

Changes in the vegetation of clear-fells and closed canopy stands in an English oak wood over a 30 year period

K J Kirby, Department of Plant Sciences, University of Oxford, OX1 3RB

Keith.kirby@bnc.oxon.org

Abstract

The vascular plant ground flora of clear-felled and undisturbed oak-stands were studied using 10x10m temporary and permanent plots over a 30 year period in a wood in southern England. Within the undisturbed stands the mean species-richness declined from 10-15 species per plot in 1981 to about 5 in 2012. The decline was negatively correlated with a decrease in openness of the tree and shrub layer over this period. In the clear-fells the species-richness in the first two growing seasons after felling was 1.5 to 3 times higher than in the undisturbed stands. Ruderal species and grasses in particular increased, but some ancient woodland indicators were present, even after a decade of openness. Change in the openness of stands appears to be a strong driver of ground flora richness up to about 50% cover; in more open conditions competition and other processes within the ground flora assemblage may come to play a greater part. Forest management has played a key role in creating canopy gaps in small ancient woods in the UK, but in future tree deaths from disease and extreme weather events are likely to increase in importance.

Keywords: conservation; ground flora; high-forest; management; protected-site management

Introduction

In cultural landscapes ancient woods have often been managed in the past and continuation of some form of management may be desirable to maintain their biodiversity (Peterken, 1977a,b; Rackham, 1990). There is much general guidance on managing woodland for biodiversity, e.g. Lindenmayer et al. (2006), Peterken (1977b), but much less empirical data to show whether the management has had the expected effect (Götmark, 2013).

The ground flora is a key part of the woodland vascular plant diversity (Gilliam, 2014). Across Europe woodland vegetation has been changing (Hermy, 2015) for a variety of reasons but including the impact of the shift to high-forest management from coppice (Buckley & Mills, 2015 a,b). During the coppice cycle the richness of the flora increases after cutting, with the increased light, rainfall and nutrient release, but then declines as the tree and shrub layer reform (Barkham, 1992). Under a high-forest regime there is a similar increase in species richness following felling as with coppicing, followed by a decline as stands enter the thicket stage (Kirby, 1988). A recovery of ground vegetation cover and richness might then be expected as the canopies age and start to open out (the understorey re-initiation stage (Oliver and Larson, 1990)). However there is a much longer period between successive gap phases (Kirby, 2009) than in coppice; plants that survive vegetatively through the closed canopy phase have to do so for longer, so more may die through lack of reserves or from being eaten by deer for example; the buried seed bank will decline more than under the shorter coppice cycles (Brown and Warr 1992); and, as less of the forest is at the open stage at any one time, the scope for invasion of gap species from clear-fells elsewhere in the woodland is less.

In 1981 surveys were carried out on the Claydon Estate in southern England that led to Sheephouse Wood being designated as a Site of Special Scientific Interest (NCC, 1989; http://www.sssi.naturalengland.org.uk/Special/sssi/sssi_details.cfm?sssi_id=1001671). One factor contributing to the designation of this site was the richness of its vascular plant assemblage. Sheephouse Wood had been managed as coppice, but in the late 19th century was converted to high forest. There had been little in the way of felling or gap creation since the 1950s. It was agreed with the owners that parts of the wood would continue to be left undisturbed. As the trees were already approaching 100 years old in the 1980s an increase in natural gap formation was expected which would benefit the flora in the mature stands, although since then evidence has emerged of declines in the ground flora of many undisturbed broadleaved woods as a consequence of increasing canopy cover (Kirby *et al.*, 2005).

Other areas were to be felled and replanted to benefit the gap-stage flora. A change in the profile of the ground flora following felling was expected with the favouring of species of light conditions and of ruderal and competitive species over stress-tolerant ones. Woodland specialist species, such as ancient woodland indicators, being often stress-tolerant and shade-tolerant, were expected to benefit less than woodland generalist plants such as brambles or grasses (Decocq *et al.*, 2005; Hermy *et al.*, 1999; Kimberley *et al.*, 2013; Kirby, 1990; Kirby *et al.* 2012).

Since 1981 the ground flora has been recorded using a small number of permanent and temporary plots in both felled and undisturbed sections of the woods to see whether these expectations were fulfilled. Although the sampling was irregular and limited this study is unusual in following through the same site over a long period (over 30 years).

Site

Sheephouse Wood is a privately-owned woodland located at National Grid Reference SP702235 (51° 54' 16" north, 0° 58' 50" west; elevation 80-105 m). The wood (58 ha) is mainly on poorly-drained clay soils (pH 5.0-6.0). Its canopy is predominantly oak (*Quercus robur*), falling within the National Vegetation Classification Type W10 (Oak-bramble-bracken woodland); around the edges and at the northern end (where the ground rises slightly) there is a richer woodland community of W8 (Ash-field maple- dog's mercury woodland) (Rodwell, 1991). This study concentrates on the main W10 (oak) stands.

The wood was worked largely as hazel *Corylus avellana* coppice with oak *Quercus robur* standards until second half of the nineteenth century, when much of it was replanted with oak to create the current high forest structure (unpublished notes, the Claydon Estate). Little management of the wood then took place until January 1984 when a block of 2.6 ha was felled; a similar-sized fell was made in August 1988; both were replanted with mixed broadleaves at 3 m spacing. Also in 1984 the understorey was cut in an area of about 1 ha in the south of the wood as a prelude to re-introducing a coppice cycle to the wood; however the oak overstorey was not thinned and no further coppice-cutting took place (Kirby, 1990). In the winter of 1985/86 some further small coupes were made in the north of the wood and the main rides were widened. No further felling took place between then and 2012.

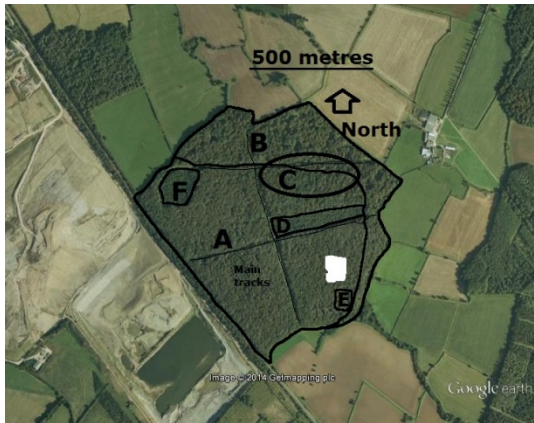


Figure 1. Sheephouse Wood: A = undisturbed oak (W10) woodland ; B = ash-maple (W8) woodland. Permanent plots were established in C (4 plots undisturbed); D (3 plots 1984 clear-fell); E (3 plots 1984 understorey removal area). Area F (1988 clear fell area) and the rest of A were sampled by temporary plots only. Area C spans the transition between the two woodland types. Underlying image from Google Earth, Copyright image@2014Getmapping plc

Methods

Field recording

Changes in the composition of the ground flora from 1981 to 2012 under different treatments were followed using either permanent or temporary 10x10 m plots.

In 1984 a study was started with the intention of using a small number of permanent plots to follow the floral changes in different treatment (Kirby, 1990) (Table 1). The permanent plots were marked by metal markers at two corners such that the same locations could be recorded each time.

- Three permanent plots were in the area that had just been clear-felled (Figure 1, area D).
- Four permanent plots were set up in undisturbed stands just to the north of the 1984 clear-fell (Figure 1, area C); (originally six plots were set up but two were partially felled during the 1986 ride-widening/small coupe fellings);
- Three permanent plots were set up in area E, where the understorey, mainly *Corylus avellana* and *Crataegus* spp., but not the overstorey, was cleared .

By 1990 it was clear that three of the four ‘undisturbed’ plots in area C were closer in composition to the W8 woodland type and that the vegetation in the majority of the wood – the W10 oak stands - was changing in a rather different way. Previously in 1981 seven temporary plots had been recorded by the Nature Conservancy Council’s England Field Unit at random locations across the W10 oakwood (one was in the area felled in January 1984), so this approach was repeated. Between 4 and 8 temporary plots were recorded in the unfelled oak stands (Table 1) between 1986 and 2012. Temporary plot positions were created afresh on each occasion at random locations within the different management areas in the wood. Additional randomly placed temporary plots were recorded in the 1984 clear-fell area to

supplement the permanent plot records. In addition the area clear-felled in 1988 was recorded using sets of six temporary plots. (The irregularity of the recording and low replication reflect the limited time available for this project.)

Table 1. Number of plots recorded by area and year (permanent plot recording indicated by italics; capital letters refer to areas shown on Figure 1).

| Year | Years since 1981 | Undisturbed (A, C) | Understorey removal (E) | 1984 clear-fell (D) | 1988 clear-fell (F) |
|--|------------------|--------------------|-------------------------|---------------------|---------------------|
| May 1981 | 0 | 7 | | | |
| Aug. 1984 | 3 | 4 | 3 | 3 | |
| May 1985 | 4 | 4 | 3 | 3 | |
| Aug. 1986 | 5 | 4 | 3 | 3 | |
| Aug. 1987 | 6 | 4 | 3 | 3 | |
| July 1988 | 7 | 4+3 | 3+3 | 3+3 | 6 |
| May 1989 | 8 | 4 | 3 | 3 | 6 |
| Aug. 1990 | 9 | | | | 6 |
| Aug. 1991 | 10 | | | 3 | |
| June 1992 | 11 | | 3 | 3 | 6 |
| June 1993 | 12 | 4 | | | |
| July 1994 | 13 | | | | 6 |
| July 1996 | 15 | 4+6 | 3 | 3+1 | 6 |
| Aug. 1999 | 18 | 6 | | 6 | 6 |
| July 2000 | 19 | 7 | | 6 | 6 |
| July 2006 | 25 | 7 | 3 | 3+3 | 6 |
| June 2008 | 27 | 4+8 | 3 | 3+5 | 6 |
| Aug. 2012 | 31 | 4+6 | 3 | 3+3 | 6 |
| Total no of records for each area (temporary+ permanent) | | 90 (50+40) | 36 (3+33) | 60 (24+36) | 66 |

In each plot, whether temporary or permanent, all vascular plant species in the field layer were listed and their cover estimated using the Domin (10-point) scale (Rodwell, 1991). Typically between 20 and 30 minutes were taken to search each plot by systematically walking over the ground. Tree and shrub seedlings (mainly *Fraxinus excelsior* and *Crataegus monogyna*) were however excluded from the subsequent analysis. Tree layer (>5m) and Shrub layer cover (2-5m high) were estimated visually on a percentage scale. A separate estimate was made of 'Open Sky' as viewed from below 2 m – the inverse of combined tree/shrub cover – to reflect the light climate experienced by the ground flora vegetation.

The 1981 records were made in May, but subsequent recording, in order to fit in with other work, was usually done in the June to August period. These later recordings may have missed some of the spring flowering species, but the vernal aspect of the flora is not well-developed over most of the wood and the presence of the commonest component *Hyacinthoides non-scripta* can still be detected from dead flower stems into August. Between

1985 and 1988 two visits were made in a season (May and July/August) and these showed no difference in species-richness recorded (Kirby 1990) in undisturbed areas.

Vascular plant names follow Stace (1991).

Data analysis

The analyses explored change in species richness in relation to the openness of the stands, differences in the composition of the vegetation between clear-fell, understorey removal, and undisturbed stands over time and by the relative abundance of different groups of species in undisturbed and disturbed woodland. The permanent plot records for different years are not independent; therefore for some of the analyses and graphical presentations permanent and temporary plot results have been separated. The main analyses were performed in Minitab (v.16) or Excel; differences in vegetation composition between plots were explored using DECORANA, run as a package from the Community Analysis Package v2.1 (www.Pisces-conservation.com).

Species were classified as woodland, or non-woodland species (Kirby *et al.*, 2012), or as regional ancient woodland indicators (Rose, 1999). Ellenberg's indicator values for light, nutrient conditions, soil wetness, as modified for British conditions Hill *et al.* (2004) and plant strategy type (Grime *et al.*, 2007; Hodgson *et al.*, 1995) were used to compare the traits of different groups of plots or species. With the Ellenberg values mean values were calculated. A mean strategy score for a group of species was calculated by converting the strategy type for each species into a percentage of the three main types: thus a stress-tolerant (S) species would be scored as 100% stress-tolerant; a competitive-ruderal species (CR) scored as 50% competitive, 50% ruderal;; a competitive-stress-tolerant-ruderal type species (CSR) 33% competitor, 33% stress-tolerant; 33% ruderal. The values were then summed to give the score for each plot for the three main strategies (C competitive; S stress-tolerant; R ruderal).

Results

Changes in stand structure

In the undisturbed stands the tree layer has increased in cover over the thirty years with little change in shrub cover (Figure 2a). (Separate measurements of cover changes made as part of a study of breeding birds in the wood confirm the increase in canopy cover, but found a decline in the shrub layer; R J Fuller personal communication.) In the 'understorey removal area' the tree layer largely parallels that of the undisturbed stands and by 2012 the shrub layer had also regrown to comparable levels.

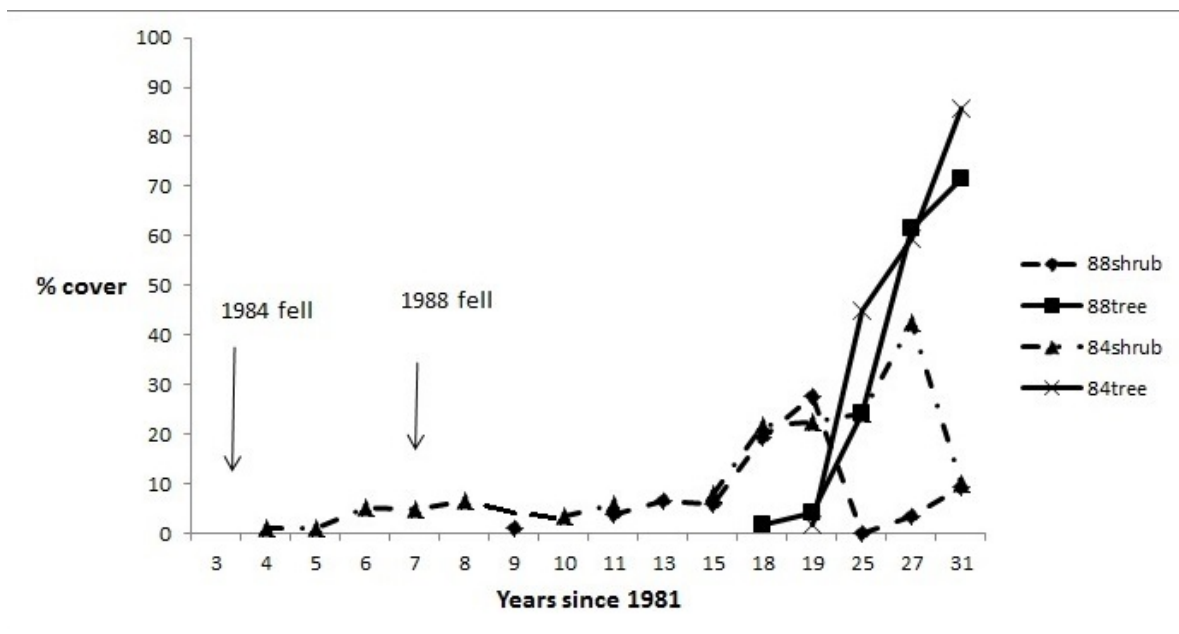
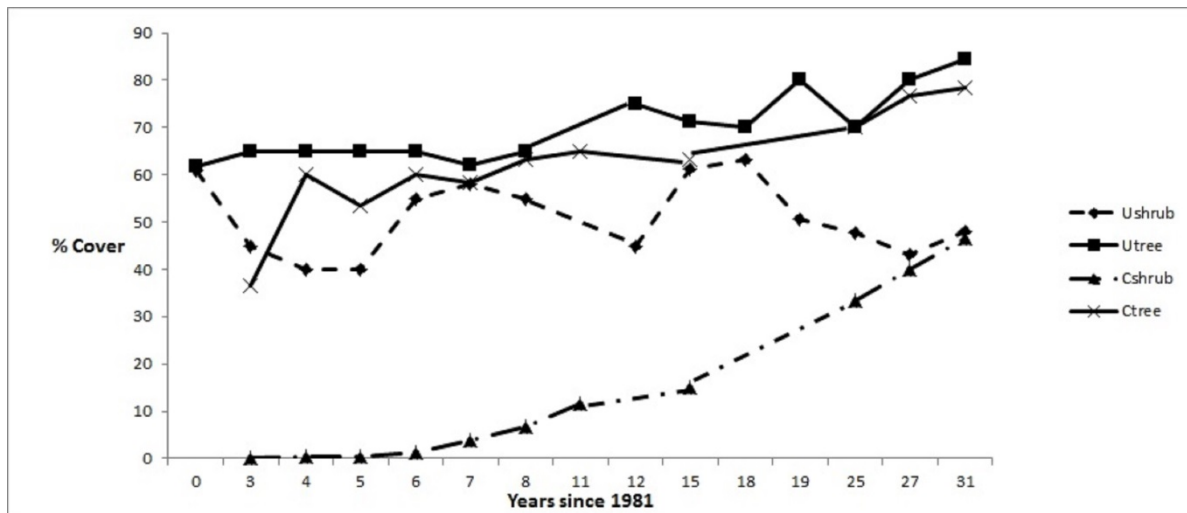


Figure 2. Changes in estimated shrub and tree cover in (a) undisturbed stands (Utree, Ushrub) and understorey removal areas (Ctree, Cshrub); and (b) the 1984 (84shrub, 84tree) and 1988 clear fell areas (88shrub, 88tree).

In the clear-fells canopy closure was initially slow because of the wide spacing between the planted trees and suppression of regeneration in the inter-rows by mowing. The 1984 clear-fell also suffered a fire which killed the trees in part of the stand. However in the last decade the cover has increased rapidly. The trees in the 1988-fell established better and have in effect caught up with the 1984-fell (Figure 2b). (The sharp decline in the shrub layer cover at around 19 years is an artefact of the canopy moving above the 5m height band and hence into the tree layer zone.)

Across recording times and stand types (Figure 3), there was a strong relationship between the degree of openness of the stand and the species richness per plot up to about 40-50% openness (linear regression $R^2=35\%$; $p<0.001$). The relationship was weaker at higher levels of openness though still significant when the records from the 1988-fell made in the

September after the felling in August (circled on Figure 3) were excluded ($R^2=11\%$; $p=0.001$). Leaving these plots out is valid since the flora had not had time to respond to the felling.

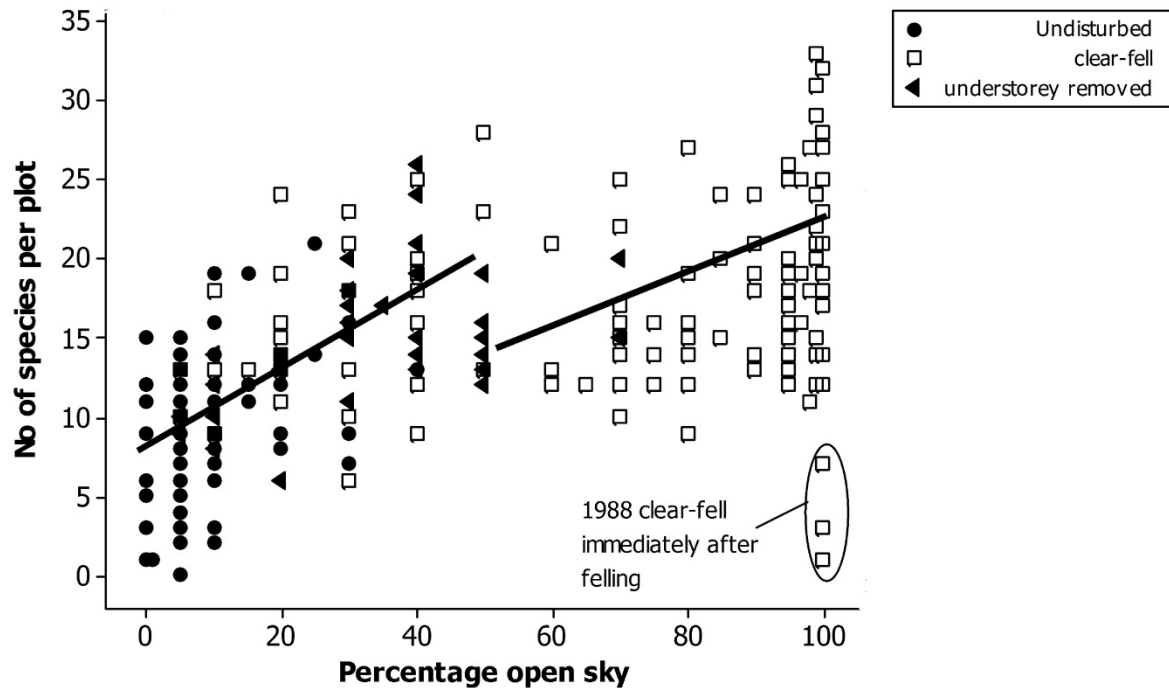


Figure 3. Species richness per plot versus estimate of ‘open sky’. Circled points are from plots recorded in September 1988, one month after the mature stand had been felled and have been excluded from the regression analysis.

Regression equations $Spp.no = 7.63 + 0.22open_{0-50\%}$; $Spp.no = 3.57 + 0.163open_{51-100\%}$.

Species-richness decline in undisturbed stands

The richness (mean number of species per plot) of the ground flora declined in the undisturbed woodland (Figure 4), based on the temporary plot samples and the one permanent plot that was well within W10 oak community (Figure 1, southern part of area C). The other three plots in area C were in the transition zone to the W8 ash-maple woodland, and varied little in richness over the thirty years. In these plots the estimates of openness slightly increased over time, for example in one case where a tree fell down, whereas in the oak stands the openness decreased significantly. It was possible that plot records from the early 1980s recorded in May had more vernal species detected and so could be biasing the results. However the relationship between species richness and canopy openness in the oak stands and the decline in richness over time remained highly significant even when these records were omitted from the analysis.

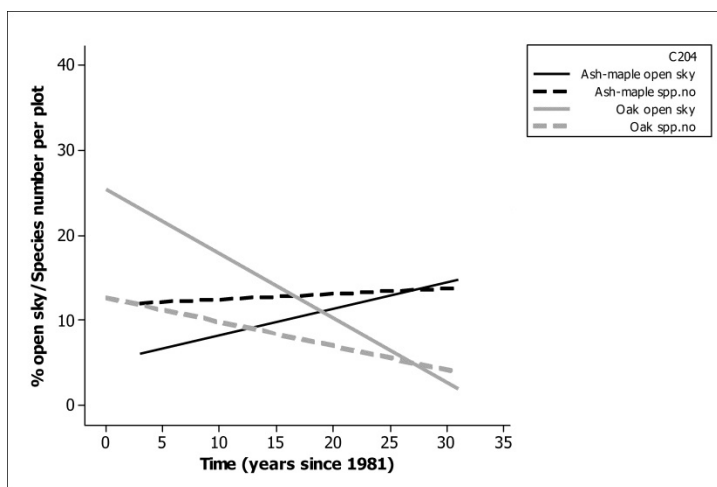
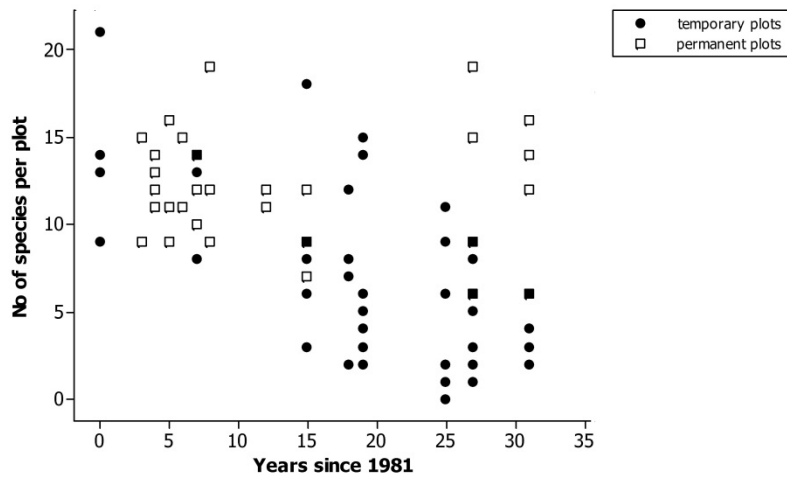


Figure 4. (a) Species number per plot for undisturbed stands 1981-2012 (b) regression lines for species richness and 'open sky' against years since 1981 separately for the plots in the W10 oak stands and the three permanent plots in area C in the transition to W8 ash-maple stands.

Oak stands: open sky = $21.7 - 0.61\text{yrs}$; $r^2 = 47\%$, $p < 0.001$ ***

Ash-maple stands open sky = $5.16 + 3.11\text{yrs}$; $r^2 = 14\%$, $p = 0.04$ *

Oak stands: spp.no = $12.5 - 0.282\text{yrs}$, $r^2 = 38\%$, $p < 0.001$ ***

Ash-maple stands: spp.no = $11.8 + 0.0633\text{yrs}$, $r^2 = 4\%$, $p = 0.26$ NS

Increased species-richness following disturbance

In the clear-fells the species richness was 1.5 to 3 times higher than found in the undisturbed oak stands (Figure 3); the one plot record from 1981 recorded in what became the 1984 clear-fell area, and the plots recorded immediately after the 1988 clear-fell (circled on Figure 3), suggest that this is not because these areas were inherently richer before felling. In the 'understorey removal' stand the initial increase in richness following disturbance was not as great as in the clear-fells but the plots were still richer than those in the undisturbed stands. The increase in species number was greater in the first two growing seasons after the disturbance compared to the subsequent value (Table 2). Since the main regrowth of shrub

and tree layers only occurred later on in the recording period (Figure 2) the initial declines in the ground flora are related to changes within the ground flora itself.

Changes in the species-profile following disturbance

The frequency of species with more than ten records across the whole recording period in the clear-fell and undisturbed plots combined was compared across these two types of stand (Table 3). More species were recorded more often in the clear-fells, particularly of grasses, *Juncus effusus* and herbs associated with disturbances such as *Chamerion angustifolium*, *Cirsium* spp., *Rumex sanguineus*. the species more common in the undisturbed woodland included more herbs and ferns and a greater proportion of regional ancient woodland indicators, but some regional ancient woodland species - the grasses *Calamagrostis epigejos* and *Holcus mollis*, and the small herbs *Potentilla sterilis* and *Hypericum pulchrum* - were more frequent in the clear-fells.

Table 3. No of occurrences of species in plots from undisturbed or clearfelled stands, across all times. Only species with at least ten records (excluding those from the Understorey removal area) have been considered.

| | | Undisturbed. | Felled | | | Undisturbed. | Felled |
|---------------------------------------|-------|--------------|--------|---|------|--------------|--------|
| No of records – all times | | 90 | 130 | | | 90 | 130 |
| Species | type | | | Species | type | | |
| A. More frequent in Undisturbed plots | | | | C. More frequent in clear-fells (continued) | | | |
| <i>Carex sylvatica</i> | AWI | 51 | 36 | <i>Anthoxanthum odoratum</i> | OW g | 5 | 42 |
| <i>Lamium galeobdolon</i> | AWI | 20 | 13 | <i>Arrhenatherum elatius</i> | OW g | 0 | 13 |
| <i>Luzula pilosa</i> | AWI | 31 | 24 | <i>Cardamine flexuosa</i> | OW | 1 | 11 |
| <i>Milium effusum</i> | AWI g | 41 | 12 | <i>Chamerion angustifolium</i> | OW | 0 | 88 |
| <i>Circaea lutetiana</i> | OW | 52 | 3 | <i>Cirsium palustre</i> | OW | 1 | 80 |
| <i>Dryopteris dilatata</i> | OW | 33 | 0 | <i>Cirsium vulgare</i> | OW | 0 | 22 |
| <i>Glechoma hederacea</i> | OW | 23 | 7 | <i>Dactylis glomerata</i> | OW g | 3 | 68 |
| <i>Poa trivialis</i> | OW g | 31 | 26 | <i>Deschampsia cespitosa</i> | OW g | 57 | 123 |
| B. Little difference in frequency | | | | <i>Epilobium montanum</i> | OW | 7 | 27 |
| <i>Anemone nemorosa</i> | AWI | 24 | 35 | <i>Galium palustre</i> | OW | 1 | 27 |
| <i>Hyacinthoides non-scripta</i> | AWI | 45 | 49 | <i>Holcus lanatus</i> | OW g | 2 | 15 |
| <i>Primula vulgaris</i> | AWI | 10 | 18 | <i>Hypericum hirsutum</i> | OW | 0 | 25 |
| <i>Brachypodium sylvaticum</i> | OW g | 6 | 5 | <i>Juncus effusus</i> | OW | 18 | 101 |
| <i>Galium aparine</i> | OW | 24 | 24 | <i>Lychnis flos-cuculi</i> | OW | 0 | 11 |
| <i>Geum urbanum</i> | OW | 4 | 6 | <i>Poa annua</i> | OW g | 0 | 10 |
| <i>Lonicera periclymenum</i> | OW | 82 | 94 | <i>Potentilla erecta</i> | OW | 1 | 38 |
| <i>Rubus fruticosus</i> | OW | 78 | 127 | <i>Rosa canina</i> | OW | 15 | 70 |
| <i>Solanum dulcamara</i> | OW | 9 | 19 | <i>Rumex sanguineus</i> | OW | 7 | 61 |
| <i>Stellaria media</i> | OW | 6 | 10 | <i>Scrophularia nodosa</i> | OW | 5 | 37 |
| C. More frequent in clear-fells | | | | <i>Senecio sylvaticus</i> | OW | 0 | 13 |
| <i>Calamagrostis epigejos</i> | AWI g | 0 | 79 | <i>Stellaria holostea</i> | OW | 10 | 42 |
| <i>Holcus mollis</i> | AWI g | 15 | 94 | <i>Ranunculus repens</i> | OW | 0 | 14 |
| <i>Hypericum pulchrum</i> | AWI | 0 | 51 | <i>Veronica officinalis</i> | OW | 0 | 17 |
| <i>Potentilla sterilis</i> | AWI | 4 | 33 | <i>Viola riviniana</i> | OW | 15 | 43 |
| <i>Agrostis stolonifera</i> | OW g | 6 | 105 | <i>Cirsium arvense</i> | NW | 0 | 50 |
| <i>Ajuga reptans</i> | OW | 20 | 47 | <i>Cerastium fontanum</i> | NW | 0 | 15 |
| | | | | <i>Glyceria spp</i> | NW g | 0 | 11 |
| | | | | <i>Lotus uliginosus</i> | NW | 0 | 59 |
| | | | | <i>Sonchus oleraceus</i> | NW | 0 | 12 |

AWI = regional ancient woodland indicator; OW other woodland species; NW non-woodland species; g grasses

The DECORANA output similarly shows the separation between the plots from the grass-dominated clear-fell areas and those in the undisturbed woodland (more herb-dominated), with the ‘understorey removal’ plots tending to be in-between the two (Figure 5a). The plots recorded immediately post-felling in the 1988 clear-fell) were grouped with the undisturbed stands. Low axis 1 scores, where most of the clear-fell plots lie, were associated with high light and moisture Ellenberg plot scores and high competitor plot scores (Table 4); whereas high axis 1 scores (undisturbed plots) had higher stress-tolerator scores.

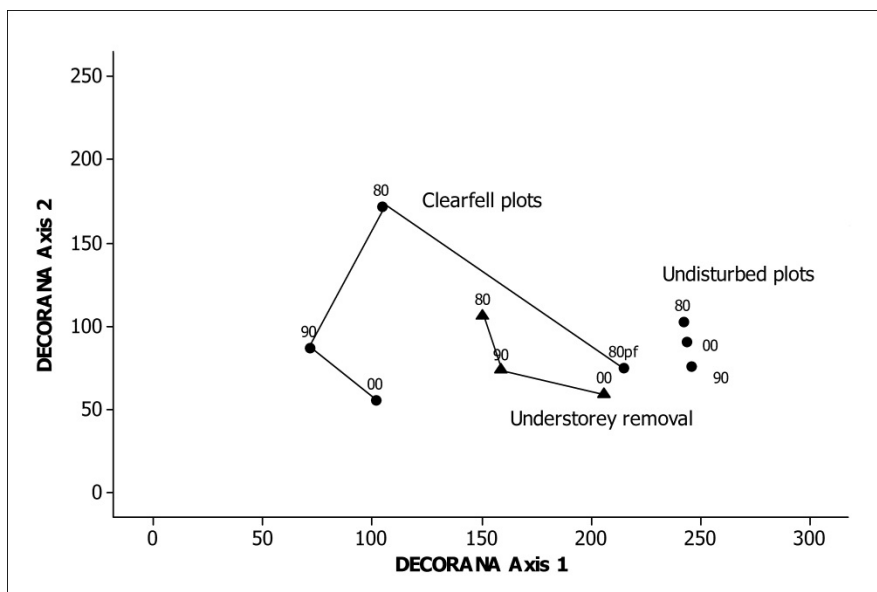
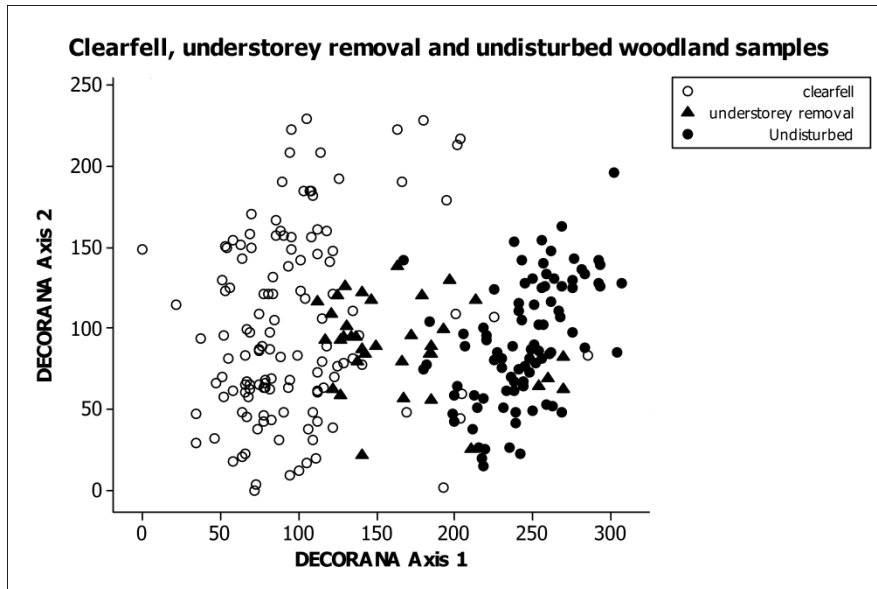


Figure 5. DECORANA output (a) Separation of different plot types according to their species composition on DECORANA axes 1 and 2; (b) Mean scores for plots grouped by decade of recording (80 = 1980s, 90 = 1990s, 00 = post 2000); 80pf represents the records for six plots in the 1988 clear-fell recorded in September 1988 immediately after felling.

The second axis of variation reflects change in the vegetation over time (Figure 5b). The data were grouped by the decade of recording, 1980s, 1990s, post- 2000 and the mean positions of plots on Axes 1 and 2 calculated for each decade. There is comparatively little variation for the undisturbed plots. The understorey removal plots were initially separate

from the undisturbed stand but are moving back towards them. The biggest initial change was in the clear-fells: non-woodland species (which tend to have high Ellenberg light scores and include more ruderal species) were most abundant in the early years of the clear-fells and contributed to the particularly high richness scores (Table 2). In the last decade vegetation appears to be starting to ‘move’ back towards that of the undisturbed woodland. The number of ancient woodland species (albeit different species) was similar in clear-fell to undisturbed woodland plots. They do however represent a higher proportion of the total species richness in undisturbed stands (Figure 6).

Table 4 Regression of mean plot scores tested against the two main DECORANA axes. The statistical significance is indicated by *= <0.05 , **= <0.01 , ***= <0.001 ; the correlation coefficient (R^2) indicates the percentage of the variation explained by this factor; while the final column shows if the association is positive or negative.

| | Axis 1 | | | Axis 2 | | |
|--|-----------------|------------------|-----|-----------------|----------------|-----|
| | Signif. | R ² % | +/- | Signif. | R ² | +/- |
| Ellenberg light values | *** | 83 | - | No relationship | | |
| Ellenberg soil wetness values | *** | 39 | - | ** | 3 | - |
| Ellenberg soil nutrient values | *** | 25 | + | *** | 8 | + |
| Grime Strategy type – competitor score | *** | 47 | - | *** | 11 | - |
| Grime Strategy type – stress-tolerator score | *** | 43 | + | *** | 13 | - |
| Grime Strategy type – ruderal score | No relationship | | | *** | 53 | + |
| Years since 1981 | No relationship | | | *** | 24 | - |

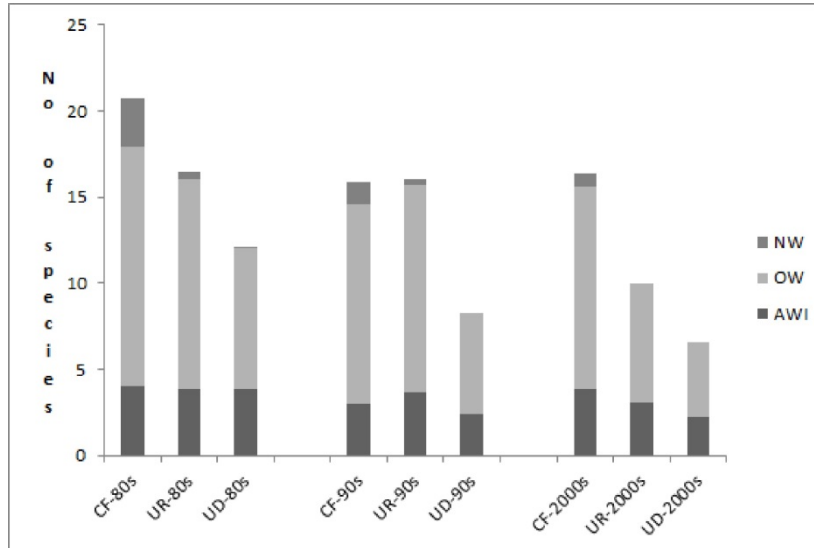


Figure 6. Contribution to mean plot richness by regional ancient woodland indicators (AWI), other woodland species (OW) and non-woodland species (NW) for plots grouped by stand (clearfell CF, Understorey removed UR, and Undisturbed UD) and by recording decade (1980s, 1990s, post-2000).

Discussion

The results from the undisturbed stands support the decline in floral richness seen in other British woods in recent decades under closed canopy high forest (Kirby *et al.*, 2005). The flora of the wood as a whole has also been recorded by walks through the stands and along the rides to detect species that are relatively scarce in the wood and hence unlikely to be picked up by small-scale plot surveys (Kirby *et al.*, 1986). Similar numbers of species were seen (88 in 1981, 80 in 2008) in a 2 hr walk and most of those seen in 1981, but not on the 2008 visit had been seen on other recent visits. This indicates that species have not necessarily been lost completely from the site, but rather it is their abundance in the closed oak stands that has been substantially reduced.

Peterken (1977b) and Rackham (1990) stressed that most ancient woodland in Britain had been managed in the past, often as coppice (as at Sheephouse until the 19th century). The frequent opening up of the canopy followed by rapid canopy closure favoured the development of rich displays of woodland flowers, characteristic bird and butterfly assemblages adapted to such conditions that are highly valued (Buckley & Mills, 2015a,b, in press).

Lengthening the period of dense canopy closure will hasten the loss of species associated with semi-shaded conditions which include some woodland specialists; however lengthening the open phase may equally be detrimental to them by allowing more opportunities for strongly competitive woodland generalists or non-woodland species to dominate (Decocq *et al.*, 2004, 2005; Itô *et al.*, 2012; Kirby, 2009; Kirby *et al.*, 2005; Kopecký *et al.*, 2013). At Sheephouse the rather open vegetation under the oak canopy with extensive areas of bare litter became a more or less complete cover of grasses within a couple of years after felling.

Opening up the stands changed the vegetation, but the increased species-richness was largely of woodland species – the non-woodland component was relatively small and declined over time. Ancient woodland species were relatively more important as components of the undisturbed stands (because there were fewer other species), but in absolute terms their richness was not much different in the clear-fells.

The clear-fells remained open for longer than would probably be considered desirable, either from a nature conservation or wood-production point of view. The delayed canopy closure has meant that there has been a little self-shading of the branches of the planted trees and many of them are of poor form. There are also indications that the cover of species such as bluebell is declining in some of the felled areas, even though no difference was detected in its frequency, as a consequence of increased grass cover. Now that the canopy has largely reformed the increased shade should reduce the abundance of the more light-demanding competitive species, particularly of the grasses *Agrostis stolonifera*, *Calamagrostis epigejos*, *Deschampsia cespitosa*, *Holcus mollis* and allow the relative contribution of woodland herbs to go up again.

Deer pressure has increased somewhat in the wood, as over most of lowland England (Ward, 2005), but it is thought that these have not been the major cause of the changes observed. Species-richness in heavily deer-grazed woods may increase, decrease or stay the same (Kirby, 2001). Deer pressure could have reduced the cover of bramble *Rubus fruticosus* in the undisturbed stands, but not necessarily its overall frequency; deer might also have been

expected to increase grass dominance in the ground flora under the canopy, not just in the clear-fells (Kirby & Thomas, 2000; Van Uytvank & Hoffman, 2009).

Sheephouse Wood is not unusual among British broadleaved woodland in its increase in canopy density over recent years (Amar *et al.*, 2010; Kirby *et al.*, 2005). Across Europe generally woods have also tended to become denser as harvesting has tended to be less than the annual increment (FAO, 2010); there has also been a comparable shift away from worked coppice to more high forest systems. Declines in ground flora abundance are therefore likely to be widespread.

The emphasis in this paper has been on the effect of changing light regimes on the ground flora, but there may also be changes in the soil conditions, particularly in pH, soil moisture, litter character and abundance and soil nutrient status caused by or happening in parallel to the structural changes (Kirby *et al.*, 2005; Van Calster *et al.*, 2007; Verheyen *et al.*, 2012). Some of the differences between the floral response to the 1984 and 1988 clear-fells for example may be because the former appeared to show a greater rise in the water table following felling than the latter.

In relatively small woods in cultural landscapes felling or thinning is generally the main gap-creation process, and hence the most important mechanism by which ground flora richness may be maintained. The frequency of gap formation is particularly important for species such as *Hypericum* spp. that rely on emergence from seed buried in the soil seed bank (Brown & Warr, 1992; Buckley *et al.*, 1997; Van Calster *et al.*, 2008). Since the 1984 and 1988 clear-fells are now closing over, should another area be felled? This may not be necessary, because we may be entering a period of increased ‘natural gap’ formation as tree deaths increase, through impacts of diseases such as ash dieback (*Hymenoscyphus fraxineus*) (Pautasso *et al.*, 2013; <http://www.forestry.gov.uk/pestsanddiseases>) or more extreme weather events such as storms (Smart *et al.*, 2014). Small gaps in high forest do not however necessarily produce the same ground flora response as larger coppice cuts: Decocq *et al.* (2004, 2005) found that selective thinning of the canopy favoured bramble, grasses and ferns (mostly woodland generalists in terms of this study) rather than vernal geophytes and other ancient forest species. At Sheephouse the ‘understorey removal’ which might be considered similar to a thinning initially produced a much smaller ground flora response than the clear-fell.

In addition, from a biodiversity perspective, it is not just the ground flora that must be considered; Sheephouse Wood for example was also designated as a site of scientific interest for its breeding bird and invertebrate assemblages, some of which benefit from closed high forest conditions (http://www.sssi.naturalengland.org.uk/Special/sssi/sssi_details.cfm?sssi_id=1001671); it also has a thriving woodland bat community. On other sites the development of humid, shaded high forest conditions may benefit the cryptogamic component of the ecosystem (although there are no data to suggest this is important at Sheephouse Wood) or species that depend on fallen dead wood (Kirby *et al.*, 1998). A decline in floral richness within some stands to favour other groups may then be part of the conservation management trade-off.

The low replication of samples in each year and irregular recording are a limitation in this study, a consequence of the work having to be fitted in amongst other programmes. However over the period of 30 years the results show consistent patterns that complement and help to validate chrono-sequence studies of forestry management effects. However while such casual observations can help to elucidate the processes underway on a particular site,

they do not detract from the need for more better-designed, structured studies of the biodiversity impacts of forest management (Gotmark, 2013).

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