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Factors determining species richness of soil seed banks in lowland ancient woodlands

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Abstract The demise of coppicing in UK ancient woodlands, combined with the planting of non-native, fast-growing conifers in the twentieth century, heightens the potential recharge value of ground flora seed banks. Soil cores from adjoining semi-natural and conifer-containing stands in four lowland ancient woods in central England were removed to establish seed bank species richness. During a fourteen-month germination trial soil from two depths yielded 6554 seedlings from 81 species, ten of which showed a strong affinity for ancient woodland conditions. *Juncus effusus* accounted for 80% of emergent seeds whilst 23 other species, including *Lysimachia nummularia* and *Potentilla sterilis*, were represented by only one individual. Species richness is described by a model that explains 40% of observed variance ($P < 0.00001$). The model has three significant variables: species richness increases as soil pH rises, and decreases with both depth and increasing time since the most recent planting/disturbance event. No difference was found in the density of seeds from species common to paired semi-natural and conifer-containing stands that were separated only by a woodland ride, suggesting prior management and environmental conditions have a greater influence on seed banks than current stand type. Sørensen similarity index values revealed poor congruence between above-ground vegetation and species in the seed bank. Taking pH measurements in conifer stands identified as younger in terms of planting/disturbance may help locate areas where greater numbers of species (including woodland specialists) are located. Caution is required, however, as these seed banks may also contain non-target, competitive species that may swamp the regeneration of woodland specialists.

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Abbreviations

ASNW Ancient semi-natural woodlands
PAWS Plantations on ancient woodland sites
AWIS Ancient woodland indicator species
GLM General linear model

Introduction

The importance of forest biodiversity is recognised at global and regional scales (UNCED 1992; EU Habitats Directive 1992). The UK Biodiversity Action Plan identifies broad-leaved woodland as supporting almost twice as many species of conservation concern as any other habitat (Biodiversity 1995). Of particular importance are ancient woodlands, which in England are defined as areas that have been continuously wooded since 1600 AD (Spencer and Kirby 1992). For centuries, the traditional management of lowland ancient semi-natural deciduous woods (ASNW) was one of selective cutting of standards e.g. oak (*Quercus* sp.) or ash (*Fraxinus excelsior*), combined with rotational coppicing of understory species e.g. hazel (*Corylus avellana*) and hawthorn (*Crataegus* spp.) (Rackham 1980). The periodic opening-up of tracts of woodland resulted in increased flowering of vernal, herb-layer species, prior to the return of a closed canopy as new standards grew and coppice stools regenerated (Rackham 2006). The twentieth century decision to plant fast-growing, non-native conifers, e.g. Norway spruce (*Picea abies*) and western red cedar (*Thuja plicata*) in UK ancient woodlands has altered not only canopy composition, but also canopy height, frequency of management and light levels reaching the woodland floor (Kirby 1988; Warr et al. 1994; Pryor et al. 2002). Areas within ancient woods that contain planted conifer stands (pure or conifer/deciduous mixes) are referred to as plantations on ancient woodland sites (PAWS). Approximately 140,000 ha of PAWS exist in Britain (Forestry Commission 2005). Pryor and Smith (2002) estimated that about 44% of surviving ancient woodland in Britain had been converted to plantations.

The impoverishment of ancient woodland ground flora resulting from the abandonment of traditional coppicing practices and/or the creation of PAWS has been well documented (Peterken 1976; Brown and Oosterhuis 1981; Warr et al. 1994). The idea that removing conifers can benefit biodiversity generally (Eycott et al. 2006a; Hill and Stevens 1981; Greatorex-Davies et al. 1993) and ancient woodland herb-layer species in particular (Godefroid et al. 2006; Hermy et al. 1999), is based on the premise that planted conifers cast continuous, deep shade and may accelerate acidification of the soil (Peterken 2001; Bossuyt et al. 2002; Ovington 1953). Managing a return to ground-flora rich ASNWs after PAWS removal is of conservation interest. This is due to the fragmented nature of UK ancient woods and the fact many woodland specialists, in particular ancient woodland indicator species (AWIS), have poor spatial dispersal abilities (Dzwonko 2001; Hermy et al. 1999; Hermy and Verheyen 2007).

As the re-colonization of cleared PAWS sites by woodland specialists from beyond forest boundaries is unlikely due to poor dispersal rates (Dzwonko and Loster 1992), seeds from the soil seed bank may act as a source of plant recharge following conifer removal/thinning or, in the case of ASNW, a return to active coppice management (Brown and Oosterhuis 1981; Warr et al. 1994; Decocq et al. 2004; Dougall and Dodd 1997). Three common themes that have emerged from past seed bank studies are: the occurrence of high numbers of propagules from early successional species known to have persistent seeds (Bossuyt et al. 2002; Kjellsson 1992; Kipfer and Bosshard 2007), the poor representation in woodland seed banks of tree species and shade-tolerant or shade-demanding herb-layer species (Brown and Oosterhuis 1981; Bossuyt and Hermy 2001) and poor congruence between above-ground vegetation and the seed bank beneath it (Staaf 1987; Falinska 1999; Olano et al. 2002). A general consensus exists that a successful return to a rich woodland-specialist ground flora from dormant seeds is unlikely (Bossuyt and Hermy 2001; Baeten et al. 2009).

The aims of this study were:

1. To determine the extent to which variance in the number of species in seed banks can be explained by the type and duration of management, and prevailing environmental conditions.
2. To establish whether seed bank composition differs under closely located PAWS and ASNW stands in the same ancient wood.
3. To assess the similarity between species richness in the seed bank and the above-ground vegetation, with particular reference to ancient woodland indicator species.

Method

Study sites

Four lowland ancient woodlands in Northamptonshire, central England were selected for the study. The furthest boundaries of all four woods are within 5.0 km radius from a central point, 52° 05′ 59″ N, 1° 05′ 43″ W. The altitude of the woods is between 140 and 150 m a.s.l. Three of the woods are documented from 1220 AD or earlier, with the fourth appearing on a 1590 AD map. Archaeological evidence suggests much earlier use of these woodland areas, (Table 4; Forestry Commission; Wilsden 1915). Despite their close proximity, these woods have clearly demarked boundaries and are unlikely to have been contiguous during the past 900 years (Table 4).

The underlying geology is boulder clay, overlain by poorly draining soils (Ordnance Survey 1969). The pH of soils in the areas studied ranges from 3.70 to 6.27 (mean pH 4.55 ± 0.69 $n = 48$). All four woods are managed by the Forestry Commission and listed on the UK Government's Ancient Woodland Inventory (MAGIC 2009).

The woods contain areas of deciduous stands (ASNW) with known tree ages/planting dates from 1907 to 1986. These stands are typically oak (*Quercus robur*) and abandoned hazel coppice, with some ash, field maple (*Acer campestre*) and understorey species that include dog's mercury (*Mercurialis perennis*), yellow archangel (*Lamiastrum galeobdolon*), sweet woodruff (*Galium odoratum*) and wood anemone (*Anemone nemorosa*). In addition, blocks within the four woods also contain mixed conifer/deciduous stands and, rarely, pure Norway spruce stands (PAWS), which were planted between 1944 and 1986. The conifer mixtures include Norway spruce and oak, Norway spruce and western red cedar, and Corsican pine (*Pinus nigra* ssp. laricio) with ash or oak.

Plot selection

Three areas in each wood where both ASNW and PAWS stands exist in close proximity were selected for sampling. Selection criteria were based on the requirement that both ASNW and PAWS areas should be adjoining, separated only by a woodland ride (approximate ride width 3.5 m), thus allowing for a stratified sampling regime that reduced variation in terms of edge effects, soil type or microclimate. Information relating to stand type and age of earliest and latest planting/disturbance at each location was obtained from the Forestry Commission. All PAWS stands, apart from one in Plumpton wood which was pure Norway spruce, were conifer mixes. At each location (defined as presence of an adjoining ASNW and PAWS site) an area to sample was chosen by selecting the mid-point of a PAWS stand along a woodland ride. From the mid-point, and 12 m into the stand, a $2 \times 2\ m^2$ site was identified by permanent wooden markers. An equivalent site across the ride in the ASNW area was marked in the same way.

Environmental data collection

Light

Canopy openness above the quadrats was measured in May 2008. At the corner of each quadrat, and oriented north, a mirror ($40 \times 60\ cm^2$) with cross hatching (104 crosses spaced 4 cm apart) was placed on the ground and the number of crosses reflecting open sky conditions (no branches or leaves) was recorded. The mean light value for each quadrat was used.

pH

A small quantity of soil (approximately $4\ cm^3$) was used from bulked samples ("Soil" section) to test the pH values for each site and depth. To deflocculate the clay particles, barium sulphate ($BaSO_4$) was added to two cubic centimetres of soil in a test tube (20:80) and 20 ml of de-ionised water added. The mixture was agitated by shaking for 30 s. A minimum of 2 min after all soil particles had settled, a hand-held, digital electrode pH meter (Hanna Instruments HI-99104), accurate to 0.01, was used to measure pH. For each sample this process was repeated and the mean value used.

Seed bank

Soil

Soil sampling took place between 18th to 28th April 2008. From the corner of each quadrat an initial soil core (14 cm × 14 cm × 25 cm) was removed. From this, a core of 5 cm × 5 cm × 23 cm was cut. This was divided into two depths (0–11.5 cm and 11.5–23 cm), with soil bagged and labelled in the field. The four cores from each depth were later bulked to give a single soil sample per depth, thus minimising spatial aggregation of propagules (Rees and Crawley 1997). A total of 192 soil cores (4 woods × 3 sites × 2 treatments (1 PAWS, 1 ASNW) × 4 corners × 2 depths) provided 48 bulked samples for germination trials.

Each bulked sample was placed in a standard (37 cm × 23 cm × 5 cm) seed tray with its base holes covered by sterile grit to aid drainage. The trays were placed at random on wooden pallets in an outdoor roofless enclosure, with a 1.5 m high perimeter of fine net to exclude animals and wind-borne seed. Trays containing sterile grit and a layer of sterile compost were placed amongst the samples as a control to check for wind-borne seed. During the trial, five *Taraxacum officinale* and three *Epilobium hirsutum* individuals appeared in the control trays and therefore these species were excluded from all results. All emerging *Hyacinthoides non-scripta* and *Ranunculus ficaria* were also excluded, as their origination from seed or bulbs could not be determined. All trays were randomly moved every three weeks during the germination trial. Slug pellets and ant powder were used to deter seedling consumption and seed robbing, respectively. The trays were watered during the 14 month trial as necessary. Recording took place on twelve occasions between 11th May and 24th September 2008, and seven occasions between 25th April and 18th July 2009. Having identified and recorded a seedling's presence it was removed and destroyed. Seedlings not readily identifiable to species level were grown on in pots and identified at a later date, including several species that flowered the following year (2009). This proved particularly important for AWIS from the families Cyperaceae and Juncaceae (*Carex* spp. and *Luzula* spp. respectively) where flowers and fruit are required for accurate identification.

Vegetation

In each $2 \times 2\ m^2$ quadrat, the percentage area without vegetation (July/August 2008), together with all species and their abundance (April, August and November 2008) were recorded. As no comprehensive UK AWIS list exists, species classed as AWIS for the purposes of this study are those that appear on a minimum of six out of ten UK regional AWIS lists produced by Natural England (Natural England 2006), Table 5. Nomenclature follows Jermy et al. (2007) for Cyperaceae and Stace (1997) for all others.

Analysis of data

Species richness

Seed bank species richness values were log transformed and tested for normality using the Shapiro–Wilk test ($W = 0.95$, $P > 0.05$, $n = 48$). A General Linear Model (StatSoft Inc. Statistica 2009) was used to test the following factors against log species richness: seedling number, depth, pH, management effect (ASNW or PAWS), canopy openness, percentage area without vegetation, time in years since earliest planting/disturbance event and time in years since most recent planting/disturbance event. Main effect factors with $P > 0.05$ were eliminated sequentially from the model by removing the least significant factor first. Overall explained variance is given as the (more conservative) adjusted r^2 value. A second analysis excluded 16 ruderal species or species which had no particular preference for woodland or wood pasture conditions (Table 5), leaving a subset of woodland and wood pasture affinity species. As one quadrat contained no species after removal of non-wood species, all values were treated as $n + 1$ to allow log transformation. These values were also tested against all factors. Exploratory analysis that used values for the two soil depths combined (the sum of two trays) gave a poorer resolution, and was not pursued.

Pair-wise comparisons of pH

Although differences between canopy type (ASNW and PAWS) are considered in the overall GLM, the possible associations between canopy type and individual pH values at matched sites and depths across rides are not explicitly explored in the model. To overcome this, differences in paired pH values were analysed using a *t* test (StatSoft Inc. Statistica 2009). All means presented in the paper are ± S.D.

Pair-wise comparisons of seed numbers

To establish whether seed bank composition differs under closely located ASNW and PAWS sites, the number of seeds from each species was compared at matched depths across rides. Where no seeds were present from a species under both management types, these double-zero results were excluded. As seed number was not normally distributed, a Mann–Whitney test was used (StatSoft Inc. Statistica 2009).

Similarity of seed bank and above-ground vegetation

The Sørensen similarity index (Magurran 2004) was calculated by comparing the total number of species in above-ground plots with the combined soil depths beneath them. This was repeated for ancient woodland indicator species.

Results

Seedling density and depth

A total of 6554 seedlings emerged in the 48 trays during the 14 month germination trial. The mean density of buried seeds per tray was 136.5 ± 97.5, $n = 48$. This corresponds to an overall density of ≈27300 seeds m^{-2}. The emergent seedlings represented 81 species, the six most common being *Juncus effusus* (5271 seedlings or 80% of all germinating individuals), *Rubus fruticosus* (380 seedlings), *Deschampsia cespitosa* (232), *Carex sylvatica* (72), *Galium uliginosum* (56) and *Hypericum pulchrum* (54). The number of seedlings germinating from soil at depth 0–11.5 cm across all woods and canopy types was 3466 (density of ≈ 14400 seeds m^{-2}), whilst 3088 seedlings germinated from soil at depth 11.5–23 cm (density of ≈ 12900 seeds m^{-2}).

Species richness

The mean number of species per tray was 7.8 ± 4.1, $n = 48$ (8 ± 4.6, $n = 24$ (PAWS) and 7.6 ± 3.6, $n = 24$ (ASNW)). The maximum number of species emerging from a single soil sample at any depth was 20 (under PAWS; Corsican pine and oak; planted in 1969), with the most species-poor quadrat yielding seedlings from only *J. effusus* (PAWS; Norway spruce/western red cedar/oak; planted in 1944).

The variance in total species richness ($r^2 = 0.4$, $F_{3,44} = 11.38$, $P < 0.00001$) across all sites and woods is explained by three significant factors: soil pH, depth, and time in years since most recent planting/disturbance event (Table 1). Species richness declines as pH falls ($P = 0.0001$) and is greatest in the top 11.5 cm of the soil ($P = 0.0001$, mean species richness is 9.8 ± 4.4 in top section and 5.9 ± 2.7 in bottom section). As time since the most recent planting/disturbance event increases, the number of species declines ($P = 0.02$). An initial GLM result revealed seedling number as significant; however seedling number was itself explained by time since most recent planting/disturbance event

Table 1 Explained variance in species richness (GLM) for all sites (total species and subset of wood and wood pasture affinity species)

	Species richness (all species)			Species richness (wood and wood pasture affinity species)		
	P	*F*	df	*P*	*F*	df
pH	0.0001	17.91	1	0.0007	13.36	1
Increasing depth in the soil	0.0001	17.26	1	0.001	11.85	1
Increasing time (years) since most recent planting/ disturbance event	0.02	6.36	1	0.02	5.94	1
Overall adjusted r^2	0.40 ($P < 0.00001$)	11.38	3.44	0.32 ($P = 0.0002$)	8.39	3.44

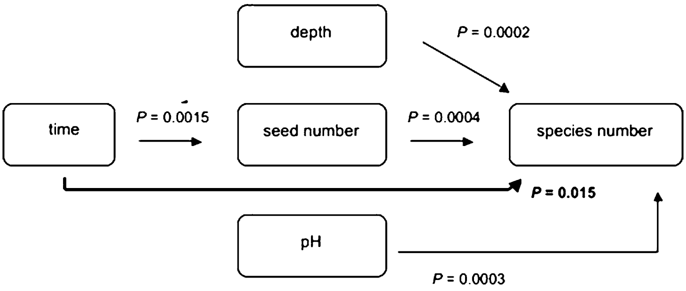

Fig. 1 The factor time since most recent planting/disturbance event as an explanation of seedling number (from an initial GLM that included seedling number)

(Fig. 1). The latter (more informative) factor is therefore included in the final model and presented in Table 1. The subset of woodland and wood pasture affinity species retained the same three explanatory factors, although with a reduced overall r^2 of 0.32 ($P = 0.0002$, Table 1).

Stand variables

Percentage bare ground

Fifteen of the twenty-four quadrats had >90% surface area without vegetation and of these five had no vegetation. Three of the sites with no vegetation were under Norway spruce canopies, with the remaining two under ASNW canopies (oak and abandoned hazel coppice).

Most recent planting/disturbance event

The dates of the most recent planting/disturbance event ranged from 1923 to 1986. Three stands (last planted/disturbed 59–60 years prior to sampling) yielded ten or more species. One of these (4A, Table 2), contained representatives from 18 species, five of which were AWIS.

Table 2 Species richness of above-ground vegetation and seed banks (combined depths), Sørensen similarity index values and number of ancient woodland species present

Wood	Site and stand A = ASNW P = PAWS	Year of earliest and most recent planting or disturbance event (single date given where values are the same)	Total number of species present in above-ground vegetation	Total number of species present in seed bank (combined depths)	Sørensen similarity index (all species)	Total number of AWIS species in seed bank (combined depths)	Sørensen similarity index (AWIS)
Bucknell	1 A	1940, 1979	0	15	0	4	0
	1 P	1973	1	16	0	2	0
	2 A	1932, 1979	2	9	0.2	1	0
	2 P	1962, 1969	7	10	0.2	2	0
	3 A	1932, 1979	0	9	0	2	0
	3 P	1980	0	11	0	3	0
Plumpton	4 A	1948	7	18	0.2	5	0.3
	4 P	1949	4	7	0	1	0
	5 A	1949	7	14	0.3	1	0.7
	5 P	1949	7	12	0.2	1	0.7
	6 A	1948, 1949	0	11	0	3	0
	6 P	1949	1	12	0	1	0
Hazelborough	7 A	1933, 1963	2	7	0	0	0
	7 P	1969	7	23	0.1	3	0
	8 A	1907, 1944	3	14	0.2	3	0
	8 P	1957, 1967	7	19	0.2	1	1
	9 A	1944	2	4	0	0	0
	9 P	1944	2	5	0.3	0	0
Whistley	10 A	1923, 1957	5	18	0.09	2	0.7
	10 P	1986	4	10	0	0	0
	11 A	1923	4	8	0.2	2	0
	11 P	1984	3	4	0	0	0
	12 A	1923, 1986	10	9	0.3	3	0
	12 P	1983	0	16	0	1	0

pH at paired sites

The *t* test revealed no significant difference in pH values at paired ASNW and PAWS sites separated by woodland rides ($T = 1.93$, $P = 0.07$, df $= 23$).

Above-ground vegetation

The number of species in above-ground vegetation of the sampled plots ranged from 0 to 10. Mean species richness was 3.5 ± 3.0, $n = 24$. At all but one sampling site in Whistley Wood (12A, Table 2) species richness was greater in the seed bank than in above-ground vegetation. The congruence between species present in both the above-ground vegetation

Table 3 Abundance and distribution of the ten AWIS present in the study, across all sites at depths 0–11.5 and 11.5–23 cm

Species	Number of samples where present at depth 0–11.5 cm	Total number of individuals at depth 0–11.5 cm	Number of samples where present at depth 11.5–23 cm	Total number of individuals at depth 11.5–23 cm	Year of most recent planting or disturbance event in stand (range given where species present in more than one quadrat)
Carex pallescens	5	33	6	11	1923–1980
C. pendula	1	1	0	0	1948
C. remota	1	1	1	1	1949
C. sylvatica	12	46	9	26	1944–1979
Hypericum pulchrum	6	34	7	20	1923–1986
Luzula pilosa	1	4	0	0	1969
Luzula sylvatica	2	3	2	2	1979–1986
Melica uniflora	2	7	1	1	1948–1986
Potentilla sterilis	1	1	0	0	1979
Veronica montana	1	8	2	3	1948–1957
Total (individuals)		138		64	

and the seed bank was poor. The Sørensen similarity index range for all plots was 0–0.3 (mean 0.1 $\pm$ 0.1, $n = 24$). Mean Sørensen index values for the different management types (ASNW and PAWS) were the same (0.1 $\pm$ 0.1, $n = 12$, Table 2).

Species rarity and presence of AWIS

Twenty-three of the 81 species were represented by a single individual, with 39 species having three or less individuals across the whole study. Trees were poorly represented, with only seven species occurring (numbers of germinating individuals given in brackets): *Acer campestre* (1), *Fraxinus excelsior* (3), *Prunus* sp. (5), *Quercus robur* (1), *Salix caprea* (13), *Salix cinerea* (2) and *Thuja plicata* (2).

Ten species of ancient woodland indicators emerged during the study. Their density and distribution across the two soil depths is given in Table 3. Of the 24 sites sampled, 79% had one or more AWIS individuals in the seed bank (Table 3). The congruence between above-ground AWIS and those in the seed bank was poor with a mean Sørensen similarity index value of 0.1 $\pm$ 0.3, $n = 24$ (Table 2).

Discussion

The results of the study suggest that a rich seed bank exists under both PAWS and ASNW areas, with individuals from 81 species (including 10 ancient woodland indicator species) successfully germinating in open tray conditions. Seedling numbers were broadly similar at the two depths; 3466 seedlings (53%) emerging from the top 11.5 cm of soil, and 3088 (47%) at the lower depth (11.5–23 cm). The seedling density for the four woods combined was $\approx$27300 seeds m^{-2}. This density is within the range recorded for other UK studies in lowland ancient woods; $\approx$700 seeds m^{-2} in abandoned coppice woods (Brown and Oosterhuis 1981) and $\approx$44700 seeds m^{-2} in managed and unmanaged oak stands (Warr et al. 1994), and is comparable to two deciduous woodland studies in Belgium; $\approx$18400 seeds m^{-2} (Godefroid et al. 2006) and $\approx$33500 seeds m^{-2} (Roovers et al. 2006).

The effect of canopy type on seed bank species richness

The two canopy types (ASNW and PAWS) do not explain observed variation in seed bank species richness between closely located sampling sites, despite the differing effects of light and leaf/needle drop. Instead, pH and timing of planting/disturbance emerge as significant factors explaining variation in species richness. These results lend support to the views of Bekker et al. (1997) and Bossuyt and Hermy (2001) that earlier land use and prior management are key factors in determining seed bank composition. Other authors (Augusto et al. 2001; Godefroid et al. 2006) have suggested that silviculture has the greatest effect on seed banks. Godefroid et al. (2006) found canopy conversion exerted effects on the composition and depth of seed banks, although canopy type and depth explained only 12% of variance.

Variables explaining observed species richness

The variance in species richness of seed banks under both ASNW and PAWS areas can be described by a model that explains 40% of the observed variation in species number ($P < 0.00001$, Table 1). The three significant factors are pH, depth in the soil and time since the most recent planting/disturbance event (when two dates are known for a site).

An increase in pH is known to positively affect the species richness of above-ground vegetation (Kirby 1988; Bruelheide and Udelhoven 2005; De Keersmaeker et al. 2004; Eycott et al. 2006b). The current model finds this trend extends to seed banks as well as above-ground vegetation (increasing species richness is observed with increasing pH, $P = 0.0001$). Although the influence of pH on seed banks has been mooted as an important factor by several authors (Brown and Oosterhuis 1981; Devlaeminck et al. 2005; Eycott et al. 2006b), to date it has not been combined with other factors in a model. Brown and Oosterhuis (1981) found a significant positive correlation ($r = 0.58$) between pH and seed bank species numbers in abandoned coppice woods in the UK. They suggested that pH determined the presence of earlier vegetation, which in turn affected the number of species represented in the seed bank. Devlaeminck et al. (2005) and Lewis (1973) suggested that, in addition to other soil properties, pH could influence seed banks through effects on seed preservation. Eycott et al. (2006b) found seed bank species richness showed a positive correlation with pH in Thetford forest (a UK pine-dominated lowland plantation) and Augusto et al. (2001), despite noting that stand type was the main influence on determining species richness, found that under similar stands (oak, pine and spruce), their Haye sampling site (pH 4.8) had greater seed bank species richness than the more acidic woodland of La Petite-Pierre (pH 3.7). These results suggest that in areas where little or no ground vegetation is present, pH could act as a proxy variable to identify areas where seed bank species richness may be relatively higher.

In the present study, depth was highly significant in the model ($P = 0.0001$), with species richness significantly lower at the deeper of the two depths. Brown and Oosterhuis (1981), Bossuyt et al. (2002) and Decocq et al. (2004) found similar results. The effect of depth on the viability and presence of seeds has been linked to three main factors. The first is age, as deeper seeds are likely to be older and therefore more may have senesced (Thompson et al. 1997).

Secondly, seed mass and shape influence the potential for vertical transportation through the soil profile (Bekker et al. 1997; Bossuyt et al. 2002). This may limit large-seeded species (especially tree species) from reaching lower depths. Thirdly, pedoturbation is greater at shallower depths (Willems and Huijsmans 1994; Dostal et al. 2005).

According to the present model, as time increases since the most recent planting/disturbance event, seed bank species richness declines ($P = 0.02$). This suggests that recently planted/disturbed areas harbour greater species richness. During tree clearance and planting, increased canopy openness may permit the establishment of stress-tolerant competitor and ruderal species (Grime 1974; Grime et al. 2007) which contribute large numbers of seeds to the seed bank. The negative effect of time on the survival of seeds in seed banks has been noted by several authors; Warr et al. (1994) found *Picea sitchensis* and *Larix* spp. stands greater than 50 years old were more species-poor than similar 20–30 year-old stands, whilst in upland conifer areas Hill and Stevens (1981) found that some seeds could survive for 50 years, but density declined beyond this and seeds almost completely disappeared after 100 years. Of note in the present study are three sites that contained $\geq$10 species despite a lack of forestry intervention for almost 60 years. Two of these, an oak/ash and a Norway spruce/oak site (4A and 5P, Table 2) planted/disturbed in 1948 and 1949, yielded 18 species (five AWIS) and 12 species (1 AWIS), respectively. This suggests that despite a decline in species richness with time, a number of species are able to persist in the soil regardless of above-ground canopy type.

Species composition

Many woodland seed bank studies have found *Juncus* spp. to be dominant (Kjellsson 1992; Bossuyt et al. 2002: Decocq et al. 2004; Kipfer and Bosshard 2007), with the present study no exception (80% of all emergent seeds were *Juncus effusus*). *Juncus* spp. 'swamping' occurs due to high reproductive output (three million seeds per plant per year, Salisbury 1976) combined with seed longevity of up to 200 years (Kjellsson 1992). Other species with known long persistence, including *Rubus fruticosus*, *Carex sylvatica* and *Hypericum pulchrum* (Kjellsson 1992), were also frequent in this study (second, fourth and sixth most common species respectively). Two of these, *C. sylvatica* and *H. pulchrum*, are ancient woodland specialists that are considered unusual beyond ancient woodland boundaries (Peterken 1974; Rackham 1980). AWIS are slow dispersers and colonisers (Dzwonko and Loster 1992; McCollin et al. 2000), often moving an average of less than 0.1 m year^{-1} (Bossuyt et al. 1999). They are considered to be poorly represented in the seed bank (Brown and Oosterhuis 1981; Bossuyt and Hermy 2001; Decocq et al. 2004). The current study found that ten of the eighty-one species were AWIS, four of which were from the genus *Carex* (Cyperaceae). Of the 24 ASNW and PAWS sites sampled, 79% contained one or more ancient woodland indicator species. In ASNW areas AWIS seed bank species richness ranged from 0 to 5 species, mean 2.2 ± 1.5, $n = 12$, whilst in PAWS areas AWIS species richness ranged from 0 to 3, mean 1.3 ± 1.1, $n = 12$. Positive identification of some AWIS was only possible by potting up individuals for observation in the following year (126 *Carex* individuals were identified to seven species in 2009, four of which were AWIS). Although time (and space) consuming, this method allows an accurate assessment of AWIS in seed banks.

Results of the non-parametric test for composition of seed banks at matched sites across woodland rides showed no significant difference in the number of individuals from each species. This suggests that despite the introduction of non-native conifers into ancient woodlands, the seed banks beneath these stands may harbour similar numbers of seeds and species to seed banks under ASNW stands.

Congruence between above-ground vegetation and the seed bank

The congruence between above-ground vegetation and the seed bank was poor (Table 2), with the Sørensen similarity index values for AWIS even lower. This result is consistent with the findings of others (Bossuyt et al. 2002; Olano et al. 2002; Eycott et al. 2006b). It suggests above-ground vegetation is a poor predictor of the type and density of seeds existing in ancient woodland seed banks under abandoned hazel coppice and conifer PAWS. Despite only 12% of the total species count in the present study being AWIS, their presence (albeit in relatively low densities, Table 3), is encouraging. It suggests that for some AWIS, temporal escape via seed dormancy is possible; two of the ten species (*Carex pallescens* and *Hypericum pulchrum*) were present in stands last disturbed in 1923. As ancient woodland landscapes become more fragmented (thereby limiting spatial movement), understanding which woodland specialists have the potential to escape unfavourable germination conditions through seed dormancy is of increasing conservation interest.

Potential use of the seed bank species richness model

Following the UK's Broadleaves Policy (Forestry Commission 1985a,b), increased value has been placed on deciduous woods, with a move from active PAWS planting to the removal and thinning of conifers (Forestry Commission 2004, 2005). Ground flora recovery through radiation of vegetation from woodland rides offers one source of recharge, however the seed bank offers additional benefits by supplementing genetic variability and introducing genotypes which may carry a memory of past selective conditions (Templeton and Levin 1979).

The model presented here suggests that younger PAWS stands with relatively higher soil pH values may possess seed banks with the greatest species richness. Keeping all other factors constant, it shows soils of pH 4.6 may support seed banks that contain up to 10 additional species over soils of pH 3.6. This increase is not sustained however; with an increase in pH from 4.6 to 5.6 yielding up to only 1.7 extra species (Fig. 2).

Using pH and stand age may allow the selection of sites that have the greatest species richness potential; however the presence of light-demanding competitors and ruderals in these seed banks may lead to the establishment of non-target species such as *Rubus fruticosus* (Bossuyt et al. 2002). This unwanted response, combined with the spatial aggregation of target species and post-seedling mortality (Baeten et al. 2009), means the probability of successfully restoring forest areas from seed banks alone is likely to be low (Bossuyt and Honnay 2008). From an evolutionary selection perspective, this highlights that successfully surviving an extended period in a dormant phase is just the first of many survival filters that species relying on temporal escape must face.

Conclusion

Germinating propagules from soil samples in ex-situ, open conditions over two seasons allows the fullest assessment of ancient woodland seed bank species richness. Micro-site differences in pH emerge as a significant factor explaining species richness. A model including the factors pH, depth and time since recent planting/disturbance explains 40% of the observed variation in species richness. The composition of seed banks under closely located PAWS and ASNW stands are not significantly different, suggesting presence of conifers is less important than past environmental conditions or management. The

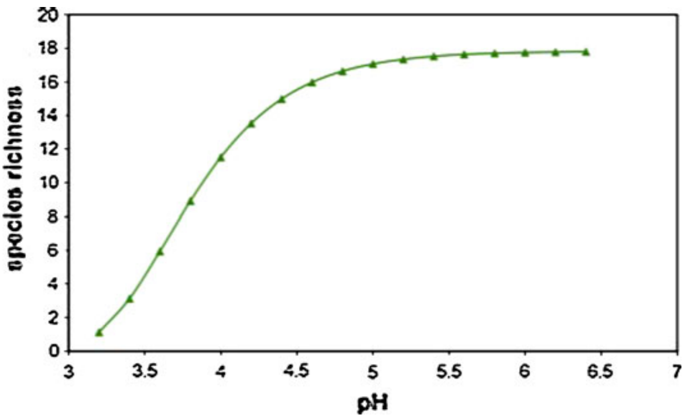

Fig. 2 Change in species richness (ASNW and PAWS sites combined) as pH increases, based on coefficients from GLM (other factors held at mean values)

similarity between extant ground flora and the seed bank is poor, highlighting that above-ground vegetation, or the lack of it, is a poor guide to seed bank species richness. Ten ancient woodland indicator species survived extended periods in the seed bank, although their potential for regeneration may be hampered by the unwanted response from light-demanding species such as *Rubus fruticosus*.

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Appendix

See Tables 4, 5.

Table 4 Earliest documented ages of woodlands in study

	Earliest documented existence	Document type and evidence of earlier occupation
Bucknell Wood	1220	Private wood. Noted as *Boggenhul* in Middle Ages. Part of larger forest associated with Wappenham Wood (no longer in existence) with enclosed pastures
		Middle Bronze Age artefact found to south of wood
Plumpton Wood	1086	Noted in domesday book
Hazelborough Forest (north)	1130	Noted in the Charter of Luffield Priory. Crown-owned wood. Part of the Royal Forest of Whittlewood which included grazing pastures and lawns for deer and cattle
Whistley Wood	1590	Noted on map of 1590. Boundary ditches dated to Iron Age/Roman period 200BC–200AD. Contained deer lawn

Source: Forestry Commission and Wilsden (1915)

Table 5 Species list (81 species)

Species	Total number of individuals germinated	Number of seed trays seeds occur in ($n = 48$)
Acer campestre	1	1
Agrostis capillaris	1	1
Agrostis stolonifera[a]	28	7
Ajuga reptans	29	14
Anthriscus sylvestris	2	1
Cardamine hirsuta[a]	2	2
Carex flacca	1	1
Carex leporina	2	1
Carex nigra	4	2
Carex pallescens[b]	44	11
Carex pendula[b]	1	1
Carex remota[b]	2	2
Carex sylvatica[b]	72	21
Cirsium arvense[a]	6	4
Cirsium palustre	10	4
Cirsium vulgare[a]	4	3
Conium maculatum	1	1
Conyza canadensis[a]	1	1
Deschampsia cespitosa	232	29
Dipsacus fullonum	1	1
Epilobium palustre	4	3
Epilobium parviflorum	2	2
Fraxinus excelsior	4	2
Fumaria officinalis[a]	1	1
Galeopsis speciosa[a]	2	2
Galium saxatile	3	1
Galium uliginosum	56	2
Glechoma hederacea	14	6
Holcus lanatus	6	3
Hypericum humifusum	3	1
Hypericum maculatum	20	2
Hypericum perforatum	11	1
Hypericum pulchrum[b]	54	13
Hypericum sp.	20	7
Isolepis setacea	1	1
Juncus bufonius	11	5
Juncus effusus	5271	48
Lolium perenne[a]	13	5
Lotus pedunculatus	22	7
Luzula campestris	8	7
Luzula multiflora	4	3
Luzula pilosa[b]	4	1
Luzula sylvatica[b]	5	4

Table 5 continued

Species	Total number of individuals germinated	Number of seed trays seeds occur in ($n = 48$)
Lysimachia nummularia	1	1
Melica uniflora[b]	8	3
Melilotus altissimus	1	1
Papavar rhoeas[a]	1	1
Phleum pratense	1	1
Plantago major	4	3
Poa annua	7	6
Poa trivialis	1	1
Polygonum aviculare[a]	2	2
Potentilla sterilis[b]	1	1
Prunus sp.	3	3
Quercus robur	1	1
Ranunculus bulbosus	1	1
Ranunculus repens	2	2
Reseda luteola[a]	1	1
Rubus fruticosus	380	35
Rumex crispus	14	4
Rumex obtusifolius	1	1
Rumex sanguineus	5	4
Salix caprea	13	8
Salix cinerea	2	2
Scrophularia nodosa	41	12
Senecio vulgaris[a]	4	4
Silene latifolia[a]	2	2
Solanum dulcamara	9	5
Sonchus asper	18	14
Stellaria holostea	7	1
Stellaria media[a]	1	1
Thuja plicata	2	1
Trifolium repens	1	1
Urtica dioica	10	3
Veronica chamaedrys	2	1
Veronica montana[b]	11	3
Veronica officinalis	4	2
Veronica polita	1	1
Viola arvensis[a]	1	1
Viola riviniana	4	4
Viola sp.	3	3
Total	6654	

[a] Indicates species eliminated from some analyses to leave 'woodland and wood pasture affinity species' list. Elimination based on species' habitat preference descriptions from Blamey et al. (2003) and Blamey and Grey-Wilson (1989)

[b] Indicates that the species appears on a minimum of 6 of 10 AWIS lists. Note: Thirteen Regional AWIS lists exist, but lists for Carmarthen, North Yorkshire and Angus are excluded for this study (Natural England 2006)

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