Five decades of ground flora changes in a temperate forest: the good, the bad and the ambiguous in biodiversity terms.

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Author contributions

All authors contributed to the data recording and commented on results and analyses; the first author was responsible for the main writing of the paper.

Highlights

- Five decades of ground flora change recorded from permanent plots at Wytham Woods
- Species-richness declined because of the loss of open-ground species.
- Vegetation cover and biomass were impacted by changing deer-levels.
- Future changes from eutrophication and consequences of Ash Dieback are discussed.
- Forest management can influence some changes; others need action at landscape scale.

Abstract

We explore how the ground flora of a temperate woodland (Wytham Woods, southern England) changed in terms of species-richness, cover and biomass over five decades; what the drivers of change were; and possible future change as a consequence of the decline in *Fraxinus excelsior* as a canopy dominant. Vascular plants were recorded from 164 permanent, 10x10 m plots, distributed as a 141 m grid, in 1974, 1991, 1999, 2012, and 2018. Species presence and frequency/abundance in each plot were estimated and used to model biomass changes. Changes in species-richness, vegetation composition and structure were analysed. Stands opened out by thinning or which became denser through tree growth gained or lost species respectively, particularly non-woodland species. Deer pressure favoured the spread of *Brachypodium sylvaticum* and reduced *Rubus fruticosus.* No obvious impacts of climate change, eutrophication or of invasive species were detected in the plot records although other signs suggest these are starting to affect the flora. Just 12 out of 235 species contributed 47% of all species occurrences, 82% of the vegetation cover and 87% of the modelled biomass. We conclude that the ground flora is highly variable over decadal timescales, but the patterns of change observed differ according to the measures used (species richness, cover, biomass, etc). Site level drivers in the short-term swamped effects of slower acting regional/global drivers. Legacy effects were seen in the greater richness of specialists in the older woodland. While some impacts can be mitigated by management, others are largely beyond control at the site level.

Key words. Long-term monitoring and surveillance; forest management; Ash Dieback; vegetation homogenisation; eutrophication; woodland vegetation change; *Rubus fruticosus*; permanent plots; woodland specialist plants.

1. Introduction

Many woodland species, including vascular plants, show declines across Britain and this may also be seen at individual sites (Kirby et al., 2005; State of Nature Partnership, 2019). Assessing increases or decreases in the ground flora is often based on monitoring permanent plots, e.g. Klynge et al. (2020). Here we describe changes over five decades from one such plot system.

The ground flora or herbaceous layer plays an important role in the functioning of temperate woodland ecosystems providing food and shelter for much of the fauna, inhibiting or facilitating tree regeneration, absorbing and releasing nutrients through its annual growth cycles. The ground flora is also valued in nature conservation terms because it often comprises about 80% of the vascular plant species in the forest and provides spectacular displays of spring flowers (Gilliam, 2014; Kirby 2020a).

However, the current composition and structure of the ground flora is influenced by conditions and events from decades or centuries earlier (Perring et al., 2018). There are differences between ancient and recent woodland floras (Peterken and Game, 1984; Rackham, 2003); the effects of past management interventions or periods of minimal intervention (Ash and Barkham, 1976; Buckley and Mills, 2015; Kirby 1988, 2015; Peterken and Mountford, 2017; Tinya 2009); the impact of grazing by large herbivores (Cooke, 2019; Kirby 2001) or extreme weather events (Smart et al., 2014). Some species may have been favoured (or not) by increasing atmospheric nitrogen deposition (Keith et al., 2009; Verheyen et al., 2012) or by climate change (De Frenne et al. 2013; Pearce-Higgins et al., 2017). These various drivers may operate alone or in combination (Bernhardt-Römermann et al., 2015; Kirby et al., 2005). Long-term measures of change in the ground flora are therefore desirable.

We analysed changes in species-richness, vegetation structure and composition collected across five decades from a long-term permanent plot system established in 1973-1976 in Wytham Woods (Dawkins and Field, 1978). Such vegetation changes may contribute to or explain variations in the populations of the fauna, that are the subject of other long-term studies in the Woods (Savill et al., 2010). Analysis of the drivers of change at Wytham may shed light on increases or decreases in plant species of conservation concern across lowland England (Plantlife, 2011). Understanding past variations also provides the context for assessing likely future change from the expected decline of European ash *Fraxinus excelsior* as a consequence of the fungal disease Ash Dieback, both in Wytham Woods and more generally across the UK (Mitchell et al., 2016; Pautasso et al., 2013).

2. Site

Wytham Woods lie about 8 km north-west of Oxford in southern England (Figure 1a; latitude 51° 46’38.4’’north; longitude 1° 20’ 23.56’’ west; elevation c.60-160m) (Savill et al., 2010). The mean soil pH from samples taken in 1974 was 6.8 (standard error 0.05); the top of the hill has shallow soils developed from Corallian Rag limestone, the lower slopes have more clay (Taylor et al., 2010). The main wood consists of 360 ha of mixed, mainly broadleaved woodland with a variety of histories summarised in Figure 1 (Kirby et al., 2014).

Figure 1. (a) Location of Wytham Woods in the UK; (b) the distribution of the permanent plots used in this study and their histories.

The main canopy trees are European ash *Fraxinus excelsior* (25% of the canopy), sycamore *Acer pseudoplatanus* (20%), beech *Fagus sylvatica* (10%) and oak *Quercus robur* (8%) (Supplementary table S1). Ash is present in 90% of the plots, has been spreading since 1974 and is the most common tree seedling or sapling (Kirby 2020b; Kirby et al., 2014). Ash Dieback was first confirmed in the Woods in 2017 and is now widespread.

Until the mid-twentieth century the Woods were actively managed, either as high forest or coppice with standards. Since 1950 about a third of the woodland, primarily the older formerly-coppiced stands, has been under minimum intervention, that is no silvicultural management takes place. Elsewhere, the main interventions since 1974 have been the thinning of 20th Century plantations (Wytham Management Committee, 2020).

Deer were largely absent from the Woods in the 19th and early 20th Century as from much of lowland Britain (Ward, 2005). A small herd of fallow deer *Dama dama* were present in the 1940s (<20 individuals) and numbers increased until the 1990s (>375 individuals). Muntjac *Muntiacus reevesi* were first seen in the Woods in 1967 (Elton 1942-1967); and roe deer *Capreolus capreolus* in the

1970s. Since the 1990s the deer populations have been reduced by shooting to c.45 fallow, c.45 roe and a small number of muntjac (Savill et al., 2010; Wytham Management Committee, 2020).

Atmospheric nitrogen deposition has increased across Britain since the mid-twentieth century and impacts on semi-natural vegetation have been widely reported from other habitats (Field et al., 2014). Woodland habitats are also considered at risk from climate change (Morecroft and Speakman, 2013).

3. Methods

3.1 Plot locations and marking procedures

In the early 1970s intersections of a 100 x 100 m grid were marked with wooden posts across the Woods (Dawkins and Field, 1978). At alternate posts, a 10x10 m vegetation plot was established giving 164 plots on a 141.1 m grid layout. The plots are 14.1 m offset from the post position on a bearing of 45^{o} true. Metal markers were buried at the post, at the south-west and north-east corners of the plot which could be subsequently re-located using a metal detector. The vegetation was recorded as part of the original project (the 1974 recording – see next section) and re-surveyed in 1991-92 (the 1991 recording); 1999-2002 (the 1999 recording); in 2011-12 (the 2012 recording) and in 2018.

3.2 The vegetation record

Dawkins and Field (1978) describe the 1974 vegetation recording. The tree and shrub records from subsequent surveys are reported in Kirby (2020b), Kirby et al. (2014) and in Supplementary Tables S1, S2. This paper uses the estimates of percentage canopy cover (>2.5 m high) made across the diagonal of the plot (Figure 2) as one surrogate for light availability for the ground flora.

Figure 2. Layout of the 10 x 10 m recording plot from Dawkins and Field (1978). (a) in profile showing the recording of the vegetation layers across the main south-west to north-east diagonal; (b) in plan view showing the positions of the 13 0.1m^2 subplots (‘circlets’).

The ground flora results presented here are based on:

- A list of vascular plant species rooted within the plot (excluding tree and shrub regeneration);
- Vegetation cover, generally less than 0.5 m high estimated along the south-west to north-east plot, but tall herbs *Rubus fruticosus* also contributed to the 0.5-2.5 m layer;
- The frequency with which a species was found rooted in a set of 13 circlets (round ‘quadrats’ covering 0.1 m^2 each) distributed across the two plot diagonals (Figure 2); the circlet positions were not precisely relocated, so species occurrences in individual circlets in a plot were not compared across recordings, only the overall frequency for the plot;
- Estimates of species cover: in 1974 a five-point scale was used for six species (*Chamerion angustifolium, Hyacinthoides non-scripta, Mercurialis perennis, Pteridium aquilinum, Rubus fruticosus, Urtica dioica*) (Table 1), previously identified as common within the Woods (Elton 1966; Osmaston 1959). In the subsequent recordings cover-abundance scores were assigned to all species using the Domin scale.

Table 1. 1974 cover scores and Domin scores with percentage cover equivalents

1974 cover score	% cover mid-point	Domin scores and % range	% cover mid-point
0	0	0	0
		1 one plant	1

1	1-5%	2.5	2	two plants	2
			3	a few plants	3
2	6-25%	15	4	4-10%	7.5
			5	11-25%	17.5
3	26-50%	37.5	6	26-33%	29
			7	34-50%	41.5
4	51-75%	62.5	8	51-75%	62.5
5	76-100%	87.5	9	76-90%	82.5
			10	91-100%	95

Recording took place between May and August except for four plots recorded in September in 1974, spread across more than one year, except for 2018, because of other work commitments. None of the 1974 surveyors could help with the subsequent re-recordings, but the first author was involved in all the recordings since 1991, providing continuity and consistency of practice. Some of the vernal flora will have been under-recorded later in the summer, but the most important of these in Wytham, *Hyacinthoides non-scripta* was still easily detected even in late August from the dead stems.

Plant species names follow Stace (2010).

3.3 Analysis of changes in species-richness, composition, and vegetation structure

Species-richness was assessed for the whole set of 164 plots; for subgroups of plots representing different woodland types (Figure 1) and as mean values for individual plots. To aid interpretation of the changes, species were grouped into Woodland specialists, often strongly associated with woodland conditions in Britain; Woodland Generalists, common in woodland but widespread in other habitats; and Non-woodland species, generally found outside woodland and mainly in glades within woods (Kirby et al. 2012).

The changing composition of the plots was assessed by calculating the similarity of a plot to its record from previous recordings using Sorensens's Similarity Index: $S= 2c \times 100/(a+b+2c)$ where c = species found on both occasions; a and b are the numbers found on only one or the other occasion. Sorensen's Index was also used to calculate the similarity between plots across each recording time, as a measure of the homogeneity of the vegetation (Keith et al., 2009). Variations in plot composition were also explored using Detrended Correspondence Analysis (DECORANA).

Vegetation cover changes were examined after converting the Domin values from the 1991-2018 recordings into a percentage value based on the mid-point of the range (Table 1). This is only an approximation of the cover but as 84% of records were for Domin values 1-3 (less than 4% cover) we did not think that more nuanced approaches such as Currall (1987) were necessary. The same approach was used with the 6-point cover score used in 1974, but these scores were only made for the six species previously judged to be common in the Woods. For the remaining species in 1974 a derived cover for 1974 was calculated using the general relationship between the cover scores from 1991-2018 Domin values (all species) and the corresponding circlet frequency value (the number of times a species occurred in the 13 circlets in that plot) plus 1 (to account for species in the 10 x 10 plot but not found in the circlets): Cover =-2.2+2.66 x circlet score; R^2 = 42%; F = 7338, DF 1, 10,233. This equation was then used to calculate a likely cover for each species in 1974 from its 1974 circlet score (Supplementary Table S3). We used the same relationship for all species: we considered developing species-specific equations, but for many species there would have been very few points so that the relationship would have been very poor. Moreover as most species were present in most plots at only very low abundance (84% of the species plot-records were given Domin scores <4% cover) any minor differences in the relationships were not likely to have a major effect.

The cover estimates were used to model biomass changes for individual species and for individual plots through the Phytocalc approach (Bolte et al., 2004; Schulze et al., 2009) according to the equation:

$$P = a \times PC^{b} \times MS^{c}$$

- P= Above ground biomass (dry matter, 105°, g m^{-2});
- PC= Percentage cover (species, species group);
- MS= Mean shoot length (above ground, cm);
- a,b,c are empirical parameters obtained by fitting measured data in the original study (Bolte et al., 2004).
- The shoot lengths used in the equations were based on 5-10 measurements across Wytham for the most common 74 species and generic values from the original studies for the remaining species.

The above should be seen as providing only a rough indication of ground flora biomass, but we used it because it should reflect changes in the potential forage for deer or shelter and nesting space for small birds and mammals better than direct vegetation cover alone.

3.4 Exploring possible causes of change

Changes in the ground flora richness 1974-2018 were compared with the corresponding change in canopy cover. Small differences in canopy cover per plot made little difference to conditions for the ground flora. Therefore, mean species-richness change was calculated separately for plots where an increase of more than 25% canopy cover was recorded over the whole period (20 plots) compared with those where the canopy decreased by more than 25% (36 plots). The effect of canopy disturbance on species-richness was also explored by comparing the change when there had been a thinning or major tree fall between two recordings with the change for woodland plots where no such disturbance had occurred.

The 1974-1999 period was characterised by an increasing deer population whereas the numbers have been brought down since. Species-change in the two periods was compared.

The distribution of plots and species along the axes of variation in the DECORANA analysis were explored using Ellenberg Indicator Values (EIV) for Light, Moisture, Reaction (pH) and Nitrogen as modified for British conditions (Ellenberg, 1988; Hill et al., 2004); and using species mean values for January Temperature, July temperature and annual precipitation requirements (Hill et al., 2004).

Statistical analyses were performed using the Minitab package (V.18; www.minitab.com) and Community Analysis Package (Pisces Publishing, 2002; www.pisces-conservation.com).

3.5 Storage of the data

A hard copy of the 1974 records and the original field sheets for subsequent recordings are currently held by the first author; copies of the data used in this paper are being prepared for deposit in the Wytham Woods Data-base https://www.wythamwoods.ox.ac.uk/research-woods and in the Oxford University Research Archive *https://ora.ox.ac.uk/objects/uuid:948a1302-5023-4216-b5a4-3e815dfe95ed*

4. Results

4.1 Variations in species richness and species types

The number of species found across all plots declined by about 20% in the first 25 years but has been fairly stable since. The mean number of species per plot was relatively stable overall apart from a small decline in 2018 (Table 2). Recording in 2018 started in June and there was a severe summer drought, such that more of the vernal species may have been missed in that year. Plots in stands that had been disturbed by planting in the twentieth century had higher than average species richness in 1974 but were little different to the semi-natural stands by 2018 (Figure 3).

Table 2. Species-richness, change over the five recordings for all plots

Recording time	1974	1991	1999	2012	2018
No of vascular plants recorded across all plots	182	171	147	158	141
Mean no per plot ± std err	16.8 ± 0.7	17.3 ± 0.8	15.5 ± 0.6	16.2 ± 0.6	13.5 ± 0.5
Range	4-62	0-49	0-45	0-43	1-39

Figure 3. Mean species richness per plot for different types of plot (see Figure 1); stands disturbed by 20th C planting are indicated by the arrows.

The Ride and Glade plots had much higher species-richness than those in closed woodland stands (Table 4), particularly in terms of the proportion of Non-woodland species (0.39) compared to Woodland specialists (0.13); the reverse was the case for the older plots such as the Pre-1800 semi-natural stands - Non-woodland species (0.07) Woodland specialists (0.25). A chi-squared test (using the species number, not proportion) comparing the different balance of species types between these plot types was highly significant: chi-squared = 34, df 2, $p<0.001$.

From 1974 to 2018 the occurrences of Non-woodland species within the 10x10 m plots declined significantly: from 33% of species and 8% of occurrences in 1974 to 27% of species and 4% of occurrences in 2018 (chi-squared for change in occurrences = 58, df = 2, $p<0.001$). The abundance of Woodland specialists remained stable.

Table 4. No/proportion of species and occurrences for Non-woodland species, Woodland generalists and Woodland specialists. Each occurrence represents the presence of a species in a 10x10 m plot at one recording time.

	Total no of species	Proportion of:			Total no of occurrences, all species	Proportion of occurrences by:		
		Non-woodland	Woodland generalists	Woodland specialists		Non-woodland	Woodland generalists	Woodland specialists
1. pre-1800, semi-natural (29)	98	0.07	0.67	0.26	2103	0.01	0.78	0.21
1a.pre-1800, disturbed (40)	125	0.18	0.58	0.24	2809	0.02	0.76	0.22
2. 19th C. semi-natural (19)	104	0.14	0.66	0.19	1332	0.02	0.80	0.18
2a. 19th C. disturbed (11)	93	0.17	0.67	0.16	682	0.04	0.79	0.17
3. 19th C. plantation (27)	120	0.21	0.61	0.18	1727	0.03	0.79	0.18
4. 20th C. wood (15)	141	0.29	0.55	0.16	1170	0.12	0.77	0.11
5. Rides and glades (23)	188	0.39	0.47	0.13	3165	0.15	0.71	0.14
All 164 plots (164)	235	0.38	0.45	0.17	12988	0.06	0.76	0.18

	No of species 1974 and 2018 compared				No of occurrences, 1974 and 2018 compared			
	All species	Non-woodland	Woodland generalist	Woodland specialist	All species	Non woodland	Woodland generalists	Woodland specialists
1974 recording only	182	61	95	26	2753	224	2127	402
2018 recording only	141	38	72	31	2220	87	1682	451
Species present in 1974 but not in 2018	60	31	27	2	186	60	123	3

4.2 Changes in vegetation structure

The percentage cover of the ground flora declined from the 1974 to 1999 recordings but recovered subsequently (Figure 4a). Part of the decline in 0.5-2.5 m cover after 1974 was due to elimination of many tall dense *Rubus fruticosus* thickets. The modelled biomass showed a much larger drop from the 1974 levels and a lesser recovery. This overall biomass change was largely caused by the change in the contribution of *Rubus fruticosus* (Figure 4b).

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Figure 4. (a) Change in layer cover and in the cover of *Rubus fruticosus*; (b) The contribution of *Rubus fruticosus* to the changes in modelled biomass.

The structure of the vegetation (its cover, height and modelled biomass) was largely determined by just twelve out of 235 species recorded. These contributed 47% of all species occurrences in the 10 x 10 m plots, 82% of the recorded vegetation cover and 87% of the modelled biomass (Table 5).

Table 5. Contribution of the twelve commonest species in terms of number of plot occurrences, mean % Cover per plot, mean biomass per plot across all five recordings.

	Mean no of plot records per recording (out of 164)	Mean % cover per plot	Mean biomass per plot (g m^{-2})
Rubus fruticosus	136	14.0	66.0
Poa trivialis	128	4.2	4.7
Mercurialis perennis	127	21.7	18.0
Brachypodium sylvaticum	126	8.6	10.4

Urtica dioica	114	8.7	7.7
Deschampsia cespitosa	104	2.6	1.1
Circaea lutetiana	98	2.1	0.8
Glechoma hederacea	85	1.9	0.9
Hyacinthoides non-scripta	80	5.2	3.4
Geum urbanum	78	1.0	0.3
Galium aparine	77	1.7	1.0
Pteridium aquilinum	76	8.0	8.4

4.3 Changes in the composition of the plots.

There was a high turnover of species: about twice as many species were recorded from a plot over the whole five recordings as were found at any one time (supplementary Figure S2). The similarity between a plot record and the previous recording for that plot decreased with increasing time between recordings (Figure 5). Shifts in the composition of the different types of woodland were also illustrated by the DECORANA analysis (Figure 6).

Figure 5 Decreasing similarity of a plot record with its previous recording with increasing time interval between recordings. The regression line is based on individual plot values but only the mean values for each year-on-year comparison are shown: i.e. 12_18 is the mean similarity for the plots in 2012 compared to 2018; 74_18 is the mean for the plots in 1974 compared to 2018). %similarity = 70 – 0.5xYear_difference; DF 1,1633, p<0.001, R^2 = 12%.

4.4 Stand openness as a driver of ground flora change

The difference in plot species richness (2018-1974) was weakly related to the estimated change in percentage canopy cover over the same period (Supplementary figure S1. Species no change = -3.9 – 0.07Canopy_change, DF=1,162; F=12.9; P<0.001; R^2=6.8%). Where there was an increase of more than 25% canopy cover between 1974 and 2018 (20 plots) mean richness declined by -9.5±2.3 species per plot; whereas where the canopy decreased by more than 25% (36 plots) the mean richness change was only -1±1.1 species. Species-richness was more likely to increase at the next recording where a disturbance such as thinning or a tree fall had occurred (50 instances across all recordings). The mean change per plot was an increase of 4.2 ± 1.1 species compared with plots where no disturbance was recorded between recordings (514 instances) where the mean change was a loss of 1.3 ±0.3 species.

In the DECORANA analysis Axis 1 scores for plots were significantly negatively correlated with the canopy cover estimates made along the diagonal of the plot (supplementary figure S4). The reduction in non-woodland and increase in woodland specialist occurrences between 1974 and 2018 was reflected in the general shift towards the low end of Axis 1 for the woodland plots while the Rides and Glade plots are separated off to the high end of the axis.

Non-woodland species clustered at the positive (low canopy cover) end of Axis 1 with Woodland-specialists which are more shade-tolerant at the negative end (Figure 6b). Axis 1 scores were positively related to Ellenberg Indicator Values for light on the species ordination (Figure 6c). The closeness of the 20th Century plantations to the Ride and Glade plots in 1974 reflected the survival of open ground (non-woodland) species from the previous land-use, but by 2018 these plots were mixed-in with those from the older woodland, i.e their flora had become more of a forest-type composition.

Figure 6 (a). DECORANA analysis output: mean positions for different groups of plots (Figure 1) across the 5 recordings; (**b)** DECORANA analysis: species distribution: Woodland specialists , Woodland generalists, Non-woodland species; (c) Mean species scores on Axis 1 set against their EIV-Light Score; (**d)**. Mean DECORANA Axis 2 score for each EIV-Reaction score group of species.

The 19th Century plantation plots (group 3, Figure 1) diverged from the other woodland plots on Axis 2. This axis separated species according to their Ellenberg Indicator Values for soil reaction (pH) (Figure 6d) and was significantly correlated with species mean precipitation requirements (Hill et al., 2004) (Axis 2 score = 793-0.71 x mean precipitation; $F=47$, DF 1, 229; $p<0.001$; $R^2=16\%$, Supplementary Figure S4). Most of the plots in this divergent group are clustered on the shallow limestone soils on the top of the hill, which may be more sensitive to drought.

4.5 Periods of increasing and decreasing deer pressure

During the period of increasing (1974-1999) deer pressure there was increasing homogenisation of the ground flora with any given pair of plots being more likely to show an increase in similarity in terms of the Sorensen's Similarity Index. This trend was reversed for the period 1999 to 2018 when the deer numbers were being reduced (Figure 7a). From 1974 to 1999 many plots showed increases in cover of *Brachypodium sylvaticum* and declines in cover of R*ubus fruticosus*, whereas the reverse pattern was seen in the 1999 to 2018 recordings (Figure 7b).

Figure 7a. Distribution of differences in the Similarity Index for any given plot-pair, during the period of increasing deer numbers (Sim_{1999}-Sim_{1974}) and decreasing deer numbers (Sim_{2018}-Sim_{1999}).

Figure 7b. Change in cover of *Brachypodium sylvaticum* and *Rubus fruticosus* in the periods 1974-1999 contrasted with that for 1999-2018.

4.6 Climate change, eutrophication, invasive species

Comparison of the mean January and mean July temperature requirements for species occurrences across the recordings provided no indication for thermophilisation of the flora. There was also no general increase in high EIV-N-score species or any relationship between EIV-N mean plot scores and axis scores in the DECORANA outputs which might indicate widespread eutrophication.

Invasive non-native ground flora species currently make up a very small part of the total flora: daffodils (*Narcissus* varieties) and snowdrops (*Galanthus nivalis*) were planted for ornament in the early 20th century but are present in only 2 plots. In the last decade, small colonies of small balsam *Impatiens parviflora* and Sicilian honey-garlic *Nectaroscordum siculum* have spread into the Woods although so far only recorded in one plot each. Himalayan balsam *Impatiens glandulifera* has been seen in the Woods but not in the plots.

5. Discussion

Over the five decades changes have occurred in the species richness, species composition, cover and biomass of the ground flora at the individual plot level. What these mean in biodiversity terms depends on which measures are used and how the plot results are combined (Klynge et al. 2020).

Species-richness declines are often regarded as ‘bad’ in biodiversity terms, but in this study the overall decline recorded in the 164 plots is mainly reduction in the Non-woodland species, linked to increasing shade as the former coppiced stands have grown into high forest and the recovery of the areas disturbed by 20th Century plantings. This might therefore be seen as a ‘good’ biodiversity outcome. The composition of the plots has become increasingly dissimilar to their composition in 1974 (‘bad’ if our aim were to maintain the 1974 state), but the movement of the younger stands, mainly plantations, towards the composition of the older semi-natural stands again could be seen as a ‘good’ result.

Gains or losses of uncommon woodland plants such as the orchid *Epipactis purpurata* (3 occurrences over the five recordings) may attract attention in nature conservation debates but the numbers involved are too small to draw reliable conclusions. The dozen common species have a greater influence on how the ground flora competes with tree regeneration, how it functions in terms of nutrient dynamics, and the habitats it provides for the fauna. The decline in *Rubus fruticosus* cover and biomass for example during the middle part of the study contributed to declines in some bird species and changes to the small mammal populations (Bush et al. 2012; Perrins and Overall, 2001); its ongoing recovery could lead to reductions in ground flora richness (Kirby and Woodell, 1998; Marrs et al. 2013) and less favourable conditions for foraging badgers *Meles meles*.

The recolonisation by roe deer – a native species – is a biodiversity gain; attitudes to fallow deer, a long-established introduction to Britain are more ambiguous; while muntjac as a recent invasive introduction is seen as generally bad for biodiversity. The desirable/acceptable level of roe and fallow (even if muntjac could be eliminated) is however a value judgement – is a grass (high deer) or *Rubus* (low deer) dominated flora the more desirable?

5.1 Likely causes of change and the role of site management

Changes in canopy density and deer pressure appear to have been major drivers of change in species-richness, species-composition and vegetation structure as in long-term vegetation studies elsewhere (Baeten et al., 2009; Cholewińska et al., 2020; Chytrý and Danihelka, 1993; Crampton et al., 1998; Fischer et al., 2009; Hedl et al., 2010; Hedwall et al., 2019; Kirby et al., 2005; Persson et al., 1987; Strubelt et al., 2019; Vild et al., 2017; Walther and Grundmann, 2001). Both the degree of shading and deer grazing are potentially within the control of forest manager through altering patterns of thinning and felling, or through fencing and culling and therefore may be used to favour the desired components of the ground flora.

World-wide invasive non-native plant species are a threat to biodiversity; for example *Alliaria petiolata* is a serious pest where it has been introduced to North American forests (Anderson et al. 1996). To date non-native invasive ground flora plants have not been significant problem in Wytham Woods: those perceived to be a possible future threat, such as *Impatiens parviflora* and *Nectaroscordium siculum,* could be controlled while they are at these current low levels.

A related issue is the potential spread of native species in response to increased nitrogen deposition. No general eutrophication signal was detected in the woodland flora at Wytham, but other observations are consistent with eutrophication starting to have an effect on the ground flora as hypothesised by Corney et al. (2008) and Verheyen et al. (2012): for example increases in *Allium ursinum* (EIV-N 7), *Alliaria petiolata* (EIV-N 8) and *Galium aparine* (EIV-N 8) (Kirby 2016). The spread of such species could be seen as 'bad' in biodiversity terms because they compete with other native plants or because they are a symptom of human-induced change.

Climate change impacts on the ground flora may have been limited to date by the microclimatic buffering provided by the canopy (De Frenne et al., 2013). Opening up of the canopy could favour thermophilisation of the ground flora (Govaert et al., 2021), providing an argument for maintaining high shade levels through the Woods. The differences in microclimate between the base and top of the hill and between north and south facing aspects could help species to survive, even if their current location in the Woods becomes less suitable (Suggitt et al., 2018).

5.2 Potential for future ground flora change because of Ash Dieback

European ash *Fraxinus excelsior* is widespread in British broadleaved woodland (Forestry Commission, 2012; Rodwell, 1991). The fungal disease Ash Dieback caused by *Hymenoscyphus fraxineus* (Pautasso et al., 2013) was first confirmed in Britain in 2012 although it had probably been present earlier (Wylder et al., 2018). Reductions in ash are expected to affect the cover and richness of the vascular plants in the field and ground layers (Mitchell et al., 2014, 2016). The disease was first confirmed in Wytham Woods in 2017 and by 2021 many ash trees showed 20-30% canopy dieback. There are concerns as to how the composition and structure of the Woods, including in the ground flora, will change as a consequence. The 2018 survey provides a detailed baseline against which we can measure such changes, while the longer-term record illustrates how other factors will need to be taken into account.

From the plot results in this study little effect on ground flora richness might be expected where ash provides less than 20% of the canopy; the canopy gaps created will be small. Where ash is more abundant and bigger canopy gaps form, then short-term increases in species-richness and the favouring of *Rubus fruticosus* growth are likely. This should favour small mammal and bird populations that favour dense vegetation in the 0.5-1.5 m height range but possibly lead to abandonment of some badger sets. However, the *Rubus* increase might be limited if deer numbers were to rise again, as in the period 1970-1990. In the longer-term, shrubs, such as *Corylus avellana, Crataegus* spp. and *Prunus spinosa*, and canopy trees such as sycamore or beech may fill the gaps (Needham et al., 2016); stands are likely to become shadier and reductions in *Rubus* cover and in ground flora richness are then expected**.**

5.3 Limitations of the present study

The results presented show that the woodland flora is not static but varies dynamically over time and space. The use of permanently marked plots means that it is easier to separate temporal and spatial effects, provided the plot relocation is precise. The buried metal markers at two plot corners made this generally possible, but in all re-recordings there were one or two plots where the markers could not be detected at the time: for example tall vegetation or piles of fallen branches can prevent the metal detector picking up a signal. However, a combination of detailed maps and the positions of large trees meant that the 10 x 10 m plot re-recordings were not more than a few metres off the original locations and in 2018 all but a handful of the original metal markers were eventually re-found.

Ideally the plots would be recorded twice in a season to avoid missing early or late growing species; all in one year, to reduce the effect of inter-annual variations; and with the same observers to reduce differences is survey capability. These requirements are difficult to reconcile for a large number of plots where the project has to be fitted in amongst other work commitments. We have therefore been conservative in identifying changes, if it seemed likely that season, year or observer bias might be a factor.

We were only able to make very rough estimates of ground flora biomass, using a model developed for German woodland, with only approximate estimates of vegetation height and cover. However, the mean values over the five recordings (from about 50 to 300 g m^{-2}) are comparable with values reported elsewhere for British woodland and Continental woodland, e.g. Landuyt et al., (2020), Ovington (1955). Dense stands of *Rubus fruticosus* were recorded with more than 400 g m^{-2} in Wytham Woods in 1974 (Kirby, 1980) which again suggests that the high biomass values for 1974 are realistic.

This is a single site study; however, Wytham Woods show many of the characteristics of other woods in the lowland England (Kirby et al., 2014), so that this unique (for the UK) long-term study of floral change can provide insights into the results from multi-site national surveillance and conservation monitoring programmes (Goldsmith, 2012; Hurford and Schneider, 2006; Kirby et al., 2002, 2005; Natural England, 2012).

5.4 Implications for other assessments of ground flora changes

- The patterns of change observed differ according to the measures used (species richness, cover, biomass, similarity/homogeneity indices).
- Different types of species and different individual species show varying patterns of change – this affects interpretation of biodiversity changes.
- Common species as well as rare ones should be studied because the former are critical to ecosystem functioning through contributing the bulk of the cover and biomass.

- Drivers of change operate at different temporal and spatial scales, gradual change associated with increased shading; more sudden effects when a gap is created; impacts of deer in the initial rapid population build-up phase are likely to be more noticeable than recovery after control measures are instigated (Tanentzap et al. 2012).
- Local drivers (changing shade levels, deer pressure) may in the short-term swamp effects of slower acting regional/global drivers such as nitrogen build-up or climate change.
- Legacy effects such as the greater richness of specialists in the older woodland, are common; woods have ecological memory built-in (Ogle et al., 2015).
- Plot recording can detect events such as the establishment of the invasive *Impatiens parviflora*, but by the time there are sufficient records to say that there is a statistically significant effect, it might be too late to manage the problem.

The Wytham plots were set up on the assumption that the vegetation would change, and that posterity would want to understand the magnitude, history, causes and consequences of those changes (Dawkins and Field, 1978). No specific assumptions were made in designing the system about what would happen or be of interest in future decades. It is a tribute to the farsightedness of the originator H.C. Dawkins that fifty years later the data collected are relevant to tomorrow's concerns such as the impact of Ash Dieback.

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References

Anderson, R.C., Dhillion, S.S., Kelley, T.M., 1996. Aspects of the ecology of an invasive plant, Garlic Mustard (*Alliaria petiolata*), in Central Illinois. *Restoration Ecology* 4, 181-191. https://doi.org/10.1111/j.1526-100X.1996.tb00118.x

Ash, J.E., Barkham, J.P., 1976. Changes and variability in the field layer of a coppiced woodland in Norfolk, England. *Journal of Ecology* 64, 697-712. https://doi.org/10.2307/2258779

Baeten, L., Bauwens, B., De Schrijver, A., De Keersmaeker, L., Van Calster, H., Vandekerkhove, K., Roelandt, B., Beeckman, H., Verheyen, K., 2009. Herb layer changes (1954-2000) related to the conversion of coppice-with-standards forest and soil acidification. *Applied Vegetation Science* 12, 187-197. https://doi.org/10.1111/j.1654-109X.2009.01013.x

Bernhardt-Römermann, M., Baeten, L., Craven, D., De Frenne, P., Hédl, R., Lenoir, J., Bert, D., Brunet, J., Chudomelová, M., Decocq, G., Dierschke, H., Dirnböck, T., Dörfler, I., Heinken, T., Hermy, M., Hommel, P., Jaroszewicz, B., Keczyński, A., Kelly, D. L., Kirby K.J., Kopecký, M., Macek, M., Máliš, F., Mirtl, M., Mitchell, F.J.G., Naaf, T., Newman, M., Peterken, G., Petřík, P., Schmidt, W., Standovár, T., Tóth, Z., Calster, H.V., Verstraeten, G., Vladovič, J., Vild, O., Wulf, M., Verheyen, K., 2015. Drivers of temporal changes in temperate forest plant diversity vary across spatial scales. *Global Change Biology* 21, 3726-3737. https://doi.org/10.1111/gcb.12993

Bolte, A., Lambertz, B., Steinmeyer, A., Kallweit, R., Meesenburg, H., 2004. Zur Funktion der Bodenvegetation im Nahrstoffhaushalt von Waldern – Studien auf Dauerbeobachtungsflachen des EU Level II-Programms in Norddeutschland. *Forstarchiv* 75, 207-220.

Buckley, G. P., Mills, J., 2015. The flora and fauna of coppice woods: winners and losers of active management or neglect. In: Kirby K. J., Watkins, C. (Eds.) *Europe's changing woods and forests: from wildwood to managed landscapes.* CABI, Wallingford, pp.129-139.

Bush, E. R., Bueesching, C. D., Slade, E. M., Macdonald, D. W., 2012. Woodland recovery after suppression of deer: cascade effects for small mammals, wood mice (*Apodemus sylvaticus*) and bank voles (*Myodes glareolus*). *PLoS One* 7 e31404.

Cholewińska, O., Adamowski, W., Jaroszewicz, B., 2020. Homogenization of temperate mixed deciduous forests in Białowieża Forest: similar communities are becoming more similar. *Forests* 11 545. https://doi.org/10.3390/f11050545

Chytrý, M., Danihelka, J., 1993. Long-term changes in the field layer of oak and oak-hornbeam forests under the impact of deer and mouflon. *Folia Geobotanica et Phytotaxonomica* 28, 225-245. https://www.jstor.org/stable/4181199

Cooke, A. S., 2019. *Munjac and Water Deer: natural history, environmental impact and management.* Pelagic Publishing, Exeter.

Corney, P., Kirby K., Le Duc, M., Smart, S., Mcallister, H., Marrs, R., 2008. Changes in the field-layer of Wytham Woods-assessment of the impacts of a range of environmental factors controlling change. *Journal of Vegetation Science* 19, 287-298. https://doi.org/10.3170/2008-8-18383

Crampton, A., Stutter, O., Kirby K., Welch, R., 1998. Changes in the composition of Monks Wood National Nature Reserve (Cambridgeshire, UK) 1964–1996. *Arboricultural Journal* 22, 229-245. http://dx.doi.org/10.1080/03071375.1998.9747207

Currall, J.E.P., 1987. A transformation of the Domin scale. *Vegetatio* 72**,** 81-87.

Dawkins, H.C.D., Field, D.R.B., 1978. A long-term surveillance system for British woodland vegetation. *Commonwealth Forestry Institute Occasional Paper 1.* Commonwealth Forestry Institute, Oxford.

De Frenne, P., Rodríguez-Sánchez, F., Coomes, D.A., Baeten, L., Verstraeten, G., Vellend, M., Bernhardt-Römermann, M., Brown, C.D., Brunet, J., Cornelis, J., Decocq, G.M., Dierschke, H., Eriksson, O., Gilliam, F. S., Hédl, R., Heinken, T., Hermy, M., Hommel, P., Jenkins, M.A., Kelly, D. L., Kirby K. J., Mitchell, F. J. G., Naaf, T., Newman, M., Peterken, G., Petřík, P., Schultz, J., Sonnier, G., Van Calster, H., Waller, D.M., Walther, G.-R., White, P. S., Woods, K.D., Wulf, M., Graae, B.J., Verheyen, K., 2013. Microclimate moderates plant responses to macroclimate warming. *Proceedings of the National Academy of Sciences* 110, 18561-18565. https://doi.org/10.1073/pnas.1311190110

Ellenberg, H., 1988. *The vegetation ecology of central Europe.* Cambridge University Press, Cambridge.

Elton, C.S., 1942-1965. *Elton Archive: notes on the Wytham Area 1942-1965*. http://ora.ox.ac.uk/objects/uuid:89c5e479-6003-45ba-bd78-8a8a12858bf1 (Accessed January 2021).

Elton, C.S. 1966. *The pattern of animal communities.* Chapman & Hall, London.

Field, C.D., Dise, N.B., Payne, R.J., Britton, A.J., Emmett, B.A., Helliwell, R.C., Hughes, S., Jones, L., Lees, S., Leake, J.R., 2014. The role of nitrogen deposition in widespread plant community change across semi-natural habitats. *Ecosystems* 17, 864-877. DOI: 10.1007/s10021-014-9765-5

Fischer, C., Parth, A., Schmidt, W., 2009. Vegetation dynamics in beech-dominated strict forest reserves. A comparison study from southern Lower-Saxony (Germany). *Hercynia* 42, 45-68.

Forestry Commission, 2012. *NFI preliminary estimates of quantities of broadleaved species in British woodlands, with special focus on ash*. Forestry Commission, Edinburgh.

Gilliam, F. S., 2014. *The herbaceous layer in forests of eastern North America.* Oxford University Press, Oxford.

Goldsmith, F. B., 2012. *Monitoring for conservation and ecology.* Springer Science & Business Media, Berlin.

Govaert, S., Vangansbeke, P., Blondeel, H., Steppe, K., Verheyen, K., De Frenne, P., 2021. Rapid thermophilization of understorey plant communities in a 9 year-long temperate forest experiment. *Journal of Ecology* 109, 2424-2447. https://doi.org/10.1111/1365-2745.13653

Hedl, R., Kopecky, M., Komarek, J., 2010. Half a century of succession in a temperate oakwood: form species-rich community to mesic forest. *Diversity and Distributions* 16, 267-276. https://doi.org/10.1111/j.1472-4642.2010.00637.x

Hedwall, P.O., Gustafsson, L., Brunet, J., Lindbladh, M., Axelsson, A. L., Strengbom, J., 2019. Half a century of multiple anthropogenic stressors has altered northern forest understory plant communities. *Ecological Applications* e01874. https://doi.org/10.1002/eap.1874

Hill, M.O., Preston, C.D., Roy, D.B., 2004 *PLANTATT: attributes of British and Irish plants.* Biological Records Centre (NERC), Cambridge.

Hurford, C., Schneider, M., 2006. *Monitoring nature conservation in cultural habitats.* Springer, Dordrecht.

Keith, S.A., Newton, A.C., Morecroft, M.D., Bealey, C.E., Bullock, J.M., 2009. Taxonomic homogenization of woodland plant communities over 70 years. *Proceedings of the Royal Society B: Biological Sciences* 276, 3539-3544. https://doi.org/10.1098/rspb.2009.0938

Kirby, K.J., 1980. Experiments on vegetative reproduction in bramble (*Rubus vestitus*). *Journal of Ecology* 68**,** 513-520.

Kirby K.J., 1988 Changes in the ground flora under plantations on ancient woodland sites. *Forestry* 61, 317-338. https://doi.org/10.1093/forestry/61.4.317

Kirby K.J., 2001. The impact of deer on the ground flora of British broadleaved woodland. *Forestry* 74, 219-229. https://doi.org/10.1093/forestry/74.3.219

Kirby K.J., 2015. Changes in the vegetation of clear-fells and closed canopy stands in an English oak wood over a 30-year period. *New Journal of Botany* 5, 2-12. https://doi.org/10.1179/2042349715Y.0000000001

Kirby K.J., 2016. A smell in the air. *Oxford Plant Systematics* 22, 15.

Kirby K.J., 2020a. *Woodland flowers: colourful past, uncertain future*. Bloomsbury, London.

Kirby K.J., 2020b. The ash population in Wytham Woods. *Fritillary* 8, 98-106.

Kirby, K.J., Woodell, S.R.J., 1998. The distribution and growth of bramble (*Rubus fruticosus*) in British semi-natural woodland and and the implications for nature conservation. *Journal of Practical Ecology and Conservation* 2, 31-41.

Kirby K.J., Latham, J., Holl, K., Bryce, J., Corbett, P., Watson, R., 2002. Objective setting and condition monitoring within woodland sites of special scientific interest. *English Nature Research Reports.* English Nature, Peterborough.

Kirby K.J., Smart, S.M., Black, H.J., Bunce, R.G.H., Corney, P.M., Smithers, R.J., 2005. Long-term ecological changes in British woodland (1971-2001). *English Nature Research Report 653.* English Nature, Peterborough.

Kirby K.J., Pyatt, D.G., Rodwell, J.S., 2012. Characterization of the woodland flora and woodland communities in Britain using Ellenberg Values and Functional Analysis. In*:* Rotherham, I. D., Jones, M.,Handley, C. (Eds.) *Working and Walking in the Footsteps of Ghosts: volume 1 the wooded landscape.* Wildtrack Publishing, Sheffield, pp. 66-86.

Kirby K.J., Bazely, D.R., Goldberg, E.A., Hall, J.E., Isted, R., Perry, S.C., Thomas, R.C., 2014. Changes in the tree and shrub layer of Wytham Woods (Southern England) 1974–2012: local and national trends compared. *Forestry* 87, 663-673. https://doi.org/10.1093/forestry/cpu026

Klynge, D., Svenning, J.-C., Skov, F., 2020. Floristic changes in the understory vegetation of a managed forest in Denmark over a period of 23 years – Possible drivers of change and implications for nature and biodiversity conservation. *Forest Ecology and Management* 466, 118128. https://doi.org/10.1016/j.foreco.2020.118128

Landuyt, D., Maes, S.L., Depauw, L., Ampoorter, E., Blondeel, H., Perring, M.P., Brūmelis, G., Brunet, J., Decocq, G., Den Ouden, J., Hardtle, W., Hedl, R., Heinken, T., Heinrichs, S., Jaroszewicz, B., Kirby, K.J., Kopecky, M., Malis, F., Wulf, M., Verheyen, K., 2020. Drivers of above-ground understorey biomass and nutrient stocks in temperate deciduous forests. *Journal of Ecology* 108, 982-997.

Marrs, R.H., Kirby K.J., Le Duc, M.G., Mcallister, H.A., Smart, S.M., Oksanen, J., Bunce, R.G.H., Corney, P.M., 2013. Native dominants in British woodland - a potential cause of reduced species-richness. *New Journal of Botany* 3, 156-168. https://doi.org/10.1179/2042349713Y.0000000028

Mitchell, R.J., Bailey, S., Beaton, J.K., Bellamy, P.E., Brooker, R.W., Broome, A., Chetcuti, J., Eaton, S., Ellis, C.J., Farren, J., Gimona, A., Goldberg, E., Hall, J., Harmer, R., Hester, A. J., Hewison, R. L., Hodgetts, N.G., Hooper, R.J. H., L., Iason, G.R., Kerr, G., Littlewood, N.A., Morgan, V., Newey, S., Potts, J.M., Pozsgai, G., Ray, D., Sim, D.A., Stockan, J.A., Taylor, A.F. S., Woodward, S., 2014. The potential ecological impact of Ash Dieback in the UK. *JNCC Report 483.* Joint Nature Conservation Committee, Peterborough.

Mitchell, R.J., Hewison, R.L., Hester, A.J., Broome, A., Kirby K.J., 2016. Potential impacts of the loss of *Fraxinus excelsior* (Oleaceae) due to Ash Dieback on woodland vegetation in Great Britain. *New Journal of Botany* 6, 2-15. https://doi.org/10.1080/20423489.2016.1171454

Morecroft, M., Speakman, L., 2013. *Terrestrial biodiversity climate change impacts summary report*. Living with Environmental Change, London.

Natural England, 2012. Environmental Monitoring in Natural England 2012. *Natural England Research Report 408.* Natural England, Peterborough.

Needham, J., Merow, C., Butt, N., Malhi, Y., Marthews, T.R., Morecroft, M., Mcmahon, S. M., 2016. Forest community response to invasive pathogens: the case of Ash Dieback in a British woodland. *Journal of Ecology* 104, 315-330. https://doi.org/10.1111/1365-2745.12545

Ogle, K., Barber, J.J., Barron-Gafford, G.A., Bentley, L.P., Young, J.M., Huxman, T.E., Loik, M.E., Tissue, D.T., 2015. Quantifying ecological memory in plant and ecosystem processes. *Ecology Letters* 18, 221-235. https://doi.org/10.1111/ele.12399

Osmaston, F.C., 1959. *The revised working plan for the Wytham Woods 1959/60-1968/69.* Department of Forestry, Unpublished MS, Oxford.

Ovington, J.D., 1955. Studies of the development of woodland conditions under different trees: III. The ground flora. *Journal of Ecology* 43**,** 1-21.

Pautasso, M., Aas, G., Queloz, V., Holdenrieder, O., 2013. European ash (*Fraxinus excelsior*) dieback – a conservation biology challenge. *Biological Conservation* 158, 37-49. https://doi.org/10.1016/j.biocon.2012.08.026

Pearce-Higgins, J.W., Beale, C.M., Oliver, T.H., August, T.A., Carroll, M., Massimino, D., Ockendon, N., Savage, J., Wheatley, C.J., Ausden, M.A., Bradbury, R.B., Duffield, S.J., Macgregor, N.A., Mcclean, C.J., Morecroft, M.D., Thomas, C.D., Watts, O., Beckmann, B.C., Fox, R., Roy, H.E., Sutton, P.G., Walker, K.J., Crick, H.Q.P., 2017. A national-scale assessment of climate change impacts on species: Assessing the balance of risks and opportunities for multiple taxa. *Biological Conservation* 213, 124-134. https://doi.org/10.1016/j.biocon.2017.06.035

Perring, M.P., Bernhardt-Römermann, M., Baeten, L., Midolo, G., Blondeel, H., Depauw, L., Landuyt, D., Maes, S.L., De Lombaerde, E., Carón, M.M., Vellend, M., Brunet, J., Chudomelová, M., Decocq, G., Diekmann, M., Dirnböck, T., Dörfler, I., Durak, T., De Frenne, P., Gilliam, F.S., Hédl, R., Heinken, T., Hommel, P., Jaroszewicz, B., Kirby K.J., Kopecký, M., Lenoir, J., Li, D., Máliš, F., Mitchell, F.J.G., Naaf, T., Newman, M., Petřík, P., Reczyńska, K., Schmidt, W., Standovár, T., Świerkosz, K., Van Calster, H., Vild, O., Wagner, E.R., Wulf, M.,Verheyen, K., 2018. Global environmental change effects on plant community composition trajectories depend upon management legacies. *Global Change Biology* 24, 1722-1740. https://doi.org/10.1111/gcb.14030

Perrins, C., Overall, R., 2001. Effect of increasing numbers of deer on bird populations in Wytham Woods, central England. *Forestry* 74, 299-309.

Persson, S., Malmer, N., Wallén, B., 1987. Leaf litter fall and soil acidity during half a century of secondary succession in a temperate deciduous forest. *Vegetatio* 73, 31-45.

Peterken, G.F., Game, M., 1984. Historical factors affecting the number and distribution of vascular plant species in the woodlands of central Lincolnshire. *Journal of Ecology* 72, 155-182.

Peterken, G.F., Mountford, E.P., 2017. *Woodland development: a long-term study of Lady Park Wood.* CABI, Wallingford, UK.

Plantlife, 2011. *Forestry Recommissioned: bringing England's woodlands back to life*. Plantlife, Salisbury.

Rackham, O., 2003. *Ancient woodland: its history, vegetation and uses in England (revised edition).* Castlepoint Press, Dalbeattie, Scotland.

Rodwell, J.S., 1991. *British plant communities: 1 woodlands and scrub.* Cambridge University Press, Cambridge.

Savill, P.S., Perrins, C., Kirby K.J., Fisher, N., 2010. *Wytham Woods, Oxford's Ecological Laboratory.* Oxford University Press, Oxford.

Schulze, I.-M., Bolte, A., Schmidt, W.,Eichhorn, J., 2009. Phytomass, litter and net primary production of herbaceous layer. In: *Functioning and Management of European Beech Ecosystems.* Springer, Berlin/Heidelberg, pp. 155-181. https://doi.org/10.1007/b82392_11

Smart, S.M., Ellison, A.M., Bunce, R.G.H., Marrs, R.H., Kirby K.J., Kimberley, A., Scott, A.W., Foster, D.R., 2014. Quantifying the impact of an extreme climate event on species diversity in fragmented temperate forests: the effect of the October 1987 storm on British broadleaved woodlands. *Journal of Ecology* 102, 1273-1287. https://doi.org/10.1111/1365-2745.12291

Stace, C., 2010. *New Flora of the British Isles (third edition).* Cambridge University Press, Cambridge.

State of Nature Partnership, 2019. *State of Nature 2019*. RSPB, Sandy, Bedfordshire.

Strubelt, I., Diekmann, M., Peppler-Lisbach, C., Gerken, A., Zacharias, D., 2019. Vegetation changes in the Hasbruch forest nature reserve (NW Germany) depend on management and habitat type. *Forest Ecology and Management* 444, 78-88. https://doi.org/10.1016/j.foreco.2019.04.030

Suggitt, A.J., Wilson, R.J., Isaac, N.J.B., Beale, C.M., Auffret, A.G., August, T., Bennie, J.J., Crick, H.Q.P., Duffield, S., Fox, R., Hopkins, J.J., Macgregor, N.A., Morecroft, M.D., Walker, K.J., Maclean, I.M.D., 2018. Extinction risk from climate change is reduced by microclimatic buffering. *Nature Climate Change* 8, 713-717.

Tanentzap, A., Kirby K.J., Goldberg, E.A., 2012. Slow responses of ecosystems to reductions in wild ungulates and strategies for achieving recovery. *Forest Ecology and Management* 264, 159-166. https://doi.org/10.1016/j.foreco.2011.10.005

Taylor, M.E., Morecroft, M.D., Oliver, H.R., 2010. The physical environment. *In:* Savill, P. S., Perrins, C., Kirby K. J., Fisher, N. (Eds.) *Wytham Woods: Oxford's ecological laboratory.* Oxford University Press, Oxford, pp. 19-28.

Tinya, F., Márialigeti, S., Király, I., Németh, B., Odor, P., 2009. The effect of light conditions on herbs, bryophytes and seedlings of temperate mixed forests in Őrség, Western Hungary. *Plant Ecology* 204, 69. DOI 10.1007/s11258-008-9566-z

Verheyen, K., Baeten, L., De Frenne, P., Bernhard-Romermann, M., Brunet, J., Cornelis, J., Decoq, G., Dierschke, H., Eriksson, O., Hedl, R., Heinken, T., Hermy, M., Hommel, P., Kirby K.J., Naaf, T., Peterken, G.F., Petrik, P., Pfadenhauer, J., Van Calster, H., Walther, G.-R., Wulf, M., Verstraeten, G., 2012. Driving factors behind the eutrophication signal in understorey plant communities of deciduous temperate forests. *Journal of Ecology* 100, 352-365. https://doi.org/10.1111/j.1365-2745.2011.01928.x

Vild, O., Hédl, R., Kopecký, M., Szabó, P., Suchánková, S., Zouhar, V., 2017. The paradox of long-term ungulate impact: increase of plant species richness in a temperate forest. *Applied Vegetation Science* 20, 282-292. https://doi.org/10.1111/avsc.12289

Walther, G., Grundmann, A., 2001. Trends of vegetation change in colline and submontane climax forests in Switzerland. *Bulletin of the Geobotanical Institute ETH* 67, 3-12.

Ward, A.I., 2005. Expanding ranges of wild and feral deer in Great Britain. *Mammal Review* 35, 165-173. https://doi.org/10.1111/j.1365-2907.2005.00060.x

Wylder, B., Biddle, M., King, K., Baden, R., Webber, J., 2018. Evidence from mortality dating of *Fraxinus excelsior* indicates Ash Dieback (*Hymenoscyphus fraxineus*) was active in England in 2004–2005. *Forestry* 91, 434-443. https://doi.org/10.1093/forestry/cpx059

Wytham Management Committee, 2020. Wytham Woods Management Plan 2021-2025. University of Oxford, Estates Department, Unpublished MS, Oxford.