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Twenty-five years on – vegetation succession on a translocated ancient woodland soil at Biggins Wood, Kent, UK

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In 1988, the topsoil layer from an ancient coppice wood, situated on the site of the rail terminal of the Channel Tunnel at Folkestone in Kent, was translocated to a receptor site a short distance away. The ground flora of the original wood was surveyed prior to translocation and monitored for 25 years at the new receptor site, where the presence or absence of species was recorded in permanent quadrats. The receptor site was planted with a mixture of broadleaved trees immediately after the soil was moved. After transference there was an increase in the abundance of open-ground species, reflected in the soil seedbank, but while many shade-tolerant species survived and some became dominant, some losses of ancient woodland indicator plants also occurred. Although it was judged to be the best available receptor site for the translocation, the comparatively drier conditions strongly influenced the field layer, while the species composition and density of the planted trees also differed from that of the canopy in the donor wood. Tree canopy uniformity at the receptor site was much greater than in the donor wood, suggesting that management interventions designed to create a more variable light environment might have been conducive to the survival of some ground flora species.

Introduction

Because infrastructure projects, such as road-building, quarrying and building construction are continually destroying semi-natural habitats of all types, the development planning process often requires some sort of compensation operation in the form of habitat creation, or the translocation of habitats to alternative sites. For many types of translocation involving grasslands, wetlands or heathlands, it may be feasible to move vegetation and soil together as intact turves, or by excavating and loose-tipping the topsoil containing seeds and vegetation (Buckley, 1989; Byrne, 1990; Pywell *et al.*, 1995; Jefferson *et al.*, 1999; Bruelheide and Flintrop, 2000; Anderson, 2003; Vécrin and Muller, 2003; Trueman *et al.*, 2007; Kiehl *et al.*, 2010; Török *et al.*, 2011). Some of these operations have been reported to be successful in terms of nature conservation (Helliwell *et al.*, 1996; Bruelheide and Flintrop, 2000; Box, 2003). In the case of woodlands, however, translocation presents many technical difficulties and usually results in the felling of the tree canopy, followed by loose-tipping of the upper soil profile containing field layer vegetation. Because of this, relatively few attempts have been made to translocate woodland, and any monitoring to demonstrate its effectiveness would need to occur over a long time period.

In the small number of cases where translocated woodland has been monitored, it has only been continued for 10 years, barely allowing for canopy closure of the replanted canopies, which is too brief a period to evaluate the success or failure of the scheme (Anderson, 2003; Ryan, 2013). In the UK, some significant areas of woodland have been translocated in connection with major projects such as the Channel Tunnel Terminal (Helliwell *et al.*, 1996), the Manchester Airport expansion (Manchester Airport plc, 1997), new railways and roads (Roberts, 2000; Cawley and Corney, 2012) and landfill schemes (Hietalahti *et al.*, 2005; Craig and Buckley, 2013; Craig *et al.*, 2015). This paper describes a much longer term monitoring exercise of 25 years, based on the translocation of a part of Biggins Wood at the Channel Tunnel Terminal site near Folkestone, Kent, in 1988. The objective was to show that what extent ground flora vegetation could be transferred successfully to a receptor site, how it established and developed from the initially open conditions until canopy closure, and whether the characteristic shade-tolerant species had persisted after 25 years. An additional objective was to determine if the origin of the soil, taken from different parts of the wood, had any bearing on the development of the vegetation at the receptor site.

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Site description

The original Biggins Wood (51°06′N, 1°08′E; 55–60 m a.s.l.) was a semi-natural woodland listed on the Ancient Woodland Inventory (Spencer and Kirby, 1992), of which ~4 ha was relatively undisturbed. It was situated at the foot of the North Downs chalk escarpment, on land sloping very gently at an average angle of ~3°. The soils were surface water gleys of the Denchworth Association, derived from clayey calcareous drift and weathered Gault (Jarvis *et al.*, 1984). Numerous seepage springs ran through the site and parts remained extremely wet throughout the growing season. The tree canopy consisted of ash (*Fraxinus excelsior*), elm (*Ulmus procera*) in the mid-stages of succumbing to Dutch elm disease, pedunculate oak (*Quercus robur*) and field maple (*Acer campestre*) over hazel (*Corylus avellana*), with willow (*Salix* spp.) prominent in the wettest areas (all scientific names follow the nomenclature of Stace (2010)). The vegetation, soils and translocation operation are fully described in Helliwell *et al.* (1996).

In the late summer of 1988, the whole wood was to be destroyed in order to make way for the Channel Tunnel Terminal development. In compensation, 20 cm thick layers of the surface soil profile from the wood were transferred to a 1.1 ha receptor site (70–80 m a.s.l.) ~270 m away to the north–west, on the edge of the chalk escarpment, using loose-tipping by dumper truck and a tracked backactor, in an attempt to salvage the least disturbed parts of the donor site. No attempt was made to maintain the original soil profile, which was thoroughly mixed during the operation. The receptor site, which had previously been prepared by stripping away 30 cm of topsoil before receiving that from the donor site, was situated on steeper ground above the donor wood and was therefore drier and more calcareous, although the soil chemistry was similar in terms of extractable P, K and Mg (Helliwell *et al.*, 1996).

The transferred soils were taken from different parts of the donor wood that were judged to be 'wet', 'moist', 'dry' or 'scrub' (the latter mainly moist, but more disturbed and less species-rich), based on their vegetation communities. Soil was transferred to the receptor site in September 1988, in dry conditions when the vegetation was relatively dormant. The placing of the translocated soil here was done in strips and then levelled using a backhoe, in such a manner as to avoid driving over it, thus avoiding any compaction. After 15 months of settlement, the mean soil depth (recorded from 400 separate auger readings) was 28 cm. Soil from the 'dry' areas of the donor site was placed along the northern edge of the more freely draining, steeper slopes (up to c. 14°) of the receptor site, whereas 'moist' and 'scrub' soils were placed lower down on much gentler slopes. The 'wet' soils were deposited at the west end of the receptor site, close to an existing area of ground water seepage.

In the following spring of 1989, the site was planted with transplants using a square grid pattern and 1.5 m spacing, with failures being later replaced in 1990 and 1991. Both the planting design and the tree species were selected by a firm of landscape architects, in which both the tree specification and their abundance differed somewhat from that in the donor woodland. The species mix consisted of *A. campestre* (8 per cent), *Alnus glutinosa* (2 per cent), *Betula pendula* (18 per cent), *C. avellana* (16 per cent), *Euonymus europaea*, (8 per cent), *F. excelsior* (20 per cent), *Malus sylvestris* (4 per cent), *Prunus avium* (4 per cent), *Q. robur* (12 per cent) and *Viburnum opulus* (8 per cent). Neither *Alnus* nor *Betula* were present in the donor wood but were planted as a temporary 'nurse' crops in order to provide early shade and to aid establishment of the vegetation. No other woody species were planted and all species in the field layer were expected to develop spontaneously from the seedbank or from vegetative fragments and propagules. Other potential colonizing sources were very limited, the nearest substantial wood being 2 km distant, with only one gappy, overmature hedgerow nearby, situated 35 m to the north of the translocated area.

Methods

The original Biggins Wood field vegetation was surveyed in 39, 1-m^2 quadrats, located on a 30 × 30-m grid in July 1985 and May 1986, followed by 15 larger, 200-m^2 quadrats in June 1986, when the breast height diameter >3 cm of all canopy trees present was measured at 1.3 m above ground, while also recording the presence and absence of vascular vegetation in the ground flora. Very uncommon species immediately adjacent to these quadrats were noted. The 200-m^2 quadrats covered ~6 per cent of the site and were located randomly in the most representative parts of the central core of the wood, avoiding disturbed edges and those areas most affected by Dutch elm disease. The smaller 1-m^2 quadrats gave a wider distributional coverage in the wood and complemented the species record, but were not included in the subsequent ordination analysis.

In May and June 1989, the presence or absence of all vascular plant species at the receptor site was recorded in 20, 200-m^2 quadrats, five replicates of which were set up in each of the four soil types identified 'wet', 'moist', 'dry' or 'scrub' communities, altogether covering ~36 per cent of the site. These data were recorded annually for 7 years until 1995. In contrast, of the 15 donor quadrats only two 'dry', 10 'moist' and three 'wet' communities were represented, approximately proportional to the area they occupied in the original wood. The additional 'scrub' areas transferred to the receptor site from the more disturbed areas of the wood were not surveyed in donor quadrats.

Weeding of the trees was carried out for 5 years, by treating the same alternate tree rows with a glyphosate spray 600–800 mm wide, repeated annually. Hand weeding of the unsprayed rows was done to avoid damaging any recovering ground flora. After this, access to the area was restricted by abundant bramble growth (*Rubus fruticosus* agg.) for 11 years, effectively preventing further survey work. The interior finally became accessible after canopy closure in 2004, when the original quadrat positions were re-marked. Recording of the ground vegetation was then resumed (at 15 years) and again in 2014 (at 25 years) when on each occasion the breast height diameter of all remaining trees was measured at 1.3 m above ground. Some very light thinning, mainly of cherry, was carried out sporadically from 2005.

Seedbank sampling

On three occasions, in December 1989, February 1992 and April 2004, the seedbank at the receptor site was sampled, taking 20 soil cores from each 200-m^2 quadrat. Cores were taken to a depth of 15 cm using a 5-cm auger, bulked and placed in seed trays in a polythene tunnel. The bulked soil from each of the 20 plots was divided into two 310 × 250 × 50-mm trays, giving 40 altogether, which were watered daily. Experimental controls of sterile compost were added to account for airbourne seeds. Emerging seedlings were identified, counted and removed during the following growing season.

Data analysis

Two sets of species data were compiled, the first set comprising all quadrats (1986–2014) from the donor and receptor sites. This included

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the presence and absence of all planted and unplanted trees, shrubs and ground vegetation, and included the 15 original donor quadrats recorded in 1986 in the three communities ('dry', 'moist' and 'wet') and the 20 receptor site quadrats, with 5 replicates each of the 'dry', 'wet', 'moist' and 'scrub' areas, that were recorded on 9 occasions (n = 180). The second set of data comprised only those quadrats at the receptor site, 1989–2014 (n = 180), minus planted trees, providing a balanced design.

The explanatory variables chosen were the three or four nominal vegetation community types 'dry', 'wet', 'moist' and 'scrub' and the time sequence. In order to aid ecological interpretation, supplementary species trait scores were derived for each quadrat. Ellenberg trait scores for light ('L'), moisture ('F'), soil reaction ('R') and fertility ('N') (Hill *et al.*, 1999) were assigned to all species present in a quadrat. For each trait separately,'L', 'F', 'R' and 'N', the mean score per quadrat was calculated by adding up all values for each species present and dividing by their total number. Species were also classified according to their primary ecological strategies based on their competitive, ruderal or stress-tolerant characteristics (Grime *et al.*, 1988) and strategy frequencies per quadrat obtained. Specialist forest species, the so-called ancient woodland indicator species, were noted (Kimberley *et al.*, 2013) and the relative percentage frequency of annuals, biennials and perennials calculated per quadrat. Also available were total basal area (BA) measurements, recorded from stem diameters measured at 1.3 m, of all woody species (trees and shrubs) per quadrat, recorded in 2004 and 2014, respectively.

Univariate statistical testing

Analysis of variance, with *post hoc* comparisons and 95 per cent confidence intervals, was performed in SPSS using the general linear model procedure (SPSS v. 23.0, Armonk, NY, USA) for each Ellenberg trait to test whether there was a significant difference in mean values between different community classes, 'wet', 'dry', 'moist' and 'scrub' at the receptor site, over the 25 years post-translocation period. A repeated measures ANOVA analysis could not be performed as the precise order of measuring plots from year to year may have varied between surveyors.

Multivariate analysis

An ordination approach using Canoco 4.5 (ter Braak and Šmilauer, 2002) was chosen to show changes in species composition of the plant communities over time, in relation to multiple variables. As the data were compositional, based on the presence and absence, with many species arriving and leaving over the monitoring interval, a weighted average approach was appropriate (Lepš and Šmilauer, 2003). Initial analysis of the vegetation data using the unconstrained ordinations of correspondence analysis (CA) produced arch effects. Therefore, to explore and compare the donor woodland vegetation with the translocated receptor site woodland vegetation over time, detrending was applied to approximate the vegetation response (ter Braak and Šmilauer, 2002, 2015). Detrended CA (DCA) by 2nd order polynomials was run on the first dataset with the planted woody species at the receptor site retained. Rare species were downweighted to reduce their influence (ter Braak and Šmilauer, 2002, 2015), with a focus on species patterns (species scaling). A nominal supplementary variable was included to display year-specific community centroids to aid interpretation. Species traits and total woody BA measurements provided supplementary variable labels. An equivalent canonical CA (CCA) tested whether the model significantly accounted for vegetation change. Additionally, partial CCAs, constrained on 'community' and 'year' and adjusted for either 'community' or 'year' were run, testing the separate effects of the community type and year.

The same DCA and CCA approach was used to explore and test the second dataset, based only on receptor site quadrats over 25 years, excluding planted trees. A further partial CCA of these data was applied to test whether the community trend was independent of year. As the time series was not recorded at regular yearly intervals (although seasonally comparable) and repeated quadrat records were not matched from year to year, a reduced (null model) Monte Carlo test with unrestricted permutations was used for all significance testing.

Results

Vegetation change at the receptor site

The survey of the donor wood contained trees whose total BA in 1986 was 25.9 ± 2.8 $m^2\,ha^{-1}$ (mean ± standard error, range of 5.0–41.3 $m^2\,ha^{-1}$). In 2004, 15 years after planting, trees on the receptor site had not achieved the same level of BA at 15.0 ± 0.7 $m^2\,ha^{-1}$ (range 5.4–15.5 $m^2\,ha^{-1}$). By 2014, 10 years later, the BA of new woodland developing at the receptor site exceeded that in the donor wood, at 30.2 ± 1.5 $m^2\,ha^{-1}$, but with a smaller range of 17.3–45.6 $m^2\,ha^{-1}$. Ash now accounted for over one-third of the BA (34.6 per cent), while cherry (*P. avium*) and field maple were co-dominant at 20.9 and 17.6 per cent, respectively, with hazel (10.0 per cent) and birch (*Betula* spp.) (5.0 per cent) present as minor components of the canopy (Table 1).

The woody species composition (by BA) of the donor site was very different to that planted at the receptor site (Table 1). No alder (*A. glutinosa*), cherry, crab apple (*M. sylvestris*) or birch was present in the donor wood, which had consisted mainly of ash, elm, oak, hazel and willow. At the receptor site, the planted 'nurse' crops, alder and birch, were beginning to stagnate or disappear after 25 years, but the ash canopy continued to expand and the early dominance of cherry, maple and hazel was maintained in spite of a combination of very limited post-2004 thinning operations and some natural self-thinning. Scattered unplanted shrubs, hawthorn (*Crataegus monogyna*) and dogwood (*Cornus sanguinea*) were present in the understorey in 2014, as was the planted spindle (*E. europaea*).

Numbers of species in quadrats at the receptor site declined steadily from an average of 58–28, as ruderal and open-ground species were gradually shaded out (Figure 1). By 2014, the average number of species per quadrat was not significantly different to that recorded in the donor wood (n = 31; t = 1.314, P = 0.20). Average Ellenberg 'L' indicator values also declined, suggesting that a more shade-tolerant flora gradually became established as the light levels decreased (Figure 1). Analysis of variance indicated that there were no significant differences in 'L' values between the different vegetation community types at the receptor site, but confirmed a significant fall in these values over the period (Table 2).

Moisture values (Ellenberg 'F') also declined throughout the receptor site over the recording period, although some 'wet' quadrats, near the edge of the new wood, included seepage ditches (Figure 1). These retained wetland species such as *Angelica sylvestris, Filipendula ulmaria, Carex pendula, Carex remota, Hypericum tetrapterum, Iris pseudacorus, Ranunculus auricomus* and *Scrophularia auriculata. Carex strigosa* and *Carex remota* which were confined to seepage areas in the donor wood did not transfer successfully to the rest of the receptor site. Higher Ellenberg 'F' values were associated with these 'wet' quadrats during the recording period which were

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Table 1 Mean BA (m^2 ha^{-1}) of woody species in 200 m^2 replicates of the donor wood (1986) and later at the receptor site (2004 and 2014), showing the percentage species composition in each year.

Woody species	1986 (n = 15) Donor wood	%	2004 (n = 20) Receptor site	%	2014 (n = 20) Receptor site	%
Fraxinus excelsior	7.58	29.3	3.00	20.4	10.45	34.6
Alnus glutinosa	–		1.70	11.6	1.29	4.3
Prunus avium	–		3.10	21.1	6.29	20.9
Acer campestre	3.06	11.8	2.55	17.3	5.30	17.6
Sambucus nigra	0.24	0.9	0.05	0.3	0.03	0.1
Euonymus europaea	0.03	0.1	0.15	1.0	0.24	0.8
Salix caprea	2.03	7.8	1.20	8.1	0.34	1.1
Salix cinerea	–		–		0.16	0.5
Betula spp.	–		0.85	5.8	1.52	5.0
Corylus avellana	2.02	7.8	0.95	6.5	3.03	10.0
Malus sylvestris	–		0.55	3.7	0.24	0.8
Viburnum lantana	0.01	0.04	–		–	
Viburnum opulus	–		–		0.06	0.2
Crataegus monogyna	0.80	3.1	0.10	0.7	0.31	1.0
Ulmus procera	6.31	24.4	–		0.13	0.4
Cornus sanguinea	0.05	0.2	–		0.07	0.2
Sorbus aucuparia	–		–		0.03	0.1
Quercus spp.	3.37	13.0	0.45	3.1	0.59	2.0
Rhamnus catharticus	0.10	0.4				
Prunus spinosa	0.29	1.1	0.10	0.3	0.08	0.3
Total BA (m^2 ha^{-1})	25.91		14.95		30.16	

Species originally planted at the receptor site are shaded.

consistently higher than in 'dry' plots. 'Moist' and 'scrub' plots also had greater 'F' values than the 'dry' quadrats, but were lower than in 'wet' plots (Table 2).

Reaction, or 'R' values, indicated that the 'dry' quadrats, situated on steeper ground at the upper edge of the receptor site, were more calcareous than other vegetation community types that were situated below on flatter topography where soil profiles tended to be deeper (Table 2). However, there was no significant change in the overall community 'R' values over time. When considering 'N' values, 'moist' quadrat vegetation appeared to be marginally less fertile than in other quadrats.

Ancient woodland indicator species

Five of the 18 ancient woodland indicator species present in the donor wood were not found at the receptor site, some of which were very uncommon and found only in single 1-m^2 quadrats in the 1985 and 1986 survey, or were immediately adjacent. Examples were *Anemone nemorosa, Sanicula europaea* and *Orchis mascula. Schedonorus giganteus* was also very occasional in the donor wood, and although it was not recorded in any of the 15, 200-m^2 quadrats, it was found frequently at the receptor site up to 1995, after which it began to disappear, and had gone entirely by 2014.

One test of translocation success is to measure the frequency or cover of the plants transferred from the donor site. In the case of Biggins Wood, a number of ancient woodland indicator species, such as the wetland species *C. strigosa* and *C. remota*, did not survive at the receptor site, while *C. pendula* and *Bromopsis ramosa* declined in frequency over time (Table 3). *Anemone nemorosa* and *R. auricomus* were both rare in the donor wood and at such low abundance that they might not have been expected to survive soil transfer, but the success of *Carex sylvatica, Primula vulgaris, Tamus communis*, *Iris foetidissima* and *Veronica montana* in 2014, along with a range of shade-tolerant plants such as *Ajuga reptans, Arum maculatum, Glechoma hederacea, Ranunculus ficaria, Rumex sanguinea, S. auriculata* and *Viola riviniana* suggested that the operation, at least for these species, had been successful. The failure of wetland plants was probably due to the drier conditions at the receptor site.

Seedbank changes

Seed banks varied in their composition at each recording interval, but there were some obvious trends. Species with short-term persistence tended to decline as the overhead canopy developed, inhibiting flowering and seed production (Table 4). This affected ruderal and competitive ruderal species in the ground flora such as *Anagallis arvensis, Cardamine flexuosa, Cirsium palustre, Epilobium adenocaulon, Picris echioides, Poa trivialis* and *Sonchus* spp., which declined in density over time. The wetland species *C. pendula, S. auriculata* and *Deschampsia cespitosa* were also much reduced by 2004, probably as a result of canopy closure on the drier site. Relatively shade-tolerant species such as *Epilobium montanum, Epilobium hirsutum, Hypericum hirsutum, R. fruticosus* and *Stachys sylvatica* increased during the period, as did *Juncus inflexus* and *H. tetrapterum*, although the latter two were more confined to the wetland plots.

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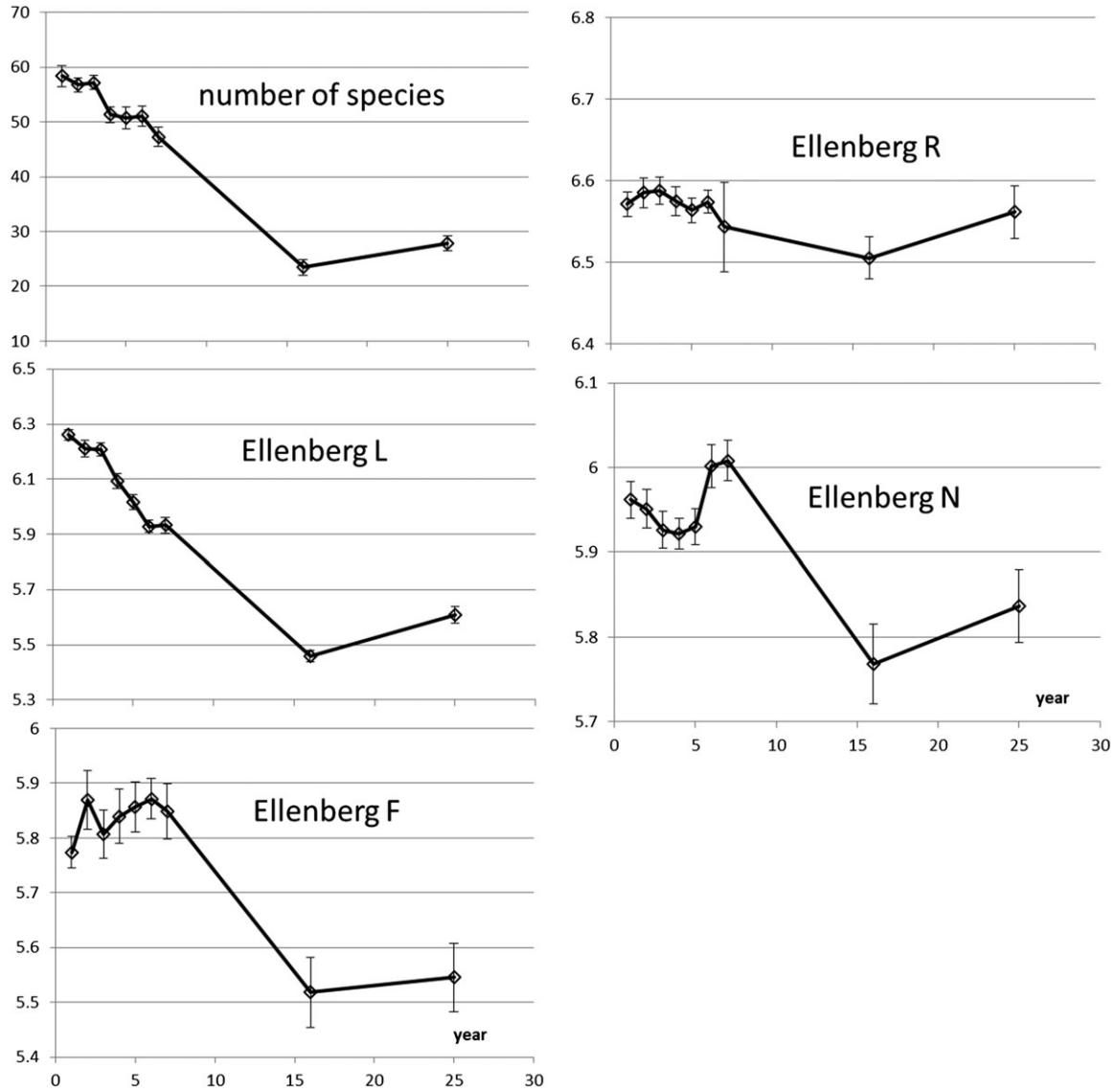


Figure 1 Changes in the number of species, and Ellenberg averages for light (L), moisture (F), reaction (R) and fertility (N) per 200-m^2 quadrat at the receptor site over a 25-year period (mean values with standard error bars).

Table 2 Comparisons of mean Ellenberg indicator values for the four different vegetation community (soil) types translocated at the receptor site over the 25-year period.

Ellenberg value	Translocated community type					Significance (*P*)	
	Overall mean (n = 180)	'wet' (n = 45)	'moist' (n = 45)	'scrub' (n = 45)	'dry' (n = 45)	Community type	Year
EL-L (light)	5.981	5.957^a	6.020^a	5.977^a	5.968^a	0.182	<0.001
EL-F (moisture)	5.777	6.016^c	5.735^a	5.745^a	5.609^b	<0.001	<0.001
EL-R (reaction)	6.563	6.502^a	6.544^a	6.563^a	6.643^b	<0.001	0.319
EL-N (fertility)	5.929	5.942^b	5.852^a	5.945^b	5.977^b	<0.001	<0.001

Different letters (a, b and c) indicate significant differences between communities (based on pairwise LSD comparisons, $P \leq 0.05$), for each Ellenberg value separately, using GLM analyses of variance.

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Table 3 Plant frequencies recorded in the original Biggins Wood in 1986 (in 15, 200 m^2 quadrats) compared with those recorded at the receptor site in 2014 (in 20, 200 m^2 quadrats).

Species	1986 (/15)	2014 (/20)	Species	1986 (/15)	2014 (/20)
Frequent species			*Tamus communis*	5	11
A. campestre	10	20	*Urtica dioica*	13	14
Adoxa mochatellina	12	11	*Veronica montana*	10	8
Ajuga reptans	13	13	*Veronica serpyllifolia*	0	9
Allium ursinum	4	2	*V. opulus*	5	6
A. glutinosa	0	10	*Viola riviniana*	8	9
Angelica sylvestris	9	3			
Anthriscus sylvestris	5	3	**Scarce species**		
Arum maculatum	13	18	*Agrostis stolonifera*	0	0
Betula pendula	0	14	*Anemone nemorosa*	1	0
Brachypodium sylvaticum	13	0	*Bromopsis ramosa*	3	0
Cardamine flexuosa	5	1	*Arctium minus*	1	0
Carex pendula	12	5	*Calystegia sepium*	0	1
Carex sylvatica	6	5	*Carex remota*	3	0
Circaea lutetiana	14	1	*Carex strigosa*	1	0
Clematis vitalba	3	16	*Cirsium palustre*	2	1
C. sanguinea	11	9	*Dactylorchis fuschsii*	1	0
C. avellana	14	19	*Deschampsia cespitosa*	5	0
C. monogyna	10	12	*Dipsacus fullonum*	0	1
Equisetum telmateia	5	1	*Dryopteris filix-mas*	3	0
Euonymous europaeus	3	18	*Epilobium tetragonum*	0	2
Filipendula ulmaria	8	0	*Equisetum arvense*	1	0
F. excelsior	14	20	*Euphorbia amygdaloides*	1	1
Galium aparine	15	5	*Hypericum hirsutum*	0	5
Geranium robertianum	9	4	*Hypericum tetrapterum*	1	4
Geum urbanum	12	4	*Iris pseudacorus*	1	0
Glechoma hederacea	12	15	*Lamiastrum galeobdolon*	1	3
Hedera helix	6	6	*Lapsana communis*	0	2
Heracleum spondyllium	6	2	*Lonicera periclymenum*	1	2
Iris foetidissima	5	12	*Mentha* spp.	1	1
Ligustrum vulgare	9	7	*Phyllitis scolopendrium*	1	0
Listera ovata	7	0	*Picris echioides*	0	3
Malus spp.	0	9	*Pimpinella major*	1	0
Poa trivialis	8	17	*Prunella vulgaris*	0	3
Primula vulgaris	10	18	*Ranunculus auricomus*	1	0
P. avium	0	18	*Ribes rubrum*	1	1
Prunus spinosa	7	8	*Rhamnus cathartica*	1	0
Quercus robur	7	9	*Rumex crispus*	0	1
Ranunculus ficaria	9	16	*S. cinerea*	0	1
Ranunculus repens	7	6	*Solanum dulcamara*	2	3
Rosa canina agg	7	12	*Sonchus oleraceus*	0	5
Rubus fruticosus	13	15	*Stachys sylvatica*	0	5
Rumex sanguineus	11	18	*Taraxacum officinale*	0	4
S. caprea	8	3	*Trifolium repens*	0	2
S. nigra	7	14	*U. procera*	5	1
Scrophularia auriculata	3	6	*Veronica chamaedrys*	1	3
Senecio jacobea	0	9	*Viburnum lantana*	1	1
Senecio vulgaris	1	5	*Vicia cracca*	0	1
Silene dioica	12	6	*Vicia sativa*	0	1

Ancient woodland indicator species are shaded.

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Table 4 Mean seedling densities (± standard error)[1] in soil samples collected from the donor wood in 1986 and at the receptor site one, three and 16 years after translocation.

Species	Density of seedlings per m^2							
	1986	SE	1989	SE	1992	SE	2004	SE
Species with short-term persistence								
Anagallis arvensis	2	–	5	–	789	320	323	7.7
C. flexuosa	968	202	107	18	46	18	–	–
C. palustre	2	–	23	–	59	16	–	–
Epilobium adenocaulon	124	61	83	–	557	177	–	–
Epilobium parviflorum	23	–	174	–	401	158	–	–
Galium aparine	53	–	119	27	16	4	–	–
P. echioides	–	–	122	24	3323	317	196	1.2
P. trivialis	648	206	3157	318	982	313	57	0.5
Sonchus asper	477	177	14	–	71	12	1	0.2
Sonchus oleraceus	248	89	104	29	240	91	–	–
Rumex sanguineus	127	–	28	–	397	101	–	–
Plantago major	8	–	6	–	22	9	–	–
Declining wetland species								
C. pendula	428	95	18	–	536	151	85	9.5
S. auriculata	267	165	271	59	2910	667	1312	9.2
D. cespitosa	225	–	52	–	149	44	–	–
A. sylvestris	9	–	1	–	29	16	–	–
Increasing shade-tolerant species								
Epilobium montanum	–	–	–	–	–	–	38	0.4
Epilobium hirsutum	–	–	5	–	90	30	171	2.0
H. hirsutum	–	–	–	–	1	–	249	2.5
R. fruticosus	11	–	1	–	–	–	75	0.9
Juncus inflexus	15	–	–	–	–	–	126	0.7
H. tetrapterum	39	–	10	–	13	–	122	0.9
Other species								
A. campestre	2	–	–	–	–	–	–	
Anthriscus sylvestris	63	–	–	–	19	–	–	–
Barbarea vulgaris	–	–	–	–	–	–	67	2.1
Calystegia sepium	–	–	–	–	–	–	3	–
Cardamine pratensis	–	–	–	–	–	–	1	0.2
C. sylvatica	–	–	–	–	19	–	–	–
Chenopodium album	3	–	–	–	–	–	–	–
Circaea lutetiana	51	13	–	–	20	6	–	–
Cirsium arvense	11	–	5	–	7	3	14	0.4
Cirsium vulgare	–	–	–	–	–	–	14	0.3
C. vitalba	7	–	–	–	–	–	1	0.7
C. monogyna	2	–	–	–	–	–	–	–
Diplotaxis muralis	–	–	–	–	–	–	3	0.2
Dipsacus fullonum	–	–	6	–	13	–	–	–
Equisetum arvense	–	–	–	–	–	–	1	–
Eupatorium cannabinum	7	–	–	–	–	–	–	–
Euphorbia amygdaloides	–	–	–	–	–	–	1	0.6
F. excelsior	15	4	–	–	–	–	–	–
Fumaria officinalis	–	–	19	–	–	–	4	0.7
Fumaria parviflora	–	–	–	–	–	–	–	–
Geranium molle	–	–	–	–	–	–	4	0.3
G. robertianum	8	–	11	–	37	10	1	0.2
G. urbanum	25	9	–	–	–	–	–	–
G. hederacea	50	17	2	–	125	19	47	0.5
Heracleum sphondylium	1	–	1	–	–	–	–	–

Continued

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Table 4 *Continued*

Species	Density of seedlings per m^2							
	1986	SE	1989	SE	1992	SE	2004	SE
Holcus lanatus	–	–	1	–	76	10	1	0.2
Hypericum perforatum	–	–	1	–	1	–	–	–
Lamium purpureum	–	–	–	–	21	–	–	–
Lolium perenne	–	–	–	–	8	–	–	–
Medicago lupulina	–	–	–	–	6	–	–	–
Melilotus altissima	2	–	–	–	3	–	–	–
Mentha sp.	–	–	–	–	–	–	6	0.4
Papaver rhoeas	–	–	5	–	1	–	–	–
Persicaria maculosa	–	–	5	–	3	–	–	–
Poa annua	–	–	2	–	–	–	6	–
P. vulgaris	2	–	1	–	3	–	–	–
Prunella vulgaris	–	–	–	–	–	–	1	0.5
Prunus spinosa	15	–	–	–	–	–	–	–
Pulicaria dysenterica	2	–	–	–	–	–	–	–
Ranunculus repens	24	–	12	–	45	16	20	0.4
Rumex obtusifolius	–	–	–	–	–	–	47	2.1
S. nigra	25	–	–	–	–	–	–	–
Senecio jacobaea	–	–	229	86	11	6	119	4.4
Senecio vulgaris	9	–	11	–	57	10	17	0.4
S. dioica	51	–	76	–	509	90	7	0.5
Sinapis arvensis	–	–	1	–	228	94	268	4.0
Sisymbrium ofticinale	–	–	–	–	–	–	1	0.2
Solanum dulcamara	6	–	–	–	1	–	–	–
Stachys sylvatica	2	–	5	–	–	–	37	0.6
Stellaria media	2	–	1	–	–	–	–	–
Taraxacum ofticinale	–	–	–	–	7	–	6	0.2
Torilis japonica	–	–	–	–	–	–	1	0.2
Trifolium repens	–	–	–	–	20	–	3	0.2
Tussilago farfara	–	–	–	–	8	–	–	–
U. dioica	112	40	2	–	6	–	9	0.3
Veronica chamaedrys	–	–	–	–	–	–	–	–
V. montana	80	32	9	–	38	12	1	0.2
Veronica persica	–	–	6	–	62	–	–	–
Vicia cracca	2	–	–	–	14	5	20	0.7
Vicia sativa	–	–	–	–	–	–	20	0.7
V. riviniana	9	–	10	–	1	–	–	–

Trends in population densities at the receptor site are indicated.
[1] For species with more than 50 per cent frequency, calculated from 20 seed trays, each one representing a 200-m^2 quadrat in the field. Species occurring in only one seed tray were omitted unless present in two or more years.

Vegetation ordination

The DCA ordination of the first dataset, including all quadrats surveyed at the donor wood and receptor site, compared their respective similarity in terms of the whole plant community, including planted trees at the receptor site. This analysis explained 17.2 per cent of the accumulated variation by the combined first and second axes, the *x*-axis of the ordination being positively related to time (excepting the donor 1986 quadrats) and woody BA, but negatively associated with the Ellenberg light (L) vector. All post-translocation year centroids followed a positive sequence, running left to right along the *x*-axis, indicating a gradually closing canopy following translocation in 1989. The *y*-axis indicated the opposed moisture (El 'F') and soil reaction (El 'R') gradients (Figure 2); indicated moisture levels (F) tended to be lower in quadrats assigned to 'dry', moist and 'scrub' associations and more calcareous in 'dry' quadrats. Bare ground and open conditions (prevailing immediately after translocation) were associated with the horizontal vectors indicating greater species numbers, competitors and ruderals (particularly annuals and biennials), many of the latter emerging from the soil seedbank, including *Sinapis arvensis, Sonchus asper* and *Papaver rhoeas*. Unplanted shrubs such as *Sambucus nigra*, *C. monogyna*, *C. sanguinea* and the woody climber *Clematis vitalba* became more prominent towards the end of the survey period. A greater

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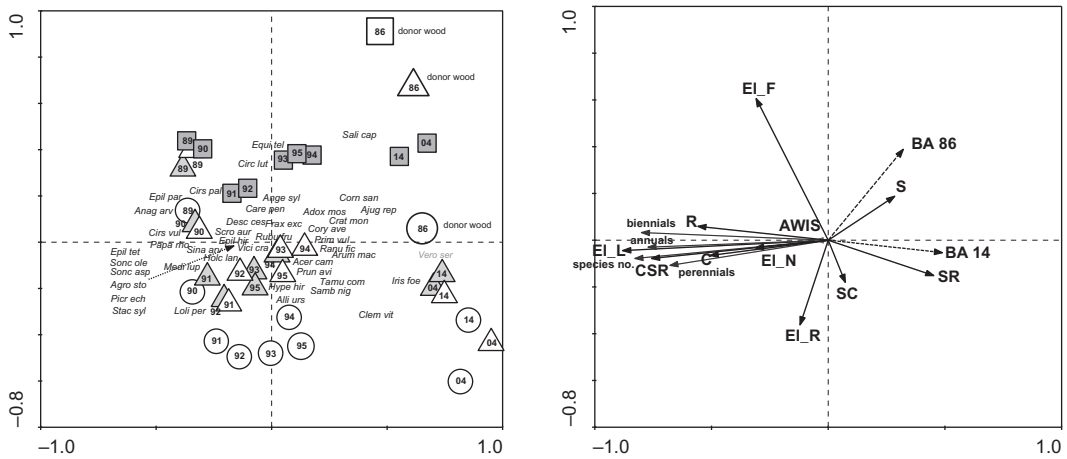


Figure 2 DCA ordination diagram (detrended by 2nd order polynomials) showing the development of the woodland flora after translocation (1989–2014), compared with donor wood vegetation in 1986. Supplementary community centroids (left) for different community types are shown for each relevant year. Planted tree species at the receptor site are included; no scrub quadrats were recorded at the donor site in 1986. The vector traits (right) are shown for primary plant strategies and Ellenberg values, together with BA values. Species fit is ≥20 per cent: species with slightly lower fit are shown in grey type. The model uses species scaling; biplot scaling and downweighting of rare species. Key to diagram: ○ = 'dry'; △ = 'moist'; △ = 'scrub'; □ = 'wet'. **Species**: *Ana arv = Anagellis arvensis; Adox mos = Adoxa moschatellina; Acer cam = Acer campestre; Agro sto = Agrostis stolonifera Ajug rep = Ajuga reptans; Alli urs = Allium ursinum; Ange syl = Angelica sylvestris; Arum mac = Arum maculatum; Care pen = Carex pendula; Circ lut = Circaea lutetiana; Cirs pal = Cirsium palustre; Cirs vulg = Cirsium vulgare; Clem vit = Clematis vitalba; Corn san = Cornus sanguinea; Cory avel = Corylus avellana; Crat mon = Crataegus monogyna; Desc ces = Deschampsia cespitosa; Epil hir = Epilobium hirsutum; Epil par = E. parviflorum; Epil tet = E. tetrapterum; Frax exc = Fraxinus excelsior; Equi tel = Equisetum telmateia; Holc lan = Holcus lanatus; Hype hir = Hypericum hirsutum; Iris foe = Iris foetidissima; Loli pere = Lolium perenne; Med lup = Medicago lupulina; Pap rho = Papaver rhoeas; Picr ech = Picris echioides; Prim vul = Primula vulgaris; Prun avi = Prunus avium; Ranu fic = Ranunculus ficaria; Sali cap = Salix caprea; Samb nig = Sambucus nigra; Scro aur = Scrophularia auriculata; Sina arv = Sinapis arvense; Sonc asp = Sonchus asper; Sonch ole = S. oleraceous; Stac syl = Stachys sylvatica; Ranu fic = R. ficaria; Rubu fru = Rubus frutucosus; Tamu com = Tamus communis; Vero ser = Veronica serpyllifolia; Vici cra = Vicia cracca*. **Traits**: Primary plant strategies: C = competitor; S = stress-tolerant; R = ruderal; SR = stress-tolerant ruderal; SC = stress-tolerant competitor; CSR = competitor/stress-tolerant/ruderal. Ellenberg indicators: EL-F = moisture; EL_L = light, EL_N = fertility; EL_R = reaction; BA = basal area in 1986 or 2014. AWIS = ancient woodland indicator plants

proportion of stress-tolerant (S) and stress-tolerant ruderal species (SR) also became more frequent as the tree canopy developed. Ancient woodland indicators were most frequent during the first 5–6 years after translocation, but declined after canopy closure.

The different soil origins of vegetation communities from the donor wood were vertically stratified on the *y*-axis, reflected in indicative Ellenberg moisture (El 'F') and reaction (El 'R') gradients. The former gradient distinguished the sequence of 'wet' community quadrats in which several wetland plant species such as *Salix cinerea, Carex riparia* and *Equisetum telmateia* were present. The soil reaction vector was orientated towards the 'dry' soil community quadrats, which were more calcareous and better drained, with 'scrub' and 'moist' communities being intermediate. By 2004 and 2014, the 'dry', 'moist' and 'scrub' quadrat centroids all tended to converge, although the 'wet' centroids retained a ground flora composition more distinct from the rest. The 1986 'wet' and 'moist' centroids, corresponding to the donor wood, were strongly influenced by the presence of wetland species such as *Salix caprea* (not present at the receptor site), along the inferred moisture (El 'F') gradient, and by the frequency of stress-tolerant species and a lower inferred soil reaction (El 'R'). The centroid representing two 'dry' quadrats recorded in 1986 was separated from the others in that year by the moisture gradient and was more similar to others representing 2004 and 2014 at the receptor site. When testing the equivalent CCA, the model was significant ($P = 0.001$), with a drop in species variance relative to the DCA of 0.5 per cent for the first and second axes together. Partial CCA testing confirmed that all years, except 1994, significantly contributed to vegetation change ($P \leq 0.05$) and that, when adjusted for years, the different communities contributed significantly to vegetation change ($P \leq 0.05$), although these results must be viewed with caution as the sample size for communities was small.

The second dataset, comprising only the receptor site quadrats minus planted trees, produced a broadly similar layout to that of the first. This DCA ordination explained 17.5 per cent of the accumulated variance by the first and second axis combined. The equivalent CCA model was significant ($P = 0.001$), with a drop in species variance accounted for by the combined first and second axis of only 2.1 per cent relative to the DCA. Partial CCA testing on 'community × year' adjusted for year, showed that the post-translocation temporal trend was influenced by community type, with 8.8 per cent of the variation explained by the communities on the combined first and second axes. This model was significant ($P = 0.001$) and clearly distinguished the different communities, even after 25 years.

The separation of the 1986 centroids at the donor site from those at the receptor site immediately after translocation in 1989 illustrates their vastly different species composition following

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translocation. Twenty-five years on, the receptor site quadrats all had much lower inferred light availabilities and increased BAs, similar to those prevailing in the donor wood. However, the donor and receptor communities still remained distinct and were separated principally by soil wetness in the donor wood and more calcareous conditions at the receptor site. High moisture levels were maintained in some quadrats at the receptor site by soil seepages, and the moist community also appeared to maintain the highest number of ancient woodland indicator species with 7 in 2014, compared with 14 in 1986.

Discussion

Like many woods in the area, Biggins wood had a history of coppicing, and in this respect the vegetation would likely have become adapted to this form of management. Thus, the periodic removal of the canopy, through coppicing, bears some analogy to its removal in a translocation operation. In coppice management, the disturbance invariably stimulates a rapid response from the seedbank, with many ruderals as well as existing perennial species benefiting from the increased light regime (e.g. Ash and Barkham, 1976; Ford and Newbould, 1977; Mason and MacDonald, 2002; Broome *et al.*, 2011). Many of these are light-demanding species of open habitats, forest edges, rides and clearings (Peterken and Francis, 1999; Bossuyt *et al.*, 2002; Erenier *et al.*, 2010; Plue *et al.*, 2010). These are able to expand rapidly and potentially compete with the recovering, shade-tolerant woodland flora. However, the translocation process creates a far greater degree of disturbance than routine coppicing resulting from the comprehensive initial soil disturbance, complete canopy removal, part-destruction of the perennial field layer and the much longer time taken to re-establish a tree canopy. In this case, it took up to 18 years to achieve canopy closure at the receptor site, whereas with coppice crops the interval may be as short as 5 years (Brown and Warr, 1992; Mason and MacDonald, 2002). The dilution of the seedbank, which would have occurred during loose-tipping and mixing of the translocated topsoil layer, did not slow the rapid expansion of competitive ruderals at a similar translocation site nearby. There is little convincing evidence that loose tipping (and inevitably mixing) of the topsoil layers is a less successful method of translocation as compared with transplanting intact 'turves' or blocks of woodland soil (Craig *et al.*, 2015). Recovery of the field layer in translocated soil would be expected to take longer, and some losses of specialist forest species might be expected in the interim.

Although the accumulated variation explained by the combined first and second axes of the ordination models was relatively low, this was to be expected when dealing with the presence–absence data, particularly when analysed by CA/CCA and considering the total variability in species composition over time (ter Braak and Šmilauer, 2015). Following destruction of the canopy, soil translocation resulted in a doubling of species numbers at the receptor site when many ruderal annuals and biennials, including competitor species, took advantage of the bare, open ground. This was a fairly short-lived phase, and by canopy closure the average number of species in quadrats resembled that in the donor wood. Both the diminishing light availability and increased dryness were driving factors in the subsequent vegetation succession, with the Ellenberg 'L' values falling from 6.3 to ~5.5, representing a semi-shaded flora, while the corresponding Ellenberg 'F' values of 5.5–5.6 at the end of 25 years still indicated a site of average dampness. While these moisture values were averages for the whole site, the 'wet' quadrats remained distinct from the others, with average 'F' values ~6.0 throughout. The inferred soil reaction 'R' values showed little change throughout the recording period, but fertility 'N' fluctuated and ultimately fell as species composition changed from a productive sward of ruderal species to a shade-tolerant ground flora. This suggested a marginal lowering of fertility over time, although the overall values indicate a site of intermediate fertility throughout. As 'R' and 'N' values are often highly correlated, the former could be the more important driver.

This translocation operation exposed the inherent difficulty in selecting a receptor site to closely match that of the donor. The receptor site chosen was in a drier situation than the position of the donor wood on the Gault clay basin, although the soil reaction was similar in other respects. In addition to the more freely draining soil profile, canopy interception and transpiration by the new tree crop contributed to the gradual drying out of the receptor site. The donor wood quadrats returned average 'F' values of 5.80 ± 0.06, compared with 5.54 ± 0.06 across the receptor site in 2014. Nevertheless, a shade-tolerant flora typical of the woodland floor had been established at the new site after 25 years, with species such as *A. reptans, A. maculatum, G. hederacea, Geranium robertianum, Geum urbanum, I. foetidissima, P. vulgaris, R. ficaria, Silene dioica, Urtica dioica* and *V. riviniana* frequent in the understorey. Several studies have shown that unthinned plantations, overmature coppices and increasing tree BAs tend to reduce species richness in the field layer (Kirby *et al.*, 2005; Van Calster *et al.*, 2008). At the Biggins Wood receptor site, planting at regular spacing, later followed by inadequate thinning, produced a dense and uniformly shading tree canopy which may have contributed to further losses of woodland ground flora. Because the new wood was even-aged and relatively uniform, there was little variation in canopy structure that could be exploited by species requiring more open conditions in canopy gaps. In the donor wood, the coefficient of variation of the BA was ~42 per cent, whereas in quadrats in the receptor site wood it was ~22 per cent in 2014.

Translocation and replanting of the receptor site profoundly altered the character of the tree canopy compared with the donor wood, both in terms of its state of maturity, being much younger, and the tree species selected for it. Although *F. excelsior* remained dominant, major components such as *U. procera* and *S. caprea* were virtually lost at the new site, although replanting with *Ulmus* would likely have been subject to disease. The 'nurse' tree crops *A. glutinosa* and *B. pendula* at the receptor site were in decline by 2014 and were relatively ineffective in providing early shade, except in the case of *Alnus* on some very small patches of 'wet' soil. On the lighter, calcareous parts of the receptor site *P. avium* grew rapidly and cast a heavy shade, while *A. campestre* was much increased by the new planting design, and that of *Q. robur* reduced.

Ancient woodland indicator species

Understorey ancient woodland indicator species that were rare and infrequent in the donor wood did not generally survive the

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soil translocation. The reasons for this include the difference of the environmental conditions at the receptor site and its considerably smaller size compared with the donor wood. As this small parcel of new woodland was also isolated from other ancient wood sources, it was unlikely to recruit indicator species from the hinterland, especially given this short timescale. Three species, *S. giganteus*, *Hypericum androsaemum* and *S. europaea* were only recorded very infrequently in the 1-m^2 quadrats, and not at all in 200-m^2 quadrats in the donor wood. As they were found later at the receptor site, it is possible that they may have been present in the transferred soil.

Conclusions and recommendations

After 25 years, the translocation exercise had succeeded in transferring some shade-tolerant elements of the ground flora from the donor wood to the receptor site, including over 70 per cent of its ancient woodland indicator species. However, the new community was significantly different from the original, principally because soil conditions were drier at the receptor site, although less so in the very restricted areas with a high water table, and, therefore, not well matched to the donor site. In future translocations, the tree species should be carefully chosen to match the prevailing topographic and edaphic factors, as well as the composition of the donor canopy. Close spacing to hasten an initial canopy cover may be an advantage at first, but tree 'nurse' crops, given that they are well suited to the site, should be removed promptly once their purpose has been served. Location of the new site as close as possible to an existing wood may provide additional colonizing sources of propagules.

Translocation creates a much greater degree of disruption compared, say, with routine coppicing, with the effects likely to persist for a much longer period. The priority for the surviving field layers is to re-establish a canopy quickly, but once developed, the long, dark phase of woodland development can become a threat to woodland-edge species and others requiring more light. This might be avoided by cluster planting, much earlier thinning or coppicing, and ultimately retaining some standard trees (Joys *et al.*, 2004) in order to simulate the variable levels of shading such as that noted in the donor wood. Such interventions would need to avoid creating too open conditions that might allow a resurgence of dominant ruderal species.

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Conflict of interest statement

None declared.

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