Restoration of broadleaved woodland under the 1985 Broadleaves Policy stimulates ground flora recovery at Shabbington Woods, southern England.

Abstract

Forestry policy and practice changes during the 20th Century led to major effects on the composition and structure of Shabbington Woods, southern England. Coppice-with-standards stands were clear-felled during the Second World War and replanted with conifer/conifer-broadleaved mixtures in which the conifer was dominant. Since 1985 broadleaves have been favoured. In 1983 the ground flora had been recorded in six plantation stands of different tree species and compared with three remnant broadleaved stands. Five $200m^2$ quadrats were taken spread across each stand. The survey was repeated using the same methods in 2015 to assess changes. In addition, in 2015, single $200m^2$ quadrats were taken in 21 other stands to put the re-recorded stands into a wider site context. In the nine re-recorded stands, six stands lost species (mean number of species per quadrat) between 1983 and 2015, only three stands gained them. Increases in species richness were associated with management (felling or thinning) or where stands had opened out through wind-throw. Species with higher Ellenberg light scores showed higher turn-over than more shade-tolerant species. In stands recorded only in 2015 oak *Quercus robur* stands derived from formerly conifer-dominant crops, showed a similar richness and species profile to the remnant broadleaved stands. Specialist woodland plants did not appear to be adversely affected by this active management of the stands. The results indicate that in terms of the ground flora at this site the 1985 Broadleaves Policy achieved one of its aims of maintaining/restoring the special character of ancient woodland.

Key Words: ancient woods, broadleaved woodland, coniferization, England, forestry policy, ground flora.

1. Introduction

Forests in western Europe have been managed for centuries with consequential effects on their composition and structure (Kirby and Watkins, 2015). Up until the 19th Century coppice and wood-pasture systems predominated (Buckley and Mills, 2015a,b; Hartel *et al*., 2015), which tended to create relatively open-structured woodland. From the 19th Century onward there was an increasing shift towards the use of high forest systems (Savill, 2015) which produce more closed-canopy, shaded conditions. Native trees and shrubs were frequently felled and replaced by more productive, often introduced species (Spiecker, 2003).

In Britain, this process was particularly intense after the Second World War (Foot, 2010; Rackham, 2003; Tsouvalis, 2000). About 38% of the ancient woods present in 1935 in England and Wales were plantations by 1985, in which the conifers were generally dominant (Spencer and Kirby, 1992). Then, in 1985, national forestry policy changed following pressure by the conservation and amenity sectors (Niemann, 2015).

Under the policy (Forestry Commission, 1985) the special interest of ancient semi-natural woodland was recognised and further conversion of broadleaved stands to conifers largely stopped. Mixed and pure conifer stands started to be restored to native broadleaves (Goldberg, 2003; Thompson and Hope, 2005; Thompson *et al*., 2003). This was given additional impetus by the UK Biodiversity Action Plans (Anon, 1994; English Nature, 1998) and more recent forest policy statements (Forestry Commission, 2005). We show here how Shabbington Woods in southern England illustrate the effects of such changing priorities on the fortunes of ancient woodland in the second half of the 20th Century.

Most forestry management involves manipulation of the woody layers that produce the main economic outputs (timber, fuel, etc) (Evans, 1984). Changes in the composition and structure of the woody layers impact on the ground vegetation which comprises the majority of the vascular plant species in woodland (Gilliam, 2014). For example, the ground flora tends to richer and more extensive in felled or thinned stands than under closed canopy crops; the flora is also usually less under rich under evergreen conifer crops than deciduous broadleaves (Kirby, 1988a; Mitchell & Kirby, 1989; Pigott, 1990).

The ground flora in turn influences patterns of tree regeneration, suppressing it in some situations, but facilitating it in others. Ground flora species affect nutrient cycling through the annual growth and rapid breakdown of their above-ground biomass; and the ground flora provides food and shelter for the fauna, from leaf-mining insects to browsing deer (Gilliam, 2014; Hermy, 2015). Therefore, if we wish to assess the biodiversity consequences of alternative forest management practices (Gotmark, 2013) we need to understand how the ground flora changes under plantations of different tree species, or under different treatments over the decades, even sometimes centuries, that the tree crop may be growing.

The changes in management that happened in the Shabbington Woods in southern England - from coppice with standards to conifer-dominated plantations, to restored broadleaved stands - are typical of what happened to ancient woodland through much of the rest of the country. Detailed historical information was available on these changes during the 20th Century at Shabbington in Thomas (1987,1988). We combined this with field surveys of the vegetation under different stands carried out in 1983 (Kirby, 1988a) and 2015 to determine the impact of shifts in forestry policies on the ground flora in particular. We sought to address the following specific questions:

- How had the composition (broadleaves versus coniferous crops) of the forest changed in response to shifting forestry policy and practice in the 20th Century;
- What were the effects on the structure of different stands, in terms of tree, shrub and ground flora cover;
- What were the patterns of the ground flora richness under different stand types;
- Were light-demanding species more likely than shade-tolerant species to show high turnover over time; did nitrogen-demanders increase; were the numbers of woodland specialists more likely to change than non-woodland species;
- Did the flora of stands where conifers had been removed show similar ground flora species composition to remnant broadleaved stands which had never been through a coniferous phase?

2. Site and Methods

2.1 Site description and management history

Shabbington Woods (1^{o}6’20” west, 51^{o}47’41” north; altitude range 72-91m) lie on gently rolling topography, about 10 kilometres north-east of Oxford. The underlying geology is primarily Oxford Clay, giving rise to heavy, poorly-drained, mainly acid soils (pH 4.0) (Kirby, 1988a). The woods cover 285 ha and are mostly ancient (Peterken, 1977). Most stands were managed as coppice or coppice-with-standards in the 19th Century (mainly oak *Quercus robur* L. over hazel *Corylus avellana* L. understorey), but this had ceased by 1900 (Thomas, 1987).

The woods were bought by Magdalen College (University of Oxford) in the 1920s and 1930s and about a quarter was replanted between 1937 and 1941 with various coniferous crops including Norway spruce *Picea abies* (L.) Karsten, pines *Pinus* spp., Lawson's cypress *Chamaecyparis lawsoniana* (A.Murray) Parl. and larch (*Larix* spp.). The College sold the woods in 1943 and much of the timber and the remaining coppice were then cut-over. The Forestry Commission acquired the woods in 1950/51 and planted them up during the next 10 years with conifers or conifer-broadleaved mixtures (Elton, 1942-1965; Thomas, 1988), again using mainly Norway spruce, pines and Lawson's cypress. Following the change in national forestry policy in 1985 (Forestry Commission, 1985) the conifers started to be thinned out.

The woods, though modified by planting, fall mainly into the British National Vegetation Classification *Quercus robur-Pteridium aquilinum-Rubus fruticosus* type (W10) with the more base-rich areas referred to the *Fraxinus excelsior-Acer campestre-Mercurialis perennis* type (W8) (Rodwell, 1991). The site was notified as a Site of Special Scientific Interest by the Nature Conservancy Council in 1981 (Natural England, 2016) primarily for its rich invertebrate fauna associated with the woodland edges and rides (Sparks *et al*., 1996)

2.2 Crop type and age class in 1950, 1980, 2010

The proportions of broadleaved and conifer crops in 1950, 1980 and 2010 in different age classes were compared (Table 1). The state of the woods in 1980 and 2010 was taken directly from contemporary Forestry Commission stock maps which give the main tree species and stand areas. The area of stands described as mixed conifer-broadleaved was allocated equally between the broadleaved and coniferous components. Three small areas that had not been replanted had a nominal 'planting' date of 1920 or 1940 on the 1980 stock map. The 1950 estimate was based on back-extrapolation from the 1980 stock map, supported by the field sheets from the 1947 forestry census (HMSO, 1952), notes from Thomas (1987) and entries from Charles Elton's diaries (Elton, 1942-65).

2.3 Ground flora survey 1983, 2015

In 1983 the ground flora in nine stands was investigated (Table 2a, Figure 1) as part of a study of plantation vegetation (Kirby, 1988a). There were three remnant broadleaved stands (mainly oak *Quercus robur*, some birch *Betula* spp. over hazel *Corylus avellana*). Five c.43 year-old plantations were chosen to explore the effects of different tree species on the vegetation (a beech *Fagus sylvatica* L. stand, a larch *Larix* sp. stand with mixed broadleaves, a mixed stand of spruce *Picea abies* and oak, a pine *Pinus sylvestris* stand, and a Lawson's cypress *Chamaecyperis lawsoniana* stand). A pre-canopy closure spruce was surveyed to show the vegetation of open, felled areas. These stands covered 35 ha (12% of the wood). Species were recorded from five 200 m^2 (14.1x14.1 m) quadrats distributed across each stand (Kirby, 1988a) with at least 50 m between each sampling position. The original quadrat positions were not marked, but in 2015 the survey was repeated using a similar distribution of quadrats. Replicate stands of each crop type were not available so differences assigned to crop type are confounded with stand location. However, the differences at stand boundaries were sharp, suggesting that the stand effect was the major cause of the differences observed.

The 2015 survey was extended to include a further 21 quadrats recorded from the rest of the woods (Figure 1) covering all but three compartments (omitted because they were impenetrable). In each compartment, a quadrat was taken in the middle of the main crop type present. Three stands were had recently been felled/part felled; eight stands were still predominantly coniferous; and ten stands had been conifer or conifer-broadleaved mixtures in 1980 but were now predominantly broadleaved.

Within each quadrat the total covers of the overstorey (more than 5 m high), understorey (2-5 m high) and ground flora (< 2 m) were estimated on a percentage scale. The cover of individual tree and shrub species cover was estimated using the 1-10 Domin scale (Supplementary Table 1) (Rodwell, 1991). All vascular plants in the ground flora were listed and assigned a cover value, again using the Domin scale.

Species names follow Stace (2010). In both 1983 and 2015 the surveys took place in the period 30th May to 15th June so that vernal species should be equally well-represented in both years. All species recorded are listed in Supplementary Table 2.

2.4 Data analysis

For the re-surveyed stands (recorded in both 1983 and 2015) the mean percentage covers of the overstorey and understorey were calculated. Differences between stands and over time were tested for significance using ANOVA for each layer separately. The Domin cover scores for trees and shrubs were converted to percentages using the mid-point of the range for each class to compare the overall cover of broadleaves and conifers in the re-surveyed quadrats in 2015 with 1983. For the extra stands recorded only in 2015 the mean cover by vegetation layer and by main tree species was calculated for the coniferous (8 quadrats), broadleaved (10 quadrats) and recently felled (3 quadrats) groups separately.

The mean percentage ground flora cover and species-richness per quadrat for 1983 and 2015 were similarly compared, using ANOVA, for the re-surveyed stands between stands and over time. The analysis of patterns in the ground flora (excluding tree and shrub regeneration) used presence/absence data because most species were recorded only at low cover (<4% in any one quadrat). However, separately, the cover of the five most abundant species across the woods was examined by converting Domin scores to percentage cover using the midpoint of the Domin range.

Ellenberg Scores (Ellenberg, 1988; Hill *et al*., 2004) for light and nitrogen were assigned to each species. These scores – on a 10-point scale – reflect a species ability to tolerate shade, or low nutrient conditions. Species were grouped according to their scores, for Light (L) (shade-tolerant score 1-5, more light-demanding 6-10) and for nitrogen (N) (score 1-5 tolerant of low nitrogen soils, or more demanding, score 6-10). Plant species were also classed, according to their broad affinity to woodland habitats: as woodland specialists, woodland generalists or non-woodland species (Kirby *et al*., 2012). Turnover of species in these different groupings between survey times was explored by looking at how many species in each group were recorded in both as opposed to only one survey. Comparisons were tested using chi-squared analysis.

The flora in the extra quadrats in 2015 that were predominantly broadleaved, but had been largely coniferous in 1983 (restored stands) was compared in terms of species richness, numbers of woodland specialists, and Ellenberg score profiles with the flora of the three re-surveyed remnant oak stands.

3. Results

3.1 Changes in the balance of broadleaves versus conifers

In 1950 the wood was largely broadleaves (92%) and less than 20 years old (Table 1) because of the felling and coppicing that had taken place in the Second World War (Thomas, 1987, 1988). The 1947 Forestry Census field sheet confirms that large areas were scrub or coppice, with much birch *Betula* spp. and few standards. The young conifer areas (6%) were from Magdalen College's 1930s plantations

The techniques used over the next 15 years by the Forestry Commission to replant the woods (Thomas, 1987) included aerial spraying and stem injection of 2,4,5-T to kill broadleaved trees (Stoakley, 1962). A first-hand description (Elton, 1942-1965) of the state of the woods in 1963 notes: '29 June 1963. We were mainly on and in the edges of Shabbington, York and Oakley Woods. The woods are a shocking sight after hormone-killing of the trees. Gaunt dead trunks by the thousand, a moss carpet below with large new *Holcus* tussocks scattered, and 1-2 ft. spruces'. By 1980 76% of the woods were coniferous.

By 2010, however, the conifer component had been reduced back to 42% of the canopy (Table 1). The change back towards broadleaves presented is a conservative estimate: some stands shown as mixed on the 2010 stock map had very little conifer left in them. The open areas (20%) include felled areas that will be regenerated as broadleaves and a meadow (5 ha) planted with spruce in the 1950s that has been returned to open meadow.

The age structure of the wood has changed from the dense young stands in 1950 (95 % <20 yrs); to mainly pole-stage crops (63% 20-40 yrs) in 1980; to mainly young-mature crops (73% >40 years old) in 2010 (Table 1).

3.2 Changes in the cover of different layers

Not surprisingly, the differences in overstorey and understorey between stands and over time were significant; but the strong interaction term indicates that the changes were stand specific (Table 2a; ANOVA table Table 2b). Two remnant oak *Quercus robur* stands (12a, 26d) showed increases in the overstorey percentage cover, in one case (26d) accompanied by a decline in the understorey. The third (14a) showed regrowth of the understorey following the coppicing that had taken place early in 1983 (Table 2a).

The beech *Fagus sylvatica* plantation (17c) showed little change in the overstorey, but unlike under the oak stands there was no understorey in either year. The *Larix*-broadleaved mixture (36a) showed a small decline in the overstorey, but by 2015 a dense understorey (64%) had developed in places of hazel *Corylus avellana* and sweet chestnut *Castanea sativa* regrowth from the stumps of thinned-out trees.

Thinning of the 1939 stand of *Chamaecyparis lawsoniana* (18e) resulted in a reduction in its overstorey (91 →72%) , and probably led to the increase in the understorey (9→ 38%) (Table 2a). The 1939 stand dominated by Norway spruce *Picea abies* (23b) in 1983 had similarly lost much of its conifer overstorey and gained in understorey (1→ 44%) and field layer covers by 2015 (3→35%). By contrast the 1973 Norway spruce crop (32a) which was still very open in 1983 had closed over by 2004, reducing the field layer (personal observation). By 2015 it had started to open-out again through thinning and wind-throw, but, though more than in 2004, understorey (29→9%) and ground flora (100→61%), were still less than in 1983. The 1939 *Pinus sylvestris* stand (23c) showed little change in the estimated cover of the overstorey between 1983 and 2015 but the depth, and hence shadiness, of that cover had increased. Underplanted western hemlock *Tsuga heterophylla* and western red cedar *Thuya plicata* had grown up amongst the pines.

In line with the stock map analysis (Table 1) the re-surveyed stands had more broadleaved cover (particularly oak *Quercus robur*) while the conifers declined (Figure 2a). The broadleaved stands recorded only in 2015 were dominated in the overstorey by oak with some birch *Betula* spp. (Figure 2b), little understorey (<10%), but a high ground flora cover (>70%) (Table 2a). In the conifer stands, Norway spruce *Picea abies* was the most common tree species, there was little ground flora cover (<20%) (Table 2a) and few species.

3.3 Changes in ground flora

As with the overstorey and understorey, differences in ground flora cover and richness were significant between stands and richness also significant over time (Table 2a, ANOVA result 2b), but also in both cases stand specific. The species richness-per-quadrat in the re-surveyed stands was similar in the two recordings (range 5-27 species in 1983, 2-25 species in 2015), but six stands lost species whereas only three showed a gain (Table 2a). The six stands where species-richness declined tended to show large increases in either overstorey, or understorey cover. The three stands where species-richness increased included one oak stand (26d) which had lost some of its understorey because of deer browsing; the P39 Lawson's cypress stand (18e) recently thinned in 2015; and the P39 spruce-oak stand (23b) which had had recent wind-throw. The species-richness of the groups of stands surveyed only in 2015, was similar to that found in the equivalent re-surveyed stands.

97 species were recorded in the nine re-surveyed stands (85 in 1983, 72 in 2015; see Supplementary Table S2). Five (*Brachypodium sylvaticum, Calamagrostis epigejos, Deschampsia cespitosa, Hyacinthoides non-scripta, Rubus fruticosus)* made up half of the total cover. None of these five averaged more than 10% cover at either recording date in the densest conifer stands. *Calamagrostis epigejos* was particularly characteristic of felled stands and large gaps in stand 36a in 2015. *Hyacinthoides non-scripta* dominated the ground flora in the beech stand, but otherwise had only low cover. *Rubus fruticosus* showed high cover in 1983 in the Scots pine stand which then had a relatively open canopy, and in the extra broadleaved stands in 2015; *Deschampsia cespitosa* had high cover in the relatively open spruce-oak stand 32a. *Brachypodium sylvaticum* increased its cover across most stands.

3.4 Changes in different groups of species

Species with high Ellenberg light scores (6-10), often non-woodland species, were more likely to be recorded in only one of the survey years, suggesting higher turn-over for these species. The more shade-tolerant species, often woodland specialists, tended to be present in both surveys (Figure 3a,c). There was no significant pattern to the Ellenberg nitrogen (N) scores (Figure 3b).

3.5 Remnant oak and restored oak stands compared

The extra quadrats recorded in 2015 in what are now predominantly broadleaved stands (restored stands) showed similar species profiles to those of the three remnant oak stands included in the 1983 and 2015 surveys, with respect to Ellenberg Light and Nitrogen scores, and species type (Figure 4).

4. Discussion

4.1 Changes in species-richness and disturbance through the forest cycle

The ground flora is not constant over the forest growth cycle: under gaps species-richness may increase and individual species increase their growth and flowering. Richness may decline again and species revert to a mainly vegetative state as conditions become more shaded. In Britain, this has been well-described for the flora under coppice regimes, e.g. Ash and Barkham (1977), Barkham (1992), Rackham (2003), Salisbury (1924). There have however been few comparable accounts of long-term changes in the flora of coppice developing into high forest or under plantations on ancient woodland sites (Brown and Oosterhuist, 1981; Buckley and Mills, 2015a).

In the Shabbington Woods and in a parallel study at Salcey Forest (Northamptonshire) (Kirby *et al*. 2017) reductions in species-richness at the quadrat were observed in more stands than showed gains in species. This parallels declines reported for largely-unmanaged broadleaved woods across England based on a comparision of records from 1971 and 2001 (Kirby *et al*., 2005), and at Sheephouse Wood which was sampled more regularly from 1981 to 2012 (Kirby, 2015). Species losses tended to be high amongst the more light-demanding, non-woodland species. This is consistent with a response to increasing shadiness associated with stands in the young-mature phase of a high forest cycle, and parallels changes in mature coppice stands.

The 'lost' species are likely to survive elsewhere in the Shabbington Woods in rides and glades managed to benefit the butterflies (Sparks *et al*., 1996; Buckley *et al*., 1997b; Natural England, 2016). In Lincolnshire Peterken and Francis (1999) found that 60% of the ground vegetation species were strongly associated with open space. Other 'lost' species may survive as buried seed (Brown and Warr, 1992; Buckley *et al*., 1997a; Van Calster *et al.,* 2008).

Increases in species-richness at the quadrat level were found in the Shabbington Woods where there had been recent canopy disturbance through thinning, felling or windthrow. This was also the case at Salcey Forest and Sheephouse Wood. Species-richness also tended to be maintained in woods affected by the 1987 great storm against the trend for woods elsewhere in the country (Smart *et al*., 2014).

Elsewhere small-scale disturbances such as single tree or group-selection felling have been reported to increase species-richness in the ground vegetation compared to unmanaged stands (Harris and Kent, 1987; Brunet *et al.,* 1996; Graae and Heskjær, 1997; Falk *et al.,* 2008). However, Godefroid *et al.* (2005) and Hannerz and Hånell (1997) found that the abundance of some vascular plant species, such as *Oxalis acetosella, Dryopteris* spp. was reduced more by clear-felling than from less drastic disturbances to the tree canopy, such as selection-type cutting.

4.2 Has broadleaved woodland restoration benefitted the ground flora?

The change in forestry policy in 1985 has led to large areas of both state and private ancient woodland (Pryor *et al*., 2002; Spencer, 2002) being put under restoration to native broadleaves. However, at the time of the policy change there was little published evidence as to whether this would reverse the reduction in the ground flora richness or abundance, seen in many coniferous/mixed plantations (Kirby, 1988a; Pigott, 1990; Mitchell and Kirby, 1989) compared to broadleaved stands.

Kirby and May (1989) found increases in species richness and ground cover in the first few years in restored stands at Dalavich Wood in Argyll, suggesting that restoration could be successful. Similarities between restored and remnant oak stands in terms of species richness and the type of species present have since been found at Salcey Forest, Northamptonshire, in a parallel study to this one (Kirby *et al.,* 2017). There was little indication at Salcey that woodland specialists had changed in abundance differently to other species and at Shabbington Woods the specialists were the most likely group to be found in both surveys.

Conditions at Salcey and Shabbington were probably particularly favourable for floral recovery. Opening up of the stands at Shabbington Woods and Salcey Forest occurred within about 50 years of canopy closure, so that the buried seed flora would still be reasonably diverse (Brown and Oosterhuist, 1981; Brown and Warr, 1992). Some species may have survived in the oak rows (Kirby, 1988a; Simmons and Buckley, 1992). The oak rows would also have provided some protection for the vegetation against heavy disturbance during felling and extraction of the conifers.

It remains to be seen how well the woodland specialist flora copes in future in the clear-felled stands recorded in 2015 at Shabbington Woods where the quadrats were dominated by *Calamagrostis epigeos*. In a study in north-eastern France Augusto *et al*. (2001) considered that up to 86 % of the native deciduous forest vegetation could be restored from the seed bank under coniferous species, but some plants typical of ancient forest might disappear during the coniferous stage. Brown *et al*. (2015) visited 104 stands (39 sites) being restored to broadleaves from conifers in 2001 and 2009 and found that most had lost plant species by the latter date. Shade-adapted species (specialists) declined more, the greater the degree of canopy opening.

The difference between the results reported here and for Salcey Forest, and those of Brown *et al*. (2015) may be partly due to differences in the survey methods used. Brown *et al*. (2015) used a different definition of 'specialist'; they also looked-for species across the whole stand. If some specialist species were present only as one or two individuals in a stand they might be lost without this being detected in the quadrats which sample a smaller area. Walking across the whole stand increases the number of species detected compared to quadrat sampling (Kirby, 1988b), but it is more difficult to relate such qualitative records to changes in the stand structure/composition.

Ground flora species might have been lost during the felling and replanting of Shabbington Wood in the 1950s. However, a visit in 1931 by Appleyard (reported in Thomas, 1987) records 32 species of which all but one (*Prunella vulgaris*) were found in this study (Supplementary Table S2). Common species in 2015, apart from *Brachypodium sylvaticum,* were all noted as locally abundant in the Forestry Commission's descriptions of the woods in the 1950s. We consider therefore that the current flora probably includes the majority of those species present at the beginning of the 20th Century.

4.3 Implications for future management of the Shabbington Woods

The management done since the 1980s has encouraged the re-development of an oak woodland flora in stands that had appeared to be almost solid conifers in the 1980s. Dense bramble layer (*Rubus fruticosus*) development following thinning was noted by Harmer *et al*. (2005, 2012) and provides a partial substitute in structural terms for the lack of a shrub layer. This is likely to favour the shade-tolerant woodland specialists over more light-demanding competitive species (woodland generalist and non-woodland species).

Future planned felling and replanting of the remaining conifer stands should lead to further diversification of the age structure of the woods. Diversification of the woody layers is also likely through natural regeneration of aspen *Populus tremula*, birch *Betula* spp., hazel *Corylus avellana,* wild service *Sorbus torminalis* and locally field maple *Acer campestre*. Even in the conifer stands the current cover of birch, oak and other broadleaves (c.16%, Figure 2b) suggests a potential to restore them to predominantly broadleaved cover in future.

Other potential changes over the next thirty years include the following.

- Closure of the overstorey and re-development of an understorey in the restored oak stands, may reduce the vegetation cover and species-richness at the quadrat level. Therefore, it would be desirable to vary the thinning regimes between stands to encourage/maintain structural diversity.
- Unlike many woods in the English midlands Shabbington Woods have relatively little ash *Fraxinus excelsior* in the canopy and so should not be too affected by Ash Dieback (Pautasso *et al*., 2013). However Acute Oak Decline (Denman *et al*., 2014) would pose a serious threat to the woodland structure and composition of the woods if it develops on the site.
- Increasing deer populations in southern England (Ward, 2005) probably contributed to the increase in grasses such as *Brachypodium sylvaticum* as at Wytham Woods (Kirby and Thomas, 2000). Blocks have been fenced against deer in the past, but maintaining the fences has proved problematic. Deer control needs to continue.

- Increased nitrogen deposition, for example following the opening of a nearby motorway in 1991, may affect the flora although it can be difficult to separate this out from the larger changes associated with changed levels of shading (Verheyen *et al.* 2012). Maintaining closed canopy stands may reduce the impacts, by keeping light rather than nitrogen as the limiting factor.
- Climate change will have an increasing impact (Kolström *et al*., 2011), although the ground vegetation will be partially buffered against the more extreme changes through the cooler, more humid microclimate under the canopy (De Frenne *et al*., 2013). Again maintaining closed stands may offset, at least temporarily, the climate change impacts on the ground flora.

Overall this study confirms that declines in ground flora species-richness may occur in stands left unmanaged, largely because many of these stands are entering the young-mature phase of the high forest cycle. Where some disturbance occurs, typically through felling or thinning, the ground flora may increase in richness. At least at Shabbington Woods a flora typical of broadleaved woodland can recover from episodes of several decades during which it had been largely suppressed by a dominant conifer crop. This provides evidence, that the restoration of broadleaved woodland encouraged under the Broadleaves Policy (Forestry Commission, 1985; Leslie, 2014) has been successful in terms of the ground flora where intervention has occurred.

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Figure legends

Figure 1. Stands included in the survey: the numbers are based on the 1983 Forestry Commission stock map; squares show those surveyed in both 1983 and 2015; triangles those surveyed in 2015 only. Details of the stands are given in Table 2a.

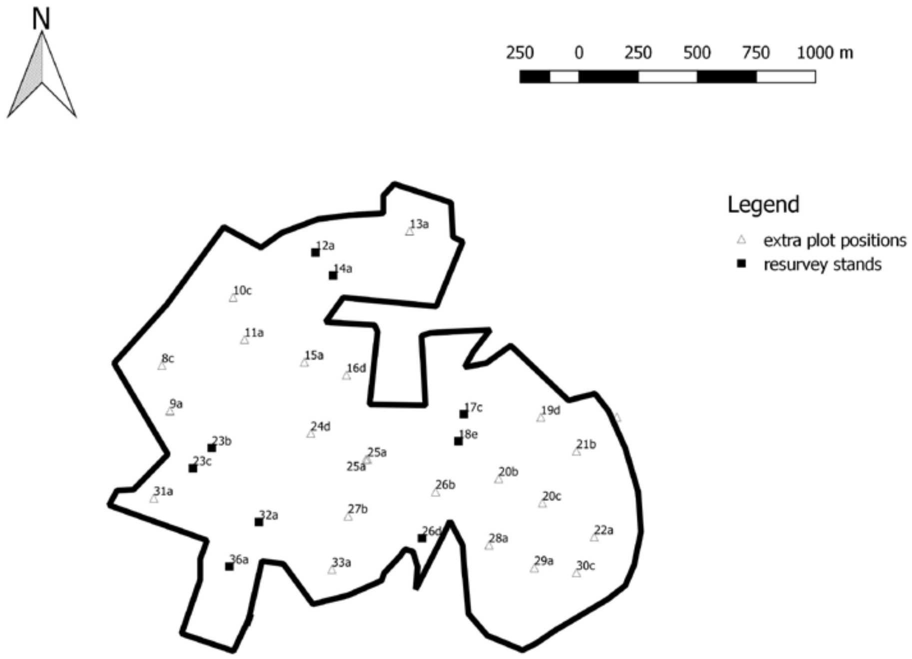


Figure 2. Overstorey composition in (a) the re-surveyed stands and (b) stands sampled only in 2015.

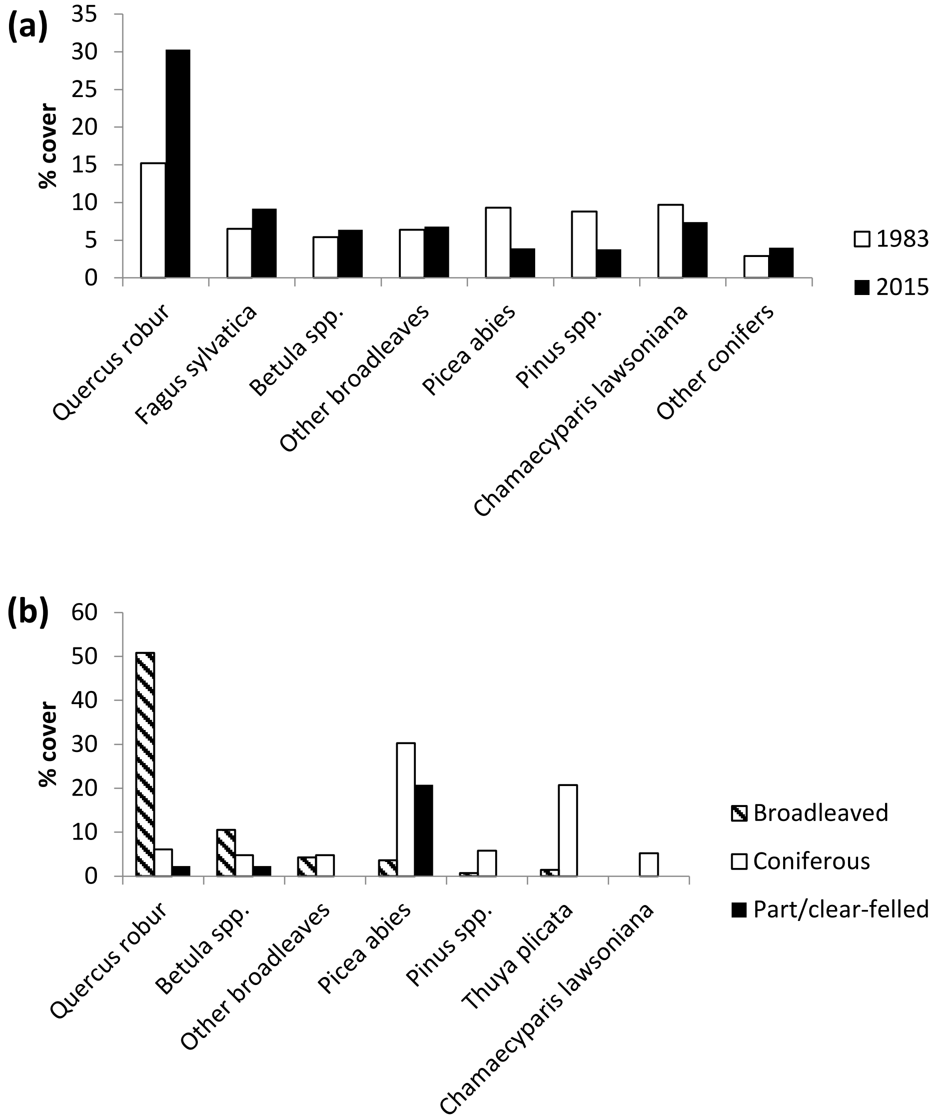
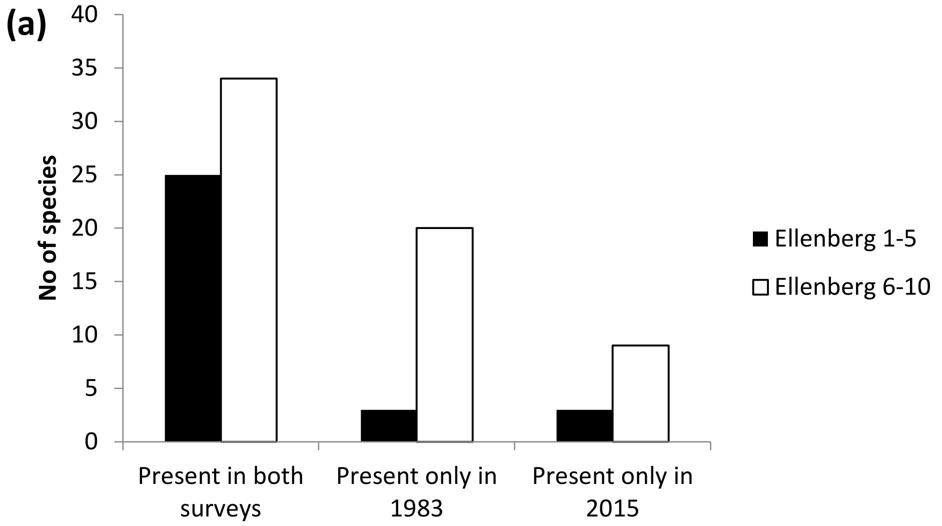
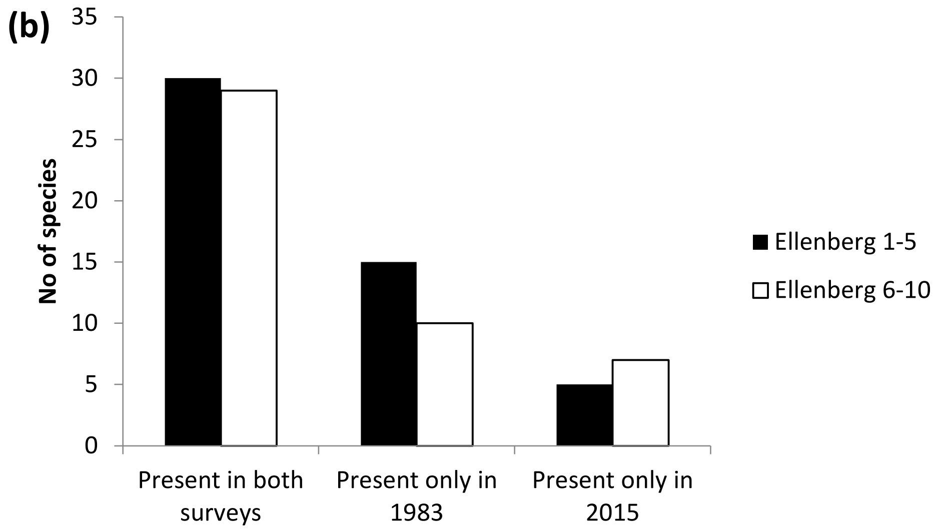
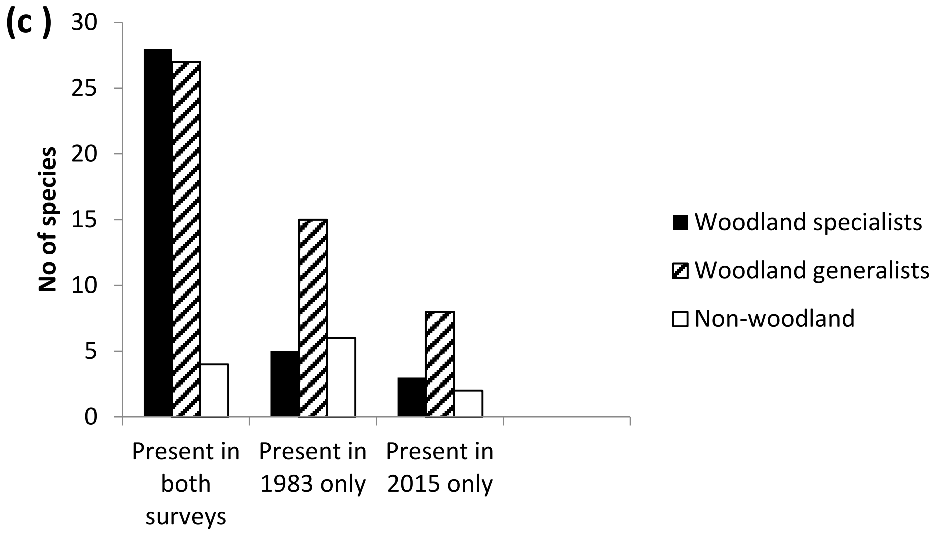


Figure 3. Characteristics of species recorded in both surveys, in 1983 only, or in 2015 only based on: (a) Ellenberg Light Scores, (b) Ellenberg Nitrogen scores, (c) Species type (after Kirby *et al.* 2012).

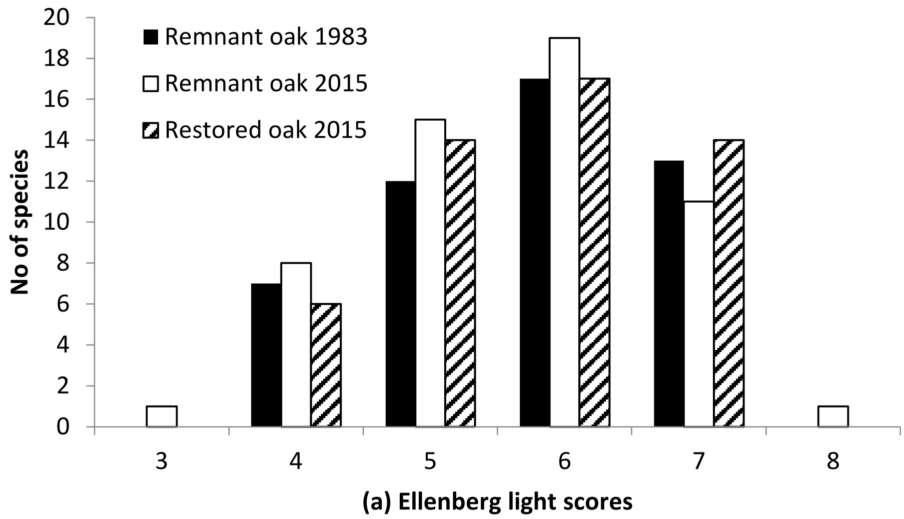


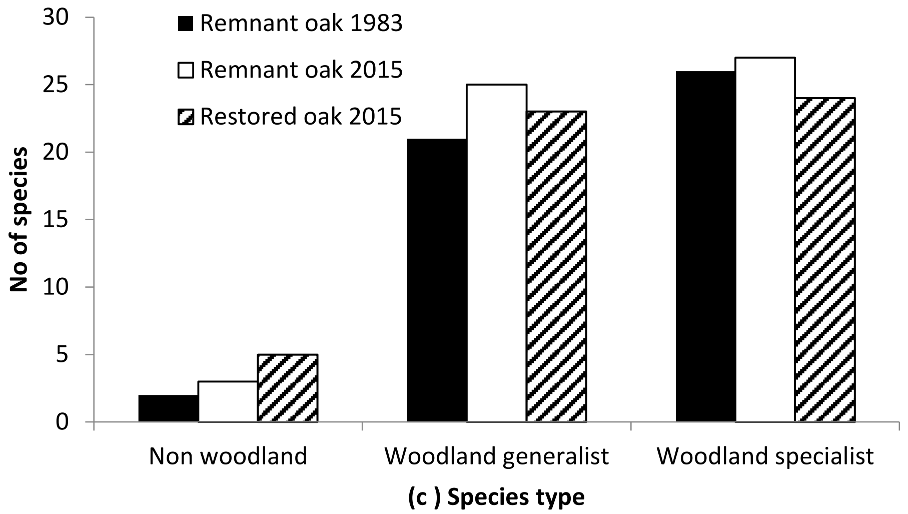




Low (1-5) versus high (6-10) Ellenberg light (L) scores Chi-squared =6.8, DF = 2, P = 0.03*; Low (1-5) versus high (6-10) Ellenberg Nitrogen (N) scores Chi-squared = 1.2, DF = 2, P= 0.5 ns; Species type (non-woodland, woodland generalist, woodland specialist) Chi-squared = 9.5, DF = 4, P=0.05*

Figure 4. Species profiles in the remnant and restored oak stands compared for (a) Ellenberg light scores; (b) Ellenberg Nitrogen scores; (c) Species type (Non-woodland species, Woodland Generalists and Woodland specialists).




Remnant oak 1983
Remnant oak 2015
Restored oak 2015
No of species
30
25
20
15
10
5
0
Non woodland
Woodland generalist
Woodland specialist
(c) Species type

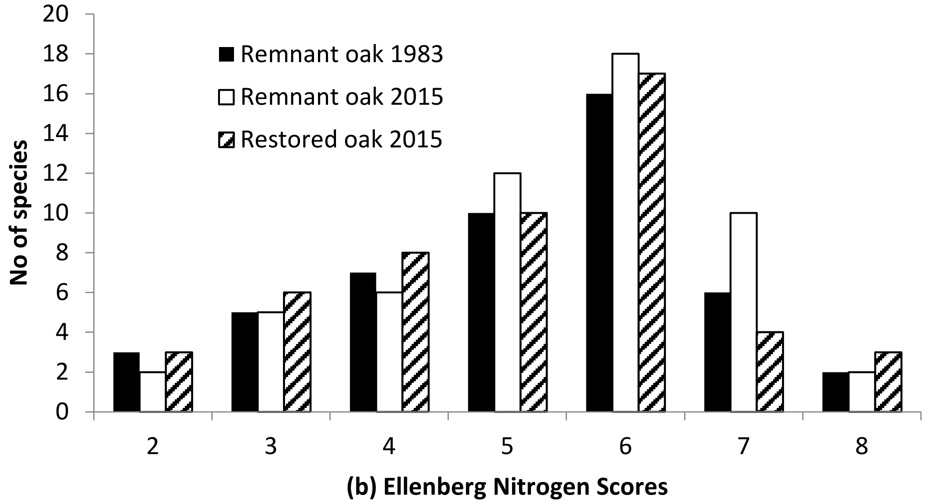

Remnant oak 1983
Remnant oak 2015
Restored oak 2015
No of species
20
18
16
14
12
10
8
6
4
2
0
2
3
4
5
6
7
8
(b) Ellenberg Nitrogen Scores

Table 1. Extent of broadleaves and conifers of different age classes in c.1950, 1980, 2010

	Extent (ha) of broadleaved and coniferous crops by age class					
Crop age (yrs)	1-20	21-40	41-60	61-80	Total Area	% of total
1950						
Broadleaves	253	8			261	92
Conifers	18				18	6
Open					5	2
1980						
Broadleaves	1	40	27		68	24
Conifers	59	140	17		216	76
Open						0
2010						
Broadleaves	4	3	54	48	109	38
Conifers	5	4	98	10	117	42
Open					58	20

Table 2 (a) Composition and structure of the stands surveyed: mean and standard errors for overstorey and understorey cover, with changes of >20% cover emboldened; mean and standard errors for ground flora cover and species-richness.

	Crop	Main woody layer change 1983-2015	Age in 1983	Extent (ha)	No of quadrats	Tree and shrub layer				Ground flora			
						Overstorey cover %	Understorey cover%	Overstorey cover %	Understorey cover%	Cover %		Richness (spp.no)	
Re-survey stands						1983	2015	1983	2015	1983	2015	1983	2015
Broadleaves in 1983													
12a	P20 oak		63	9	5	**44 ±2**	**72±6**	62±2	52±7	**11±2**	**36±10**	13.6±2	9.6±1
14a	P40 oak	U/storey regrowth	43	5	5	52±12	60±3	**0**	**66±7**	27±6	33±9	19.0±2	11.8±1
26d	P30 oak		53	2	5	**34±4**	**56±4**	**76±2**	**56±5**	**36±10**	**56±5**	18.4±4	25.2±2
17c	P37 beech		46	3	5	96±2	93±2	7±4	4±1	53±14	70±14	8.4±1	2.8±0.5
Mixed mainly broadleaved in 1983													
36a	P39 Larch/ash/oak	Thinning/ u/storey	44	5	5	88±3	70±9	**9±4**	**64±8**	81±4	62±14	21.8±2	15.4±3

		growth											
Mainly conifer in 1983													
18e	P39 Lawson's cypress	Thinning	44	3	5	**91±3**	**72±4**	5±0	7±2	**9±1**	**37±8**	9.8±1	13.6±1
23b	P39 Spruce/oak	Thinning/wind-throw	34	3	5	**99±1**	**64±6**	**1±1**	**44±9**	**3±1**	**35±12**	5.4±2	14.8±5
32a	P73 Spruce	Canopy closure /thinning	10	4	5	**3±1**	**68±6**	**29±3**	**9±2**	**100**	**61±14**	26.8±2	20.2±3
23c	P39 Scots pine	U/planting grwoth	44	3	5	90±4	85±3	4±2	24±9	**75±5**	**10±4**	22.0±1	5.6±2
Stands recorded in 2015 only													
Part/clear-felled[1]		Felling	varied	12	3		23±23		27±13		72±21		22.3±6
Coniferous[2]			"	26	8		77±4		11±6		17±6		8.6±2
Broadleaved[3]		Thinning	"	35	10		74±4		8±3		73±7		22.1±2

[1]Quadrats in felled or partly felled stands 15a, 19d, 21b (formerly Norway spruce, planted 1954-1959)

[2] Quadrats in conifer dominated stands 8c, 11a 13a, 20d (Norway spruce planted 1956-1962), 10c (Scots pine planted 1958), 16d (Lawson's cypress planted 1959), 27b, 31a (western hemlock planted 1960)

[3]Quadrats in broadleaved stands 20b, 22a, 24d, 26b, 28a, 29a, 30c, (formerly Norway spruce-oak mixtures planted 1954-1958); 9a, , 33a (formerly Norway spruce planted 1960-1962 but with oak regrowth); 25a (formerly Lawson's cypress-oak mixture planted 1939).

Table 2b. ANOVA details for comparisons of layer cover and ground flora richness from the re-surveyed stands.

		Overstorey cover			Understorey cover			Ground flora cover			Ground flora richness		
Factor	DF	SS	F ratio	Sig.	SS	F ratio	Sig.	SS	F ratio	Sig.	SS	F ratio	Sig.
Stand	8	33926	34.7	***	36724	39.4	***	40765	12.9	***	2669	13.8	***
Year	1	514	4.2	*	4855	41.6	***	18	0.05	ns	1901	7.9	**
Interaction	8	18239	18.6	***	21331	22.9	***	2303	7.4	***	1314	6.8	***
Error	72	8800	18.7		8396			28371			1738		
Total	89	61478			71306						5912		

DF Degrees of Freedom, SS sum of squares, Sig. Significance ***P<0.001;** P<0.01; * P<0.05; ns non significant

Supplementary Table S1. Domin score (Rodwell, 1991)

Domin score	Cover range
1	< 4%, few individuals
2	<4%, several individuals
3	<4% many individuals
4	4-10%
5	11-25%
6	26-33%
7	34-50%
8	51-75%
9	76-90%
10	91-100%

Supplementary Table S2. Ground flora species recorded and their characteristics (Kirby et al., 2012; Hill et al., 2004).

Scientific name	1 Non-woodland, 2 woodland generalist, 3 woodland specialist	On Brown et al. 2015 specialist list	Ellenberg light score	Ellenberg nitrogen score	No of records in re-surveyed stands 1983 (45 quadrats)	No of records in re-surveyed stands 2015 (45 quadrats)	No of records in extra stands recorded in 2015 only (21 quadrats)	Recorded in Hell Coppice and York Wood, May 1931, from Thomas (1987)
WOODLAND SPECIALISTS								
Anemone nemorosa	3		5	4	30	13	2	*
Arum maculatum	3	1	4	7	6	4	0	
Athyrium filix-femina	3		5	6	1	1	0	
Brachypodium sylvaticum	3		6	5	31	38	16	
Bromopsis ramosa	3	1	4	7	5	1	0	
Betonica officinalis	3		7	3	7	0	1	
Calamagrostis epigejos	3		7	6	10	22	13	
Carex pendula	3	1	5	6	0	0	1	
Carex remota	3	1	4	6	2	9	6	
Carex sylvatica	3	1	4	5	27	28	9	*
Euphorbia amygdaloides	3	1	4	6	8	10	4	*
Fragaria vesca	3		6	4	5	0	0	*
Geranium robertianum	3		5	6	3	6	3	
Holcus mollis	3		6	3	22	10	12	
Hyacinthoides non-scripta	3		5	6	32	26	4	*
Hypericum hirsutum	3		6	5	3	6	4	*
Hypericum pulchrum	3		6	3	8	8	8	
Hypericum tetrapterum	3		7	4	0	1	1	
Lamiastrum galeobdolon	3	1	4	6	6	11	0	*
Lonicera periclymenum	3	1	5	5	31	32	13	
Luzula pilosa	3		5	3	27	10	6	

Luzula sylvatica	3		5	4	0	1	0	
Melampyrum pratense	3		5	3	0	3	2	
Mercurialis perennis	3		3	7	6	2	0	
Milium effusum	3	1	4	5	4	4	4	
Moehringia trinervia	3	1	4	6	4	0	1	
Neottia ovata	3		6	5	1	0	0	*
Poa nemoralis	3	1	4	5	3	0	0	*
Potentilla sterilis	3	1	5	5	8	7	4	*
Primula vulgaris	3		5	4	22	7	3	*
Schedonorus gigantea	3		5	7	11	3	0	
Scrophularia nodosa	3		5	6	4	10	7	*
Stachys sylvatica	3	1	6	8	7	5	3	
Stellaria holostea	3		5	6	5	5	7	
Tamus communis	3	1	6	6	3	2	1	
Valeriana officinalis	3		6	5	4	3	2	
Vicia sepium	3		6	6	0	0	3	
Viola riviniana	3		6	4	38	22	6	*
WOODLAND GENERALISTS								
Agrostis capillaris	2		6	4	1	0	0	
Agrostis stolonifera	2		7	6	21	18	15	
Ajuga reptans	2	1	5	5	7	11	6	*
Alliaria petiolata	2		5	8	1	0	0	
Angelica sylvestris	2		7	5	3	1	0	
Anthoxanthum odoratum	2		7	3	14	10	12	
Anthriscus sylvestris	2		6	7	0	1	0	
Arctium minus	2		6	5	2	0	0	
Arrhenatherum elatius	2		7	7	3	1	4	
Cardamine flexuosa	2		5	6	0	1	1	
Carex hirta	2		7	6	2	0	0	
Carex riparia	2		7	7	1	0	1	*
Chamerion angustifolium	2		6	5	4	0	0	*

Circaea lutetiana	2		4	6	9	5	4	
Cirsium palustre	2		7	4	4	2	3	*
Cirsium vulgare	2		7	6	1	0	0	
Dactylis glomerata	2		7	6	11	13	11	
Deschampsia cespitosa	2		6	4	39	40	18	*
Digitalis purpurea	2		6	5	0	1	3	
Dryopteris dilatata	2		5	5	15	7	13	
Dryopteris filix-mas	2		5	5	12	9	8	
Epilobium hirsutum	2		7	7	0	3	0	*
Epilobium montanum	2		6	6	4	4	0	
Festuca rubra	2		8	5	3	1	0	
Ficaria verna	2		6	6	5	6	1	*
Filipendula ulmaria	2		7	5	1	2	0	*
Galium aparine	2		6	8	10	12	8	
Galium palustre	2		7	4	0	7	2	*
Geum urbanum	2	1	4	7	5	4	0	
Glechoma hederacea	2		6	7	6	7	5	*
Holcus lanatus	2		7	5	1	0	0	*
Juncus conglomeratus	2		7	3	1	0	0	*
Juncus effusus	2		7	4	18	17	16	
Lapsana communis	2		6	7	1	0	0	
Luzula multiflora	2		7	3	1	1	5	
Myosotis arvensis	2		7	6	2	0	0	
Poa annua	2		7	7	1	0	0	
Poa trivialis	2		7	6	19	10	7	
Potentilla erecta	2		7	2	6	4	5	
Potentilla reptans	2		7	5	1	2	0	
Pteridium aquilinum	2		6	3	1	0	0	
Ranunculus repens	2		6	7	0	1	0	*
Rosa canina	2	1	6	6	23	16	4	
Rubus fruticosus	2		6	6	34	32	20	

Rumex sanguineus	2	5	7	10	9	10	
Scrophularia auriculata	2	7	7	0	0	1	
Senecio sylvaticus	2	7	6	0	0	2	
Solanum dulcamara	2	7	7	0	2	1	
Stellaria media	2	7	7	0	1	0	
Succisa pratensis	2	7	2	2	0	0	
Taraxacum officinale agg.	2	7	6	0	0	1	
Urtica dioica	2	6	8	3	3	9	
Veronica officinalis	2	6	4	11	0	0	*
NON-WOODLAND SPECIES							
Alopecurus pratensis	1	7	7	3	0	0	
Carex flacca	1	7	2	3	10	2	
Carex otrubae	1	6	7	0	1	3	
Carex pilulifera	1	7	2	2	4	6	
Cerastium fontanum	1	7	4	0	0	1	
Cirsium arvense	1	8	6	3	0	0	
Glyceria spp	1			0	1	2	*
Hieracium spp	1			1	0	0	
Lathyrus pratensis	1	7	5	2	3	0	
Lotus pedunculatus	1	7	4	2	2	0	
Luzula campestris	1	7	2	5	0	0	
Polygala vulgaris	1	8	3	1	0	0	
Senecio jacobaea	1	7	4	0	0	1	
Vicia cracca	1	7	5	1	0	0	