

# Long-term changes in the flora of oak forests and of oak:spruce mixtures following removal of conifers

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## Abstract

Ground vegetation changes under coppice regimes have been well described but less work has been done in Britain on the changes that take place under managed high-forest. In 1982/3 sixty 14.1 x 14.1 m quadrats were recorded across stands of oak (*Quercus robur* L.) and spruce (*Picea abies* (L.) H.Karst.)/oak mixtures, of various ages in Salcey Forest, southern England. In 2014 the survey was repeated and changes in the ground flora over this 31 year period in the different crop types were compared. There was a decline in the species richness (number of species per quadrat) in most stands, mainly of species with a high Ellenberg light score, even under mature oak (>100 years old) where no intervention had taken place. Plant species richness increased in stands that had been felled or heavily thinned. The flora of stands where the spruce had been removed leaving a predominantly oak canopy had become similar in richness and individual species frequency to the mature oak crops, supporting the case for restoration of plantations on ancient woodland sites. The changes in the frequency of Woodland specialist plants were similar to those for other woodland species.

**Key words:** understorey vegetation, plantations, conifer, broadleaved, Ellenberg values, Woodland specialist plants

## Introduction

As trees grow they change the local environment around and below them, affecting the associated biodiversity (e.g. Hunter, 1990). Thus at any one point the vegetation will vary in its abundance and composition over the lifetime of the trees above it (Gilliam, 2014; Hermy, 2015). In Britain many broadleaved woods were managed for centuries as coppice (Rackham, 2003; Buckley and Mills, 2015a) and the changes in species composition and richness over the coppice rotation (generally less than 30 years) have been well-described (Ash and Barkham, 1976; Ford and Newbould, 1977; Buckley and Mills, 2015b).

During the twentieth century many former coppice stands developed through deliberate intervention, or neglect, into high-forest. The area of broadleaved woodland has steadily increased in Britain since 1947, but the area of coppice is now less than a fifth of what it was then (Hopkins and Kirby, 2007; Forestry Commission, 2012). In such high-forest stands there are likely to be fewer opportunities for species that depend on survival as buried seed during the closed canopy phase of coppice (van Calster *et al.*, 2008). The periods of dense shade may be longer in unmanaged or even-aged stands (Baeten *et al.*, 2009); or the frequency of interventions may be greater, but each intervention less severe, where the stands are regularly thinned or selectively felled (Decocq *et al.*, 2004).

Other former coppices were converted to plantations dominated by non-native conifers between 1935 and 1985 (Spencer and Kirby, 1992). In these there was a change in tree species type as well as in forest structure. While the initial felling in such conversions might boost plant richness in ways comparable to a coppice cut, the flora then tended to become impoverished once the conifer canopy closed as a result of increased shade and a change in litter type (Kirby, 1988; Mitchell and Kirby, 1989; Pigott, 1990).

A change in forestry policy in 1985 reversed the trend for conifer conversion in broadleaved woods; many stands that had been so converted are now being restored to native broadleaves (Forestry Commission, 1985; Goldberg, 2003; Thompson *et al.*, 2003; Foot, 2010). There can be rapid recovery of woodland vegetation cover within a few years after such restoration begins (Kirby and May, 1989); in a study in France Augusto *et al.* (2001) considered that it would be possible to restore up to 86 % of the native deciduous forest vegetation from the seed bank under coniferous species. However, these latter authors also found that some plant species typical of ancient forest may have disappeared during the coniferous stage, especially under Norway spruce (*Picea abies* (L.) H.Karst.) and Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco). Brown *et al.* (2015) similarly noted some loss of species even where stands were restored to native broadleaves gradually and concluded that specialist plants were particularly affected. Godefroid *et al.* (2005) found that some forest species (such as *Carex remota*, *Circaea lutetiana*, *Dryopteris dilatata*, *Oxalis acetosella*) declined in clear-cuts in old beech high forest in Belgium. Studies in eastern North America have also found that the flora may take more than a century to recover after clear-felling (Wyatt and Silman, 2014).

In this study changes in the flora in a large forest in southern England were explored through a comparison of surveys carried out in 1982/3 and 2014. The objectives were to examine:

- how the age structure and composition of the forest changed in response to forestry policies;
- whether the richness of the flora of mature (> 100 year-old) high-forest plantations dominated by oak (*Quercus robur* L.) changed and, if so, what types of species were involved;
- whether the flora of mixtures of Norway spruce and oak that developed after the removal of the spruce was similar to that of mature (> 100 year-old) oak plantations;
- whether the species that increased in the more open stands were the same as those that declined where stands became more shaded;
- whether there was a difference in the trends for Woodland specialist plants (Kirby *et al.*, 2012) compared to more generalist species?

Although based on a single-site this study is unusual in providing a long-term test of the effectiveness of aspects of a major change in forestry policy. The outcomes can inform the implementation of forestry policy and practice in lowland England and be relevant to discussions about the management of forest biodiversity elsewhere in Europe. Analogous patterns may be seen in the herbaceous layer of forests in eastern North America (Gilliam, 2014), although the different history of land-use limits direct comparisons.

## Site

Salcey Forest is a large (489 ha) wood straddling the Northamptonshire-Buckinghamshire county boundary (National Grid Reference SP 810513; 52°09' north, 0°49' west) in southern England. The site is located on a gently undulating plateau at 100-130 m altitude. The solid

geology is of Jurassic oolitic limestone producing imperfectly-drained brown clay soils of moderate to high fertility.

Salcey Forest is ancient woodland, i.e. it is believed to have been wooded since at least AD 1600 (Spencer and Kirby, 1992). It was formerly a royal hunting forest consisting of a series of coppices around a central deer lawn. In the mid-nineteenth century (nominally 1847) the site was re-planted with oak which developed into high-forest stands of oak over hazel understorey (*Corylus avellana* L.). Some of these stands were felled and replanted, mainly with oak, in the first decades of the twentieth century. The Forestry Commission initiated a more active programme of felling and replanting after the Second World War, with a particular emphasis on mixtures of oak and Norway spruce.

The dominant vegetation type in the mature broadleaved stands is *Fraxinus excelsior*-*Acer campestre*-*Mercurialis perennis* woodland (W8) in the British National Vegetation Classification (Rodwell, 1991). Ash (*Fraxinus excelsior* L.) might therefore be expected to have a stronger presence in the canopy and the current levels of oak are in part a consequence of it being favoured by past management.

## Methods

### *Changes in the age structure and broadleaved/conifer balance*

The proportions of broadleaved and conifer crops in the forest were determined for c.1900, 1940, 1980 and 2010. The state of the wood in 1980 and 2010 was estimated directly from Forestry Commission stock maps which give the main tree species and compartment areas. The 1940 and 1900 estimates were based on back-extrapolation from the 1980 stock map, assuming that all twentieth century plantings were derived from felling of 1847 oak stands: discussions with the local forest managers and others involved with the site in 1982 indicated that this was the case.

The area of mixed conifer-broadleaved stands was split equally between the broadleaved and coniferous components. This probably under-estimates the contribution of the conifers in young crops: more conifer rows than broadleaves were generally planted and the faster-growing conifers tended to dominate the early canopy. On the other hand, the conifer contribution may be over-estimated from the recent stock-map, because during the 2014 survey some stands classed as mixed appeared to have very little conifer left in them.

### *Field surveys*

In 1982/3 the first author and colleagues from the then Nature Conservancy Council recorded 60 14.1x14.1 m (200 m<sup>2</sup>) quadrats in 22 compartments spread across the wood (Figure 1, Table 1). In 2014 the authors repeated the 1980s survey. The original quadrat positions were not marked but the same compartments were sampled with the same number and size of quadrats as in 1982/3. In both surveys quadrats in the same compartment were located at random and at least 50 m apart.



**Figure 1.** Distribution of stands surveyed according to 1982 compartment numbering which is used throughout this paper (Table 2, column 3).

**Table 1.** Extent of the crop types included in the 1982/3 field survey

Crop type	Total extent in forest (ha)	Stands sampled 1982/3		
		Extent (ha)	No of compartments	Total no of quadrats
1847 oak plantations	119	35.0	5	10
1900s oak plantations	72	24.5	5	10
1930s oak plantations	30	5.5	1	5
1970s oak plantations	21	9.5	1	5
1940s Norway spruce/oak mixtures	58	38	5	10
1950s Norway spruce/oak mixtures	34	22	3	10
1970s Norway spruce/oak mixtures	19	18	2	10

Within each quadrat visual estimates were made of the overall percentage cover of the ground flora layer, the understorey layer (roughly 2-5m high), overstorey layer (>5m high). These data were used in interpreting recent management changes, but the main interest was the change in the ground flora composition.

All vascular plant species were listed and assigned a cover score using the 10-point Domin scale (Rodwell, 1991). In the analyses tree and shrub regeneration were excluded and the following simplifications of the data made to account for potential effects of differences in the timing of the surveys and in the skills of the surveyors (Kirby *et al.*, 1986).

- The 1982/3 surveys were done in May-June, whereas the 2014 survey had to be in August to fit in with other work. Records for early spring species that were not detected at all in 2014 were therefore excluded from the analyses (*Conopodium majus* 2 records, *Ranunculus auricomus* 10, *Ranunculus ficaria* 27). Records for *Arum maculatum* and *Hyacinthoides non-scripta* were retained in the analysis because these

species were detectable in 2014 from the dead flower stalks, but their frequency and abundance may have been underestimated.

- The different surveyors may not have recorded species consistently across the two surveys. Records for the following species pairs were amalgamated as follows (number of records involved): *Hypericum maculatum* was combined with *H. tetrapterum* (1), *Holcus lanatus* combined with *H. mollis* (9), *Poa nemoralis* combined with *P. trivialis* (9) *Ribes nigrum* combined with *R. rubrum* (4) and *Rubus caesius* combined with *R. fruticosus* (4).

Between them these two adjustments affected only 66 out of over 2700 records. Throughout the paper plant names follow Stace (1991).

## Data analyses

### *Changes in species occurrence across the two surveys*

The total number of species found across the sixty quadrats at each survey date was compared and the most frequent species listed.

The frequency with which a species was recorded in 2015 was plotted against its frequency in 1982/3 and three groups distinguished. Species which had 10 or fewer records across both surveys combined were classed as ‘scarce’. Species with more than 10 records across the two surveys were split into those showing a decline in the number of quadrats in which they were recorded of at least 10 occurrences - classed as ‘declining’ species - and those showing little difference (<10) in frequency between the two survey periods were classed as ‘stable’ species. No species showed large increases in recorded frequency.

Ellenberg light scores, as modified for British conditions (Hill *et al.*, 2004), were used to help interpret possible causes of the changes taking place. Differences between survey times in the numbers of species recorded with high (6-10) or low (1-5) scores were tested for statistical significance using chi-squared comparisons. Similarly differences in the light scores of the ‘declining’ versus ‘stable’ or ‘scarce’ species were examined.

Species were classified as Non-woodland species, Woodland generalists, or Woodland specialists using the approach described by Kirby *et al.* (2012). The Woodland specialist list was derived from a combination of different ancient woodland indicator lists. Differences between survey times in the numbers of species in each category were tested for statistical significance using chi-squared comparisons; and again separately the characteristics of the ‘declining’ versus ‘stable’ or ‘scarce’ species were compared. Plant Strategy Types (Grime *et al.*, 2007) were also noted (Supplementary Table S1) but no clear patterns emerged with respect to these.

Brown *et al.* (2015) used a different definition of specialist plants, although in terms of the species found in Salcey Forest most of their species are also in the Kirby *et al.* (2012) Woodland specialist list (Supplementary Table S1).

### *Comparisons between compartments and crop types in terms of species richness and composition*

The 1982/3 survey had been designed to look at the difference between a range of crop types and ten quadrats each were allocated to compartments representing 1847 oak, 1900s oak, 1940s oak-spruce, 1950s oak-spruce, 1970s oak-spruce stands (Table 1; Kirby, 1988): together these crop types made up about 70% of the Forest. Where only two suitable compartments were available for a particular crop type (stands less than 2 ha were generally avoided because of potential edge effects) five quadrats were recorded in each; where there

were more compartments up to five were sampled with two to four quadrats in each, so as to give ten quadrats in total. In 1983 five quadrats each were recorded in compartments planted with oak in 1935 and in 1971 to complement the previous year's work.

By 2014 the original 1982 groupings of compartments were no longer useful as a basis for comparisons because not all compartments in a group had been treated in the same way in the intervening years: for example, while four of the 1847 oak compartments had been left untouched during this time, one had been felled and replanted. Therefore, initially the changes in species-richness were examined at the compartment level.

For each compartment the mean species richness (number of species per quadrat) was calculated based on the 2 to 5 quadrats recorded in that compartment in each survey. This allowed us to consider changes in richness that might be the result of interventions specific to that compartment, independently of the changes that might or might not be happening in other compartments that had been the same crop type in 1982/3. Change in the spatial distribution of species-richness between 1982/3 and 2014 was noted by looking at where the richest quadrats had been in 1982/3 compared to where the highest richness occurred in 2014.

The compartments were then grouped, and groups compared, according to the general pattern of intervention that had occurred between 1982/3 and 2014 (Table 2).

- Eight mature (>100 years-old) oak stands had had little intervention either immediately prior to the 1982/3 survey or the 2014 survey. This consisted of four compartments of oak planted in 1847 and four compartments of 1900s oak. As the least disturbed parts of the forest over this period changes in species-richness and in the species character were expected to be the least.
- Four compartments of 1940s oak-spruce mixtures were being thinned in 1982/3 and had by 2014 been restored to almost pure oak stands.
- Four compartments in 1982 were pre-canopy closure or open because of recent thinning; these had become more closed by 2014;
- Six compartments that had been closed canopy in 1982 had gone through an open phase between then and 2014, either following felling and replanting, or recent heavy thinning.

To explore the degree of recovery of the vegetation in the four 1940s oak-spruce mixture compartments their mean species richness was compared with the four 1847 oak stands and the four 1900s oak stands using a one-way ANOVA. Sorensen's Similarity Index (Moore and Chapman, 1986) was then used to test how close the vegetation composition was under these restored oak stands compared to the 1900s and 1847 mature oak stands using the 2014 records. Each comparison was based on the combined list (total count) from the two quadrats recorded in each of the different compartments. The index was then calculated as follows.  $\text{Similarity (\%)} = (2C) * 100 / (A+B)$  where A and B are the total number of species recorded in the two compartments being compared; C is the number of species that are common to the two lists.

Each of the four 1847 mature oak compartments was compared with the other three 1847 mature oak compartments (six comparisons in total) to estimate the mean percentage similarity within that crop type; the same process was followed for the four 1900s oak compartments and the four 1940s restored oak compartments.

262 **Table 2** Details of compartments and how they were categorised

1982/3 crop planting year	Extent (ha)	Compartment no 1982/3	2014	No of quadrats	Mean spp no per quadrat 1982/3      2014		State 1982/3	State 2014	Comment
<i>Mature oak, little/no intervention 1982/3-2014</i>									
1847	3.0	1a	2037a	2	25.0	10.5	Mature oak/hazel	As 82	These stands were mature oak (with occasional ash) in the canopy, with generally a well-developed understorey of hazel and other shrubs; ground flora generally covering more than half the quadrat. By 2014 there appeared to be more areas of extensive litter with little vegetation cover.
1847	9.5	22	2035b	2	38.0	24.5	Mature oak/hazel	As 82	
1847	7.0	27	2039b	2	25.5	15.5	Mature oak/hazel	As 82	
1847	8.0	54a	2049b	2	29.0	19.0	Mature oak/hazel	As 82	
1908	6.0	16b	2033f	2	31.0	23.5	Mature oak	As 82	The stands consisted of tall, thin-crowned oaks forming a more or less closed-canopy, over a scattered understorey of hazel and other shrubs, and a well-developed ground flora. The general structure was similar in 2014, but the ground flora cover was more patchy.
1905	2.0	21b	2035g	2	35.0	14.0	Mature oak	As 82	
1906	7.5	34b	2042d	2	34.0	15.5	Mature oak	As 82	
1904	2.0	41a	2045g	2	25.5	12.5	Mature oak	As 82	
<i>Restored young oak plantations derived from mixed Norway spruce-oak plantings</i>									
1944	12.0	3b	2037b	2	22.0	16.5	Row mixture, oak/NS,part thinned	Now mainly oak	These stands were planted as alternating bands of oak (5 rows), spruce (5 rows) with 1-2 m between rows and 1-2 m spacing within rows. The ground flora was sparse in unthinned stands, mainly surviving under the oak component. However where thinning was underway in 1982/3 the ground flora had already started to increase in cover and richness. Removal of the most of the spruce by 2014 left an oak dominated canopy with well-developed ground flora cover.
1943	10.0	8c	2032b	2	29.0	20.0	Row mixture, oak/NS part thinned	Now mainly oak	
1944	1.0	16a	2033i	2	37.0	18.0	Row mixture, oak/NS part thinned	Now mainly oak	
1945	7.0	50b	2046d	2	34.0	24.0	Row mixture, oak/NS part	Now oak/hazel	

thinned

*Stands with open canopies in 1982/3 that had become more closed by 2014*

1931	5.5	35a	2042c	5	32.2	10.4	Recently thinned oak, little understorey	Closed oak over dense hazel	This compartment was planted with oak and had had a well-developed understorey of hazel and other shrubs. In 1982/3 these had been coppiced and the overstorey lightly thinned. The ground flora layer was extensive and dominated by tall grasses. By 2014 the understorey had regrown and the ground flora cover was much reduced.
1979	10	12f	2034a	5	46.2	10.8	Row mixture, oak/NS; pre canopy-closure	Pole stage dense canopy; oak/NS	These stands were planted as bands of 2 rows oak, 3 rows spruce, but in 1982/3 had not yet closed canopy. There was extensive cover of tall grasses and scramblers such as <i>Rosa</i> spp. and <i>Rubus fruticosus</i> . By 2014 the stands were closed-canopy, with few gaps, little if any understorey, or ground flora cover.
1977	8.5	15a	2033e	5	21.8	7.6	Row mixture; oak/NS; pre canopy-closure	Pole stage dense canopy; oak/NS	
1973	9.5	36a	2042a	5	30.0	16.0	Pre canopy-closure oak.	Closed canopy	This compartment was planted with oak in bands of 5 rows with strips of c5 m left unplanted between bands for natural regeneration. By 1982/3 the oak had not closed canopy and the ground vegetation was extensive and dominated by tall grasses. By 2014 the gaps between the rows had filled with self-sown ash and <i>Salix</i> spp.; there was a more-or-less complete tree layer cover, a developing understorey layer, but the ground flora cover was less extensive.

*Stands which went through a more open phase between 1982/3 and 2014*



1847	7.5	47a	2049c	2	27.5	26.0	Mature oak over hazel	Felled/replanted; oak-birch 1984	In 2014 compartment 47a (felled and replanted 1984) consisted of a dense growth of young planted oak and birch ( <i>Betula</i> spp.) with a well-developed ground flora.
1915	7.0	7b	2032c	2	24.5	29.5	Mature oak	Recent heavy thinning	Canopy open following recent heavy thinning; ground vegetation forming almost full cover.
1947	8.0	51b	2047d	2	13.0	20.5	Row mixture, oak/NS Unthinned	Spruce thinned out; now oak/hazel	Planted as alternating bands of oak (5 rows), spruce (5 rows) with 1-2 m between rows and 1-2 m spacing within rows; ground flora was very sparse, surviving mainly under the oak component; it had spread widely by 2014.
1955	7.5	42a	2045b	3	18.3	19.3	Row mixture, oak/NS	Felled, replanted oak/pine, p98	These stands were planted as bands of 2 rows oak, 3 rows spruce, but often the oaks had died. In 1982/3 there was little shrub layer and only a very sparse ground flora (mainly under gaps where a tree had died or under the oak where it survived). The compartments sampled were all felled and replanted in 1998 with oak and some <i>Pinus</i> spp. By 2014 they also included much self-sown ash and a variety of shrubs with a well-developed ground flora cover.
1957	6.5	44c	2047a	3	14.3	24.7	Row mixture, oak/NS	Felled, replanted ash p98.	
1956	8.0	52	2047a	4	13.2	23.5	Row mixture, oak/NS	Felled, replanted ash p98.	

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Each 1847 oak compartment was then compared separately to each of the four 1900s oak compartments (16 comparisons in total) to obtain a mean similarity between 1847 and 1900s oak stands, i.e. similarity across crop types. This process was repeated comparing each 1847 oak compartment with each of the four 1940s restored oak stands (16 comparisons in total); and finally each of the four 1900s oak compartments was separately compared with each of the four 1940s restored oak stands (16 comparisons in total). The mean values for these three sets of comparisons were then compared by one-way ANOVA.

### ***Species change where major increases or decreases in richness occurred***

The two groups of compartments which had major interventions either just before the 1982/3 recording or just before the 2014 survey collectively showed the biggest gains and losses of species-richness per quadrat between 1982/3 and 2014 (Table 2). The frequency of each species in 2014 was plotted against its frequency in 1982 for each of these groups of compartments separately to determine whether all species declined/increased uniformly. The change then was expressed in terms of the difference in the percentage number of quadrats in which a species occurred (i.e out of 20 quadrats for the compartments which closed over during the intervening period, and out of 16 quadrats for those that had an open phase during this period). A one-way ANOVA was used to test whether the mean percentage change differed for the two groups of compartments for all species. The mean change for the different species groups (Non-woodland, Woodland generalist, Woodland specialist) within each group of compartments was tested separately, again using one-way ANOVA.

All analyses were carried out using Excel and Minitab packages.

## **Results**

### ***Changes in the age structure and broadleaved/conifer balance***

In 1900 the forest would have been mostly young (c.53 year-old) oak stands. By 1940 the felling and replanting had affected about a third of the wood, but virtually all was still broadleaved (Table 3). In 1980 slightly less than a quarter of the original 1847 plantings survived (now c.130 years old) and young conifers covered about a third of the Forest. By 2010 there had been a further slight decline in the extent of 1847 oak stands, the conifer area had reduced and in particular there were far fewer young conifer stands. From being composed of a single age-class of young broadleaves in 1900, by 2014 a very wide range of age classes were present (Table 3).

**Table 3.** Extent (ha) of different crops and ages in 1900, 1940, 1980 and 2010

Age class (years)	1-20	21-40	41-60	61-80	81-100	101-120	121-140	141-160	161-180	Total extent	%
1900 broadleaved	0	0	489	0	0	0	0	0	0	489	100
1900 coniferous	0	0	0	0	0	0	0	0	0	0	0
1940 broadleaved	39	91	0	0	353	0	0	0	0	483	99
1940 coniferous	0	6	0	0	0	0	0	0	0	6	1
1980 broadleaved	38	49	40	92	0	0	117	0	0	336	69
1980 coniferous	102	48	3	0	0	0	0	0	0	153	31
2010 broadleaved	23	80	23	98	56	26	0	0	99	405	83
2010 coniferous	4	19	57	1	3	0	0	0	0	84	17

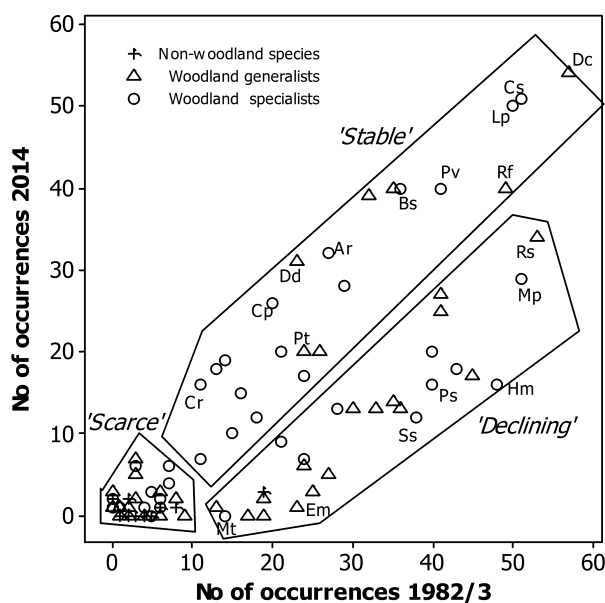
### Changes in species occurrences across the two surveys

101 species were recorded across all 60 quadrats in 1982/3 compared to 74 species in 2014 (Supplementary Table S.1).

The list included 35 species that were only recorded in the first survey and 8 only recorded in the second period. Most of these species were present in 3 or fewer quadrats in the year in which they were recorded (23 out 35 from 1982/3; all 8 from 2014). Notable exceptions were *Taraxacum officinale* (19 records), *Chamerion angustifolium* (17 records) and *Moehringia trinervia*, (14 records), all from 1982/3.

The most frequently recorded species were (in 1982/3 and 2014, with occurrences out of 60 in each case): *Brachypodium sylvaticum* (36,40), *Carex sylvatica* (51,51), *Circaea lutetiana* (32,39), *Deschampsia cespitosa* (57,54), *Dryopteris filix-mas* (35,40), *Lonicera periclymenum* (50,50), *Mercurialis perennis* (51,29), *Primula vulgaris* (41,40), *Rosa* spp. (53,34), *Rubus fruticosus* (49,40).

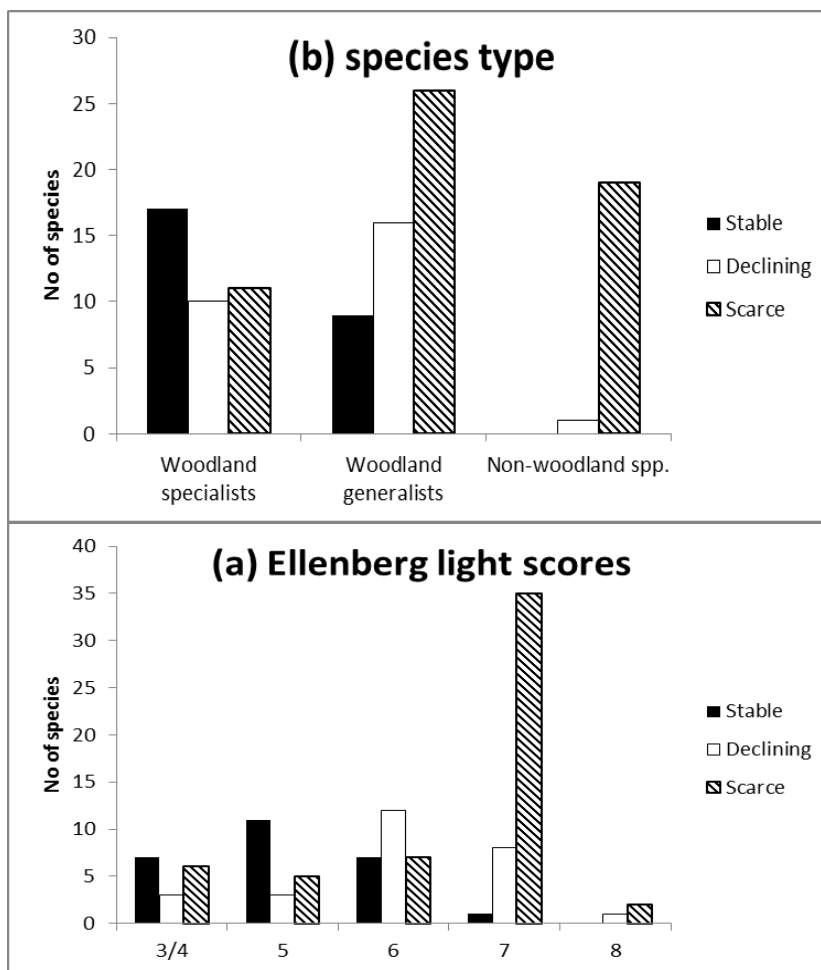
The number of quadrats in which a species occurred in 2014 was plotted against that for 1982/3 with the three groups of species (scarce, stable, declining) distinguished (Figure 2).



**Figure 2.** Species frequency in 2014 compared to that for 1982/3 for all quadrats.

Selected species marked: Ar *Ajuga reptans*, Bs *Brachypodium sylvaticum*, Cp *Carex pendula*, Cr *C. remota*, Cs *C. sylvatica*, Dc *Deschampsia cespitosa*, Em *Epilobium montanum*, Hm *Holcus mollis*, Lp *Lonicera periclymenum*, Mp *Mercurialis perennis*, Mt *Moehringia trinervia*, Ps *Potentilla sterilis*, Pt *Poa trivialis*, Pv *Primula vulgaris*, Rf *Rubus fruticosus*, Rs *Rosa* spp., Ss *Stachys sylvatica*. Non-woodland species, Woodland generalists and Woodland specialists are based on Kirby *et al.* (2012).

There were highly significant differences (Figure 3) between the groups in terms of the numbers of Woodland specialists, Woodland generalists and Non-woodland species (chi-squared = 31, degrees of freedom 4,  $p < 0.001$ ) and in the distribution of Ellenberg light scores (for number of species with score of 6-10 versus scores of 1-5 chi-squared = 21, degrees of freedom 2,  $p < 0.001$ ). The 'stable' group were more likely to be relatively shade-tolerant (Ellenberg light values 1-5 (Hill *et al.*, 2004)), with a higher proportion of Woodland specialists. The 'declining' group had more Woodland generalists and species with higher Ellenberg light scores. There was also a slight, but non-significant tendency for the 'stable' group to have elements of stress-tolerance, e.g S, SC, (Grime *et al.*, 2007) in their strategy type (Supplementary Table S1). The 'scarce' group included most of the Non-woodland species records and was even more biased towards those with high Ellenberg light scores (6-10) (Figure 3).

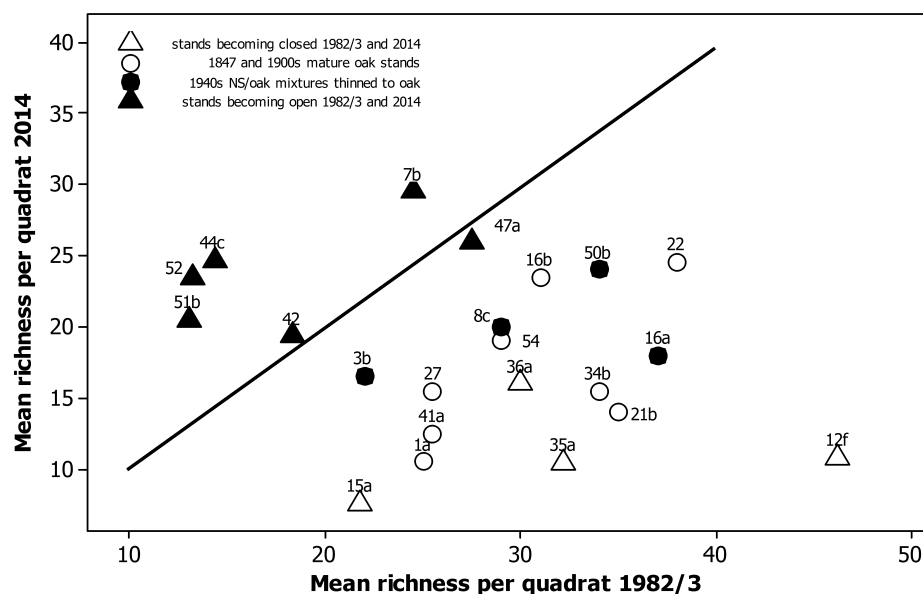


**Figure 3.** (a) Ellenberg light score distribution and (b) species types distribution for stable, declining and scarce species

### *Changes in compartment species richness*

Mean species richness per quadrat had declined in about three-quarters of the compartments (Table 2, Figure 4): no quadrats had more than thirty species in 2014 and most had fewer than twenty. There was also a change in where the richest compartments occurred. The richest

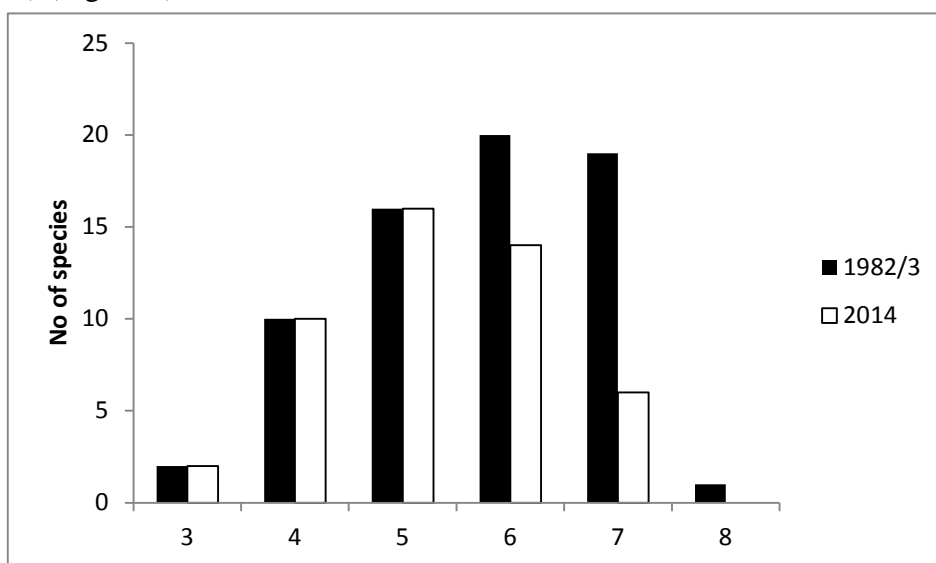
areas in 1982/3 were in the north-east (compartments 12f, 15a) and south-west (compartments 35a, 36a) of the forest, whereas more of the richer areas in 2014 were in the south-east (compartments 22, 44c, 47a, 50b, 52) (Table 2, Figure 1).



**Figure 4.** The mean richness per quadrat for each compartment in 1982/3 and 2014 by compartment for different crop types (Table 2). Compartments above the line gained species; those below had lower species richness.

#### *Change in undisturbed mature oak stands*

Four of the original five ‘1847 oak’ compartments and four of the ‘1900s oak’ compartments appeared to have had little or no intervention in the intervening years. These still showed declines in species richness (Table 2, Figure 4). The mean reduction in species richness per quadrat was  $10.6 \pm 1$  for the four 1847 oak compartments and  $12 \pm 2$  species for the 1900s oak compartments, due to fewer occurrences of high light-demanding species (Ellenberg scores 6–10) (Figure 5).



**Figure 5.** Species recorded in the undisturbed 1847 and 1900s mature oak compartments grouped by their Ellenberg light scores.

### *Similarity of restored oak to mature oak stands*

In the four 1940s Norway spruce-oak compartments (3b, 8c, 16a, 50b) where thinning out of the spruce had just started in 1982, most of the spruce had gone by 2014. By 2014 the species richness per quadrat for these compartments overlapped that of the 1847 and 1900s mature oak stands (Table 2, Figure 4) and there was no significant difference in the mean species richness for these three crop types (Table 4a). The 1940s stands restored to oak showed slightly more variability (lower similarity within crop type than the 1900s or 1847 mature oak stands (Table 4b). However, there was no significant difference between the similarity comparisons for 1847 oak:1940s restored oak and that for 1847 oak:1900s oak (Table 4c), i.e. the flora of these restored stands was as comparable to the 1847 oak stands as that from the 1900s oak compartments.

**Table 4.** Similarity of undisturbed and restored oak compartments.

a. Mean species richness

Crop type	1847 oak	1900's oak	1940's restored oak	
No of compartments	4	4	4	
Mean species richness	17.4±3	16.4±2	19.6±2	
Anova table	Df	SS	F	P
Crop type	2	22	0.48	0.6 ns
Error	9	208		
Total	11	230		

b. Similarity within crop type<sup>1</sup>

Crop type (number of compartments)	No of comparisons	Mean similarity (%±se)
(a) Within crop type <sup>1</sup>		
1847 oak stands (4)	6	67±3
1900s oak stands (4)	6	64±3
1940s restored oak (4)	6	55±2

(c) Similarity between crop types<sup>2</sup>

Crop type (number of compartments)		No of comparisons		Mean similarity (%±se)
1847 oak (4) /1940s restored oak (4)		16		56±2
1847 oak (4)/1900s oak (4)		16		55±2
1900s oak (4)/1940s restored oak (4)		16		61±2
Anova table	Df	SS	F	P
Crop type	2	292	2.1	0.14
Error	45	3165		
Total	47	3457		

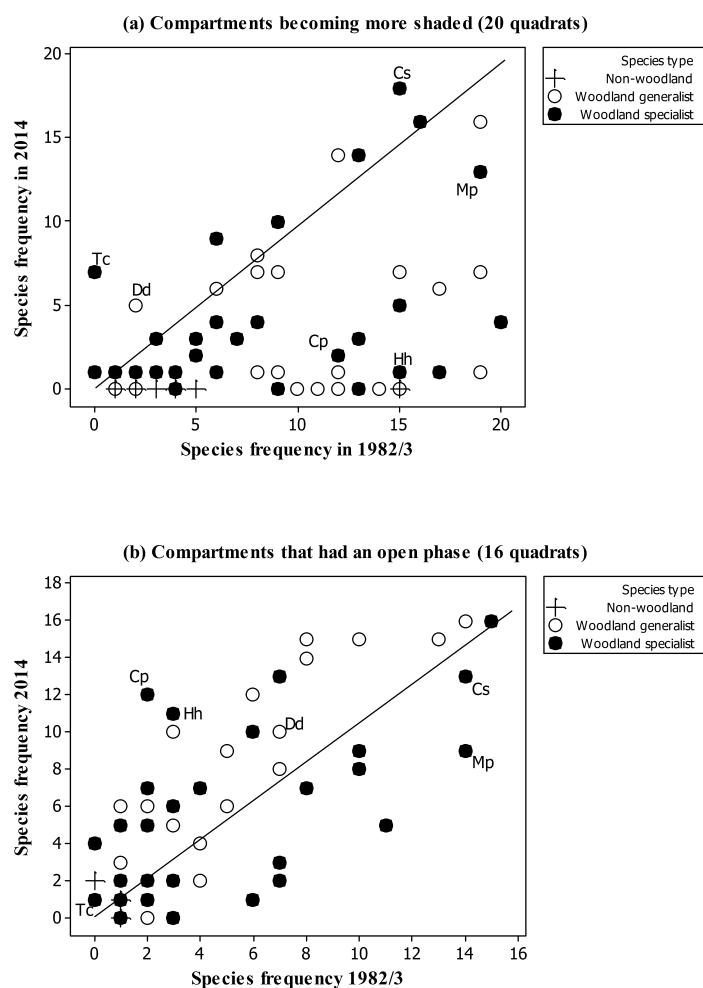
1. Each compartment in a crop type was compared with the other three and the mean similarity calculated.

2. Each compartment in the first crop type was compared in turn with each of the four compartments in the second crop type and the mean similarity calculated.

### Species change where major increases or decreases in richness occurred

Figure 4 showed that as expected species-richness had declined in compartments that tended to become more closed during the period between the two surveys decreased in species-richness, whereas compartments that had an open phase tended to increase in richness. In the compartments that became more closed a few species retained their frequency (points close to the 1:1 line in Figure 6a) but most, including some that had been very frequent in 1982/3, declined (points below the line) and overall ground flora cover was also much reduced (Figure 6c). In the compartments which had an open phase more species retained or in some cases increased their occurrence by 2014 (Figure 6b). Species that were already frequent in 1982/3 clearly could not increase much in frequency, but might increase their abundance within quadrats, so contributing to the overall increase in ground flora cover (Figure 6c).

Individual species showed different patterns: for example *Carex pendula*, *Hypericum hirsutum* increased a lot in one set of compartments (Figure 6b) but declined in the other (Figure 6a), whereas others such *Tamus communis*, *Carex sylvatica* increased somewhat in the closing compartments (Figure 6a) but showed little increase in the more open compartments (Figure 6b). *Dryopteris dilatata* showed small increases in both sets of compartments while *Mercurialis perennis* declined in both. Overall the difference in mean between the two sets of compartments in mean percentage change in occurrence for all species was significant (Figure 6d; Table 5a). However there was no difference between the mean response for the different species groups (Non-woodland, Woodland Generalists, Woodland specialists) (Table 5b).



**Figure 6.** Changes in species frequency 1982/3 and 2014 (a) for compartments becoming more shaded; (b) compartments with an open phase (lines indicate equal frequency in the two recording times); (c) changes in percentage field layer cover; (d) mean % change in occurrence for different species groups. (Species abbreviations Cp *Carex pendula*, Cs *Carex sylvatica*, Dd *Dryopteris dilatata*, Mp *Mercurialis perennis*, Tc *Tamus communis*).



**Table 5.** ANOVA tables for changes in species occurrence in compartments closing over versus those that had an open phase 1982/3-2014 (see Figure 6d)

a. Change in % of quadrats in which a species occurred (all species)

	No of species	Mean change in % of quadrats (2014-1982/3)		
Compartments with open phase	74	8.2 ±2		
Compartments closing over	92	-23.1±3		
Anova table	Df	SS	F	P
Compartment type	1	4029	70	0.000 ***
Error	164	94174		
Total	165	134468		

b. Change in % of quadrats in which a species occurred grouped by species type within each set of compartments

Compartments with open phase				
Anova table for species type comparison*	Df	SS	F	P
Species type	2	1302	1.6	0.2 NS
Error	71	28536		
Total	73	29838		
Compartments closing over				
Anova table for species type comparison*	Df	SS	F	P
Species type	2	2229	1.6	0.2 NS
Error	89	62107		
Total	91	64336		

\*Non-woodland, Woodland generalist, Woodland specialist.

## Discussion

In some North American studies recovery from the effects of clear-felling, particularly among the specialist flora, may take more than a century (Wyatt and Silman, 2014). Similarly, Hannerz and Hånell (1997) found that various vascular plant species were more at risk from clear-felling than from shelterwood interventions in wet northern boreal forests. However Heinrichs and Schmidt (2009) considered there was not likely to be a negative effect from using clear-cutting in the conversion of old spruce stands to more mixed forests. In these studies, the baseline for judging the diversity of the woodland ground flora was undisturbed or 'old-growth forest' or old managed high forest stands. In Britain old growth did not survive into historic times (Rackham, 2003) although some stands, including the 1847 oak compartments at Salcey might be considered to be moving towards such a state; and even managed broadleaved high forest stands >100 yrs old are not common (Forestry Commission,

2012). Instead our conservation reference points tend to be stands that had been managed under the organised regular disturbance regimes of coppice or coppice-with-standards, such as was the case for Salcey Forest prior to 1847.

The structure and composition of Salcey Forest has not been stable for any period of more than a few decades over the last 200 years. Coppice changed to young broadleaved high forest; parts of that were then felled whilst other areas matured; conifers were introduced and dominated large areas, now they are being removed. This changing pattern is likely to have occurred in many other ancient woods because it has been driven by broad forestry policy trends. These in turn reflect society's changes in demand for woodland goods and services: for example, for small roundwood versus larger timbers; for broadleaves versus conifers; for wood production versus biodiversity (Rackham, 2003; Foot, 2010).

No records exist for the effects on the flora of Salcey Forest of the original conversion of a coppice-with-standards system to young oak high-forest in 1847. Presumably the site went from a mosaic of open, recently cut stands with other patches of dense regrowth (Buckley and Mills, 2015a) to relatively uniform even-aged young oak stands across most of the forest in 1900. The current spread of age classes (Table 3) is re-building that age structure mosaic, albeit probably at a coarser spatial scale.

The vegetation and species richness will wax and wane in stands across the forest in response to variations in stand structure associated with different age classes. Across just the thirty years between the two field surveys there have been major changes in the species richness, as measured by number of species per quadrat, at the compartment level and in the patterns of richness across the site as a whole. It is unlikely that any of the species recorded only in 1982/83 have been lost from the site itself; much of the plant species-diversity in a large site such as Salcey Forest may be in or on the edges of open spaces such as rides (Peterken and Francis, 1999). Nevertheless, the study demonstrates that the scale at which data on species presence or abundance is collected affects the conclusions that might be drawn about effects of forest management on plant biodiversity.

The flora differences, not unexpectedly, appear to be driven primarily by changes in light availability: the main species declines are amongst the more light-demanding species. Felling or thinning increased species richness in the ground flora, but this then declined through periods of subsequent tree growth, analogous to the changes in coppice (Barkham, 1992). Brunet *et al.* (1997) similarly found that richness increased following management interventions in Swedish oak and beech forests, while Zhang *et al.* (2016) describe the rise and subsequent decline in the ground vegetation in early open stages of ponderosa pine plantations in northern California. However, Härdtle *et al.* (2003) caution that while light may be the limiting factor in some woodland types, factors such as moisture or nutrient availability may limit the light response to thinning in others.

Reductions in the frequency of light-demanding species were seen even in the apparently undisturbed 1847 and 1900s mature oak stands. Similar species richness declines in unmanaged broadleaved woodland in Britain over recent decades have been recorded elsewhere (Kirby *et al.*, 2005; Kirby, 2015). While the signal from the vegetation was that these stands had become more shaded the estimates of canopy and shrub cover did not reflect this. These were however only subjective assessments and may have been too imprecise to pick up the effective change in light levels for the ground flora; for example, through increases in canopy depth as the trees grew.

At some future date there may be major canopy break-ups with gap formation; however, so far, these 100-160 year-old oak stands have proved much more stable than the mixed species old-growth stands studied by Peterken and Jones (1987) in the Wye Valley. Graae and Heskjær (1997) comparing managed and unmanaged stands in Denmark similarly found a tendency for species richness to decline with stand age in unmanaged stands that were still largely closed canopy.

There are also likely to be interactions with other factors such as increasing deer populations in southern England (Ward, 2005), climate change (de Frenne *et al.*, 2013), or increased nitrogen deposition (Verheyen *et al.*, 2012). These might be having an effect on the abundance of particular species: for example, the decline in the shade-tolerant *Mercurialis perennis* and maintenance of the frequency of *Poa trivialis* (a high light-demander) against the general trends could be mediated by increased deer pressure (Kirby, 2001). High-light demanding species are also often relatively large, fast-growing plants (e.g. *Angelica sylvestris*, *Cirsium palustre*, *Filipendula ulmaria*) which might also make them more palatable to deer.

The 1940s Norway spruce-oak mixtures, from which most of the conifers have now been removed to restore pure oak stands, showed similar species richness per quadrat and similar species composition to the undisturbed stands by 2014. This supports the case for restoration of plantations on ancient woodland sites for biodiversity reasons. The success of development of the native woodland ground flora was probably helped at this site by the survival of species within the oak rows in the original mixed planting (Kirby, 1988).

There was no indication that the richness of Woodland specialists, as defined by Kirby *et al.* (2012), were adversely affected by opening the canopy in contrast to the findings of Brown *et al.* (2015). The latter used a different definition of specialist plant but at Salcey their species, as a group, tended to do slightly better (and certainly no worse) than either the flora as a whole or Woodland specialists as defined in this study (Supplementary Table S.1). Four of the eighteen species present at Salcey on Brown *et al.*'s list did decline strongly between the two surveys, but in one case, *Arum maculatum* (43:18), this was probably an artefact, because of the later timing of the 2014 survey compared to that in 1982/3. The other three *Moehringia trinerva* (14:0), *Potentilla sterilis* (40:16), and *Stachys sylvatica* (38:12) are not uncommon in recently cut coppice or clear-fells and are tolerant of at least mild disturbance (Grime *et al.*, 2007); it thus seems unlikely felling or thinning contributed to their decline.

### ***Implications for future management***

The changes in the structure and composition of Salcey Forest have largely been driven by economic and policy decisions; only in the last few decades has conservation of biodiversity been a significant objective. Forest managers thus have a reasonably high degree of control over how patterns of richness change over time and over the site through the manipulation of changes in the openness of the canopy (Kerr, 1999). For the future they need to consider the following.

- The recent declines in plant richness at Salcey may not continue. The 1847 oak stands may start to break up, perhaps exacerbated by the impact of climate change or diseases such as Acute Oak Decline.

- Ash which has increased since 1982, as might be expected from the classification for this site as *Fraxinus excelsior-Acer campestre-Mercurialis perennis* type vegetation (Rodwell, 1991), is also likely to decline because of the impact of ash dieback (Pautasso *et al.*, 2013), providing another source of gaps and subsequent young growth.
- Even if the gap formation in the older stands is slower than expected over the next few decades there should be sufficient opportunities for light-demanding species to increase elsewhere through further restructuring of the remaining conifer/mixed stands. A combination of felling and thinning should provide a variety of large and small gaps across the forest.
- The likely future decline in the oldest stands (c.98 ha of 1847 oak) means that attention should be focussed on ensuring that some of the c.80 ha of oak and ash in the 81-120 year age class are identified to be grown on for the next century to provide the next generation of very old stands.

The diversity of a forest for other species groups (birds, bats, saproxylic invertebrates) does not necessarily follow that for the vascular plants (indeed sometimes it is the complete reverse) but the same principle applies that species abundance is likely to vary across the tree layer's life cycle, and hence to vary in space as well.

Many of these conclusions will apply to British and continental broadleaved woods more generally. Long-term dynamics of woodland need to be considered when assessing biodiversity patterns (Verstraeten *et al.*, 2013; McCarthy, 2014) and there are likely to be shifts in the patterns of species richness around a site over time, as seen with plant richness at Salcey Forest.

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**Supplementary Table S1. Total no of species occurrences in 1982/3 and 2014**

Col. 1 Species names after Stace (1991)

Col. 2,3 Ellenberg Light and Nutrient scores after Hill *et al.* (2004)Col. 4 Plant Strategy Types after Grime *et al.* (2007). Main strategy types C competitor; S stress-tolerator; R ruderal, plus various combinations of these, e.g. CR competitive-ruderal.Col. 5 Woodland species type after Kirby *et al.* (2012: NW Non-woodland; WG Woodland generalist; WS Woodland specialist; \* listed as Woodland specialist in Brown *et al.* (2015)

Col. 6,7 No of occurrences (out of 60 quadrats) at each recording time

Species name	Ellenberg Light score	Ellenberg nutrient score	Plant Strategy Type	Woodland species type	1982/3 occurrences (n=101)	2014 occurrences (n=74)
<b>'Scarce' (10 or fewer occurrences in total)</b>						
<i>Agrostis stolonifera</i>	7	6	CR	WG	4	0
<i>Alliaria petiolate</i>	5	8	CR	WG	1	0
<i>Alopecurus pratensis</i>	7	7	C/CSR	NW	1	0
<i>Athyrium filix-femina</i>	5	6	C/SC	WS	3	6
<i>Cardamine flexuosa</i>	5	6	R/SR	WG	3	5
<i>Carex flacca</i>	7	2	S	NW	2	0
<i>Carex pilulifera</i>	7	2	S	NW	0	2
<i>Carex strigose</i>	3	6	-	WS	5	3
<i>Centaurea nigra</i>	7	5	CSR	NW	3	0
<i>Cerastium fontanum</i>	7	4	R/CSR	NW	2	0
<i>Cirsium vulgare</i>	7	6	CR	WG	4	0
<i>Clematis vitalba</i>	6	5	SC	WG*	4	1
<i>Dactylis glomerata</i>	7	6	C/CSR	WG	8	2
<i>Dryopteris affinis</i>	5	5	SC/CSR	WS	0	2
<i>Epilobium hirsutum</i>	7	7	C	WG	3	2
<i>Epipactis helleborine</i>	4	4	S	WS	0	1
<i>Festuca rubra</i>	8	5	CSR	WG	1	0
<i>Fragaria vesca</i>	6	4	CSR	WS	5	0
<i>Galeopsis tetrahit</i>	7	6	R/CR	WG	2	1
<i>Galium mollugo</i>	7	4	CSR	NW	2	2
<i>Galium odoratum</i>	3	6	SC/CSR	WS*	0	1
<i>Galium palustre</i>	7	4	CR/CSR	WG	6	3
<i>Glyceria</i> spp.			-	NW	1	0
<i>Hedera helix</i>	4	6	SC	WG	3	7
<i>Heracleum sphondylium</i>	7	7	CR	WG	6	0
<i>Hypericum tetrapterum</i>	7	4	CSR	WS	6	1
<i>Juncus articulatus</i>	8	3	CSR	NW	2	0
<i>Juncus conglomeratus</i>	7	3	C/SC	WG	9	0
<i>Juncus inflexus</i>	7	5	SC	NW	8	1
<i>Lapsana communis</i>	6	7	R/CR	WG	1	0
<i>Lathyrus pratensis</i>	7	5	CSR	NW	6	1



<i>Lotus pedunculatus</i>	7	4	C/CSR	NW	5	0
<i>Luzula pilosa</i>	5	3	S	WS	1	1
<i>Lychnis flos-cuculi</i>	7	4	CSR	WG	2	0
<i>Melica uniflora</i>	4	5	S/SC	WS*	0	1
<i>Mentha aquatic</i>	7	5	C/CR	WG	1	0
<i>Mentha arvensis</i>	6	6	CR	WG	1	0
<i>Milium effusum</i>	4	5	S/CSR	WS*	0	2
<i>Plantago major</i>	7	7	R/CSR	NW	1	0
<i>Poa pratensis</i>	7	5	CSR	NW	3	0
<i>Potentilla erecta</i>	7	2	S/CSR	WG	1	0
<i>Potentilla reptans</i>	7	5	CR/CSR	WG	0	1
<i>Prunella vulgaris</i>	7	4	CSR	WG	1	0
<i>Ranunculus acris</i>	7	4	CSR	NW	4	0
<i>Rubus idaeus</i>	6	5	SC	WG	0	3
<i>Rumex acetosa</i>	7	4	CSR	WG	1	0
<i>Scrophularia auriculata</i>	7	7	CR	WG	1	1
<i>Senecio jacobaea</i>	7	4	R/CR	NW	1	0
<i>Senecio vulgaris</i>	7	7	R	NW	2	0
<i>Sonchus oleraceus</i>	7	7	R/CR	NW	5	0
<i>Stellaria graminea</i>	7	4	CSR	WG	2	0
<i>Stellaria media</i>	7	7	R	WG	9	0
<i>Tussilago farfara</i>	7	6	CR	NW	1	0
<i>Valeriana officinalis</i>	6	5	CSR	WS	6	2
<i>Veronica beccabunga</i>	7	6	CR	NW	1	0
<i>Veronica officinalis</i>	6	4	S/CSR	WG	1	0

**‘Stable’ (<10 difference  
in no of occurrences  
between 1982/3 survey  
and 2014)**

<i>Ajuga reptans</i>	5	5	CSR	WG*	27	32
<i>Brachypodium sylvaticum</i>	6	5	S/SC	WS	36	40
<i>Bromopsis ramosa</i>	4	7	CSR	WS*	24	17
<i>Carex pendula</i>	5	6	S/SC	WS*	20	26
<i>Carex remota</i>	4	6	CSR	WS*	11	16
<i>Carex sylvatica</i>	4	5	S	WS*	51	51
<i>Circaea lutetiana</i>	4	6	CR	WG	32	39
<i>Deschampsia cespitosa</i>	6	4	SC/CSR	WG	57	54
<i>Dryopteris dilatata</i>	5	5	SC/CSR	WG	23	31
<i>Dryopteris filix-mas</i>	5	5	SC/CSR	WG	35	40
<i>Festuca gigantea</i>	5	7	CSR	WS	16	15
<i>Geranium robertianum</i>	5	6	R/CSR	WS	13	18
<i>Geum urbanum</i>	4	7	S/CSR	WG*	21	20
<i>Hyacinthoides non- scripta</i>	5	6	SR	WS	7	4
<i>Lamiastrum</i>	4	6	S/SC	WS*	14	19

<i>galeobdolon</i>						
<i>Lonicera periclymenum</i>	5	5	SC	WS*	50	50
<i>Myosotis sylvatica</i>	6	5	CSR	WS	7	4
<i>Oxalis acetosella</i>	4	4	S/CSR	WS	29	28
<i>Poa trivialis</i>	7	6	CR/CSR	WG	24	20
<i>Primula vulgaris</i>	5	4	S/CSR	WS	41	40
<i>Ribes rubrum</i>	5	6	SC	WS*	7	6
<i>Rubus fruticosus</i>	6	6	SC	WG	49	40
<i>Stellaria holostea</i>	5	6	CSR	WS	11	7
<i>Tamus communis</i>	6	6	C/CR	WS*	15	10
<i>Veronica chamaedrys</i>	6	5	CSR	WG	26	20
<i>Vicia sepium</i>	6	6	C/CSR	WS	18	12
<b>'Declining' (&gt;10 more occurrences in 1982/3 survey than 2014)</b>						
<i>Angelica sylvestris</i>	7	5	C/CR	WG	33	13
<i>Arctium minus</i>	6	5	CR	WG	24	6
<i>Arum maculatum</i>	4	7	SR/CSR	WS*	43	18
<i>Calamagrostis epigejos</i>	7	6	C/SC	WS	40	20
<i>Cardamine pratensis</i>	7	4	R/CSR	WG	13	1
<i>Chamerion angustifolium</i>	6	5	C	WG	17	0
<i>Cirsium arvense</i>	8	6	C	NW	19	3
<i>Cirsium palustre</i>	7	4	CR	WG	27	5
<i>Epilobium montanum</i>	6	6	CSR	WG	23	1
<i>Filipendula ulmaria</i>	7	5	C/SC	WG	19	2
<i>Galium aparine</i>	6	8	CR	WG	36	13
<i>Glechoma hederacea</i>	6	7	CSR	WG	41	27
<i>Holcus mollis</i>	6	3	C/CSR	WS	48	16
<i>Hypericum hirsutum</i>	6	5	S/CSR	WS	28	13
<i>Juncus effusus</i>	7	4	C/SC	WG	35	14
<i>Mercurialis perennis</i>	3	7	SC	WS	51	29
<i>Moehringia trinervia</i>	4	6	SR	WS*	14	0
<i>Potentilla sterilis</i>	5	5	S	WS*	40	16
<i>Ranunculus repens</i>	6	7	CR	WG	30	13
<i>Rosa (cf canina)</i>	6	6	SC	WG	53	34
<i>Rumex sanguineus</i>	5	7	CSR	WG	45	17
<i>Scrophularia nodosa</i>	5	6	CR	WS	21	9
<i>Solanum dulcamara</i>	7	7	CSR	WG	25	3
<i>Stachys sylvatica</i>	6	8	C/CR	WS*	38	12
<i>Taraxacum officinale</i>	7	6	R/CSR	WG	19	0
<i>Urtica dioica</i>	6	8	C	WG	41	25
<i>Viola riviniana</i>	6	4	S	WS	24	7

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