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Colonisation of farmland deciduous plantations by woodland ground flora

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ABSTRACT

Newly planted broadleaved woodlands under agri-environment schemes lack floral diversity. The dispersal range and colonisation rates of herbaceous ground flora in thirty newly planted broadleaved woodlands in Northern Ireland were investigated during spring and early summer (2017). The colonisation rates of 14 species conventionally recognised as Ancient Woodland Indicator Species (AWIS) and Woodland Indicator Species (WIS) together with Lesser Celandine were assessed and the maximum dispersal distances from potential source populations was measured. The study found that the nine selected AWIS colonise new habitats significantly more slowly ($p < 0.001$) than the four woodland study species and colonisation rates corresponded approximately to the classifications AWIS and WIS. The effect of twelve selected habitat variables on species colonisation rates revealed that greater species dispersal range was associated with the management of the sources both within and bordering to the newly planted broadleaved woodlands. Ensuring connectivity to mature deciduous woodlands with an integrated, riparian zone together with a mosaic of inter-connected, species-rich hedges increased species dispersal. These results suggest succession from grassland into woodland only begins with the planting of trees. Colonisation of woodland plant species should be a key objective of establishing newly planted broadleaved woodlands within farmland afforestation schemes and should be facilitated by active management practices.

KEYWORDS

Herbaceous colonisation;
woodland management

Introduction

An extensive deciduous forest once covered much of northwest Europe. Depletions and fragmentation of this forest commenced with the arrival of agriculture during the early Neolithic (*ca.* 6,500 BP; Smith & Goddard, 1991), continuing to the present day driven by human population growth and the demands for food and raw materials. These effects are seen within Irish forests and is one of the most dramatic examples of the conversion of ancient forest to farmland which is generally dominated today by grass production. The forest cover (populated by various tree species) as well as the understory species and herbaceous flora have been subjected to severe habitat loss and fragmentation (Mitchell, Bennett, & Gonzalez, 2013; Vellend, 2003), and a subsequent impoverishment of biodiversity (Humphrey, Peace, Jukes, & Poulsom,

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2004; Watts, 2006). In contrast to Britain, Ireland does not have any documented ancient woodlands (Peterken, 1981; Rackham, 1986), although some areas have been wooded more or less continuously from 1600 onwards. Attempts at re-afforestation, initiated from the seventeenth century onwards, have met with limited enduring success and Northern Ireland (NI) currently has only 6% forest cover with less than 1% considered semi-natural, broadleaf woodland (Cooper & McCann, 2002). In a further effort to increase deciduous woodland cover, Farm Woodland Schemes supported by the Department of Agriculture, Environment and Rural Affairs (DAERA) have promoted the planting of small woodlands on farms as well as encouraging positive management of existing tree cover. Recently these initiatives have been part of general agri-environmental schemes. Whilst welcome, such is the level of isolation of mature woods in Northern Ireland, it is not clear whether newly planted broadleaved woodlands are colonised by herbaceous flora typical of deciduous woods (Goldberg, Kirby, Hall, & Latham, 2007; Verheyen, Guntenspergen, Biesbrouck, & Hermy, 2003). The homogenisation of the landscape leading to continuous areas of grass-dominated fields with narrow hedges (Graham, Gaulton, Gerard, & Staley, 2018) and the consequent reduction of the flora of hedgerows and earth banks (Cooper & McCann, 2002) may also decrease the capacity of plants to colonise newly planted woodlands and, thus, compromise the development of a woodland ecosystem (Peterken & Game, 1984). These remaining remnants of ancient land use are key factors in maintaining species richness in agricultural landscapes (Schmitz, Sanchez, & de Aranzabal, 2007).

Colonisation factors

The fragmentation of ancient and mature woods causes difficulties with dispersal (*the spread*) and the colonisation (*the establishment of species within a habitat*) of herbaceous plants (Goldberg et al., 2007; Ratcliffe, Peterken, & Hampson, 1998). Species survival in such a landscape is dependent on habitat connectivity and the species rate of spread (Matlack & Monde, 2004), and the spatial relationship between colonisation and habitat formation (Norden et al., 2014; Rotherham, 2011). Habitat patch connectivity is therefore vital in the persistence of populations in a disjointed landscape (Matlack & Monde, 2004; Holyoak, Leibold, Mouquet, Holt, & Hoops, 2005; Nicol & Possingham, 2010). In European agricultural systems, hedges play a significant role in connectivity of biological communities (Schmitz et al., 2007). Their management and structure is important in retaining biodiversity and thus have considerable conservation importance (Hill, Fasham, Tucker, Shewry, & Shaw, 2005; Peterken & Game, 1984) particularly where they contain relics of woodland flora (Peterken & Game, 1984; Matlack & Monde, 2004; Rose, 2006; Schmitz et al., 2007). However, surviving or recreated natural or semi-natural habitats, such as newly planted broadleaved woodland, are also important in maintaining diverse communities (Deckers, Hermy, & Muys, 2004). The spatial relationships of linear and non-linear habitats therefore determine the ability for species to colonise new areas (Humphrey et al., 2015).

The facility to colonise new habitat is also characteristic of each plant species with some species requiring a mosaic of different habitats and others requiring rare and localised conditions (Montoya, Rogers, & Memott, 2012). Established networks that have a short

timeframe can enhance the ability of a fast-moving species to expand its range whereas species with slow colonisation require more permanent habitat corridors (Matlack & Monde, 2004). Landscape connectivity, therefore, controls abiotic and biotic spatial patterns (Mitchel et al., 2013). The interaction between connectivity and multiple ecosystems however is poorly understood (Mitchel et al., 2013).

Poor colonisation of plants and animals may limit the development of plant communities in newly planted broadleaved woodlands (Norden et al., 2014). Further, temporal effects on dispersal range may relate to r-selected or K-selected species traits. The former is vulnerable to competition, produce many propagules and consequently dominate ephemeral habitats, whilst, the latter having long generation times and low reproduction rates, are persistent and have limited dispersal ability. In stable habitats, K-selected species are successful competitors and thus dominate communities.

Evaluation of the efficacy of afforestation and agri-environment schemes should be an integral part of conservation management (Arlettaz et al., 2010; Memmott et al., 2010). Therefore, to ensure that communities in newly planted broadleaved woodlands attain higher levels of biodiversity, research is required on how to establish ground flora indicative of mature and ancient woodlands (Vickers, Rotherham, & Rose, 2000). This should focus on understanding variation in plant dispersal and colonisation and how this is influenced by landscape and environmental factors (Tilman, 1999).

The aims of this study therefore, were to: (1) investigate the distribution and abundance of herbaceous plant species in newly planted broadleaved woodland; (2) determine the classification of the herbaceous plants with respect to their colonisation rates; (3) identify environmental and landscape factors that might influence colonisation rates of herbaceous plants in these newly planted broadleaved woodlands; and (4) develop evidence-based proposals for the siting and subsequent management of newly planted broadleaved woodlands to improve the colonisation rates of woodland ground flora.

Study area and methods

Study sites

Thirty newly planted broadleaved woodlands (established 1996 to 2006) across Northern Ireland (Figure 1) were selected for detailed survey in 2017, with many of the woods close to small urban populations. The total area of woodland surveyed was 51 ha and the individual sites' size ranged from 0.3 ha to 5.7 ha. The altitude of the sites extended from 21 m (min) to 167 m (max) above sea level and soil pH ranged from 4.14 to 6.98. Twenty-two of the woods had public access, 4 had limited public access and 4 were private. Planting dates were collated through conversation with landowners or using Woodland Trust (WT) management plans.

Sampling design Belt transect

A number of methods can be used to determine species abundance (Glaves, Rotherham, Wright, Handley, & Birbeck, 2009). However, for this study a variation on the belt transect method was used to monitor changes in vegetation across the

Figure 1. Distribution of selected newly planted broadleaved woodland sites (sites are grouped into single point where applicable).

selected sites (Hill et al., 2005). Quadrats were not used since many of the study species were limited in their distribution and consequently vegetation cover density was not measured, but species distance from habitat source was recorded. Each wood was surveyed twice, in late April or early May and secondly in late May or early June. The woods' internal circumference (2.5 m away from the boundary) was walked and any study species located 2.5 m either side of this transect was recorded. When a study species was located, the distance to the seed or vegetative source in the newly planted broadleaved woodland boundary or internal location was measured with a measuring wheel. On completion of the first transect, a further transect was walked 5 m from the first, again measuring the dispersal distance between source and the located study species. This method was repeated until the middle of the wood was reached. Where the exact location of the source plants could not be located, the distance to the nearest boundary was measured.

Habitat analysis

Twelve habitat variables were selected as potentially influencing the dispersal and colonisation of the study species (Table 1).

Table 1. Description of the habitat variables recorded for modelling colonisation rates ($\phi = \beta/A$) per year ($n = 30$).

Variable	Measurement	Mean (SD)	Min	Max
Tree Species	Tree species at point of colonisation: Oak, Ash, Birch, Willow spp./Hazel, Rowan, Hawthorn, Cherry, Apple, Field Maple, Sycamore, Horse Chestnut Beech Scots Pine, non-native	-	-	-
Mean tree spacing	Distance between trees (m)	2.54 (0.64)	1.86	4.74
Habitat Connectivity	Distance to nearest mature broadleaved/mixed wood (Km)	0.674 (1.015)	0	3.6
Total perimeter of site	Boundary edge distance (m)	580.43 (330)	193.5	1573.9
Source boundary type	Colonising plant source description: Hedgerow, Mature Wood, Riparian, Hedge Bank, Hedgerow & ditch, Thicket or Copse	-	-	-
Linear length (m) of the source habitat	Distance of wood edge type (bordering & internal) (m)	379.62 (380.22)	0	1405.3
Soil Texture	Predominant soil texture of site: Sandy Loam, Silt, Loam, Clay Loam, Clay Silt, Sandy Loam	-	-	-
pH	Mean of the pH of site	5.07 (0.614)	4.15	6.92
Maximum altitude at site	Height above sea level (m)	69.1 (39.91)	21	167
Topography of site	Difference in min and max altitude	11.17 (7.46)	0	35
Previous land use	Land use prior to plantation as classified by Fossitt: (2007) Improved Agricultural grassland (GA1), Amenity grassland improved (GA2), Dry Meadow & grassy verge (GS2), Wet grassland (GS4), Spoil and bare ground (ED2), Conifer Plantation (WD4), Improved Agricultural grassland with wet grassland. (GA1 & GS4), Amenity grassland improved with some wet willow-alder- ash woodland (GA2 & WN6), Amenity grassland improved with Spoil and bare ground (GA2 & ED2)	-	-	-
Current manager/ owner	Owner (and manager) of planted site: Woodland Trust, DAERA, Private	-	-	-

- (a) Tree species – the canopy above each study species location was recorded (presence/absence) as each category of wood is linked to its own ground flora (Fossitt, 2000).
- (b) Mean tree spacing – (density may increase or decrease shading) measured using the nearest neighbour method as described by Wheeler, Bell and Cook (2011) (mean distance (m) of 5 adjacent trees).
- (c) Habitat connectivity – each site's distance to the closest existing mature broadleaf/mixed wood was either measured in the field or, where distance was more than 100 m, using Ordnance Survey maps of Northern Ireland. This was to record the general characteristics of the sites' wider landscape features, in other words the sites connectivity.
- (d) Total perimeter of each site was measured in the field (m), but where dense vegetation made this impossible, Google Earth supplemented field measurements.

This measurement was to provide information on the length of the possible entry points of the study species' sources.

- (e) The general structure and shape of the source habitat was recorded within seven broad categories as this was expected to affect study species diversity. These source habitats were either at the boundary or located within the study sites. The general condition of a hedge (where present) was not considered in the study, since the newly planted broadleaf woodland may have had a negative or positive effect on plant growth, but rather its construction. Double and single rows of the hedge shrubs were put into a single category of hedge.
- (f) The linear length (m) of the source habitat was recorded directly in the field. This included both internal linear lengths and boundary linear length of source.
- (g) Soil texture, particle size directly influences water-holding capacity and nutrient availability (Wheater et al., 2011). Field assessments of the soil texture were measured (3 samples each), using the American Scale mechanical analysis texture designation (Townsend, 1973; Trudgill, 1989).
- (h) Soil pH influences plant growth and soil samples were collected at each site using a random sampling method (3 samples each). To ensure accuracy the soil pH was analysed using a PHTS 200 meter and a Combo pH & EC (Hanna) meter. The difference in pH range from both metres was 0–0.75. The mean pH level for each site was used.
- (i) Altitude of the sites including the maximum and minimum heights above sea level was recorded using Google Earth. The maximum altitude (m) was used to represent the site.
- (j) The topography of a site can affect the distribution of plants (Wheater et al., 2011). Therefore, the altitude range (difference between maximum and minimum heights (m)) within each site was also calculated. The internal meso-topography was not considered, as each site had limited colonisation from the selected study's species. Although individual plant growth may be affected by meso- topography it was not seen to be a feature of the dispersal of the study species.
- (k) The sites previous land use may influence subsequent colonisation characteristics as each habitat has its own vegetation types (Averis, 2013). Data on previous use were collected either through conversation with owners, or through analysis of the WT management plans (Woodland Trust, 2017). Neighbouring habitat was also examined as well as the site's current grassland species. These three pieces of information were used to determine a site's previous use and habitat was subsequently classified according to Fossit (2000). It is important to note that Lesser Celandine does occur in some grassland but is largely restricted to shaded sites (Nicholson, 1983).
- (l) The current manager/owner of each newly planted broadleaved woodland site – 22 sites were owned by the WT, 4 by DAERA and 4 were privately owned.

Study species

The study investigated dispersal and colonisation in 14 representative herbaceous species, subdivided into three species types (Table 2)

- (1) Ancient woodland indicator species (AWIS) which are woodland specialists as identified by Kirby, Pyatt, and Rodwell (2003/2012) and are a group of plants strongly linked to a native deciduous woodland environment but occur less often in other habitats.

Table 2. Study species classified into AWIS, WIS and LC including life form, species frequency (5 very common and characteristic of the habitat, 4 common and 3 widespread), and agency of dispersal.

Study Species	Study classification	Life Form (Grime et al., 2007)	Woodland abundance* (Grime et al., 2007)	Agency of dispersal (Grime et al., 2007)
Bluebell (<i>Hyacinthoides non-scripta</i>)	AWIS	Geophyte (buds below soil surface)	5	Unspecialised capsule
Common Dog Violet (<i>Viola rivinana</i>)	AWIS	Hemicryptophyte (buds at soil level)	3	Seed with an elaiosome (dispersed short distance by ants)
Golden Saxifrage (<i>Chrysosplenium oppositifolium</i>)	AWIS	Chamaephyte (buds < 250 mm above soil level)	3	Unspecialised
Greater Stitchwort (<i>Stellaria holostea</i>)	AWIS	Chamaephyte (buds < 250 mm above soil level)	5	Unspecialised capsule
Hart's Tongue (<i>Asplenium scolopendrium</i> syn. <i>Phyllitis scolopendrium</i>)	AWIS	Fern – Not specified in Grime et al. (2007)	Not specified in Grime et al. (2007)	Wind – Spore – Not specified in Grime et al. (2007)
Primrose (<i>Primula vulgaris</i>)	AWIS	Hemicryptophyte (buds at soil level)	5	Seed with an elaiosome (dispersed short distance by ants)
Ramsons (<i>Allium ursinum</i>)	AWIS	Geophyte (buds below soil surface)	5	Unspecialised capsule
Wood Anemone (<i>Anemone nemorosa</i>)	AWIS	Geophyte (buds below soil surface)	5	Animal – dispersule with an awn or with spiny calyx teeth
Wood Sorrel (<i>Oxalis acetosella</i>)	AWIS	Hemicryptophyte (buds at soil level)	5	Animal – dispersule adhesive through the secretion of mucilage
Enchanter's nightshade (<i>Circaea lutetiana</i>)	WIS	Geophyte (buds below soil surface)	4	Animal – dispersule with an adhesive burr
Jack-in-the-Pulpit (<i>Arum maculatum</i>)	WIS	Geophyte (buds below soil surface)	5	Animal -dispersule by an ingested berry
Herb Bennet (<i>Geum urbanum</i>)	WIS	Hemicryptophyte (buds at soil level)	5	Animal – dispersule with an awn or with spiny calyx teeth
Male Fern (<i>Dryopteris filix-mas</i>)	WIS	Fern – Not specified in Grime et al. (2007)	Not specified in Grime et al. (2007)	Wind – spore – Not in specified in Grime (2007)
Lesser Celandine (<i>Ranunculus</i> – includes spp. <i>verna</i> & ssp. <i>fertilis</i>)	Not <i>ficaria</i> classified	Geophyte (buds below soil surface)	4	Seed with an elaiosome (dispersed short distance by ants)

- (2) Woodland indicator species (WIS), as identified by Fossit (2000) which are found in various woodland types, but crucially they are not considered as woodland specialists by Kirby et al. (2003/2012).
- (3) Lesser Celandine (LC) (*Ranunculus ficaria*), was also included in the study and is abundant in recently planted woodlands throughout NI (personal observation). Significantly it is not considered as an ancient woodland species or a woodland species either by Kirby et al. (2003/2012) or Fossit (2000) but is considered a shade tolerant species (Grime, Hodgson, & Hunt, 2007).

All 14 species are reasonably widespread in woodlands (Peterken, 1974, 2000; Spencer, 1991), tolerant to adverse conditions and are relatively long lived (Wright & Rotherham, 2011). The selected species (9 AWIS, 4 WIS plus LC) are easily identified, are widespread and common and have a distribution range throughout NI (Table 2). They tolerate a wide range of soil types and pH, but with seven selected species avoiding soils with a pH of <4.5, however only three of the sites fell marginally below this value (Table 1). It is recognised that the 14 species although common within NI, may not always be present, due to biodiversity loss, in the newly planted broadleaf woodland's surrounding habitat. Therefore, not all sites had the 14 selected species in the boundary habitat. Where this occurred, their absence was recorded, but only those species present could be used to determine dispersal range and colonisation rates.

Grime et al. (2007) described a functional approach to species type showing life form, abundance within woodland, and agency of dispersal. All plant species of interest have passive modes of dispersal with density of seed often low immediately under the plant, rising to a peak close by and steeply falling with distance (Begon, Townsend, & Harper, 2006). However, eight of the study species also have a "mutualistic agent" (Begon et al., 2006) where seed destination and dispersal are more uncertain. Wood Anemone (*Anemone nemorosa*), Enchanter's Nightshade (*Circaea lutetiana*) and Herb Bennet (*Geum urbanum*), for example, have seeds that may catch in animal fur, and Jack-in-the-pulpit (*Arum maculatum*) has a berry which is often ingested by birds or small mammals, thereby also increasing their respective dispersal ranges.

Results

The data collected were analysed using SPSS version 25. The main dependent variable used in this research was the colonisation rate per year (ϕ) and for each study species this was calculated by using the maximum dispersal range (β), divided by the plantation age (A) using the formula $\phi = \beta/A$.

This was examined for normality using three measures – visual assessment of distribution when plotted on a histogram as well as two statistical tests, Kolmogorov – Smirnov and Shapiro – Wilk. Using these indicators, the colonisation rates ($\phi = \beta/A$) as calculated were assessed as not normal and non-parametric univariate analyses were carried out (Mann Whitney (MW); Kruskal Wallis (KW)). Multivariate analysis employed generalised linear

models which were run to determine the relative contribution of the habitat variables on species colonisation rate ($\phi = \beta/A$). A total of 7 models (all defined *a priori*) including the full model were tested, and the best fit model was determined based on Akaike information criteria calculations.

Study species maximum distance of colonisation

The mean maximum distance of colonisation in rank order for each of the 14 species where present across all 30 newly planted broadleaved woodland sites is shown in Table 3. The distribution and variation associated with each species is shown in the combined box plot (Figure 2).

Table 3. Rank order of maximum distance of colonisation for the 14 herbaceous species (n = 323).

Rank	Species	Max distance (m)	SD
1	Herb Bennet (<i>Geum urbanum</i>)	28.71	23.48
2	Enchanter's nightshade (<i>Circaea lutetiana</i>)	27.12	15.78
3	Male Fern (<i>Dryopteris filix-mas</i>)	24.80	19.82
4	Lesser Celandine (<i>Ranunculus ficaria</i>)	23.73	18.20
5	Wood Anemone (<i>Anemone nemorosa</i>)	19.30	15.28
6	Greater Stitchwort (<i>Stellaria holostea</i>)	17.25	11.07
7	Jack-in-the-Pulpit (<i>Arum maculatum</i>)	16.58	12.62
8	Bluebell (<i>Hyacinthoides non-scripta</i>)	15.11	14.18
9	Golden Saxifrage (<i>Chrysosplenium oppositifolium</i>)	14.92	15.36
10	Ramsons (<i>Allium ursinum</i>)	12.05	8.27
11	Primrose (<i>Primula vulgaris</i>)	10.83	11.13
12	Hart's Tongue (<i>Asplenium scolopendrium</i>)	8.81	10.97
13	Common Dog Violet (<i>Viola rivinana</i>)	7.66	7.23
14	Wood Sorrel (<i>Oxalis acetosella</i>)	3.72	2.40

Figure 2. Rank order of maximum colonisation rate for the fourteen herbaceous species (n = 323).

Study species colonisation rates ($\phi = \beta/A$)

The frequency of each species and their maximum dispersal (m) was recorded at each site to calculate the colonisation rate ($(\phi = \beta/A)$ (AWIS, $n = 110$; WIS $n = 146$; LC, $n = 67$)). On analysis, it was found that there was a significant difference between the colonisation rates ($\phi = \beta/A$) of the three groups (AWIS v WIS $U = 5373$ $p < 0.001$; AWIS v LC $U = 2240$ $p < 0.001$; WIS v LC $U = 4565$ $p = 0.555$) and confirmed that the colonisation rates ($\phi = \beta/A$) of the ancient woodland indicator species are significantly slower than the colonisation rates ($\phi = \beta/A$) of either the woodland indicator species or Lesser Celandine. The distribution of the three groups are shown in [Figure 3](#) below.

The effect of four of the variables on the colonisation rate ($\phi = \beta/A$) (tree species, source boundary type, soil texture and previous land use) on the classified groups (AWIS, WIS) and lesser celandine (LC) were analysed and are summarised in [Table 4](#). Current

Figure 3. Distribution of colonisation rates for the groupings of the study species ($n = 323$).

owner effects were not analysed due to insufficient representative data. The effect of the source on the colonisation rates ($\phi = \beta/A$) of the species groupings revealed a significant effect ([Table 4](#)). The riparian habitat source was found to have the greater number of species. With respect to the 9 representative AWIS, the presence of a mature broadleaved/mixed woodland was the next most important habitat source followed by hedge banks, whereas with the four representative WIS the next best habitat source was the hedge and ditch.

Regrouping of the data

To investigate the natural groupings of the 14 selected study species based upon their respective colonisation rates ($\phi = \beta/A$) a hierarchical cluster analysis was performed. This produced sets of homogenous indicator plants described in the dendrogram ([Figure 4](#)) and

revealed the natural groupings (colour coordinated). This closely corresponds to the predetermined groupings (Fossit, 2000; Kirby et al., 2003/2012, and own observation) used within the study. The composition of the new groupings with new descriptive labels can be seen in Table 5. The analysis subdivided the colonisation rates ($\phi = \beta/A$) of the 3 original species classifications into 4 types: (1) the ancient edge huggers, where colonisation rate ($\phi = \beta/A$) was slower and therefore they are more likely to be found at the periphery of a newly planted broadleaved woodland; (2) the Expansionists, which can colonise more quickly; (3) the Woodland Dispersers, which were rarely present in newly planted broadleaved woodlands; and (4) the Exploiter, which was frequently found and was also able to rapidly colonise newly planted broadleaved woodland. The main finding, however, was that the colonisation rate ($\phi = \beta/A$) of the species was comparable to the original classifications, Ancient Woodland Indicators (1 and 2),

Table 4. The effect of tree species, boundary type, soil texture and previous land use on the colonisation rate ($\phi = \beta/A$) of AWIS, WIS and the study species ($n = 323$).

Study Species	Tree species	Source Boundary	Soil texture	Previous land use
Ancient Woodland Indicator Species (AWIS)	H = 8.820, df = 6, p = 0.184 Not significant	H = 19.220, df = 5, p = 0.002 The "riparian" source significantly increased colonisation rates compared to either a "hedge bank" (post-hoc p = 0.003) or "hedge & ditch" habitats (post-hoc p = 0.038)	H = 6.155, df = 3, p = 0.104 Not significant	H = 13.797, df = 4, p = 0.008 Colonisation rate was significantly higher on GA2 land-use than GA1. All other land-use types were not significantly different.
Woodland Indicator Species (WIS)	H = 4.926, df = 6, p = 0.553 Not significant	H = 31.935, df = 5, p < 0.001 Mature woodland habitat significantly increased colonisation rates compared to either, "hedge & ditch" (post-hoc p < 0.001), "hedge bank" (post-hoc p < 0.0001), or "hedge row" (post-hoc p = 0.001)	H = 9.496, df = 3, 0.023 Colonisation rates on sandy soils were significantly lower than on clay soils (post-hoc p = 0.033), loams (post-hoc p = 0.017) and silts (post-hoc p = 0.014). All other soil textures were not significantly different.	H = 4.246, df = 4, p = 0.374 Not significant
Lesser Celandine (<i>Ranunculus ficaria</i>)	H = 4.811, df = 6, p = 0.568 Not significant	H = 2.014, df = 5, p = 0.001 The mature broadleaved/mixed woodland' source significantly increased colonisation rates compared to "trees and shrubs" (post-hoc p = 0.015) and "hedge rows" (post-hoc p = 0.006)	H = 1.481, df = 3, p = 0.687 Not significant	H = 10.113, df = 4, p = 0.039 No differences were found post hoc Not significant

Figure 4. Cluster analysis dendrogram using average linkage between groups, revealing the natural groupings.

Table 5. Species groups based on colonisation rates ($\phi = \beta/A$).

Group Name	Indicator Species
Ancient Edge Huggers	(1) Ransom, (2) Wood Sorrel, (3) Harts Tongue Fern, (4) Dog Violet, (5) Wood Anemone
Expansionists	(6) Primrose, (7) Greater Stitchwort, (8) Golden Saxifrage, (9) Bluebell, (10) Enchanters Nightshade
Woodland Dispersers	(11) Jack in the pulpit, (12) Male Fern, (13) Herb Bennet
Exploiter	(14) Lesser Celandine

Woodland indicator species (3) and Lesser Celandine (4). The only species that transferred between categories was Enchanters Nightshade (*Circaea lutetiana*).

To further illustrate the analysis a “fingerprint” technique (generated for this study) was used which plotted the source of the study species (indicated by the central point of origin in the diagram) to the maximum point of colonisation rate ($\phi = \beta/A$) as a series of concentric rings. The fingerprints (Figure 5) show a change in the maximum colonisation rate ($\phi = \beta/A$) for each group. Group 1, the Ancient Edge Huggers, display a pattern of stepped rings, whereas Group 2, the Expansionist have a concentrated core, but a colonisation rate ($\phi = \beta/A$), which is ultimately further than the Ancient Edge Huggers. Group 3 the Woodland Dispersers are almost identical to the Woodland Indicator Species (as noted above). The visual analysis of the Exploiter (LC) also shows a similar relationship

Figure 5. Fingerprint analysis of original groupings and groupings after cluster analysis.

to the Woodland Dispersers (WIS excluding Enchanter's Nightshade). The division of the AWIS into Ancient Edge Huggers and the Expansionists (including Enchanter's Nightshade *Circaea lutetiana*) shows a more complex relationship. The colonisation rate ($\phi = \beta/A$) of the Ancient Edge Huggers is shown in short steps, whereas the Expansionists' initial steps are shorter, but their dispersal range is further.

Regression analysis and model selection

Six models using seven variables were selected *a priori* to determine the best combination on the study species' colonisation rate ($\phi = \beta/A$) using regression analysis (Table 6). The seven habitat variables that were chosen and included in the full model were soil pH, altitude, perimeter of plot, linear length of source habitat, distance to nearest mature broad leaved/mixed wood, mean tree spacing, and altitude range. Correlations between variables were tested and no pair had a coefficient >0.5 , hence, all were retained for the analysis. Models with a $\Delta AIC_c < 2$ were considered to have substantial

Table 6. Selection of candidate models for colonisation rates ($\phi = \beta/A$) as ordered by decreasing AICc.

Model	k	AIC _c	ΔAIC _c	wAIC _c
Altitude + perimeter of plot + linear length of source habitat	3	889.820	0.000	0.414085
Altitude + perimeter of plot + linear length of source habitat + distance to nearest mature broadleaved/mixed wood	4	890.940	1.12	0.251156
Soil pH + altitude + perimeter of plot + linear length of source habitat + distance to nearest mature broadleaved/mixed wood + mean tree spacing + range of altitude	7	894.451	4.631	0.152334
Linear length of source habitat	1	924.308	34.448	0.092395
Soil pH + mean tree spacing + range of altitude + perimeter of plot	4	934.267	44.447	0.05604

support. In addition, AIC_C weights (wAIC_C) which indicate relative support of a model were calculated for each model. The model best explaining the colonisation rates ($\phi = \beta/A$) for the 14 herbaceous species had an AIC_C weight of 0.414085 and included altitude, perimeter of plot, and total linear length of source habitat.

Discussion

The results from this study provide evidence for the management of newly planted broadleaved woodlands ensuring greater diversity and colonisation for the herbaceous plants colonising newly established plantations. The study revealed that, within the selected 30 newly planted broadleaved woodland sites, the colonisation rate ($\phi = \beta/A$) of the selected ancient woodland indicator species was significantly lower than that of both the woodland indicator species and lesser celandine. This finding also supports established guidelines of species definitions. However, Kirby et al., 2003/2012 suggested that there is inevitably a degree of arbitrary interpretation in the species lists.

The research did reveal the main variables that affected the dispersal of the 14 herbaceous plants. The nine representative ancient woodland indicator species colonisation rates ($\phi = \beta/A$) were significantly increased when the seed source was from a riparian habitat. This is contrasted with the colonisation rate ($\phi = \beta/A$) of the four representative woodland indicator species and lesser celandine, which was significantly improved if the seed source was from a mature broadleaved/mixed woodland habitat. Loam sites were found to favour the four woodland indicator species which may be related to the differing growth habit strategies employed. Interestingly, the research indicated that tree species did not affect the colonisation rates ($\phi = \beta/A$) of the 14

selected herbaceous plants, surprising perhaps as many woodland species are associated with the older forest canopies. However, that may be because of the relative age of the newly planted broadleaved woodlands as opposed to the ability of the herbaceous plants to colonise within the timeframe studied.

The results from the regression analysis indicated the preferred combination of variables that should be utilised to improve the respective colonisation rates ($\phi = \beta/A$). The best fit model provides evidence for the management measures that could be undertaken for habitat restoration and improving recently planted woodland diversity. The colonisation rates ($\phi = \beta/A$) of the selected plant species were significantly increased with lower altitudes and an increase of the linear length of source habitat. The length of the mature broadleaved/mixed woodland perimeter was also selected as an explanatory variable within the best model fit. This variable, however, is associated with the linear length of edge type used as source. In addition, the study highlighted the importance of the source type to the subsequent colonisation potential for the 14 selected indicator species.

The relationship between Lesser Celandine and mature broadleaved/mixed woodland as a source revealed an apparent conflict. When the distance to the wood was short, the colonisation rate ($\phi = \beta/A$) was further. This contrasts with the reduced colonisation rate ($\phi = \beta/A$) of Lesser Celandine when the linear length of the mature broadleaved/mixed woodlands edge used as source lengthened. This seems counterintuitive, but it is likely that

the considerable shade from a lengthy canopy of an existing mature broadleaved/ mixed wood may negatively influence Lesser Celandine's dispersal and colonisation. It is a shade tolerant species rather than a woodland specialist (Grime et al., 2007). This finding may warrant further investigation.

In summary, the creation of any woodland ecosystem is multifaceted, and the species richness and interactions in ancient woodlands is highly complex. This study shows that the colonisation rate ($\phi = \beta/A$) of the nine representative ancient indicator species is significantly slower than the other study species and source boundary type is critical in promoting faster dispersal. Therefore, this research indicates (based upon these 14 species) that wherever possible newly planted woodlands should be sited along riparian zones and next to existing mature broadleaved/mixed woodlands thereby improving the potential of increased herbaceous colonisation into newly planted broadleaved woodlands. In addition, to further improve colonisation rates ($\phi = \beta/A$) of these nine representative ancient woodland indicator species, newly planted broadleaved woodlands should be sited at lower altitudes. These suggested woodland management practices are shown in the model (Figure 6) where the ideal site requires a combination of habitat features.

Figure 6. Newly planted broadleaved woodlands site with ideal habitat variables for improvement in the representative colonisation rates.

The provenance of seed is also important, and the managers and owners of the sites have the dilemma; do they increase colonisation by bringing in plants from elsewhere possibly causing a founder effect or wait until the woodland species are self-sown and, therefore, genetically endemic. The problem with self-seeding is that there may only be a few woodland plants growing locally or a few species may even be locally extinct. The study has found that dispersal range and therefore colonisation rates ($\phi = \beta/A$) vary with edge type, and, therefore, it is suggested that before any herbaceous planting occurs, the edges of the site are surveyed to determine what is present and enhance any management practices that reduce the potential for alien species to colonise newly planted broadleaved woodlands. In a few sites, “exotic” or alien species were observed so every effort should be made to prevent this occurring. Improved connectivity does have the potential to increase the chances of this happening.

Conclusion

The intrinsic value of our woods cannot be overstated. Newly planted woodlands are a small step towards addressing habitat fragmentation (Matlack & Monde, 2004), but they need conservation corridors for source populations to establish and disperse (Deckers et al., 2004). The succession from grassland into woodland, has only begun with the planting of trees, as ground flora diversity is needed to assist in the establishment of a true woodland biome. As identified in the study, the nine representative of ancient woodland indicator species colonise slowly, yet given the right site and habitat management, they can migrate more rapidly. This study identified factors that increased the colonisation rates ($\phi = \beta/A$) of woodland herbaceous plants and more generally addressed the potential of evaluating afforestation schemes. Testing of all restoration schemes would assist conservation action plans (Arlettaz et al., 2010; Humphrey et al., 2015) and enable any necessary re-adjustment of conservation policy. A regeneration of our woodlands, which includes the ground flora will not only help to increase biodiversity but will foster a healthy and vibrant natural landscape.

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No potential conflict of interest was reported by the authors.

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References

- Arlettaz, R., Schaub, M., Fournier, J., Reichlin, T. S., Sierro, A., Watson, J. E. M., & Braunisch, V. (2010). From publications to public actions: When conservation biologists bridge the gap between research and implementation. *Bioscience*, 60(10), 835–842.
- Averis, B. (2013). *Plants and habitats, an introduction to common plants and their habitats in Britain and Ireland*. Edinburgh: Ben Averis.
- Begon, M., Townsend, C. R., & Harper, J. L. (2006). *Ecology: From individuals to ecosystems*. Oxford: Blackwell.
- Cooper, A., & McCann, T. (2002). *Technical report of the Northern Ireland countryside survey*. Belfast: University of Ulster & the Department of Environment & Heritage Service.
- DAERA. (2016). *Statistical review of northern agriculture* (pp. 33–38). Belfast: Department of Agriculture, Environment, and Rural Affairs.
- Deckers, B., Hermý, M., & Muys, B. (2004). Factors affecting plant species composition of hedgerows: Relative importance and hierarchy. *Acta Oecologica*, 26(1), 23–37.
- Fossit, J. A. (2000). *A guide to habitats in Ireland* (pp. 48–58). Dublin: The Heritage Council.
- Glaves, P., Rotherham, I. D., Wright, B., Handley, C., & Birbeck, J. (2009). *A report to the Woodland Trust. Field surveys for ancient woodlands: Issues and approaches*. Sheffield: Hallam Environmental Consultants Ltd., Biodiversity & Landscape History Research Institute, and Geography, Tourism & Environmental Change Research Unit, Sheffield Hallam University.
- Goldberg, E., Kirby, K., Hall, J., & Latham, J. (2007). The ancient woodland concept as a practical conservation tool in Great Britain. *Journal for Nature Conservation*, 15(2), 109–119.
- Graham, L., Gaulton, R., Gerard, F., & Staley, J. (2018). The influence of hedgerow structural condition on wildlife provision in farmed landscapes. *Biological Conservation*, 220, 122–131.
- Grime, J. P., Hodgson, J. G., & Hunt, R. (2007). *Comparative plant ecology; a functional approach to common British species*. Sheffield: Castlepoint Press.
- Hill, D., Fasham, M., Tucker, G., Shewry, M., & Shaw, P. (2005). *Handbook of biodiversity methods survey, evaluation and monitoring*. Cambridge: Cambridge University Press.
- Holyoak, M., Leibold, M. A., Mouquet, N. M., Holt, R. D., & Hoops, M. F. (2005). *Metacommunities: Spatial dynamics and ecological communities*. London: University of Chicago.
- Humphrey, J. W., Peace, A. J., Jukes, M. R., & Poulson, E. L. (2004). Multiple-scale factors affecting the development of biodiversity in UK plantations. In O. Honnay, K. Verheyen, B. Bossuyt, & M. Hermý (Eds.), *Forest biodiversity: Lessons from history for conservation* (IUFRO Research Series 10, pp. 143–162). Wallingford: CABI Publishing.
- Humphrey, J. W., Watts, K., Fuentes-Montemayor, E., Macgregor, N. A., Peace, A. J., & Park, K. J. (2015). What can studies of woodland fragmentation and creation tell us about ecological networks? A literature review and synthesis. *Landscape Ecology*, 30(1), 21–50.
- Kirby, K. J., Pyatt, D. G., & Rodwell, J. (2003/2012). Characterisation of the woodland flora and woodland communities in Britain using Ellenberg values and functional analysis. In I. D. Rotherham, M. Jones, & C. Handley (Eds.), *Working and walking in the footsteps of ghosts volume 1: The wooded landscape* (pp. 66–86). Sheffield: Wildtrack Publishing.
- Matlack, G. R., & Monde, J. (2004). Consequences of Low Mobility in Spatially and Temporally Heterogeneous Ecosystems. *Journal of Ecology*, 92(6), 1025–1035.

- Memmott, J., Cadotte, M., Hulme, P. E., Kerby, G., Milner-Gulland, E. J., & Whittingham, M. J. (2010). Putting applied ecology into practice. *Journal of Applied Ecology*, 47(1), 1–4.
- Mitchel, M.G. E., Bennett, E. M., & Gonzalez, A. (2013). Linking landscape connectivity and ecosystem services provision: Current knowledge and research gaps. *Ecosystems*, 16(5), 894–908.
- Montoya, D., Rogers, L., & Memmott, J. (2012). Emerging perspectives in the restoration of biodiversity-based ecosystem services. *Trends in Ecology & Evolution*, 27(12), 666–672.
- Nicholson, G. C. (1983). Studies on the distribution and the relationship between the chromosome races of *Ranunculus ficaria* in South-East Yorkshire. *Watsonia*, 14, 321–328.
- Nicol, S., & Possingham, H. P. (2010). Should metapopulation restoration strategies increase patch area or number of patches? *Ecological Applications*, 20, 566–581.
- Norden, B., Dahlberg, A., Brandrud, T. E., Fritz, O., Ejrnaes, R., & Ovaskainen, O. (2014). Effects of ecological continuity on species richness and composition in forests and woodlands: A review. *Ecoscience*, 21(1), 34–45.
- Peterken, G. F. (1974). A method for assessing woodland flora for conservation using indicator species. *Biological Conservation*, 6(4), 239–245.
- Peterken, G. F. (1981). *Woodland conservation and management*. London: Chapman and Hall.
- Peterken, G. F. (2000). Identifying ancient woodland using vascular plant indicators. *British Wildlife*, 11, 153–158.
- Peterken, G. F., & Game, M. (1984). Historical factors affecting the number and distribution of vascular plant species in the woodlands of central Lincolnshire. *Journal of Ecology*, 72(1), 155–182.
- Rackham, O. (1986). *The history of the countryside*. London: Dent.
- Ratcliffe, P. R., Peterken, G. F., & Hampson, A. (1998). *A forest habitat network for the Cairngorms* (Research, Survey and Monitoring Report No. 114). Battleby, Redgorton, Perth: Scottish Natural Heritage.
- Rose, F. (2006). *The wild flower key, how to identify wild flowers trees and shrubs in Britain and Ireland*. London: Warne.
- Rotherham, I. D. (2011, August–September). New insights into the ancient woodland paradigm. In M. Bürgi (Ed.), *Problems and possibilities on the border between historical ecology and environmental history and archaeology* (p. 75). Birmensdorf, Switzerland: Conference Proceedings: Frontiers in Historical Ecology.
- Schmitz, M. F., Sanchez, I. A., & de Aranzabal, I. (2007). Influence of management regimes of adjacent land uses on the woody plant richness of hedgerows in Spanish cultural landscapes. *Biological Conservation*, 135(4), 542–554.
- Smith, A. G., & Goddard, I. C. (1991). A 12,500 year record of vegetational history at Sluggan Bog, Co. Antrim, N. Ireland (incorporating a pollen zone scheme for the non-specialist). *New Phytologist*, 118(1), 167–187.
- Spencer, J. (1991). Indications of antiquity: Some observations on the nature of plants associated with ancient woodland. *British Wildlife*, 2, 90–102.
- Tilman, D. (1999). The ecological consequences of changes in biodiversity: A search for general principles. *Ecology*, 80(5), 1455–1474.
- Townsend, W. N. (1973). *An introduction to the scientific study of the soil* (pp. 24–38). London: Edward Arnold.
- Trudgill, S. (1989). *Soil types; A field identification guide*. Telford: FSC Publications.
- Vellend, M. (2003). Habitat loss inhibits recovery of plant diversity as forests regrow. *Ecology*, 84(5), 1158–1164.
- Verheyen, K., Guntenspergen, G. R., Biesbrouck, B., & Hermly, M. (2003). An integrated analysis of the effects of past land use on forest herb colonization at the landscape scale. *Journal of Ecology*, 91, 731–742.
- Vickers, A. D., Rotherham, I. D., & Rose, J. C. (2000). Vegetation succession and colonisation rates at the forest edge under environmental conditions. *Aspects of Applied Biology*, 58, 351–356.
- Watts, K. (2006). British forest landscapes: The legacy of fragmentation. *Quarterly Journal of Forestry*, 100, 273–279.

Wheater, C. P., Bell, J. R., & Cook, P. A. (2011). *Practical field ecology, a project guide*. Oxford: Wiley-Blackwell.

Wright, B., & Rotherham, I. D. (2011). Assessing woodland history and management using vascular plant indicators. *Aspects of Applied Biology*, 108, 105–112.