Fifty years of change across British broadleaved woodlands

A resurvey and analysis of the "Bunce" sites 1971-'01-'21

S.M.Smart[1], C.Walker[1], A.R.J.Sier[1], F.Seaton[1], K.J.Kirby[2], C.M.Wood[1]

1: UKCEH, 2: University of Oxford

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Contents

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1. Executive Summary

a. In 1971 103 woods across Britain were selected as representative of a wider sample of 2453 woods (> 4 ha) surveyed in the late 1960s. Within each of the 103 woods sixteen 200m^2 plots were located using a stratified random design and records made of soils, tree and shrub composition, ground flora, dead wood, signs of management and other features. These were revisited in 2001[2].

b. In the third and latest survey 97 sites were revisited and the plots re-recorded as close to the original plot locations as possible. The original recording methods were used. The data from the 1971, 2001 and 2021 surveys were combined and analyses of change over time undertaken to address two broad questions; what has changed over time and what were the likely causes?

1. Losses of plots and changes in vegetation type

a. Between 1971 and 2001 sixteen of the 103 sites were affected by change in land use and 38 plots (2.3%) out of a total 1,648 locations were lost, with about equal contributions from urban development and agricultural activities.

b. Between 2001 and 2021 a further 21 plots (1.3% of the original total) were lost to other land-use. One plot was lost to encroaching gardens while three plots all in one site were lost to the construction of a new lake. The biggest cause of loss was the incorporation of woodland edge into grazed and often improved agricultural land.

c. Fitting of the 2021 plot data to the National Vegetation Classification gave the following rank order in terms of the top units matching most frequently to each plot; W8>W10>W9>W11. Reassuringly, this corresponds with the ordering of area estimates of the most common NVC types across Britain.

d. As in the 2001 survey we suggest that the latest observations are broadly representative of the extent of broadleaved woodland types and their ecological status in Britain.

2. Woodland ownership and signs of management

a. The distribution of woodlands among categories in 2021 has changed little since 2001 with most sites being in private ownership.

b. Plots in forestry ownership showed the most evidence of recent gap-creation while signs of recent gap creation in plots in sites owned by private individuals and those owned by conservation bodies dropped to around 10% in the latest survey having been higher in 1971 and 2001 (c.18% of plots in these earlier surveys).

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[2] The second and third surveys were carried out over the years 2001 to ’03 and then 2020 to ’22. We refer to these simply as the ’01 and ’21 surveys.

c. Signs of historical disturbance; sawn dead wood, old stumps and derelict coppice remain common in the data.

3. Soil changes

a. Mean fresh soil pH differed significantly between each pair of survey years whilst Soil Organic Matter (SOM) was stable across the 50-year interval. Mean soil pH increased by 0.18 (0.27-0.08 HPD) in the 50-year interval.

b. The pattern of soil pH change was very similar to that seen in low intensity habitats that included broadleaved woodland ,in the GB-wide Countryside Survey (CS) between 1978 and 2019. In both surveys soil pH increased from the 1970s to 2000 and then decreased through to the present but resulting in a net increase over the whole period.

c. We found that reduction in sulphur deposition explained significant variation in soil pH differences between surveys. The slope of the relationship between soil pH and reduction in sulphur deposition changed over the 50 year period consistent with recent recovery and peak sulphur deposition in the early 70s. Larger increases in pH over time are associated with the largest declines in sulphur deposition.

3. Changes to tree and shrub species

a. In terms of frequency across the survey plots, the rank order of the most common trees and shrubs remained the same over the 50-year period. The most common species in order of frequency in plots were Oak species > Ash > Hazel > Birch species.

b. The biggest observed changes were a further reduction in Elm, continuing its ongoing decline between 1971 and 2001, and a remarkable increase in Holly. Its increase up to 2021 saw it jump two places becoming more frequent between plots than Hawthorn and Beech.

c. Stand development and the pattern of recruitment to older, fewer stems continued with a 60% loss of stem numbers from 1971 to 2021 and an increase in mean basal area.

d. The overall impression is that most sites have continued to follow a common trend of stem exclusion and recruitment into older classes from woodland sites dominated by many more younger stems in 1971. Initial analysis indicates that widespread recovery from the legacy of post-WWII timber extraction is likely to be a partial explanation for this highly directional cross-site trend.

e. Changes among individual species were largely a continuation of the 1971 to 2001 pattern:

    i. Sycamore, Ash, Birch and Oak lost stems in the smallest size classes but gained in the larger ones;
    ii. Holly gained in all DBH classes overall. Unlike most other species it recruited high numbers into the youngest age-classes even in 2021.

iii. Hazel lost stems over the 50 years from the smallest class (<5cm DBH). The presence of so many young stems in 1971 relative to later years would be consistent with more active coppice management in 1971. However, the low number of signs of recent coppice in that year suggests that the coppice cycles initiating this younger cohort must still have happened some years prior to 1971.

f. Open habitats (rides, glades etc) became less common up to 2021 but with the biggest reduction between 1971 and 2001. Also, records of micro-habitats (wet features, ditches, streams, rock and soil exposures) declined in frequency over the 50 years.

g. Signs of grazing reduced for all animals apart from deer species. Signs of the impact of deer increased from 12% of plots in 1971, to 24% on 2001 to 33% in 2021.

4. Ground flora changes

a. Plant species richness increased significantly between 2001 and 2021 but this did not compensate for the large reduction between 1971 and 2001. Over the 50-year interval, mean species richness per 200m^2 plot decreased by 22% of 1971 values.

c. Species that increased since 2001 appear to be a non-random draw of the ground flora. Ferns, woodland sedges and competitive but shade-tolerant woodland specialists such as Bluebell and Wild Garlic increased as did species of more fertile conditions. Consequently, mean Ellenberg N increased significantly over the 50-year period as did total cover of woodland specialists.

d. We found no significant effect of cumulative nitrogen deposition in explaining change in mean Ellenberg N over time leaving open the possibility that the effect is obscured by more influential drivers. A possible explanation is that lack of woodland management and therefore reduced offtake of nutrients has driven an endogenous increase in fertility in addition to external inputs from N deposition and nutrient surplus from surrounding land.

5. Possible causes of woodland change

Ash dieback (AD)

a. Signs of the disease were present in 21% of the pots surveyed in 2021. We found that the presence of AD was correlated with increased forb cover and increased species richness (probably caused by light reaching the understorey).

b. Species richness changes associated with AD were further moderated by an interaction with deer grazing since species richness only increased in the presence of AD under high deer grazing where herbivory seems to have reduced the competitive effect of Bramble.

Herbivory

a. The only significant herbivore for which we had estimates of impact risk were deer species. We found that high deer risk was correlated with several effects realised over the 50-year interval; lower Bramble cover, higher species richness realised in canopy gaps associated with Ash dieback, suppressed tree and shrub regeneration and higher mean basal area of trees and shrubs.

Intensive land-cover, land-cover change, canopy gaps and distance to site edge
a. Distance-to-edge effects were very small with no overall significant effect across surveys reflecting subtle differences between surveys (positive richness versus distance effect in 2021 and the reverse in 1971).

b. The presence of canopy gaps had a significant positive effect on species richness but there was no interaction with the amount of intensive land-cover surrounding each site, nor distance to site edge. Gaps also had no significant effect on mean Ellenberg N (fertility).

c. Relatively larger effects were attributable to site size and % intensive land-cover around each site. A model that included survey date day difference, year of survey, soil pH, site area and % intensive land-cover in 2021 explained 45% of the total cross-year and between-plot and site variation in mean Ellenberg N.

Climate change
a. There was a significant increase in the proportion of southerly distributed species in plots between 1971 and 2021 and on average this proportion was higher if sites had become warmer in the summer. Species that increased were also likely to be beneficiaries of the shift toward a closed woodland canopy and greater shade.

b. The increase in Holly in surveyed plots was also correlated with a warming climate. Holly seedlings, regenerating younger stems (<1.3m) and bigger stems (>1.3m) increased in frequency where sites had become warmer in winter. Change in mean DBH of Holly stems was not correlated with climate change.

c. Changes in mean DBH across all trees and shrubs was also correlated positively with change in summer temperature but the rate of increase was lower at sites that were already in the warmest parts of the country. Overall, stand development has been accelerated by a warmer climate in Britain.

Sulphur and nitrogen deposition
a. Significant associations between soil pH change and sulphur and nitrogen deposition were present in the data and it is also probable that the increase in soil pH has driven changes in the ground flora, summarised as positive shifts in mean Ellenberg N and R values.

b. A weak but detectable interaction was found between understorey response to high nitrogen deposition and reduction in sulphur deposition. This is consistent with a mechanism whereby increased macronutrient availability associated with recovering pH can stimulate a greater eutrophication signal in the vegetation where N deposition is elevated.

c. We suspect that canopy growth and increased shading may have obscured stronger underlying relationships with pollutant deposition. New gaps from storm events, Ash dieback or management could unlock more widespread effects in the future, especially under climate change.

6. Conclusions and implications; an update since 2001

a. The biggest species-specific changes are the loss of Elm, the spread of Ash dieback and the rise of Holly. In terms of the most common species the canopy composition of the woods has not changed greatly over the 50-year period but structurally the woods are now older, comprising bigger and fewer stems. This pattern is remarkable because it is synchronous across so many of the sites. While legacy effects of post-war disturbance are a partial explanation, it seems that other large-scale legacy effects must be at work such as the long-term decline in broadleaved woodland management.

b. These changes have favoured shade-loving plants and will have also favoured conditions suitable for other biota not recorded in the survey such as shade-loving invertebrates. These changes will filter preferentially for a subset of specialist species rather than providing heterogenous conditions that support a potentially bigger species pool of shade and gap-phase species.

c. Some of the results indicate a degree of recovery from past damage, for example the increase in soil pH associated with reduced sulphur deposition. Moreover, in the last 20 years, several shade-loving and nutrient-demanding plants have increased resulting in a slight recovery in the plant diversity of the woodland understorey. Woodland specialists of better-lit conditions remain less frequent than in 1971.

d. The impact of Ash dieback requires careful interpretation. The increase in species richness in gaps caused by the disease has locally reversed the trend for reduced understorey species richness and non-random filtering for shade-loving plants. However, this outcome needs to be considered alongside the severity and impact of Ash mortality which has yet to play out across GB and could yet drive declines in the wide range of species facultatively and some obligately dependent on the second most common tree across this representative sample of British woodlands.

e. The apparently positive effect on plant species richness associated with AD interacting with high deer risk is also likely to be transient if the Ash canopy is replaced with other tree species such as Sycamore. An alternative possibility is that these gaps become a more permanent feature if high deer herbivory continues to prevent tree and shrub regeneration and drives an increase in shade-intolerant understorey species. The plant species composition of these gaps will then be context-dependent and shaped by other factors such as N deposition and climate change.

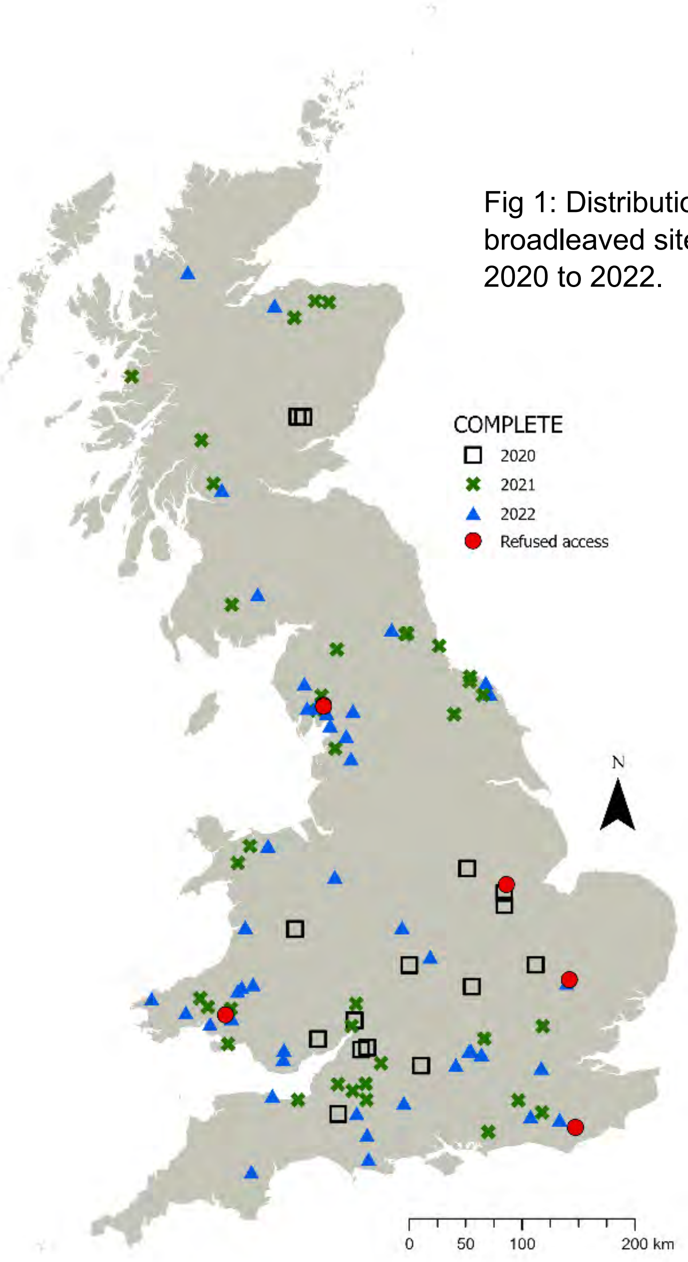
f. The major drivers affecting the woods in the last 50 years are climate warming, ongoing reduction in management interventions that create gaps but an increase in global change-driven gaps from Ash dieback and extreme weather. Deer herbivory has also increased.

g. We have found correlative evidence of the impact of all these drivers. Importantly, observed ecological changes are best explained when interactions between drivers are included in many of the models. It therefore seems likely that future change will not be simply attributable to one or more drivers operating in an additive way but resulting from non-linear effects where driver impacts are amplified or suppressed by interactions between each other and with historical legacy effects. This emphasises the importance of vigilance and ongoing monitoring to measure these interplaying forces and to underpin the development of potentially new forms of mitigation and adaptative management in the face of novel combinations of stressors.

2. Introduction

In 1971 103 woods across Britain were selected as representative of a wider sample of 2,453 woods (> 4 ha) surveyed in the late 1960s (see Kirby et al 2005 for further details). Within each of the 103 woods sixteen square 200m^2 plots (14.14 x 14.14m) were located using a stratified random design and records made of tree and shrub composition, ground flora and other attributes within each plot. Here we summarise the results of an analysis of status and change across these "Bunce" broadleaved woodland sites surveyed for the first time in 1971, then in 2001-'03 (reported in Kirby et al 2005) and again most recently in 2020-'22.

Fig 1: Distribution of the broadleaved sites surveyed from 2020 to 2022.



3. Methods

3.1 Field survey

Re-finding the quadrat locations on each site
When the baseline was established in 1971 the locations of the 16 quadrats per site were simply marked as an 'X' on 2 ½ inch maps. Whilst high resolution GPS grid references were recorded in the latest survey and will allow for high precision re-finding in the future the 2001 and latest campaigns had to use these base maps as the only source of locational information. The full approach to re-finding the previous approximate locations is detailed in Smart et al (2022). In brief surveyors used a GPS to walk to the centroid of each of the digitised X's from the base maps and without agonizing too much over the accuracy of the location, set up the plot for recording (Fig 2). At this point the tree species composition data from the previous survey was inspected to build confidence that the plot was not in the completely wrong area of the woodland but also bearing in mind the possibility that change to the canopy could have occurred in the intervening 20 years. This approach was trialled in 2016 by S.Smart and visiting ecologists from Ghent University. We concluded that using the previous tree data was an effective and recommended aide to avoid setting up the plot in the wrong area but required careful judgement in its use. The approach was demonstrated to the surveyors in one-to-one training days at the start of each campaign. The benefits of attempting to refind previous locations rather than deploy new random points was demonstrated after the 2001 survey. We adopted the same approach in 2021. Some refinding error is inevitable, however. We assume that this error is randomly distributed in subsequent analysis but that the means of any measurements at each plot are autocorrelated over time.

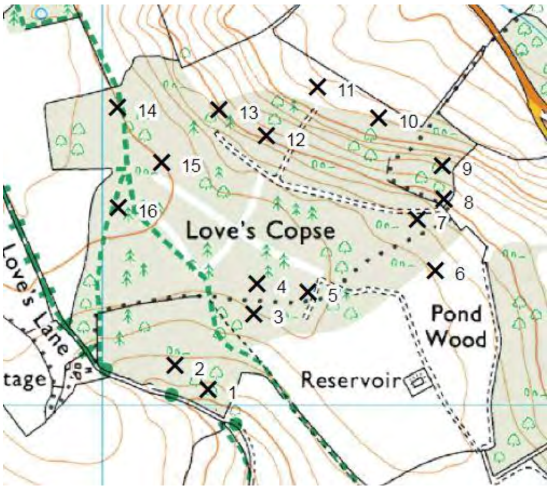


Fig 2: Digitised plot locations transcribed onto a 1:10,000 OS map from the original 2 ½ inch paper map from 1971.

In each $200m^2$ quadrat in each woodland in 1971, 2001 and 2021[3] observations were made of the following:

1. Tree and shrub canopy; Diameter-at-Breast-Height (DBH), count of stems >=1.3m, tree or shrub species composition, presence of regeneration (stems >25cm and <1.3m).
2. Understorey; presence and % cover of all vascular plants plus a selected list of bryophytes and lichens plus tree and shrub seedlings.
3. Plot attributes; presence of bare ground and litter, presence of micro-habitats, signs of grazing, dead wood and many others.

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[3] The second and latest surveys took place from 2001 to 2002 and from 2020 to 2022, respectively. For convenience we refer to these as the 2001 and 2021 surveys.

4. Soil; a 5x15 cm soil core was extracted and subsequently processed for Loss-on-Ignition and pH,

At site level, a suite of additional attributes was also recorded. Full field survey methods are detailed in Kirby et al (2005) and in the Survey Handbook (Smart et al 2022).

Methods and observations new to the latest survey are as follows:

1. Presence of tree disease in each plot with accompanying photos.
2. Presence and % of leaf browning and defoliation in each plot.
3. Signs of recent storm damage in each plot.
4. GPS coordinates stamped and digitally stored.
5. Five photographs of each plot; four taken horizontally at chest height from the centre of the plot and along each cardinal bearing. One upward facing photo of the canopy taken by resting the camera on the top of the plot centre post.

3.2 Response variables

Summary metrics for the ground flora in each plot were calculated as follows:

- species richness
- Shannon diversity
- Simpson diversity
- Nectar-producing plant richness
- butterfly larval food plant richness
- mean Ellenberg R (soil reaction)
- mean Ellenberg N (fertility)
- % cover of different growth forms including forbs, ferns, grasses and sedges.

Three summary metrics were also calculated based upon the trees and shrubs recorded in each plot:

- tree species richness
- stem count per plot
- mean basal area (sum of basal area across recorded stems/number of stems per plot)
- mean Diameter at Breast Height (sum of DBH classes across recorded stems/number of stems per plot)

Shannon and Simpson diversity were calculated using the proportion of vascular plant cover, as the total cover estimate per plot could exceed 100 due to layering of the vegetation. Nectar producing plants were identified using the list compiled by Baude et al (2016) and butterfly larval food plants were identified using the list compiled by Smart et al (2000). Ellenberg scores for each plant species were obtained from PLANTATT (Hill et al, 2004).

All summary metrics were limited to vascular plants only. Some species were also aggregated into amalgamated species groupings due to the differing levels of taxonomic resolution applied in each survey (e.g. combining *Viola riviniana* and *Viola reichenbachiana*). This resulted in a unique list of 795 vascular plant species plus amalgams recorded across all three surveys (compared to 856 vascular plant species pre-amalgamation). If Ellenberg scores varied across the different members of the amalgamated grouping the average was calculated. Mean Ellenberg scores were calculated both with and without cover weighting.

An all-GB list of Ancient Woodland Indicator (AWI) species was compiled from Glaves et al., (2009). In addition, a broad list of non-woodland specialists was compiled based on negative Common Standards Monitoring species for British habitats aggregating the lists compiled by the Botanical Society of Britain & Ireland for use in the National Plant Monitoring Scheme (see Appendix A). This comprises many generalist, ecologically wide-ranging and weed species but also species of wetter condition or lower fertility that are nevertheless not specialised to woodlands but are found in less intensively managed semi-natural habitats outside of woodlands or where suitable patches occur within woodlands (see for example the distinctions made in Jamoneau et al 2011 and Kimberley et al 2013).

Response and explanatory variables were also assembled to address three questions pertaining to climate change effects across the 50-year time-series. Interpolated 1km square estimates of four climate variables were averaged and attached to each site for the 20 years preceding each survey. Because the values of these variables at each site reflect overall geographic differences in climate – northern and western sites are cooler and wetter than southern and eastern sites – the values were centred by the cross-year mean at each site thereby removing this overall spatial variability and allowing attribution of changes explicitly to differences in climate over time. This also means that the overall mean climate for a site can also be used as an explanatory variable that is not confounded with change in climate.

Many analyses exploring the links between climate and woodland change are clearly possible with the survey data. We focus on addressing three questions that illustrate potential and are likely to be of high priority in any list of such questions.

i. Have southerly distributed species increased in abundance?

ii. Is climate change implicated in the rise of Holly?

iii. Is climate warming accelerating stand-development and canopy growth?

Species expected to increase with a warmer climate were selected based on their membership of the six Southern-temperate biogeographic elements listed in Hill & Preston (1997) plus the Submediterranean-Subatlantic group. Distribution maps in that paper showed that all these species had distributional ranges that, while sometimes widespread, were centred in southern Britain. Many rarer species in these groups were likely to be restricted in their distribution for additional reasons related to dispersal and habitat requirements but such species are also rare or absent in the woodland plots.

3.3 Explanatory variables and detecting the causes of woodland change

Based on the results from the analysis of the previous two surveys and other sources of published evidence, we selected a series of hypotheses to test regarding possible causes of woodland change. The varying effect of each hypothesised driver was conveyed by explanatory variables drawn from the survey data or from independent sources that were then matched to the spatial location of each woodland site. The plausibility of a driver impacting the woodlands is more likely where its effects are consistent with a well understood mechanism and where effects have been detected elsewhere in other independent datasets including where the driver may have been experimentally manipulated. Sources of evidence in support of the possible role of a range of drivers are listed in Table 1.

Table 1: Drivers of broadleaved woodland change and hypothesised effects in the Bunce survey time-series[4]. Entries in italics refer to evidence from the analysis of change in the Bunce surveys between 1971 and 2001.

Woodland change	**Driver**	**Evidence from other studies**
Enhancement of forest growth where suitable species can respond. Reduced growth and enhanced species turnover if associated with extremes.	Climate warming	Wu et al (2014) Charru et al (2017)
Changes in species composition of the understorey.	Climate warming	Kirby et al (2005); De Frenne et al. (2019); Stevens et al., (2015)
Increase in nutrient-demanding species e.g. competitive grasses and, plants with higher Ellenberg N values, change in soil pH.	Nitrogen deposition	Kirby et al (2005); Gilliam (2006); Segar et al. (2022)
Increased soil pH. Increase in plant species with higher Ellenberg R values.	Declining sulphur deposition	Kirk et al (2006); Seaton et al (2023); Rose et al (2016)
Changing presence and abundance of exotic shrubs and trees. Change in balance of shade-loving versus shade-intolerant plants in the understorey and regenerating juvenile tree and shrub stems. Increase in species with high Ellenberg N values reflecting increased nutrient accumulation because of reduced biomass offtake.	Historical and current woodland management; gap-creation versus canopy closure	Kirby et al (2005); Perring et al (2018); Depauw et al (2020)
Increase in weedy generalists and nutrient-loving species at the edge of woodlands; greater impact in small sites and where gaps in the canopy are present because light-limitation is alleviated; increased species richness at edges where specialists and generalists may co-exist.	Land-use change around site; edge effects	Kirby et al (2005); Burst et al (2017); Bergés et al (2016); Govaert et al (2020); Jamoneau et al (2011)

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[4] We only list those drivers for which we can assemble explanatory variables either from external sources or where proxies were recorded as part of the survey. For example squirrel damage is not explicitly recorded and so we omit this possible impact from the table because we cannot test for its effect in the survey data.

Change in balance of palatable species; increase in grazing-tolerant grasses and decline in grazing-sensitive species especially woodland specialists; reduced tree regeneration.	Herbivory	Ignacio-Ramirez et al (2018); Pellerin et al (2010); Morecroft et al (2001)
Increased disease signs and mortality. Changes in understorey plant species composition where disease causes canopy gaps and light is admitted to the understorey.	Tree disease	Cracknell et al (2023); Coker et al (2019); Mitchell et al (2014); Brunet et al (2023); Hardová et al (2017)

Climate data

The average summer rainfall, winter rainfall, winter average minimum temperature, and summer average maximum temperature were calculated over the twenty years pre-survey for all plots based on 1 km HadUK-Grid interpolated estimates from the UK Met Office (Met Office et al., 2022).

Atmospheric deposition data

Sulphur oxides, oxidised nitrogen and reduced nitrogen deposition were based upon modelled estimates of anthropogenic emissions across the UK at a 1km scale from 1750-2100 (Tomlinson et al., 2023). Unless otherwise stated all units are tonnes km^2. Multiply by 10 to convert to kg ha^{-1}.

Deer grazing

Deer risk at the site level was categorised into low, moderate and high for all sites based on expert assessment and observations[5]. Deer risk at Scottish sites was estimated using the R Shiny app in Spake et al. (2020). In total there were 36 low, 35 moderate and 32 high risk sites across the GB-wide sample of sites.

Land cover and land cover change

Land cover within a 1km buffer zone around each site was extracted from Land Cover Map 2015, recommended as the best map for our purpose by Dr Clare Rowland (satellite land cover change team lead at UKCEH). Intensive land use was defined as total % arable plus improved grassland in each buffer. A land-use change metric was also constructed as the difference between the Dudley Stamp land-cover layer and the LCM2015 layer in the 1km buffer zone around each site (Appendix B). Because of lack of direct equivalence in the two classifications it was only possible to construct a ‘moorland & heath’ category that we could reliably apply to both the 1930s Stamp data and LCM2015. This was based on aggregation of what we assumed to be equivalent land cover types in in each dataset. It was not possible to separate the effects of grassland intensification for example because neutral versus improved grassland are not adequately differentiated in either system.

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[5] We thank David Jam and colleagues at the Forestry Commission for their expert assessment of risk at broadleaved sites in Wales and for pointing us to the indicative deer risk layer for England at https://www.forestergis.com/Apps/MapBrowser/

Other explanatory variables were drawn from the attributes recorded at each site and plot. These were especially important where they were recorded at plot level. Unlike the site-level covariates they can potentially explain variation in change over time and in space between the high-resolution locations recorded within each wood as well as between sites. Important explanatory variables recorded by surveyors were:

- presence of Ash dieback,
- gaps in the canopy,
- micro-habitat presence
- signs of recent management.

In some cases plot-level variables were used as explanatory variables mediating relationships between external drivers and understorey response. Examples include the use of mean DBH as an expression of shade and canopy closure and soil pH mediating the effect of pollutant deposition on understorey species composition.

3.4 Statistical modelling

We used several statistical approaches to answer two broad questions; what changed over time? (a model containing year only as a fixed effect) and what may have caused the change over time? (a model containing year of survey as well as the fixed effects of possible explanatory variables and their interactions where justified by a plausible mechanism – see Table 1). Depending on the response and explanatory variable we added in random effects of plot nested within site, to account for repeated recording over time and to account for variability due to exchangeable differences between sites and plots over time that were not attributable to the systematic effect of an explanatory variable. See Appendix C for further details regarding analytical methods. As in Kirby et al (2005), all modelling of changes between surveys accounted for an additional effect of difference in day-date of survey between campaigns. Modelling showed that on average a 30 day later survey resulted in a 7% decrease in species richness.

3.5 Assigning plot data to the National Vegetation Classification (NVC)

The plant species compositional data from the latest survey were assigned to the NVC to assess the representativeness of the data as done previously in Kirby et al (2005) by comparing the results with area estimates of groups of like community types and with the results for previous surveys.

Species lists from each plot were assigned to the NVC (Rodwell 1991) using the pseudo-quadrat approach (Tipping et al 2013) implemented in the assignNVC R package (Harrower et al 2020)[6]. The method avoids species-richness bias associated with matching directly to the over-enriched constancy tables of the NVC and instead matches a quadrat species list with species lists realised as random draws from the published NVC tables conditional on the constancy of each listed species. The top 5 matching coefficients were extracted for each surveyed quadrat and the total count of each NVC unit in these coefficients expressed

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[6] This package is currently being developed further as a free R Shiny app. Contact S.Smart (ssma@ceh.ac.uk) or C.Harrower (corr@ceh.ac.uk) for further information.

as a percentage of the total number of matches i.e. number of total quadrats * 5 as the denominator.

4. Results

4.1 Numbers of sites and plots visited in the latest survey

Ninety seven of the 103 woodland sites were surveyed between 2020 to 2022 (Fig 1). Despite protracted diplomacy, permission was denied to revisit six of the sites. In one case the owner wanted paying for access. In another two, storm damage was considered to pose too much of a risk. In another, the owner had very recently died and the family did not want to be disturbed. In the remaining two no particular reason was given.

Among the surveyed sites, varying numbers of the 16 plots per site were recorded dependent upon permission being gained to access sub-compartments in different ownership. Plots were occasionally not recorded if the location was considered too dangerous or where the plot appeared to sample an area that was no longer woodland and for which permission had not been obtained. In total 1460 200m^2 plots were recorded in full in the latest survey representing an absence of 11% of the original locations compared to 2% not recorded in 2001.

4.2 Losses of plots and changes in vegetation type

Between 1971 and 2001 16 of the 103 sites were affected by major change in land use and 38 plots (2.3%) out of a total 1648 locations were lost, with about equal contributions from urban development and agricultural activities.

Between 2001 and 2021 a further 21 plots (1.3% of the original total) were lost to other land-use. Only one plot appeared to be lost to encroaching gardens while three plots all in one site were lost to the construction of a new lake. A plot at the edge of Papworth wood was lost to an extension of an access road to the hospital. In all other cases unprotected woodland edges were converted with varying intensity to grazed wood pasture, grass-heath and improved grassland (see Appendix F).

4.3 Representativeness of the sample and assignment to the National Vegetation Classification

When assigned to the National Vegetation Classification the most common groups represented were the W10,11 Oakwoods and the W8,9 Ash-Elm woods reflecting the rank order of these groups in the area estimates of Cooke & Kirby (1994) and from figures derived more recently from National Forest Inventory data (Kirby, K. unpublished note). Most of the woodland NVC groupings assigned in 2021 broadly correspond to the ordering of the independent area estimates. However, the Birch-Willow woods W1-4 are relatively under-represented in the Bunce data in the latest survey (Fig 2).

Fitting of the survey data to the NVC will have been blurred by lack of discrimination of *B.pendula* versus *pubescens* and *Q.robur* versus *petraea*. Lack of exhaustive recording of the bryophytes – a legacy from the 1971 survey methodology – will also tend to bias fitting away from bryophyte-rich communities. However, the largest number of fits in the 2021 data were to W8>W10>W9>W11. Reassuringly, this corresponds with the ranking of national area estimates of NVC types in Cooke & Kirby (1994).

As in the 2001 survey we suggest that the latest observations are broadly representative of the extent of woodland types and their ecological status in Britain.

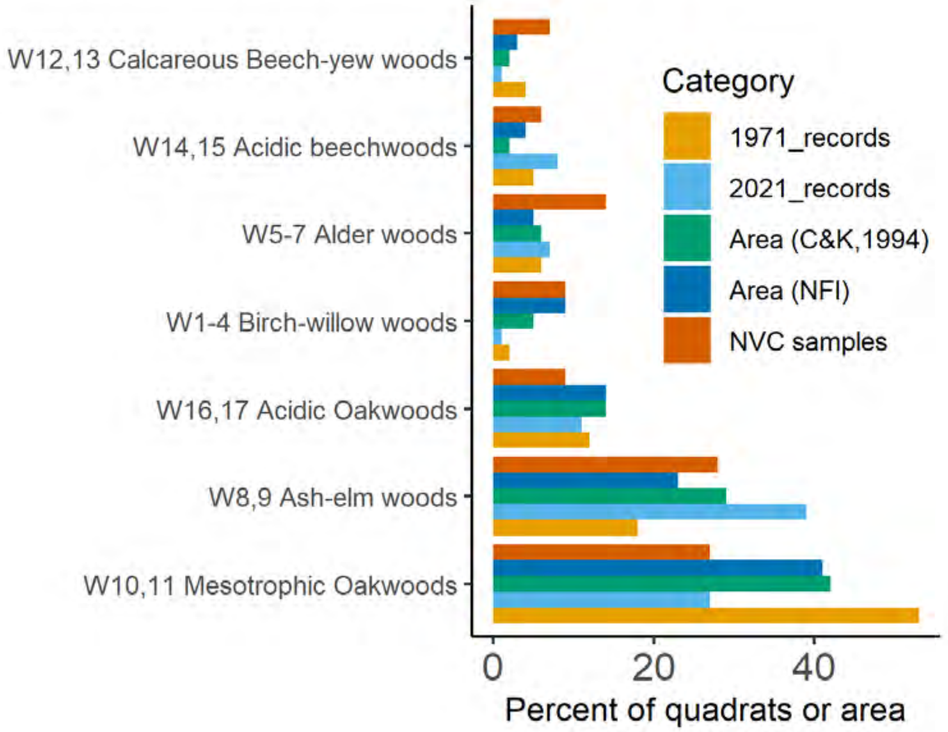


Fig 2: The NVC groupings are ordered by the area of each of these estimated from the National Forest Inventory (Kirby, unpublished).

4.4 Woodland ownership

Owners of the woodland sites were assigned to three categories using the same approach applied in 2001. Private ownership was assigned where named individuals, a farm or estate, were owners. Forestry was assigned where the owner was identifiable as an enterprise whose primary focus was forestry including private as well as public bodies. Similarly, conservation/heritage was inferred where site owner names included nature reserves, town and district council parks as well as the statutory agencies and trusts motivated partly or wholly by conservation and heritage objectives. The consequence is that the private category will have included enterprises where management objectives could include conservation, heritage and forestry but where we have no way of knowing who these enterprises are and to what extent these goals may have driven ecological change across their sites.

The distribution of woodlands among categories in 2021 has changed little since 2001 with most sites being in private ownership (Fig 3a).

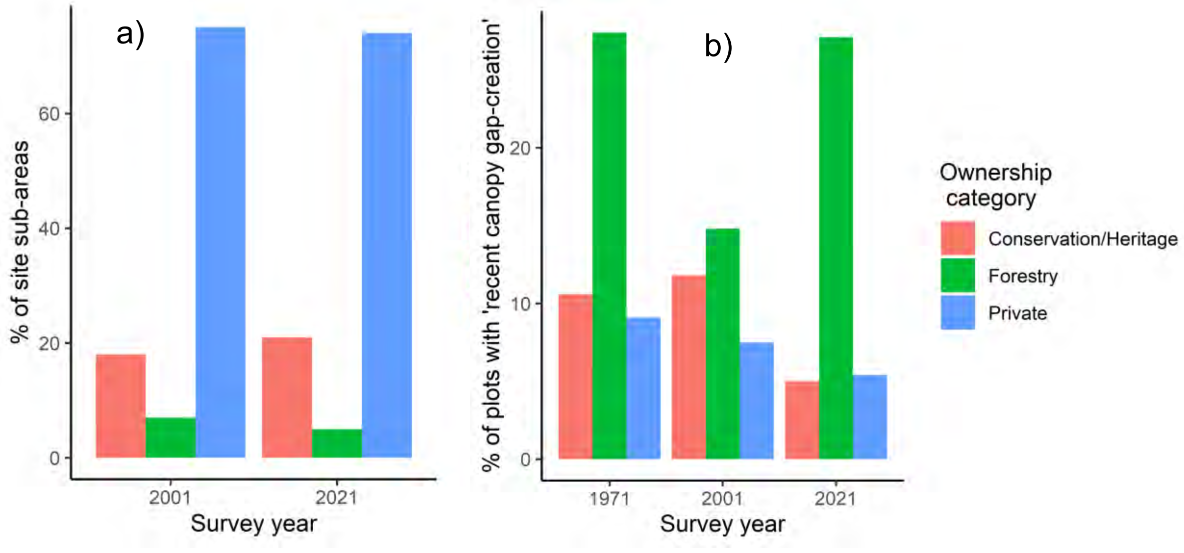


Fig 3: a) Distribution of owner types among broadleaved woodland sites and their sub-areas in 2001 compared with 2021, b) % of surveyed plots in each year with recorded signs of *recent* management that create gaps in the canopy (recently cut coppice & recent tree stumps). Note that we do not know who owned the woodland sites in 1971 hence in b) all sites are classified by their ownership status in 2021.

4.5 Signs of management and presence of dead wood

Plots in forestry ownership unsurprisingly showed the most evidence of recent gap-creation while plots in private and conservation ownership with signs of recent gap creation dropped to around 10% in the latest survey having been higher in 1971 and 2001 (c.18% of plots in total affected in these earlier surveys) (Fig 3b). Recently cut coppice and recent felling are therefore rarer now than in both previous surveys.

Dead wood has increased slightly with more records of fallen uprooted stems, branches >10cm diameter and fallen and broken limbs (Fig 4). The increases in deadwood undoubtedly reflect the impact of storms since 1971 including the major events in 1987, 2020 and 2021 (Fig 4). Surveyors were asked to note these impacts in the 2021 survey (Fig 5).

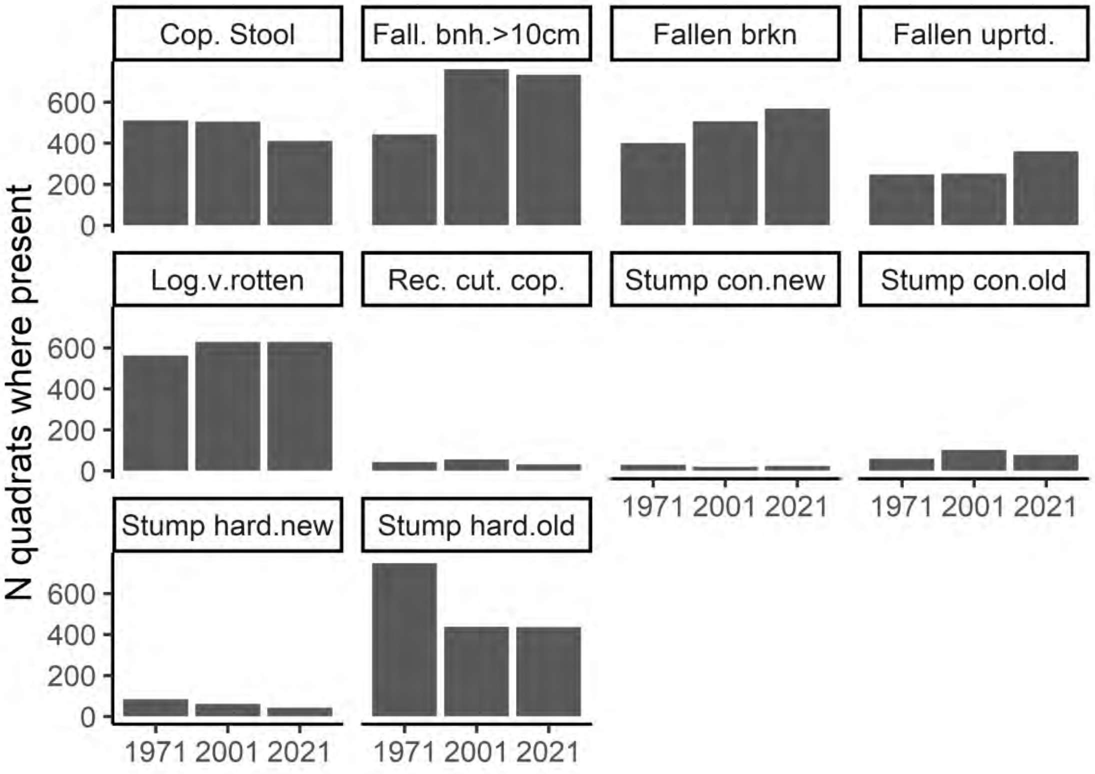


Fig 4: Counts of attributes in recorded plots in each survey relating to management and deadwood**.**

4.6 Changes in the woodland canopy; mean basal area, DBH class distribution and stem count

Over the last 22 years there has been a loss of stem numbers (Fig 6), an increase in mean basal area (Fig 7) and a net loss of stems from the younger age classes (Fig 9). Therefore, the directional pattern of woodland change seen between 1971 and 2001 has continued. This is consistent with an ongoing process of canopy ageing, stem exclusion under competitive thinning and recruitment into older DBH classes.

Fig 5: Storm damage at the Bunce broadleaved sites recorded from 2020-’22. Circles are proportional to the frequency of plots with damage noted.

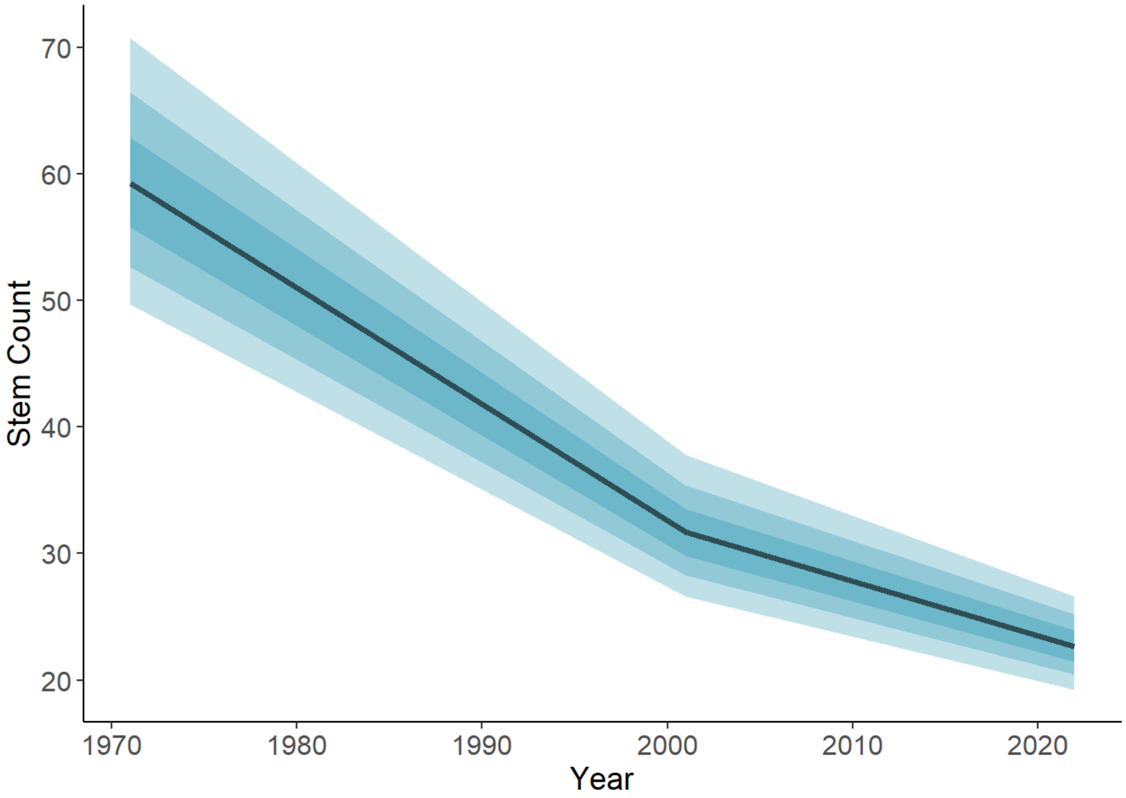


Fig 6: Change in mean stem count of trees and shrubs per repeat plot.

Patterns of change in individual species were largely a continuation of the dynamics noted between 1971 and 2001 (Fig 9):

i. Sycamore, Ash and Birch all lost stems in the lowest size classes but gained in the larger ones (Fig 9a,b,f). Hence, despite Ash dieback being present in 21% of plots in 2021, Ash still gained live, yet presumably now often infected, older individuals.

ii. Oak saw a less dramatic reduction from 2001 to 2021 in younger stems with many still apparent in 2021. The total number of individuals in the older, larger classes did not change greatly over time (Fig 9e).

iii. Hazel lost stems over the 50 years from the smallest class (<5cm DBH) (Fig 9c). The presence of so many young stems in 1971 relative to later years would be consistent with more active coppice management in 1971. However, the low number of signs of recent coppice in that year (see Fig 4) suggest that the coppice cycles initiating this younger cohort must have happened some years prior to 1971.

iv. The shade-tolerator Holly showed a different pattern with more young stems in 2001 and ’21 (Fig 9d). See section 3.11.2 for further analysis of the increase in Holly.

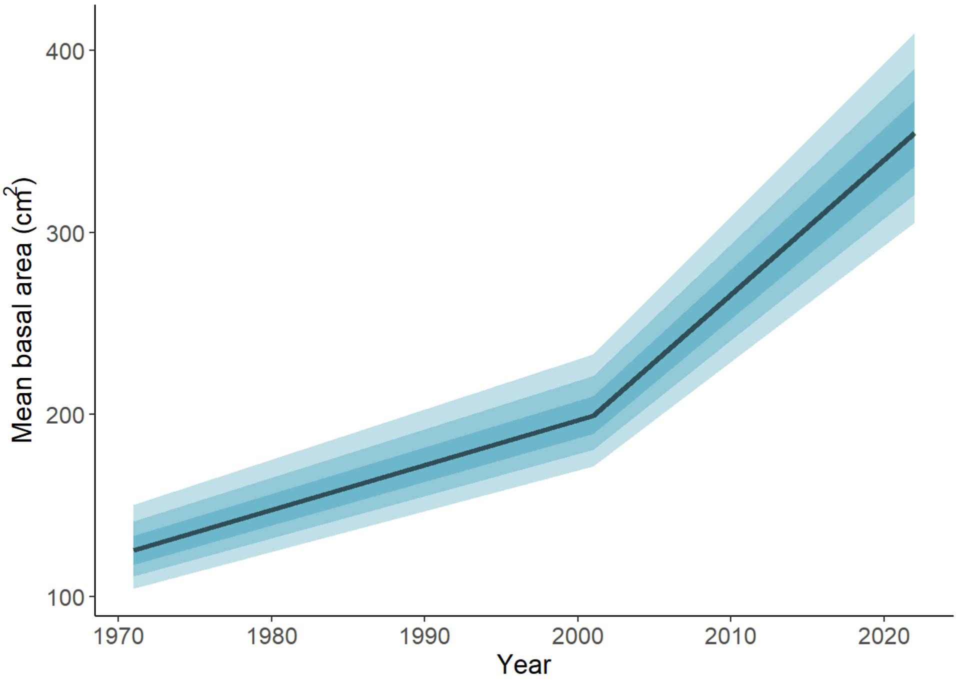


Fig 7: Change in mean basal area of trees and shrubs per repeat plot.

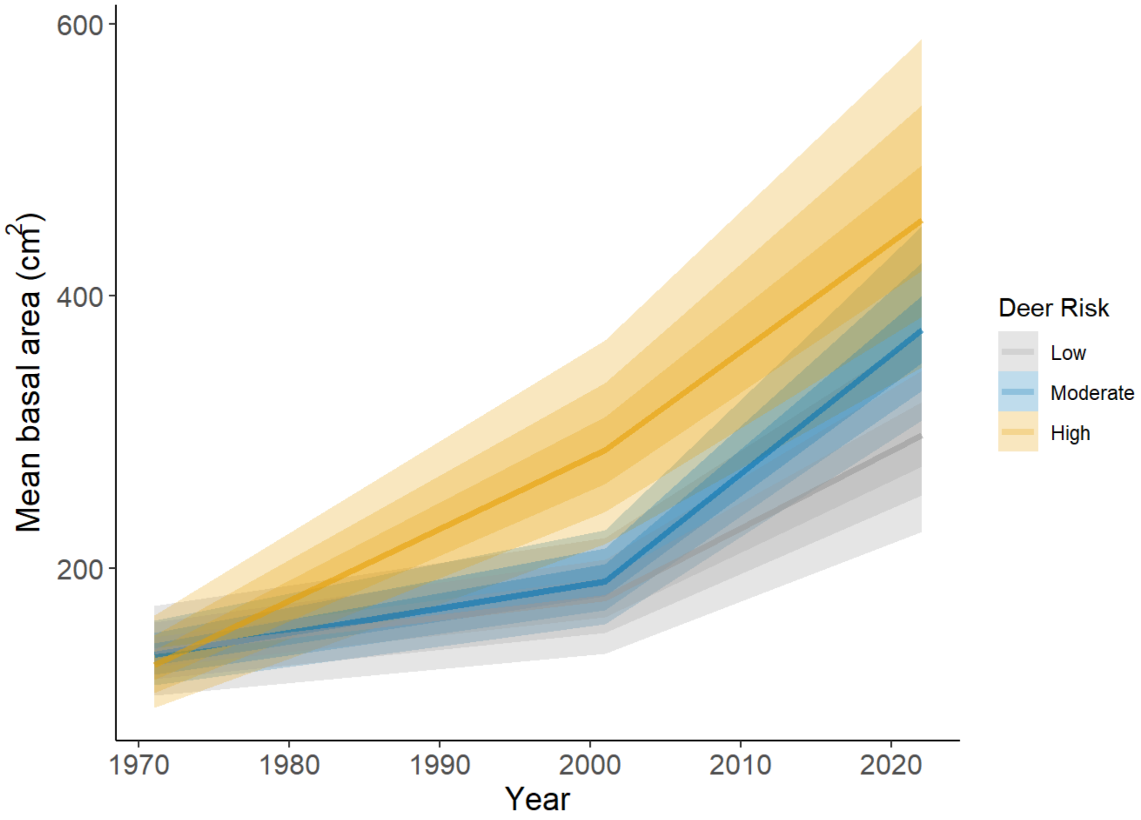


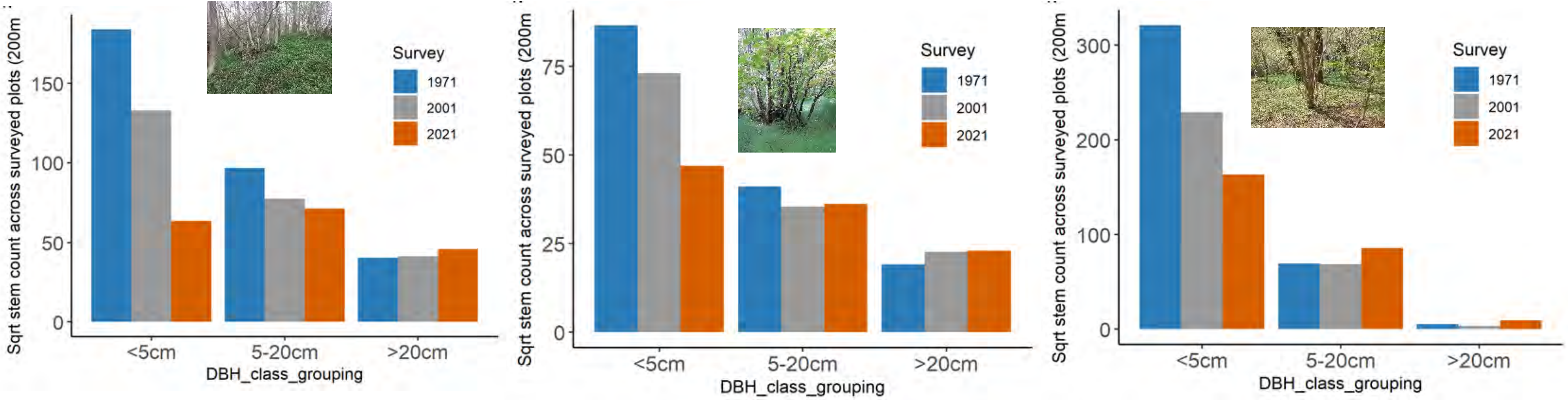
Fig 8: Change in mean basal area by deer risk.

The changing shape of the DBH class distributions for each survey year indicate a common pattern of stand development across sites. Younger stems dominate in 1971 and reduce in number moving from 2001 to 2021 as stems are thinned by competition.

The overall impression is that most sites have continued to follow a common trend of stem exclusion and recruitment into older classes from woodland sites dominated by many more younger stems in 1971.

The full cross-site DBH class distribution is shown for Oak (*Quercus petraea* and *robur* combined) in Fig 10. Along the stem age (i.e. DBH) gradient younger stems reduce in numbers. They are most abundant in 1971 and gradually recruit into older classes hence the grey (2001) and then orange (2021) bars have higher counts within each class.

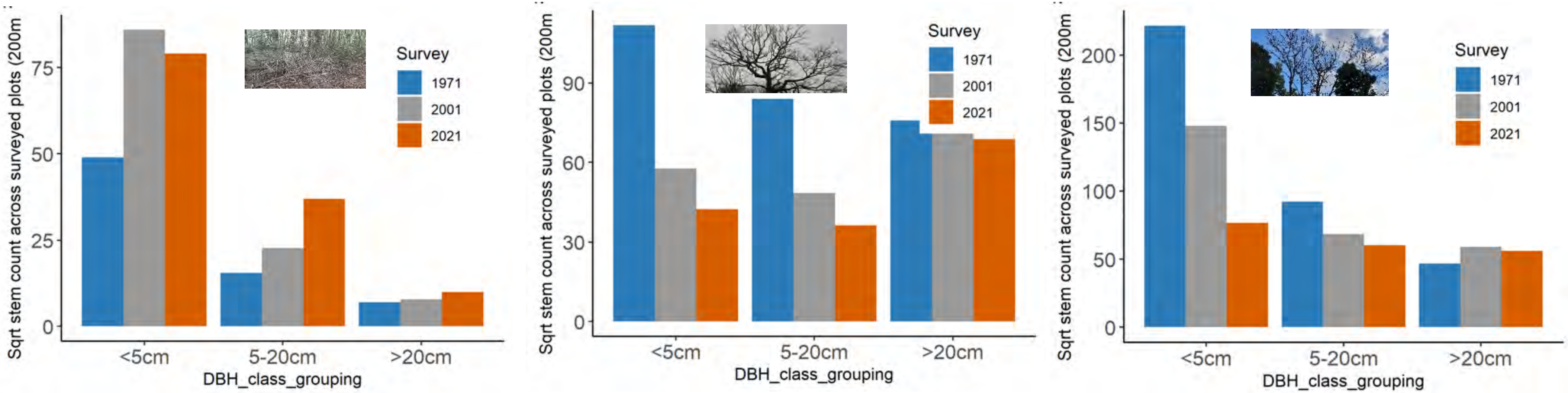
Fig 9: Square-root transformed stem count by Diameter at Breast Height by survey year summed across 200m^2 plots repeated in each survey. Note different scales on Y axes.



a) Birch

b) Sycamore

c) Hazel

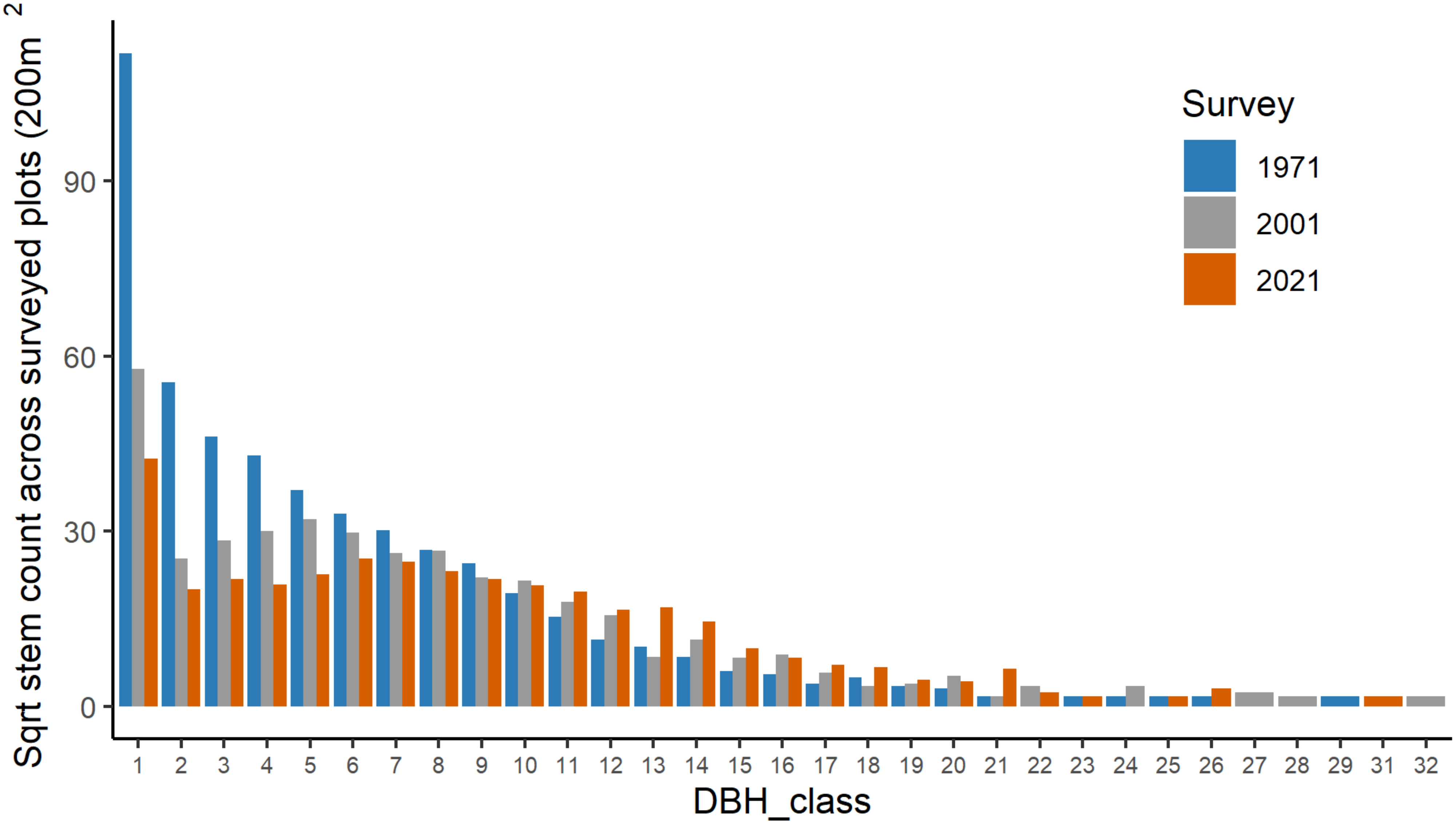


d) Holly

e) Oak

f) Ash

Fig 10: DBH class distribution for Oak stems (Q*uercus petraea* & *Q.robur* combined). Note that the y axis is square-root transformed counts of stems summed across plots repeated in every survey.



An additional effect of deer herbivory was explored (Fig 8). Despite the uncertainties involved in these estimates, the results of our analyses convey plausible relationships between deer herbivory levels and survey observations. We found that mean basal area achieved higher levels at high deer risk and then progressively lower as risk declined (Fig 8). A possible explanation is that herbivory has reduced the density of younger stems elevating mean basal area because larger stems remain.

4.7 Species composition of the canopy dominants – has the tree and shrub canopy changed over 50 years?

The rank order of 11 of the most common tree species has remained the same over the 50-year interval, hence the broad character of the woodland canopy has not changed. Two shade tolerators – Beech and Holly - have increased in plot-frequency. The expansion of Holly now places it above Hawthorn and Beech in its ranking (Fig 11).

Most species were less frequent in 2021 than in the previous surveys, because of stand thinning and reductions in stand density. This is a typical pattern of stand development following disturbance such that in 2021 British woodlands are now made up of fewer but bigger trees.

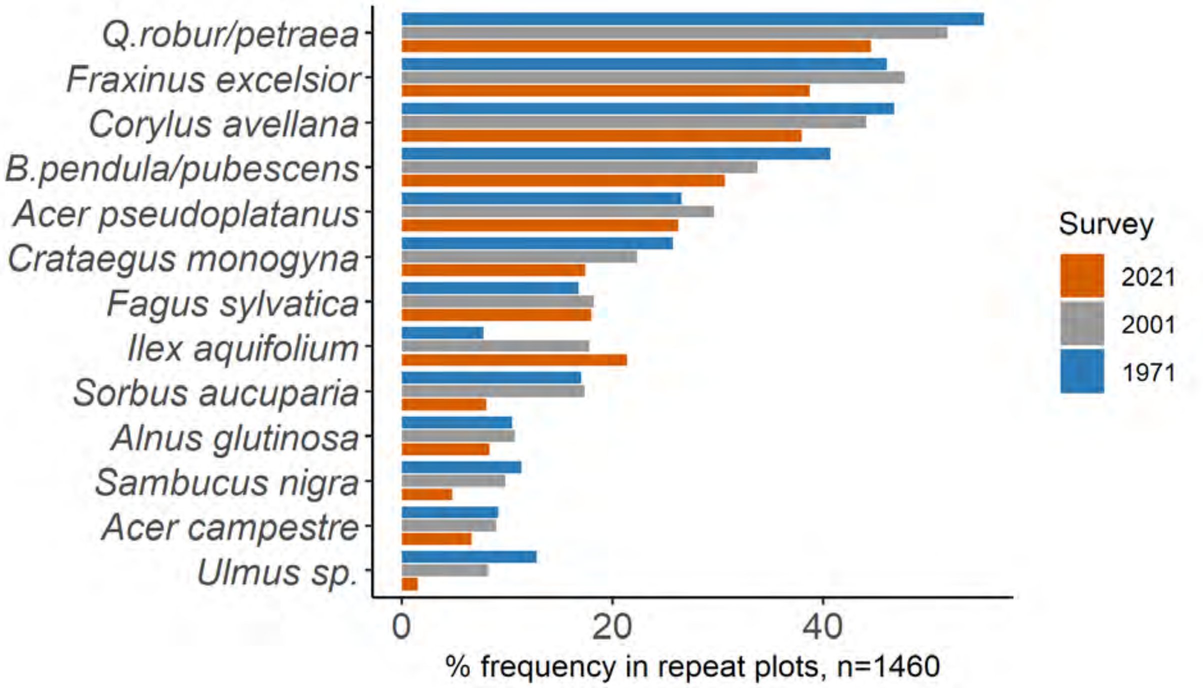


Fig 11: Between-plot frequency of the most common tree species in the broadleaved woodland sample in each survey. Tree species are ordered by frequency in 2001.

4.8 Changes in presence of regenerating stems (>0.25cm and <130cm in height)

Tree and shrub stems less than <130cm in height but >25cm were recorded as 'regenerating stems' in each plot in each survey. Ash was the most common contributor but declined over the 50-year period as did Birch, Sycamore and Hazel, all trends that are consistent with the loss of stems from the youngest DBH classes over time (Fig 12).

The shade-tolerator Holly was remarkable in that it increased over time with a marked jump between 2001 and 2021.

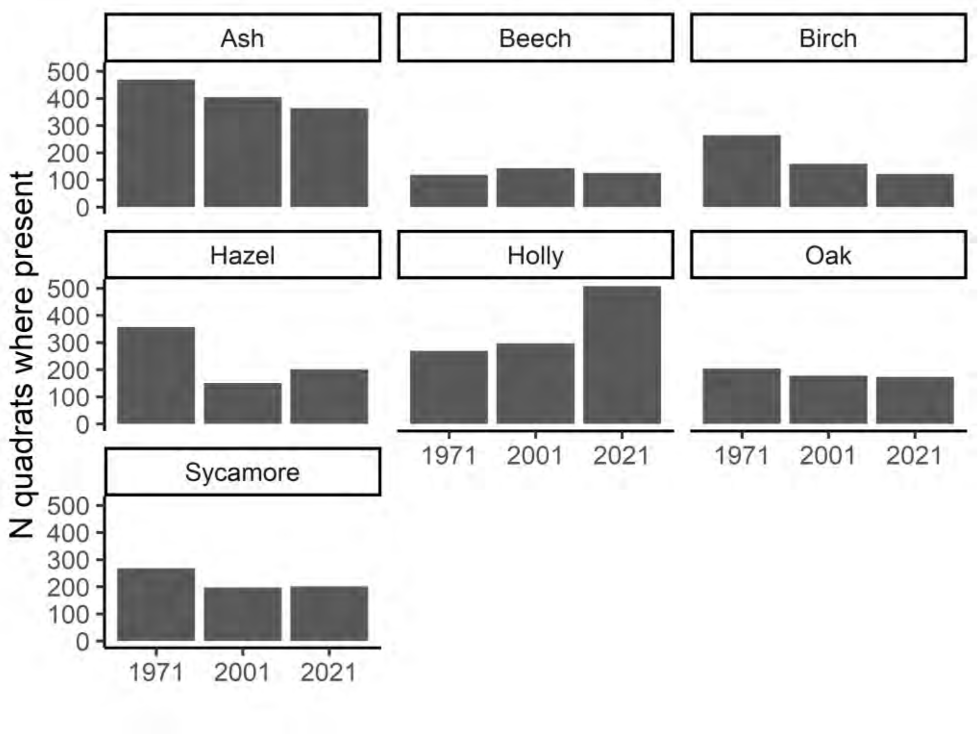


Fig 12: Change in presence of regenerating stems (>25cm and <130cm).

The relationship between deer risk and proportion of plots that show regeneration of any tree species over time is complicated by high variability but also that stems in 1971 and 2001 were more frequent in high deer risk sites pointing to the operation of a confounding factor (Fig 13). From 2001 to 2021 there was a significant increase in count of the youngest stems in low deer risk sites and a consistent lower increase and decline in moderate and high risk sites respectively but the differences were not significant (i.e. the 95% parameter interval included zero).

4.9 Presence of other habitats and changes in micro-habitat diversity within plots

Open spaces (glades and paths) became less common up to 2021 but with the biggest reduction between 1971 and 2001 (Fig 14).

The number of micro-habitats noted in each plot also declined but only between 1971 and 2001. This mainly reflects reduction in exposed soil and rock habitats (Fig 15)[7], which is consistent with vegetation and canopy growth covering up these features.

The pattern adds a further mechanism to explain the loss of numerous light-loving earlier successional species reported in Kirby et al (2005) as the woodlands became more shaded after 1971.

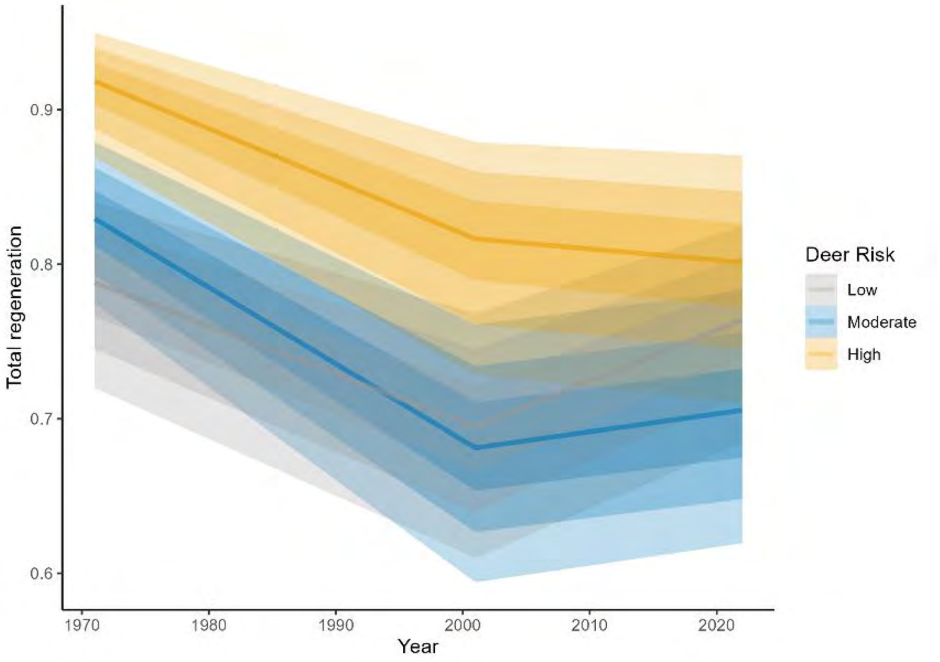


Fig 13: Proportion of plots with regenerating stems across surveys by deer risk status.

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[7] Micro-habitats comprise the following: Stumps>10cm, rot holes, dry/wet streams and ditches, stones and boulders, scree, embankments, exposed organic soils, sand & gravels, rock ledges, walls, cliffs, gully, ponds/lakes, quarry/mine workings.

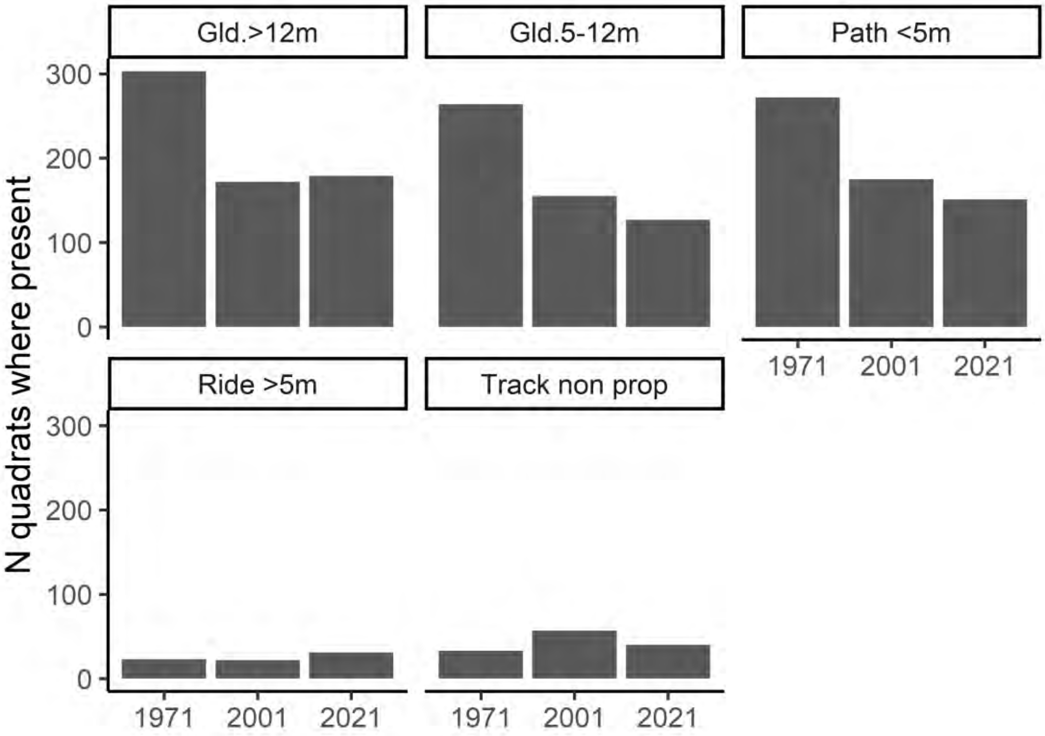

Fig 14: Presence of open spaces in the woodland plots in each survey. Gld = glades, defined as areas without a tree or shrub canopy.

4.10 Signs of grazing

There is inevitably much uncertainty in the extent to which surveyors can detect signs of grazing animals where present.

Signs of the presence of sheep, red deer, cattle and horses were uncommon and reduced slightly over time from low levels in 1971. However, signs for 'other deer' were commonly noted and increased markedly over time suggesting that a range of deer species constitute the greatest herbivore presence in the woodland sample. Signs were noted in 33% of plots by 2021 (Fig 16). Detection of the possible impact of deer on the woodland understorey is detailed below in section 10.

Increases in signs of deer are consistent with the known increases in numbers across Britain since the early 1970s (Coomber et al 2021; Ward 2005).

Squirrel damage was not recorded and so constitutes an impact that we are unable to explore in the survey data.

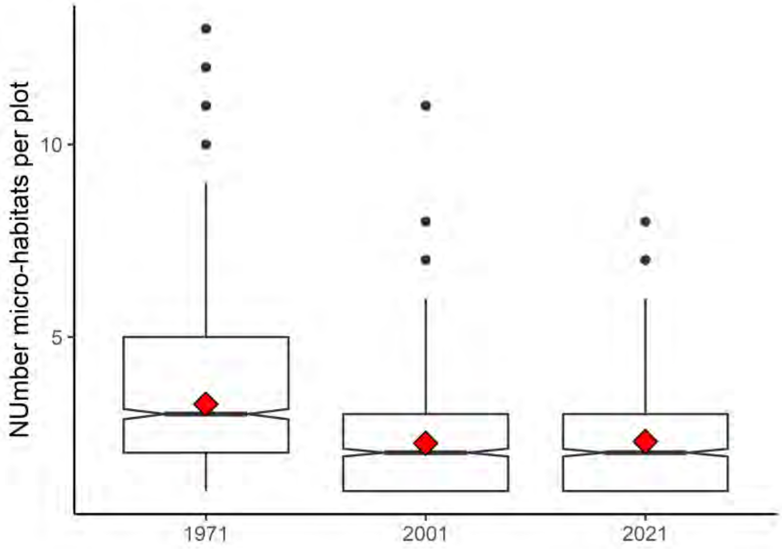

Fig 15: Presence of habitats that impart small-scale heterogeneity within sample plots. The red diamond is the mean. The middle line in each box indicates the median, the upper and lower edges are the 66 and 33% tiles respectively and the whiskers and dots indicate the non-outlier range and outliers respectively.

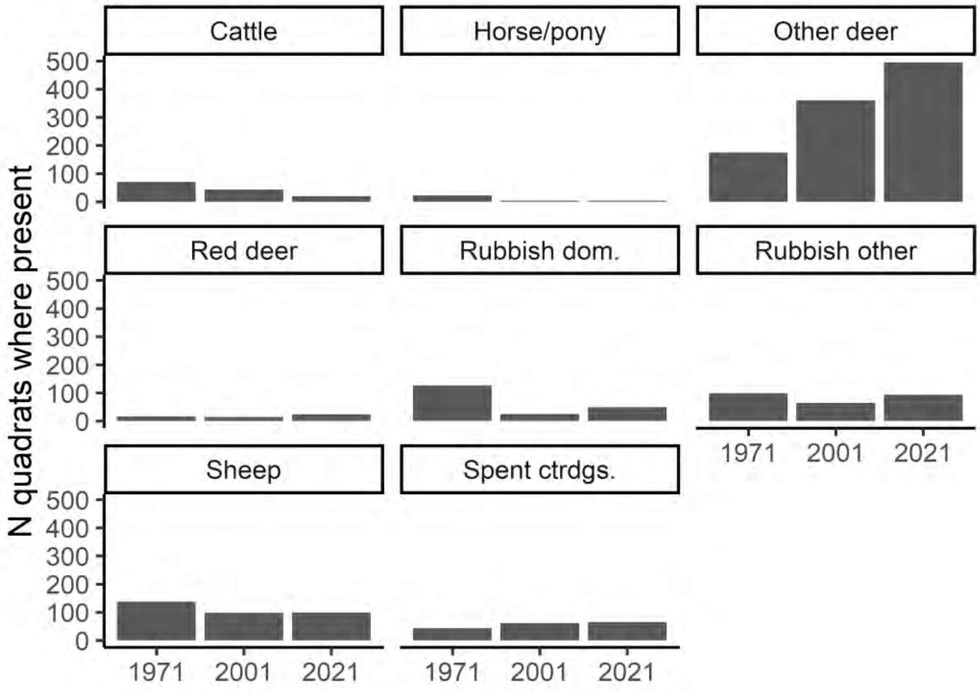

Fig 16: Signs of grazing animals and presence of rubbish in surveyed plots.

4.11 Presence of rubbish in the surveyed plots

Surveyors also recorded domestic rubbish and other litter where present including spent shotgun cartridges. Rubbish was recorded in 10% of plots and cartridge cases in 6% of plots in 2021 with minor changes over time but a reduction in domestic rubbish since 1971. This may simply reflect its lack of visibility as the woodlands closed up to some extent in subsequent years (Fig 16).

4.12 Changes in ground flora species richness and composition

Species richness declined significantly between 1971 and 2001 and then increased again significantly between 2001 and 2021 but was still significantly lower than the 1971 mean value (Fig 17). The 1971 to 2001 change was partially explained by a statistical model that included positive effects of the October 1987 storm, grazing signs and presence of woodland gaps as having a positive effect on species richness whilst increases in tree basal area had a negative effect. Between 2001 and 2021, species richness increased. An obvious question is why this reversal occurred.

Table 2. Species that increased or decreased the most in frequency of occurrence between plots over the 50-year period. Figures are % frequency across repeated plots and % change is the overall change in % frequency from 1971 to 2021. Trees and shrub entries refer to seedlings only.

a) Increasers

Name	**1971**	**2001**	**2021**	**% change**
Ilex aquifolium	20	24	36	16
Hyacinthoides non-scripta	29	34	44	15
Arum maculatum	10	11	23	13
Galium aparine	21	21	31	10
Ranunculus ficaria	0	4	10	10
Carex remota	6	8	15	9
Anemone nemorosa	9	11	17	8
Teucrium scorodonia	0	0	7	7
Polystichum setiferum	0	1	7	7
Phyllitis scolopendrium	2	4	8	6
Taraxacum agg.	7	7	13	5
Juncus effusus	16	15	21	5
Rumex conglomeratus/sangui	10	13	15	5
Carex pendula	4	6	9	5
Lapsana communis	0	0	4	4
Allium ursinum	5	6	9	4

b) Decreasers

Name	**1971**	**2001**	**2021**	**% change**
Viola riviniana/reichenbiana	45	27	22	-23
Castanea sativa	18	8	2	-16
Epilobium montanum	23	9	8	-15
Oxalis acetosella	48	36	34	-14
Betula seedling/sp	22	15	9	-13
Pteridium aquilinum	46	36	34	-12
Deschampsia flexuosa	27	15	16	-12
Ajuga reptans	21	11	9	-12
Sorbus aucuparia	27	14	16	-11
Galium saxatile	22	11	11	-11
Quercus seedling/sp	35	21	25	-11
Luzula pilosa	20	8	10	-11
Fragaria vesca	16	7	6	-11
Lonicera periclymenum	42	31	32	-11
Chamerion angustifolium	13	5	3	-10

Clues can be sought in the identity of the apparent winners and losers over time and in the way indicator variables have changed where these variables imply changes in conditions such as mean Ellenberg scores for fertility (N) and soil pH (R) or track species considered to be specialised and therefore most characteristic of long-continuity woodlands (Ancient Woodland Indicators) or species more common in the wider landscape and in a wider range of habitats and including those favoured by disturbance and high fertility (see for example the similar distinction made between forest and non-forest plants in Jamoneau et al 2011). The latter are defined here as the total list of negative Common Standards Monitoring indicators for British habitats minus trees and shrubs (see Appendix A).

Table 3. Species that increased or decreased the most in mean cover over the 50-year period. Figures are % mean cover across repeated plots and % change is the overall change in % cover over time from 1971 to 2021[8].

a) Increasers

Name	**1971**	**2001**	**2021**	**% change**
Hyacinthoides non-scripta	0.6	4.3	5.2	4.6
Dryopteris dilatata/carthusiana	1.5	2.1	3.0	1.5
Allium ursinum	0.0	0.8	1.2	1.2
Brachypodium sylvaticum	0.5	0.7	1.5	1.1
Lolium perenne	0.1	0.9	1.2	1.0
Carex pendula	0.1	0.4	1.0	1.0
Deschampsia cespitosa	1.6	1.4	2.5	0.9
Poa nemoralis/trivialis	0.7	1.7	1.5	0.8
Rubus fruticosus agg.	10.1	10.3	10.9	0.8
Anthoxanthum odoratum	0.8	0.7	1.5	0.7
Dryopteris affinis/f-mas	1.2	1.1	1.9	0.7
Galium aparine	0.3	0.5	0.9	0.7
Anemone nemorosa	0.1	0.4	0.7	0.6
Urtica dioica	1.2	2.9	1.8	0.6

b) Decreasers

Name	**1971**	**2001**	**2021**	**% change**
Deschampsia flexuosa	2.6	1.6	1.0	-1.6
Pteridium aquilinum	8.7	7.5	7.2	-1.5
Holcus mollis	3.2	2.0	1.9	-1.3
Mercurialis perennis	6.3	6.9	5.6	-0.7
Agrostis capillaris	2.1	2.7	1.5	-0.5
Lamiastrum galeobdolon	0.7	0.3	0.2	-0.5
Chamerion angustifolium	0.5	0.1	0.1	-0.4
Agrostis canina sens.lat.	0.5	0.6	0.2	-0.3
Glechoma hederacea	0.6	0.4	0.4	-0.2
Agrostis stolonifera	0.7	0.8	0.5	-0.2
Festuca ovina agg.	0.2	0.3	0.1	-0.2
Filipendula ulmaria	0.5	0.4	0.3	-0.1

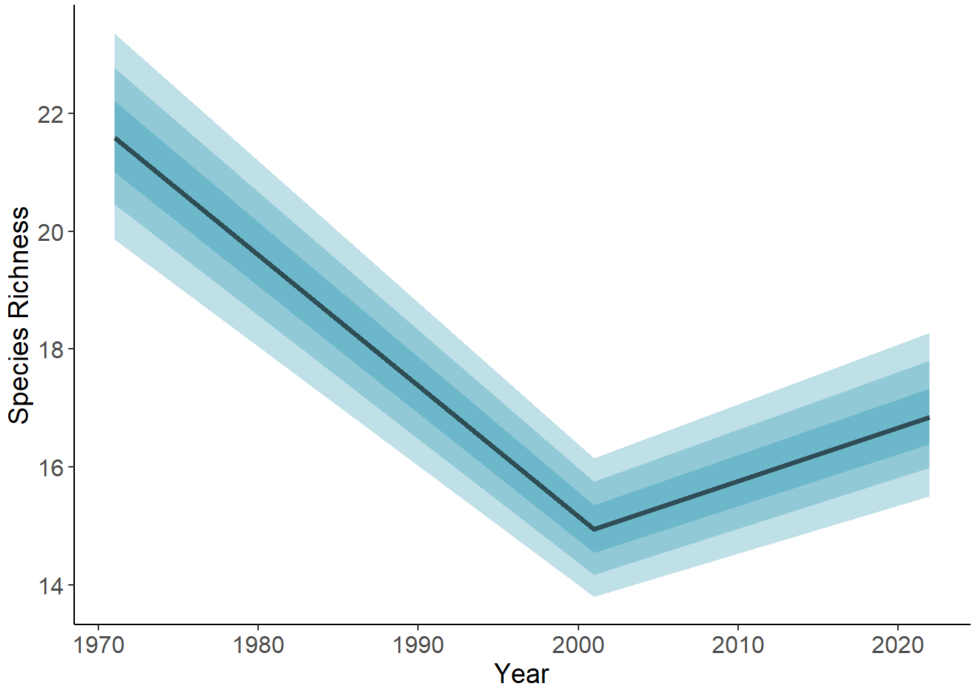

Fig 17: Change in plant species richness having accounted for a mean effect of day-difference in survey dates between each survey.

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[8] Note that low frequency and cover of vernal species in 1971 will partly reflect the generally later dates of survey in that year. While we account for day-date differences between surveys in our models, this can only apply an average correction which will not fully correct for extreme cases such as *Ranunculus ficaria* (now *Ficaria verna*) – see Table 1.

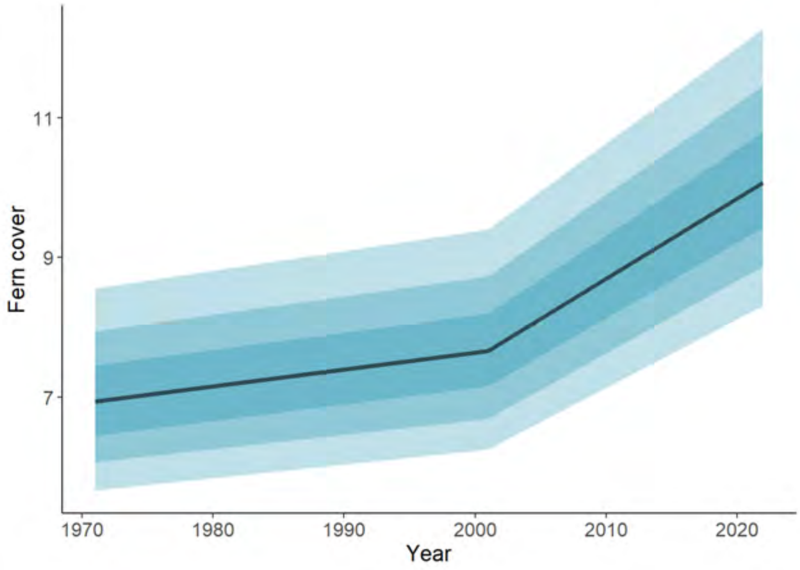


Fig 18: Change in total (%) cover of ferns over time.

Winners and losers (those frequent or high cover plants that changed most over time) are a mixed group (Tables 2 and 3). Increased abundance (cover or frequency) of ferns (*Drypoteris* species, *Phyllitis scolopendrium*) (Fig 18) and tree seedlings *(Ilex aquifolium)* coupled with a decrease in light-demanding species such as *Galium saxatile* and *Chamanerion angustifolium*, are consistent with 50 years of stand development, canopy closure and increased shade. Other signals are also present. Species of more fertile conditions increased including *Galium aparine, Carex pendula, Lolium perenne, Taraxcum* agg. and *Urtica dioica*. The trend for an increase in species of more fertile conditions is also supported by the 50-year significant increase in mean Ellenberg fertility score (Fig 19). Mean Elleberg R (an indicator of soil pH) also increased to a lesser and more variable extent (Fig 20). Grass species of better lit and grazed situations decreased such as *Agrostis capillaris* and *Festuca ovina*.

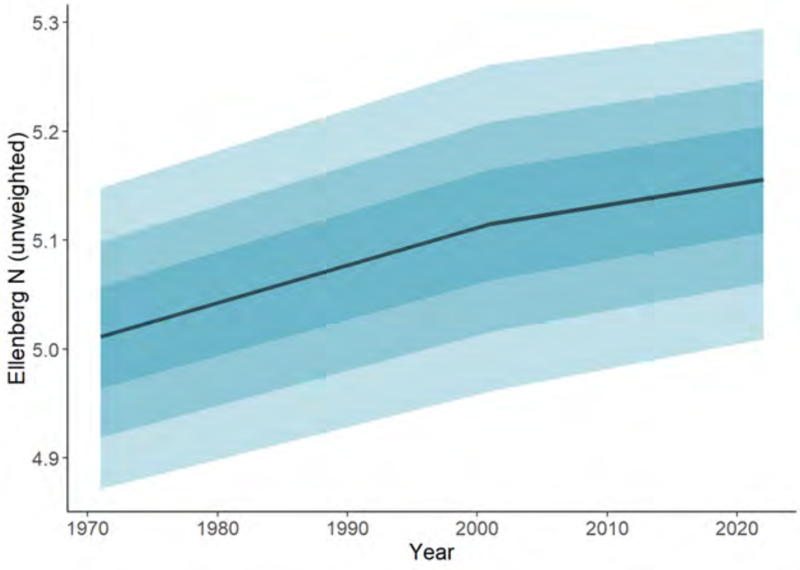


Fig 19: Change in mean Ellenberg N (fertility) values over time across repeated plots having accounted for survey day-date differences.

To further our understanding of the decline then recent increase in understorey species richness we tested whether, as richness changed, the proportion of different kinds of species changed (also see Appendix D). For example, the reduction and uptick in richness would be evaluated differently if increasing richness tended to favour woodland and wider landscape generalists whilst woodland specialists declined or remained at low levels. Note the subtlety of this analysis; we already know that Ancient Woodland Indicator richness exhibited the same pattern as total species richness. Here we ask whether, as species richness changed, the proportion of the species pool became dominated by woodland specialists or wider countryside plant species.

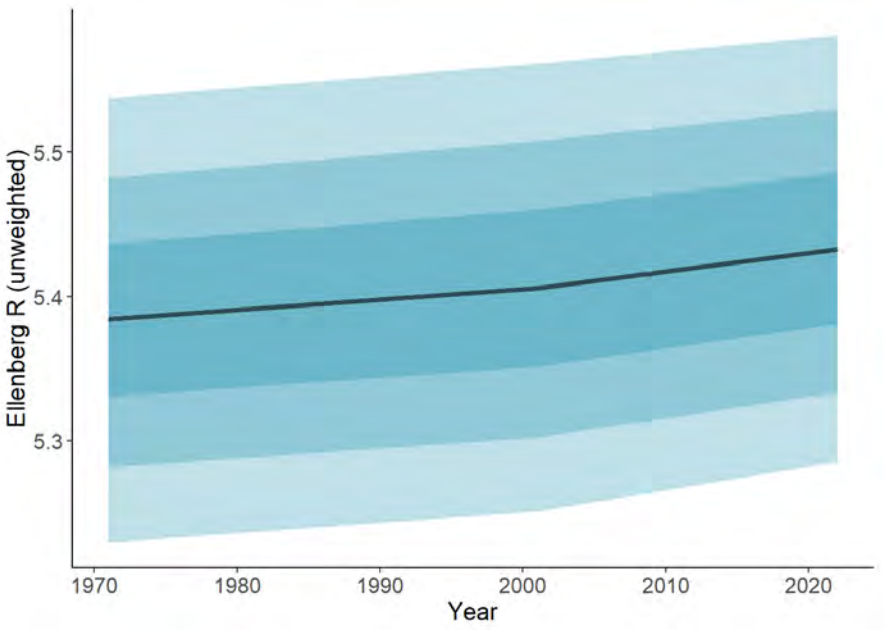


Fig 20: Change in mean Ellenberg R (soil pH) values over time across repeated plots having accounted for survey day-date differences.

Results showed that the *proportion* of AWI species in each plot did not change over time and was estimated as 42%, 42% and 43% of the mean richness in plots in 1971, 2001 and 2021 respectively. The proportion of wider-ranging, non-woodland plants (negative CSM species minus trees and shrubs) was estimated at an average 26%, 28% and 28% in 1971, 2001 and 2021 where 1971 values were significantly lower than both later surveys but 2001 and 2021 were not different. The results tend to indicate that changes in richness have not involved strong preferential filtering for either specialised or generalist plants. However, it seems likely that other different groupings of plants might reveal such trait-based segregation over time, for example dividing AWI species into more versus less shade-loving species (Kimberley et al 2013). Indeed, when the proportion of negative CSM species are analysed over time but additionally factoring in the presence of canopy gaps (glades, paths and rides) the interaction between their presence and the latest survey year was highly significant. Plotting the data shows that whilst the overall mean proportion has changed relatively little over time this conceals a divergence most apparent in the latest survey where these *non*-woodland specialist species have become more frequent in gaps but less frequent under the canopy (Fig 21).

Given the trend toward more shaded, less disturbed understoreys we would expect shade-loving species to thrive. Modelling change over time in % cover indeed shows this to have been the case for *Allium ursinum*, *Hyacinthoides non-scripta* and *Mercurialis perennis*, three common perennials capable of exploiting stable, shaded conditions (Fig 22). They have either held their ground or increased in cover between 1971 and 2021. The increase in summed % cover of ancient woodland indicators as well as summed fern and sedge cover (Figs 18 & 22) also imply a recovery phase in the last 20 or so years following the dramatic drop in richness from 1971 to 2001 but where recovery is filtering in favour of more shade-tolerant species and woodland specialists that are often clonal or large plants inherently capable of increasing in cover; competitive stress-tolerators in Grime’s CSR scheme.

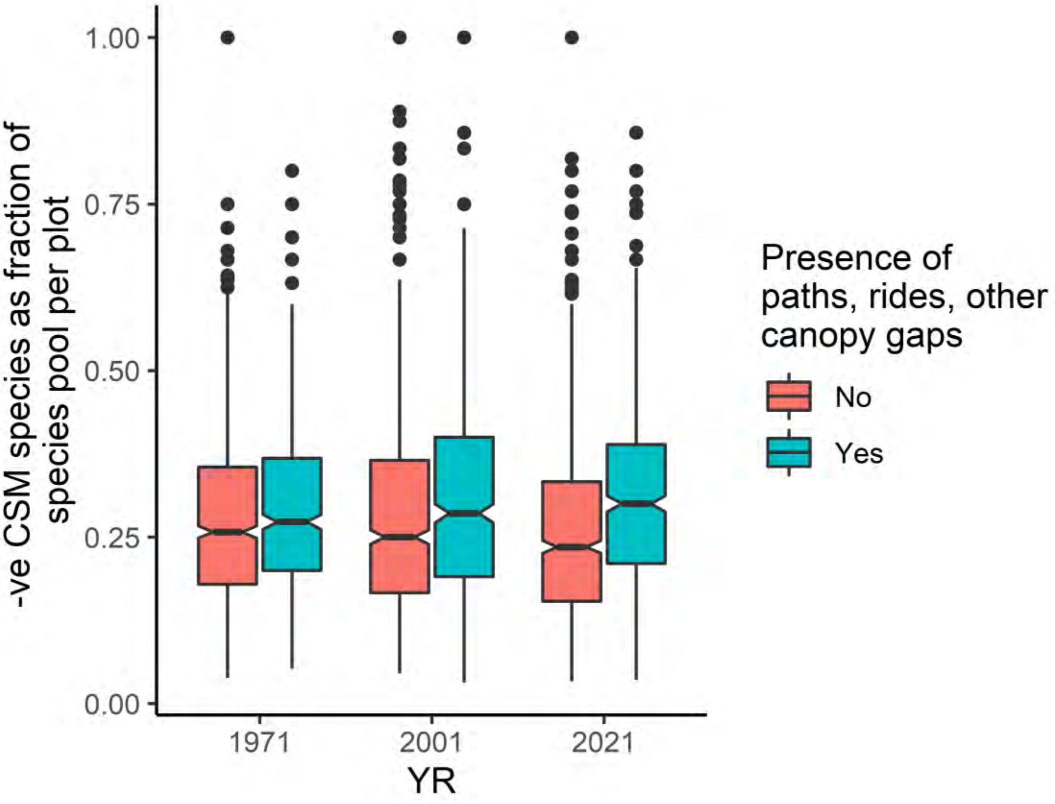
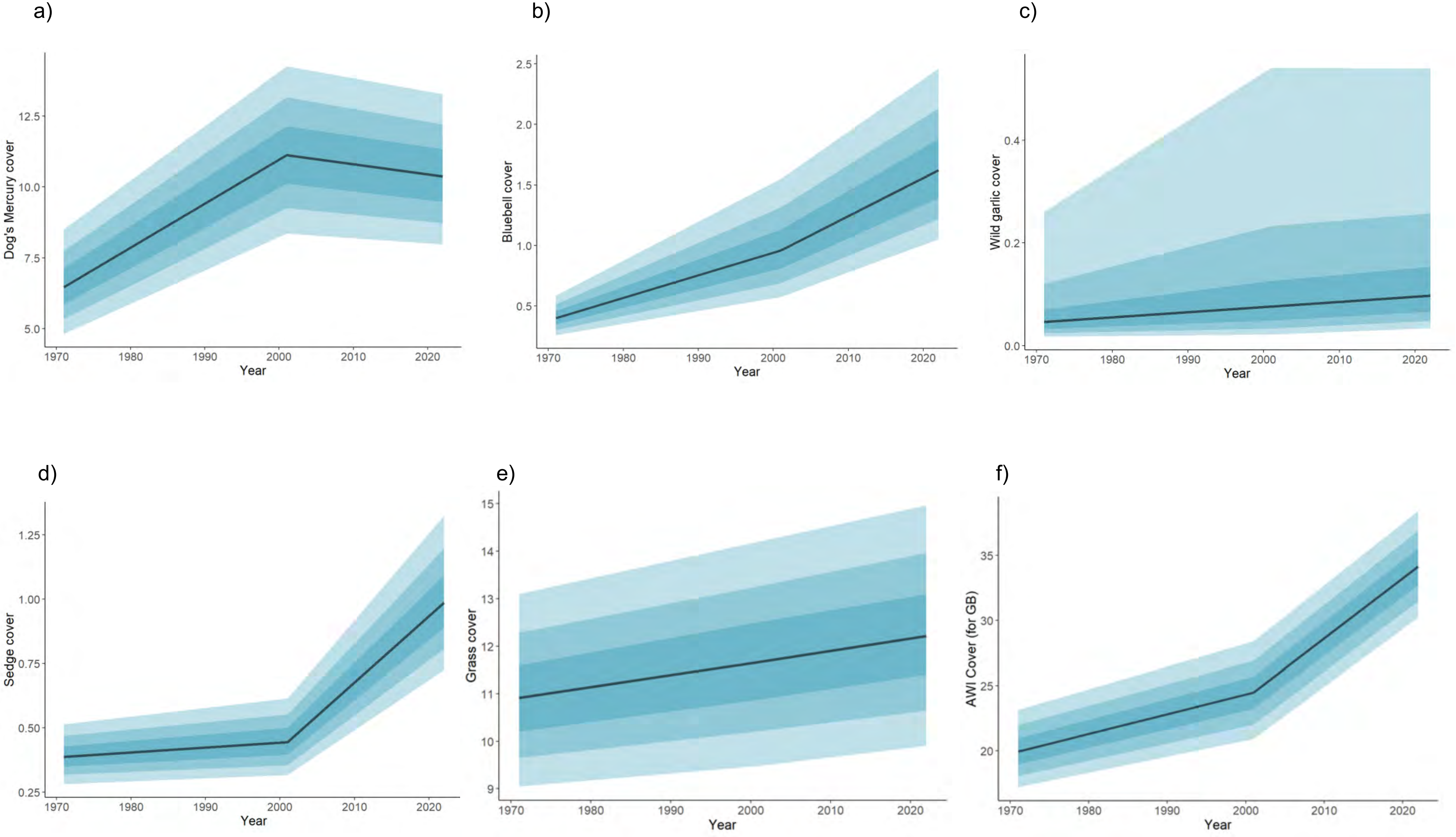


Fig 21: Negative CSM species for all habitats minus trees and shrubs, as a proportion of the total number of species recorded in each plot, by survey year and whether the plot coincided with a gap in the canopy. The middle of each box indicates the median, the upper and lower edges are the 66 and 33% tiles respectively and the whiskers and dots indicate the non-outlier range and outliers respectively.

Fig 22: Modelled changes in % cover of common woodland understorey dominants, a) Dog's Mercury (*Mercurialis perennis*), b) Bluebell (*Hyacinthoides non-scripta*), c) Wild Garlic (*Allium ursinum*). Modelled changes in summed % cover of d) sedges, e) grass (Poaceae) and f) Ancient Woodland indicators.



Stronger, yet nonetheless still correlative evidence of the drivers of changes in the understorey comes from modelling species compositional change along gradients where the possible driving forces vary from high to low. In sections 4.14 to 4.17 we summarise attempts to understand and isolate the impacts of Ash dieback, deer grazing, intensive land-use surrounding each woodland, distance of plots to the edge of the wood, climate & climate change and atmospheric pollutant deposition.

4.13 Soil change since 1971; pH and Soil Organic Matter (SOM)

Mean fresh soil pH differed significantly between each pair of survey years (Fig 23) whilst SOM was stable across the 50-year interval (Fig 24). Overall, soil pH increased by 0.18 (0.27-0.08 HPD) in the 50-year interval.

The direction and magnitude of soil pH change is very similar to that seen in the low intensity habitats, including broadleaved woodland, that were sampled in the GB-wide Countryside Survey (CS) between 1978 and 2019 (Seaton et al 2023). In both surveys soil pH increased from the 70s to around 2000 and then decreased through to the present but resulting in a net increase over the whole period. The changes in CS were partly explained by reduced sulphur deposition with an additional positive effect of rainfall during the field season.

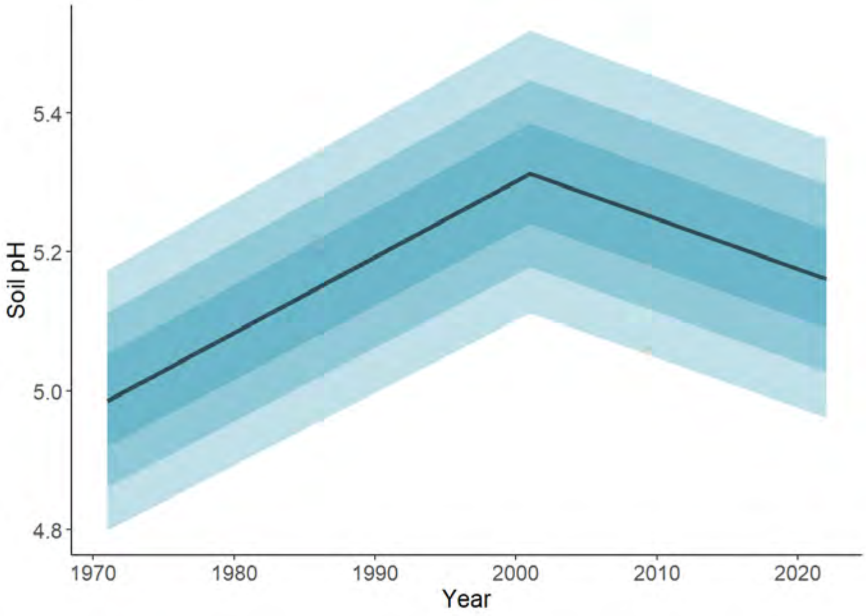


Fig 23: Change in fresh soil pH in the broadleaved plots.

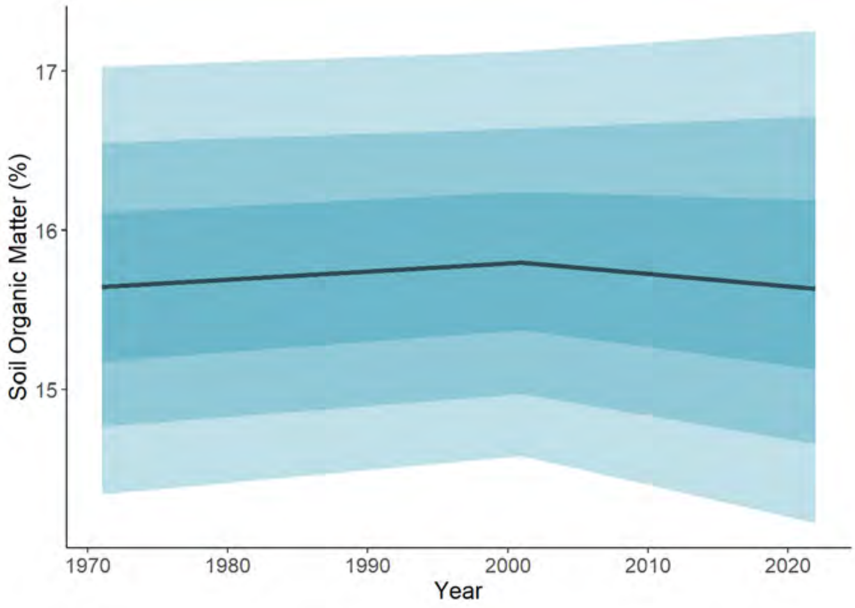


Fig 24: Change in Soil Organic Matter in the broadleaved plots.

The annual rates of change in soil pH within time intervals across each survey are remarkably similar hinting at shared driving variables that are not solely a function of habitat identity since a wide range of semi-natural habitats were included in the CS sample (Fig 25). The role of atmospheric pollutant deposition alongside other drivers in explaining pH change in the woodland sample are explored further in section 4.17.

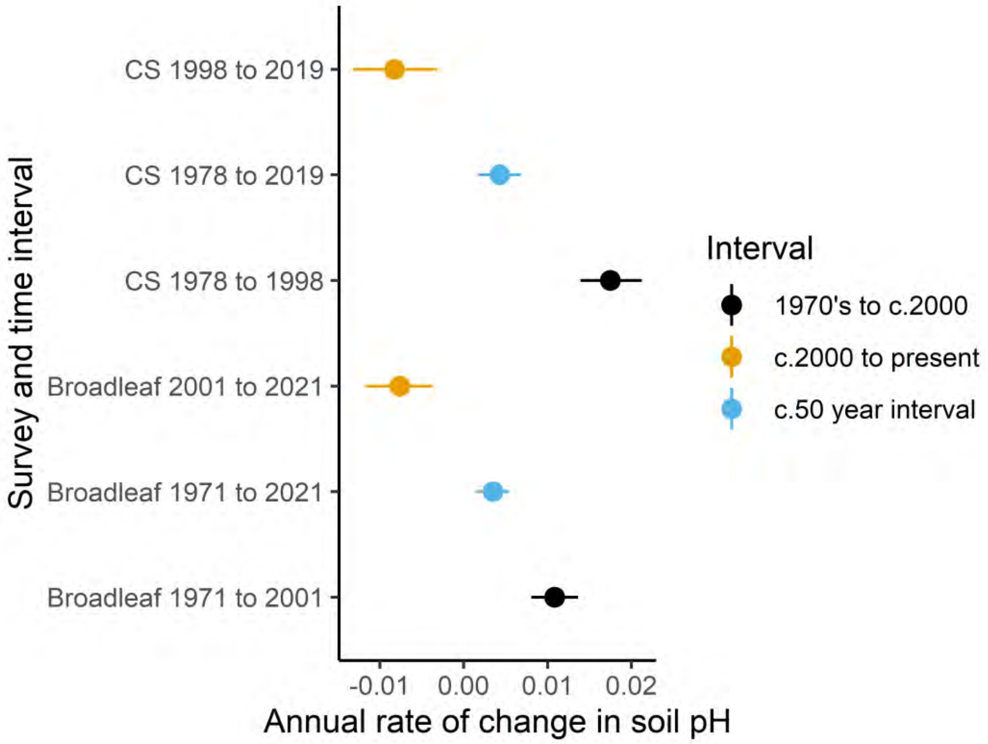


Fig 25: Annual rates of change in soil pH per year based on the differences between survey years within Countryside Survey (Seaton et al 2023) and between the broadleaved woodland survey years. Means (+/- Highest Posterior Density interval).

4.14 Ash dieback, deer impacts and the interaction between the two

Signs of Ash dieback disease were noted in 21% of the most recently surveyed plots (Fig 26). This number plus their geographic spread provides a robust sample for examining impacts on the ground flora and interactions with other drivers. Here we focus specifically on deer risk and explore how these two factors might also interact with plant cover and Bramble (*Rubus fruticosus* agg.) given that the latter strongly dominated many understoreys and its growth is favoured by better-lit woodland gaps.

Species richness in plots that had Ash dieback was higher in 2021 than plots with Ash but without Ash dieback (plots without Ash dieback had ~90% (83-97%) of the richness of plots with Ash dieback), and this was compared to the surveys in previous years having the same richness (i.e. before Ash dieback had an impact there was no difference in richness – indicating no confounding factors) (Fig 27). Plots without Ash showed lower species richness overall. Interestingly, there was no effect of Ash dieback on Shannon diversity and Simpson diversity indicating that the increase in species richness was driven by an increase in the number of low cover species present rather than potential dominants.

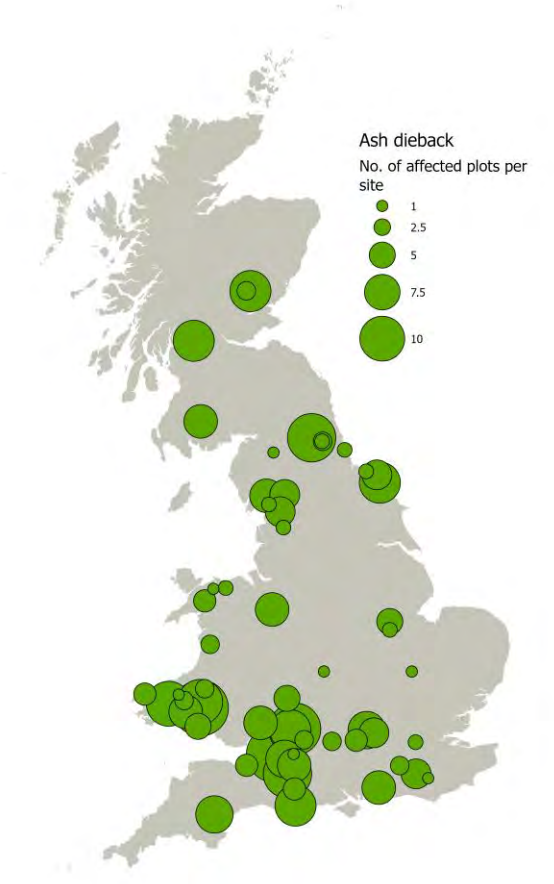


Fig 26: Numbers of plots per site with signs of Ash Dieback present in the 2020-’22 survey. Circles are proportional to the number of plots with signs present.

Further analysis showed that inclusion of several mediating relationships improved model fit. Bramble cover tended to increase only in low deer risk sites, with twice as much Bramble cover on average in 2021 in low risk compared to moderate and high-risk sites (Fig 28). Increasing Bramble cover was negatively correlated with forb cover which was in turn positively associated with species richness. Presence of Ash dieback also appeared to elevate forb cover and species richness leading to the best fitting model shown in Fig 29.

The addition of two climate variables also led to better model fit. Higher winter rainfall had a positive effect on species richness but a negative effect on Bramble cover while higher winter minimum temperature had positive effects on both (Fig 29). Adding summer rainfall and temperature did not improve model performance.

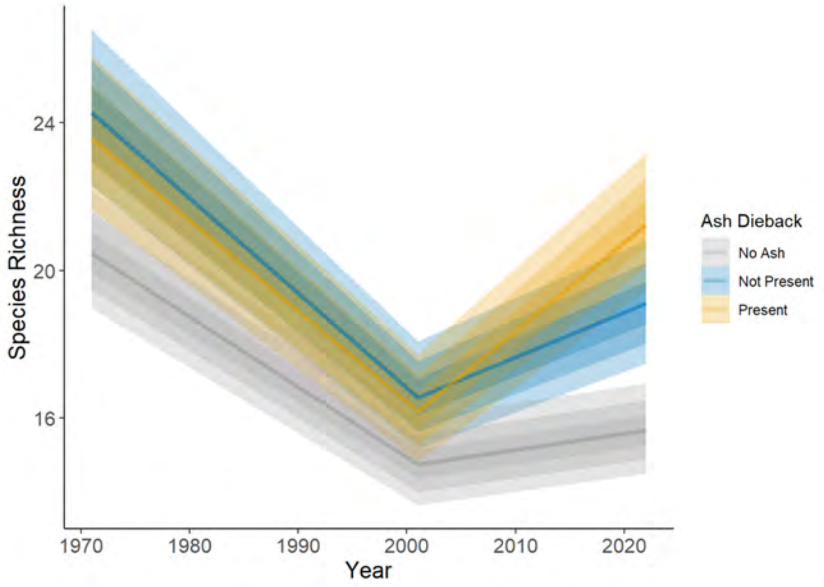


Fig 27: Plant species richness changes by presence of Ash and Ash Dieback over time.

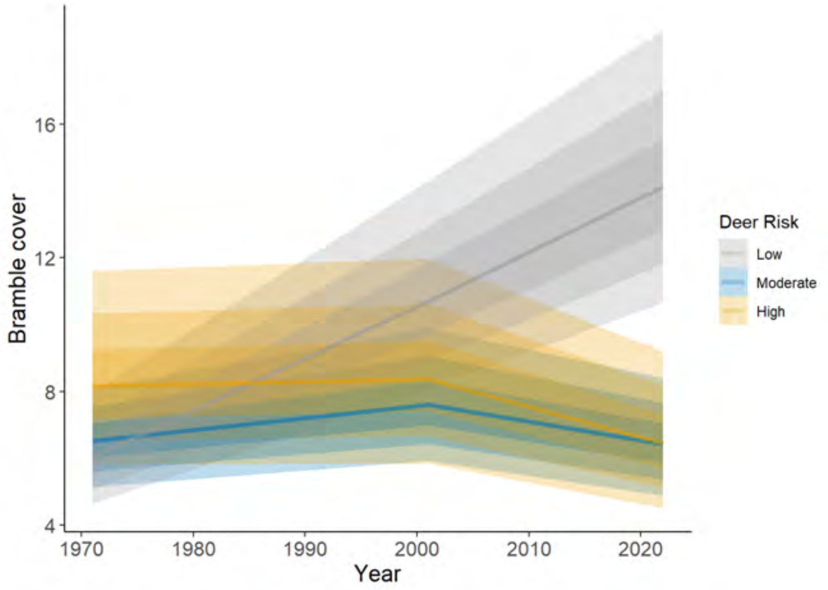


Fig 28: Bramble (*Rubus fruticosus* agg.) % cover in each survey year crossed with deer risk.

In summary, in recent years Ash dieback has led to increased forb cover and increased species richness most likely associated with better-lit understories. Bramble has rapidly spread in low deer grazing areas but has remained stable in high and moderate deer grazing areas. Species richness changes are mediated by an interaction between Ash dieback and deer grazing since species richness has only been able to increase due to Ash dieback under high deer grazing. Forb cover has been able to increase due to Ash dieback under all levels of deer grazing. This suggests that species richness changes under Ash dieback and high deer grazing are due to deer preventing potentially dominant forbs from taking over.

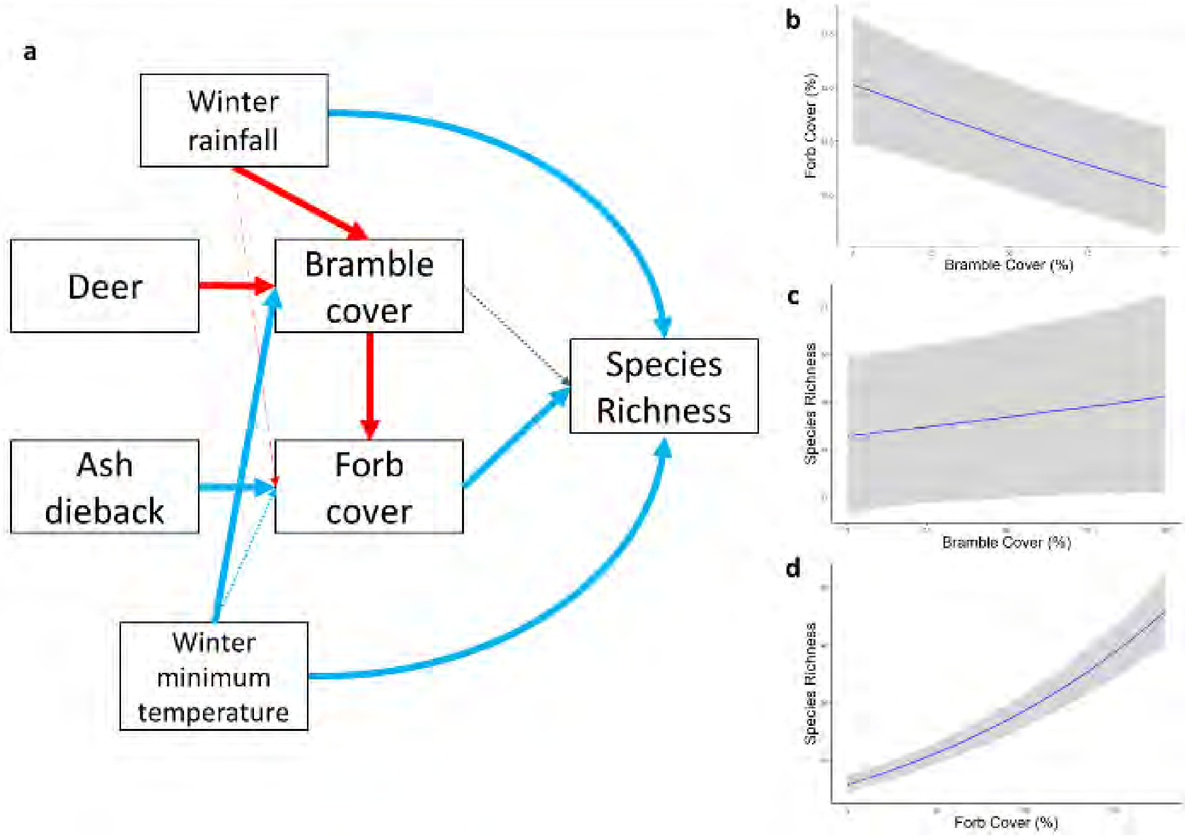


Fig 29: Best fitting model of the direct and indirect effects of correlated potentially causal factors on understorey species richness. Thick red and blue lines indicate statistically significant relationships. a) Multivariate model diagram, b) to d) are graphs of the separate effects of the mediating variables forb cover and Bramble cover.

4.15 The influence of intensive land cover and land cover change around each site and interactions with distance to woodland edge, site area and presence of gaps

The effect on understorey species richness of plot distance to the edge of the woodland was on average not significant across years and sites. This appeared to be because the individual within-year relationships differed, hence there was a significant interaction between distance to edge of site and year of survey (Fig 30). In the latest survey species richness increased with distance into the woodland whilst in 1971, the opposite was true. The effects are however very small relative to the variation in the data but the 2021 relationship seems consistent with the modest increase in shade-tolerant species seen since 2001. The species-area relationship could also indirectly be at work here since larger sites by definition will have plots that are farther from the edge. This would require the extra species that have increased in the last 20 years to occurr preferentially within the interior of the site.

The presence of gaps within each plot had a significant positive effect (Fig 31) on species richness but there was no interaction with the amount of intensive land-cover surrounding each site, nor distance to site edge. Gaps also had no significant effect on mean Ellenberg N (fertility) but see Fig 21 above where we did see an increasing proportion of more generalist species in gaps over time (Fig 32).

Interestingly there were significant effects of distance to edge of site on mean Ellenberg N(fertility) values and the negative relationship steepened over time so that by 2021 fertility scores were higher at the site edge and lower farther from the edge than in 1971 (Fig 33).

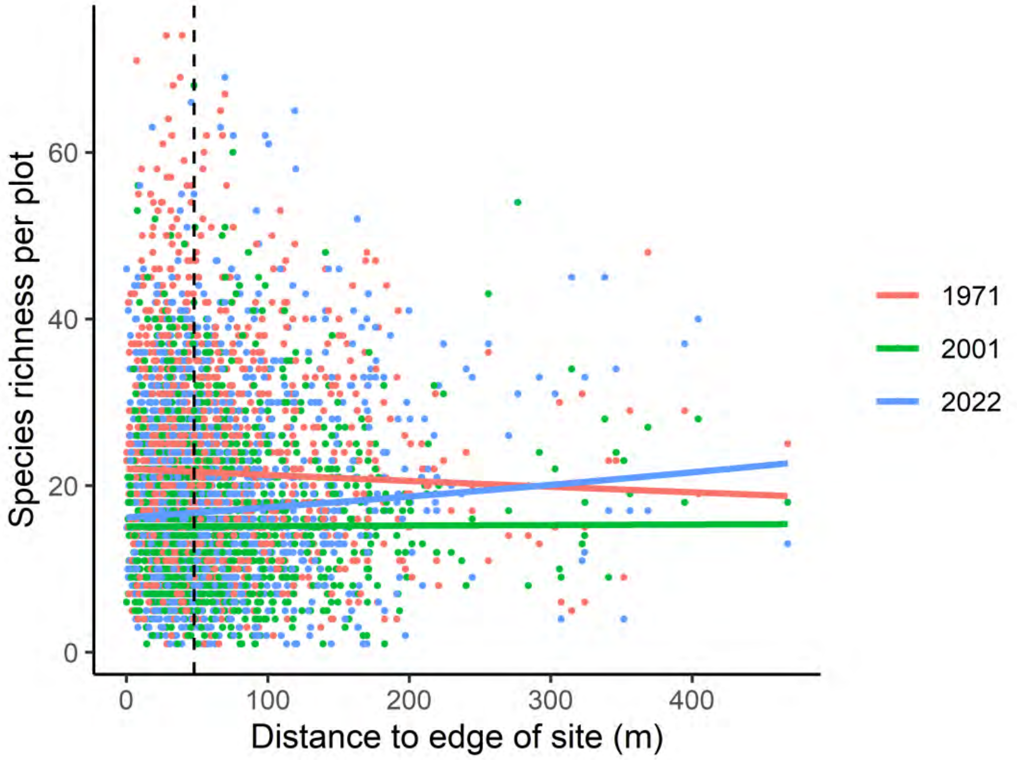


Fig 30: Understorey species richness by distance of plots from site edge across surveys. The vertical line is the median distance to edge of site. Coloured lines are the model predictions for each year.

Far bigger effects were attributable to site size and % intensive land cover (arable + improved grassland) around each site (Figs 34 & 35). This is a complex model that requires careful interpretation of potential cause and effect. Firstly, site area is unevenly distributed with most woodlands in the sample being <60ha in size and very few representing large sites. Hence there is much scope for the site area effect being confounded with other factors that are correlated with size. Similarly, the strong effect on mean Ellenberg N attributable to the proportion of intensive land-use in the 1km buffer around each site could also reflect the fact that smaller woodland sites with higher intensity of land-use are embedded in landscapes on more naturally productive soils irrespective of human activity. We tried to account for this by including plot-level soil pH as an additional predictor because this tends to have a positive correlation with macronutrient availability and therefore fertility unless pH is at the very high end of the gradient. The modelled lines in Figs 34 & 35 show predicted responses to site area and % intensive land cover having fitted the average effect of soil pH. Hence, there is still a residually significant relationship with site area and intensive land-use even after fitting soil pH variation.

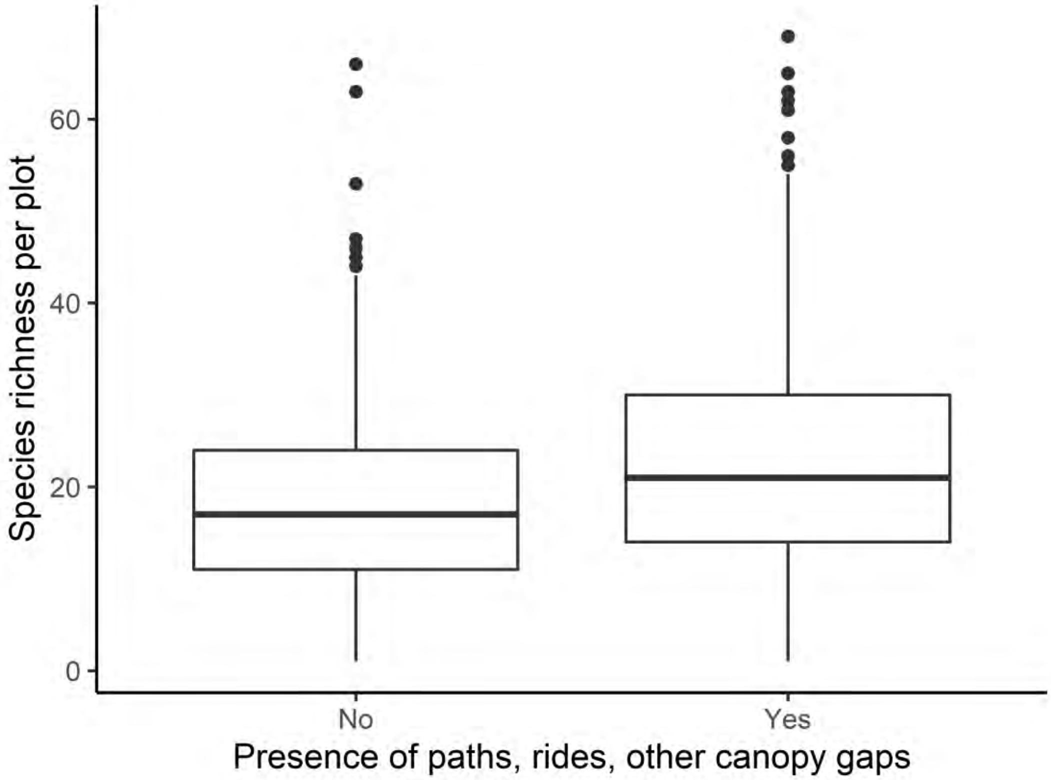


Fig 31: Understorey species richness in all surveyed plots from all years by presence of canopy gaps. Boxes are the median (+/-33%tile). Whiskers are the non-outlier range of the data.

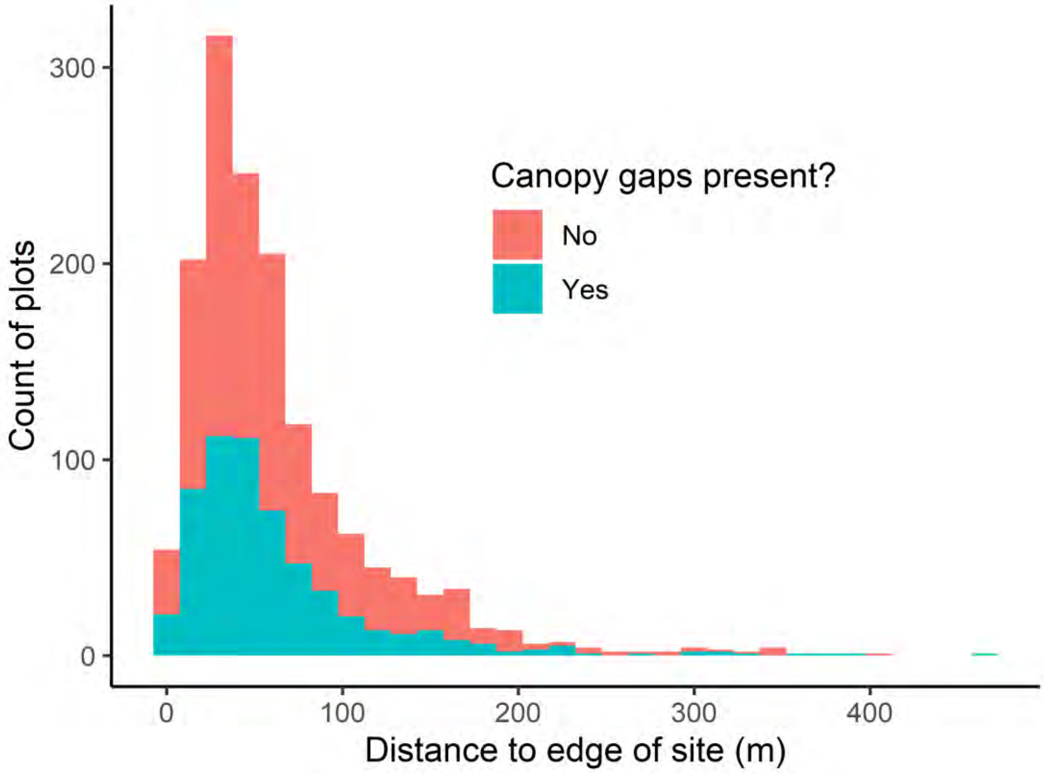


Fig 32: Presence of canopy gaps versus distance of gaps to edge of the woodland sites.

The best fitting model included survey date day difference, year of survey, soil pH, site area and % intensive land-cover in 2021. All terms were significant and the model explained 45% of the total cross-year and between-plot and site variation in mean Ellenberg N excluding random effects. This is a high level of explanatory power for such geographically dispersed and ecologically variable data.

This model estimates that a change from 0 to 100% intensive land-cover increases mean Ellenberg N by 1.62 units, which is 23% of the gradient of fertility values across the British flora (range 1-8). The area effect works in the opposite direction estimating a reduction of mean Ellenberg N by one unit for every 137ha increase in site size. The interpretation of the model needs to be heavily caveated. These are spatial predictions and space does not readily substitute for time (Damgaard 2019) especially in woodlands where legacy effects of residual fertility can be virtually permanently fixed into soils, rhizosphere and vegetation (Dupouey et al 2002; Diedhiou et al 2009). The implication is that reducing the intensity of land-use around sites and increasing site size will at least be a precautionary tactic. Whilst not directly reducing fertility within the woodland it would increase the extent to which the woodland was buffered from intensive land-use. However high place-based uncertainty attaches to the timescale and magnitude of the response of woodland ecosystems to these mitigation actions. Temporal responses to management that increase site size and reduce land-use intensity around sites are likely to be non-linear, lagged, context dependent and subject to deflection by climate change and extreme weather.

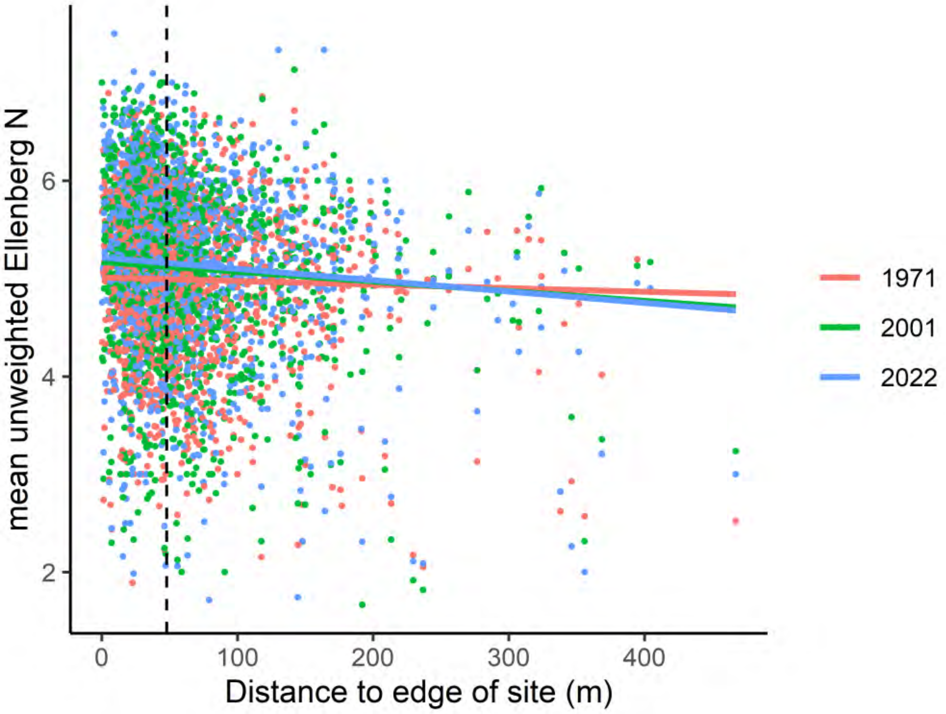


Fig 33: Data points for plots in all survey years and modelled predictions of mean Ellenberg N per plot given distance to site edge. The slopes for 2001 and 2022 differed significantly from and steepened relative to 1971.

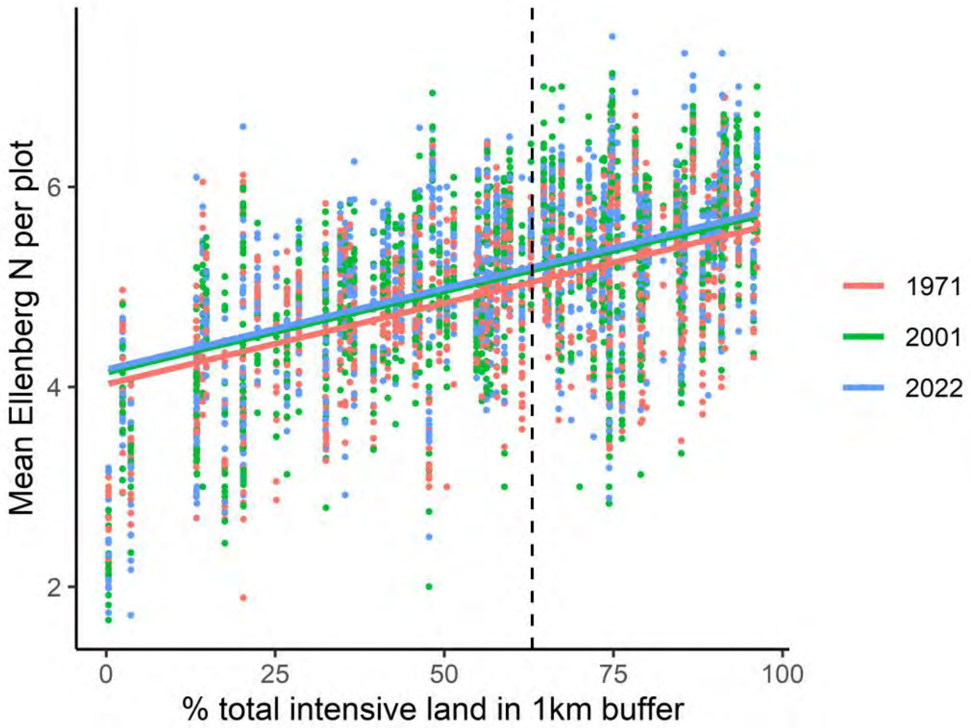


Fig 34: Data points for plots in all survey years and modelled predictions of mean Ellenberg N given % intensive land-cover in the 1km buffer around each site. The vertical line is the median percentage.

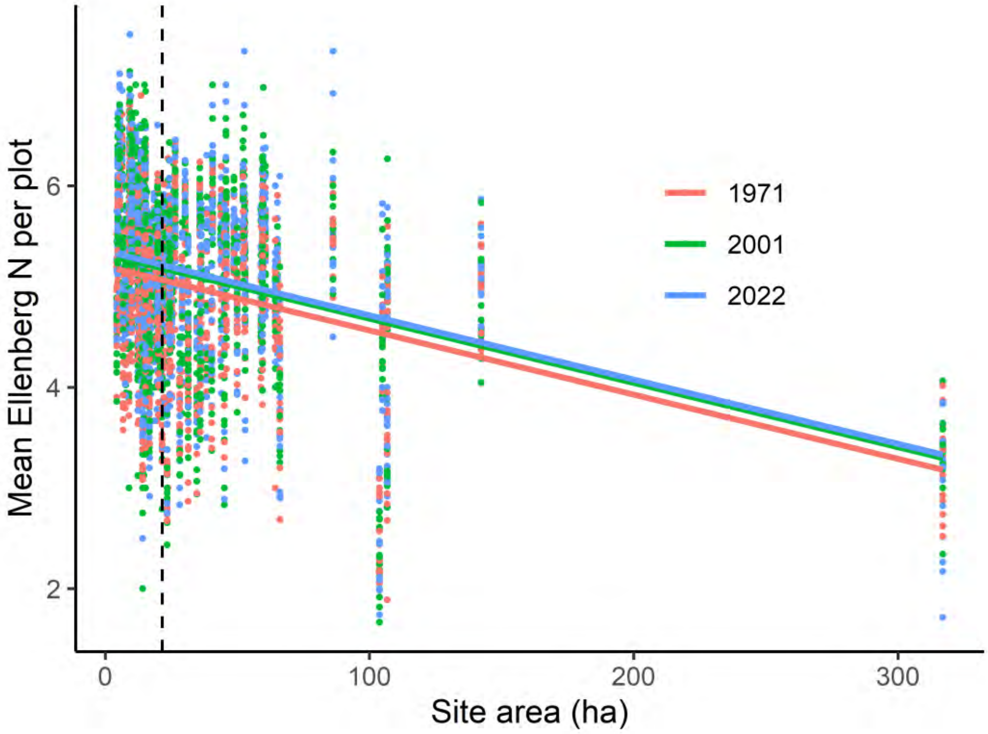


Fig 35: Data points for plots in all survey years and modelled predictions of mean Ellenberg N given variation in site area. The vertical line is the median value.

4.16 The effects of climate change

Have southerly distributed species increased in abundance?

There were significant increases in the proportion of southerly distributed species in plots between all survey years through time. On average this proportion was higher if sites had become warmer in the summer (Fig 36). Change in summer rainfall had no significant effect. We presumed that these species would favour gaps, greater light and greater warmth but there was no significant overall effect of gap presence and no year by gap interaction terms were significant.

The southerly species involved are a mixed bag ecologically. Changes seem very consistent with the strong effect of a closing canopy filtering for shade-tolerators over time versus more light-demanding species. The beneficiaries comprise shade-tolerant plants that can withstand or take advantage of these influential changes in light regime, persisting while other species decline. However, the outcome of these probably shade-driven changes still leaves southerly species with greater representation in the reduced pool per plot relative to 1971. The most common increasing southerly species included *Ilex aquifolium, Polystichum setiferum, Carex pendula* and *Hedera helix*, while common decreasers included *Lonicera periclymenum, Dactylis glomerata, Holcus lanatus, Digitalis purpurea* and *Lotus corniculatus*. Notably, the last four are all less shade-tolerant.

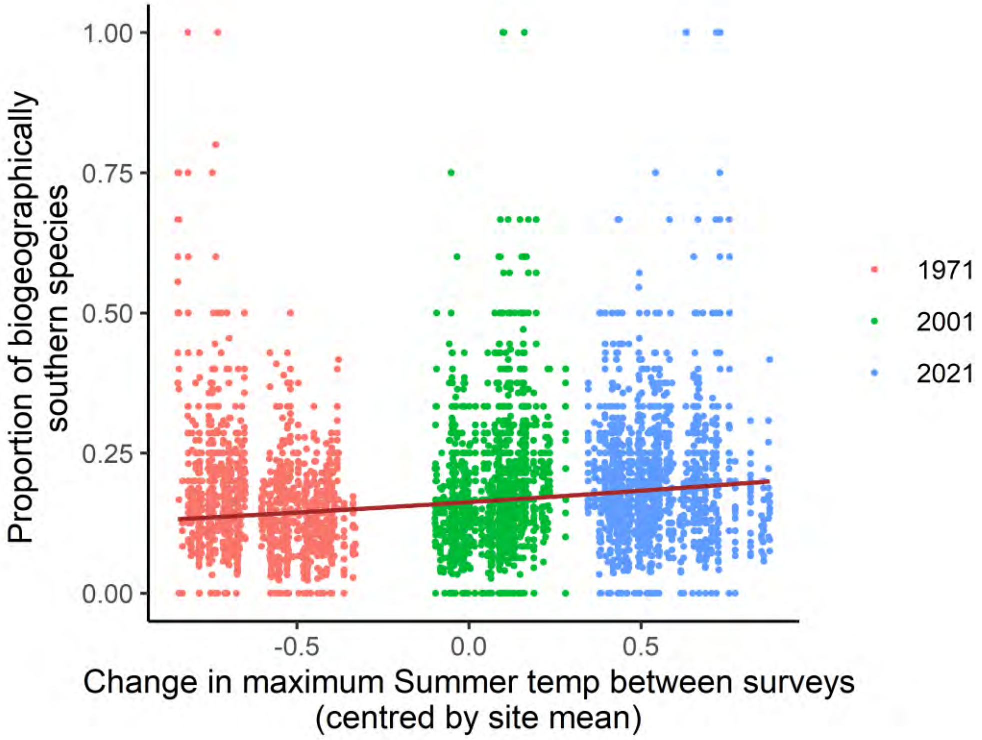


Fig 36: Number of plant species with a southerly biogeographic range as a proportion of the total number of species recorded in each plot. The line is the predicted proportion in each plot by change in maximum summer temperature at each site on the x axis. Points are also coloured by year of survey showing clearly how the 20-year pre survey maximum temperature has increased across all sites in the 50-year period.

Is climate change implicated in the rise of Holly?

The increased abundance of Holly across the 50-year period could be related to grazing pressure and to a changing climate. Bañuelos et al (2004) showed that Holly responded positively to warmer winter temperatures in Denmark and so we modelled Holly changes across time in terms of change in mean winter minimum temperature crossed with deer risk.

The survey data allows separate models to be constructed of Holly populations at different stages of growth. Hence, separate models were constructed for seedling counts, regen stems (<1.3m and >25cm), stem counts (>1.3m) and also mean DBH (stems >1.3m).

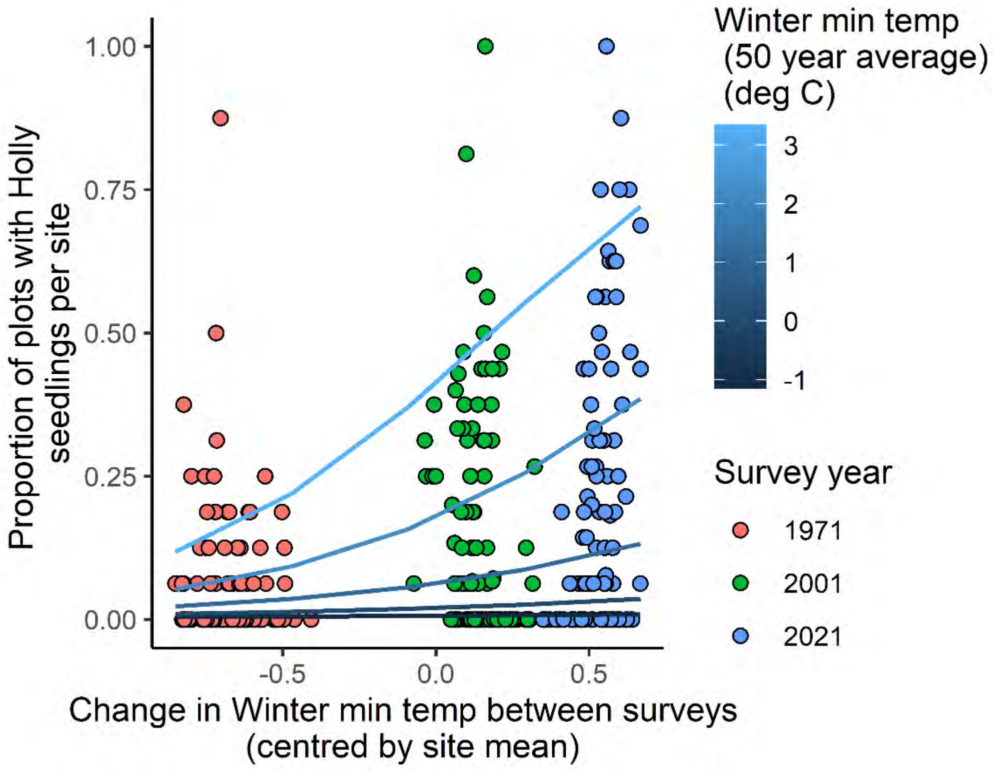


Fig 37: Proportion of plots containing Holly seedlings in each survey. Lines are the fitted predictions from the best-fitting model that included winter min temp change and overall average winter minimum temperatures at each site and their interaction.

Holly seedlings

Remarkably, even though we used 20-year average climate data preceding each survey year, we see that sites increased by just over 1 deg C on average in the 50-year period with a clear separation between the three surveys. When overall winter minimum temperature averaged across the survey years was included in the model we also found a significant interaction with change in winter temperature over time (Fig 37). The increase in Holly seedlings was stronger at sites that started out warmer in winter.

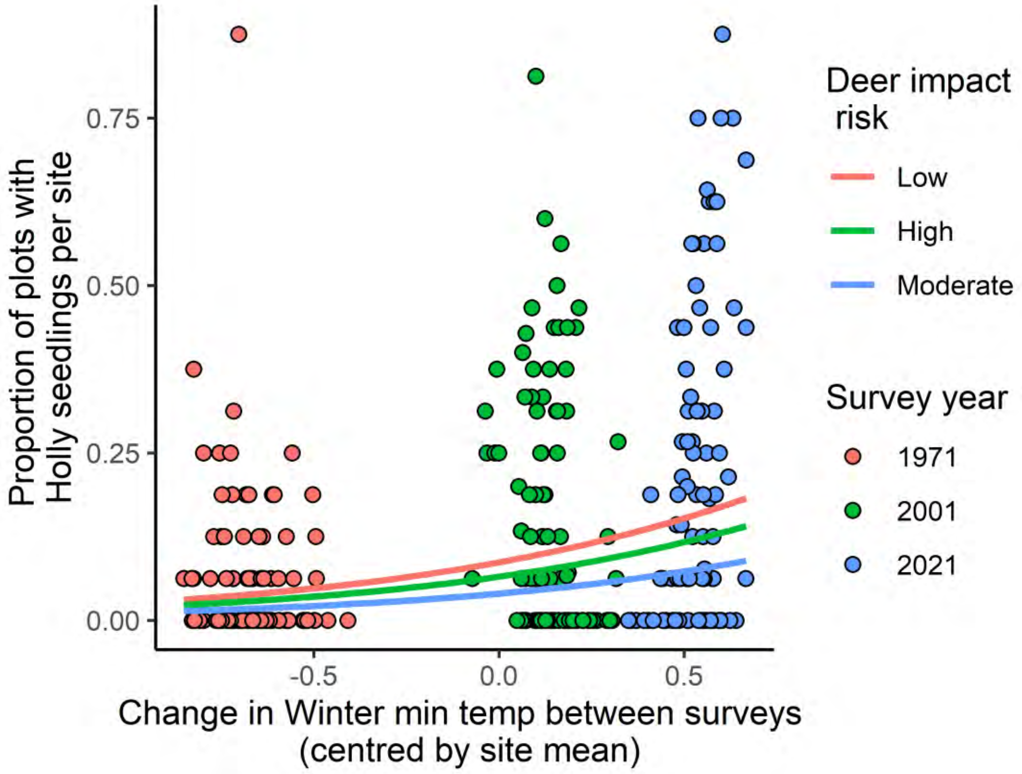


Fig 38: Proportion of plots containing Holly seedlings in each survey. Lines are the fitted predictions from the best-fitting model that included winter min temp change and deer risk and their interaction.

The increase in Holly seedling counts with warmer winters was also modified by deer Risk but in a way that defies easy interpretation (Fig 38). The increase was greatest at Low-risk sites, consistent with the palatability of Holly, but then exhibited the next highest increase at High-risk sites with Moderate-risk sites seeing the lowest rate of increase. Further work is required to identify mediating factors such as the presence and change in cover of other palatable species such as Bramble moderating the response of Holly to herbivory.

Holly regeneration (stems <1.3m and >25cm)

The proportion of plots on each site with Holly regeneration increased consistently over the 50-year period with a statistically significant increase between 2001 and the latest survey (Fig 39). The best fitting model with the fewest parameters included overall mean winter minimum temperature at each site plus winter temperature change plus the interaction between the two (Fig 40). Just as for seedling count, the result suggests that a significant fraction of the increase in Holly regen over the 50-year period is explainable by a shift to warmer winters and that the increase is more marked at sites that are in parts of Britain that have warmer winters overall. Holly regen was also slightly more frequent in 1971 on those sites with warmer winters (Fig 40).

Interactions with deer risk were also significant (Fig 41). Since Holly is a palatable species it seems counterintuitive that more of an increase is observed in higher deer risk sites. Speculatively, it could be that deer preferentially graze other species that could outcompete Holly regen.

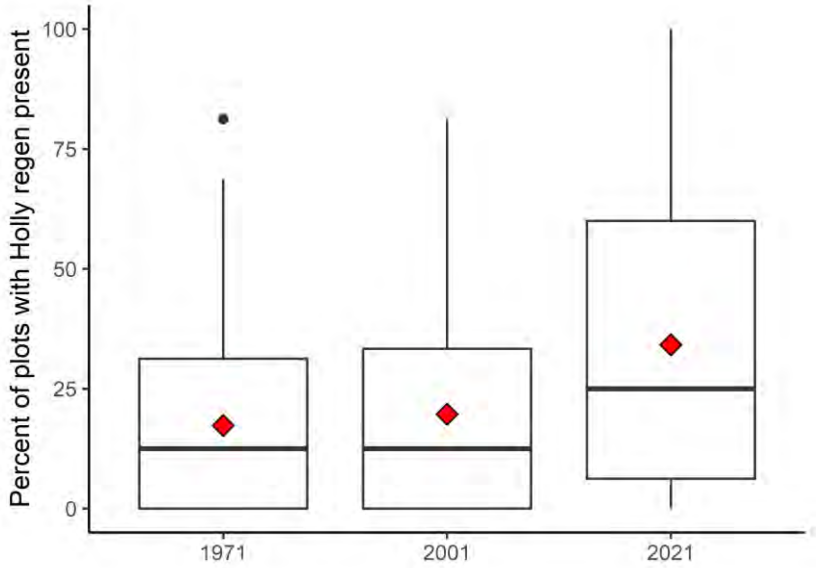


Fig 39: Proportion of plots in each survey site in each year that contained Holly regen. Mid-line in each box is the median. The red diamond is the mean and the boxes delimit the 33% and 66%tiles with whiskers being the non-outlier range.

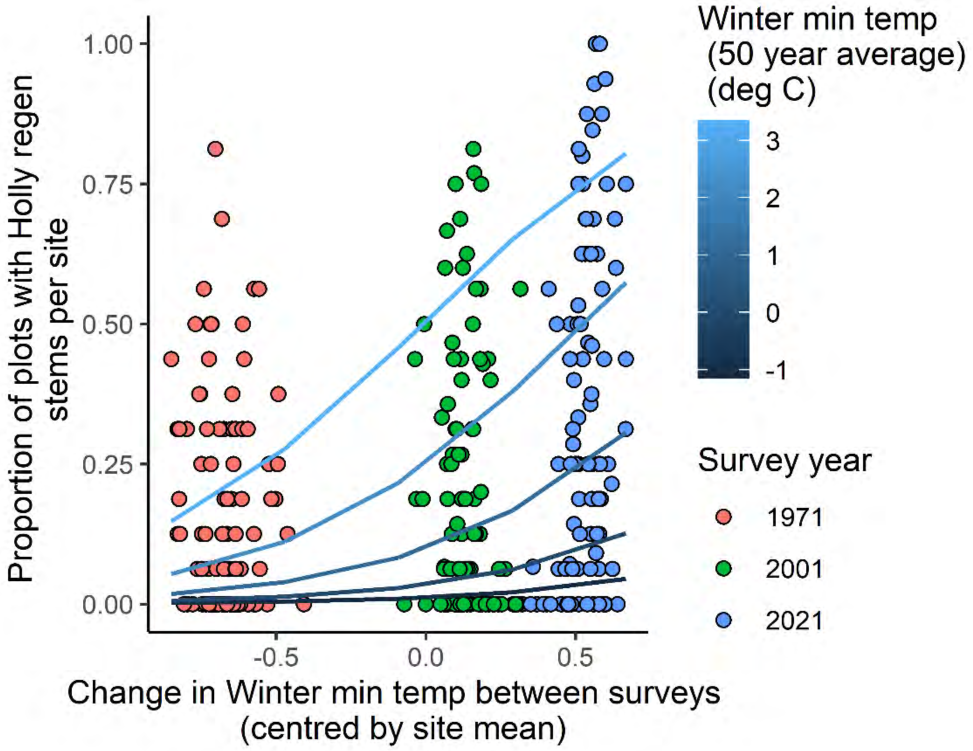


Fig 40: Proportion of plots on each site containing Holly regen by change in mean winter temperature between surveys (mean centred to remove overall geographic variation in temperature). The lines show the effect of a significant interaction between temperature change and the average temperature at each site. Warmer sites showed the greatest response to temperature change.

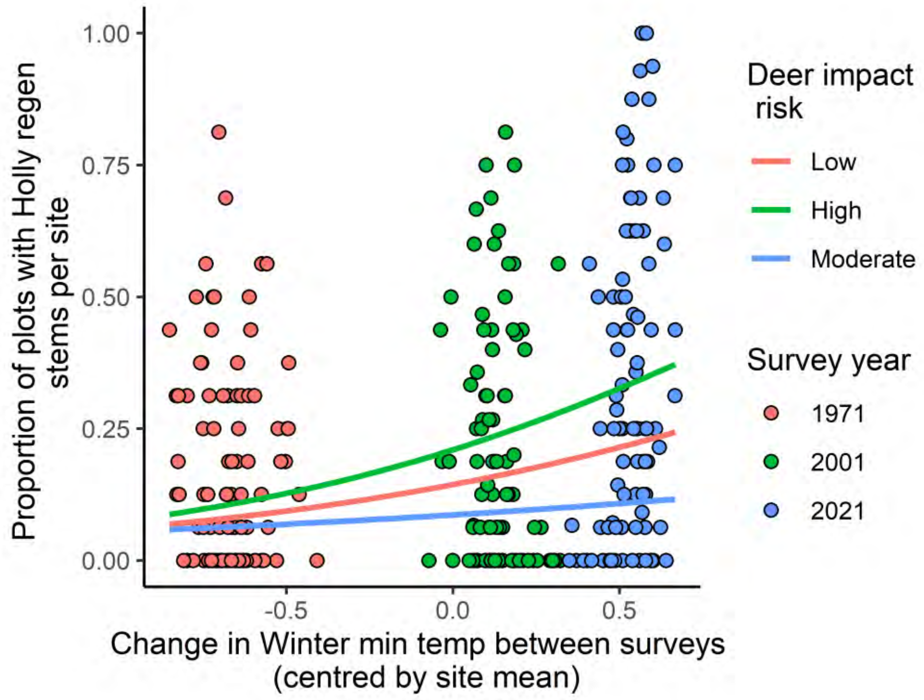


Fig 41: Proportion of plots in each site with Holly regen by winter temperature change but adding in modelled lines showing the interaction with deer risk.

Holly stem counts and mean DBH (>1.3m)

The proportion of plots across sites that contained Holly stems >1.3m increased steadily across the 50-year period with significant differences between all pairs of surveys (Fig 42). However, mean DBH did not change significantly between surveys (Fig 43) as expected if the age-class distribution of stems remained relatively constant over time (Fig 9d). Moreover, deer risk levels also made no difference to the proportion of plots on each site with Holly stems >1.3m.

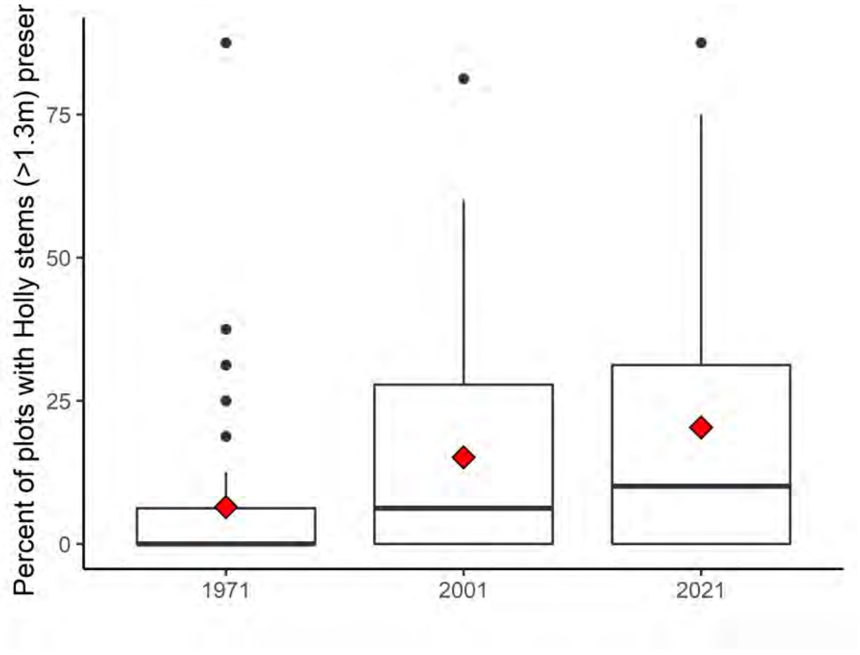


Fig 42: Proportion of plots with Holly present in each site and survey.

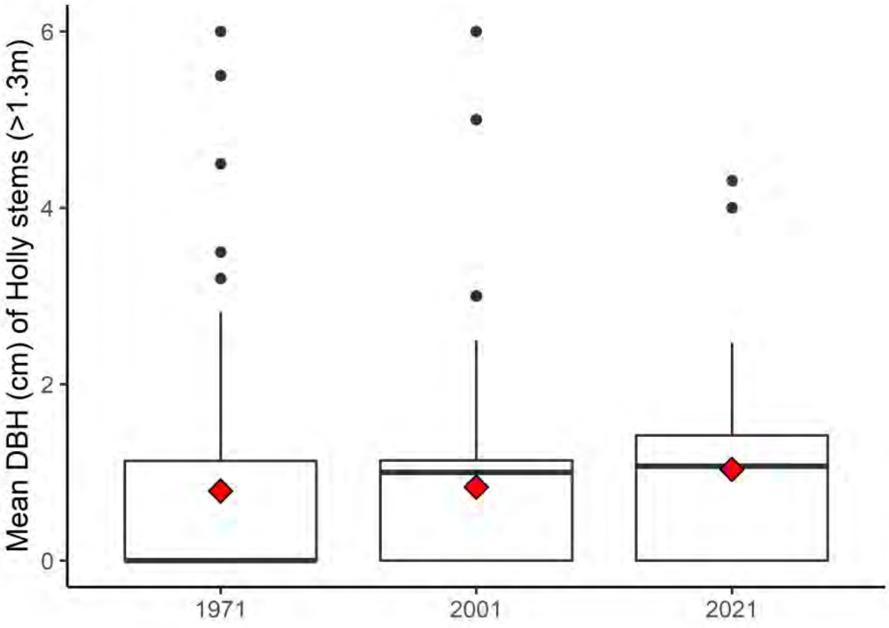


Fig 43: Mean DBH of Holly stems across plots and sites and surveys.

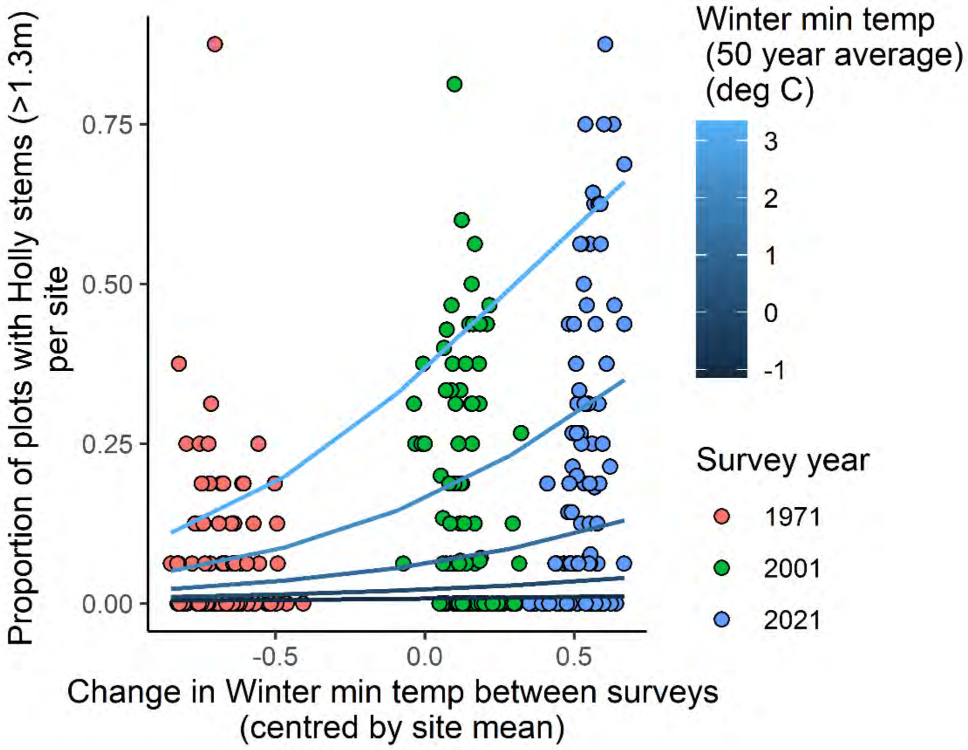


Fig 44: Proportion of plots on each site containing Holly stems >1.3m tall by change in mean winter temperature between surveys (mean centred to remove overall geographic variation in temperature). The lines show the effect of a significant interaction between temperature change and the average temperature at each site. Warmer sites showed the greatest response to temperature change.

Deer risk did not explain any spatial variation in the pattern of change over time in either stem count or mean DBH. However, stem counts did show a positive relationship with winter temperature change increasing more in number of plots occupied at sites that were in warmer parts of Britain (Fig 44) and displaying a strikingly similar pattern to seedling and regen dynamics and suggesting that all age-classes have responded positively to a warming climate by increasing the numbers of individuals across sites. The diameter distribution of stems has not been impacted as expected if the recruitment of young stems and subsequent stem-exclusion has been constant across populations.

Is climate warming accelerating stand-development and canopy growth?

Mean basal area across all shrubs and trees increased across the 50-year period (Fig 7). This pattern is consistent with stand development and tree ageing across the sample in turn associated with a response to the more open conditions and younger age-class distributions that were present in most sites in 1971 (see Kirby et al 2005 and section 4.6). Given this clear directional trend we ask whether the rate of stand development was enhanced by climate warming.

Mean summer maximum temperature increased over time (Fig 45) hence warming is clearly correlated with year of survey, which is also correlated with increasing DBH increment as trees age. However, the best model included year, summer maximum temperature change and overall mean summer maximum temperature to differentiate sites that were in warmer parts of Britain (Fig 45).

The summer maximum temperature change term explained unique additional variation over and above year of survey indicating that a growth enhancement was detectable. The interaction with overall mean summer temperature was negative however indicating that the warming enhancement was reduced at sites that were already warmer in summer (Fig 45). This points to a possible threshold effect where warming in an already warm location limits growth via drought or heat stress.

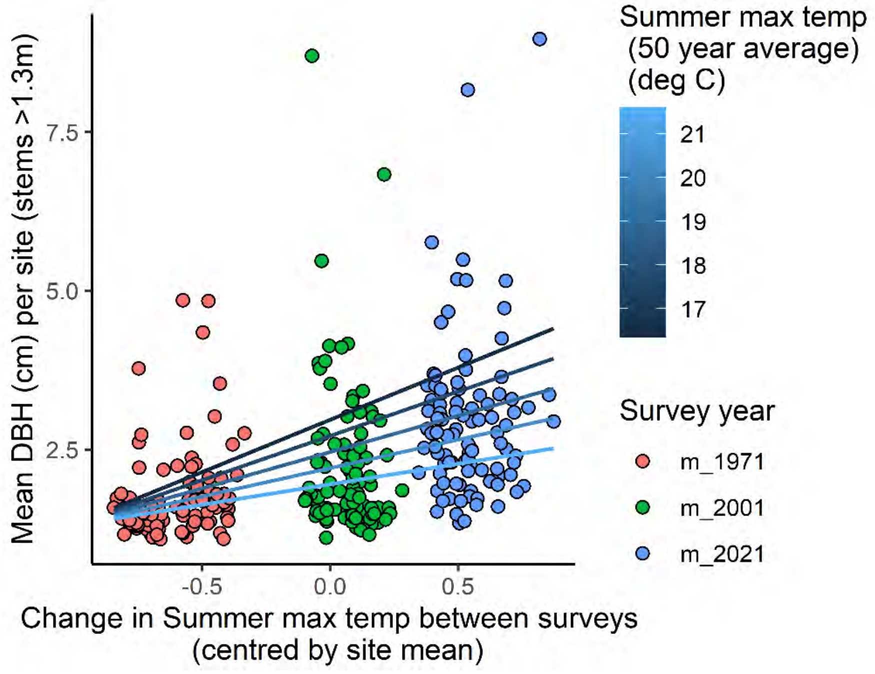


Fig 45: Mean DBH of all trees and shrub stems >1.3m in height across the three surveys by change in summer maximum temperature over time. The modelled lines also show the

significant interaction with the mean maximum summer temperature at each site across the survey years. Mean DBH increased less at sites that were overall warmer in summer.

Thus, there is evidence for an enhancement of forest growth by climate warming but this enhancement has an upper climatic limit that is already reached in the warmer parts of Britain. The variation attributable to climate is likely to be small though and with individualistic variation between species. Overall, the best model explained 22.4% of the total variation across plots and sites, excluding random effects.

4.17 Response of the broadleaved woodlands to atmospheric deposition of nitrogen (N) and sulphur (S)

Here we examine the effects of modelled atmospheric pollutant deposition (nitrogen (N) and sulphur (S)) on soil pH and the understorey vegetation. S deposition dropped to varying extents across all sites from 1971 onwards (Fig 46a). Most sites in Scotland had N deposition rates that were below the lower empirical Critical Load (CL) for N by the latest survey. About 70% of sites overall had deposition loads that were above the lower empirical CL, and 30% that were still above the higher empirical CL by the latest survey (Fig 46b).

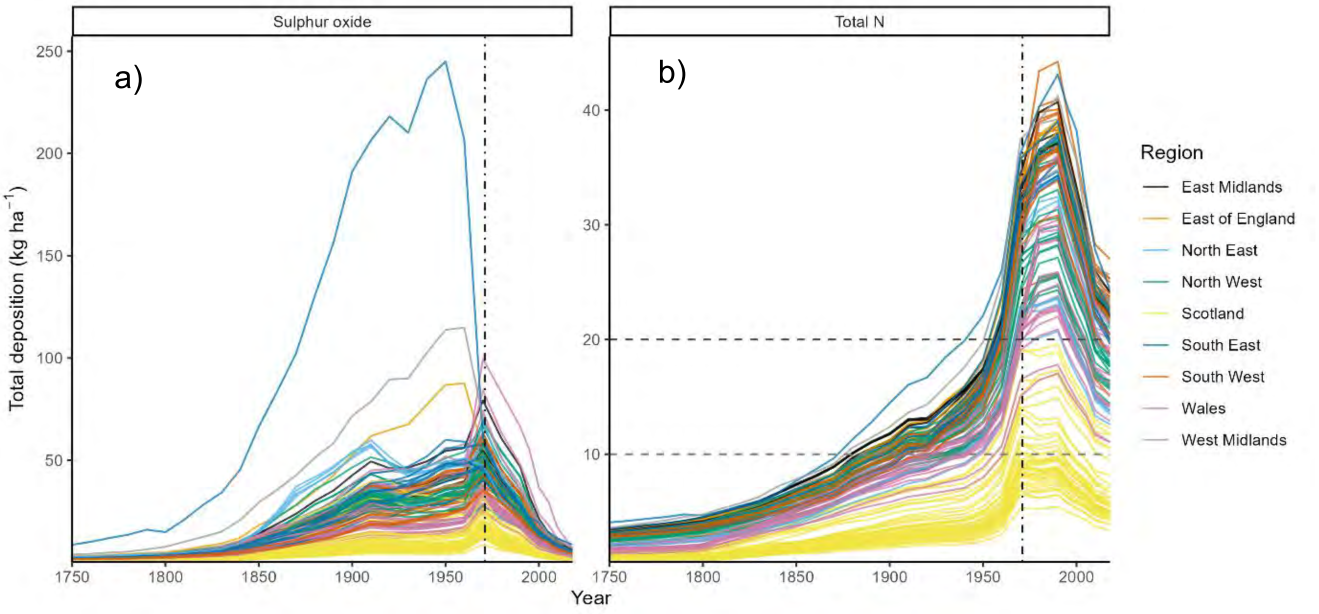


Fig 46: Modelled change in atmospheric deposition of a) sulphur and b) nitrogen across the broadleaved woodland sites. The time series is from 1750 to 2018. Vertical dashed lines indicate the first survey in 1971. Horizontal dashed lines indicate the current upper and lower limits of the empirical critical load for N for broadleaved woodland[9] .

There is good evidence that reductions in S deposition have driven a recovery in soil pH across Britain in the last 50 years (Seaton et al 2023; Kirk et al 2006). In contrast to the previous analysis of just the 1971 and 2001 data, we now detect a significant relationship between modelled S deposition change at the broadleaved woodland sites and change in soil pH (Fig 47). Interaction terms between reduction in S deposition and year were significant and the direction of these different slopes within each year are consistent with

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[9] https://www.apis.ac.uk/critical-loads-and-critical-levels-guide-data-provided-apis#_Toc279788052

recovery; the 1971 slope is negative presumably because this period coincided with peak S deposition driving down soil pH. By 2001 and 2021 these areas saw the greatest reduction in deposition and the slope had become positive suggesting recovery is underway (Fig 47).

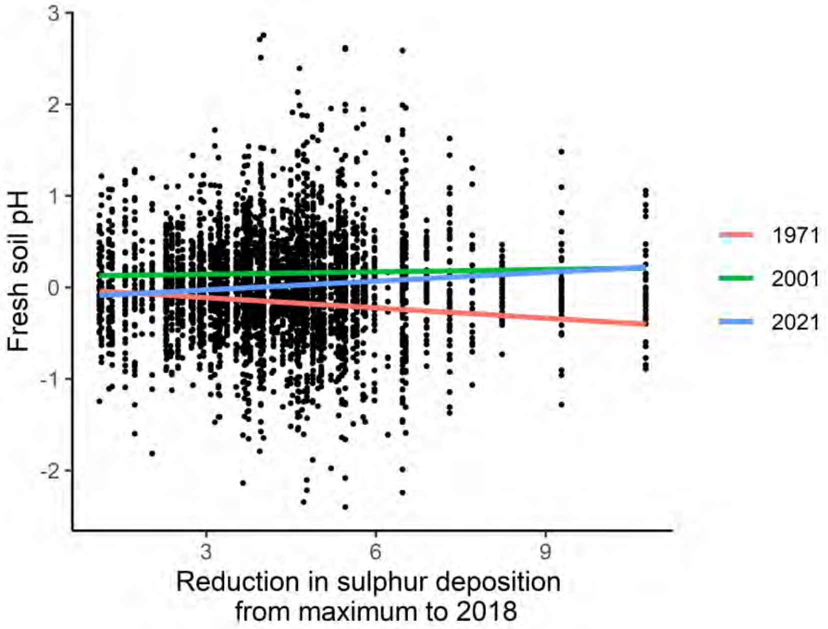

Fig 47: Fresh soil pH change (centred by the cross year, within plot mean) by the reduction in S deposition per site (tonnes per km^2) from the modelled maximum in the last 60 years to 2018

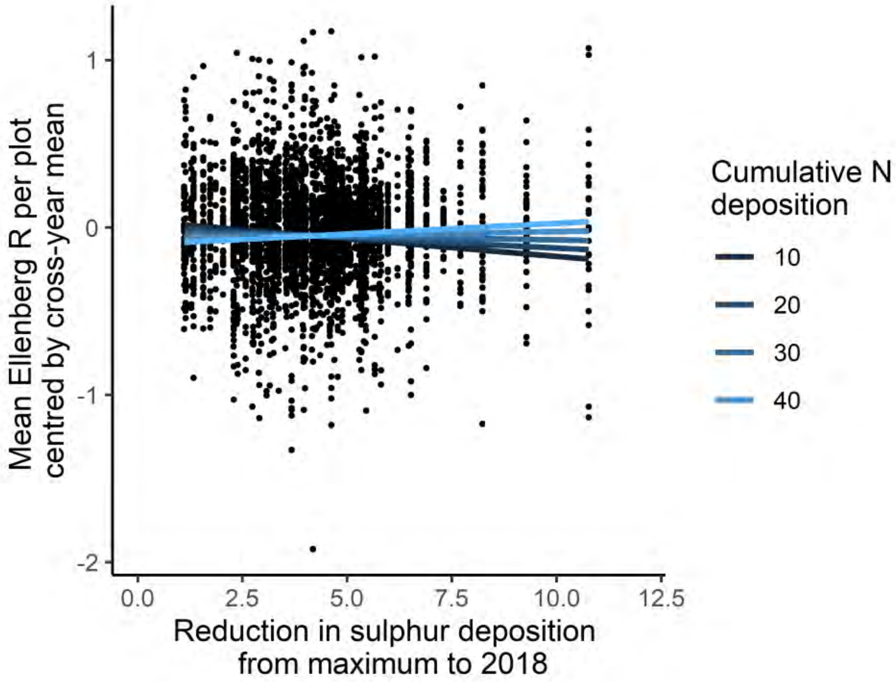

Fig 48: Fresh soil pH change (centred by the cross year, within plot mean) by the reduction in S deposition (tonnes per km^2) per site from the modelled maximum in the last 60 years to 2018. Also shown are the modelled relationships between Ellenberg R and S deposition at different levels of cumulative N deposition (tonnes per km^2 1750-2018). The slopes differ significantly but have low explanatory power.

While we have captured signals of the impact of S and N deposition in the data these drivers explain a small fraction of the variaion in the data. There are likely to be other factors that interact to supress or amplify these effects. For example vegetation and soils at low pH are less responsive to eutrophication effects (Stevens et al 2011) while canopy-induced light limitation will also suppress the response of shade-intolerant nitrophilous species (Smart et al 2014; Smart et al 2006; Verheyen et al 2012). In this respect it is significant that we found a greater proportion of generalist species in better lit woodland gaps (Fig 21).

We also found a weak signal consistent with recovering soil pH driving an enhanced vegetation eutrophication response to higher N loading (Fig 48). The interaction term between changing S and cumulative N deposition on mean Ellenberg R change was statistically significant but the effect is clearly small relative to variation across the data. It does suggest that vigilance is required particularly in areas that have persistently high N deposition but where S deposition has reduced greatly driving up soil pH. Whilst the suppression of phosphorus-induced eutrophication by acidification has been seen in European freshwater systems (Schneider et al 2018), to our knowledge it has not been captured in the terrestrial domain nor linked to high N loading (but see Rose et al 2016). Smart et al (2014) speculated on its occurrence in woodlands where canopy gaps resulting from the 1987 storm could have alleviated light limitation providing conditions for an enhanced eutrophication response but in those sites it was likely that low background soil pH reduced the chance of this effect being detectable.

5. Discussion

5.1 Caveats and limitations when inferring drivers of woodland change

Our aim was to attribute spatio-temporal variation in the survey data to potential causal drivers of change. The analyses and results, whilst based on a uniquely long-term and large-scale sample of broadleaved woodlands over 50 years, are not drawn from a controlled experiment and so confounding and correlated yet unmeasured factors could also be responsible in part for some of the effects that we attribute to one or more causes (Smart et al 2012). Experimental manipulation is however difficult if not impossible for drivers such as the legacy effects of historical management and climate change (Perring et al 2018a). Consequently, the correlative evidence from long-term, large-scale studies such as the Bunce survey are a uniquely valuable contribution to the evidence base but also have clear weaknesses when inferring cause and effect. The body of evidence becomes stronger where the results from a range of methods at varying scales are consistent (Landuyt et al 2023). Analysis of large-scale observational data can also offer unique insights into the consequences of interactions between drivers at realistic scales – see for example section 4.14 where we describe the complex relationships between Ash dieback, herbivory and the mediating role of understorey dominants (see also Perring et al 2018b).

Unravelling the interplay between driving variables using landscape scale survey data imparts realism and relevance to the results but the detection of effects is also hostage to other factors beyond the control of the observer. These include variation in the length of driving gradients; the shorter this gradient then the less likely that signal can be isolated from noise making it advantageous to be able to collect and analyse data from a large sampling domain. Also, if gradients differ in length then for an equivalent potential effect and residual error, attribution is more likely to the driver represented by the longer gradient (Smart et al 2012). In addition, time lags such as species' extinction debts and colonisation credits can lead to underestimation of effects yet to play out (Ridding et al 2020; Watts et al 2020 and see below). Lack of detection of an effect in large-scale observational data is not necessarily good evidence that the effect is not present or will not occur.

A further caveat applies to the representativeness of the survey data for wider inference. That is, the extent to which our conclusions regarding the direction and nature of woodland change and the role of possible drivers apply more generally to broadleaved woodlands in Britain. The sample of woods is not a strict 'probability' sample where stratification of the entire population and then random, replicated sampling within strata confers lack of bias and therefore builds confidence in scaling up from the sample to the population. The 'Bunce' survey design is non-standard. Each of the sites, 97 of which were visited in every survey, represent the centroids of 103 clusters formed from a multivariate classification of 2453 broadleaved woods >4ha that were surveyed in the late 60s. This larger survey was designed to be nationally representative. Coupled with our NVC analysis (section 4.3) these aspects build confidence in our ability to infer results to the wider population of such woods across Britain. Further work is possible to explore and validate the representativeness of the survey sample (see Boyd et al 2022).

5.2 The one thing that doesn't change is that woodlands keep changing

The woodland sites present a broad picture of stability in terms of their size, the integrity of their boundaries and the rank order of the canopy dominants. The open and youthful woodlands encountered in the 1971 survey may well have been shaped by an acute episode of post-WWII timber removal whose operation across sites resulted in a period where light was admitted to the disturbed woodland floor leading to unusually high understorey species richness in 1971 as more light-demanding plants coexisted with shade-tolerators (Appendix E). Subsequently, there has been an ongoing process of stand development and stem exclusion resulting in more shaded understoreys composed of fewer, larger stems (Fig 49) and where plant species of more open situations declined.

Over the last 20 years these more light-demanding species have shown little sign of recovery but a subset of ferns and shade-tolerant sedges and woodland specialists have increased in cover and frequency driving plant species richness up again but still resulting in a net 22% reduction over the 50-year period. Species that have benefited have also tended to include those favoured by higher nutrient levels while species that are less-shade tolerant, associated with very low fertility and lower soil pH have tended to decline (4.12 and Appendix D). Since we could find no correlative link with N deposition we speculate again, as we did in 2005, that reduced offtake of nutrients in wood products has driven an endogenous increase in productivity while N deposition must still have been a significant source of external nutrient input.

Some of the trends in plant species that we see in the past 50 years in the Bunce woodlands are consistent with changes in occupancy of woodland plant species from other recording schemes in Britain despite recording being at very different resolutions. The Local Change project revisited a subset of tetrads (2x2km) squares across Britain in 2004 and reported changes that had occurred since previous recording in the mid-1980s (Braithwaite et al 2006). Among species with an affinity for woodlands southerly species increased while increasing species also comprised shade-tolerators including the fern *Polystichum setiferum*, the sedges *Carex remota* and *C.sylvatica* and the common woodland specialist *Allium ursinum*. Woodland species of more acidic substrates also declined whilst species of more fertile conditions increased and species of less fertile conditions declined; all trends that are consistent with our results (see Table 4.4. in Braithwaite et al 2006 for a comparison of Local Change and change in the Bunce plots up to 2001). Against a backdrop of overall stability in plants of broadleaved woodland the most recent plant atlas also noted that species of open ground have tended to decline whilst shade-tolerators such as *Dryopteris dilatata* and *Carex pendula* have increased over the 70-year period (Walker et al 2023)[10].

The remarkable feature of the linked changes in age-class distribution, shade, species composition and richness that we see in the Bunce woodlands is their apparency across so many of the survey sites resulting in strong directional change over time from a common level of openness and youthful age-class distribution in 1971. The apparently synchronous nature of the 50-year trend indicates that change is not a function of varied local management decisions, which would be expected to result in similarly varied trajectories of change, but likely to have been driven by common factors driving similar effects across most sites. The evidence suggests that a widespread reduction in management is responsible, specifically a reduction in interventions that create gaps in the canopy and therefore admit light into the understorey. Signs of gap-creation and management are rarer than ever in the most recent data even though historical signs of management are still to be seen in the form of sawn old dead wood, rotting stumps and derelict coppice (Appendix F). While the evidence suggests a plausible role for the influence of post-WWII disturbance it is also apparent that the survey plots coinciding with the most natural stand type in the 1947 Forest Census – uneven-aged high forest – were still undergoing a trajectory from younger cohorts of trees and recruiting into fewer and older stems (Appendix E, Figs 2 & 4). We suggest that a long-term decline in traditional management may be responsible coupled with the wake of timber removal going even farther back to the first World War.

In other respects the woodlands appear stable – the tree canopy species composition and distribution of NVC types has changed relatively little over the 50 years - but there are also directional changes whose long-term dynamics have yet to be played out. In addition to the changes in tree age-class distribution, increased canopy shading and the filtering of understorey plant assemblages we have seen three major impacts on tree and shrub abundance; Elm has declined due to Dutch Elm Disease, Holly has increased – correlatively linked to warmer winters - and Ash has been infected and debilitated by dieback. The changes in these three species indicate how even amongst a pool of trees and shrubs undergoing a largely similar trajectory, individualistic responses to global change occur with major effects that are yet to cascade though the system (Maes et al 2018). The rise of Holly

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[10] Both Local Change and the BSBI plant atlases estimate change in occupancy across 2x2km and 10x10km grid squares respectively so that substantial increase or decrease in abundance is possible within squares without registering as an absence or new presence. Also, in these schemes plant species are grouped as broadleaved woodland based on their known affinity with the habitat type rather than the results reflecting an analysis of records specifically within woodlands.

may yet reveal a further twist since an open question is to what extent its increase includes new populations of the introgressive hybrid *Ilex* x *altaclerensis*[11]

It should not come as a surprise that woodlands do not stand still (Ellison 2013; Peterken 2023). They are alive and responsive to the changing world around them; human exploitation, disease, herbivory, pollution and climate change including extreme weather comprise a mixture of natural 'pulsed' stressors plus unnatural 'press' stressors that originate from outside the woodlands and are human in origin (Smith et al 2009; Garcia et al 2014). Peterken (2023) provides ample evidence of how woodlands in Britain have changed in response to an accumulation of influences in the recent past but against a backdrop of much longer impacts of human activity. It is the influence of modern land-use surrounding woodlands, novel pollutants and no-analogue future climate that subject woodlands to new pressures (Kirby 2020). These will play out in ways that may challenge the relevance of applying reference conditions drawn from the present or from historical data, especially if the mortality of characteristic canopy species' starts to increase with the cumulative effects of climate change (Broadmeadow et al 2005; Dodd et al 2021; DeSoto et al 2020). It is possible that setting and monitoring new goals for woodland survival and expansion could be aided by developing novel indicators that subsume taxonomy and phyto-sociology and rather reflect function and resilience; such indicators might for example measure complexity (Bullock et al 2022), a property likely to confer resilience. This may not mean new, costly nor complex measurements but potentially new synthesis of measurements of heterogeneity and woodland structure (Maskell et al 2023), trait diversity (Sakschewski et al 2016), wider habitat configuration (Hodgson et al 2022) as well as more obvious quantities such as woodland area (Maskell et al 2023). Interactions between species are a key functional building block of complexity and whilst challenging to measure directly (Villa-Galavíz et al 2020) can, for example, be approximated using databases of dietary preference and interactions (Smart et al 2000; Redhead et al 2018).

Woodlands are also likely to experience lagged effects. The potential for these is important to acknowledge though hard to predict (Watts et al 2020). Drivers that operate now and in the past may have impacts that have yet to propagate through the woodland ecosystem so that future dynamics are better predicted by past states. This emphasises the need to consider pre-emptive mitigation of these drivers now even though evidence of their full effect may not be apparent for years to come (Whittet et al 2019). Extinction debts and colonisation credits resulting from the lagged effects of climate change, change in woodland area and surrounding land-use are all likely and supported by evidence, albeit correlative (Kimberley et al 2015; Ridding et al 2020). Over a 44-year period in France (1965-2008) plants and animals in lowland woodlands were estimated to have responded to only 0.02 deg C of a 1.11 deg C warming (Bertrand et al 2011) indicating a stored effect of climate change yet to work its way through the ecosystem.

The interaction with gap creation is likely to be critical in the playing out of these lag effects. The tree canopy buffers the climate in the woodland interior so that understories in gaps will

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[11] https://plantsbiodiversityecosystems.wordpress.com/2020/02/06/a-suspected-introgressive-population-of-ilex-aquifolium-and-ilex-x-altaclerensis-satlburn-yorkshire-uk/ and https://plantatlas2020.org/atlas/2cd4p9h.7bz

be exposed to greater climate variation. Thus, tree disease and storm-induced gaps are likely to be a significant additional trigger for mediating climate change impacts on regenerating tree seedlings, younger stems, soils and the understorey and its invasibility by other plants and animals (De Frenne et al 2021; Hardová et al 2017). A knowledge gap here is to better understand how future climate change exposure interacts with surrounding land-use to impact British woodlands (Dodd et al 2021; Schulte to Buhne & Pettorelli, 2023). If future effects are not approximated well by phenomena in past and present, there is a clear need for ongoing monitoring to be able to understand mechanisms, causes and consequences of change. To gain most understanding and benefit, parallel model development would be useful, generating predictive hypotheses to be compared with observations. Increased belief in the forecasting ability of models and their use in guiding management options should then result from an ongoing cycle of comparison of predictions with observations, model reappraisal and further development (Watts et al 2020; West et al 2023; Honrado et al 2016).

5.3 Which trends have continued since 2001 and what is new?

When reporting the results of the change between the 1971 to 2001 surveys we wrote of the sense that woodlands were becoming socially, economically and ecologically disconnected from the wider landscapes in which they were embedded (Kirby et al 2005). Increasing shade, lack of relevance of woodlands as a source of saleable products and a woodland environment less conducive to being permeated by humans at leisure or at work portended almost a sealing up of these woodlands under closing canopies. This had benefits and disbenefits; good for shade-loving biota sensitive to disturbance (Hambler & Speight 1988) but not good for shade-intolerant, pulse-disturbance species of more open conditions yet not favoured by high nutrient loads and high grazing pressure (Kimberley et al 2013; Swallow et al 2019). Many of these species are not necessarily woodland specialists but rather exploit woodlands as a refuge of last resort in the face of unfavourable conditions in the wider, intensively farmed landscape (Smart et al 2006). In the last 20 years this trajectory has continued. In parallel, several shade-tolerant plants have increased and woodlands have accumulated more dead wood, a more continuously closed canopy comprising older and fewer trees probably resulting in a less variable and cooler average climate at the woodland floor relative to outside the wood (De Frenne et al 2019). The likelihood that these trends are typical of British broadleaved woodlands and have impacted higher trophic levels is also supported by evidence of changes in the abundance and distribution of organisms recorded in other surveillance programs. Invertebrates of early seral stages of woodland development declined from 1992 to 2012 (Thomas et al 2015). A more recent study has also confirmed the overall decline of invertebrates specialised to woodland clearings although more generalist species of intermediate woodland cover and woodland edge increased (Bowler et al 2023). Birds are another very well recorded group in Britain. Here the link between declining woodland gap-creation and changing species abundance is perhaps less clear because of varied species requirements and the fate of migrants in their winter quarters. Between the mid-1980s and 2003-’04 woodland specialists declined more markedly than woodland generalists (Hewson et al 2007). Quine et al (2007) also characterised decreasing species as more likely to favour open canopies and ecotonal areas.

Looking forward in 2001 there seemed few obvious agents that would drive new canopy disturbance. The October 1987 storm had left its mark, reversing the trend for plant species loss in the understorey (Smart et al 2014) yet this impact was localised to south-east England. The consequence of Dutch Elm disease was also apparent, a trend that has continued up to the present. However, any effects of the reduced frequency of Elm species on the openness of the canopy seemed to be eclipsed by the national-scale reduction in management interventions as previously more widespread ‘traditional’ management and exploitation of woods for a diverse range of products declined (Peterken 2023). We did not foresee Ash dieback, however. In the latest survey we see a clear signal of the impact of this disease on canopy and understorey species richness (44% of plots had Ash and 49% of these showed signs of disease). In addition, recent storm impacts were also very evident and reported in 5% of plots in 2021.

The long-term consequences of the impact of Ash dieback cannot be reliably inferred from the recent signals we see in the survey data. Ongoing monitoring is required to test at least two alternative hypotheses regarding woodland development. Firstly, it seems likely that other tree species will fill the canopy gaps resulting from Ash mortality. If these beneficiaries cast greater shade and have more suppressive litter then any positive impact on species richness will be transient. Without intentional gap-creation understorey plant species richness will continue to be influenced by further canopy closure and shading. A second pathway is plausible. If deer impacts remain high enough to suppress tree regeneration then canopy gaps could persist with ground layer vegetation increasingly shaped by herbivory, which would favour grazing-tolerant and often non-woodland, shade-intolerant species (Kimberley et al 2013; Morecroft et al 2001). In addition, these gaps will also be influenced by context-dependent climate and pollution drivers. For example, high herbivory promotes different suites of winners and losers at high versus low N deposition (Segar et al 2022; Morecroft et al 2001).

The woodland canopy has a known moderating effect on the understorey vegetation and soils emphasising the importance of managing the tree and shrub layer to mitigate the effects of drivers such as pollutant deposition and climate change (Landuyt et al. 2020; Verheyen et al. 2012; Zellweger et al. 2020). Alleviated light limitation in gaps can drive increased plant species richness but the identity of the species that respond positively can again depend on interactions between global change drivers. We have shown that Bramble (*Rubus fruticosus* agg.) can strongly dominate in gaps and suppress light-demanding plants, an effect also found experimentally (Harmer et al 2017). In the latter study generalists and woodland specialists both benefited from Bramble control measures. However, where Bramble is controlled by deer herbivory not all plant species respond in the same way. Morecroft et al (2001) showed that higher deer pressure favoured grass species whilst forbs decreased, implicating differences in palatability and grazing tolerance in selecting species that would benefit from the debilitation of Bramble by deer. The role of Bramble in mediating the impact of deer herbivory and additional light availability on understorey plant assemblages highlights the importance of common native dominants as an influence on more subordinate plant species and their associated animal species especially if these dominants are favoured by pollution and climate change (Marrs et al 2011).

5.4 Concluding remarks; evidence, threat, hope

The sensitivity of woodland ecosystems to peripheral land-use, climate change, pollution, forest management, storm impacts and disease are well known and we present unique new evidence quantifying how all these drivers are likely to have shaped woodland canopies, understoreys and soils over the last 50 years across Britain. Their future severity and novel interactive effects may well present new challenges to those who manage and value woodlands because the adaptive capacity of a woodland and its biota will not have been shaped by exposure to these new configurations of stressors that have no analogue over evolutionary timescales (Williams & Jackson 2007; Kirby 2020).

Based on our results and the uncertain future for broadleaved woodlands three strands of activity seem desirable:

1) Growing new woodlands in the right places to buffer existing woodlands: Much effort, resource, scientific and policy interest now focusses on tree planting and natural regeneration across Britain. The challenge is to achieve connectedness and larger size without negatively impacting existing habitat (Walker et al 2022). Because long-continuity woodlands have species compositions and structures that reflect their age and situation in the landscape, adjacent planting on agriculturally modified land will require species-specific and sometimes long time periods to accumulate woodland biota even if in close contact with source populations. While woodland plant community assembly is possible focussing particularly on common woodland species (Harmer et al 2001; Broughton et al 2021) long to very long-lasting land-use legacy effects may inhibit restoration of soils, specialist plants and the soil microbiome and therefore require management of expectations regarding restoration targets (Dupouey et al 2002; Diedhiou et al 2009). Even in semi-natural settings planted buffer zones are likely to be different to adjacent core areas. For example, planted or regenerating woodland on previously grazed acid grassland will accumulate a different community than an adjacent Upland Oak woodland in a rocky ghyll. The difference will however translate into an increase in beta diversity across the local landscape.

2) Ongoing monitoring of woodland sites: Continuing to monitor a sub-sample of the Bunce sites would seem desirable because of the inevitably that the woodlands will keep changing. Yet the dynamics we have described over the last 50 years do not allow accurate prediction of the way these multiple factors will play out, hence continued vigilance is needed. Moreover, several drivers are likely to increase in the severity of their operation resulting in even stronger joint effects but whose outcomes are uncertain. Ash dieback and storminess will inevitably drive increasing gap creation interacting with strengthening climate change. Among semi-natural habitats in Britain Wilson & Pescott (2023) estimated that broadleaved woods were second only to calcareous grasslands in their probable exposure to climate change over the next 20 to 60 years. While we detected average impacts of climate warning on understorey and canopy growth, acute effects were not so apparent even though they are likely to drive cumulative impacts in the future (De Soto et al 2020) and be of increasing concern to woodland managers (Hemery et al 2020).

While there seem obvious benefits in continuing to monitor it is worth noting that the baseline series of sites is fixed and therefore no plots in new woodland can enter the time-series. Over time the site series might reduce in representativeness if more sites are refused access. Joint analysis of change in these long-established woodlands with younger secondary, newly planted or naturally regenerating woodland would also provide a more balanced and comprehensive picture of how broadleaved woodlands of different continuity and age are changing across Britain relative to the large number of ancient woodlands that make up the Bunce sample (Watts et al 2016).

3) Mobilising the positivity of the ‘Bunce’ woodland owners: The positivity and interest of many of the site owners was very apparent during the survey. Many owners who did not actively manage their sites wanted to do so but lacked guidance on setting objectives and achieving these through practical intervention. We have sought to inform owners by making the summary observations for each site available via an R shiny app with an instance tailored to each of the sites. Plot photographs, interpretation notes and other information could be readily added to the shiny platform providing a further avenue for keeping the owners engaged and interested in the future of their site because they are better informed about its past and present. Practical options might include encouraging a willing cohort to subdivide the site into non-intervention versus managed, assuming resources were not an obstacle to management. Less ambitiously but also very useful, if the goal were to simply repeat the ecological measurements at more regular intervals it is possible that the recording protocols could be streamlined and simplified relying less on taxonomic expertise for example and more on easier, photographic recording of woodland structure, light levels and species but also indicators of grazing pressure and presence of dead wood. DBH recording can also be repeated only requiring the ‘citizen scientist’ to be familiar with a more manageable smaller list of tree and shrub species.

There are hopeful signs that this positivity is more widespread among custodians of British broadleaved woodlands. Hemery et al (2020) found that ‘Improving/protecting nature’ was the most important objective in their national survey of 642 owners which predominantly focussed on broadleaved woodlands with large amounts of Ancient Woodland and PAWS. This analysis also showed that many owners were motivated by a worldview that acknowledged the existence of the climate and biodiversity crises correlating with keenness to engage in positive action for nature and carbon storage.

Fig 49: Summary of 50 years of change in the 'Bunce' broadleaved woodlands.

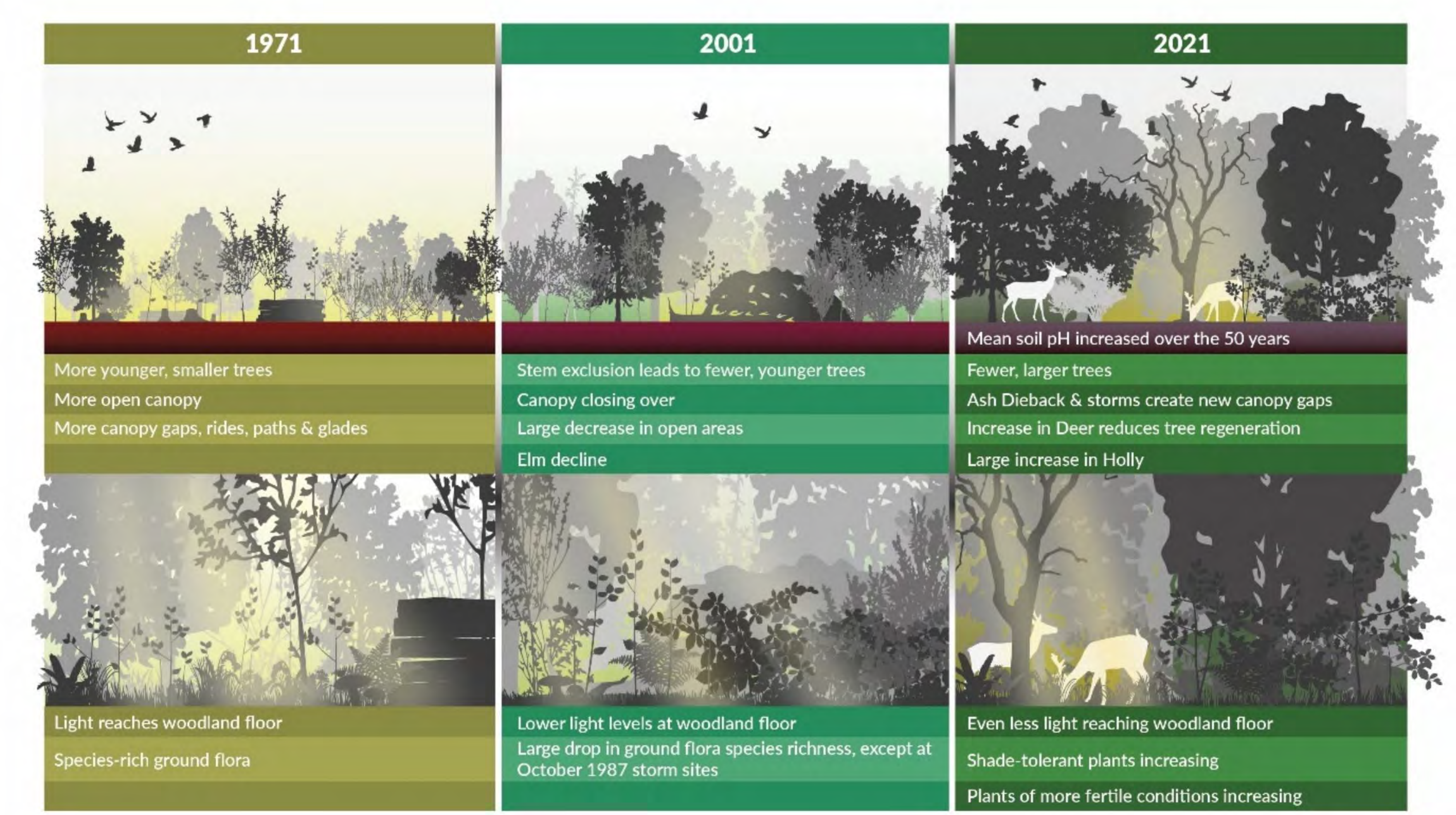
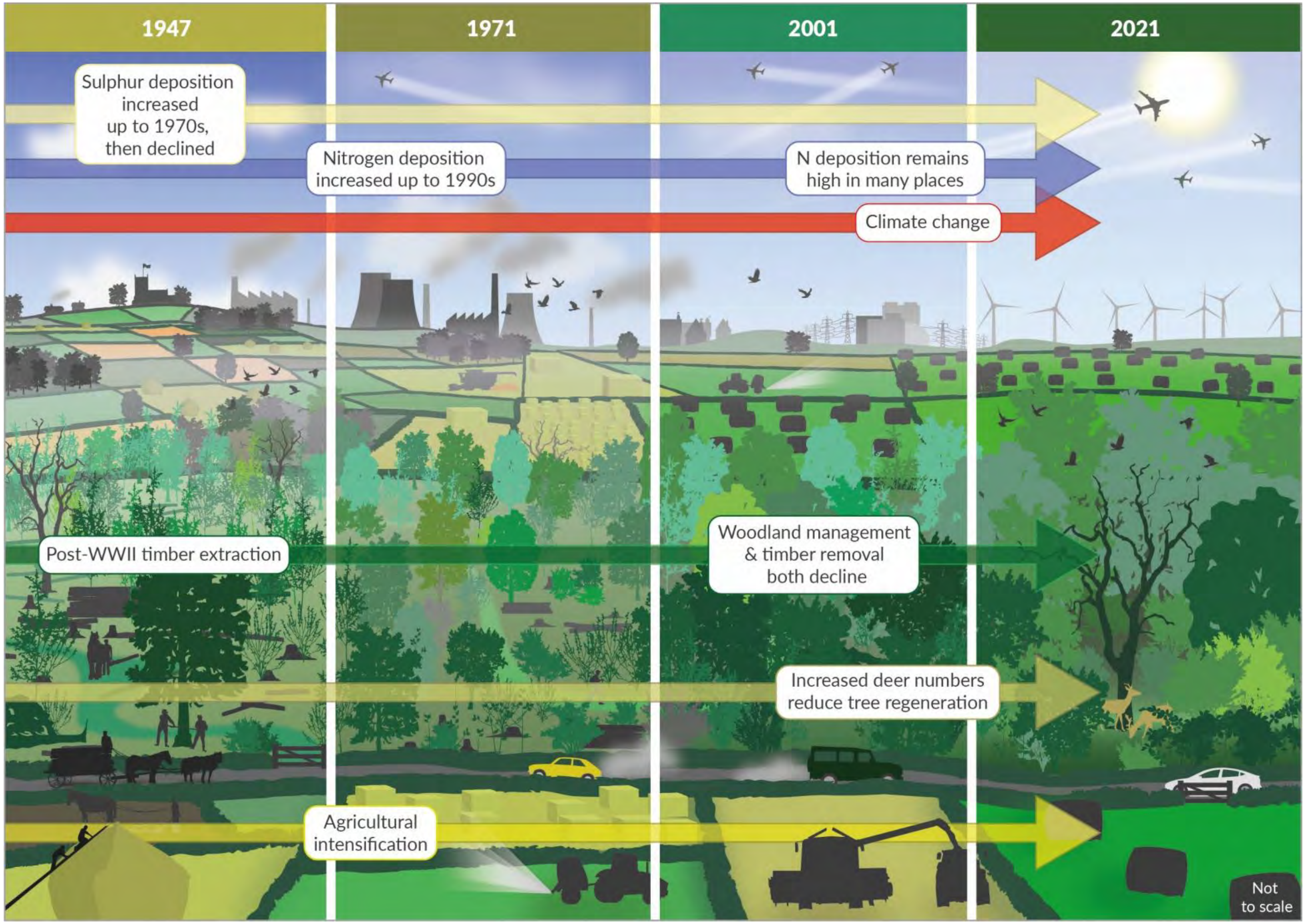


Fig 50: Summary of the probable major drivers of change across the ‘Bunce’ broadleaved woodlands.



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7. Appendices

7.1 Appendix A: Negative Common Standards Monitoring indicator species for British habitats excluding trees and shrubs.

The list was compiled by the Botanical Society of Britain and Ireland in 2015 in preparation for the roll-out of the National Plant Monitoring scheme[12].

Agrostis capillaris
Agrostis stolonifera
Alopecurus geniculatus
Anthoxanthum odoratum
Anthriscus sylvestris
Arrhenatherum elatius
Azolla filiculoides
Bellis perennis
Brachypodium pinnatum
Bromopsis erectus
Bromus hordeaceus
Carduus crispus
Cerastium fontanum
Cetranthus ruber
Chamerion angustifolium
Cirsium arvense
Cirsium palustre
Cirsium vulgare
Cotoneaster integrifolius
Crassula helmsii
Cynosurus cristatus
Dactylis glomerata
Deschampsia cespitosa
Deschampsia flexuosa
Elodea canadensis
Elodea nutallii
Elytrigia repens
Holcus mollis
Impatiens glandulifera
Juncus articulatus
Juncus conglomeratus
Juncus effusus
Juncus inflexus
Juncus squarrosus
Lemna gibba
Lemna minor
Lolium perenne
Mimulus guttatus
Nardus stricta
Oenanthe crocata
Parietaria judaica
Phalaris arundinacea
Phelum pratense
Phragmites australis
Plantago major
Poa annua
Poa humilis
Poa trivialis
Potentilla erecta
Pteridium aquilinum
Ranunculus acris
Ranunculus repens
Rubus fruticosus agg.
Rumex conglomeratus

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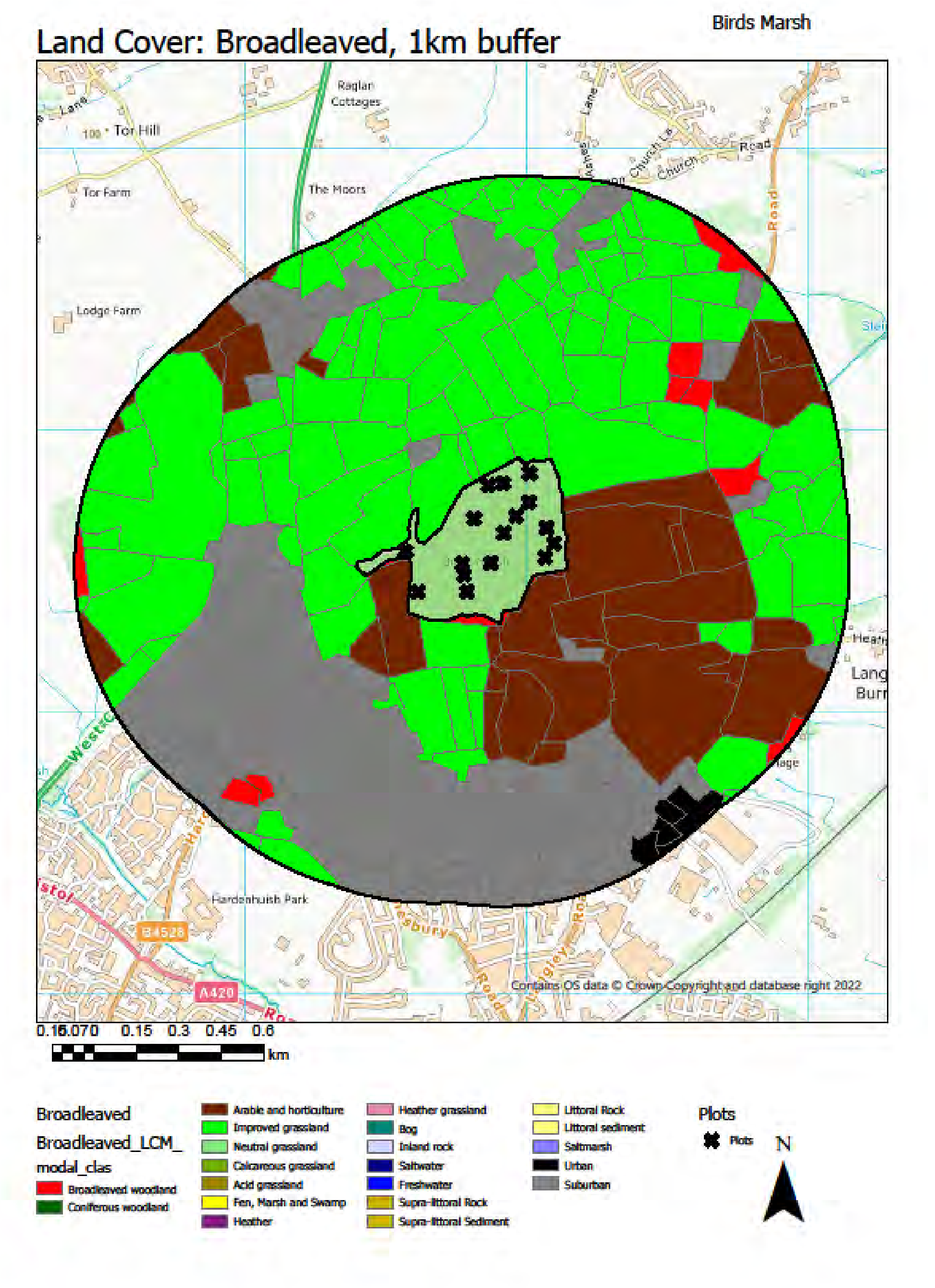
[12] https://www.npms.org.uk/

Epilobium brunnescens
Epilobium ciliatum
Epilobium hirsutum
Epilobium lanceolatum
Epilobium montanum
Epilobium obscurum
Epilobium parviflorum
Epilobium roseum
Epilobium tetragonum
Equisetum arvense
Fallopia japonica
Schenodorus arundinacea
Festuca ovina
Festuca rubra
Galium aparine
Galium saxatile
Gaultheria shallon
Glyceria maxima
Helictotrichon pubescens
Heracleum mantegazzianum
Heracleum sphondylium
Holcus lanatus
Rumex crispus
Rumex obtusifolius
Sagina procumbens
Sambucus nigra
Senecio jacobaea
Senecio squalidus
Senecio sylvaticus
Senecio viscosus
Senecio vulgaris
Sonchus arvensis
Sonchus asper
Sonchus oleraceus
Stellaria media
Trifolium repens
Trisetum flavescens
Typha angustifolia
Typha latifolia
Urtica dioica

7.2 Appendix B: Example of the 1km buffer around each site and land cover composition according to Land Cover Map 2015.



7.3 Appendix C: Further details on analytical methods.

Model fitting sought to identify a Minimum Adequate Model; that is a model with as few parameters as possible, with the lowest AIC value and where, if fixed effects are not statistically significant, then they are only included where an interaction term specified *a priori* is statistically significant (Crawley 2007).

The change in each summary metric over time was modelled either using generalized linear mixed models in a frequentist approach or within a Bayesian hierarchical framework. The latter was implemented using the brms package as an interface to Stan (Bürkner, 2017; Carpenter et al., 2017). Response variables were modelled as a function of survey year (treated as categorical), with the day of year the plot was surveyed also included as a predictor (centred on the 19th July, scaled so that 30 days was equal to one unit change), and a hierarchical effect of plot nested within site on the model intercept.

For the change over time models only the effect of the survey year was also allowed to vary by site in a hierarchical effect. Count variables were modelled using either the negative binomial family (brms) or the Poisson and binomial families (glmer or lmer functions in the lme4 R package and applying a correction to parameter estimates and *p* values for over or under-dispersion[13]). Continuous variables were modelled using the Gaussian family and change in % cover using a hurdle gamma family. The hurdle gamma family was chosen for cover as the total cover of any growth form was bounded at zero but could, and frequently did, go above 100% due to the different canopy levels included in the calculation. Within the hurdle gamma models the count and cover-based models had normal priors with mean 2 and standard deviation 1 on the year effect (no intercept was included in the model), a unit normal prior on the day of year effect, a Student T prior on the hierarchical effects with 5 degrees of freedom, mean 0 and scale 1. The negative binomial models also had a gamma prior with shape 0.1 and inverse scale 0.1. The cover models also had a gamma prior with shape 0.1 and inverse scale 0.1 on the shape parameter, and the priors on the hurdle effects were normal with mean -1 and standard deviation 1 for the year effects, a unit normal for the day of year effect and a Student T prior on the hierarchical effects with 2 degrees of freedom, mean 0 and scale 1. The Gaussian models had normal priors on the year effects with mean 6 and standard deviation 2, plus a unit normal prior on the day of year effect and Student T priors with degrees of freedom 5, mean 0, and scale 3. All prior distributions were tested by sampling only from the prior, and examining the prior predictive distribution to confirm it was biologically feasible.

Bayesian models were run with four chains each with 6000 iterations, of which 2000 were warmup and a thinning rate of 4. Default control parameters were used for the Stan sampler, other than for the fern cover model where adapt_delta was set to 0.9. All models

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[13] Written by Ben Bolker http://bbolker.github.io/mixedmodels-misc/glmmFAQ.html#overdispersion

had Rhat less than 1.01 and both bulk and tail effective sample sizes greater than 1000. Convergence was also assessed through visual inspection of the rank histogram overlay plots. Fit to the data was assessed using graphical posterior predictive checks, and judged acceptable for all metrics other than the cover weighted Ellenberg R scores which are therefore not presented in our results. Comparisons between the years were conducted using estimated marginal means, and the 95% HPD of each comparison calculated. The tidybayes package was used to plot the 50%, 80% and 95% intervals of each effect.

A multivariate model to investigate the effects of Ash dieback (i.e. with multiple response variables) was fit using brms. Within this model Bramble cover, forb cover, and species richness were all modelled together as a function of survey year, Ash dieback, deer risk, day of year, climatic variables, and a site/plot hierarchical effect on the intercept. Forb cover was also modelled as a function of Bramble cover, and species richness as a function of both Bramble cover and forb cover. Response families, priors and number of iterations were as detailed above within the individual models, and no residual correlation between the responses was modelled. To compare multivariate models with differing configurations 10-fold cross validation was used, with site being used as a grouping variable. Note that because of the computing time required to run brms models, Bayesian approaches were limited to tests of change in summary metrics over time and the analysis of Ash dieback effects.

All data manipulation and analysis was done using R version 4.2.2 (R Core Team, 2022), brms version 2.18.0 (Bürkner, 2017), rstan version 2.26.13 (Stan Development Team, 2022), emmeans version 1.8.4-1 (Lenth, 2023), tidybayes version 3.0.3 (Kay, 2023), dplyr version 1.1.0 (Wickham et al., 2023), ggplot2 version 3.4.0 (Wickham, 2016), sf version 1.0-9 (Pebesma, 2018), terra version 1.7-3 (Hijmans, 2023), lme4 version 1.1-30 (Bates et. al. 2015), lmerTest versions 3.1-3 (Kuznetsova A. et. al. 2017), modelbased version 0.8.6 (Makowski D. et.al. 2020), modelr version 0.1.11 (Wickham 2023), parameters version 0.21.0 (Lüdecke D, et.al. 2020).

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7.4 Appendix D: An analysis of changes in individual plant species frequency between the three surveys

1. Introduction

While plant species populations respond individualistically to their environment shared traits confer shared sensitivity to changes in conditions that can non-randomly filter the plant community leading to identifiable groups of winning or losing species (Kopecký et al 2012). Here we delve deeper into the changes in abundance of plant species in the woodland understories sampled over the three surveys. We determine whether species that have increased, decreased or remained stable between each survey exhibit certain combinations of traits that help to characterise them as winners or losers and whether these traits also help suggest which drivers may have been responsible. Analyses both in the main body of this report and in Kirby et al (2005) have correlated vegetation change with a range of drivers including reduced sulphur deposition, long-term lack of canopy disturbance and climate warming. The reduction in mean plant species richness between 1971 and 2001 and then slight recovery from 2001 from 2021 saw an overall reduction in species of open, better-lit conditions and an increase in shade-tolerant species including some with a more southerly biogeographical affinity and some that can exploit increased fertility (see 4.12).

Our objective here is to add to these analyses by examining overall patterns of significant change in *individual plant species* over the 50 years. We provide summaries of change in terms of Ellenberg scores for soil pH, light and fertility, growth form, canopy height and by grouping plants by direction of change and by their status as either nectar-providers, recognising the importance of broadleaved woodlands for pollinating insects (Baude et al 2016), and by their status as woodland specialists and hence plants for which long-continuity woodland is especially important.

2. Methods

Since mean plant species richness declined between 1971 and 2001 and then increased between 2001 and 2021 we treated frequency differences in each species across each pair of years as separate two-tailed tests. That is we tested whether the size of the mean difference between each pair of years was large enough to lead us to reject the null hypothesis of no change at the 5% level. Analyses were simplified by reducing the sample of plots and sites to only those in which the species occurred in at least one survey in each pair, thus removing joint absences. We also restricted analysis to vascular plants with >=10 records in any one year of a pair of survey years. The variable of interest was change in percentage occupancy of plots across sites hence we analysed each species in each site as the difference between the proportion of plots occupied between surveys. This removed the need for a random effect on site and the complication of estimating change as a function of site and plot-level presence/absence data. Since we know that refinding error attaches to each plot we also paired the % frequencies at the site and not plot level. The only covariate we included in each model was date-day difference between surveys to account for change resulting from differences in survey date in each survey.

The probability of the change occurring by chance was estimated using a bootstrapped distribution of the modelled estimate of the mean difference in % occupancy having fitted date-day difference. We explored whether estimated increases, decreases or lack of change among groups of species could be understood in terms of change along environmental gradients, implied by the attributes of the plant species, in turn associated with plausible driving variables. For example, increases in species with high Ellenberg fertility values point toward the impact of changes in the availability of macro-nutrients.

A subset of species that did not change significantly at the 5% level (bootstrapped 95% CI included zero) were included in graphical summaries and in a CART analysis following the approach used in Smart et al (2003). That is we identified those non-significant tests that had the statistical power to detect at least the median absolute difference in % frequency among significant test results. This was done to try and avoid the inclusion of species whose sample size and variance in % change between surveys was likely to have resulted in low power and therefore high Type 2 error. We did this step by extracting the median significant difference in % frequency within each year pair but across all significant species changes for that year pair and adding this value to the bootstrapped sample values for each non-significant test result and then selecting for inclusion in the CART analysis those species whose adjusted 95%tiles did not include zero (Kleinman & Huang 2016).

Bootstrapping of the differences in % frequency between year pairs and for each species used the boot package (Canty & Ripley 2024) and the boot.ci function selecting the 'bca' non-parametric bootstrap based on 100 samples, with replacement, of the site-paired differences. CART analysis was implemented using the ctree function in the R packages party (Hothorn et al 2006) and partykit (Hothorn & Zeilieis 2015).

3. Results and discussion

The CART diagram in Figure 1 partitions the significantly increasing, decreasing and stable species into groups based on a hierarchy of shared attributes. As well as canopy height, growth form and Ellenberg R, N and wetness values, the paired survey year for each species test was added to allow the analysis to potentially separate groups of species by survey interval.

The best-fitting tree diagram first separated changes in the more recent interval between 2001 and 2021 from the 1971 to 2001 interval and the 50-year changes between 1971 and 2021 (Fig 1). More increases were seen in this recent period relative to the greater number of decreases known to have occurred over the 50 years and between 1971 and 2001. However, combinations of the attributes provided were not useful in defining groups of species making up these most recent changes. The clearest attributes differentiating the species changing between 1971 to 2001 and 1971 to 2021 were Ellenberg N values and growth form. Species associated with low fertility were more likely to decrease irrespective of growth form (also Fig 2). This was a relatively large group of less shade-tolerant species including *Campanula rotundifolia, Carex nigra, Deschampsia flexuosa, Erica cinerea, Galium saxatile, Hypericum pulchrum, Potentilla erecta, Stachys officinalis* and *Succisa* *pratensis*. Species of moderately fertile conditions (values >3 but <= 5) were most likely to remain stable with smaller numbers of increasers and decreasers. Having an Ellenberg N value >5 was more likely to result in increasing frequency but only if a non-graminoid monocot or a sedge. These species included the shade tolerators *Arum maculatum, Allium ursinum and Hyacinthoides non-scripta* and the sedges *Carex sylvatica* and *Carex remota*.

Species with higher Ellenberg N values also tend to have higher Ellenberg R values since higher soil pH is associated with higher fertility apart from at the very highest soil pH values. Certainly many of the less shade-tolerant decreasers with low Ellenberg N were also notably acidophilous while increasing species have an affinity for higher pH as well as higher fertility. These include *Mercurialis perennis, Listera ovata, Filipendula ulmaria, Alliaria petioloata, Glechoma hederacea, Lathyrus pratensis, Veronica chamaedrys* and *V.montana*.

Neither canopy height nor Ellenberg Light values were good separators of winners from losers over the 50 years (Figs 4 and 5). Changes in % frequency were also not well differentiated by growth form (Fig 6). Forbs saw the greatest change over the 50 years with just under half of all forb species tested decreasing between 1971 and 2021 (Fig 6).

Status as an Ancient Woodland Indicator also did not clearly separate species by their direction of change. The clearest pattern is that most species whether woodland specialist or not, did not change over time but of those species that did change, increases were more likely to occur in the last 21 years whilst overall more species decreased than increased (Fig 7). The same pattern and interpretation applies to nectar or non-nectar plants (Fig 8). Overall, over the 50- year interval most nectar plants did not change but of those that did more decreased than increased (Fig 8).

Overall 45% of the species tested did not change in % frequency between surveys[14].

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[14] Note that because of the exploratory nature of the analysis we did not apply any correction for multiple testing hence be aware that 11 tests are likely to have been significant by chance at the 5% level out of a total of 215 significant results.

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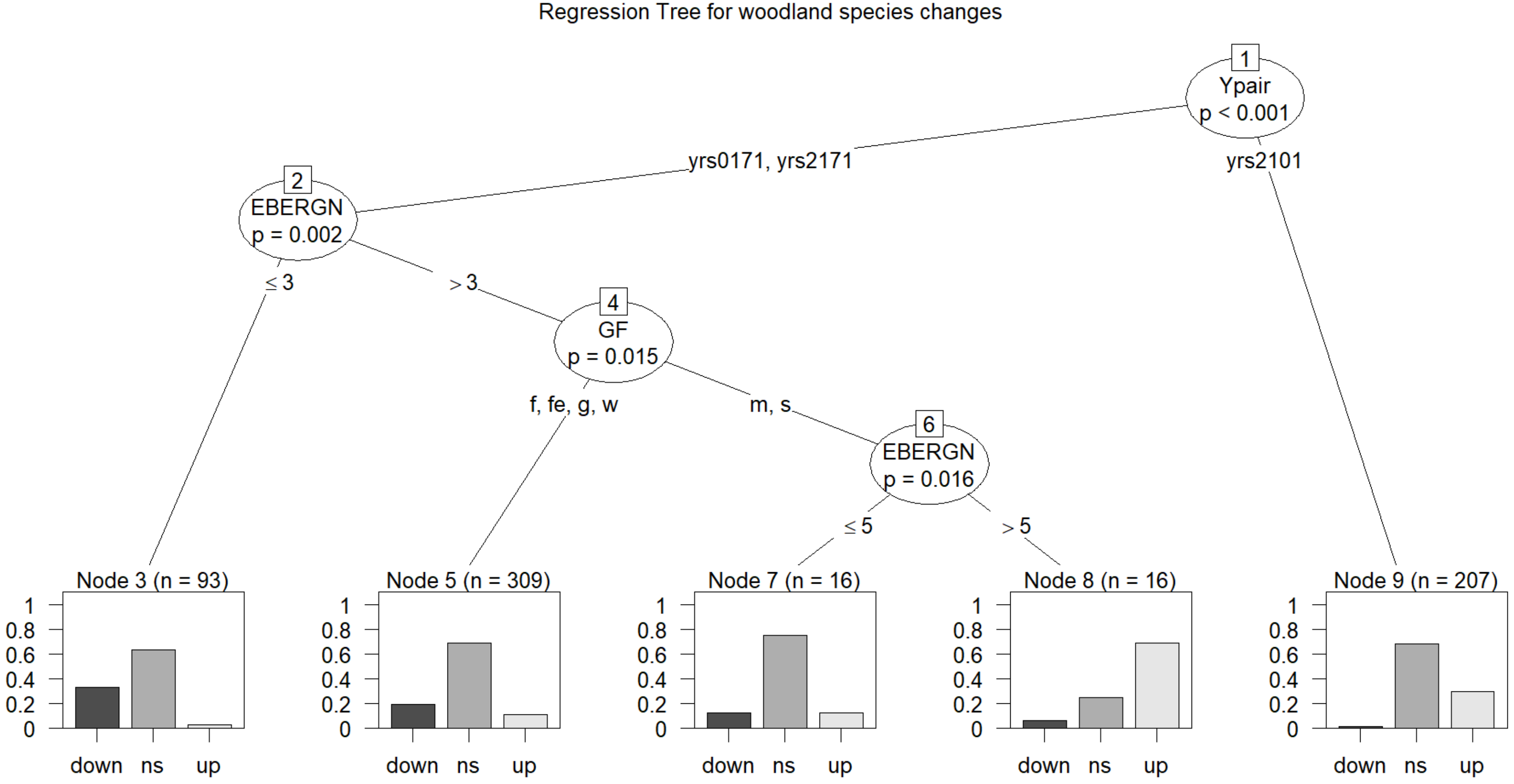

Figure 1: Classification and Regression Tree showing how differences in numbers of plants increasing, decreasing or remaining stable between surveys could be explained by their attributes. EBERGN = Ellenberg N values, GF=growth form (f=forb, fe=fern, g=grass, w=tree/shrub seedlings, m= non-grass monocots, s=sedges). Yrs0171, yrs2171, yrs2101 are the paired differences between 1971 and 2001, 1971 and 2021 and 2001 and 2021 respectively. The number of plant species results classified in each node is shown in brackets.

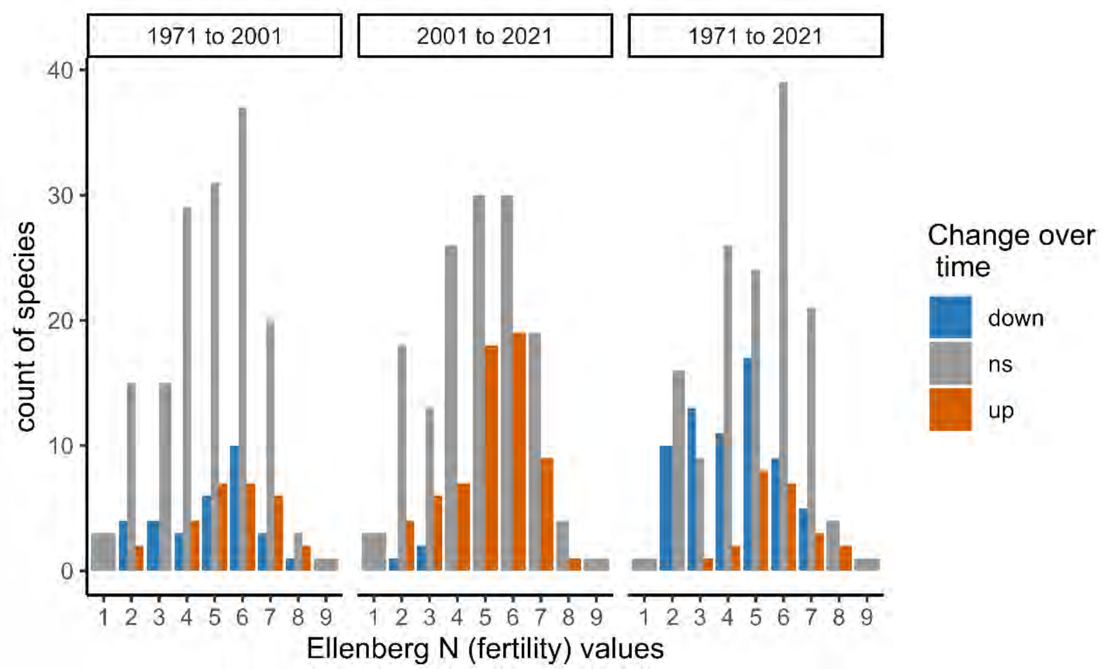

Figure 2: Significantly changing and stable species (ns) summarised by Ellenberg N (fertility) value.

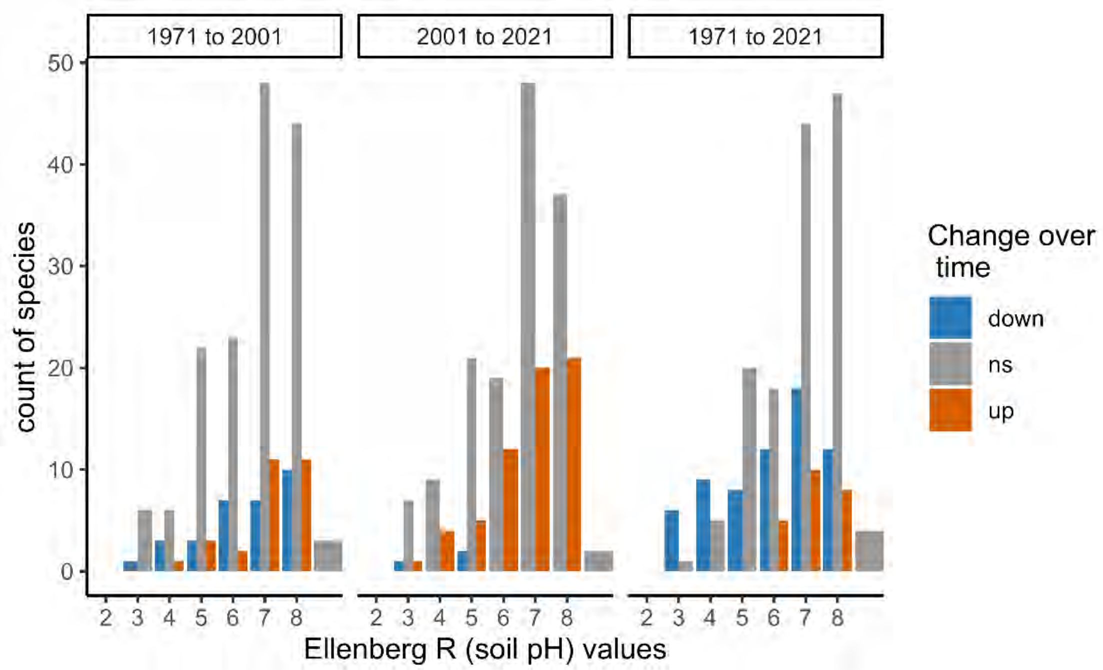

Figure 3: Significantly changing and stable species (ns) summarised by Ellenberg R (soil pH) value.

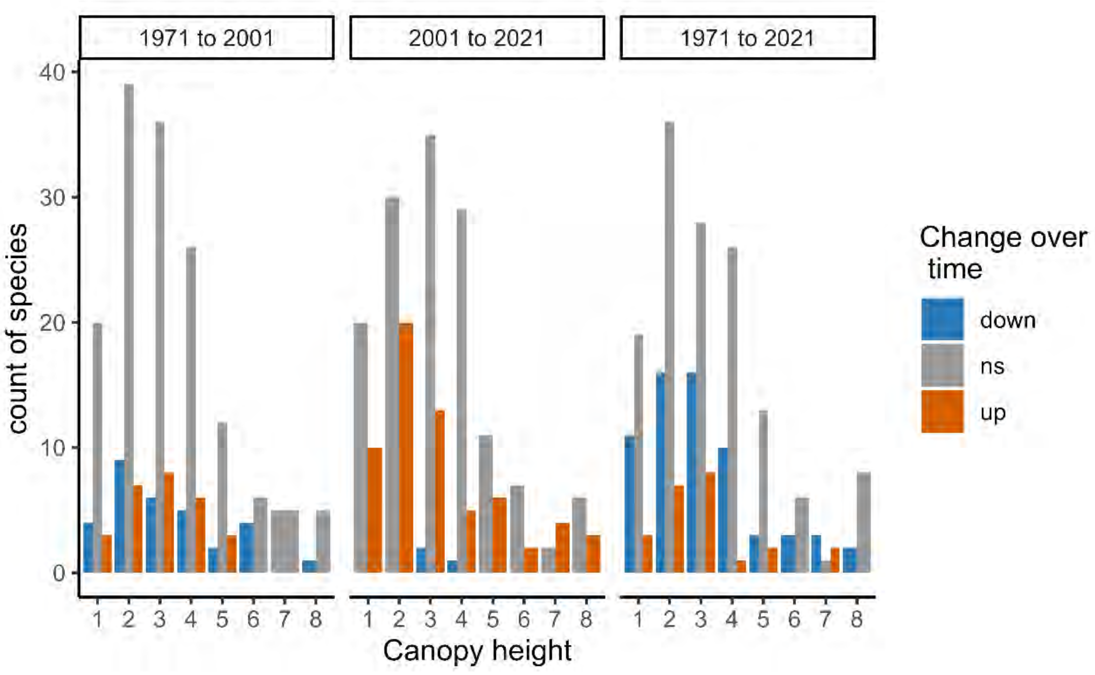

Figure 4: Significantly changing and stable species (ns) summarised by an ordinal classification of average canopy height as follows: 1, <100mm; 2, 101-299mm; 3, 300-599mm; 4, 600-999mm; 5, 1 – 3m; 6, 3.1-6m; 7, 6.1 – 15m; 8, >15m.

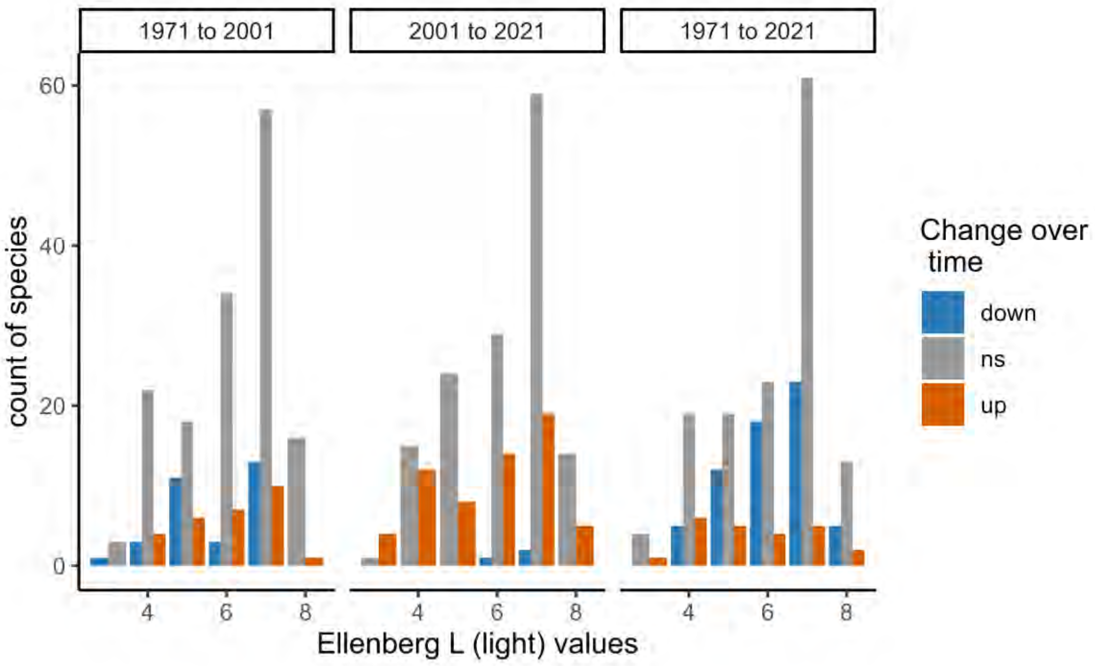

Figure 5: Significantly changing and stable species (ns) summarised by Ellenberg L (light) value. High values are associated with greater shade-tolerance.

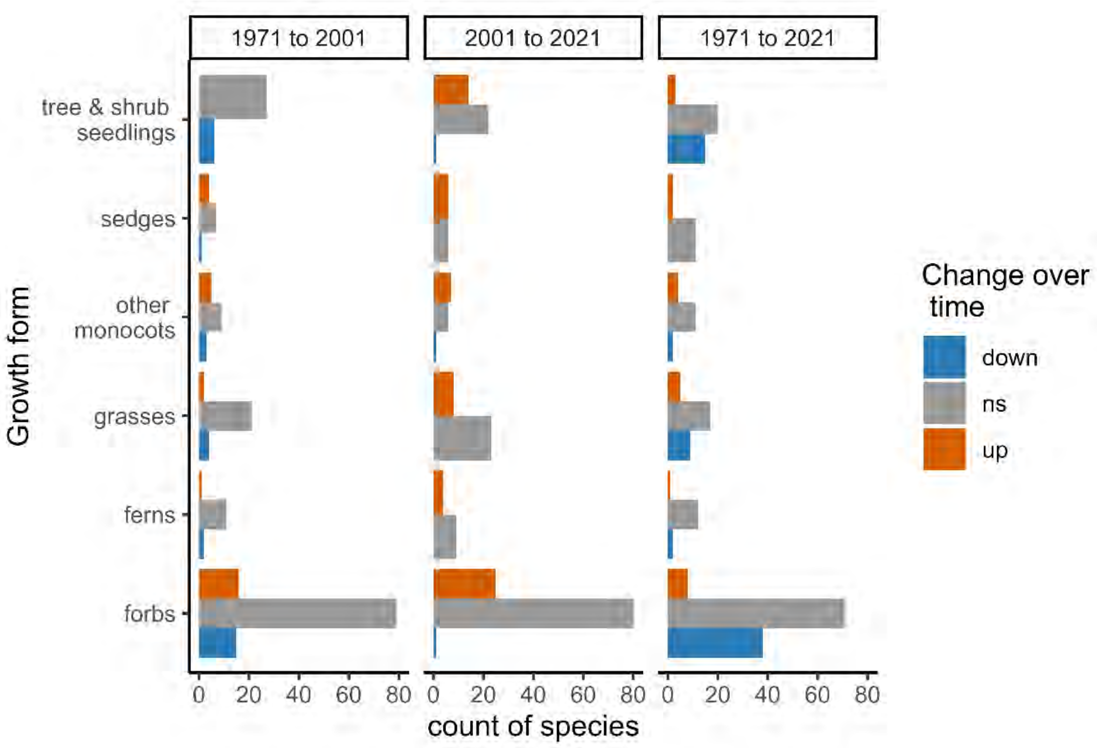

Figure 6: Significantly changing and stable species (ns) summarised by growth form.

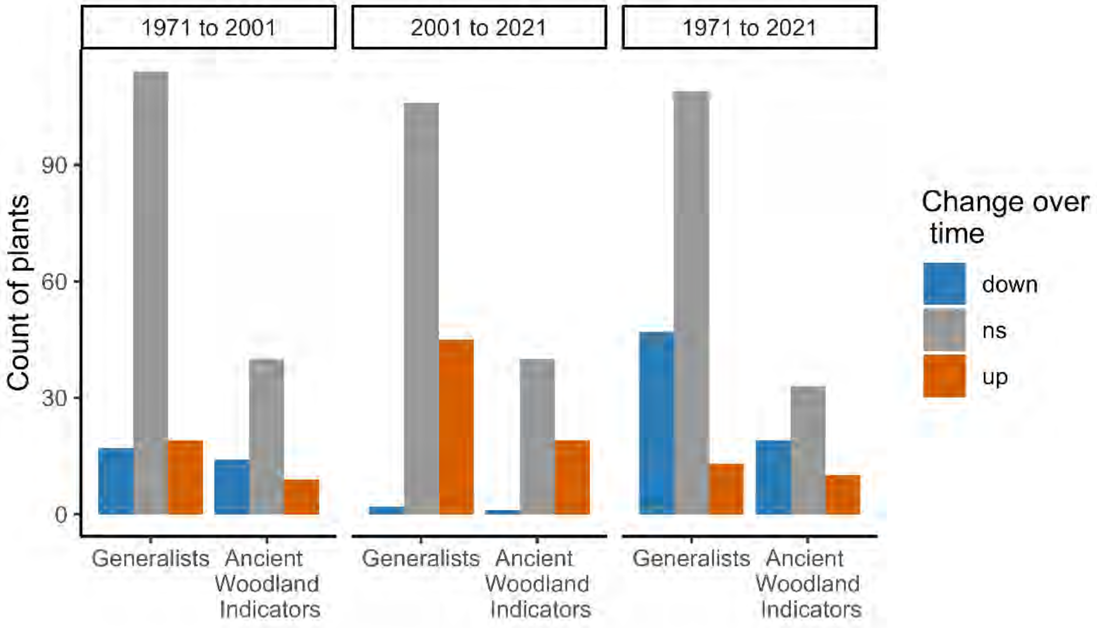

Figure 7: Significantly changing and stable species (ns) summarised by status as a woodland specialist associated often with long-continuity woodland or a habitat generalist associated with lower quality habitat.

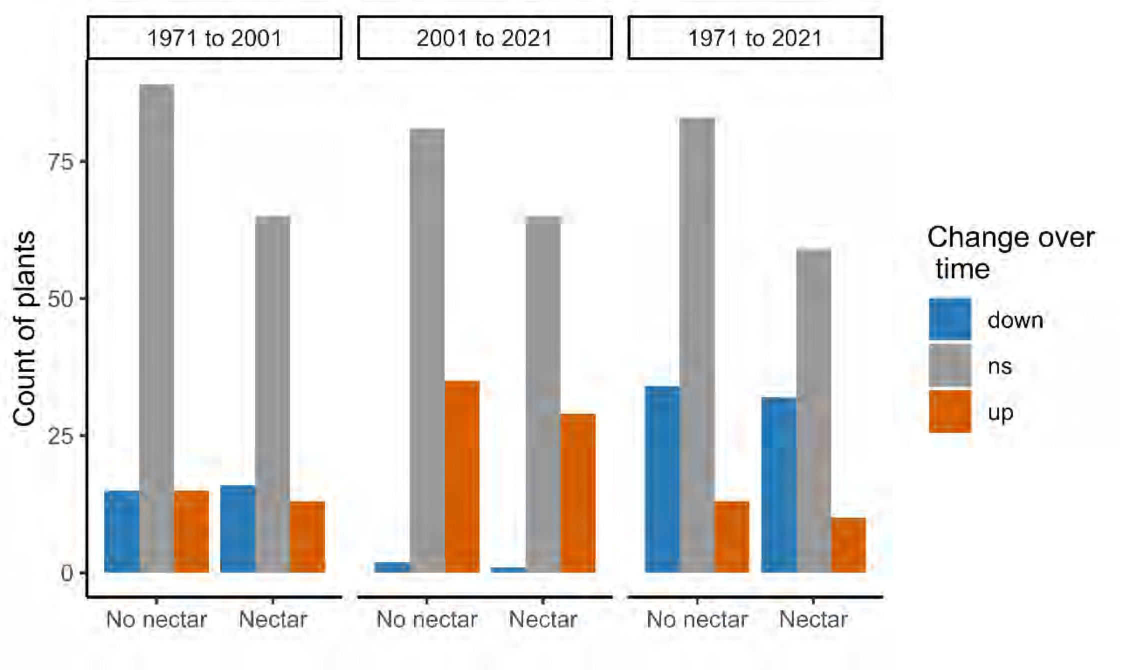

Figure 8: Significantly changing and stable species (ns) summarised by whether they are important nectar-providers or not according to the analysis and database of Baude et al (2016).

7.5 Appendix E: Testing the War-Torn Woodlands Hypothesis - Was the widespread removal of timber at the end of World War II the reason for trees being younger and understories more species-rich in 1971?

Catherine Walker & Simon Smart

1. Introduction

A key driver of woodland change is management of the tree canopy. Due to the relatively slow development of woodland ecosystems, the impacts of past management may persist over long periods of time. Cycles of traditional coppicing and thinning management have been performed in woodland across Europe for hundreds of years, but this form of management began to decline in the late 19th and early 20th Century (Innes et al., 2013).

In Britain, the decline in management of broadleaved woodland was interjected by a disturbance event that affected woodlands across Britain. The Second World War halted imports of timber to Britain, therefore there was extensive felling of native woodlands to meet demand (Meiggs, 1949).

In the 80 years since the Second World War, the decline in traditional management, for the most part, continued, and areas of woodland that were re-established through planting or natural regeneration post-war have steadily moved through the stages of succession.

Due to management decline, the successional trajectories of British broadleaved woodland were subject to less disturbance since the Second World War than before. As a result, woodlands that were re-established post-war were likely to be single cohort stands (Oliver and Larson 1990). Single cohort stands regenerate after a major disturbance and are generally characterised by a homogeneous canopy structure in the mid-stages of succession. Following the initial rapid growth of the stand initiation phase of succession, woodlands reach the optimum or stem exclusion period (Hilmers et al. 2018; Oliver & Larson, 1990). This period is characterised by canopy closure as trees fill space. Understorey plant species richness is generally low in this stage as the closed canopy limits light availability on the woodland floor (Hilmers et al. 2018).

Multi cohort stands are produced by multiple asynchronous patch disturbances in a woodland, resulting in a more heterogeneous canopy structure. Gap formation in the development of multi-cohort stands provides light for more plant species to establish on the woodland floor. Due to minimal management post-war, many British broadleaved woodlands did not experience the frequency of minor disturbances that would produce canopy heterogeneity at this mid-point in succession.

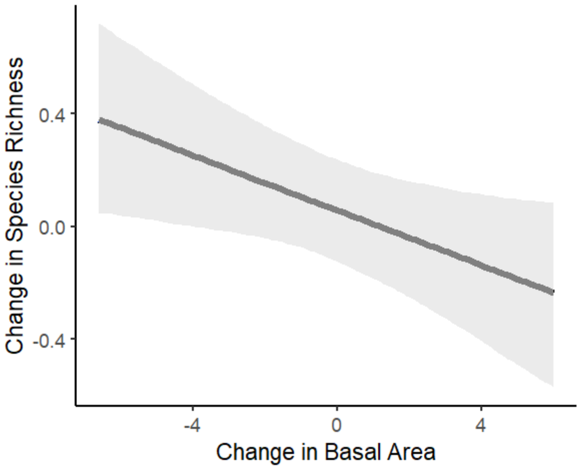

Fig 1: Change in mean basal area versus change in understorey species richness between 1971 and 2001 in the Bunce broadleaved woodland sites.

Therefore, understorey species richness may have been unusually high across British forest in the decades immediately following timber extraction post-WWII and then experienced synchronous and unusually steep decline as a result of shading because succession has tended not to be deflected by traditional management (Fig1).

We compared the observations from national surveys of the canopy structure and understorey species composition carried out in 1971 and 2001. We tested the hypothesis that woodlands that were re-established following wartime felling had moved into the stem exclusion stage of single cohort stand development by 2001. If this was the case, we expected canopy structure in war-time felled woodland to have shifted between 1971 and 2001 from many small stems of the stand initiation stage towards fewer, larger stems of the stem exclusion stage. We expected these differences to be linked to the decline in understorey species richness across British broadleaved woodland. This hypothesis is referred to as the War-Torn Woodlands Hypothesis (WTWH). In summary we sought to answer the following questions:

1. How has the structure of the woodland canopy (stem density, stem basal area and variance in stem basal area) changed in stands that were felled in the Second World War compared to those that were not felled?
2. Is there a causal link between wartime felling, canopy structure in re-established woodland and understorey species richness?

Identifying whether widespread war-time felling was still affecting canopy structure and woodland species richness 50 years later is an important step towards predicting future woodland succession. It also helps guide appropriate evaluation of recent changes in species richness and composition. For example, if post-war timber extraction affected many sites then the high species richness observed in 1971 may not be typical and the size of the subsequent decline in richness needs to be seen in that light.

2. Methods

The 1947 Census of British Woodland

To investigate whether war-time felling affected canopy structure and understorey species richness decades later, historical data was sought to quantify the extent of woodland felling during the World War ii. The 1947 Census of British Woodland is a unique dataset that provided this historical link. Following the timber supply crisis of the Second World War, this census was a government-run stock-take of post-war timber reserves across British woodland (Forestry Commission, 1952). Carried out between 1947 and 1949, the census detailed tree species composition, age classes of trees, and woodland condition. Woodland condition comprised ten 'type' categories. This study focused on the following categories, which identify woodland as broadleaved high forest, or having evidence of felling in the Second World War:

- Broadleaved High Forest (BHF) – Trees grown as standards to maturity.
- Scrub – Inferior growth, either the initial stages of natural regeneration following felling or sparse high forest on poor quality sites.
- Devastated – Areas of scattered trees, usually after selective felling.
- Felled after 1939- Woods that had not been restocked or naturally regenerated following felling.

416 original data sheets and 114 woodland maps from the 1947 Census were viewed and photographed in the National Archives in Kew, London, and the National Records of Scotland in Edinburgh. Data sheets consisted of tick boxes to record woodland attributes, and data were digitised into an excel spreadsheet. Woodland maps consisted of 6-inch Ordinance Survey (OS) maps produced between 1900 and 1930. Woodland area was divided into stands according to species composition and/or the categories of woodland condition (Forestry Commission, 1952). Stands had been outlined and numbered by hand on the 6-inch OS maps.

Data from the 1947 census were gathered for 95 sites in the Bunce woodland survey. Some sites were not present in the 1947 census. For some, it was due to them being managed by the Forestry Commission at the time and they were therefore surveyed in a separate census, which has not been archived. Sites were further removed if they did not contain at least one BHF stand and at least one stand of either scrub, devastated or felled woodland. This was to ensure that data from the same sites could be paired to compare the effect of high forest condition to the effect of the management conditions. Under these criteria, 83 sites were finally selected for analysis.

To link the 1947 census data to the Bunce Woodland Survey, digitisation of the outlined 6-inch maps was performed, which allowed for the Bunce survey plots to be overlaid onto the 1947 stands. Digitisation of the maps was performed using the *Georeference* and *Trace Raster* tools in QGIS to create polygons of the outlined stands (QGIS Development Team, 2019). The quality of the digitisation was restricted by the quality of the scanned maps in the archives, and there was subsequent variation in alignment of the old maps with modern digital maps. To account for this, all Bunce plots that were less than 5m away from a stand edge were removed from subsequent analyses.

Initial exploration of the data resulted in further categorisation of the woodland stand conditions. It was possible to include subgroups of stand age in the BHF category. Age classes were included as tick boxes to identify stand age at ten and twenty-year increments. There was also an option to include broader age classes in the 'remarks' section of the survey sheet. Due to the range of different age classes and the subsequent small number of woods falling into some of the age classes, BHF stands were instead categorised as 'Even' or 'Uneven' aged. The rationale behind this was that even-aged stands were more likely to be planted, commercial stands, which might indicate different management history to uneven-aged stands.

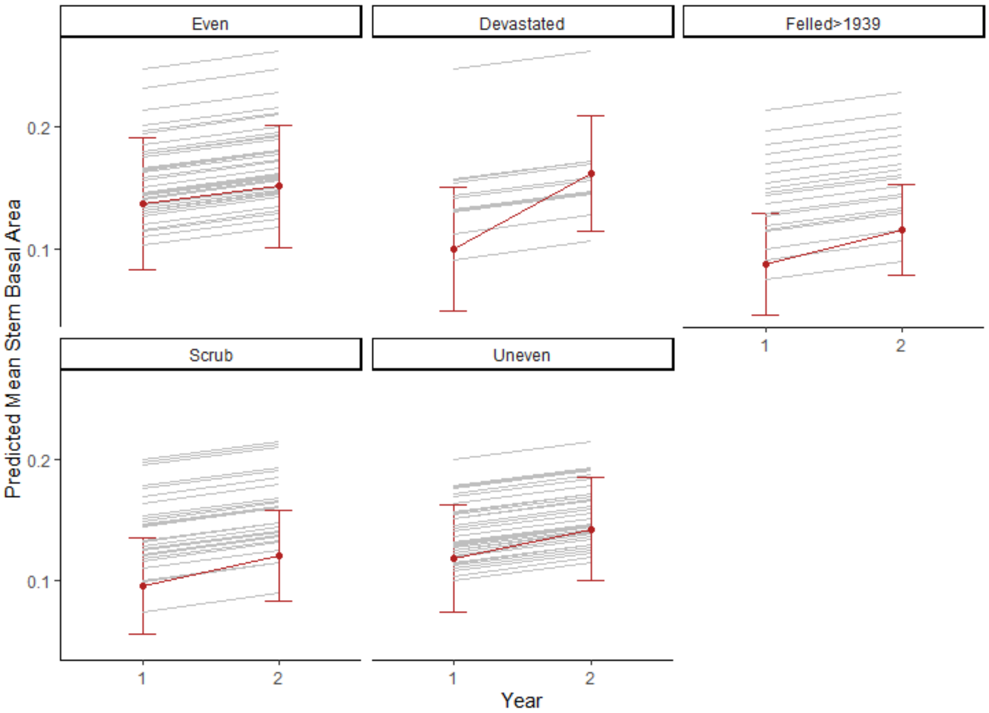

Fig 2. Mean predicted basal area plot in year 1 (1971) and year 2 (2001) for each 1947 management type is shown in red. Error bars show the standard deviation. Grey lines show the random intercept estimates for each site.

Analysis

Hypotheses were tested using mixed models (glmer/lmer R functions). Tests of Differences in paired plot response variables included the 1971 values as a covariate to account for regression to the mean effects (Mazalla & Diekmann 2022).

3. Results

In 1971, mean basal area was significantly lower in stands that had been felled in 1947 ('devastated', 'scrub' and 'felled after 1939') compared to stands that were BHF in 1947.

This suggests that 24 years after disturbance, stands carried a legacy impact on basal area dating back to the period of felling in the 1940s (Fig 2).

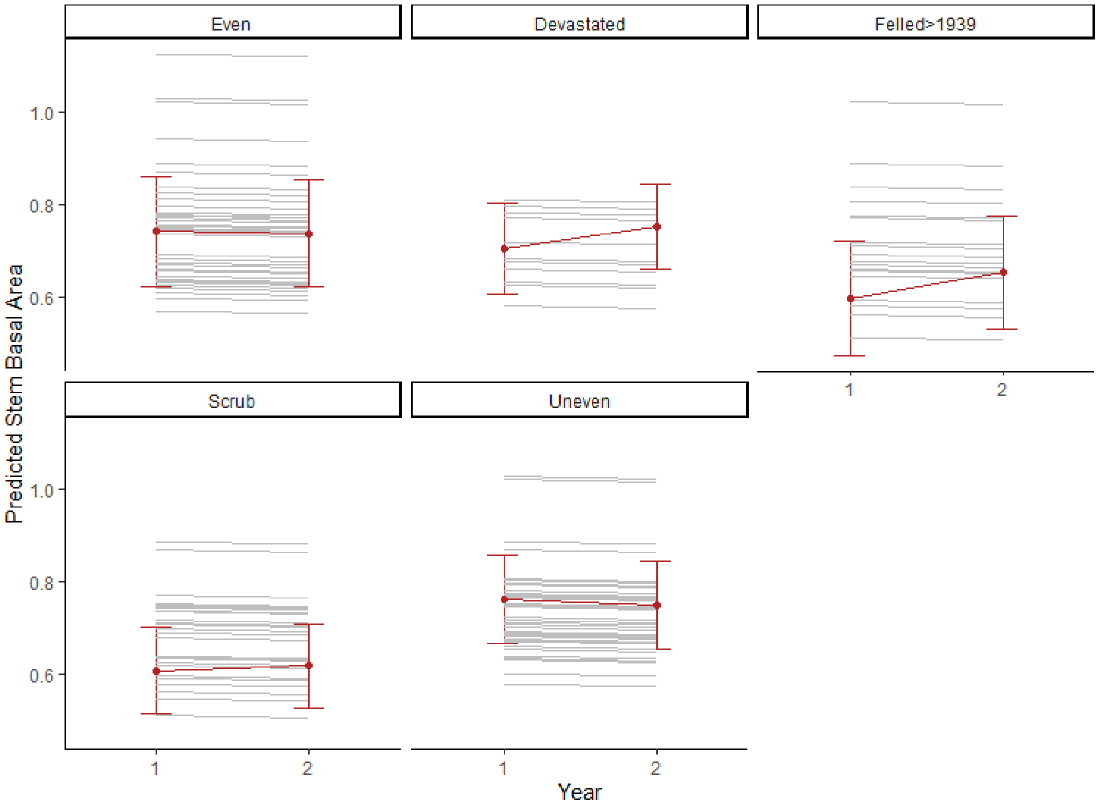

Fig 3. *Total* stem basal area per plot in year 1 (1971) and year 2 (2001) for each 1947 management type is shown in red. Error bars show the standard deviation. Grey lines show the random intercept estimates for each site.

At plot level, there was a significant interaction between devastated and year, suggesting that the increase in mean stem basal area is more marked in historically devastated woods (Fig 2) as predicted by the WTWH.

At plot level, total basal area was significantly lower in felled and scrub plots than even aged BHF. At site level, total basal area was significantly lower in felled, devastated and scrub plots than even aged BHF, uneven aged BHF had significantly higher basal area (Fig 3).

At plot level, stem density was significantly higher in felled plots than even aged BHF across both years. At plot level there was a significant negative interaction between 'felled after 1939' and year, and 'scrub' and year. Stem density decreased with year to a significantly greater extent in these historic management types (Fig 4).

Interestingly, 1947 management types other than uneven-aged BHF increased in total basal area suggesting that irrespective of the magnitude of change most woodlands in the sample showed net directional stand development over time rather than no change where the latter would be more consistent with dynamic and asynchronous gap-creation and post-disturbance canopy growth (Fig 3). Therefore, uneven-aged BHF is the woodland type that seems least obviously impacted by legacy effects of historical and widespread canopy disturbance. This is also consistent with the WTWH.

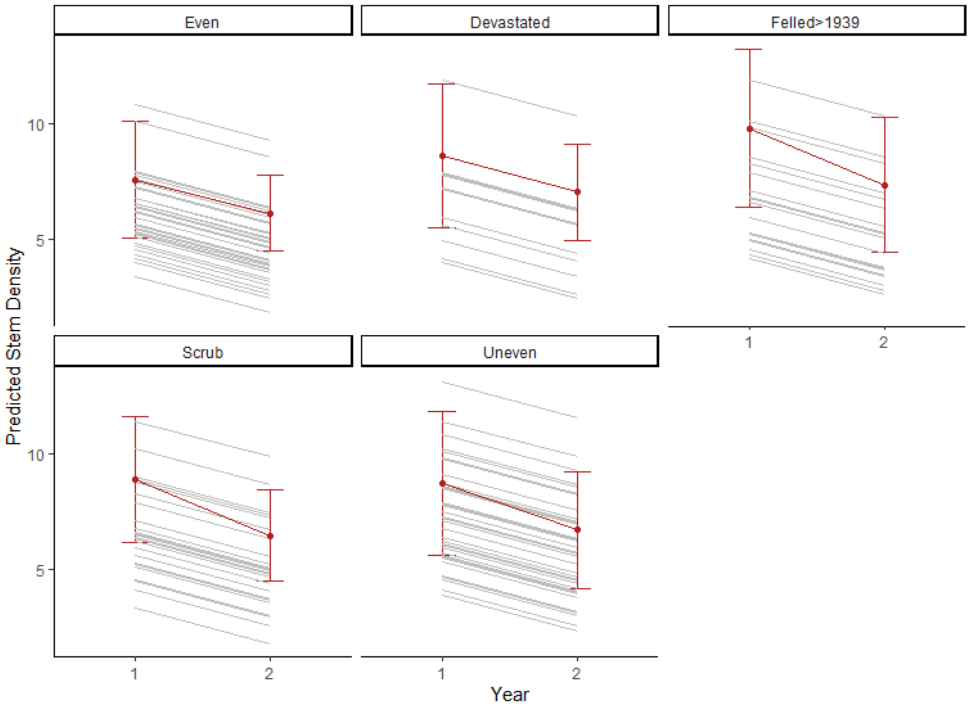

Fig 4. Mean predicted stem density per plot in year 1 (1971) and year 2 (2001) for each 1947 management type is shown in red. Error bars show the standard deviation. Grey lines show the random intercept estimates for each site.

4. Conclusions and further work

The ‘devastated’, ‘felled after 1939’ and ‘scrub’ categories all showed different rates of change in either mean basal area or stem density between 1971 and 2002 versus BHF in 1947. This provides correlative evidence that changes in canopy structure known to influence understorey species richness differed between stands impacted versus those not impacted by WWII wood extraction. This is evidence of a legacy effect of disturbance consistent with the WTWH. A next step in the testing of this hypothesis will be to determine whether 1947 forest management status explains understorey species richness change mediated via changes in the tree canopy.

The results also strongly suggest that the WTWH cannot be the entire explanation of changes in canopy and understorey because it is apparent that mean basal area increased in all forest types including BHF not felled in 1947 (Fig 2). This broader trajectory could be due to further legacy impacts of the long decline in woodland traditional management as well as pulsed canopy disturbance associated with the first World War.

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7.6 Appendix F: Examples of the impact of woodland loss, historical and recent management

Recent timber extraction

Recent felling of timber was a rare occurrence across the broadleaved woodlands. At Wellhanger copse, a site in Hampshire, mature Ash had been removed from one of the plots in the last 5 years. This resulted in a rich understorey with a diverse mix of open ground, generalist and woodland specialist species and even a crop volunteer. Being shaped by this 'pulsed' disturbance event the assemblage is likely to change rapidly over time as taller species gradually dominate and filter out light-loving species. That is unless there were an increase in grazing pressure.

Table 1: Species list from Wellhanger copse where Ash had been clearfelled.

Species	% Cover
Bare ground/litter/water/rock/mud	30
Rubus fruticosus agg.	30
Mercurialis perennis	20
Pteridium aquilinum	15
Galium aparine	5
Rubus idaeus	5
Arrhenatherum elatius	5
Urtica dioica	5
Holcus lanatus	5
Bryum sp.	1
Thamnobryum alopecurum	1
Brachypodium sylvaticum	1
Circaea lutetiana	1
Dactylis glomerata	1
Geum urbanum	1
Lamiastrum galeobdolon	1
Poa trivialis	1
Alliaria petiolata	1
Carex sylvatica	1
Cirsium vulgare	1
Epilobium hirsutum	1
Festuca gigantea	1
Hypericum perforatum	1
Juncus bufonius sens.lat.	1
Lapsana communis	1
Poa annua	1
Rumex obtusifolius	1
Senecio erucifolius	1

Stellaria graminea	1
Triticum aestivum	1
Veronica seedling/sp	1
Arctium agg.	1
Dryopteris filix-mas	1
Glechoma hederacea	1
Agrostis stolonifera	1
Clematis vitalba	1
Lolium perenne	1
Plantago major	1
Potentilla reptans	1
Potentilla sterilis	1
Prunella vulgaris	1
Ranunculus repens	1
Rumex sanguineus	1
Scrophularia nodosa	1
Silene dioica	1
Veronica serpyllifolia	1

At another site, this time in SW Wales, mature Ash had also been felled in the last 2 years stimulating strong dominance by Bramble that was also very dense throughout the rest of the woodland. The owner used the felled and seasoned wood in his cabinet-making business and also produced charcoal. He was extremely keen to carry on managing the woodland but was nearing retirement and had been unsuccessful in his attempts to recruit an apprentice whom he hoped would take over the business. Difficulty lay in finding someone who would make a long term commitment but also had a second income given the low profitability of the enterprise. In the photograph the owner is wrapping a chain around a felled Ash prior to hoisting it up the steep slope.

Table 2. Species recorded in a plot in one of the Welsh sites where Ash had been clearfelled recently.

Species	% Cover
Rubus fruticosus agg.	55
Bare ground/litter/water/rock/mud	15
Brachythecium rutabulum	15
Thuidium tamariscinum	15
Hyacinthoides non-scripta	15
Veronica montana	5
Galium aparine	5
Dryopteris affinis	1
Galium mollugo	1
Hedera helix	1
Potentilla sterilis	1
Veronica chamaedrys	1
Circaea lutetiana	1
Epilobium sp.	1
Ranunculus repens	1
Epilobium montanum	1
Geranium robertianum	1
Lonicera periclymenum	1
Athyrium filix-femina	1
Dryopteris dilatata	1

Storm impacts

Recent storm impacts were recorded in 5% of plots. In some sites in south-east England, fallen dead wood was still evident dating back to the October 1987 storm. This event was associated with increased species richness between 1971 and 2001, a different trajectory to most of the sites, which saw dramatic reductions in understorey plant species richness. Felled trees provide new opportunities for a range of species to colonise as described evocatively in Tony Whitbread's account of the aftermath of the 1987 storm "When the Wind Blew". An uprooted tree simultaneously creates a mosaic of new niche space – exposed soil and wetter hollows at ground level, dead wood of varying size and decomposability, soil associated with the exposed root plate that may be tall enough to be beyond reach of herbivores and experiences greater fluctuations in temperature and wetness since the other hugely influential consequence is to admit light into the woodland floor. Examples from the Bunce woodlands are shown above from Whitbarrow in Cumbria and Pen-yr-Alt on the coast in south-west Wales.

Neglected coppice stools

These were an extremely common feature of all three surveys. Coppice stools were common but recently cut coppice very infrequent. Two examples are shown below. The first is from a site in Somerset. Here coppiced Sycamore forms a canopy over a shade-tolerant assemblage with high cover of soft shield-fern (*Polystichum setiferum*) and many bryophytes present. The second example is in NW Lancashire. Here a richer assemblage on wetter soil was recorded yet still dominated by shade-tolerant forbs and bryophytes.

Table 3. Fern-dominated assemblage under Sycamore coppice.

Species	% Cover
Bare ground/litter/water/rock/mud	70
Polystichum setiferum	40
Acer pseudoplatanus	1
Brachythecium rutabulum	1
Eurhynchium praelongum	1
Fissidens bryoides	1
Amblystegium serpens	1
Hedera helix	1
Pteridium aquilinum	1
Rubus fruticosus agg.	1
Rumex sanguineus	1
Atrichum undulatum	1
Eurhynchium striatum	1
Fraxinus excelsior	1
Ilex aquifolium	1
Mnium hornum	1
Urtica dioica	1
Phyllitis scolopendrium	1
Total bryophyte	1

Table 4. Assemblage under Sycamore coppice in New Laund wood, NW Lancashire.

Species	% Cover
Equisetum telmateia	50
Mercurialis perennis	30
Bare ground/litter/water/rock/mud	25
Chrysosplenium oppositifolium	15
Total bryophyte	15
Eurhynchium praelongum	10
Veronica montana	10
Brachypodium sylvaticum	10
Brachythecium rutabulum	5
Calliergon cuspidatum	5
Cardamine flexuosa	5
Oxyrrhychium hians	1
Pellia epiphylla	1
Poa trivialis	1
Atrichum undulatum	1
Carex remota	1
Circaea lutetiana	1
Filipendula ulmaria	1
Geum urbanum	1
Mnium hornum	1
Plagiomnium undulatum	1
Potentilla sterilis	1
Dryopteris dilatata	1
Fraxinus excelsior	1
Ranunculus repens	1
Deschampsia cespitosa	1
Stachys officinalis	1
Carex sylvatica	1
Dryopteris affinis	1
Dryopteris filix-mas	1

Signs of historical management

Old hardwood stumps in varying stages of decomposition were a common feature throughout the sample of woodlands. Sawn but left logs such as that below in Riding Mill Wood in NE England, were also frequently encountered providing evidence that many sites saw episodes of felling that must have resulted in a greater number of open areas in the past. Recently cut stumps were rare even in 1971 (see Fig 4 in the main report).

Loss and modification of woodland habitat

Conversion of woodland to other land cover types was rare with 1.3% of the original total number of plots being converted or modified. The most frequent driver appeared to be intensification involving the spread of productive species and increased grazing underneath a scattered, residual canopy of shrubs and trees at the woodland edge. The proximity of intensive ‘press’-disturbed agricultural grassland is illustrated below. Here grazed, semi-improved pasture is directly adjacent to part of the Pen-yr-alt woodland site in SW Wales. The grazed pasture abuts the woodland edge and, in the picture, all five Injurious Weeds (listed in the Weeds Act 1959 plus *Senecio jacobaea* added to the list in 2003) were present plus dense stands of *Urtica dioica*. There is no dispersal barrier to these species entering the wood but a number of factors probably reduce the likelihood of incursion and establishment. The edge of the wood is very densely dominated by *Rubus fruticosus* agg whilst the interior covers densely shaded and undisturbed wet woodland on low ground. Canopy disturbance coupled with drying of the peaty soil could readily create suitable conditions for weed spread.

The example below is from the south-east of England. Here, grazing and probably fertilizer inputs and re-seeding at the woodland edge have resulted in a zone of productive wood pasture replacing part of the original woodland. The green, homogenous colour palette tells the whole story additionally evidenced by the species composition of the plot which is dominated by Perennial rye-grass (*Lolium perenne*).

A striking feature of the plot is the long tail of subordinate species at <5% cover. Similar to the Ash clearfell plot at Wellhanger copse, a diverse range of species were recorded with affinities for disturbance, wood pasture and elevated productivity. Here though the dominance of the agriculturally-favoured grass is clear and it may only be reduced light levels under the tree canopy that limit the vigour of the dominant providing opportunities for persistence of the other species present.

Table 5. Species recorded in newly intensified wood pasture at the edge of a site in the south east of England.

Species	% Cover
Lolium perenne	80
Bare ground/litter/water/rock/mud	5
Cardamine hirsuta	1
Cirsium vulgare	1
Poa annua	1
Poa trivialis	1
Ranunculus repens	1
Rumex obtusifolius	1
Rumex sanguineus	1
Taraxacum agg.	1
Urtica dioica	1
Vicia sativa	1
Brachythecium rutabulum	1
Carex pendula	1
Cerastium glomeratum	1
Cirsium arvense	1
Cirsium palustre	1
Convolvulus arvensis	1
Dicranella heteromalla	1
Festuca rubra agg.	1
Lotus corniculatus	1
Plantago major	1
Rubus fruticosus agg.	1
Rumex crispus	1
Sonchus asper	1
Stachys sylvatica	1
Veronica serpyllifolia	1
Carex strigosa	1
Geranium molle	1
Juncus bufonius sens.lat.	1
Medicago arabica	1
Plantago lanceolata	1
Trifolium repens	1
Barbula sp	1

Bryum sp.	1
Eurhynchium praelongum	1
Petasites fragrans	1
Prunella vulgaris	1
Stellaria graminea	1
Veronica hederifolia	1
Achillea millefolium	1
Barbula convoluta	1
Bellis perennis	1
Calliergon cuspidatum	1
Epilobium sp.	1
Leucanthemum vulgare	1
Total bryophyte	1
Trifolium dubium	1
Veronica chamaedrys	1
Physcomitrium pyriforme	1

The example below illustrates complete change of habitat type impacting three of the 16 plots on the site. The species composition of the three plots was not recorded for obvious reasons but the location had evidently changed from broadleaved woodland following the creation of a new lake.
The only other wholesale changes of land-use recorded between 2001 and the recent resurvey were one plot having been subsumed within an encroaching garden and a plot that appears to have been lost to an extension of an access road to the Royal Papworth Hospital, Cambridgeshire.

7.7 Appendix G: End of survey wash-up meeting: 23rd November 2022

Present: Simon Smart, Claire Wood, Paul & Michelle Losse, Sue & Roger Ward, Andy McMullen, Lucia Ruffino, Hilary Wallace.

Impacts *Thinking about factors that affect the woodlands you visited what did you see most evidence for?*

Broadleaved Woods

- Ash dieback is obvious throughout, although there are signs the Ash is being quite resilient – lots of seedlings, and isn't making a huge gaps in the woods. Ash seemed to be the most common 'regeneration' species. Young and old trees seem more resilient.
- Maybe more evidence of disease in the canopy, but hard to see. Bit of *phytopthera* in juniper wood, and a bit of larch disease noticed.
- Drought apparent in 2022 in the south – everything wilting, even the Bramble.
- Sycamore and Beech are often shading out ground flora.
- Rhododendron encroachment did not seem to be a big issue at our sites
- Lack of management apparent at many of the privately owned sites. Woods well fenced. Many fallen trees and Bramble. Overgrown (especially Wales sites).
- Bracken, Bramble, *Holcus*, *Dactylis* evident (nitrogen response?)
- Previous thinning and temporary tracks have left gaps now filled with scrub and Bramble.
- Lack of active coppice management (signs of old coppicing)
- Pickreed – some plots are now in grassland, not woodland. Also, other sites, quite a lot of plots with no trees now.
- Evidence of Non-natives – Cherry laurel, Himalayan balsam, exotic conifers. But didn't get a sense they'd increased.
- Grants for woodland planting (sometimes inappropriate).
- Evidence of parts of sites being lost to development.
- Dulwich – noticed a lot of Holly. Had been an increase 1971-2001. Landowner said they'd tried to keep cutting it back, but failing.
- Sensed a difference between the narrow valley side woods and the larger landscape woods – grazing?
- Maybe less Rowan now? Lots of seedlings, but few regen/saplings.
- Pheasant pens – shooting seems less popular. A lot of existing pens seem derelict. Bird flu, expensive food?

- Squirrels like Sycamore – which sometimes is planted in order to take the brunt of squirrel damage.
- Fallen trees are generating new stems from branches.

Condition

- Some sites lacked variety (e.g. Wales – high canopy, bluebells, Bramble). Often the linear ones were botanically dull (Wales).
- Fern & bryophytes increased 1971-2002. Not sure if increased again?
- Paul's sites would have failed condition assessments on at least one criteria (e.g. lack of regeneration, non-natives etc.)
- Often management entails destructive clearance with heavy machinery – but not apparent in our sites.

Storms

- Storms etc. good for dead wood?
- Allt-ddu and Dol-y-garnedd wood – next to it, a site has been clear felled which made plots difficult to access but also left it vulnerable to wind blow.
- Quite a bit storm damage in NE and NW English sites.

Lessons Learnt/Next time. *Any ways we can improve the survey for next time around? Old species: Lookup list/update species list, especially bryos*

- Plot locations – next time there will be 3 locations to look for, but photos and GPS should help.
- Soils – better guidance for difficult soils. Unsure as to whether keeping horizons intact was essential. Often had to trowel into bag.
- Pass on surveyor notes to the next surveyors
- UKCEH Parking sign to put in cars
- Overall, well-organised and well-supported by UKCEH.

Favourite Woods *What was your favourite woodland and why?*

- Allt-ddu and Dol-y-garnedd wood
- General spring flora, Pike Gill
- Medmenham
- Coulin
- Craighall (also worst!)

Photos *What could we do with all the photos you collected?*

- Will be useful for next surveyors.

Contact

enquiries@ceh.ac.uk

@UK_CEH

ceh.ac.uk

Bangor

UK Centre for Ecology & Hydrology
Environment Centre Wales
Deiniol Road
Bangor
Gwynedd
LL57 2UW

+44 (0)1248 374500

Edinburgh

UK Centre for Ecology & Hydrology
Bush Estate
Penicuik
Midlothian
EH26 0QB

+44 (0)131 4454343

Lancaster

UK Centre for Ecology & Hydrology
Lancaster Environment Centre
Library Avenue
Bailrigg
Lancaster
LA1 4AP

+44 (0)1524 595800

Wallingford (Headquarters)

UK Centre for Ecology & Hydrology
Maclean Building
Benson Lane
Crowmarsh Gifford
Wallingford
Oxfordshire
OX10 8BB

+44 (0)1491 838800

UK Centre for
Ecology & Hydrology