

Irregular silviculture and stand structural effects on the plant community in an ancient semi-natural woodland

D.C. Alder^{a,b,*}, B. Edwards^a, A. Poore^c, J. Norrey^b, S.J. Marsden^b

^a Dorset Environmental Records Centre, Dorset History Centre, Bridport Road, Dorchester, Dorset DT1 1RP, UK

^b Department of Natural Sciences, Manchester Metropolitan University, Chester Street, Manchester M1 5GD, UK

^c The Estate Office, Rushmore Estate, Tollard Royal, Salisbury, Wiltshire SP5 5PT, UK

ARTICLE INFO

Keywords:

Woodland stand management
Coppice plant groups
Woodland structure
Canopy openness
Continuous cover silviculture
Ancient woodland indicator plants
Species richness
Understorey
Rubus fruticosus
Irregular High Forest

ABSTRACT

Plants associated with traditional forms of coppice management are affected by changes in, or cessation of, stand management which produce differences in structure, usually in the direction of high forest. The habitat structure, ground flora richness, and composition of an ancient woodland in southern England were compared across three distinct management treatments: traditional Coppice (the cyclical cutting of underwood on rotations), Limited Intervention (representing the effective cessation of management), and Irregular High Forest silviculture (a form of continuous cover forestry using single and small group selective tree harvesting). Coppice and Irregular silviculture showed a more complex woody stand structure whereas Limited Intervention was strongly correlated with closed-canopy, single-storied structures and no developing understorey. Increased bramble *Rubus fruticosus* cover was strongly associated with Irregular silviculture, bare ground mostly with the limited intervention closed-canopy stands. Distinct plant-habitat associations were identified across stand management types with the greatest differences between Limited Intervention and the two active interventions. Overall vascular plant species and Coppice group species were lowest in Limited Intervention stands. Using ancient woodland indicator and Coppice plant species and groups, we found a similar community pattern between Coppice and Irregular silviculture. More ancient woodland species were accommodated within the comparatively heterogenous woodland habitat associated with active silvicultural interventions of Coppice and Irregular High Forest management. The study indicates that the introduction of Irregular silviculture as practiced here can conserve most ancient woodland and Coppice plants associated with traditional coppicing, a practice which has declined significantly in the UK since the late 19th Century.

1. Introduction

The woodland ground flora contributes to biological diversity and plays an important role in the ecological functioning of temperate woodland via nutrient cycles, soil formation and resource provision for other species (Decocq et al., 2004, Ford & Newbould, 1977, Jaroszewicz et al., 2021). Specialist ancient forest and woodland plants e.g., ancient woodland vascular plants (Rose, 1999), are distinguished by their associations with light and dark phases relating to canopy openness, edaphic factors and adaptation to periods of shade and stress tolerance (Naaf & Wulf, 2010, Gilliam, 2007, Peterken, 1993). Generalist species are characterised by a wider ecological niche related to open and ruderal habitats often associated with external woodland edges and higher nutrient levels influenced by agriculture (Hermý, 2015). Abandonment of coppicing can reduce plant species diversity as succession leads to

closed canopy and conditions where only specialist shade-adapted woodland plants can persist (Campetella et al., 2011). This is a limiting factor favouring species with higher light demands which restrict their flowering phenology to the short vernal periods prior to canopy closure (Ottaviani et al., 2019).

In the United Kingdom, woodland specialists associated with ancient woodland are important as determining criteria for the ageing of a woodland and for its inclusion within the ancient woodland inventory (Spencer & Kirby, 1992, Goldberg, 2015) and are an important means of conservation evaluation (Rose, 1999, Goldberg et al., 2007, Kimberley et al., 2013). Supposedly, Coppice-adapted plants are relicts of species assemblages in ancient woodlands with a direct physical link to the past activities of people and provide both biological and archaeological value (Nordén, et al., 2014, Barnes & Williamson, 2015). However, it is not entirely clear how these species respond to changes in silviculture

* Corresponding author at: Dorset Environmental Records Centre, Dorset History Centre, Bridport Road, Dorchester, Dorset DT1 1RP, UK.

<https://doi.org/10.1016/j.foreco.2022.120622>

Received 4 May 2022; Received in revised form 18 October 2022; Accepted 31 October 2022

Available online 9 November 2022

0378-1127/© 2022 The Author(s). Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

practice (von Oheimb & Härdtle, 2009) or the lack of it (Peterken & Mountford, 2017).

Over many centuries, simple Coppice, stands comprising only a coppiced layer and Coppice with standards, a predominant coppiced layer (the ‘underwood’) with a low-density upper layer of un-coppiced trees were the predominant practices in ancient woodlands across much of western and Mediterranean Europe (Rackham, 2003). Plants, which became to be regarded as ‘Coppice-adapted’, particularly vernal spring flowering species, were likely responding to the oscillations of light through opening of the canopy every 10–30 years (Hermy & Verheyen, 2007, Buckley, 2020). Forest-edge specialists, or ruderal species (opportunistic plants with a broad tolerance of conditions), responding to pulses of light through new openings and disturbances, can also tell us much about the species potentially ‘in waiting’ contained within the seed bank of woodland soils from historical legacies (Grime et al., 1988, Verheyen et al., 2003, Hermy, 2015). Traditional coppicing, in which the production of underwood is the primary aim, became less economically attractive in the UK during the 19th century, had declined significantly by the 1980’s (Buckley & Mills, 2015a). This decline has been associated with conversion of simple Coppice and Coppice-with-standard stands to high forest by planting and through neglect (Peterken & Mountford, 2017). The rising dominance of sawtimber, and firewood, and the demise of underwood markets, within the woodland economy and the substantial rise in the impact of deer browsing since the 2nd World War led to significant changes in woodland structure (Mason, 2007, Hopkins & Kirby, 2007).

Across Europe, Coppice management is still practiced on a significant scale reflecting a long history and importance associated with the use of underwood (see, e.g., Buckley, 2020). Coppice was likely to have been dynamic in varying rotation lengths, in response to societal demands as resource needs changed (Szabó, 2010). Coppice management has been shown to maintain favourable conditions for vascular plant species diversity including in woodlands where it has been reintroduced following abandonment suggesting a legacy effect that may be important for their conservation (Ewald et al., 2018). Structural characteristics of Coppice woodland succession can exert strong effects on vascular plant richness and diversity and are essential to our understanding of sustainable silvicultural management (Bartha et al., 2008, Bricca et al., 2020). In France, Coppice stands comprise canopy-forming species (e.g., lime *Tilia cordata*, hornbeam *Carpinus betulus*, ash *Fraxinus excelsior*, birch *Betula pendula/pubescens*) with an overstorey dominated by oak *Quercus spp.* The stemmed coppice layer (taillis) is cut on long rotations (30 years plus) and is combined with the removal of a proportion of the overstorey (Rochel, 2015). The conversion of Coppice to Irregular High Forest management, the keystone silvicultural system associated with the somewhat wider term Continuous Cover Forestry (CCF), has been a developing trend in France over the last 25 years and has provided a model for the silviculture practiced on the study site (Susse et al., 2011). This involves more frequent interventions than under the Coppice regime, and the use of permanent timber harvesting extraction racks (trackways) is important to avoid increased disturbance to the ground layer particularly on heavier soils (Sanchez, 2017). Studies in Europe identified that an increasing intensity of disturbances through mechanised forest operations can lead to more ruderal species and reduced numbers of forest specialist plants which may be at a competitive disadvantage (von Oheimb & Härdtle, 2009). Spatial heterogeneity associated with a mix of actively managed Coppice and abandoned stands has been found to be important in maintaining species richness of woodland specialist plants although this depends on locality and scale (Campetella et al., 2016, Tardella et al., 2019). Understanding the influence of management on woodland specialist plants is crucial because of the functional value they provide in respect of nutrient and decomposition cycles (Chelli et al., 2022).

In UK stands previously managed on shorter underwood rotations, longer periods of shade may negatively impact several woodland specialists, yet increased periods of openness may increase the numbers of

more light demanding and competitive plants (Kirby, 2015). Therefore, species richness as a metric may mask the impacts of silviculture to woodland specialist plants (Boch et al., 2013). Irregular silviculture, a form of continuous cover forestry (hereafter CCF), (Puettmann et al., 2015), which aims at permanently irregular structures and uses selective harvesting of single, or small groups of trees leads to a mixed size structure and species composition, and through stand manipulation and gap creation utilises natural regeneration of successive cohorts (Sanchez, 2017, Susse et al., 2011). Studies in beech *Fagus sylvatica*-dominated European forests showed how Irregular High Forest may reduce homogenisation of the ground flora and retain forest specialists (von Oheimb & Härdtle, 2009).

The benefits of changing to Irregular High Forest Management for biodiversity, including ancient woodland plants adapted to traditional Coppice management or indeed unmanaged woodland, mostly remain unclear (Coll et al., 2018, Bürgi, 2015). Very little is known about silvicultural changes in ancient broadleaved woodland and the resulting environmental gradients that influence the plant community (Hermy & Verheyen, 2007, Buckley, 2020, Bergès & Dupouey, 2021). There is considerable interest in the promotion of natural processes in building resilience in the face of climate change, including the adoption of CCF alongside Coppice (Forestry Commission, 2020, Department for Environment, Food & Rural Affairs, 2021). Silvicultural management systems including Irregular High Forest, are also likely to become important as an adaptive response to reducing disease transmission such as ash *Fraxinus excelsior* die-back *Hymenoscyphus fraxinaea* (Short & Shawe, 2018).

Using a range of plant groups (Rackham, 2003, Kimberley et al., 2013), we explored the responses of vascular plants in ancient woodland with a focus on ancient woodland indicator plants and coppice plant groupings to the introduction of this novel silviculture in a working ancient semi-natural broadleaved woodland (for a definition see Spencer & Kirby, 1992) in southern England together with a comparison between the actively managed stands and those assigned to a Limited Intervention treatment. Assuming the woodland flora across our study had a common origin and shared a similar land-use history, it also seems reasonable to believe that any variation in species and groups between the actively managed and limited intervention stands is potentially due to management decisions over the last thirty years (Depauw et al., 2020). We 1) compare variation across Irregular High Forest, traditional Coppice and Limited Intervention stands using structural measures and assessed plant species composition, richness, and relative abundances. We then asked 2) whether there are species similarities between stand management types and 3) can we identify indicator species for each which help explain stand structural characteristics and inform silvicultural management?

2. Methods

2.1. Study area

The study area sits within 442 ha of semi-natural broadleaf woodland, across two contiguous blocks on the Rushmore Estate, in the Cranborne Chase, southern England (110–190 m a.s.l; 395724.26 E, 117963.15 N; Fig. 1). The principal National Vegetation Classification (NVC) (Rodwell et al., 1998), and European Nature Information System EUNIS categories of woodland that could be assigned to codes (Latham et al., 2018) relate to broadleaf stands on base-rich and mesotrophic soils (Rodwell et al., 1998), and were: W8 *Fraxinus excelsior* – *Acer campestre* – *Quercus robur* – *Corylus avellana* – *Mercurialis perennis* – *Eurhynchium praelongum* – *Rubus fruticosus* – *Hyacinthoides non-scripta* (EUNIS G1.A22 *Fraxinus* – *Sorbus aucuparia* – *Mercurialis perennis* forests) associated with base-rich soils within which W10 *Quercus robur* – *Betula pendula* – *Corylus avellana* – *Rubus fruticosus* – *Pteridium aquilinum* – *Lonicera periclymenum* – *Hyacinthoides non-scripta* (G1.A11 Mixed Atlantic *Quercus* forests with *Hyacinthoides non-scripta*) that fall within

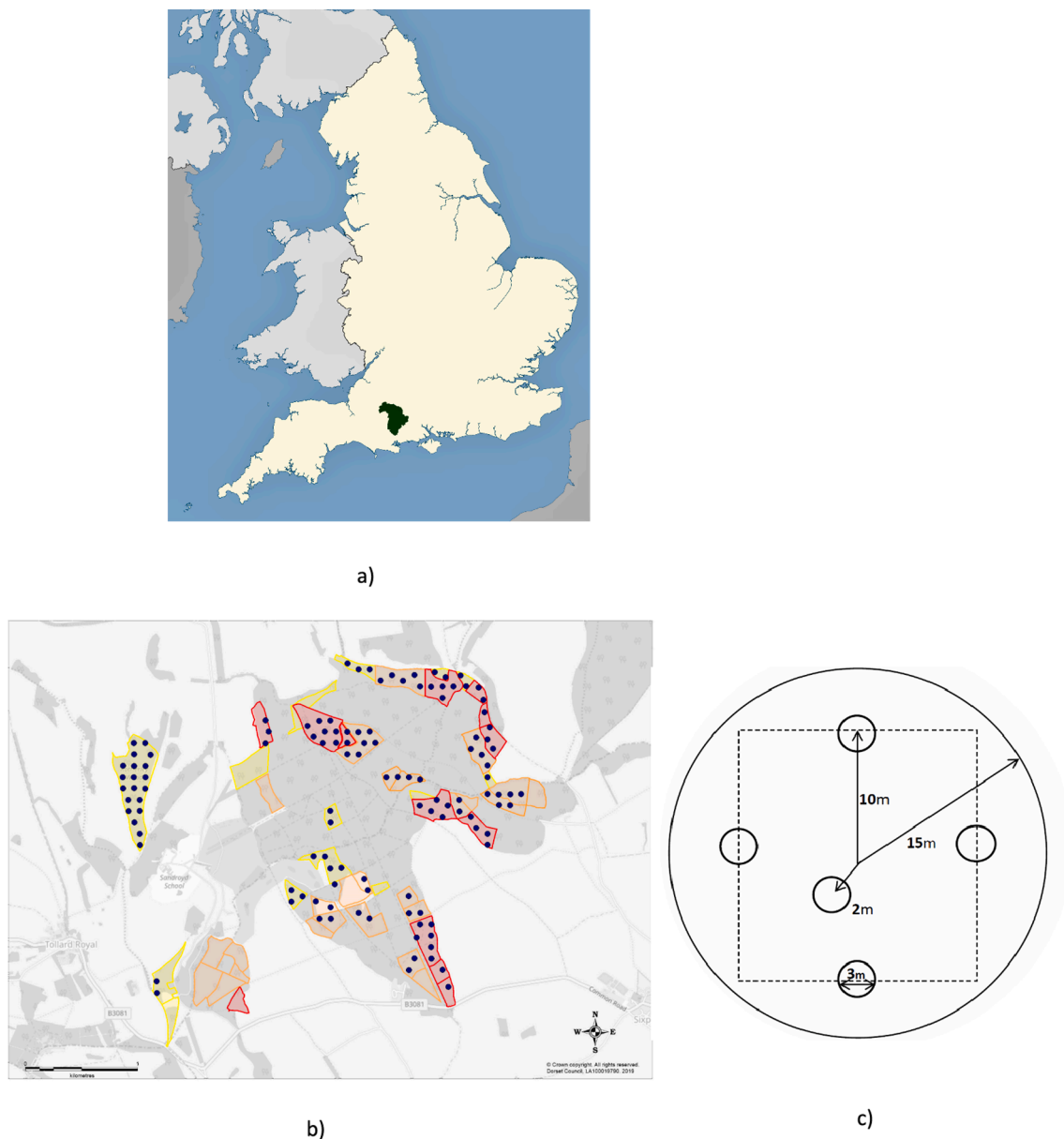


Fig. 1. Location of study: a) study location in southern England, UK; b) sampling points across study area for the collection of vegetation, structural and plant community measures within locations of. Woodland stand types indicated by colour; Yellow – Limited intervention, Orange – Coppice, Red – Irregular High-Forest; c) example of plot layout for measuring habitat structures and from where plant species and community features were recorded in a 20×20 m quadrat and 3 m diameter circular sub-plots. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the broad category of lowland mixed deciduous woodland (Rodwell et al., 1998). The dominant tree and shrub species are ash *Fraxinus excelsior*, pedunculate oak *Quercus robur*, field maple *Acer campestre*, silver birch *Betula pendula*, downy birch *Betula pubescens*, hazel *Corylus avellana*, spindle *Euonymus europaeus*, hawthorn *Crataegus monogyna*, sallow *Salix cinerea*, goat willow *Salix caprea*, dogwood *Cornus sanguinea* and blackthorn *Prunus spinosa*. There is scattered mature and veteran whitebeam *Sorbus aria*, and more locally distributed beech *Fagus sylvatica* and sycamore *Acer pseudoplatanus*.

2.2. Silvicultural management

The 442 ha of semi-natural woodland on the Rushmore Estate woodlands were historically managed under a coppice and coppice with standards system for many centuries (Poore, 2016). Originally mixed underwood of ash, hazel, birch, maple and whitebeam was cut on lengthening rotations during the early Modern Period, but during the

18th & 19th centuries underwood species composition was altered to increase the proportion of hazel and the area became a centre of the hazel underwood trades. The area under coppice management declined after the 1st World War and was accompanied by a long-term natural process of high-forest development, largely through the development of pole-stage ash within the coppice stands. Systematic coppice management had largely ceased in the 1980's but given the designation of site as a Site of Special Scientific Interest, a major project was undertaken from 1990 to restore areas of coppice, create a wide ride network, and allocate areas to a limited intervention treatment. Because of the precarious economic basis of coppice management efforts were also made to develop a diverse high forest management approach which could supplement coppice management in maintaining and enhancing biodiversity on the site (Poore, 2016).

We evaluated three broadleaved stand management types (Fig. 2). We define woodland management as harvesting of woody material and the stand as the silvicultural unit at which forest management was

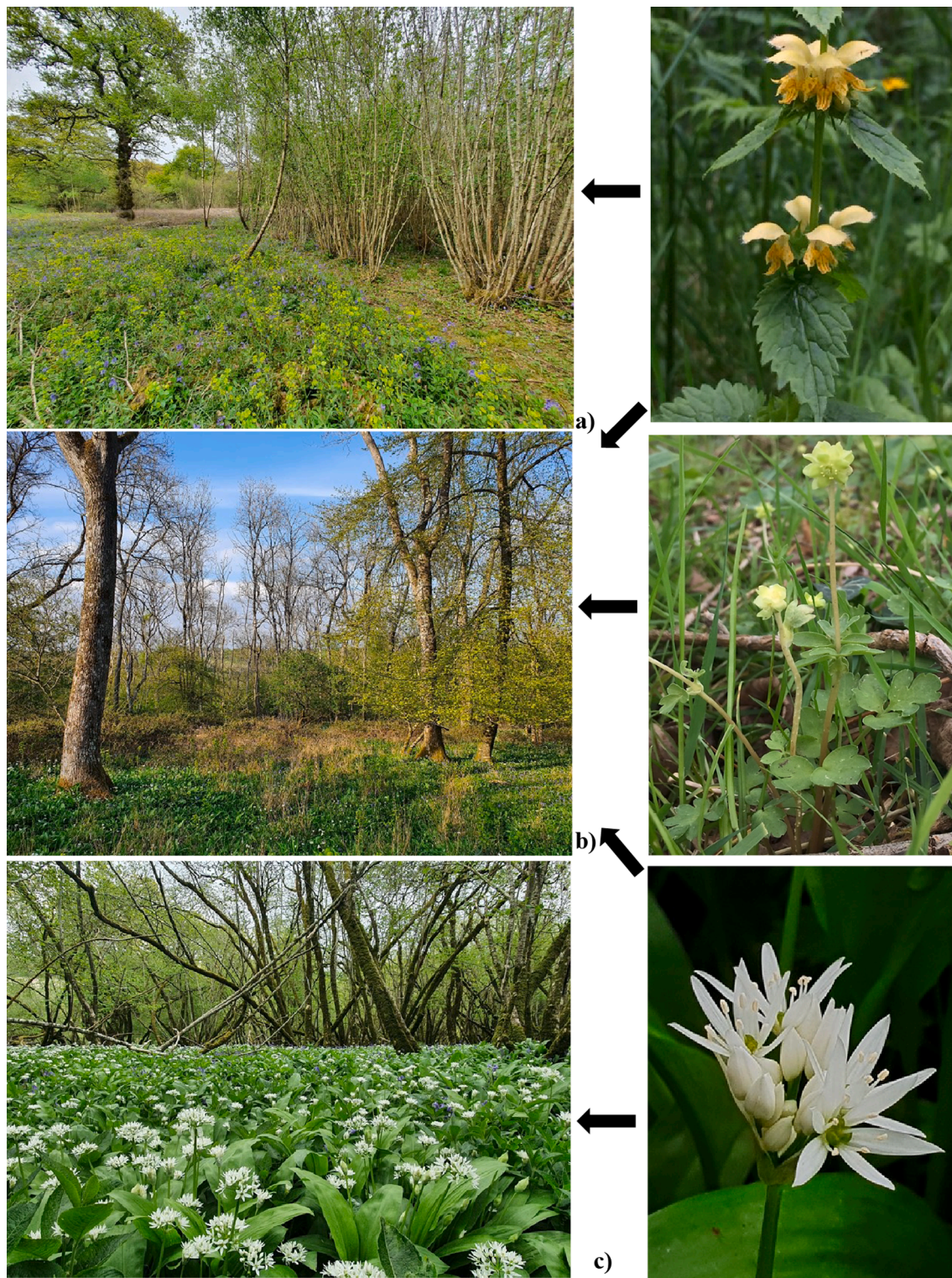


Fig. 2. Stand management types and examples of AWI plants associated with each (see [Table 3](#) in results, arrows depict strongest association with a stand type in the examples), a) coppice with *Lamiastrum galeobdolon* in a diverse ground layer, mix of recently felled coppice and 7-year-old stems b) Irregular High Forest, varied tree sizes, canopy gaps with a patchily distributed understorey including bramble and variable ground layer composition including *Adoxa moschatellina* and c) limited intervention with *Allium ursinum* ground layer, dense shade no understorey. Rushmore, UK, April 2022.

undertaken.

Coppice stands (covering 59.0 ha of the project area) include both simple coppice and coppice with standards with up to 20 % cover of upper canopy trees. It should be noted, however, that effective underwood production requires a maximum cover of 10 % upper canopy trees

([Harmer & Howe, 2003](#)). Underwood cycle lengths vary with use: hazel dominated coppice cut every 8–15 years, birch coppice was managed on two rotations, with birch for horse jumps cut at 3–4 years and the remainder on > 25 year cycles for wood fuel. There was a broad representation of growth stages across our study site, with a mean age of

coppice during the study of 7.3 ± 3.9 (SD) years with 0–5 years ($n = 10$), 6–9 years ($n = 19$), and 12–15 years ($n = 11$). Basal areas were in a range of 2–24 m²/ha⁻¹. At each cutting, the entire panel (felling) between 0.5 and 1.5 ha of underwood is removed leading to even-aged regrowth (Harmer & Howe, 2003).

Irregular High-Forest stands (covering 52.9 ha) were transformed from unmanaged coppice stands from the mid-1980's. They had already undergone some transition to a high forest structure over the preceding 20 – 50 years. This transformation involves the selective removal of harvestable trees and of weaker growing specimens and cutting the residual hazel and birch dominated understorey to increase light levels reaching the woodland floor. The aim is, however, for a suitable proportion of the understorey to re-grow, both for silvicultural reasons (to control seed bed conditions) and in order to create a complex habitat structure where the shrub layer is integrated within the high forest structure. The aim is to increase incremental growth and vigour of the retained trees to increase their resilience, enhance their economic value, promote natural regeneration of trees and shrubs and establish a range of tree size-classes.

With regard to the overall growing stock size, 'moderate stocking' is aimed for with basal areas (>7.5 cm diameter at breast height) in the range of 17–24 m²/ha⁻¹. Lower stocked areas still in transition can have a range of 10–16 m²/ha⁻¹. Understorey is dense in places yet patchily distributed as influenced by previous management and the effects of deer browsing. Species diversity is encouraged and individual trees with particular biodiversity values are retained, including senescent and standing deadwood (Susse et al., 2011). Irregular silviculture as practiced in our study involves interventions every 8–15 years (Poore, 2016). An intervention involves cutting all, or more usually a proportion, of the understorey, prior to selective removal of canopy trees as part of timber harvesting (Susse et al., 2011).

Limited Intervention stands (covering 43.4 ha) are closed canopy stands, with a higher tree density and basal area in the range 18–40 m²/ha⁻¹, and more limited understorey due to a period of between 30 and 50 years without formal silvicultural intervention. Some closed-canopy have also been created by areas of abandoned overstood hazel that were last cut ≥ 50 years ago (Poore, 2016).

Such structures appear to be typical of ancient woodland which has become neglected with closed canopy and understorey which is sparse or has grown up to become part of the woodland canopy layers (Amar et al., 2010, Hopkins & Kirby, 2007).

2.3. Field sampling

Plots were selected with each location a minimum of 100 m apart, and to reduce the influence of proximate habitats, plots were located a minimum distance of 30 m from stand edges stratified equally across the 3 stand management types ($n = 120$). Measurements of habitat structural variables were collected within a 30 m diameter circle (0.07 ha) with five sub-plots of 3 m diameter within each (four located at the cardinal points at 10 m radii and one at 2 m off-centre along a random compass bearing (Fig. 1) (Bibby et al., 2000)). The plant community data were collected within a 20 × 20 m quadrat at each plot (Kent, 2012). Fieldwork was conducted between 1st May and 31st July.

Within each plot, the following habitat structural measurements were recorded:

- Percentage of canopy openness was measured at each circular sub-plot with a spherical convex mirror densiometer (Lemmon, 1956) taken at 1.5 m above ground to gauge light levels.
- To calculate understorey density using the proportion of the shrub layer cover at 0.5 m and 2 m height bands, a percentage score of obscurations to the nearest 5 % was visually estimated. At each cardinal point of the plot at the sub-plot centres understorey density was visually assessed against a 50 × 30 cm chequer board with 10 × 10 cm squares (Alder et al., 2018).

- Percentage cover of bramble was visually estimated overall within the plot because it can exert an important influence over the vascular plant community (Harmer et al., 2017), and % area of bare ground without plant growth or deep litter was visually estimated.
- Vascular plant richness and % cover (as an estimate of abundance of each plant species) at each plot within the quadrat scored using the Domin scale, subsequently converted to mid-point % categorical variables adapted from Kirby et al. (2022) (Supplementary Table S.1).

Vascular Plant groups (supplementary Table S.2 with all species recorded and their groupings).

We used all vascular plant species identified to compare species richness between the three stand management types described above.

Species were differentiated by groups. For ancient woodland in the UK, Rackham (2003) developed an approach based on Coppice-associated plants which represent phytocoenological groups (Borhidi 1995), described as follows:

- Spring plants; species which flower early in the year and being vernal species have set seed by mid-summer.
- Summer plants; shade resistant summer flowering which actively grow during canopy leaf-cover.
- Buried seed plants; species which prolifically germinate following canopy opening with a persistent seed bank capable of withstanding decades of shade lying dormant until conditions become favourable with an increase in light.
- Mobile plants; windblown species that move around woodland, typically are short-lived biennials and are more abundant in open conditions though some may persist as perennial.
- Non-responsive plants; which are shade tolerant species and do not respond to canopy openings or may decline.

Finally, species have been checked against the list of Ancient Woodland Indicators – (hereafter AWI).

Ancient Woodland Vascular Plants are species with a direct association with woodland identified as being of ancient origin and are therefore a specialist group indicative of continuity (Rose, 1999, Peterken, 2000). Furthermore, with traits of dispersal limitation and sensitivity to intensive disturbance regimes their distinctiveness makes Ancient Woodland Vascular Plants important as a group on which to base conservation evaluation in UK woodland (Kimberley et al., 2013).

2.4. Data analysis

Differences in the percentages of individual habitat structural measures, and species richness for each plant group, across stand management types were tested using generalised linear mixed models (GLMMs), with Arcsine data transformation and Poisson distribution respectively (Bates et al., 2015). Plot nestedness (pseudoreplication) was accounted for by including stand unit number as a random effect in the models (Alder et al., 2021). Principal components analysis (PCA) was performed on the habitat structural variables to identify the main gradients and relative contribution of each variable to these (Alder et al., 2018).

A non-metric multidimensional scaling (NMDS) ordination (using the package 'vegan' (Oksanen et al., 2020)) was used to explore Ancient Woodland Indicator plant composition and percentage cover across stand types. NMDS ranked the species in order and used the Bray-Curtis coefficient (Kent, 2012) between samples to create a dissimilarity matrix of plant communities for the stand types. An analysis of similarity (ANOSIM) was performed on the resulting ranked data using a non-parametric multiple permutation test (999 runs) for testing differences in the plant communities (McCune et al., 2002).

We used indicator species analysis (ISA) which combines abundances and frequencies of the plant occurrences to group those AWI species most strongly associated with particular stand management types

(Dufrene, & Legendre, 1997). Indicator species values were calculated across a range between 0 (no indication) or 100 (exact indication). Indicator values were also calculated for combinations of stand types using an extension of the indicator species analysis method (De Cáceres et al., 2010). Values were tested using a permutation test run 999 times. ISA was performed using the package ‘indicspecies’ version 1.7.8 (De Cáceres, 2010). All data analysis was run using R version 4.1.0 (R Core Team, 2021) with figures produced using ggplot2 (Wickham et al., 2016). Significance was set at $P < 0.05$.

3. Results

3.1. Habitat structural measures across stand management types

Understorey densities in Irregular stands were intermediate between Limited Intervention and Coppice stands (See supplementary Table S.3). In the Coppice understorey densities at the 2 m height layer were significantly greater than in both other stand types. Bramble density was highest in Irregular over both other stand types, although the densities were as wide ranging in Coppice as Irregular. Canopy openness was greater in Irregular over Limited stands, while the latter was strongly associated with bare ground compared with the intervention stands. The first two PCA axes accounted for 67.1 % of original variation, Table 1. Axis 1 was associated with increasing bare ground and sparser understorey, especially at 0.5 m height, which was itself closely related to bramble *Rubus fruticosus* cover. For Axis 2, increasing canopy openness correlated with Irregular High Forest while understorey density at 2 m height associated with coppice and represented a closed understorey canopy, Fig. 3 a.

3.2. Vascular plant and group richness

A total of 91 vascular plant species were identified from seven plant groups including from all five of Rackham’s Coppice plant groups (Rackham, 2003), ancient woodland indicators (AWI), and ‘other’ species which included several AWI that were not categorised as Coppice plant species (see supplementary Table S.2). While there were differences in species richness between different stand types, this varied depending on the plant group (Table 2). Four of the seven plant groups: All vascular plants; AWI’s; Spring plants; and Buried seed plants, were similar between the two active intervention stands while significantly lower in Limited Intervention plots. There were no significant differences between species richness across stand types for Summer and Non-responsive plant groups. Irregular stand type had significantly more Mobile plant species than Limited while Coppice was not significantly different from either.

3.3. Ancient woodland indicator species

The AWI plant community varied significantly between stands (ANOSIM statistic R: 0.13, $P < 0.001$) while NMDS for ancient woodland indicator species cover, had a stress value of 0.19 indicating a good fit of the data (McCune et al., 2002). Ordination ellipses (95 % confidence) revealed distinct spatial patterns with most AWI species cover associated with Coppice followed by Irregular. Limited intervention plots had more

Table 1

Factor loadings/correlations for habitat structural variables on the first two Principal Components axes with percentage variation given in parenthesis.

Habitat Variable	Axis 1 (45.4 %)	Axis 2 (21.7 %)
Bare ground	0.43	-0.14
Bramble	-0.47	0.17
Canopy openness	-0.30	0.69
Understorey density 0.5mht	-0.58	-0.12
Understorey density 2mht	-0.41	-0.68

variation in their AWI plant communities, and generally AWI plant cover correlated strongly with open canopy, yet also included plots with dense understorey and bramble cover (Fig. 3b). As with the PCA, both NMDS Axis 1 and 2 reflect a gradient from closed to open canopy; Axis 1 is positively associated with increasing understorey complexity and open canopy from bare ground while Axis 2 follows a transition from open, bare ground with a lack of understorey complexity to some bramble cover.

The frequency of occurrences across all 25 AWI species at plots ordered along the two main habitat structural (PCA) gradients are shown in Fig. 4. Axis 1 shows that most common species separate evenly between the active interventions and limited, while for both axis 1 and axis 2 less common species are more frequent in the active interventions. (See supplementary Table S.4 for correlations between AWI species and PCA factor scores for axis 1 and 2).

3.4. Stand type indicator species

Indicator species analysis (ISA) identified 22 species with a significant association with a particular stand type or stand type pair (Table 3). These included nine of the twenty-five AWI species from four Coppice plant groups. The Spring vernal species were all included in both coppice and Irregular and reinforce the results from the pairwise group tests which show richness in limited intervention decreases. Most differences between Coppice and Irregular were for either Buried seed plants or Summer perennials, while Limited Intervention had only one Non-responsive species which it shared with Irregular.

4. Discussion

4.1. Structural effects of silvicultural management

A primary aim of Irregular silviculture is the adoption of ecologically sustainable methods (Susse et al., 2011, Sanchez, 2017). An important objective of sustainable forest management is for forest managers to consider the potential impacts, following restructuring of woodlands, upon a range of taxonomic groups especially in ancient woodlands (Bricca et al., 2020, Larrieu et al., 2019, Brown et al., 2015). Irregular silviculture in temperate broadleaf woodland does appear to positively benefit other groups such as birds (Alder et al., 2018), and bats (Alder et al., 2021). Generally, we found Irregular silviculture has created dynamic woodland structures across a continuum not unlike a Coppice woodland with a broad range of age classes in varying stages of growth (Alder et al., 2018), although we recognise it may not be directly analogous (Bürgi, 2015). Irregular silviculture in our study retained several characteristics of early successional understorey associated with traditional coppicing (Sanchez, 2017) with a significantly more open canopy than Limited Intervention. In mixed hazel and birch coppices such as those within our study the ground flora is adapted to the rapid turnover of light to shade, and woodland species with varied requirements can persist side by side according to the stage of the coppice cycle (Buckley & Mills, 2015b, Kirby et al., 2017). Notably, we did not detect a significant difference in openness between Coppice and Limited stands which reflects the way we measured canopy openness in Coppice below understorey closure at 2 m height. The proportion of Coppice at <3 years age in our study was 10 % and so the majority was actively growing with closed canopy at around the fourth or fifth year since cutting (Mitchell, 1992). The creation of larger canopy gaps which remain open for many years can be detrimental to coppice adapted plants as the community can shift to grassland (Barkham, 1992) or develop a ruderal community (Klug et al., 2019). Although not tested, our study area had localised patches of woodland with high grass cover which may have been due to increased canopy opening followed by incursion by deer *Cervidae* (Kirby et al., 2022, Joys et al., 2004).

Within-stand gap creation in the Irregular High-forest stands is patchier than even-aged high-forest and regeneration of woody species

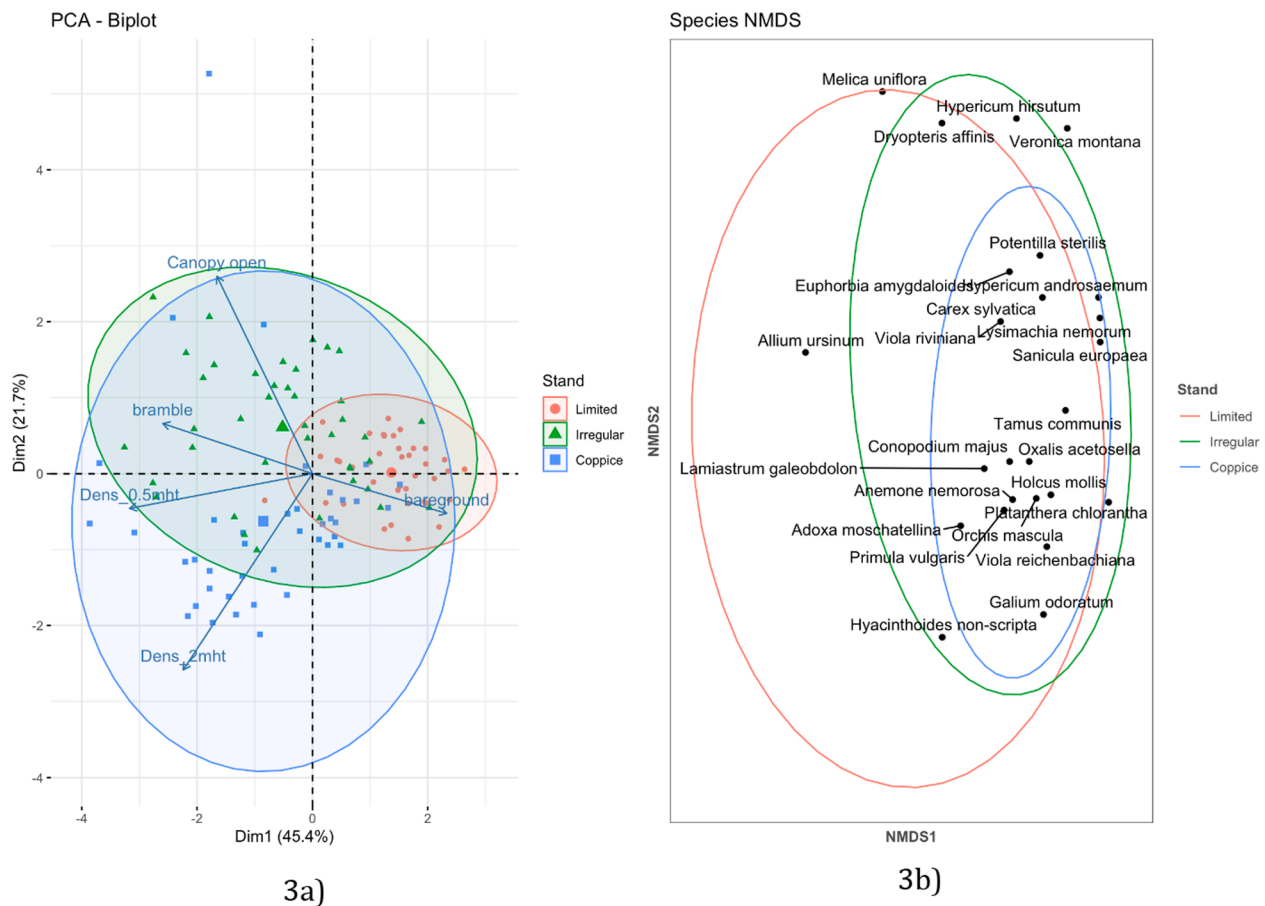


Fig. 3. Ordinations from Principal Components Analysis factors 3a) of the main habitat structural variables associated with the three stand management types, Non-metric Multidimensional Scaling biplot showing NMDS 1 and 2 positions 3b) for Ancient Woodland Indicator plant species % cover with 95% confidence ellipses for habitat / species separation across stand types.

Table 2

Results of GLMM and pairwise comparisons of species richness for seven plant groups across the stand management types; medians are given with range shown in parenthesis. Those pairs of stand types which differ significantly are shown between columns, the values across rows indicate whether the difference is positive or negative; L – Limited, I – Irregular, C – Coppice with those in bold denoting significant difference from pairwise test $P < 0.05$.

Woodland Plant Group	Limited	Irregular	Coppice	P
All vascular plants	8 (3 – 25) IC	18 (10 – 31)	16 (9 – 32)	<
Ancient Woodland Indicators	2.5 (0 – 14) C	7.5 (1 – 13) L	8 (2 – 12) L	0.016
Spring plants	1.5 (0 – 6) C	3.5 (0 – 6)	4 (0 – 6) L	0.033
Summer plants	1.5 (0 – 9)	3 (1 – 6)	4 (0 – 7)	0.116
Buried seed plants	2 (0 – 8) IC	6 (2 – 14) L	5.5 (1 – 14) L	<
Mobile plants	0 (0 – 2) I	1 (0 – 5) L	1 (0 – 4)	0.006
Non-responsive plants	3 (1 – 5)	3 (1 – 6)	2 (0 – 5)	0.458

becomes more varied with a wider range of age-classes (Alder et al., 2021). This is unlike clear-cutting or more intensive even-aged high-forest management which can result in an increase in transient and non-woodland plants (Tinya et al., 2019). Irregular High Forest management, as we have shown, produces both early successional and old growth characteristics important for maintaining biodiversity in temperate European woodlands, features which are often under-represented (Hilmers et al., 2018). Despite the presence of deer, which are managed through a culling regime designed to significantly reduce

their impact, our study showed how bramble *Rubus fruticosus* flourished within Irregular stands following canopy opening. This may indicate an effect of increased ground disturbance combined with reduced density and competition from the rapid understorey regrowth typically associated with the coppice cycle. Decocq et al. (2005) and Harmer et al. (2017) found that bramble decreased overall plant species richness in selectively cut forests, which was not the case in our Irregular stands. Van Calster et al. (2008) found a similar increase in bramble cover during canopy opening, yet increases in species richness in the herb layer correlated with uneven-aged high forest compared with even-aged and was related to edaphic factors influenced by silviculture. The impact of bramble can be varied according to land-use history (Hédél et al., 2021), local site conditions, the degree of canopy opening and the development of a competing woody understorey (Harmer et al., 2017). We found bramble was generally absent in Limited Intervention stands and suppressed in closed canopy coppice. However, despite highest cover values, bramble presence did not appear to have a negative effect for any plant group in Irregular stands. Bramble in these stands is selectively controlled where higher densities are deemed likely to suppress tree regeneration although this is infrequent and targeted. The rapid development of a woody understorey in gaps is generally desirable in Irregular stands as it negates such intervention and increasing understorey density within the 2-metre height band (analogous to Coppice at 3–5 years) may help in this respect.

Limited Intervention stands in our study appear to be typical of ancient woodland in lowland Britain which has become neglected and homogenously structured with closed canopy and a sparse understorey, or abandoned coppice that has grown up to become part of the woodland canopy (Amar et al., 2010, Hopkins & Kirby 2007). Species diversity in

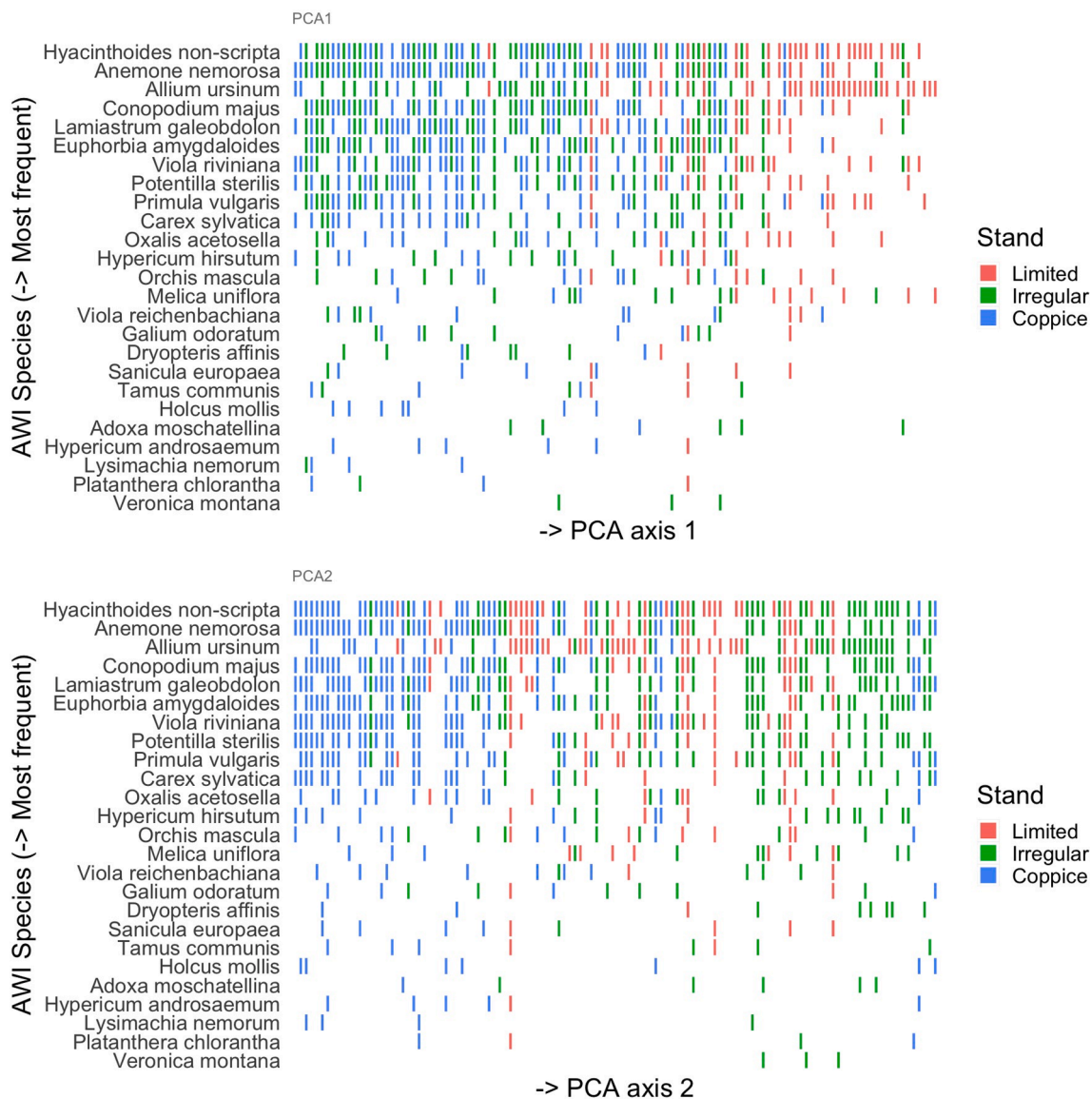


Fig. 4. Occurrence of ancient woodland plant species at each plot ($n = 120$; coloured by stand type) ordered along ordination axes 1 and 2 of the PCA.

UK ancient woodlands is associated with structural heterogeneity (Peterken & Game 1984, Peterken & Mountford 2017) and our results suggest that Irregular High Forest management may offer a feasible alternative to coppicing where it is no longer practiced. The proximity of small canopy gaps created (every 7–10 years) within and between Irregular stands may retain habitat conditions suitable for ancient woodland indicator species (Klug et al., 2019). Chelli et al. (2021) suggest canopy heterogeneity developed by larger trees with a complex vertical distribution (as found in Irregular High Forest) may modulate the light heterogeneity in abandoned coppice and drive functional diversity.

4.2. Vascular plant groups and species responses

Most woodland plant groups in our study were tolerant of Irregular silviculture management, with the main differences in the plant communities being between managed and unmanaged stands. In central Europe the conversion to High Forest from traditional Coppice has been associated with losses of forest plant species of high conservation value (Müllerová et al., 2015). While our study found Summer perennials and Non-responsive groups were not significantly different across the three

stand types, overall vascular plant richness was highest in Irregular High Forest followed by coppice. However, plant species richness *per se* does not necessarily provide a measure of the conservation value of a woodland, because it also includes both generalist and common non-woodland species (Kirby et al., 2022, Hupperts et al., 2020, Boch et al., 2013, Bartha et al., 2008, von Oheimb & Härdtle 2009).

Decoq et al. (2005) found more ruderal and generalist plant species in a selective high-forest system that originated from a coppice with standards silviculture. Such effects may be related to the actual treatment on a site sensitive to soil compaction, in particular the lack of defined, permanent timber extraction racks leading to a wider area of the woodland subject to disturbance (Harmer et al., 2010). Moreover, even where ruderal/generalist plants occur they are likely to diminish as the stand structure develops (Bartha et al., 2008). While we did not detect a significant difference between Coppice and Irregular, Buried seed plant richness was significantly higher in the Irregular than Limited Intervention stands, which included widespread species which are more typical of disturbed soils. ISA identified 9 Buried seed species in Irregular with only 5 (of the same) species in Coppice (including bramble) while Limited Intervention had none. None of 4 Buried seed species ISA identified uniquely in Irregular are AWI. Following Hill et al. (2000) and

Table 3

Results of Indicator Species Analysis across stand types; Coppice plant groups are shown in superscript, Nr – Non-responsive, Bu – Buried seed, Sp – Spring, Su – Summer perennial, Mo - Mobile.

Ancient Woodland Species		Limited	Irregular	Coppice	Test	P
<i>Adoxa moschatellina</i> ^{Nr}	Moschatel		✓		0.34	0.02
<i>Allium ursinum</i> ^{Nr}	Ramsons	✓	✓		0.76	<0.001
<i>Carex sylvatica</i> ^{Bu}	Wood sedge		✓	✓	0.59	0.002
<i>Conopodium majus</i> ^{Sp}	Pignut		✓	✓	0.82	<0.001
<i>Euphorbia amygdaloides</i> ^{Bu}	Wood Spurge		✓	✓	0.76	<0.001
<i>Holcus mollis</i> ^{Su}	Creeping Soft-grass			✓	0.42	<0.001
<i>Hypericum androsaemum</i> ^{Su}	Tutsan			✓	0.35	0.05
<i>Lamium galeobdolon</i> ^{Sp}	Yellow Archangel		✓	✓	0.8	<0.001
<i>Primula vulgaris</i> ^{Sp}	Primrose		✓	✓	0.66	0.004
Other Vascular Plants						
<i>Arctium</i> spp ^{Mo}	Lesser/Greater Burdock		✓	✓	0.37	0.045
<i>Ajuga reptans</i> ^{Bu}	Bugle		✓	✓	0.42	0.02
<i>Circaea lutetiana</i> ^{Mo}	Enchanter's Nightshade		✓		0.37	0.011
<i>Cirsium arvense</i> ^{Mo}	Creeping Thistle		✓	✓	0.4	0.024
<i>Cirsium palustre</i> ^{Mo}	Marsh Thistle			✓	0.5	0.001
<i>Clematis vitalba</i>	Traveller's Joy			✓	0.38	0.047
<i>Dactylis glomerata</i> ^{Bu}	Cock's Foot grass	✓			0.39	0.006
<i>Deschampsia caespitosa</i> ^{Su}	Tufted Hair-grass	✓		✓	0.75	0.001
<i>Eupatorium cannabinum</i> ^{Su}	Hemp Agrimony			✓	0.45	0.005
<i>Ficaria verna</i> ^{Bu}	Lesser Celendine		✓		0.44	0.023
<i>Galium aparine</i> ^{Bu}	Cleavers		✓		0.6	0.001
<i>Geranium robertianum</i> ^{Bu}	Herb Robert		✓		0.45	0.001
<i>Rubus fruticosus</i> agg. ^{Bu}	Blackberry		✓	✓	0.96	0.001
<i>Rumex sanguineus</i> ^{Bu}	Wood Dock		✓	✓	0.39	0.022

Hill et al. (2004) we identified these species as generalists found in a broad range of temperate habitats in light (L) levels with an Ellenberg L value of 6, comparatively higher than other species of this group such as Bugle *Ajuga reptans* and the AWI species, Wood spurge *Euphorbia amygdaloides* with Ellenberg L values of 5 and 4 respectively. Of these Buried seed species cleavers *Galium aparine* is a species with an Ellenberg N (Nitrogen) value of 8 for nutrient rich soils. It is likely to have responded to soil disturbance following harvesting which may explain why Cock's-foot grass *Dactylis glomerata* was similarly commonest in Irregular stands (von Oheimb & Härdtle 2009). We did not test for soil compaction in our study, although species such as cleavers are known to be intolerant of compact soils (Godefroid & Koedam 2004).

Ancient woodland plants are susceptible to nutrient enrichment, especially nitrogen, which may arise through atmospheric deposition or localised agricultural drift (Kirby 2020). There have been concerns over the impact of canopy opening after many decades of neglect which releases the so-called 'nutrient time-bomb', yet this remains uncertain (Verheyen et al., 2012). While there were significantly more mobile species in Irregular stands than Limited Intervention, Coppice had a similarly high number. Buried seed species such as perennial nettle *Urtica dioica* were found as much in Limited Intervention stands as in Irregular and may be a response to localised enrichment especially of phosphates, (Capstick et al., 2019) from pheasant *Phasianus colchicus* rearing rather than silviculture (Sage et al. 2005).

4.3. Woodland management implications

We recognise that our study is limited to one site with its own historical ecology which poses difficulties in making general recommendations (Hédl, et al., 2021). Nevertheless, we did not detect many significant differences between the ancient woodland plant communities of Coppice and Irregular stands. Neither did we find strong evidence of negative effects, e.g., from competitive exclusion, as a result of increases in species such as bramble and cleavers. This may be because Irregular High Forest as practiced in our study has a relatively low rate of disturbance compared to clear-felling (Harmer et al., 2010). Brown et al. (2015) found that ancient woodland plants were able to withstand high levels of exotic tree removal during restoration of ancient woodlands, although there may be a reduction in those shade adapted species initially. Clearly the intensity and methods of silvicultural practice vary

which can greatly influence the resulting woodland plant community (Hermy 2015). For ancient woodlands however, Irregular silviculture as we have found appears to be benign and a preferable option to management neglect and the potential demise of specialist woodland plants as a result of closed canopy, shading and intense grazing by deer (Rackham 2008, Van Calster et al., 2008, Roleček et al., 2017).

Despite evidence of there being a time-lag between cause and effect of climate change in temperate forests (Bertrand et al., 2011) stand manipulation offers the prospect to evaluate responses of different taxonomic groups (Larrieu et al., 2019). At Rushmore coppice management is likely to continue as part of the mix of management types albeit greatly reduced compared to the early 19th century. This provides a unique opportunity for long-term comparison with Irregular High Forest management in an ancient woodland, see for example Kirby et al. (2022) and recommendations therein. The Rushmore Estate woodlands are particularly valuable in this respect with an important historical ecology and intimate mix of traditional and novel silvicultural management types for assessing how woodland plants respond (Bergès & Dupouey 2021). The interaction between canopy and woody understorey (and bramble) is likely to be important and warrants further research (Chelli et al., 2022, Landuyt et al., 2019, Dölle et al., 2017, Brown et al., 2015). Importantly, investigating how environmental conditions are moderated for Coppice adapted plants of ancient woodlands (Buckley 2020, Cervellini et al., 2017, Boch et al., 2013). This is important for ground flora because of the effects of increased temperatures (thermophilisation) following canopy opening in a changing climate (Zellweger et al., 2020, Schall & Heinrichs 2020, Landuyt et al., 2019). Moreover, Ash die-back *Hymenoscyphus fraxineus* will alter the canopy cover and the ground-layer composition, including natural regeneration of woody species (Mitchell et al., 2016, Broome et al., 2019).

The dynamics of woodland flora is complex and varies within a season as well as between sites and to fully understand changes in the patterns of woodland plants, long term studies in a range of stand management types is key (Keith et al., 2009, Hédl & Chudomelová 2020). To fully comprehend responses to the conditions produced by silvicultural management on woodland flora requires understanding of the management histories across a range of sites (Bricca et al., 2020, Barnes & Williamson 2015, Spencer 1990). Slow dispersing ancient woodland plants may be particularly vulnerable to changes in climate

and nutrient enrichment even though they may be buffered from its effects initially (Hermy 2015). Improving our knowledge of the impacts from raised temperatures (Govaert et al., 2020) is vital for ecosystem services where the ground flora plays an important role (Mitchell et al., 2014, Mitchell et al., 2016, Kirby et al., 2022).

Natural restructuring which creates a range of successional habitats and old growth can take centuries to establish in formerly managed woodland (von Oheimb et al., 2005, Peterken & Mountford, 2017). However, the choices for high-forest are varied and Irregular silviculture appears to offer a broad range of structures and habitat conditions (Alder et al., 2021). Using plant indicators based around AWI and Coppice-adapted groups (Rackham, 2003) we feel offers a robust mixture of species indicators to guide ancient woodland management (Ellis, 2015, Lelli et al., 2019, Swallow et al., 2020) (.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

We are grateful for the assistance given by the Rushmore Estate, Trustees, the managing agent Mr Phillip Gready, along with Ian Burt, Andy Taylor, Rob Taylor and Don Taylor for practical help. Rhiannon Rogers and Jon Corkill of Dorset Environmental Records Centre helped with fieldwork and GIS support respectively. We are especially indebted to our funders, The Golden Bottle Trust and the Henry C. Hoare Charitable Trust, and are grateful to Dr Annabel King for the recommendation. We acknowledge the generous support of Forestry Commission (England). Keith Kirby and two anonymous reviewers made many valuable comments which significantly improved the text.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2022.120622>.

References

- Alder, D.C., Fuller, R.J., Marsden, S.J., 2018. Implications of transformation to Irregular silviculture for woodland birds: A stand wise comparison in an English broadleaf woodland. *For. Ecol. Manage.* 422, 69–78.
- Alder, D.C., Poore, A., Norrey, J., Newson, S.E., Marsden, S.J., 2021. Irregular silviculture positively influences multiple bat species in a lowland temperate broadleaf woodland. *For. Ecol. Manage.* 483, 118786.
- Amar, A., Smith, K.W., Butler, S., Lindsell, J.A., Hewson, C.M., Fuller, R.J., Charman, E. C., 2010. Recent patterns of change in vegetation structure and tree composition of British broadleaved woodland: evidence from large-scale surveys. *Forestry* 83 (4), 345–356.
- Barkham, J.P., 1992. The effects of coppicing and neglect on the performance of the perennial ground flora. In: Buckley, P. (Ed.), *Ecology and Management of Coppice Woodlands*. Springer, Dordrecht, pp. 115–146.
- Barnes, G., Williamson, T., 2015. Rethinking ancient woodland: the archaeology and history of woods in Norfolk. University of Hertfordshire Press.
- Bartha, S., Merolli, A., Campetella, G., Canullo, R., 2008. Changes of vascular plant diversity along a chronosequence of beech coppice stands, central Apennines, Italy. *Plant Biosyst.-An Int. J. Dealing with all Aspects of Plant Biol.* 142 (3), 572–583.
- Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* 67 (1).
- Bergès, L., Dupouey, J.L., 2021. Historical ecology and ancient forests: Progress, conservation issues and scientific prospects, with some examples from the French case. *J. Veg. Sci.* 32 (1), e12846.
- Bertrand, R., Lenoir, J., Piedallu, C., Riofrio-Dillon, G., de Ruffray, P., Vidal, C., Pierrat, J.C., Gégout, J.C., 2011. Changes in plant community composition lag behind climate warming in lowland forests. *Nature* 479 (7374), 517–520.
- Bibby, C.J., Burgess, N.D., Hillis, D.M., Hill, D.A., Mustoe, S., 2000. Bird census techniques. Chapter 11 Description and Measurement of Bird Habitat 250–277. Elsevier.
- Boch, S., Prati, D., Müller, J., Socher, S., Baumbach, H., Buscot, F., Gockel, S., Hemp, A., Hesse, D., Kalko, E.K., Linsenmair, K.E., 2013. High plant species richness indicates management-related disturbances rather than the conservation status of forests. *Basic Appl. Ecol.* 14 (6), 496–505.
- Borhidi, A., 1995. Social behaviour types, the naturalness and relative ecological indicator values of the higher plants in the Hungarian flora. *Acta Botanica Hungarica* 39, 97–181.
- Bricca, A., Chelli, S., Canullo, R., Cutini, M., 2020. The legacy of the past logging: How forest structure affects different facets of understory plant diversity in abandoned coppice forests. *Diversity* 12 (3), 109.
- Broome, A., Ray, D., Mitchell, R., Harmer, R., 2019. Responding to ash dieback (*Hymenoscyphus fraxineus*) in the UK: woodland composition and replacement tree species. *Forestry: An Int. J. Forest Res.* 92 (1), 108–119.
- Brown, N.D., Curtis, T., Adams, E.C., 2015. Effects of clear-felling versus gradual removal of conifer trees on the survival of understory plants during the restoration of ancient woodlands. *For. Ecol. Manage.* 348, 15–22.
- Buckley, P., 2020. Coppice restoration and conservation: a European perspective. *J. Forest Res.* 25 (3), 125–133.
- Buckley, P., Mills, J., 2015a. Coppice silviculture: from the Mesolithic to the 21st century. In: K.J. Kirby, C. Watkins (Eds.), *Europe's changing woods and forests: from wildwood to managed landscapes*. CABI, (2015) Wallingford, UK, 77–92.
- Buckley, P., Mills, J., 2015b. The Flora and Fauna of Coppice Woods: Winners and Losers of Active Management or Neglect? In: K.J. Kirby, C. Watkins (Eds.), *Europe's changing woods and forests: from wildwood to managed landscapes*. CABI, (2015) Wallingford, UK 129–139.
- Bürgi, M., 2015. Close-to-nature forestry. In: K.J. Kirby, C. Watkins (Eds.), *Europe's changing woods and forests: from wildwood to managed landscapes*. CABI, (2015) Wallingford, 107–115.
- Campetella, G., Botta-Dukat, Z., Wellstein, C., Canullo, R., Gatto, S., Chelli, S., Mucina, L., Bartha, S., 2011. Patterns of plant trait–environment relationships along a forest succession chronosequence. *Agric. Ecosyst. Environ.* 145 (1), 38–48.
- Campetella, G., Canullo, R., Gimona, A., Garadnai, J., Chiarucci, A., Giorgini, D., Angelini, E., Cervellini, M., Chelli, S., Bartha, S., 2016. Scale-dependent effects of coppicing on the species pool of late successional beech forests in the central Apennines, Italy. *Appl. Vegetation Sci.* 19 (3), 474–485.
- Capstick, L.A., Sage, R.B., Hoodless, A., 2019. Ground flora recovery in disused pheasant pens is limited and affected by pheasant release density. *Biol. Conserv.* 231, 181–188.
- Cervellini, M., Fiorini, S., Cavicchi, A., Campetella, G., Simonetti, E., Chelli, S., Canullo, R., Gimona, A., 2017. Relationships between understory specialist species and local management practices in coppiced forests—Evidence from the Italian Apennines. *For. Ecol. Manage.* 385, 35–45.
- Chelli, S., Bricca, A., Cutini, M., Campetella, G., Cervellini, M., Tsakalos, J.L., Canullo, R., 2021. Large standard trees and deadwood promote functional divergence in the understory of beech coppice forests. *For. Ecol. Manage.* 494, 119324.
- Chelli, S., Ottaviani, G., Tsakalos, J.L., Campetella, G., Simonetti, E., Wellstein, C., Bartha, S., Cervellini, M., Canullo, R., 2022. Intra-and inter-specific leaf trait responses of understory species to changes in forest maturity. *For. Ecol. Manage.* 506, 119977.
- Coll, L., Ameztegui, A., Collet, C., Löf, M., Mason, B., Pach, M., Verheyen, K., Abrudan, I., Barbat, A., Barreiro, S., Bielak, K., 2018. Knowledge gaps about mixed forests: What do European forest managers want to know and what answers can science provide? *For. Ecol. Manage.* 407, 106–115.
- Department of Food, Environment & Rural Affairs. 2021. The England Trees Action Plan 2021–2024. May 2021. The UK Government. Online: <https://www.gov.uk/government/publications/england-trees-action-plan-2021-to-2024> Accessed 20/6/2022.
- De Cáceres, M., Legendre, P., Moretti, M., 2010. Improving indicator species analysis by combining groups of sites. *Oikos* 119 (10), 1674–1684.
- Decocq, G., Aubert, M., Dupont, F., Alard, D., Saguez, R., Wattez-Franger, A., DeFoucault, B., Delelis-Dusollier, A., Bardat, J., 2004. Plant diversity in a managed temperate deciduous forest: understory response to two silvicultural systems. *J. Appl. Ecol.* 41, 1065–1079.
- Decocq, G., Aubert, M., Dupont, F., Bardat, J., Wattez-Franger, A., Saguez, R., De Foucault, B., Alard, D., Delelis-Dusollier, A., 2005. Silviculture-driven vegetation change in a European temperate deciduous forest. *Ann. Forest Sci.* 62 (4), 313–323.
- Depauw, L., Perring, M.P., Landuyt, D., Maes, S.L., Blondeel, H., De Lombaerde, E., Brümelis, G., Brunet, J., Closset-Kopp, D., Czerepko, J., Decocq, G., 2020. Light availability and land-use history drive biodiversity and functional changes in forest herb layer communities. *J. Ecol.* 108 (4), 1411–1425.
- Dölle, M., Petritan, A.M., Biris, I.A., Petritan, I.C., 2017. Relations between tree canopy composition and understory vegetation in a European beech-sessile oak old growth forest in Western Romania. *Biologia* 72 (12), 1422–1430.
- Dufrène, M., Legendre, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecol. Monogr.* 67 (3), 345–366.
- Ellis, C.J., 2015. Ancient woodland indicators signal the climate change risk for dispersal-limited species. *Ecol. Ind.* 53, 106–114.
- Ewald, J., Hedl, R., Chudomelová, M., Petřík, P., Šipoš, J., Vild, O., 2018. High resilience of plant species composition to coppice restoration—a chronosequence from the oak woodland of Gerolfing (Bavaria). *Tuexenia* 38, 61–78.
- Forestry Commission, 2020. Managing England's woodlands in a climate emergency. A guide to help foresters and agents implement adaptation actions. Version 2. Forestry Commission. Online. Date accessed 15/9/2021.

- Ford, E.D., Newbould, P.J., 1977. The biomass and production of ground vegetation and its relation to tree cover through a deciduous woodland cycle. *J. Ecol.* 201–212.
- Gilliam, F.S., 2007. The ecological significance of the herbaceous layer in temperate forest ecosystems. *Bioscience* 57 (10), 845–858.
- Godefroid, S., Koedam, N., 2004. Interspecific variation in soil compaction sensitivity among forest floor species. *Biol. Conserv.* 119 (2), 207–217.
- Goldberg, E., Kirby, K., Hall, J., Latham, J., 2007. The ancient woodland concept as a practical conservation tool in Great Britain. *J. Nat. Conservation* 15 (2), 109–119.
- Goldberg, E., 2015. 22 The UK's Ancient Woodland Inventory and its Use. In: Kirby, K.J., Watkins, C., (Eds.), *Europe's Changing Woods and Forests: From Wildwood to Managed Landscapes*, CABI (2015) Wallingford UK, 326–336.
- Grime, J.P., Hodgson, J.G., Hunt, R., 1988. Comparative plant ecology: a functional approach to common British species. Unwin, Hyman, London.
- Harmer, R., Howe, J., 2003. The silviculture and management of Coppice woodlands. Forestry Commission.
- Harmer, R., Kerr, G., Thompson, R., 2010. Managing native broadleaved woodland. The Stationary Office Ltd (TSO).
- Harmer, R., Kerr, G., Stokes, V., Connolly, T., 2017. The influence of thinning intensity and bramble control on ground flora development in a mixed broadleaved woodland. *Forestry: Int. J. Forest Res.* 90 (2), 247–257.
- Hédl, R., Chudomelová, M., 2020. Understanding the dynamics of forest understorey: Combination of monitoring and legacy data reveals patterns across temporal scales. *J. Veg. Sci.* 31 (5), 733–743.
- Hédl, R., Cousins, S.A., Decocq, G., Szabó, P., Wulf, M., 2021. The importance of history for understanding contemporary ecosystems: Insights from vegetation science. *J. Veg. Sci.* 32 (3), e13048.
- Herm, M., Verheyen, K., 2007. Legacies of the past in the present-day forest biodiversity: a review of past land-use effects on forest plant species composition and diversity. In: Nakashizuka, T. (Ed.), *Sustainability and Diversity of Forest Ecosystems*. Springer, Tokyo.
- Herm, M., 2015. Evolution and changes in the understorey of deciduous forests: lagging behind drivers of change. In: Kirby, K.J., Watkins, C., (Eds.), *Europe's Changing Woods and Forests: From Wildwood to Managed Landscapes*, CABI (2015), pp. 174–192.
- Hill, M.O., Roy, D.B., Mountford, J.O., Bunce, R.G., 2000. Extending Ellenberg's indicator values to a new area: an algorithmic approach. *J. Appl. Ecol.* 37 (1), 3–15.
- Hill, M.O., Preston, C.D., Roy, D.B., 2004. PLANTATT-attributes of British and Irish plants: status, size, life history, geography and habitats. Centre for Ecology & Hydrology.
- Hilmers, T., Friess, N., Bässler, C., Heurich, M., Brandl, R., Pretzsch, H., Seidl, R., Müller, J., 2018. Biodiversity along temperate forest succession. *J. Appl. Ecol.* 55 (6), 2756–2766.
- Hopkins, J.J., Kirby, K.J., 2007. Ecological change in British broadleaved woodland since 1947. *Ibis* 149, 29–40.
- Hupperts, S.F., Webster, C.R., Froese, R.E., Lilleskov, E.A., Marcarelli, A.M., Dickinson, Y. L., 2020. Increasing ground-layer plant taxonomic diversity masks declining phylogenetic diversity along a silvicultural disturbance gradient. *Can. J. For. Res.* 50 (12), 1259–1267.
- Jaroszewicz, B., Borysowicz, J., Cholewińska, O., 2021. Forest floor plant diversity drives the use of mature spruce forests by European bison. *Ecol. Evol.* 11 (1), 636–647.
- Joys, A.C., Fuller, R.J., Dolman, P.M., 2004. Influences of deer browsing, Coppice history, and standard trees on the growth and development of vegetation structure in Coppiced woods in lowland England. *For. Ecol. Manage.* 202 (1–3), 23–37.
- Keith, S.A., Newton, A.C., Morecroft, M.D., Bealey, C.E., Bullock, J.M., 2009. Taxonomic homogenization of woodland plant communities over 70 years. *Proc. Royal Soc. B: Biol. Sci.* 276 (1672), 3539–3544.
- Kent, M., 2012. *Vegetation description and data analysis: a practical approach*. John Wiley & Sons.
- Kimberley, A., Blackburn, G.A., Whyatt, J.D., Kirby, K., Smart, S.M., 2013. Identifying the trait syndromes of conservation indicator species: how distinct are British ancient woodland indicator plants from other woodland species? *Appl. Veg. Sci.* 16 (4), 667–675.
- Kirby, K.J., 2015. Changes in the vegetation of clear-fells and closed canopy stands in an English oak wood over a 30-year period. *New J. Botany* 5 (1), 2–12.
- Kirby, K., 2020. *Woodland Flowers: Colourful past, uncertain future*. Bloomsbury Publishing.
- Kirby, K.J., Buckley, G.P., Mills, J., 2017. Biodiversity implications of Coppice decline, transformations to high forest and Coppice restoration in British woodland. *Folia geobotanica* 52 (1), 5–13.
- Kirby, K.J., Bazely, D.R., Goldberg, E.A., Hall, J.E., Isted, R., Perry, S.C., Thomas, R.C., 2022. Five decades of ground flora changes in a temperate forest: The good, the bad and the ambiguous in biodiversity terms. *For. Ecol. Manage.* 505, 119896.
- Klug, B., Tintner, J., Heinz, I., Matiasch, L., 2019. Species composition change with different silvicultural methods—evidence of a long-term study over two decades in a Pannonian oak-hornbeam forest. *Austrian J. Forest Sci./Centralblatt für das gesamte Forstwesen* 136 (3), 199–218.
- Landuyt, D., De Lombaerde, E., Perring, M.P., Hertzog, L.R., Ampoorter, E., Maes, S.L., De Frenne, P., Ma, S., Proesmans, W., Blondeel, H., Sercu, B.K., 2019. The functional role of temperate forest understorey vegetation in a changing world. *Glob. Change Biol.* 25 (11), 3625–3641.
- Larrieu, L., Gosselin, F., Archaux, F., Chevalier, R., Corriol, G., Dauffy-Richard, E., Deconchat, M., Gosselin, M., Ladet, S., Savoie, J.M., Tillon, L., 2019. Assessing the potential of routine stand variables from multi-taxon data as habitat surrogates in European temperate forests. *Ecol. Ind.* 104, 116–126.
- Latham, J., Hall, J., Holl, K., Perry, S., Goldberg, E., 2018. Guidelines for the Selection of Biological SSSIs. Part 2: Detailed Guidelines for Habitats and Species Groups. Chapter 2a Woodlands, Wood Pasture and Parkland, and Veteran Trees. Joint Nature Conservation Committee, Peterborough.
- Lelli, C., Bruun, H.H., Chiarucci, A., Donati, D., Frascaroli, F., Fritz, Ö., Goldberg, I., Nascimbene, J., Tottrup, A.P., Rahbek, C., Heilmann-Clausen, J., 2019. Biodiversity response to forest structure and management: Comparing species richness, conservation relevant species and functional diversity as metrics in forest conservation. *For. Ecol. Manage.* 432, 707–717.
- Lemmon, P.E., 1956. A spherical densiometer for estimating forest overstorey density. *Forest Sci.* 2 (4), 314–320.
- Mason, W.L., 2007. Changes in the management of British forests between 1945 and 2000 and possible future trends. *Ibis* 149, 41–52.
- McCune, B., Grace, J.B., Urban, D.L., 2002. *Analysis of ecological communities*, Vol. 28. MjM software design, Gleneden Beach, OR.
- Mitchell, R.J., Beaton, J.K., Bellamy, P.E., Broome, A., Chetcuti, J., Eaton, S., Ellis, C.J., Gimona, A., Harmer, R., Hester, A.J., Hewison, R.L., 2014. Ash dieback in the UK: a review of the ecological and conservation implications and potential management options. *Biol. Conserv.* 175, 95–109.
- Mitchell, R.J., Hewison, R.L., Hester, A.J., Broome, A., Kirby, K.J., 2016. Potential impacts of the loss of *Fraxinus excelsior* (Oleaceae) due to ash dieback on woodland vegetation in Great Britain. *New J. Botany* 6 (1), 2–15.
- Mitchell, P.L., 1992. Growth stages and microclimate in coppice and high forest. In: Buckley, G.P. (Ed.), *Ecology and Management of Coppice Woodlands*, Chapman & Hall, London, 31 – 51.
- Müllerová, J., Hédl, R., Szabó, P., 2015. Coppice abandonment and its implications for species diversity in forest vegetation. *For. Ecol. Manage.* 343, 88–100.
- Naaf, T., Wulf, M., 2010. Habitat specialists and generalists drive homogenization and differentiation of temperate forest plant communities at the regional scale. *Biol. Conserv.* 143 (4), 848–855.
- Norden, B., Dahlberg, A., Brandrud, T.E., Fritz, Ö., Ejrnaes, R., Ovasainen, O., 2014. Effects of ecological continuity on species richness and composition in forests and woodlands: a review. *Ecoscience* 21 (1), 34–45.
- Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R., 2020. *vegan: community ecology package*. R package version 2 (0–2), 2012.
- Ottaviani, G., Götzenberger, L., Bacaro, G., Chiarucci, A., de Bello, F., Marcantonio, M., 2019. A multifaceted approach for beech forest conservation: Environmental drivers of understorey plant diversity. *Flora* 256, 85–91.
- Peterken, G.F., 1993. *Woodland conservation and management*. Springer Science & Business Media.
- Peterken, G., 2000. Identifying ancient woodland using vascular plant indicators. *British Wildlife* 11 (3), 153–158.
- Peterken, G.F., Game, M., 1984. Historical factors affecting the number and distribution of vascular plant species in the woodlands of central Lincolnshire. *The J. Ecol.* 155–182.
- Peterken, G., Mountford, E., 2017. *Woodland development: a long-term study of Lady Park Wood*. CABI, Wallingford, UK.
- Poore, A., 2016. *Rushmore Estate Woods; management plan 2016–2026*. Estate Office, Tollard Royal, Wiltshire.
- Puettmann, K.J., Wilson, S.M., Baker, S.C., Donoso, P.J., Drössler, L., Amente, G., Harvey, B.D., Knoke, T., Lu, Y., Nocentini, S., Putz, F.E., 2015. Silvicultural alternatives to conventional even-aged forest management—what limits global adoption? *Forest Ecosyst.* 2 (1), 1–16.
- Rackham, O., 2003. *Ancient woodland, its history, vegetation and uses in England*, New ed. Castlepoint Press, Dalbeattie.
- Rackham, O., 2008. *Ancient woodlands: modern threats*. *New Phytol.* 571–586.
- Rackham, O., 2006. *Woodlands*. Harper Collins UK.
- Rochel, X., 2015. 19 Forest Management and Species Composition: A Historical Approach in Lorraine, France. In: K.J. Kirby, C. Watkins (Eds.), *Europe's Changing Woods and Forests: From Wildwood to Managed Landscapes*, CABI (2015), pp 279 – 289.
- Rodwell, J.S. (Ed.), 1998. *British plant communities: volume 1, woodlands and scrub (Vol. 1)*. Cambridge University Press.
- Roleček, J., Vild, O., Sládký, J., Repka, R., 2017. Habitat requirements of endangered species in a former Coppice of high conservation value. *Folia Geobotanica* 52 (1), 59–69.
- Rose, F., 1999. Indicators of ancient woodland. *British Wildlife*, 10, 241–251. British Wildlife Publishing.
- Sage, R.B., Ludolf, C., Robertson, P.A., 2005. The ground flora of ancient semi-natural woodlands in pheasant release pens in England. *Biol. Conserv.* 122 (2), 243–252.
- Sanchez, C., 2017. *Pro Silva Silviculture: Guidelines on Continuous Cover Forestry/Close to Nature Forestry Management Practices*. Forêt Wallonne, Namur, Belgium.
- Schall, P., Heinrichs, S., 2020. Comment on “Forest microclimate dynamics drive plant responses to warming”. *Science* 370 (6522).
- Short, I., Hawe, J., 2018. Ash dieback in Ireland—A review of European management options and case studies in remedial silviculture. *Irish Forestry* 75, 44–72.
- Spencer, J., 1990. Indications of antiquity: some observations of the nature of plants associated with ancient woodland. *British Wildlife* 2 (2), 90–102.
- Spencer, J.W., Kirby, K.J., 1992. An ancient woodland inventory for England and Wales. *Biol. Conserv.* 62, 77–93.
- Susse, R., Allegrini, C., Bruciamacchie, M., Burrus, R., 2011. Management of Irregular Forests: developing the full potential of the forest. Association Futaie Irreguliere. English translation P. Morgan, p. 144p.
- Swallow, K.A., Wood, M.J., Goodenough, A.E., 2020. Relative contribution of ancient woodland indicator and non-indicator species to herb layer distinctiveness in ancient semi-natural, ancient replanted, and recent woodland. *Appl. Veg. Sci.* 23 (4), 471–481.

- Szabó, P., 2010. Driving forces of stability and change in woodland structure: A case-study from the Czech lowlands. *For. Ecol. Manage.* 259 (3), 650–656.
- Tardella, F.M., Postiglione, N., Tavoloni, M., Catorci, A., 2019. Changes in species and functional composition in the herb layer of sub-Mediterranean *Ostrya carpinifolia* abandoned coppices. *Plant Ecol.* 220 (11), 1043–1055.
- Tinya, F., Kovács, B., Prättälä, A., Farkas, P., Aszalós, R., Ódor, P., 2019. Initial understory response to experimental silvicultural treatments in a temperate oak-dominated forest. *Eur. J. Forest Res.* 138 (1), 65–77.
- Van Calster, H., Baeten, L., Verheyen, K., De Keersmaeker, L., Dekeyser, S., Rogister, J.E., Hermy, M., 2008. Diverging effects of overstorey conversion scenarios on the understory vegetation in a former Coppice-with-standards forest. *For. Ecol. Manage.* 256 (4), 519–528.
- Verheyen, K., Honnay, O., Motzkin, G., Hermy, M., Foster, D.R., 2003. Response of forest plant species to land-use change: a life-history trait-based approach. *J. Ecol.* 91 (4), 563–577.
- Verheyen, K., Baeten, L., De Frenne, P., Bernhardt-Römermann, M., Brunet, J., Cornelis, J., Decocq, G., Dierschke, H., Eriksson, O., Hedl, R., Heinken, T., 2012. Driving factors behind the eutrophication signal in understory plant communities of deciduous temperate forests. *J. Ecol.* 100 (2), 352–365.
- von Oheimb, G., Härdtle, W., 2009. Selection harvest in temperate deciduous forests: impact on herb layer richness and composition. *Biodivers. Conserv.* 18 (2), 271–287.
- von Oheimb, G., Westphal, C., Tempel, H., Härdtle, W., 2005. Structural pattern of a near-natural beech forest (*Fagus sylvatica*) (Serrahn, North-east Germany). *For. Ecol. Manage.* 212 (1–3), 253–263.
- Wickham, H., Chang, W., Wickham, M.H., 2016. Package 'ggplot2'. Create Elegant Data Visualisations Using the Grammar of Graphics. Version 2 (1), 1–189.
- Zellweger, F., De Frenne, P., Lenoir, J., Vangansbeke, P., Verheyen, K., Bernhardt-Römermann, M., Baeten, L., Hédl, R., Berki, I., Brunet, J., Van Calster, H., 2020. Forest microclimate dynamics drive plant responses to warming. *Science* 368 (6492), 772–775.