability) change, potentially facilitating plant establishment (Humphrey et al., 2015; Peterken & Game, 1984). It may take decades to develop a structure similar to that of an ancient mature woodland (Fuentes-Montemayor et al., 2021; Whigham, 2004) and create conditions suitable for woodland specialist plants. However, few studies have studied the impact of local woodland structure, such as tree size and density which change over time, on plant species establishment (Peterken & Game, 1984). Species community changes over time are often examined through comparisons of old versus young woodlands (Brunet et al., 2021; Kimberley et al., 2014; Naaf & Kolk, 2015), but there is a lack of data on the pattern of plants colonising new woodlands through time.

Spatial proximity to source populations is also important for species colonisation within newly created habitats, especially in highly fragmented and degraded landscapes (Watling et al., 2011). Whilst woodland creation sites located close to older or ancient woodlands have higher plant species richness (Brunet et al., 2021; Hughes et al., 2023; Naaf & Kolk, 2015), it is unclear at what spatial scales this relationship occurs as spatial proximity is rarely considered beyond a simple categorisation of contiguous or isolated (Brunet et al., 2021; Hughes et al., 2023). Furthermore, the spatial composition and configuration of the wider landscape, including the amount of other woodlands and smaller woody features (e.g. hedgerows and clusters of trees) in the surrounding matrix, is often overlooked (Humphrey et al., 2015), despite having a positive influence on woodland species colonisation in the few studies that do include it (Jamoneau et al., 2011; Liira et al., 2012; Peña et al., 2011; Petit et al., 2004).

Studying the effects of restoration on biodiversity empirically is challenging as it is difficult to run experiments over the temporal scales necessary to detect effects of restoration (Jackson & Sax, 2010; Tilman et al., 1994), and to ensure both ecological realism and the ability to apply experimental control and replication (Debinski & Holt, 2000; Haddad, 2012). Consequently, there is a scarcity of studies conducted at appropriate spatial extents and temporal resolutions to inform ecological restoration policy and practice. Yet it is this sort of evidence that is urgently needed to test the efficacy of past restoration actions and inform the design of future restoration schemes (Watts et al., 2020). 'Natural experiments' which overlay an experimental design on a landscape that has been modified previously provide a way of overcoming these spatial and temporal challenges (Carpenter et al., 1995; Diamond, 1986; Stockton et al., 2005).

The UK has a long history of woodland degradation and loss coupled with over a 100 years of restoration action, both of which have been well documented in historical maps (Harmer et al., 2015). This provides a unique opportunity to study the effects of woodland restoration that has occurred over the past 160 years within highly fragmented and agriculturally dominated landscapes. The Woodland Creation and Ecological Networks project (WrEN) is a long-term,

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large-scale natural experiment that aims to assess the effects of past woodland creation on current biodiversity to inform future conservation actions (Watts et al., 2016). During project development, woodland creation sites were systematically selected to span a wide range of relevant local and landscape attributes to test their influence on the occurrence, abundance and diversity of a wide range of taxonomic groups (Watts et al., 2016).

In this study, we examine the vascular plant community across the WrEN network of post-agricultural woodland creation sites. Our study is the first to consider the relative influence of an extensive suite of local attributes (including woodland structural metrics) and landscape-level attributes (including composition and configuration of the surrounding matrix) on the colonisation of all plants at appropriate temporal and spatial scales to inform policy and practice. By using a Structural Equation Model approach both direct and indirect effects of these attributes can be examined, allowing us to identify potential mechanisms, for example age acting through increased time for colonisation and/or through woodland development. We answer the following questions:

1. Is ground flora species richness in woodland creation sites similar to that found in old growth woodlands?
2. What is the relative influence of local and landscape-level attributes on the occurrence and species richness of woodland plants in woodland creation sites?
3. How does the plant community composition change over time, and does it move towards assemblages found in old growth woodland communities?

2 | MATERIALS AND METHODS

2.1 | Study sites

We surveyed vascular plants in 102 woodland creation sites between May and July 2015 and 27 'old growth' woodlands in June and July 2016, distributed across Central Scotland and the Midlands of England. The woodland creation sites were part of the long-term, large-scale natural experiment Woodland Creation and Ecological Networks (WrEN) project (Watts et al., 2016; www.wren-project.com) and were all discrete broadleaved woodlands surrounded predominately by agricultural land. Sites were systematically selected to represent a gradient in woodland age (10 to 160 years at the time of survey; Table S1), woodland size (0.5–32 ha), proportion of broadleaved woodland within 3 km (1.3%–17%) and distance to nearest broadleaved woodland (7–1573 m). All sites had been planted with a range of tree species on former agricultural land, without remnant woodland biodiversity or a persisting soil seed bank. Therefore, the presence of species within these new woodlands represents successful colonisation, presumably mediated by attributes of the woodland sites and the landscapes around them. Old growth woodlands acted as a comparison to the more recently created woodlands; they were selected to have similar characteristics (e.g. patch size, degree of connectivity and amount of surrounding woodland) and were located in the same landscapes as the woodland creation sites. We selected the old growth sites using the Ancient Woodland Inventory, which defines Ancient as continuously wooded since 1750 in Scotland and since 1600 in England (Forestry Commission, 2011; Spencer & Kirby, 1992), although they are likely to be much older. Study sites were >1 km from each other (in most cases >3 km).

2.2 | Botanical surveys

The presence of all vascular ground flora (shrubs, climbers, forbs, graminoids and ferns) were recorded at each site by an experienced botanist, who conducted a thorough search across the full woodland area, recording all species encountered. Taxonomic agglomerates (e.g. *Taraxacum officinale* agg.) were treated as single species. Following the classification of Kirby et al. (2012), species were classified as woodland specialist, woodland generalist (defined as 'other woodland' by Kirby et al., 2012) or non-woodland. In Kirby et al. (2012), woodland specialists were defined as species that were exclusively or mainly found in British woodlands based on records from the National Vegetation Classification tables, Ellenberg Indicator Values and Functional Attributes. Woodland generalists were defined as species that are frequently found within woodlands but are also common in many non-woodland habitats. Non-woodland species are those that are more commonly associated with other land cover types, such as grasslands.

2.3 | Local and landscape variables

In each planted and old growth woodland, we measured the following local variables at the level of woodland site: age, patch area, structural tree metrics (stem density and diameter at breast height [DBH]) and canopy cover. For woodland creation sites, age was determined by inspecting digital scans of Ordnance Survey historical land-use maps from the 1840s to 1990s (An Ordnance Survey/EDINA supplied service http://digimap.edina.ac.uk/). We calculated the approximate age of each woodland patch by identifying the time when the woodland first appeared on the historical maps (giving a range of 10 to 160 years). Old growth woodlands were categorised as >250 years using the Ancient Woodland Inventory. Woodlands were split into four development stages based on their age and following Oliver and Larson (1996): stand initiation = 0–30 years (*n sites* = 32), stem exclusion = 31–80 years (*n* = 28), understorey re-initiation = 81–160 (*n* = 42), and old growth >250 years (*n* = 27). Woodland area was generally consistent between development stages (Figure S1) with slightly larger woodlands on average found in the youngest stage (stand initiation). Woodland area was calculated in hectares (ha) in ArcGIS Desktop 10 (Advanced licence, http://www.esri.com/). Vegetation surveys were conducted using the point-centred quarter method along an edge-to- interior transect (Ferris-Kaan & Patterson, 1992), with points established every 15 m along an edge-to- interior transect (transect length varying with size of woodland). At each point, a cross

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of two perpendicular lines (one of them following the direction of the transect) was established to divide the surrounding area into four quarters. Within each quarter, we measured the distance from the centre point to the nearest tree (used to calculate stem density) and the diameter at breast height of this tree measured (DBH; trees ≥7 cm DBH). Canopy cover (%) was estimated using a sighting tube with an internal crosshair (Ferris-Kaan & Patterson, 1992); if the crosshair intersected canopy vegetation, the presence of canopy was recorded. Ten measurements were taken per point along the transect, at 1 m intervals perpendicular to each point.

Landscape variables were included in the analysis to capture the spatial arrangement of the surrounding landscape, including both the composition and configuration. For composition, the proportions of land with broadleaved woodland cover, trees outside of woodlands (calculated as the proportion of buffer covered by tree canopy not included in woodlands) and semi-natural vegetation (other than woodland) were calculated within buffers surrounding the study sites (buffer sizes = 100, 250, 500, 1000, 1500, 2000, 2500, 3000 m). To capture the configuration of surrounding landscape, the distance to the nearest broadleaved woodland (m) was measured. See Supporting Information Appendix 1 for more detail on how these variables were calculated. All spatial analysis was carried out using the 'Simple Features' (Pebesma, 2018) and 'Raster' (Hijmans, 2023) packages in R Statistical Software (v4.2.1; R Core Team, 2022).

2.4 | Statistical analyses

2.4.1 | Species occurrence and richness across woodland development stages

We tested for differences in species richness across the four stages of woodland development using a linear regression model (question 1). We ran three separate models for the species classifications (woodland specialist, woodland generalist, and non-woodland), with total number of species found in each woodland as the response variable and development stage as a fixed effect. A Tukey post hoc test was used to determine significant pairwise differences in species richness between stages.

2.4.2 | Drivers of woodland plant species richness in woodland creation sites

We analysed the relative influence of a wide range of variables on plant species richness in woodland creation sites (question 2; $n = 102$; excluding old growth woodlands), using a Structural Equation Modelling approach (SEM). SEM is a multivariate statistical framework that tests whether a priori hypothesised direct and indirect causal relationships between variables are supported by observed data. We used ecological theory to construct a metamodel (Figure 1) testing the influence of landscape attributes (likely mediating species colonisation) and local attributes (likely influencing habitat suitability and thus species establishment) on species richness (total count of either specialist or generalist species per site). We ran separate models (following the same metamodel) for woodland specialists and generalist, both modelled using a generalised linear model (GLM) with a negative binomial distribution. SEMs were performed in the 'piecewiseSEM' R package (Lefcheck, 2016) and model fit was evaluated using Fisher's C and Chi Squared statistics, with values of $p > 0.05$ indicating the model was supported by the observed data. See Supporting Information Appendix 1 for full details on SEM variable selection, hypotheses, and model specification for each direct and indirect pathway on species richness.

To investigate whether patterns observed for overall specialist richness remained for individual species, we tested the influence of

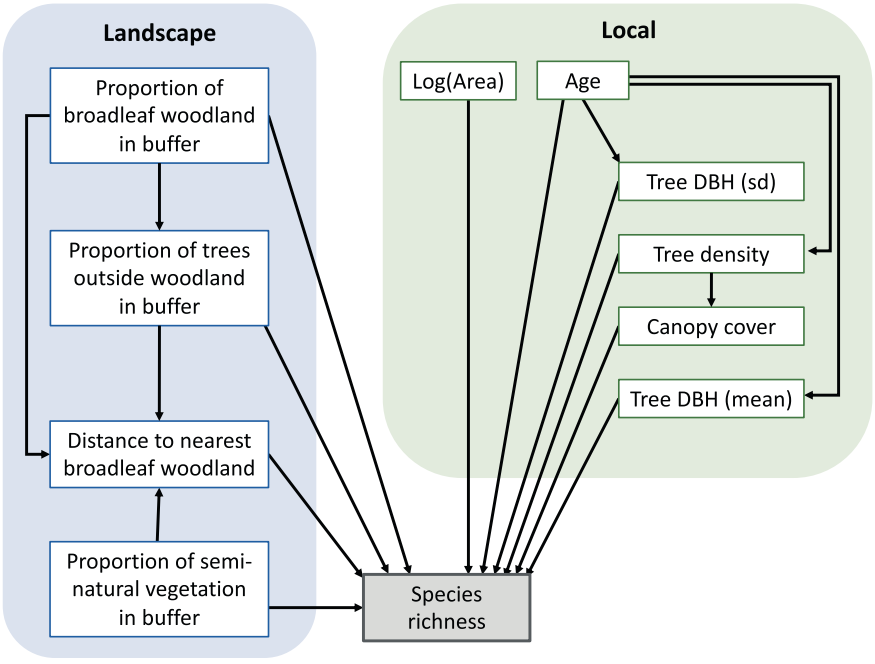


FIGURE 1 Hypothetical structural equation metamodel showing potential local and landscape drivers of woodland plant species occurrence within newly created woodlands. Full details on these variables are within the main text and Supporting Information Appendix 1.

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local and landscape variables on species occurrence for the 10 most common specialist species using GLMs (i.e. 10 models). For each model, the response variable was the presence or absence of the species in each woodland (1 or 0, respectively), and a binomial error distribution was used. There were 10 main fixed effects, which included the four landscape variables and six local variables included in the SEM (Figure 1). Region (Scotland or England) was added as a fixed effect in all models to control for regional differences but was not a variable of interest.

2.4.3 | Plant community composition across woodland development stages

To compare compositional similarity of the full plant community (woodland specialists and generalists, and non-woodland species) across the four development stages (question 3) we conducted an ordination using non-metric multi- dimensional scaling (NMDS) on a Jaccard dissimilarity matrix. Ordinations were conducted on site-level data, based upon the presence/absence of species per site using the 'vegan' package (Oksanen et al., 2007). Based on results of the SEM, we assessed the effect of development stage and woodland structure (standard deviation of tree DBH) on community composition using a permutational multivariate analysis of variance (PERMANOVA), with 999 permutations to calculate significance. Finally, a similarity percentage procedure (SIMPER) was performed in 'vegan', to determine which plant species contributed the most to differences between development stages.

3 | RESULTS

3.1 | Patterns of plant species occurrence and richness over time

Across all woodlands (creation and old growth), the ground flora was dominated by woodland generalist species (Figures 2 and 3), with generalists making up the 15 most recorded species across sites. In woodland creation sites the three most common generalists were *Urtica dioica* (96.1% of sites), *Galium aparine* (86.3%) and *Rubus fruitcosus* (78.4%) and in old growth woodlands these were *U. dioica* (85% of sites), *R. fruitcosus* (81.5%;) and *Pteridium aquilinum* (81.5%). The three most common specialists in woodland creation sites were *Silene dioica* (37.3%), *Dryoteris affinis* (35.3%) and *Hyacinthoides non-scripta* (33.3%) and in old growth sites were *H. non-scripta* (77.7%), *Geranium robertianum* (59.3%) and *Mercurialis perennis* (55.6%).

Of the 201 species recorded across the 129 woodlands (102 woodland creation +27 old growth), 47 were specialists, 85 generalists and 69 non-woodland species (Figure 2). A total of 113 species (i.e. 56.2%) were shared between woodland creation and old growth sites (26 specialists, 62 generalists and 25 non-woodland species), 73 species (36.3%) were recorded only in woodland creation (16 specialists, 15 generalists and 42 non-woodland species) and 15 (7.5%) species only in old growth sites (5 specialists, 8 generalists and 2 non-woodland species).

There were significant differences in the number of specialist and non-woodland species between woodland development stages, but not for generalist species (Figure 3). The number of specialists in the woodland creation sites increased with age (a mean of 2.7 [SE ± 0.34]) specialist species per site in stand initiation sites (0–30 years) and 4.6 (SE ± 0.63) in understorey re-initiation sites (80–160 years; Figure 3 and Table S2), although this was only marginally significant ($p = 0.078$). We found significantly more specialists and fewer non-woodland species in old growth woodlands (mean = 7.6 ± 0.76 specialist species and 2.3 ± 0.34 non-woodland species; >250 years) than in any development stage of woodland creation sites (<160 years; Figure 3 and Table S2).

3.2 | Drivers of woodland plants occurrence and richness in woodland creation sites

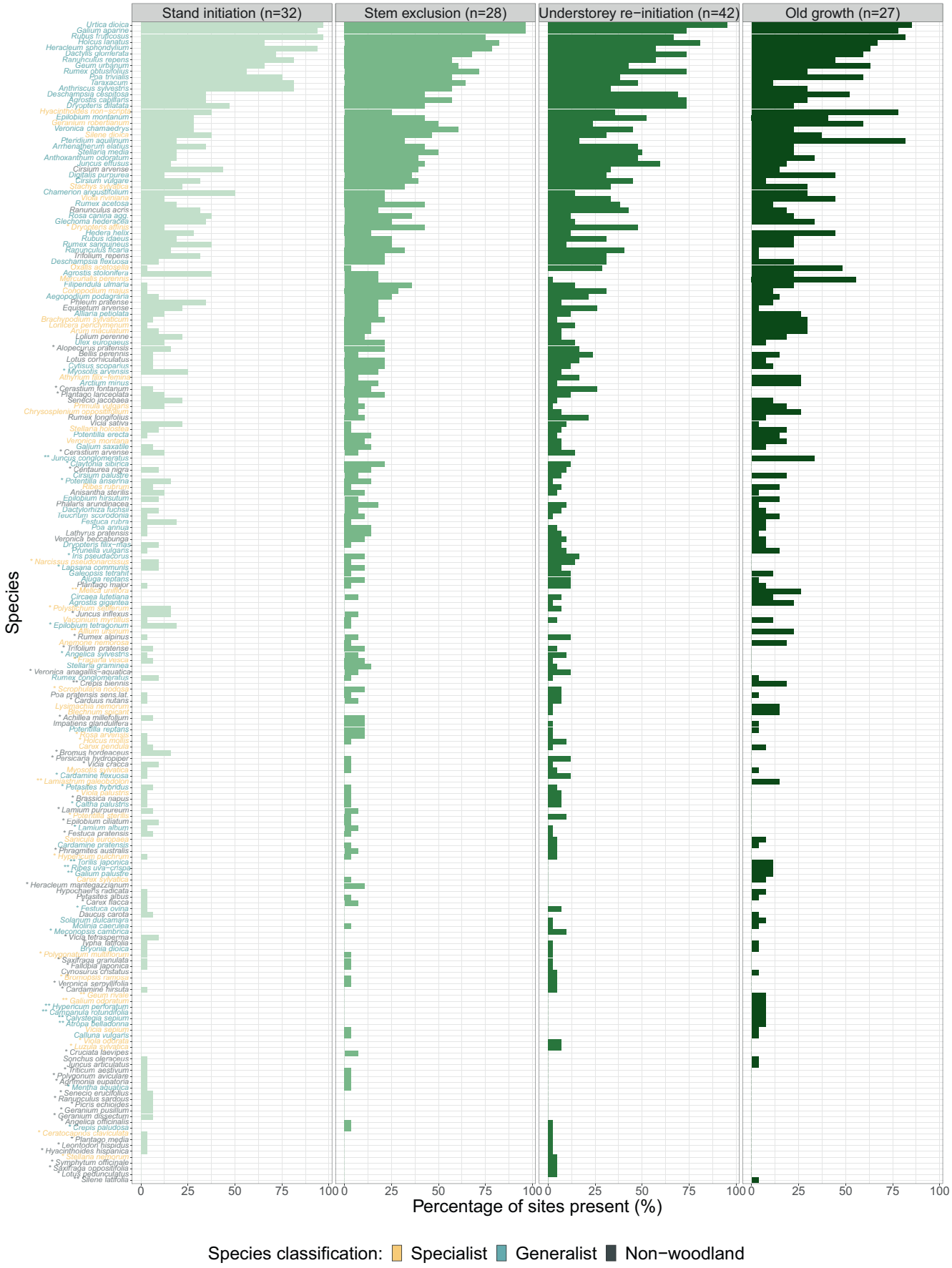
Overall, local (site-level) variables had a stronger influence on the occurrence of woodland specialist and generalists than did characteristics of the surrounding landscape. There were more specialist and generalist species in larger woodland creation sites (Figure 4a,b and Table S3). Age indirectly increased the number of specialist plants, through increased variation in tree size (i.e. standard deviation of tree DBH; Figure 4a and Table S3) in older sites. The quadratic age term on variation in tree size indicated a non-linear relationship, with variation in tree size starting to plateau at ~80 years (Figure S2). For generalists, we detected the same indirect relationships with age as we found with specialists, but there was also a direct negative effect of age on generalist species richness (Figure 4b and Table S3). Tree density had an indirect negative effect on both specialists and generalists, mediated through variation in tree size (Figure 4a,b and Table S3). We found no effect of landscape variables on either specialists or generalists (Figure 4a,b and Table S3).

For the 10 most common specialists (found in 10%–37% of woodland creation sites; Table S4) the most important predictors were all local factors ($p < 0.05$; Table S4), including canopy cover (negative relationship for *D. affinis* and positive relationship for *G. robertianum*), area (positive relationship for *S. dioica*), age (positive relationship for *Oxalis acetosella*), tree density (negative relationship for *G. robertianum*) and region (*Conopodium majus* being most common in Scotland).

3.3 | Shifts in plant community composition over time

Plant community composition varied by woodland development stage but, unlike plant species richness, this was not significantly driven by variation in tree size (Figure 5; PERMANOVA—development stage: $R^2 = 0.1$, $p < 0.001$; tree dbh SD: $R^2 = 0.007$, $p = 0.4$). Some older woodland creation sites were compositionally similar to

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FIGURE 2 Occurrence of all plant species found in 102 woodland creation sites, separated by development stage, and 27 old growth woodlands. Species are ranked by total frequency across all 129 sites and coloured by species woodland classification based on Kirby et al. (2012). Symbols indicate the following: **=species only recorded in old growth woodlands and *=species only recorded in woodland creation sites.

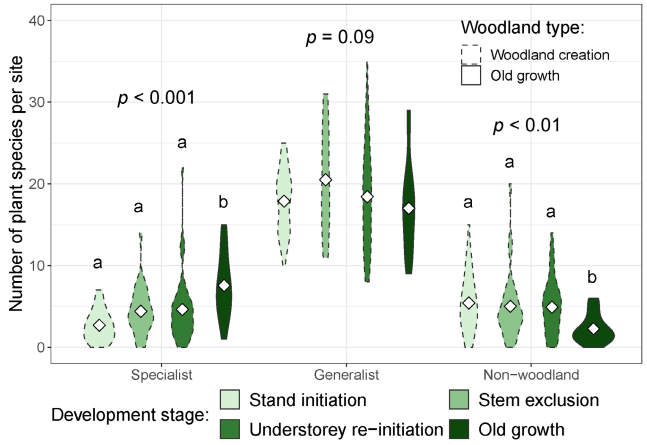


FIGURE 3 Summary of woodland specialists, woodland generalist and non-woodland species found in 102 woodland creation sites and 27 old growth woodlands in Scotland and England. Violin plot showing the total number of species per site, split by woodland development stage. Stand initiation = 0–30 years (*n sites* = 32), stem exclusion = 31–80 years (*n* = 28), understorey re-initiation = 81–160 (*n* = 42), and old growth >250 years (*n* = 27). *p*-values based on ANOVA of Linear Model (Number of species ~ Development stage). Different letters indicate significant pairwise differences between stages based on a Tukey post hoc test, underlined letters indicate marginally significant differences ($p = 0.078$).

old growth woodlands, dominated by specialist species (Figure 5 and Figure S3), but others were more distant, dominated by generalists and non-woodland plants (Figure 5 and Figure S3).

The SIMPER analysis identified 16 species (Figure 5 and Figure S4) that significantly contributed to driving part of the observed differences in the species compositions between different development stages (Figure 5 and Table S5). Three specialists, *G. robertianum*, *H. non-scripta* and *M. perennis*, and one generalist species, *P. aquilinum*, were more common in old growth communities (Figure 2 and Figure S4); generalists *Agrostis capillaris*, *Deschampsia cespitosa*, *Dryopteris dilatata* and *Juncus effusus*, were characteristic of older woodland creation sites (80–160 years), and generalists *Chamerion angustifolium*, *Anthriscus sylvestris* and *Taraxacum*, most common in the youngest woodlands (<30 years).

4 | DISCUSSION

In this study, we use a natural experiment approach to investigate the influence of an extensive suite of local and landscape attributes on the colonisation and establishment of vascular plants. This was conducted at appropriate temporal and spatial scales to inform ecological restoration policy and practice. We used a space-for-time approach to investigate plant community composition at different stages of woodland development, to determine whether the plant assemblages in new woodlands change over time towards those found in old growth woodlands. Our results show that woodland creation sites are readily colonised by woodland generalists but host fewer woodland specialist species and more non-woodland plants than old growth woodlands. Woodland plant richness (specialists and generalists) within woodland creation sites was primarily driven by woodland area and variation in tree size (which was higher in older woodlands), and surprisingly not by features of the surrounding landscape. Whilst the species composition of some older creation sites (80–160 years since planting) was very similar to those found in old growth woodlands, other older creation sites appear to be on a different trajectory.

4.1 | Slow colonisation of woodland specialist plants

We found that, on average, old growth woodlands had significantly higher numbers of specialist species than did woodland creation sites (see also Naaf & Kolk, 2015; Vellend et al., 2006). The oldest woodland creation sites (81–160 years) had on average ~2 more specialist species (mean = 4.6) than the youngest (<30 years; mean = 2.7), indicating that establishment is increasing over time. However, our results indicate that it is a very slow process, and it may take centuries to approach the species richness found in old growth woodlands. This long temporal lag in establishment of woodland plants within newly created post-agricultural woodlands is thought to be driven in part by life history and functional traits of these specialist species (Naaf & Kolk, 2015).

Species with traits facilitating long distance dispersal (e.g. tall habit, dispersed by wind or vertebrates, low diaspore mass and non-clonal growth) have been found in other studies to colonise woodland creation sites faster (Brunet et al., 2021; Naaf & Kolk, 2015) and to be the species that reach very isolated (>100 m from nearest woodland) woodlands (Brunet et al., 2021). By contrast, most specialist woodland plant species are poor dispersers and are generally slow to colonise new woodlands (Kirby et al., 2012), which limits their ability to reach isolated sites. This is exemplified by some of the specialist species that in this study had much higher occurrence in old growth woodland than in woodland creation sites. For example, *M. perennis* was present in only 6% of woodland creation sites but in 56% of old growth woodlands, and *Anemone nemorosa* was found in only one woodland creation site (<1%) but 18% of old growth woodlands. These two species are clonal, short in habit and dispersed short distances by ants; thus life history and functional traits are likely limiting their colonisation into new woodlands sites.

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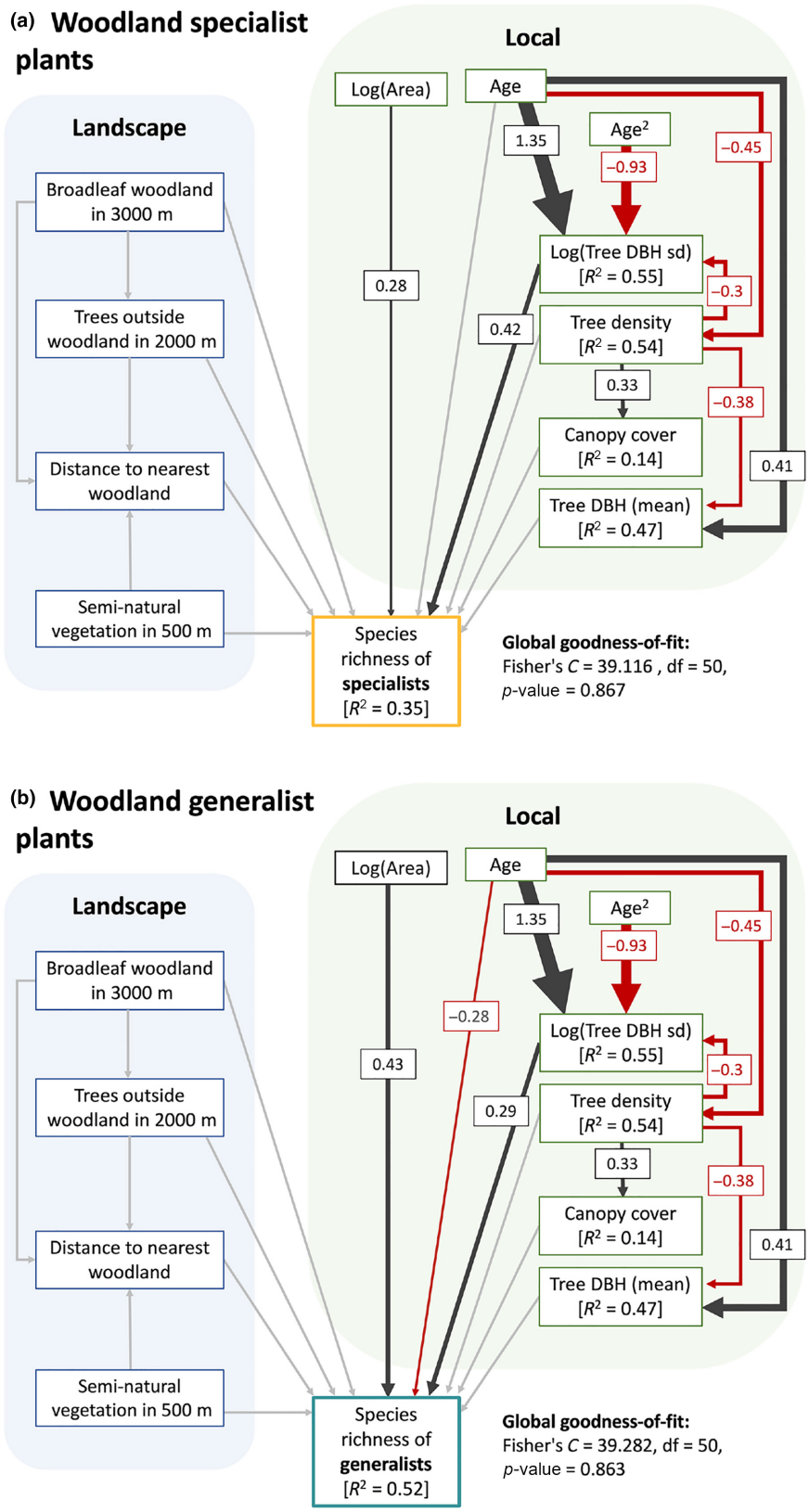


FIGURE 4 Structural equation model showing local and landscape-level drivers of plant species richness for (a) woodland specialists and (b) woodland generalists within 102 woodland creation sites in Scotland and England. Significant positive relationships shown with black lines, and significant negative relationships in red. Numbers are standardised path coefficients from the SEM. Significant correlated errors (i.e. correlated variables with no causal explanation) included in the model are not shown (see Supporting Information Appendix 1 text and Table S3 for details).

Even once a specialist species arrives at a new woodland it may not be able to establish due to unfavourable abiotic (e.g. soil nutrients) and biotic conditions (e.g. competition with other species) of the site. Young, recently created, woodlands on former agricultural lands will likely have very fertile soils, rich in nitrogen, phosphorus and calcium (Peterken & Game, 1984); additionally, competition from quick dispersing species that favour high light and nutrient-rich environments may further limit the establishment of slow dispersing specialist species (Brunet et al., 2021; Baeten & Verheyen, 2017). In this study, young woodlands (<30 years), were

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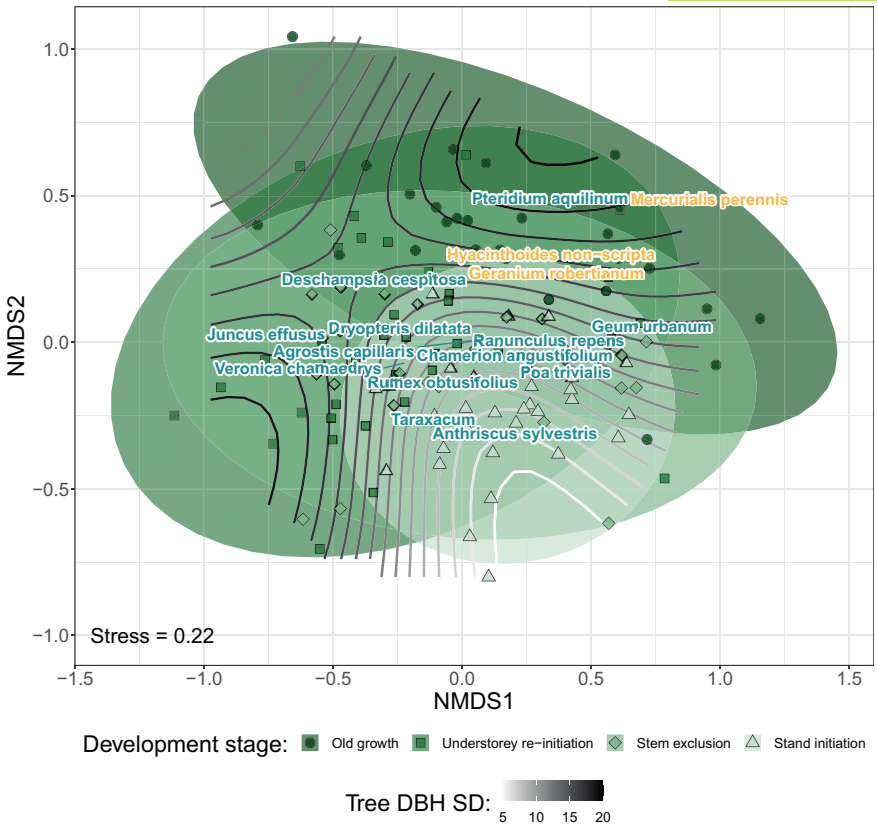


FIGURE 5 Non-metric multidimensional scaling (NMDS) of plant species composition based on occurrence data (Jaccard distance) for different aged woodland creation sites ($n = 102$) and old growth woodlands ($n = 27$). Each symbol represents one woodland community and is based on occurrence data of all species found within woodland sites, including woodland specialist and generalist, and non-woodland species. Development stage is split into: Stand initiation = 0–30 years (*n sites* = 32), stem exclusion = 31–80 years ($n = 28$), understorey re-initiation = 81–160 ($n = 42$), and old growth >250 years ($n = 27$). Contour lines represent the variation of tree structure (as measured by the standard deviation of tree DBH). Results of Permutational Multivariate Analysis of Variance, with 999 permutations were: development stage, $p = 0.001$; tree DBH SD $p = 0.446$. Species names are the 16 species that were the top ten most influential for each pairwise comparison of development stages (see Table S5 for full results), which were significant at $p < 0.05$ based on permutation-based *p*-value. They are coloured by their habitat affiliation: specialists = orange and generalists = blue.

dominated by nutrient loving generalist species, such as *Urtica dioica*, *Rubus fruticosus*, *Heracleum sphondylium* and *Galium aparine*, and competition from these species was likely a barrier to establishment for some specialists. One limitation of this study is the lack of local information on soil nutrients. While sites were carefully selected to be within relatively homogenous agricultural landscapes in lowland central Scotland and midlands of England with the same former land-uses and overall soil types (Watts et al., 2016), there will likely be variation between sites that influences the plant community.

4.2 | Changes in community composition over time

This study shows that as woodlands age, the plant communities in them change. The species communities found in some older woodland creation sites are starting to resemble those communities found in old growth woodlands, occupied by more woodland specialist plants. However, the community analysis indicates that not all older creation sites are following this trajectory, with some compositionally far from the old growth woodlands. These older woodland creation sites have the high variation in tree size expected of older woodlands (Fuentes-Montemayor et al., 2021), but their communities are dominated by more generalist species, such as *Dryopteris dilatata* and *Juncus effusus*. Whilst our survey method provided a complete site-level species list, we lack data on abundance of each species, which would provide more insight into what species within these communities are dominant and which are rare. Thus, these results are likely conservative, and we predict stronger relationships using abundance data.

While some planted woodland creation sites may gradually become compositionally similar to old growth woodlands, these results indicate that some might never follow that trajectory. On average, old growth woodlands had more specialists and fewer non-woodland plants, but there were several specialists recorded only in woodland creation sites ($n = 16$ species), more than those recorded only in old growth ($n = 5$ species). The old growth woodlands in this study were selected to be comparable to the woodland creation sites (i.e. small, isolated, and in similar agricultural landscapes), but perhaps these attributes have led to the selection

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of lower quality sites which do not provide suitable conditions for some woodland plants. Most old growth woodland in the UK is highly fragmented (Reid et al., 2021), and there are likely no true 'pristine' ancient woodlands remaining in the UK and across many other temperate regions. However, larger, and less fragmented old growth woodlands will likely have even higher richness of specialists and contrast even more strongly with some of the woodland creation sites in this study.

It is common when planting new woodlands to use old growth woodlands as a reference for success, following the 'field of dreams' approach (Hilderbrand et al., 2005); this approach assumes that once the physical structure of a woodland (e.g. the mix of dominant tree species and vegetation structures found in old growth woodlands) is restored, species composition and ecosystem function will self-assemble in a predictable manner. Our study suggests that the trajectory may not necessarily be so predictable. Indeed, some researchers and practitioners are now starting to rethink how we measure restoration success, with a greater focus on multifunctionality and ecosystem resilience, rather than purely on species composition (Bullock et al., 2021). Thus, further studies should investigate whether these older woodland creation sites with different species community compositions are similar to old growth woodlands in terms of ecosystem functioning and resilience.

4.3 | Influence of local woodland attributes

In line with other studies, we found a positive effect of area (log transformed) on the number of woodland specialists and generalists based on the well-established species–area curvilinear relationship (Petit et al., 2004; Pierik et al., 2010; Usher et al., 1992). We also identified a strong relationship between specialists and generalists and local woodland attributes (e.g. tree density and variation in tree size) driven by age. Variability in tree size is associated with higher species richness of woodland plants, and increases with woodland age, plateauing around 80 years. Woodland area has previously been proposed as a surrogate for habitat quality or heterogeneity (Humphrey et al., 2015), but based on the results of this study we suggest that variation in tree size may be a more useful proxy for habitat quality, indicating healthy forest dynamics with natural regeneration occurring (Fuentes-Montemayor et al., 2021). Active woodland management to encourage large and structurally complex woodland creation sites, through a reduction of tree density, may, therefore, facilitate the establishment of woodland plants. Our findings reinforce previous studies from the WrEN project on rodents and Diptera which also found a positive association between variation in tree size and species richness and abundance (Fuentes-Montemayor et al., 2020; Fuller et al., 2018). Future studies could utilise remotely sensed data to measure tree structure (e.g. LiDAR; Yao et al., 2012), scaling up assessment of woodlands across landscapes.

4.4 | Weak effects of landscape attributes

Unexpectedly, we found no influence of the surrounding landscape on species richness (specialists and generalists) or on the presence of the 10 most common specialists. This is contrary to previous studies linking plant richness (or occurrence) and distance to nearest woodland (Brunet et al., 2021; Hughes et al., 2023; Naaf & Kolk, 2015) or amount of woodland in the surrounding landscape (Jamoneau et al., 2011; Liira et al., 2012; Peña et al., 2011; Petit et al., 2004). Those studies found that proximity to existing mature woodland is an important driver of plant colonisation and suggested that being more than 100 m away from nearest woodland may still incur a significant colonisation credit (i.e. lower richness than nearby old growth woodlands) after considerable time (~100 years; Brunet et al., 2021; Hughes et al., 2023). In comparison, woodland creation sites in this study were relatively isolated with a median distance of 153 m to the nearest broadleaf woodland (mean 218 m; range 7–1573 m), and 66% of woodlands over 100 m from the nearest woodland. In addition, for most of our study sites the closest old growth 'ancient' woodland was over 1.5 km away (median distance = 1639 m; mean = 2006; range = 24–8210 m). Evidence suggests that even relatively short distances between woodland patches create ecological isolation and limit colonisation (Humphrey et al., 2015), so seed sources of many plants are likely to have been limited in the areas immediately surrounding the sites. We also predicted that smaller woody features (such as hedgerows) in the landscape may increase connectivity and colonisation of these woodlands, as Liira and Paal (2013) reported for generalists, but not specialist species; however, we found no effect on either group. Our results suggest that there may be thresholds of distance between woodlands beyond which the structure of the surrounding landscape no longer has a significant influence on woodland plant colonisation and establishment.

4.5 | Conclusion and management suggestions

This study indicates that woodland specialist plants are very slow to colonise woodland creation sites, potentially taking several centuries. The woodlands included in our natural experiment are typical of woodland creation sites being established within agriculturally dominated landscapes; therefore, our results likely reflect plant colonisation and establishment within many new woodlands in the UK and similar landscapes. Here we outline management suggestions to help species colonise new woodland patches and facilitate their establishment and spread within these woodlands.

Our results highlight the importance of creating large and structurally complex woodland creation sites. They also support considering active woodland management to enhance structural complexity, through a reduction of tree density and an increase variation in tree size. Whilst heterogeneity is expected to increase through time as woodlands develop, management or lack of this can help or hinder the development of understorey and tree

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regeneration (Fuentes-Montemayor et al., 2015). Tree thinning can enhance structural complexity and accelerate the transition to later successional stages, whilst protection from over-grazing by livestock or native herbivores can help tree regeneration and increase structural complexity (Fuentes-Montemayor et al., 2020). This study also reinforces the need to create new woodland adjacent or in close proximity to remnant mature source woodlands to facilitate colonisation by woodland plants and maximise conservation benefits (Tscharntke et al., 2012). For some species that have very low occurrence even in the oldest creation sites (81–160 years; e.g. specialists *Mercurialis perennis* and *Anemone nemorosa*), colonisation may need to be facilitated through translocations or direct sowing (Worrell et al., 2021). These combined actions to create large, structurally complex woodlands, adjacent or close to existing woodlands may further facilitate the establishment of woodland plants faster than would occur naturally.

AUTHOR CONTRIBUTIONS

Elisa Fuentes-Montemayor, Kirsty J. Park, Nicholas A. Macgregor and Kevin Watts conceived the ideas. Elisa Fuentes-Montemayor, Kirsty J. Park, Nicholas A. Macgregor and Kevin Watts designed methodology; Peter Carey collected the botanical data; Matt Guy calculated the landscape metrics; Emily H. Waddell and Kevin Watts analysed the data; Emily H. Waddell and Kevin Watts led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

Authors report no conflict of interest in this study.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

The data supporting the results are available from DataSTORRE: Stirling Online Repository for Research Data: http://hdl.handle.net/11667/229 (Waddell et al., 2024).

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SUPPORTING INFORMATION

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

Figure S1. Area of 102 woodland creation sites and 27 old growth woodlands in Scotland and England split by development stage of woodland.

Figure S2. Correlation matrix for 13 variables recorded in 102 woodland creation sites, showing bivariate scatterplot with fitted line (lower triangle), heatmap of pearsons correlation coefficient (upper triangle) and histogram of each variable (diagonal).

Figure S3. Non-metric multidimensional scaling (NMDS) of plant species composition based on occurrence data (Jaccard distance) for different aged woodland creation sites ($n = 102$) and old growth woodlands ($n = 27$).

Figure S4. The 16 most influential species to plant community dissimilarity based on similarity percentage procedure (SIMPER analysis), split by percentage of sites each species was found within each development stage.

Table S1. Summary statistics of all variables in 102 WrEN woodland creation sites included in the Structural Equation Models.

Table S2. Number of specialist, generalist and non-woodland plant species found across 102 WrEN and 27 old growth woodlands, split by development stage.

Table S3. Model output from Structural Equation Model testing local and landscape-level drivers of plant species richness for woodland specialists and woodland generalists within 102 woodland creation sites in Scotland and England.

Table S4. Results of General Linear Models testing the effect of local and landscape level predictors on the presence of the ten most common woodland specialist plant species found within 102 UK woodland creation sites.

Table S5. Output of similarity percentage procedure (SIMPER analysis) testing plant species contributions to the observed differences between plant communities found in 102 UK woodland creation sites and 27 old growth woodlands split into four development stages.

Appendix 1. Variable selection and model specification for Structural Equation Model (SEM) metamodel.

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