Ecological Characteristics of Ancient Semi-Natural Woodlands undergoing transformation to an Irregular High Forest silviculture in southern Britain

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2022

Ecological Characteristics of Ancient Semi-Natural Woodlands undergoing transformation to an Irregular High Forest silviculture in southern Britain

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A thesis submitted in partial fulfilment of the requirements of the
Manchester Metropolitan University
for the degree of
Doctor of Philosophy

Department of Natural Sciences

Manchester Metropolitan University

2022

Abstract

Ancient woodlands in lowland Britain are repositories of cultural and ecological histories which reflect a long association with human intervention since the Mesolithic. The interests of ancient woodland are valued by society yet demands on woodlands beyond providing woodland produce have increased. Uncertainties around anthropogenic climate change are driving land-use policies towards more resilient outcomes and sustainable forest management is part of the response. Irregular silviculture is one method to achieve continuous cover forestry in the United Kingdom and is promoted as an appropriate method of sustainable forestry management and has been practised at the study site, Rushmore estate since the 1980s. As an exploited resource ancient woodlands were significant in the development of European society providing fuel, building materials and furnace charcoal for metallurgy. Coppice management was prevalent over many centuries, at its height between the 13th and 19th centuries. Despite intensive exploitation, woodland species adapted alongside to form distinct communities against a backdrop of a farming landscape which was more benign than that which modern agriculture has created, causing woods to become isolated remnants of semi-natural habitats. Changes in the way woodlands were generally managed across Europe reflected the increasing sophistication of technology and demands on the types of wood resources required especially during the industrial revolution. The progression of Silviculture as a science ran parallel and many of the traditional coppice-based products became obsolete. High forest silviculture developed as coppice subsided alongside the arrival of plantation management with a focus on producing increasing quantities of timber for construction to meet national demands and security of supply. By the middle of the 20th century coppicing of most ancient woods ceased; woods became either neglected or converted to high forest often with non-native conifers planted which changed conditions for many of the ancient woodland species associated with continuity of coppice management. Under-management is a conservation threat to many species associated with a more heterogenous stand structure. Continued management by coppicing however, remains economically tenuous. This study in the Cranborne Chase with a long history of coppice management across its ancient woodlands provided a unique opportunity to compare habitat structures between active coppice silviculture, Irregular high forest, transitional stands in the early stages of silvicultural management and limited intervention stands, those neglected between 30-50 years previously. Using a combination of descriptive, multivariate analysis, correlations and modelling with pairwise tests between stand types of the effects of silvicultural management, or the lack of it, upon three different taxonomic groups; birds, bats and plants associated with ancient woodland. Irregular high forest was found to positively influence all three taxonomic groups. Significantly, Irregular silviculture retained many species of conservation interest including the conservation red-listed Marsh Tit *Poecile Palustris* and Barbastelle Bat *Barbastella barbastellus* which is listed internationally as near-threatened by the International Union for the Conservation of Nature. Both were found to occupy Irregular stands at greater levels of abundance and activity respectively compared to either coppice or limited intervention stands. For ancient woodland indicator plants and coppice-associated plants as derived by Rackham (2003), there was no significant difference between coppice and Irregular stands. Structural comparisons between Irregular and limited intervention stands were strikingly different with lower basal area, stand structural variation and developing understorey associated most strongly with the former. Irregular silviculture provides structural heterogeneity and complexity associated with early successional growth typical of the coppice cycle and more open woodland, but also older growth features, e.g., deadwood, of mature stands related to larger diameter trees. Both sets of attributes provide important functional resources for a range of woodland species analogous to a woodland successional gradient. This study has identified that Irregular high forest produces a broad ecological ‘bandwidth’ of environmental conditions for woodland species. Active silvicultural management that includes Irregular in ancient woodland is preferable to neglect associated with limited intervention because it appears to retain structural characteristics important to several groups of woodland species of intrinsic conservation value.

Acknowledgements

Throughout childhood my parents allowed me to indulge my passion for nature despite many times bearing the brunt of escapees; newts, slowworms, water boatmen, invading our home. It was, however, the late Beryl and Brian Williams who, with no children of their own took me and several other children during the late 70’s early 80’s under their wings and patiently taught us how to identify birds and their habitats on winter evening slide shows and countless fieldtrips to the likes of Maidenhead Thicket and Pagham Harbour. My mentor in the world of work was Nick Hoskins an excellent botanist and horticulturalist who, despite my lack of confidence as a young man, encouraged me to ignore the self-doubt and use my love of nature in a way I never thought possible. Your friendship and wisdom has meant much to me over the years, thank you. To my friends, Mike Carson, David Percival, Gerard Gorman and Kyle Turner with whom I have badger-watched, bird-watched and shared ideas, thank you. I will always be indebted to the Churchill Fellowship for the incredible opportunity it gave me to visit Hungary in 2002 and gain insight into the ecology and conservation of central European forests; here the seed was sown.

Professor Stu Marsden while steering me along an academic pathway has encouraged, cajoled, and taught me to look at things differently and I will always be indebted to him, while enjoying his friendship and good humour throughout. Dr Stuart Newson of the British Trust for Ornithology has become a good friend too and his expertise, especially in bioacoustics, has been invaluable during the study design and analysis. Dr Danny Norrey at MMU has been vital in helping me address the many statistical challenges along the way. Dr Robyn Grant gave steadfast advice during my annual progress reviews. Professor Rob Fuller, former Research Director at the British Trust for Ornithology has been a wonderful ally to our research and brought a wealth and depth of experience. Similarly, Dr Keith Kirby gave a good deal of his time reviewing the manuscript on plants and significantly enhanced my understanding of the value and nuances of their role as ancient woodland indicators.

Dr Annabel King, a highly respected friend and colleague kindly made the recommendation to the research project funders, The Golden Bottle Trust and Henry Hoare Charitable Trust.

Thank you very much one and all for such an incredible opportunity. It was a chance discussion with Andy Poore, consultant forester to the Rushmore Estate which triggered the research project on the Rushmore Estate. Andy has imparted his extensive knowledge and been integral to the success of this research, and I value the collaboration between us. The Rushmore Estate has been an incredible outdoor laboratory, a culturally and ecologically rich landscape. Thanks are due to Becky Beavis, Ian Burt, Andy Taylor, Rob Taylor and Don Taylor who accommodated my requests for logistical support. To Mark Hooper for cutting access paths through dense bramble so we could position sampling stations. I must have tried the patience of these people several times for which I sincerely apologise! Thanks are due to the managing agent at Rushmore, Mr Phillip Gready, for his support and interest.

My good friends at Dorset Environmental Records Centre; Rhiannon Rogers for her field assistance, good company and diligently managing the budget, to Jon Corkill for GIS expertise and support and Bryan Edwards for botanical fieldwork and discussions on ancient woodland plants, thank you. It was a pleasure to work alongside Dr Phil Sterling and Mike Jeffes who were studying the moth population, both made useful comments on the study design. Dr Daniele de Rigo kindly sent the graphic and references from the Atlas of European Forest Trees. To Dr Mike Allen for use of his graphic in Figure 14 and discussion on the prehistoric landscape of the Chase woods, whose work alongside that of Dr Martin Green has captured my imagination, thank you. Finally, to Heather Kiel my long-suffering partner whose love and support has got me through the trying times and shared in the best of days too. Thank you.

Table of Contents

Abstract……………………………………………………………………………………….....iii

Acknowledgements……………………………………………………………………………v

Chapter 1 Introduction: Biodiversity and Silviculture………………………………....1

1.1 Woodlands from Holocene to the Anthropocene……………………………………………………1

1.1.1 Woodland Conservation Preamble………………………………………………………………………1

1.1.2 British Woodlands Historical Ecology………………………………………………………………….9

1.1.3 Ancient Woodlands - Concepts, Classifications and Designations……………………………11

1.1.4 Ecological Characteristics of Ancient Woodland - Categories and Communities……..14

1.1.5 Conservation Rationale in Ancient woodland………………………………………………………20

1.2 Silvicultural management in British Ancient Woodlands……………………………………….24

1.2.1 Drivers of change in woodland management since 1600……………………………………24

1.2.2 From Coppice to High Forest Systems; a British and European Context…………………26

1.2.3 High Forest; a British and European Context……………………………………………………….30

1.2.4 Irregular Silviculture; transformation from Europe to Britain……..............................34

Chapter 2 Study Area: Description and Overview of Research………………....38

2.1 Study Area: Background and Description………………………………………………………………38

2.1.1 Study Area: Description of Research Woodlands…………………………………………………38

2.1.2 The Cultural Significance of Woodland Development in Cranborne Chase……………...41

2.1.3 Silvicultural Description of the Study Area ……………………………………………………………48

2.1.4 Conservation Rationale for Cranborne Chase Woods…………………………………………..52

2.2 Overview of the Research ………………………………………………………………………………………55

2.2.1 Aims and Objectives ……………………………………………………………………………………………55

2.2.2 Study Design……………………………………………………………………………………………57
2.2.3 Outline of the Research Chapters…………………………………………………………………..62
2.3 References……………………………………………………………………………………………………64

Chapter 3 The structure and composition of vegetation and its response to silviculture………………………………………………………………………………95

3.1 Structural Characteristics of the ancient semi-natural woodlands……………………………95
3.1.1 Introduction...95
3.1.2 Methods……………………………………………………………………………...........................96
3.1.3 Results…………………………………………………………………………………………………….96

Structural Characteristics

Dominant Floristic Cover

3.1.4 Discussion…………………………………………………………………………………………………105
3.1.5 References………………………………………………………………………………………………..108

3.2 Paper 1 Irregular silviculture and stand structural effects on the plant community in an ancient semi-natural woodland……………………………………………………………………………… 112
3.2.1 Background and Details of Authors Contributions....……………………………………………112
Paper 1 Irregular silviculture and stand structural effects on the plant community in an ancient semi-natural woodland…………………………………………………………………………….....113

Chapter 4 Woodland Birds………………………………………………………………..129

4.1 Paper 2 Implications of transformation to irregular silviculture for woodland birds: A stand wise comparison in an English broadleaf woodland………………………………………..129
4.1.1 Background and Details of Authors Contributions....……………………………………………129

Paper 2 Implications of transformation to irregular silviculture for woodland birds: A stand wise comparison in an English broadleaf woodland……………………………………………130

Chapter 5 Bats……………………………………………………………………………………………140

5.1 Paper 3. Irregular silviculture positively influences multiple bat species in a lowland temperate broadleaf woodland……………………………………………………………………………140
5.1.2 Background and Details of Authors Contributions..140

Paper 3 Irregular silviculture positively influences multiple bat species in a lowland temperate broadleaf woodland ……………………………………………………………………………141

Chapter 6 Discussion..159

6.1 Context of the research...159
6.2 Synopsis of results..162
6.3 Woodland Management Implications...165
6.4 Future research...168
6.5 References..171

Appendices..182
Appendix 1 Glossary of terminology and abbreviations used.....................182

List of Figures and Tables

Figure 1. Qualitative evolution from the pre-industrial society to two subsequent transitions…….4

Figure 2. Pollen diagram showing relative percentage of species from Longmoor Bog, Wokingham, Berkshire, United Kingdom………………………………………………………………….11

Figure 3. Relationship between woodland age and degree of naturalness in British woodland (Forestry Commission 2003)……………………………………………………………………….14

Figure 4. National Vegetation Classification for UK woodland with relationship to geographical location, main soil characteristic and dominant stand tree species…………..16

Figure 5. Herb Paris *Paris quadrifolia*, an uncommon woodland plant associated with ancient woodland which is adapted to deep shade emerging in early spring before leave-burst of canopy trees. Dorset, May 2022……………………………………………………………………17

Figure 6. The woodland Dor snail *Clausilia bidentata* commonly found on tree trunks in broadleaf temperate woods, Dorset, June 2021…………………………………………………………..20

Figure 7. Expected relationships between forest management, habitat attributes and the resources provided for biodiversity……………………………………………………………………….23

Figure 8. Schematic representation of a successional stand development model following major disturbance and removal of overstorey. (Adapted from Harmer *et al*. 2010) …………25

Figure 9. Silvicultural classification system for high forest adapted from Matthews (1991), high forest systems regenerate through natural seeding or via planting; coppice is included as a type of intensive even-aged system on short cycles, regeneration is vegetative from coppice stools……………………………………………………………………………………………………….27

Figure 10. Example of a commercial charcoal production clamp showing a burn above, with soil placed over the stack of cut and prepared logs, below. A method in use since the Iron-age. Hungary 2002……………………………………………………………………………………………......30

Figure 11. Location of woodlands contributing to the AFI network, Annee = Year, Nombre = Number of woods in each region……………………………………………………………………………37

Figure 12. Location of Rushmore Estate study area within Cranborne Chase and West Wiltshire Downs Area of Outstanding Natural Beauty in central southern England, United Kingdom…….39

Figure 13. Neolithic flint working, Chase wood, Sixpenny Handley, Dorset, September 2014……42

Figure 14 Contrasting postglacial woodland development between the Wessex Chalklands including Cranborne Chase, and the South Downs of Sussex. (Figure © Mike Allen, from Allen (2017))…….42

Figure 15 Model of woodland-scrub-grassland development adapted from Vera (2000) and added to by Kirby (2004) with additional break-up degeneration phase of woodland……43

Figure 16 An engraving from 1857 of a Cranborne Chase Keeper in his protective forest night dress, cutlass and staff, Rushmore 1815………………………………………………………………45

Figure 17. Don Taylor, Hurdle-Maker constructs a hazel hurdle from the coppice he has recently cut, a process followed by successive generations of coppice-workers for at least 500 years in the Chase woods. Rushmore, Wiltshire, April 2014……………………………………..47

Figure 18. Produce from an area of pure Birch Betula spp coppice cut on a 3–4-year rotation stacked awaiting collection for use as horse jumps and revetments for river bank restoration. March 2014……………………………………………………………………………………………47

Figure 19. The Cranborne Chase woodlands……………………………………………………………………50

Figure 20. Ancient woodland locations used in the study across the Rushmore Estate 2014 -2016; stand descriptions are given……………………………………………………………………………..51

Figure 21. Variable plot as used in the study within which all structural habitat measures were collected from circular plots and vascular plant data from within the 20mx20m quadrat. Point counts and Acoustic activity measures for birds and bats respectively were collected at the plot centre. Plot adapted from Hansen and Hounihan (1996)…………………...58

Figure 22. Locations of all study plots; 310 were used for woodland birds across four stand treatments with 120 for birds, bats, vascular plants, moths and congruence shown as circles for three stand types, mauve limited intervention, green Irregular high forest and blue coppice ……….59

Figure 23. Chequer board as used to estimate woodland understorey density across a horizontal plane. Three height bands were sampled 0.5 m, 1.5m and 2 m to look at variation in structure across the understorey strata. Spherical densiometer on right for measuring canopy cover………………………………………………………………………………………………61

Figure 24. Principal Components Analysis ordination graph of habitat structural measures for the wider area of ancient semi natural woodland. Stand management types are shown………98

Figure 25. Principal Components Analysis ordination graph of habitat structural variables with correlations of floristic variables and bare ground for the wider woodland area of ancient seminatural woodland. Mean positions of the four stand types are shown…………99

Figure 26. Hazel coppice. Previous winters felling evident through open area and standard Oak; the adjacent dense understorey of regrown coppice stools can be clearly seen, (above). Preparing ‘sails’ (below) for a Hazel hurdle placed upright into the mould behind

Don Taylor (Hurdle-maker) with binders woven through. Pole material prepared, ready to be worked. March 2022……………………………………………………………………………………………102

Figure 27. Limited intervention stand composed of Ash and overstood Hazel coppice last managed c.50 years previously; heavily shaded and higher basal area than other stands with evidence of self-thinning stems falling to the woodland floor. The ground flora is dominated by vernal species flowering and storing carbohydrate reserves in their bulbs before canopy leaf-burst. April 2022……………………………………………………………………………….101

Figure 28. Irregular stand with open canopy, mixed sizes of trees and variable, patchy understorey of Bramble, Hawthorn and Hazel interspersed with openness as shown by the emergent ground flora of vascular plants and grasses. April 2022…………………………………103

Figure 29. Transition stands comprised of even-aged trees at pole-stage and not mature therefore requiring transformation to restructure age-classes and encourage natural regeneration; the first thinning has taken place the previous winter with Hazel understorey having been cut which can be seen resprouting. Further trees are marked to be felled to open the canopy. May 2014…………………………………………………………………………………………104

Table 1. IUCN Protected area definition, management categories and governance types……..7

Table 2. Summary of ancient semi-natural broadleaved woodland and current silvicultural management at Rushmore used in the study…………………………………………………………….49

Table 3. Median values of habitat structural variables measured across the four stand types; lower and upper quartiles in parenthesis and results of ANOVA tests for random effects (stand number) and fixed effects (stand type) Pairwise comparisons using Tukey's post-hoc test, for stands; C - coppice, I - Irregular, L - Limited intervention and T - Transitional; those in bold are highly significant P < 0.005……………………………………………….98

Table 4. Spearman's Rank Correlations of main structural and floristic variables sampled across all four stand management types……………………………………………………………………99

Table 5. Principal Component scores of significant habitat and floristic variables used in the community analysis across each of four stand types. Values in bold are significant at P = 0.05 ……..105

Silver-washed fritillary *Argynnis paphia* nectaring on a white Marsh thistle *Cirsium palustre,* Chase Wood, Sixpenny Handley, Dorset, July 2013.

"I wish that we would not fight for landscapes that remind us of who we think we are. I wish we would fight, instead, for landscapes buzzing and glowing with life in all its variousness."
Author: Helen Macdonald
Macdonald, H. 2014. H is for Hawk. Jonathan Cape, London. 300pp.

"What better life could there be - to get my living out of the land as much as my ancestors had ever done."
Artist: Paul Nash
Haycock, D. B. 2016. Paul Nash, Outline: An Autobiography and Other Writings. Lund Humphries Publishers Ltd, London. 280 pp.

Chapter 1 Introduction: Biodiversity and Silviculture

1.1 Woodlands from Holocene to the Anthropocene

1.1.1 Woodland Conservation Preamble

The starting point of the Anthropocene is subject to considerable argument; empirical evidence points to rates of change in nature e.g., habitat loss and species extinctions occurring in the last 300 years, which are of an unprecedented order of magnitude (Soriano 2020). The Anthropocene epoch, in which *Homo Sapiens* have affected the entire world biome, has amplified in society a sense of urgency to understand and address the causes of ecological destabilisation which, ultimately will lead to global societal conflicts (Steffen *et al*. 2007, Steffen 2021). Unsustainable exploitation of the earth's resources has not only deprived future generations of landscapes and their component biodiversity, it has compromised ecosystem functioning to the extent that it undermines the health of these systems and their resilience to change (Roe *et al*. 2019).

Globally 1.6 billion people are directly reliant on forests and woodlands (hereafter used interchangeably) for their livelihoods, yet losses of intact forests are widely reported with over half of tropical forests destroyed since the 1960's, and more than 3.7 million hectares of European forests degraded through human-induced actions (IUCN 2021). The Common International Classification of Ecosystem Services (CICES) defined ecosystem services as the contributions that ecosystems make to human well-being, and distinct from the goods and benefits that people subsequently derive from them (Haines-Young and Potschin 2018). As well as provision of resources (provisioning services); timber for construction, wood-fuel and food, forests and woodlands provide a range of other ecosystem services; (regulatory services), acting as carbon sinks, maintaining the functioning of watersheds and nutrient cycles and moderating climate processes (Grantham *et al*. 2020). Additionally, forests provide non-consumptive 'goods' (cultural services) through aesthetic, spiritual, intellectual, physical and experiential interactions with humans (Mae *et al*. 2016). Moreover, forests and woodlands are the most biodiverse terrestrial habitats on earth

(IUCN 2021) and account for most terrestrial species on our planet including 75% of vertebrate species (FAO and UNEP 2020). Many species such as birds and mammals are important dispersers of seeds aiding forest regeneration while fungi, and invertebrates form important components of the nutrient cycling and decomposition (FAO and UNEP 2020). We are only just beginning to understand the value of the complex interactions between fungi and trees which are vital in the functioning of forest ecosystems including the carbon exchange (Johnson *et al*. 2016) and resilience to drought in a changing climate (Simard 2021, Pickles and Simard 2017). Throughout the quaternary period of 2.6 million years European forests have been subject to significant changes in extent, composition, and structure as a result of a globally changing climate and glacial oscillations, with periods (measured in tens of thousands of years) alternating between the extreme cold of the glaciations and the warm interglacial (Birks and Birks 2004). The influence of human-induced impacts to woodland cover from the Mesolithic period (9600 - 4000 BC) , has also profoundly affected the characteristics of forest and woodland vegetation as palaeoecological studies indicate (Birks and Tinner 2016). The wooded landscapes of Europe were therefore highly dynamic in both space and time; our understanding of long-term ecological change and historical legacies can provide guidance as society wrestles with the possible future trajectories of ecosystem and resource disruption as a consequence of human-induced climate change (Birks 2012). This is perhaps the greatest challenge of our times as we tackle the consequences of increased greenhouse gas emissions resulting from human activity since the onset of the industrial revolution c1800 AD (United nations undated).

The transition towards a bio-based economy is defined as ‘reliance on biological processes and natural ecosystems, use natural inputs, expend minimum amounts of energy and do not produce waste as all materials discarded by one process are inputs for another process and are reused in the ecosystem’ (Mubareka *et al*. 2016, Johansson 2018). The forest-based sector as part of a bio-based economy is expected to significantly contribute to sustainable development as society phases out fossil fuels and returns to a sustainable pre-industrial pathway (Figure 1), which minimises waste, embeds carbon in timber construction, substituting carbon heavy resources like concrete, and provides renewable biomass fuel (Mubareka *et al*. 2016). Sustainable forest management (SFM) ‘aims to maintain and enhance the economic, social and environmental values of all types of forests, for the benefit of present and future generations' (FAO 2020[1]). Or as Weatherall *et al*. (2022) suggest, forest workers and users (stakeholders) are more likely to describe it as 'a way of managing trees so that when some of them are harvested, the forest survives'. Sustainable forest management may already mitigate climate change by preserving and enhancing environmental values for the benefit of present and future generations. Yet, given the multiple objectives of SFM in providing ecosystem services, forest managers must prioritise each which inevitably leads to trade-offs (Weatherall *et al*. 2022). The development of so-called Climate-Smart-Forestry (CSF) and adaptive forest management (AFM), the 'adaptation of trees, woods, and forests (to a range of dynamic climate change scenarios) and the use of forestry to mitigate climate change as the priority for SFM, so that other ecosystem services can be provided now and, in the future,' (Yousefpour *et al*. 2017, Weatherall *et al*. 2022). Promoting heterogeneity and diversity for genetic resilience is a key objective of the adaptive approach at multiple landscape scales (Yousefpour *et al*. 2017).

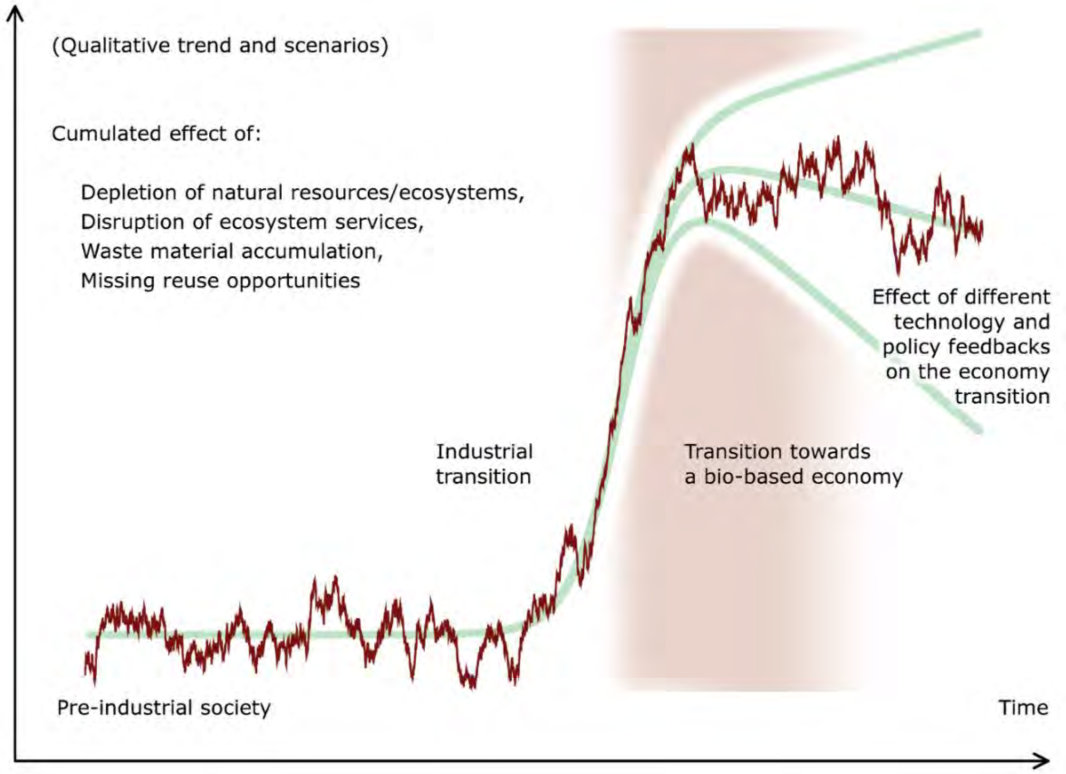

Figure 1. Qualitative evolution from the pre-industrial society to two subsequent transitions. First, the transition to the industrial society and economy illustrated by a sharp rise in resource use. Then, toward a bio-based economy based on use of renewable resources. The short-term patterns of the actual evolution may be complex since they are subject to several sources of local fluctuations. The qualitative future trend will also depend on the cumulative feedback effect due to different potential technology and policy scenarios. ((Mubarecka *et al.* 2016), reproduced by kind permission of the author: Dr. Daniele de Rigo).

Inappropriate management depreciates the ecological integrity of forest and woodland systems as a result of modifications to its structure and composition and is often a precursor to deforestation as its value diminishes (Grantham *et al*. 2020). Biodiversity loss is known to disproportionately effect the functioning of forest and woodland ecosystems, reducing the capacity for resilience and adaptation to changes including those caused by humans (Betts *et al*. 2017). Understanding the ecological processes of forest and woodland habitat heterogeneity in readiness of future adaptation to climate change and novel pests and diseases is critical for sustainable resource management (Spiecker 2002). Reduction of forests and woodlands worldwide regardless of protection status, has shown a worrying increase (Leberger *et al*. 2020) with mean losses per annum of 4.2 million hectares in the decade from 2010 (FAO 2020[2]). In addition to halting such declines, there is a strong desire to establish monitoring systems which seek to measure the effectiveness of protection of forest and woodland resources beyond simply establishing protected areas so that quality as well as quantity can be better evaluated (Leberger *et al*. 2020). Indeed, evidence is emerging of the value of forest and woodland governance and management systems which link positive outcomes between socio-economic and nature conservation objectives (Powlen *et al*. 2021). Despite direct threats posed to forests and woodlands by climate change, wild fires and the introductions of pests and diseases (San-Miguel-Ayanz *et al*. 2016), policies towards global mitigation of climate related impacts will need to include major contributions from the forest management sector (Gamborg and Larsen 2003, Roe *et al*. 2021). As a result, the future sustainable management of forests and woodlands is likely to depend on a robust yet flexible range of management systems which integrate relevant biodiversity metrics into decision-making processes for forest practitioners and policy-makers alike (Lõhmus *et al*. 2020, Vizzarri *et al*. 2022).

Most European forests and woodlands have undergone management interventions to some degree, influenced by local conditions (abiotic and biotic) and anthropogenic demands typically leading to distinctive wooded landscape typologies with strong cultural linkages (Wascher 2005). Indeed, European forests and woodlands are a complex and heterogenous mix of these characteristics leading to highly localised peculiarities of woodlands and the resources found within them and influencing where they sit within a framework for protection and governance (Table 1). The anthropic factor often dominates the way woods and forests have developed over centuries and millennia intensifying the variability to be found across the European continent (San-Miguel-Ayanz *et al*. 2016). For instance, wood-pastures (traditional sylvo-pastoral systems associated with high nature value, many of which have been present since the medieval period) are found throughout Europe, and show considerable variations between and within biogeographic regions reflecting a blend of their dynamic characteristics creating a range of habitat mosaics within distinctive geographies (Rotherham 2013, Plieninger *et al*. 2015). Similarly, coppice woodlands have existed since the neolithic period c.4,500 years BCE, are generally closed canopy understorey woods where livestock are excluded, being found throughout Europe they vary in their harvesting rotation lengths (repeated cycles of cutting of stems which regrow) between 5 and 30 years depending upon the uses at a particular point in history (Buckley and Mills 2015). Wood-pasture and coppice are widely recognised for their nature conservation value yet each has faced challenges in keeping apace with societal demands and the resulting economic consequences (Kirby and Watkins 2015). There have been some fundamental changes in the way people have exploited European forests and woodlands since the 17th century with a reduction of 153,000km^2 of coppice, an increase of 818,000km^2 in high forest management and 593,000km^2 increase in coniferous woodland, at the expense of broadleaved woods (McGrath *et al*. 2015). Following the introduction of plantation forest management to Europe in the 18th and 19th centuries the use of fast-growing trees typically non-native species has become prevalent in countries with a low tree species richness; Sitka spruce *Picea sitchensis* in the UK, *Eucalyptus* in Portugal and False acacia *Robinnia pseudoacacia* in Hungary (Quine 2015, Savill 2015). Introduced trees alter the composition of land cover and associated plant and animal communities which can lead to losses of semi-natural habitats with impoverished biodiversity (Souvalis 2000). False acacia is highly invasive, negatively affecting semi-natural habitats including native woodlands and grasslands (Vítková et a. 2017, own observation 2002). Between 1950 and 1980 many ancient and semi-natural woodlands in the UK were planted with non-native coniferous species which led to significant changes to the structure and composition of these woods and their native ground flora (Kirby 1988). Policy changes in the UK during the mid-1980's led to a shift towards native broadleaf restoration and removal of conifers from Ancient Woodland Sites (Forestry Commission 1985). Since then, improved silvicultural planning over woodland creation site selection, especially avoiding sensitive semi-natural habitats, and the design and management of new plantations can provide opportunities which incorporate a range of public goods including biodiversity (Quine 2015). Increasingly we are beginning to understand and value the use of natural processes for native woodland establishment on former agricultural land undertaken passively which can efficiently contribute to increasing woodland cover although this relies on nearby semi-natural woodland to act as a donor (Broughton *et al*. 2021). The importance of forest and woodland management in cultural landscapes is recognised where it sustains varied tree composition and important ecological assemblages in protected areas (Borrinni *et al*. 2013).

Table 1. IUCN Protected area definitions, management categories and governance types. IUCN describes a protected area as: A clearly defined geographical space, recognised, dedicated and managed, through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural values. The definitions are shown as seven conservation management categories (one with a sub-division), summarized below. For this study we are primarily concerned with IV, V and VI.

1a Strict nature reserve: Strictly protected for biodiversity and also possibly geological/ geomorphological features, where human visitation, use and impacts are controlled and limited to ensure protection of the conservation values

1b Wilderness area: Usually large unmodified or slightly modified areas, retaining their natural character and influence, without permanent or significant human habitation, protected and managed to preserve their natural condition

II National Park: Large natural or near-natural areas protecting large-scale ecological processes with characteristic species and ecosystems, which also have environmentally and culturally compatible spiritual, scientific, educational, recreational and visitor opportunities

III Natural monument or feature: Areas set aside to protect a specific natural monument, which can be a landform, sea mount, marine cavern, geological feature such as a cave, or a living feature such as an ancient grove

IV Habitat/species management area: Areas to protect particular species or habitats, where management reflects this priority. Many will need regular, active interventions to meet the needs of particular species or habitats, but this is not a requirement of the category

V Protected landscape or seascape: Where the interaction of people and nature over time has produced a distinct character with significant ecological, biological, cultural and scenic value: and where safeguarding the integrity of this interaction is vital to protecting and sustaining the area and its associated nature conservation and other values

VI Protected areas with sustainable use of natural resources: Areas which conserve ecosystems, together with associated cultural values and traditional natural resource management systems. Generally large, mainly in a natural condition, with a proportion under sustainable natural resource management and where low-level non-industrial natural resource use compatible with nature conservation is seen as one of the main aims.

1.1.2 British Woodlands, Historical Ecology

Towards the end of the last glacial maximum, approximately 16,000 years BCE much of Britain was open tundra, a largely treeless landscape analogous with the modern day sub-arctic region (Birks and Tinner 2016). At the start of the Holocene epoch the climate ameliorated and the vast ice-sheet retreated, trees and shrubs gradually returned from the southern refuges that had escaped the intense cold of the ice-age. This was the start of the current interglacial period, one in which the woodland cover of today is the result of a mixture of environmental and anthropogenic influences (Rackham 1990, Peterken 2015). The succession towards woodland reflected the climatic periods that followed the retreat of the ice-sheet, with Birch *Betula spp* and Pine *Pinus sylvestris* establishing during the earlier pre-boreal period approximately 8,500-7500 years BCE (Peterken 1981, Huntley 1990). During subsequent climatic periods additional tree and shrub species expanded their ranges into Britain so that by the relatively warm and wet Atlantic period of 3000 years BCE, woodland composition was similar to that which now exists in semi-natural woodlands, (Huntley 1990, Birks *et al*.1975). By which time the rising sea-levels had effectively cut-off Britain and Ireland from the European land-mass, preventing further species from colonising (Rackham 1990). It is likely that between 6500 years BCE and 4000 years BCE woodland extent throughout Britain and Europe had reached its maxim (Zanon *et al*. 2018). A factor influencing the period which follows is the increasing effect of humans on the vegetation of Britain and Europe. The original wildwood that arose following the ice age (Rackham 1990) was changed and as people cleared the trees for domesticated livestock, they began to have a selective effect on the relative proportions of trees that remained (Kirby and Watkins 2015). Pollen analysis, (see Figure 2), has helped to reveal the relative changes between species as they spread from the southern refuges and were later affected by human activities across the landscape (Peterken 2015). A significant change is detected at the beginning of the Neolithic c.4300 years BCE when settled farming and resultant woodland clearance gave rise to a significant increase in plants of cultivated and open habitats especially *Poaceae,* grasses and cereals, and heather *Calluna vulgaris* (Peterken 2015).

In addressing biodiversity loss and the climate emergency, woodland ecologists today look to the past environmental and anthropogenic evidence to gain insight into possible future trajectories for woodlands to support intact assemblages of species within resiliently functioning habitats (Birks and Tinner 2016). Indeed, there has been much debate, and diverging views, on the relative proportions of openness and woodland cover that existed in prehistory and the drivers, natural and human that created such conditions and the pattern of shifting vegetation dynamics over space and time (Vera 2000, Kirby 2004, Hodder *et al*. 2009). Woodland clearance across Britain continued through the Bonze-age and Iron Age so that by the Roman conquest the original wildwood had probably vanished (Rackham 1990). What followed across much of the country was the development of nearly every remaining woodland into some form of management to support local demands for fuel, construction and a settled existence on a predominantly farmed landscape. I briefly explore the prehistory and history of the study area below in 1.3, as this demonstrates the localised characteristics and interplay between environment and people from the Mesolithic through to the Medieval period and the ways these factors influenced the woodland composition found there today and the way it is managed.

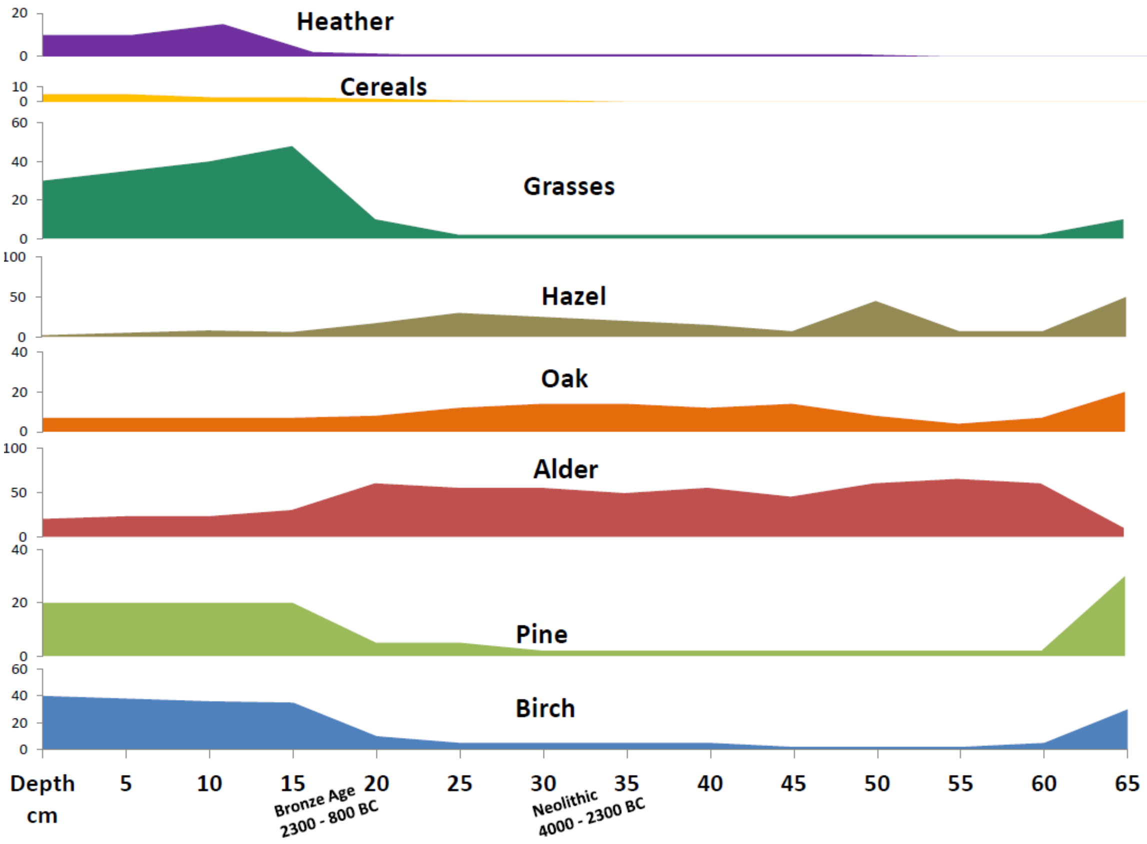

Figure 2. Pollen analysis diagram showing relative percentage of species from Longmoor Bog, Wokingham, Berkshire, United Kingdom. Increasing depth represents increasing age with the 35cm – 65cm band approximating to the Mesolithic period, pre-farming, hunter-gatherer human culture. (Redrawn from data source University of Reading). Key: Heather *Calluna vulgaris*, Cereals *Poaceae*, Grasses *Poaceae*, Hazel *Corylus avellana*, Oak *Quercus spp*., Alder *Alnus glutinosa*, Scots Pine *Pinus sylvestris*, Birch *Betula pendula/pubescens*.

1.1.3 Ancient Woodlands in Britain - Concepts, Classifications and Designations

Ancient woodland in Great Britain is generally recognised to be woodland that is likely to have been continuous woodland cover since at least 1600. AD (1750 in Scotland), (Goldberg *et al*. 2007). The concept was formally promoted by Peterken (1977, 1981) and Rackham (1976, 1990) following their extensive research into the historical ecology of woodlands across Britain. Evidence of ancient woodlands can be based on old estate and Tythe maps, Saxon charters, historical survey records and early editions of ordnance survey maps (Glaves *et al.* 2009). The use of biological indicators of ancient woodlands has been primarily based on phytosociological classifications pertaining to associations between stand (tree and shrub community) composition and ground flora communities (Peterken 1983). An Ancient woodland inventory was started by the Nature Conservancy Council in 1981 and published a decade later (Spencer and Kirby 1992). Ancient woodlands include some which are believed to have a direct link back to the Atlantic period 3000 years BCE, alongside those which may have been subject to varying degrees of human intervention (Goldberg *et al*. 2007). More recent studies have highlighted how varied woodland cover is likely to have been across Britain with some woods cleared entirely or partially as evidence of earth works from Neolithic to the Roman period, 4300 years BCE down to 50 years CE,indicate (Rackham 1990, Barker 1998, Peterken 1981, Day 1993). Ancient woodland which is believed to have had no intervention or has developed from a natural succession following a natural disturbance e.g., a landslip, are termed Primary ancient woodlands, while those that arose following clearance are termed Secondary and/or recent (Peterken 1981). However, this distinction becomes considerably more blurred depending upon location and the available historical and archaeological record; woodlands which were believed to demonstrate continuity of woodland cover from their phytosociological associations have been found, from detailed pollen studies, to have undergone considerable structural changes resulting from human interventions (Bradshaw *et al*. 2015). Studies in Norfolk by Barnes and Williamson (2015) highlight the ebb and flow of woodland cover in response to the vagaries of human influence based around resource use or neglect, which could be especially dynamic. Ancient woodlands could become enclosed to prevent livestock entering and harvested for their underwood as coppice, or subject to emparkment and fenced to become parkland for deer especially from the Saxon period onwards (Rackham 1990). Examples exist of open common and farmed land rejuvenating as secondary ancient woodland in some cases after decades or centuries of continual use (Rotherham 2018, Barnes and Williamson 2015). It seems likely that there are few, if any, woods in the British Isles that have not been affected by human activities, and we should value this cultural association as much as any other archaeology in our landscape (Rotherham 2018). Perhaps as Barnes and Williamson (2015) suggest, the blurring of the distinction between ancient and recent woods does not reduce the importance of the former as much as it raises it for the latter. Box 1 summarises the types of woodland cover to be found in the British Isles which includes ancient woodlands (Kirby and Watkins 2015) while Figure 3 illustrates the relationship between woodland age, degrees of naturalness in respect of ancient and modern woodland (Forestry Commission 2003).

In the UK ancient woodland over 2 hectares has been identified and included in a national inventory, the most recent of which covering England and Wales was undertaken in 1992 (Spencer and Kirby 1992). While the inventory did not confer any additional protection to woodlands at the time it has since been used to inform guidance and planning policy. Ancient woodlands are recognised in the National Planning Policy Framework (NPPF 2021) with a presumption against loss or deterioration unless there are wholly exceptional circumstances (MH C and LG 2021). The Keepers of Time policy document (DEFRA 2022) sets out the UK government's position for protecting,restoring and sustainably managing the UK's ancient woodland and veteran trees for the benefit of society. In addition to influencing planning decisions the policy has promoted the updating of the ancient woodland inventory (Spencer and Kirby 1992) which, since 2006 includes additional ancient woodlands smaller than 2 hectares. The Keepers of Time policy has been brought in line with a wider suite of policies and environmental targets to attain net zero signifying the important role that ancient woodlands contribute towards Nature Recovery Networks following the Environment Act 2021 (DEFRA 2022).

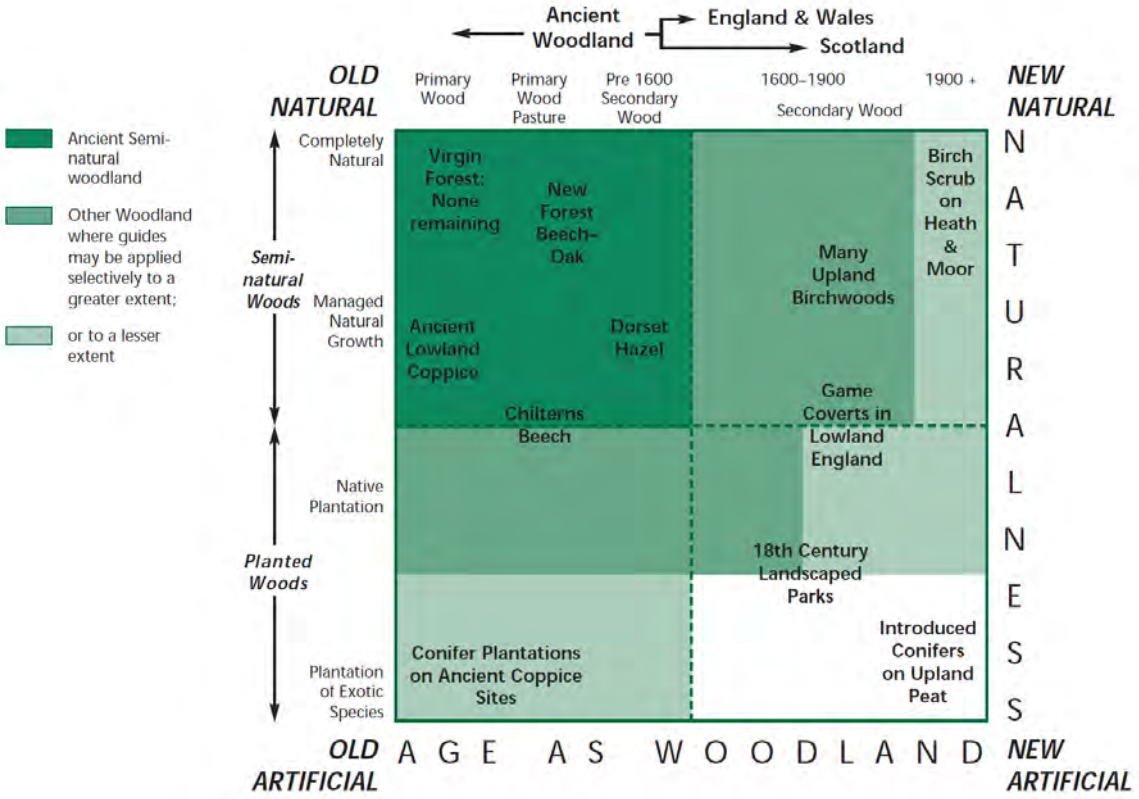

Figure 3. Relationship between woodland age and degree of naturalness in British woodland (Forestry Commission 2003). Not all ancient woodlands contain old trees and may have been managed continuously for many centuries, similarly semi-natural woodlands may have developed since 1600 CE and contain similar ecological characteristics as ancient woods which may be more prevalent when they have regenerated close by.

1.1.4 Ecological Characteristics of Ancient Woodland - Categories and Communities

This section considers some of the main communities associated with Ancient semi-natural woodlands and the principal objectives of conservation management for them. Alongside knowledge of woodland history an overarching objective for woodland managers is to understand the community of plants including the tree and shrub composition and associated higher (Tracheophytes) and lower (Bryophytes) plant assemblages (Kirby and Hall 2019). It was during the preparation of the seminal work*, A Nature Conservation Review* (Ratcliffe 1977), when conservation scientists realised there was an urgent need to better define and interpret the vegetation of Great Britain. The result was the National Vegetation Classification (NVC) system which aimed to produce a systematic categorisation of the main plant communities found in the UK (Rodwell 1991). There are twenty-five communities for the volume on woodlands and scrub which were based on 2,648 samples from ancient and recent woods throughout Britain with eighteen main woodland types categorised (Rodwell 1991). Using phytosociological associations of woods surveyors captured data across plots of varying size according to the scale of the community being sampled with fine-grade ground flora and bryophytes sampled in the smallest quadrats through to understorey, scrub and canopy trees in the larger (Rodwell 1991). Prior to NVC Peterken (1981) proposed thirteen categories based around the tree stand type linked to soils and soil moisture. Both systems reflect geographical and edaphic affiliations and include additional sub-categories in an attempt to capture subtle variations. Rackham (1980) adopted a similar approach to Peterken (1981) and was critical of the NVC as being less detailed and comprehensive than either (Rackham 2003). However, conservation scientists believe NVC aligns better with similar phytosociological assessments in Europe particularly the European Nature Information System (EUNIS), (Davies *et al*. 2004) where the aim is more about understanding how communities of vegetation relate to one another as much as the processes, including anthropogenic, by which they arose (Rodwell 1991). Usefully, for cross referencing, Peterken stands are included in the synonymous index of Rodwell (1991) while Latham *et al*. (2018) give the corresponding EUNIS woodland categories used in Europe. Of the NVC classifications eighteen main woodland communities have been identified (Figure 4), while Rackham (2003) lists fifty-four tree communities. Of those woodland NVC communities five do not fit within ancient woodland as they all relate to successional woodland on recently disturbed or restored land e.g., *Salix spp*. Willow Carr (Marren 1990).

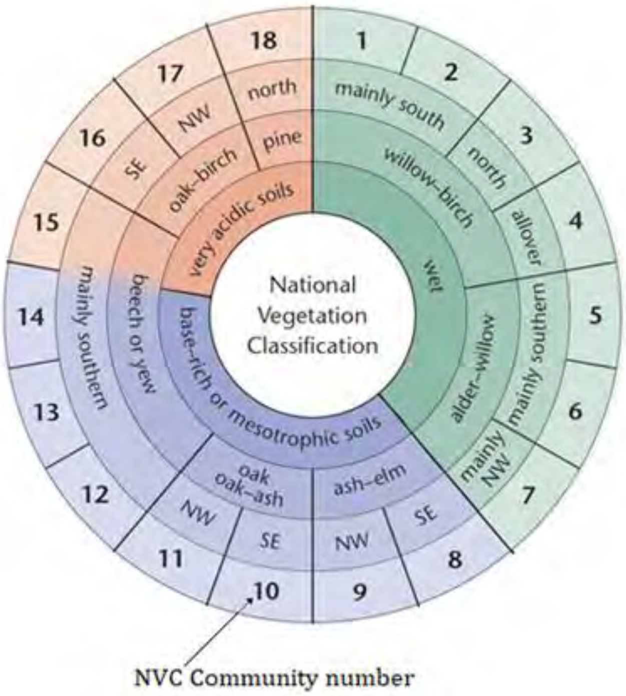

Figure 4. National Vegetation Classification for UK woodland with relationship to geographical location, main soil characteristic and dominant stand tree species. Communities 1,2,3,4 and 6 are rarely associated with ancient woodland communities in Britain as they are frequently disturbed through human activities or mostly through early successional re-initiation in wetlands and river systems. Adapted from Whitbread and Kirby (1992).

Ancient semi-natural woodlands (a spectrum of woodlands that represent both ancient woodlands and those which originated in historic times) are generally species rich, so that catering for an individual species conservation is fraught with difficulties; it is better to consider broader community integrity (Fuller and Peterken 1995). Despite most ancient woodlands having been influenced by people over many centuries or millennia (Rackham 2003), they still retain important vestiges of woodland species which were believed to be present in the wildwood (Watkins 1990). Although this assumption has been challenged more recently as woodlands have been shown to have been more dynamic and subject to periods of clearance, tillage and grazing followed by abandonment (Barnes andWilliamson 2015). Nevertheless, Barnes and Williamson (2015) recognise that the value of woodlands of more recent origin can be as important as those truly ancient woodlands as much because they have a strong archaeological and cultural value. Indeed, recent woods often include many of the species associated with continuity across a broad bandwidth of ecological conditions especially where they are part of an otherwise ancient countryside which has retained many of the features of the past despite alterations to its structure (Rackham 1990). Formerly wooded common land and wood-pastures can retain some of their characteristic vegetation long after it had been cleared e.g., during the feudal system of land-use from the 13th Century; the so called 'shadows and ghosts' of lost woods in the landscape (Rotherham 2017).

A crucial aim of woodland nature conservation is to provide conditions which replicate those to which most ancient woodland species are adapted (Peterken and Game 1984). Although, as mentioned previously, our knowledge of conditions of prehistoric woodlands is a useful guide, we are unlikely to ever know for sure what the primeval woodlands (referred to as the wildwood) looked like and indeed so much is likely to have changed in the 5000 years since humans settled the landscape (Fuller and Freeman 2021). Certainly, the landscapes of Britain were varied in the Mesolithic (Allen 2017). The species assemblages present in ancient (and some recent) woodlands today have survived in spite of human intervention, and many because of it (Rackham 2008).

Figure 5. Herb Paris *Paris quadrifolia*, an uncommon woodland plant confined to ancient woodland which is adapted to deep shade emerging in early spring before leave-burst of canopy trees. Dorset, May 2022.

Possibly the best-known species strongly associated with ancient woodlands are vascular plants (ancient woodland indicators – AWI's) which have adapted to the cycles of cutting trees, primarily of underwood since the neolithic period (Rackham 2003). The distinctiveness of these plant communities and their persistence in ancient woodlands is bound up with the activities of management, as such they are very useful as bio-indicators (Figure 5), for monitoring changes including those driven by human-induced climate anomalies (Ellis 2015). While they may be found beyond ancient woodlands, they exist within semi-natural habitats which have not been modified other than having their tree cover removed or changed (Webb and Goodenough 2018). Nevertheless, ancient woodland indicator plants are a valuable resource demonstrating continuity due to their low dispersal capacity and regional distinctiveness (Swallow *et al*. 2020). There are similarly distinct communities of Lichens which are indicators of woodland continuity and slow dispersal as they are restricted to particular niches; probably the best known in lowland British ancient woodlands is *Lobaria pulmonaria* the tree lungwort. Bryophytes, mosses and liverworts, that are associated with ancient woods tend to be found in the cooler, wetter parts of Britain with important communities found in the Atlantic oak-woods of the western sea-board, including the wholly epiphytic species *Ulota calvescens* (Marren 1990). Fungi are an incredibly diverse Kingdom with many species found in woodland across different niches (Laessøe and Petersen 2019). They are critically important in the functioning of the ecosystem in recycling nutrients and carbon while creating microhabitats e.g., cavities and wet rots, for a range of other species including cavity-using bats and birds but also specialist saproxylic invertebrate communities (Lonsdale *et al*. 2007). Indeed, standing and fallen deadwood is an essential component of functioning woodlands (Hodge and Peterken 1998) with many species e.g., wood-boring beetles *Coleoptera* which use deadwood as breeding habitats. Several species of wood-boring beetles of the *Cerambycidae* also require open sunny areas within woodland as they feed on nectar of various woodland vascular plants (Kirby, 2013). Deadwood is widely associated with old growth associated with mature and veteran trees typicaly over 250 years old, which are entering a degenerative phase in their lifecycle and are especially important (Siitonen *et al*. 2015, Read 2000). Land snail *Gastrapoda* assemblages are valuable in demonstrating the gradients between closed canopy shaded damp woods through to open and dryer habitats (Allen 2017). Several species are associated with fallen deadwood and moist conditions in deep leaf-litter e.g., *Carychium tridentatum* others use bark substrate on living trees e.g., dor snail *Clausilia bidentata* (Figure 6), while some are associated with more open edge habitats on dryer calcareous soils including *Pomatias elegans* (Allen 2017). Land snails are a very useful group in helping to understand past habitat changes including woodland clearance (Evans 1972). Probably the best-known invertebrate community associated with ancient woodlands in Britain are butterflies *Lepidoptera*, with many restricted to native broadleaf and mixed woods (Warren andKey 1991). Several woodland butterflies have a strong dependency on open habitats following gap creation e.g., Pearl-bordered fritillary *Boloria euphrosyne* found in areas of clear-felled woodland and actively coppiced seminatural woods, where they benefit from the thermophilic conditions (Kirby 2001). For vertebrate groups, birds *Aves* and bats *Chiroptera*, woodlands provide breeding and roosting opportunities for cavity dwelling species and nesting locations in dense scrub for several bird species, and foraging resources in terms of substrate, foliage and fruits (Fuller 1995, Ferris and Humphrey 1999). Small mammals such as wood mouse *Apodemus sylvaticus* and bank vole *Myodes glareolus* exert an important influence as seed predators in woodland affecting tree regeneration, and whose populations respond to changes in understorey cover including that caused by deer (Buesching *et al*. 2011). Wild deer in many UK ancient woodlands pose a serious concern as their populations are believed to have been increasing for at least 200 years, as browsers and selective grazers of woodland vegetation this has had negative consequences for other species e.g., woodland birds (Gill and Fuller 2007) and Hazel Dormouse *Muscardinus avellenarius* (Goodwin *et al*.2018). Roe *Capreolus capreolus* and red *Cervus elaphus* deer are both native to Britain and along with feral non-native species such as Reeve's muntjac *Muntiacus reevesii* and Sika *Cervus nippon* influence woodland with positive and negative impacts depending upon browsing levels, creating structural heterogeneity at different thresholds but with severe levels leading to loss of vegetation affecting sustainable woodland management, woodland biodiversity and ecosystem functioning (Eichhorn *et al*. 2018, Brake *et al*. 2020). Of the vertebrate groups birds and bats may be especially valuable as indicators of both varying structure and composition of woodland vegetation and act as a proxy for other taxonomic groups (Ferris and Humphrey 1999). Within ancient and seminatural woodlands a mix of stages of woody growth from early successional through to old growth along with temporary and permanent open habitats across varied aspects and sizes within the woodland provides a range of opportunities for many species; their conservation within each individual wood will vary depending upon local site conditions and characteristics, and regional distinctiveness (Peterken 1981).

Figure 6. The woodland Dor snail *Clausilia bidentata* commonly found on tree trunks in broadleaf temperate woods, Dorset, June 2021.

1.1.5 Conservation Rationale in Ancient woodland

At the time of Domesday 1086 AD Britain's ancient woodlands were probably less than 20% of land cover and by the late 19th century this figure diminished to under 6% (Rackham 1990). Within 50 years until the mid-1980's at least 40% of England's ancient woodland was destroyed most through conversion to intensive agriculture, with further degradation through felling and replanting with conifers (Rackham 2006). The picture across 20th century Britain was similar, with additional losses of semi-natural habitats e.g., species rich semi-natural grasslands, in between the remaining woodlands which compounded the effects of fragmentation as woods became increasingly ecologically isolated (Hopkins and Kirby 2007). The ecological quality of the ancient woodlands which remain is clearly important for nature conversation. Partly in response to the requirement for national governments to monitor biodiversity under article 7 of the global Convention on Biological Diversity, (https://www.cbd.int/) a National Forest Inventory (NFI) was undertaken between 2010-2015 and included an assessment of woodland ecological condition in Britain (Forestry Commission 2020). The stratified and random sampling covered native species woodlands, including ancient woods, and produced outputs from 15 metrics to inform future policy decisions around the management of UK woodlands and conservation of its biodiversity. Among the key findings for native woodland which includes ancient seminatural woods, was that only 7% was in favourable ecological condition with most 91% in the intermediate condition category (Forestry Commission 2020). Of special reference was a paucity of open habitat with 83% in unfavourable condition, and secondly the volume of deadwood was in unfavourable condition in 80% of samples within native woodlands. In more than 40% of sampled woods grazing pressure, mostly from deer *Cervidae*, was unfavourable as it affected natural regeneration. These findings generally accord with other recent national surveys notably the repeat woodland bird survey where changes in the structure and composition of woods were compared between the 1980's and 2003-4 (Amar *et al*. 2010). Canopy closure and structural changes leading to shading and homogenisation of the woodland stands was common. There were regional differences yet most localities exhibited increased understorey (sub-canopy) cover suggesting structures were following a similar pattern of change most as a result of under-management (Amar *et al*. 2010). In contrast to the NFI woodland ecological condition findings for deadwood (Forestry Commission 2020), Amar *et al*. (2010) found there was an increase in deadwood between the 1980's and 2003-4 which they suggest was down to self-thinning by regenerating even-aged stems as they competed for the available resources.

Ancient woodlands in Britain are complex terrestrial habitats and have been subject to considerable conservation interest and efforts in the latter half of the 20th century by the statutory agencies, wildlife conservation charities and local authority countryside departments (Rackham 2003). During this time questions were raised about the benefits of reinitiating traditional woodland management practices without full consideration of alternative approaches based on the restoration of past habitats of the late Holocene

(Hambler and Speight 1995). Rackham (2003) countered this view arguing that any objectives for ancient woodland conservation must consider a broader ecological philosophy which include the archaeological, cultural alongside ecological interests. The characteristics of woodland that help promote biodiversity conservation in ancient woodlands are varied and will depend upon a range of local site-based factors which include management history (Woodland Trust 2020). Restoration of traditional practices such as coppice management may be worthwhile but should be guided by prior site evaluation for species of conservation interest (Watkins 1990). Perhaps, as Rackham (2003) suggested, 'varied styles of management are needed, even if some are less fashionable than others.' Indeed, Rackham (2008) argued that one threat to ancient woods is a lack of human intervention through periodic harvesting of trees and underwood (coppice); the increased shade in British woodlands has led to a reduction in woodland plants including communities associated with permanent grasslands found in woods (Peterken and Francis 1999). Conversely, modern day threats to ancient woods are mainly driven by human exploitation as external influences from pollution, nutrient enrichment from fertilizer, importation of pest species and diseases and increased browsing from an exceptionally high deer population (Rackham 2008). Evidence suggests pre-industrial landscapes (c. 1200–1750) including woodland in Britain would have been subject to varying degrees of intensive exploitation (including of deer), often at very localised levels creating a spatially diverse and highly heterogeneous landscape (Fuller *et al*. 2017). A combined knowledge of the needs of those species present, and understanding of past practices will allow for the better management of those surviving in ancient woodland where historic assemblages persist – with 'greater emphasis on physical disturbance and variability in prescriptions both temporally and spatially,' (Fuller *et al*. 2017). It is highly probable that unlike modern land use, which has partitioned woodland from farmland management systems, a more integrated and intimate pattern of exploitation existed (Rackham 1986). This varied over time depending upon changing resource needs and so allowed for the creation of localised and heterogeneously dynamic woodland management over the centuries (Fuller *et al*. 2017). Replicating the broad range of resource needs of ancient woodland species, (Figure 7), in the highly fragmented modern-day agricultural landscape is challenging, yet woodland management provides an opportunity to address at least some of these requirements (Fuller 2013).

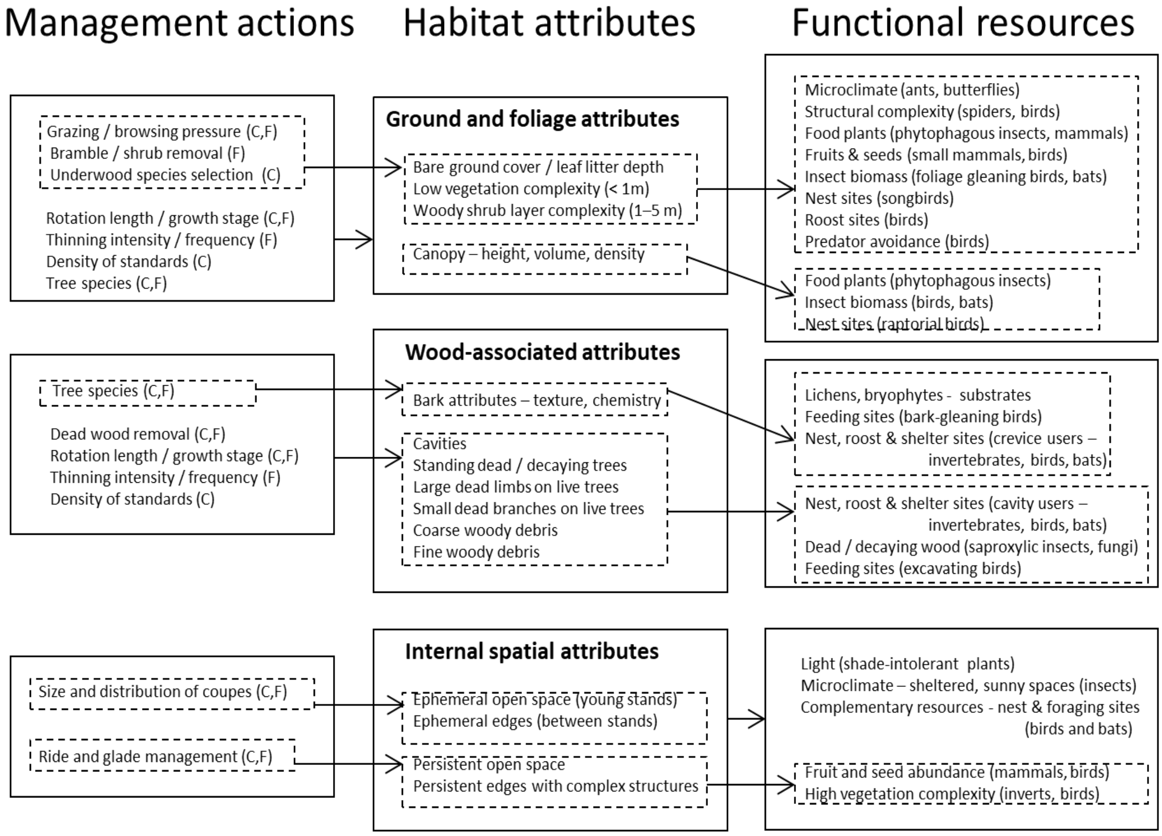

Figure 7. Expected relationships between forest management, habitat attributes and the resources provided for biodiversity. The linkages should be regarded as hypotheses based on existing knowledge of the broad resource needs of exemplar species groups and in many cases need verification through research. Management actions and decisions (left) affect three broad sets of habitat attributes (centre). These attributes affect resource provision for species living within forests (right). Relevance of management actions to active coppice and high forest (which I discuss below in 1.2) is indicated by (C) and (F), respectively. Relevant sources include Fuller and Warren (1991); Clarke *et al*. (2011); Fuller, Smith and Hinsley (2012). Reproduced from Fuller (2013) courtesy of John Wiley and Sons Licence number 5277670539219.

1.2 Silvicultural management in British Ancient Woodlands

1.2.1 Silvicultural systems

Silviculture is a process of tending trees within a woodland or forest to a point when they are harvested to meet a particular demand following which they are replaced (Ashton and Kelty 2018). In Europe, including Britain, coppice systems were the earliest known methods of managing trees although by the 18th and 19th Centuries the rise of high forest silviculture following a more systematic approach and attitude towards forestry as a science began to prevail (Savill 2015). Today methods for silvicultural management reflect the fundamental understanding of natural disturbances which typify the response of woodland vegetation through natural succession (Harmer *et al*. 2010). Stand development for instance, following a major storm, effectively reinitiates the ecological succession when most of the trees within an area have been blown down (Figure 8). In reality the duration at each stage is subject to variation dependent upon prevailing conditions with some sites taking most time in the stem exclusion phase or before where regeneration is halted through the effects of browsing herbivores (Harmer *et al*. 2010). The selection of a particular forest management system is related to site history as well as soil type, exposure and social, environmental and economic objectives and constraints. Undertaking any intervention including felling by thinning, clear-felling an entire stand or selectively felling individual trees or small groups can mimic natural disturbances and is useful in maintaining or enhancing particular species composition and diversity depending upon the scale at which it is undertaken (Harmer *et al*. 2010, Kuuluvainen *et al*. 2021). Nevertheless, care in manipulating the stand structure is required where the rate of change to which woodland species have adapted maybe slower than that being proposed and may negatively impact some species groups e.g., slow colonising plants, or destabilise remaining trees through increased exposure to wind (Ashton and Kelty 2018).

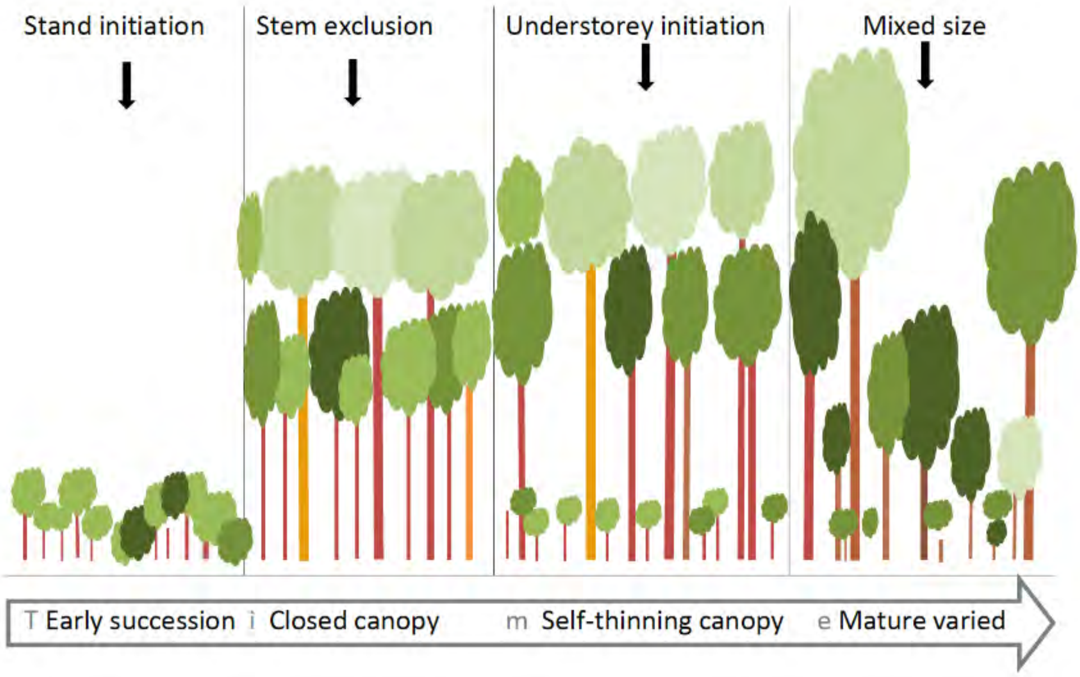

Figure 8. Schematic representation of a successional stand development model following major disturbance and removal of overstorey. (Adapted from Harmer *et al*. 2010).

Thinning is a term used to describe a broad spectrum of felling intensities from highly selective of individual trees, to groups of trees or removal of most trees (Kerr and Haufe 2011). Depending upon the objectives of management thinning at the stem exclusion stage is often undertaken to facilitate reduced competition of the crowns of canopy trees allowing dominant trees to increase their incremental stem growth yield for timber production (Harmer *et al*. 2010). In reality thinning meets multiple objectives often in the same stands; a) to enable re-initiation of the understorey through natural regeneration (or from planted saplings where regeneration is unreliable), by allowing more light to penetrate the woodland floor; b) to promote the viability of the most economically desirable trees that have been retained following removal of lower quality competitors; and c) for the benefit of habitat diversity where nature conservation is a priority to encourage structures to support the various functional resources. It can therefore, speed up processes found within the successional model or indeed arrest the succession at a desired point as found in the coppice management system described below. The natural restructuring of even-aged woodland can take in excess of 160 years to reach a mixed size stage ranging from open habitats in early seral stages to old growth characteristics associated with senescent trees (Peterken 1996). Different forest management categories may be classified by their method of regeneration and different age-classes of trees (Figure 9), which influences the structure of the stand, and may be considered along a gradient of intensity of management from clear-felling or coppicing to single tree selection (Savill 2015).

1.2.2 Drivers of change in woodland management – the coppice era.

Ancient woodlands in Britain were subject to silvicultural management which developed from the late Holocene wildwood. The earliest known use of round-wood derived from woodland management comes from Starr carr in Yorkshire, UK where archaeological evidence of cut and worked willow *Salix spp* and aspen *Poplus tremula* was identified, used as a platform for brushwood and possibly as a landing stage for boats, dated to the Mesolithic 9,000 years BCE (Conneller *et al*. 2012). Another early example known as the Sweet track, found during archaeological investigation in the Somerset levels, was an elaborate mixture of worked, split wooden poles constructed in the Neolithic 3800 years BCE, to enable passage across the wetland moors (Brunning 1995, Rackham 1990). Archaeology informs us that wood was widely used but very little evidence exists of systematic woodland management before and during the Roman occupation of Britain. The picture becomes clearer in the Anglo-Saxon period as place names revealed attachment to woodland and Anglo-Saxon charters describe the landscape within perambulations of settlements during land exchange . However, the 1086 AD Domesday presents us with the clearest idea of how much woodland existed; of more than 12,000 settlements with sufficient information approximately half possessed woodland (Rackham 1990). From the Norman conquest of 1066 AD, the management of woodlands could be broadly split into two forms, wood-pasture (or sometimes called pasture-woodland), and coppice. First wood-pasture which could be sub-divided into commons where ordinary people (commoners) were able graze livestock and collect fire-wood. Medieval deer parks were typically areas of wood-pasture subject to emparkment within a park-pale fence and were used primarily for maintaining deer for hunting and food. Secondly, Royal forests and their equivalent private chases used primarily for the benefit of ‘beasts of the chase’ including deer *Cervidae* and wild boar *Sus scrofa* as hunting preserves for the likes of Royalty, Noblemen and their followers (Rotherham 2018). Second, and more widespread, woods became coppice with frequent successive harvesting of the understorey, a system which changed little for at least 650 years until the start of its economic demise during the mid-19th century (Mason 2007).

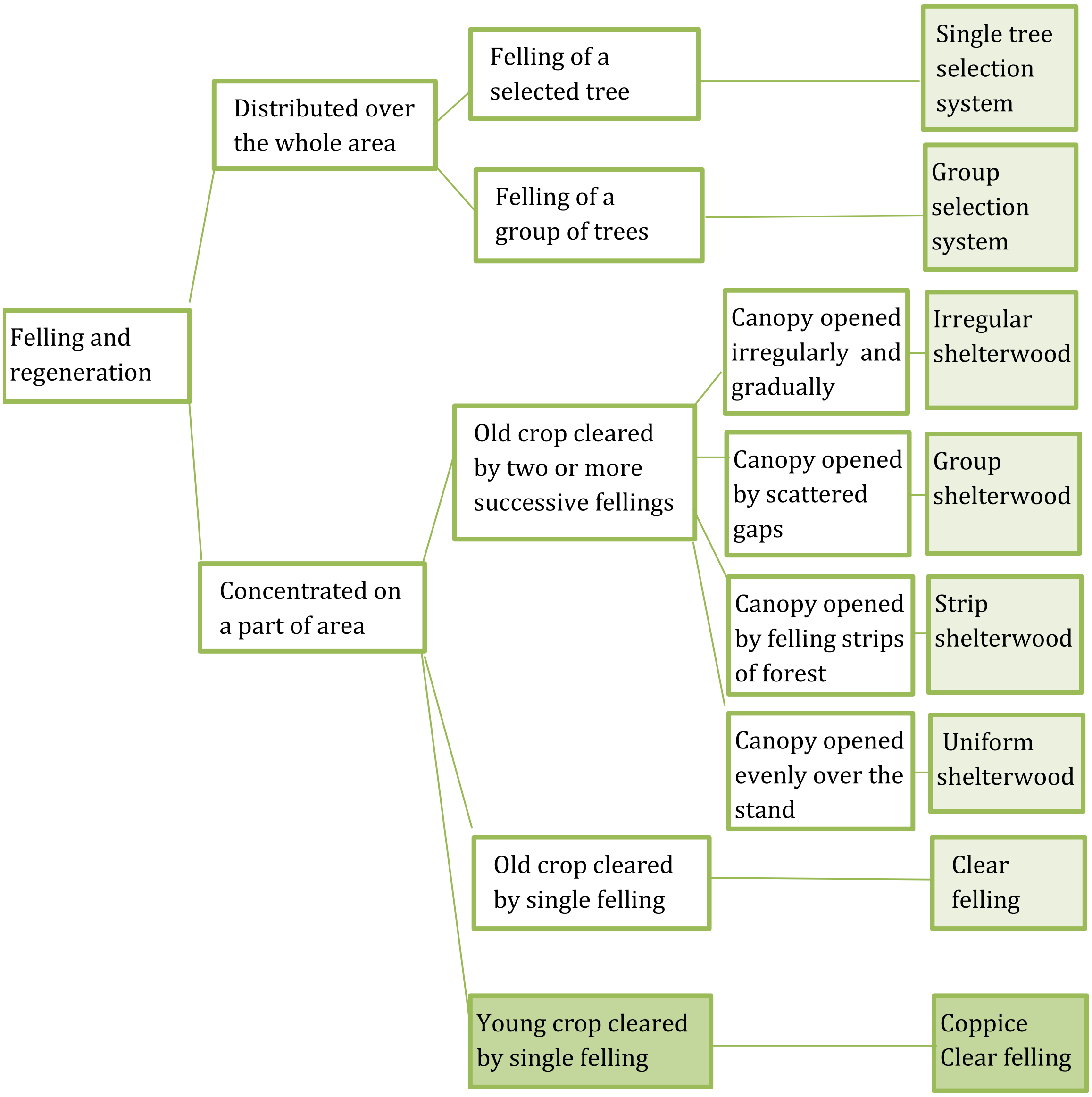

Figure 9. Silvicultural classification system for high forest adapted from Matthews (1991), high forest systems regenerate through natural seeding or via planting; coppice is included as a type of intensive even-aged system on short cycles, regeneration is vegetative from coppice stools.

Coppice could be woodland or parts of woods entirely subject to cyclical harvesting of underwood on rotations ranging between 7 and 30 years, known as simple coppice, or as coppice with standards (Harmer and Howe 2003). The latter included taller canopy trees (the standards) harvested for their timber on much longer rotations exceeding 70 years selecting i.e., Oak for construction of buildings and ships (Colebourn 1983, 1989). Throughout the Middle Ages up until the 19th century, coppice had become a highly regularised system of woodland management with woodlands divided up by internal plots through the construction of wood banks to demark ownership and tenure (Buckley andMills 2015). Coppice woodland was mostly enclosed to prevent grazing of livestock and deer, although in some woods temporary grazing was permitted once regrowth had reached a certain age at which it could withstand grazing animals moving through (Best 1998). Coppice products ranged from wattle and daub used in the construction of buildings, woven hurdles linked to sheep husbandry, firewood and the production of charcoal (Figure 10), used to smelt iron from the iron-ore up to the arrival of coal in the 18th century (Morris 2009). Before the widespread advent of coal in the 19th century charcoal was very important across Britain and Europe to fire the furnaces for glass production (Buckley and Mills 2015). The scale of the coppice industry is illustrated by the requirements for provisioning furnaces across Europe; a large 16th century furnace in the Forest of Dean required 53km^2 of managed coppice woods to sustain it (Crossley 2013), while the furnace at Bagot's Park, Staffordshire used approximately 1560 tonnes of wood a year from 19 ha of 15-year-old coppice (Crossley 1967). The use of Oak *Quercus spp*. bark for the leather tanning industry was also an important use of coppice but by the 19th century synthetic chemicals were developed and together with coal replacing charcoal, coppice wood as a resource began to decline (Buckley and Mills 2015). Coppice management developed by the 18th and 19th centuries to the extent that species were selected for particular use and planted to become almost pure stands of one or two species, Hazel *Corylus avellana* a good example in southern England in response to the burgeoning demand for sheep hurdles (Peterken 2015). Coppice management continued throughout the 19th century and into the middle of the 20th but demands for underwood declined substantially during this period, and accelerated between the 1947 and 2000 census of woodlands in Britain with an 80% reduction (Buckley and Mills 2015). As coal became more easily available demand for charcoal diminished across Europe, although its production continued in parts of central Europe well into the 20th century (Máliš *et al*. 2021). The rapid advancement of iron foundry technologies alongside the establishment of the railway network in Britain led to a corresponding reliance on coal much earlier than many other parts of Europe (Evans and Rydén 2017). Woodland management at this point continued along a trend for high forest silviculture and the arrival of plantation forestry which had begun in the 18th century, and succeeded coppice as the primary system (Savill 2015). Most ancient woodland in lowland Britain had been coppiced and following abandonment of this practice those which were not converted to high forest silviculture became closed canopy, even-aged and high forest from neglect (Kirby *et al*. 2017). Despite a revival of interest in coppicing particularly in nature reserves in the latter part of the 20th century, coppicing on a commercial scale is a specialised and limited in scale reflecting niche markets in the UK (Harmer and Howe 2003).

Figure 10. an example of a commercial charcoal production clamp showing a burn, above, with soil placed over the stack of prepared logs, below. A method in use in Europe since the Iron-age. Börzsöny, Hungary 2002.

1.2.3 High Forest; a British and European Context

High forest silviculture developed in earnest from the 18th century at a time when there were huge demands for timber resources to supply the needs of a growing population across an increasingly industrialised Europe (Savill 2015). Coppice silviculture (reliant on underwood harvesting) became redundant or was altered to timber production from the harvesting of canopy trees either through allowing coppice to develop as overstorey, e.g., through singling, from naturally regenerated seedlings, or were replanted using nursery grown stock (Harmer *et al*. 2010). There was also a switch from local supplies of wood to increased trade in timber between neighbouring European countries which prior to the advent of canals, railways and roads had been near impossible (Savill 2015). While woodfuel was still important for most people in the 18th and 19th centuries there were moves by governments to ensure strategic supplies of timber were available, for instance for naval use (Williams 2002). The burgeoning demand and growing concern for security of supplies was largely responsible for the development of new systems for producing trees which could be sustained, as well as predictable for future use (Williams 2002). This led to more regulated systems of governance which replaced the archaic, often complex forest laws in countries such as Britain (Rackham 1990) and especially France, where, simultaneously Forestry management was given a higher profile so that it became an important element of the state economy (Rochel 2015). In Germany in 1713 AD, Hans Carl von Carlowitz published *Silvicultura oeconomica* which proposed methods for sustainable yields across longer felling rotations alongside promoting the planting of fast-growing coniferous species, particularly Norway spruce *Picea abies* (Bürgi *et al*. 2015). This approach was adopted throughput central Europe and the mountainous regions of Italy and Slovenia (Johann 2006). Forestry was becoming a profession and taught in several Universities in Germany towards the end of the 18th century, and as a result there was wider adoption of plantations and even-aged high forest (Savill 2015). However, despite a move towards a reduced number of harvestable species, high forest systems of the 19th and 20th centuries could be varied and refined to suit conditions which included the use of natural regeneration (Troup 1928). A more scientific approach to silviculture which arose from the German forestry schools reflected a European social and economic context undergoing considerable changes in how land was used and timber resources were becoming increasingly valued during the 19th century (Johann 2006).

The variability of high forest systems is considerable across modern-day Europe; and particularly in mixed species forests requires detailed understanding and ecological expertise in the implementation of suitable management systems for the prevalent environmental conditions (Pach *et al*. 2018). Today we generally recognise three forms of high forest systems (See Figure 9); a) selection system, b) shelterwood system, and c) clear-felling creating even-aged stands, although there are many variants around these (Harmer *et al*. 2010). The foundations of ecologically minded forestry were well established by the turn of the 20th century using Continuous Cover Forestry (a broad approach covering a wide range of forest management systems and ideas, but also referred to as ‘back to nature’, and ‘close to nature’ in parts of Europe) which were based on natural processes including natural regeneration, developing a mixed-age cohort of trees and selection harvesting of single or small groups of trees (Johann 2006). Shelterwood systems, common in France, rely on natural tree regeneration following a thinned canopy, which once young saplings are sufficiently established, is removed, although there is usually a succession of preparatory thinning to develop the crowns of seed-bearing trees (Pach *et al* 2018). The result is a mixture of a partly even-aged stand development over much of the cycle, although this could be varied depending upon location and conditions (Peterken 1996). Clear-felling following even-aged high forest management involves the felling of an entire block of trees; anything between 1 and 20 hectares at maturity, (although UKWAS includes areas > 0.25ha with no upper limit (UKWAS 2018)) and became common especially in monoculture plantation forestry during the 19th and 20th century (Savill 2015). Some authorities have suggested that adopting this system mirrored an attitude towards nature, of dominance and subjugation which was prevalent during the industrial revolution (Johann 2006). However, modern day even-aged forestry can be varied and include systematic thinning of trees before a final felling of the entire block, followed by replanting of native or non-native trees or by relying on natural regeneration from either (Savill 2015).

The First World War gave impetus to the establishment in Britain of the Forestry Commission in 1919 such had been the demands on timber resources and difficulties in securing them during the early part of the 20th century (Raum 2020). In Britain, with a comparatively low number of tree species compared to mainland Europe, high forest has become the dominant silviculture with coniferous plantation accounting for more than half the area under production (Harmer *et al*. 2010). For broadleaf woodland high forest accounts for 97% which is a combination of managed woods and those which were formerly managed and developed a high forest structure (Hopkins and Kirby 2007). There are today many examples of lowland broadleaf woodlands which were neglected e.g., abandoned coppice which has become closed-canopy overstorey and even-aged (Hopkins and Kirby 2007). During the 20th century following the establishment of the Forestry Commission the area of woodland cover in Britain increased from 4.7% to 13.5% (Harmer *et al*. 2010). The ensuing large-scale afforestation primarily entailed planting introduced Sitka spruce on open land including areas of semi-natural habitat such as moorland and bogs of the uplands, much of which was in Scotland, with financial incentives and tax breaks to help offset costs for landowners (Tsouvalis 2000). During the 1980's the nature conservation movement highlighted the ecological problems of widescale planting on important upland moorland habitats (Avery and Leslie 1990) along with effects on some water catchments with increased acidification from chemical changes in soils caused by coniferous leaf-litter (Ormerod and Gee 1990). Coniferous species such as Sitka spruce being relatively fast growing are commonly harvested before 60 years old and remain economically important in many areas of northern and western Britain (Quine 2015). Broadleaved plantations are generally associated with new woodland creation in Britain since the introduction of the broadleaved policy of 1985 which encouraged amenity tree planting, or following removal of conifers from previously broadleaved woodland (Harmer *et al*. 2010). Broadleaf trees managed under high forest silviculture are harvested between 50 and 160 years old depending upon species, quality and uses (Kerr and Evans 1993). In Britain perhaps the best-known example of a continuous cover system is in the Chiltern Hills which developed following transformation to favour Beech *Fagus sylvatica* to supply the furniture industry (Peterken 1981). High forest management generally dominates much of European forestry although its ecologies will depend on its origin, species mix and subsequent management; on one hand high forest derived from the long-term traditional management of ancient woodland coppice, on the other non-native plantation. With 44% of all woodland known to be certified under the UK woodland assurance scheme, (a sustainable silviculture standard designed to reflect the requirements set out in the governmental UK Forestry Standard (UKWAS 2018)), there is likely to be a significant proportion of under-managed woodland in Britain today (Forest Research 2021). For England 41% of woodlands are estimated to be unmanaged (Royal Forestry Society 2019).

1.2.4 Irregular Silviculture – Transformation from Europe to Britain

The 19th century gave rise to an increasing move towards selective systems of forestry in Europe as an alternative response to the purely economic and production utility of clear-cutting even-aged plantations (Johann 2006). This was primarily down to concerns over the vulnerability of homogenous stands to insect outbreaks, storm susceptibility and frost damage alongside a better understanding of plant and soil sciences (Jacobsen 2001). Despite considerable debate over definitions, there are many variations of selective and irregular management; the principles revolve around utilising adaptation to site conditions and avoidance of clear-cutting with varying degrees of reliance on natural regeneration of trees (Bürgi 2015). At the turn of the 20th century ecology was in its infancy yet understanding ecological concepts in the natural succession of woodland vegetation and working with woodland dynamics in tree species selection, helped to further promote the idea of close-to-nature-silviculture (Bürgi 2015). Key to this was knowledge of localised site conditions, soils, topography, tree growth, especially incremental increase in stem volume and climatic constraints. A move away from clear-cutting to sustain timber resources was adopted by the French forester Adolphe Gurnaud who promoted the concept of optimal distribution of tree size-classes in every compartment which was a fundamentally different approach (Pommerening *et al*. 2004). The ideas of Gurnaud centred around the way forest compartments must be managed, independently of each other maintaining high growth rate, where timber yield and volume increment are assessed by comparing subsequent inventories; the amount removed is equal to the increment if the forest is in “balance”. Importantly, tree selection is made by foresters based on their experience and knowledge of the forest, which has helped it win support by private woodland owners opposed to constraints imposed by state forestry (Nocentini 2021). Ideas around single tree selection were further developed by Alfred Möller a German mycologist who saw the forest as an organism and that maintaining it as a functioning ecosystem was integral to sustaining silvicultural management (Bürgi 2015). Möller’s ‘Dauerwald’ (continuous forest) ideas from the 1920’s shaped the Working Group on Close -to - Nature Silviculture, which eventually became Pro Silva Europe an organisation which continues today to promote the principles of continuous cover forestry through a country wide network (Bürgi 2015).

The demise of coppice and rise of even-aged stands in Britain was largely as a result of the drive towards high forest management, particularly plantations managed through clear-cutting and replanting of coniferous species between 1945 and 1980 (Hopkins and Kirby 2007). The remaining broadleaved woodlands in lowland Britain developed into high forest from coppices because they were largely unmanaged (Kirby *et al*. 2005). Despite the continued increase of plantations across Europe during the 20th century (McGrath *et al*. 2015) there was a strong revival in the development of CCF during the 1980's and adoption of ideas around mimicking natural disturbances through selective felling. From this time the use of CCF and CNF has been adapted to include mixed and broadleaved forests across France in particular but adopted by a few in the UK and Ireland mostly by private landowners, despite opposition from state-run forestry (Bürgi 2015). Recent studies have highlighted how CCF can support a range of ecosystem services making it increasingly attractive in providing various social, economic and environmental benefits which modern forestry is expected to provide (Kerr 1999, Pukkala *et al*. 2016). Moreover, CCF is being promoted by the UK Forestry Commission and Natural England as a way of increasing resilience and adaptation of forest management systems to the effects of a changing climate (Forestry Commission 2020, Rural Payments Agency and Natural England 2020). Today an estimated 30% of European forests are managed under a form of CCF yet uncertainties remain around its wider adoption to meet with the range of demands placed on forest and woodlands due in part to lack of evidence of its suitability and limited experience in the forest management sector (Mason *et al*. 2022).

In British nature conservation there have been divergent opinions expressed over the merits of restoring coppice management in lowland broadleaved woodlands. Hambler and Speight (1995) challenged what they saw as the dogmatic views surrounding the use of traditional coppice. They argue such an approach caters for comparatively few organisms associated with early successional scrub at the expense of later seral stages where a more dynamic habitat complexity can develop and thus a broader compliment of habitat niches supporting a wider assemblage. Nevertheless, the demise of coppicing has led to a corresponding reduction of some species associated with the continuity of gap creation in British woods, e.g., birds including nightingale *Luscinia megarhynchos* and butterflies like the pearl bordered fritillary *Boloria euphrosyne* (Fuller and Warren 1991). There is a genuine concern too for the loss of cultural association and species affiliated with a coppice system prevalent since at least the neolithic (Rackham 2006). A particular challenge in Britain is to accommodate a range of species along the successional gradient model found in woodlands which may go some way to address concerns across the spectrum of debate (Colak *et al*. 2003). A key question is can high forest management systems achieve the necessary structures to maintain species associated with traditional landscape practices (Kirby *et al*. 2017)? Or indeed adopt natural woodland processes whilst including anthropogenic intervention (Colak *et al*. 2003). In a changing environmental context that includes climate driven impacts and those from rising deer numbers, there is increasing focus on wilding land using natural processes where CCF may be complimentary (Bennett and Morgan 2018). The Association Futaie Irrégulière is a group of foresters mainly managing broadleaved forests and woodlands in France based on single tree selection; the network promotes dissemination of knowledge and has established research stands across the country which has, since the early 1990's, included several woodlands in the UK (Susse *et al*. 2011), (Figure 11). The collection of forest mensuration data includes overall stand condition, individual tree performance, biological data mainly focussed on deadwood and microhabitat features associated with old growth characteristics, alongside economic performance and provides a powerful tool for maximising income using irregular silviculture (Susse *et al*. 2011). For nature conservation CCF including irregular may offer potential for a broad range of species associated with early succession and old growth characteristics e.g., the retention of important habitat trees (Gustafsson *et al.* 2020). High forest systems with mixed growth stages in CCF managed forests are analogous with natural woodland, more so than coppice which is primarily based on the transient stages of young woodland growth (Peterken 1996). Another characteristic of the transformation towards CCF management is that it is purported by its advocates to be flexible in being adaptive to changing circumstances and that resilience (to retain overall woodland structure and function) is integral by following ecologically based principles (Diaci *et al*. 2011, Brang *et al*. 2014). However, the development of multi-aged forestry also requires experiential insight from foresters about how they may skilfully manipulate forests and woodlands towards resilience and sustainability, in an increasingly dynamic market to meet with the multiple demands of society (O'Hara 2015). The current UK Forestry Standard promotes the restructuring of even-aged woodlands to uneven-aged to create diverse mosaics of species, sizes, ages, spatial scales and regeneration cycles (UKWAS 2018). As humanity faces threats from a changing climate and increased expectations are placed on forests and woodlands to provide a range of ecosystem services and public goods, CCF and CNF silviculture is likely to be tested to provide a suite of novel solutions in the coming decades (O'Hara 2015, Gamborg and Larsen 2003).

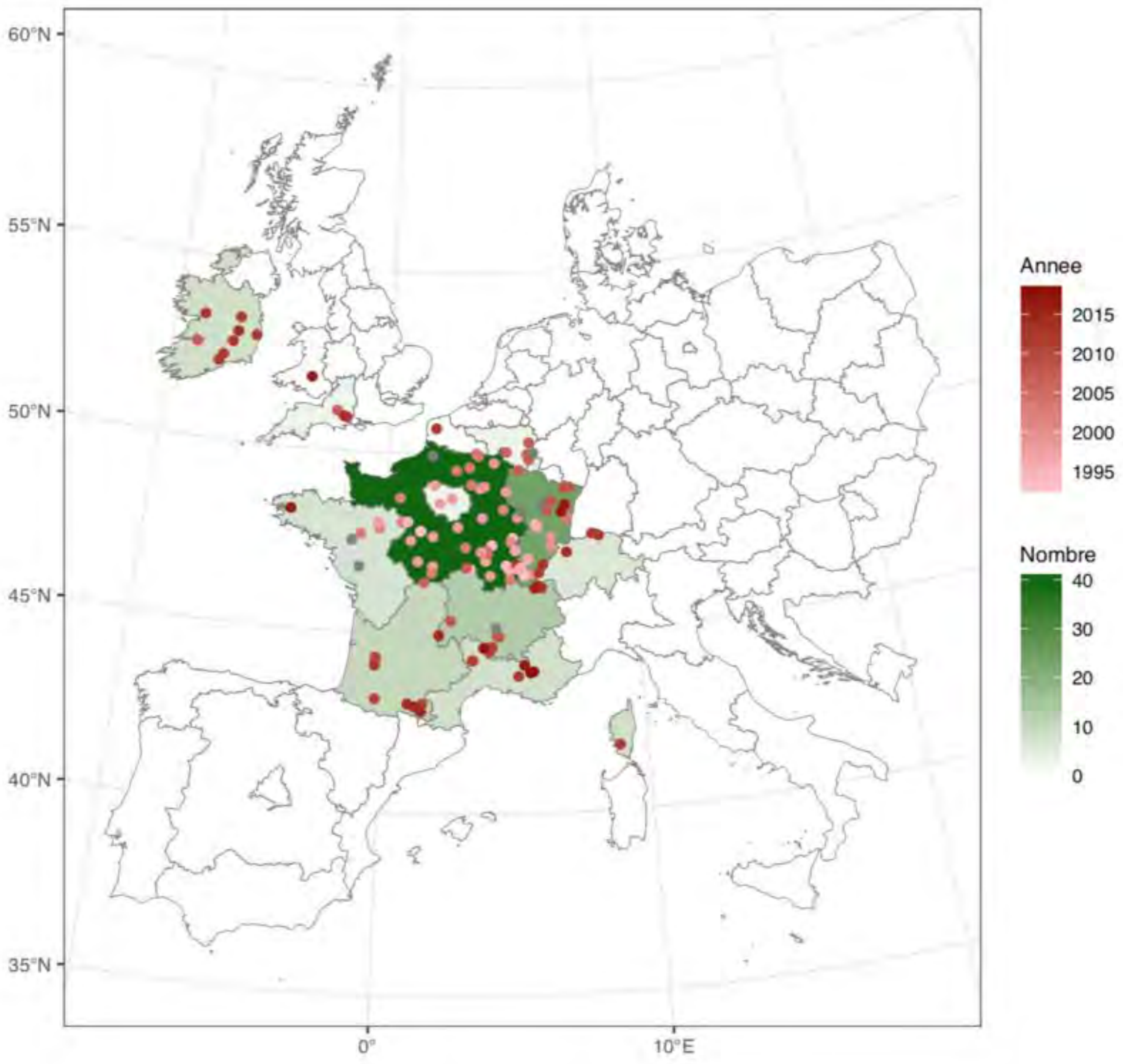

Figure 11. Location of woodlands contributing to the AFI network, Annee = Year, Nombre = Number of woods in each region.

Chapter 2 Study Area Description and Overview of Research

2.1 Study Area: Background and Description

2.1.1 Study Area: Description of Research Woodlands

The study area on the Rushmore Estate lies within the Cranborne Chase and West Wiltshire Downs Area of Outstanding Natural Beauty on the Dorset, Wiltshire border Latitude: 50°.95’ North, Longitude: -2°.08’ West, (Figure 12). The underlying geology is chalk laid down from marine sediments during the late Cretaceous period 66 to 100 million years ago. The landscape is one of rolling chalk downland with expansive chalk plateau which arose after the major geological uplifting around 37 million years ago and has been subsequently influenced through post-glacial wash and erosion (Natural England 2013). The Rushmore Estate woodlands are predominantly found on the plateau and gently sloping dry valleys between 100 metres and 260 metres above sea level but extending to the top of the escarpment. The soils reflect the parent rock in being rendzinas with chalky, flinty material on the plateau and exposed slopes, typically with high pH, due to free calcium, although deeper soils of brown-earth have developed where woodland cover has persisted over many centuries. Clay with flints maybe moderately acidic where the influence of chalk is not prevalent, elsewhere soils that developed a mull humus may be neutral pH (Smith 1980). There is no surface water within the woodlands estate although the porous nature of the soils and underlying chalk has a high water holding capacity and is not drought-prone (Poore 2016). Average rainfall is 896mm (Met Office Undated). The Ecological Site Classification version ESC 4 (Forest Research https://www.forestresearch.gov.uk/tools-and-resources/fthr/ecological-site-classification/) identifies the site which has a warm, moderately exposed and moist climate. The soils are slightly dry moisture status and rich nutrient status.

Figure 12. Location of Rushmore Estate study area within Cranborne Chase and West Wiltshire Downs Area of Outstanding Natural Beauty in central southern England, United Kingdom.

The Rushmore estate sits entirely within the designated landscape of the Cranborne Chase and West Wiltshire Downs Area of Outstanding Natural Beauty established in 1981 (Natural England 2013). The primary purpose of AONB designation is ‘conserving and enhancing the natural beauty’ of the area. In 1991, the Countryside Commission stated ‘In pursuing the primary purpose of designation, account should be taken of the needs of agriculture, forestry and other rural industries and of the economic and social needs of local communities.’ Particular regard should be paid to promoting sustainable forms of economic and social development that in themselves conserve and enhance the environment (CCand WWD AONB 2019). The AONB landscape is also of international importance. The International Union for the Conservation of Nature (IUCN) recognise it as a Category V Protected Landscape which they define as: *A protected area where the interaction of people and nature over time has produced an area of distinct character with significant ecological, biological, cultural and scenic value, and where safeguarding the integrity of this interaction is vital to protecting and sustaining the area and its associated nature conservation and other values.* (Lausche 2011). In 2013, the IUCN UK Committee reaffirmed the Category V status of all AONBs, confirming the significant contribution they make to conserve the UK’s biodiversity (CC and WWD AONB 2019). The Rushmore woodlands form part of the Wooded Chalk Downlands Landscape Character Area (3a).

The key aims under the Cranborne Chase and West Wiltshire Downs Area of Outstanding Natural Beauty Management Plan 2020- 2024 (CCand WWD AONB 2019) for "Conserving and Enhancing the Outstanding landscapes" are:

- All natural resources in the AONB are sustainably managed.
- Wildlife thrives in the AONB and is able to move freely around the area.
- The natural environment to be healthy and resilient to the effects of climate change.

The Rushmore study area covers 442 hectares of ancient semi-natural broadleaved woodland all of which is within the Cranborne Chase woodland Site of Special Scientific Interest (SSSI). The Rushmore woodland form 91% of the SSSI (Poore 2016). The SSSI was designated in 1989 under the Wildlife and Countryside Act (1981). "Cranborne Chase SSSI is one of the largest tracts of ancient semi-natural woodland in southern lowland England. It is a mosaic of oak / ash / maple / hazel woodland on base rich soils influenced by the underlying chalk, interspersed with oak / birch / hazel woodland on base poor soils of the overlying surface deposits" (Natural England undated). Due to historical continuity of woodland cover and because the Rushmore estate woodlands are the most extensive and contiguous tract in central southern England, the site has the most diverse lichen assemblage in the region outside of the New Forest (Natural England 2013). The Rushmore Estate woodlands are a mixture of two National Vegetation Communities (NVC), being composed of W8 Ash *Fraxinus excelsior*, Field Maple *Acer campestre,* and W10 Oak *Quercus robur*, Ash *Fraxinus excelsior* stand types (Rodwell 1991). The latter includes stands of Birch *Betula pendula* which in some areas forms the dominant stand, while Beech *Fagus sylvatica*, Oak and Field Maple stands are locally prominent with Whitebeam *Sorbus aria* on the dryer soils (NCC 1989). There is a rich assemblage of shrub species representative of variations in the soil with Spindle *Euonymus europaeus*, Holly *Ilex aquifolium*, Dogwood *Cornus sanguinea*, locally common Butcher's broom *Ruscus aculeatus*, Old Man's beard *Clematis vitalba* and Bramble *Rubus fruticosus*. The ground flora is especially rich and one of the primary reasons for the SSSI designation with 57 species of ancient woodland indicator plants (AWI) recorded alongside nationally important lower plant communities (NCC 1989).

2.1.2 The Cultural Significance of Woodland Development in Cranborne Chase

With a rich landscape history, the area of Cranborne Chase has been subject to considerable archaeological studies which has revealed chronological insights into its vegetation history and land-use patterns from the Mesolithic onwards (Green 2000, Allen 2002). The chalklands of Cranborne Chase has produced more prehistoric evidence of human activity at this time than any other chalk landscape in Britain (Green and Allen 1997). Analysis of pollen and land snail assemblages from deposits found within a naturally sunken shaft (known as the Fir tree shaft) in the chalk at Down Farm, Sixpenny Handley suggest humic soil conditions were present with Boreal woodland (i.e., Mesolithic- c. 7,500–5,000 BCE), cover likely to have comprised Scots pine *Pinus sylvestris* and hazel *Corylus* avellana (Green and Allen 1997). Furthermore, analysis of deposits from peatlands of the Allen Valley within Cranborne Chase suggest these Mesolithic woodlands were considerably more open and patchily distributed than the presumed closed canopy climax woodland (French *et al*. 2003). Given the recurring amount of charcoal found within the strata of the Fir tree shaft and the considerable quantity of flint scatters, (Figure 13), it has been suggestested humans were influencing the characteristics of the vegetation of the Cranborne Chase chalklands during the Mesolithic (Allen 2002, French *et al*. 2003). However, and in contrast to other chalkland regions in southern Britain, (Figure 14), this evidence suggests the landscape was already lightly wooded with open grassland, because soils were not fully developed as either light brown-earth or Rendzinas more commonly associated with thin soils of chalk downland (Allen and Gardiner 2009). It appears that the hunter-gatherer people of the time were attracted to the ecological diversity of those mosaics of wooded/open habitats which were occupied by wild animals including deer which they exploited along with a range of fruits and seeds (Allen and Gardiner 2009). The development of the native vegetation and interaction between people and ungulates in Cranborne Chase, has direct relevance to models of past woodland equilibrium postulated by ecologists particularly Vera (2000) and Kirby (2004), (Figure 15), and further referenced by palaeoarchaeologists Allen and Gardiner (2009) and Allen (2017), in their research on Cranborne Chase. Recent discussions around modern rewilding of landscapes have focussed on trying to understand a) the degree of woodland cover and openness in the Holocene and, b) what we might be able to usefully derive from our understanding of landscape characteristics that may have been prevalent before farming began in the Neolithic, towards current land management philosophies (Hodder *et al*. 2009). Pertinent to which is the understanding of natural processes used in CCF and irregular silviculture, which is having resonance with several of its promoters who contend that rewilding is complementary (Bennett and Morgan 2018).

Figure 13. Neolithic flint working, Chase wood, Sixpenny Handley, Dorset, September 2014.

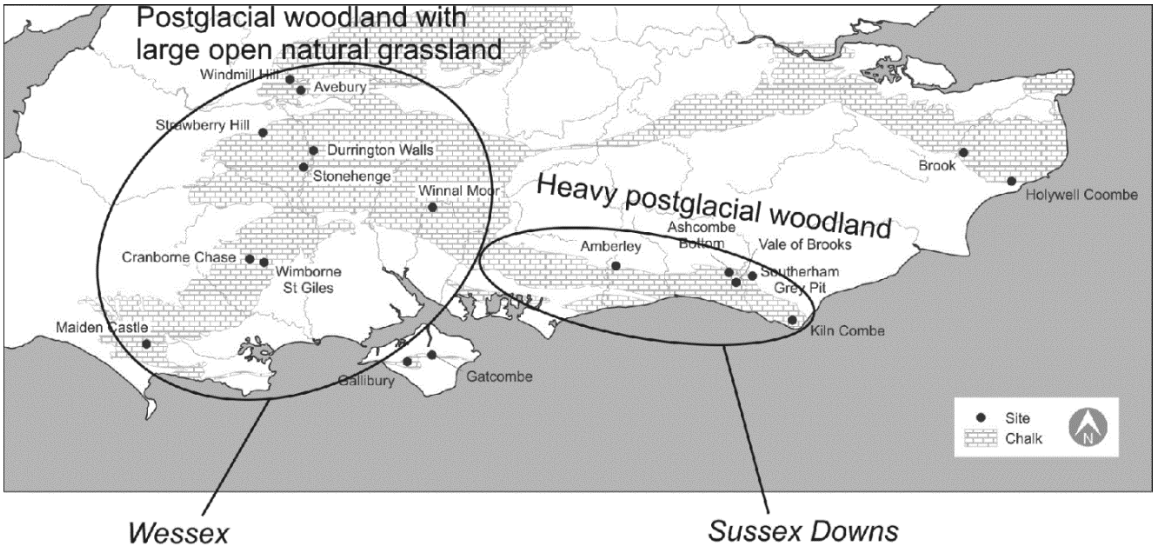

Figure 14. Contrasting postglacial woodland development between the Wessex Chalklands including Cranborne Chase, and the South Downs of Sussex. Evidence suggests the former was more open in character while the latter was densely wooded. (Figure © Mike Allen, from Allen (2017)).

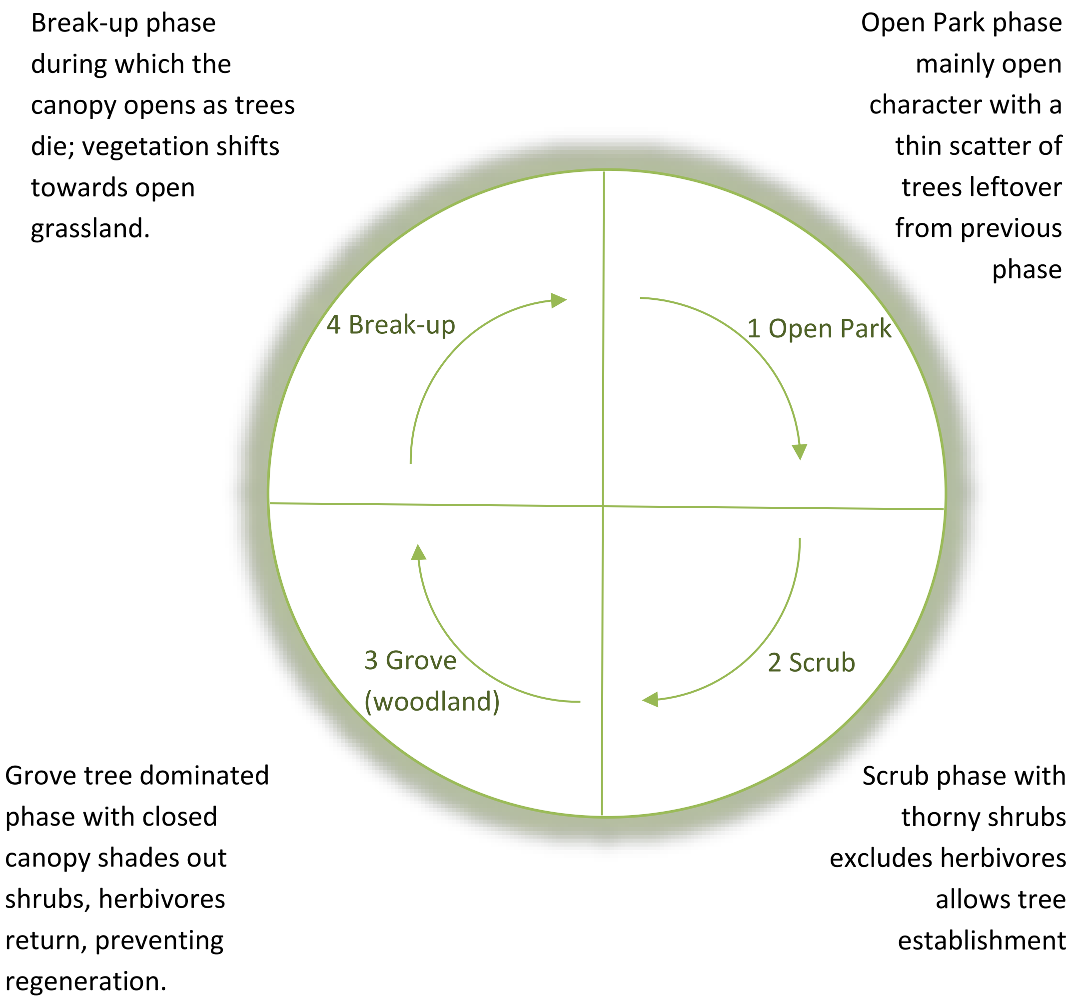

Figure 15. Model of woodland-scrub-grassland development adapted from Vera (2000) and added to by Kirby (2004) to include a break-up degeneration phase of woodland.

The expansion of human settlement across Cranborne Chase chalklands reflected the relatively close proximity of a diverse range of habitats, and continued throughout the Neolithic and Bronze Age. The area developed into a sacred landscape full of social and cultural meaning as is evident from the hundreds of prehistoric burial and ritualistic earthworks of the area (Green 2000). By the time of the Roman occupation 43 AD a more regularised system of land management existed with clearance of woodland followed by cultivation of the lighter soils (Rackham 1986). This was set to change following the demise of the Roman empire in 410 AD as the Saxon settlers occupied river valley locations and the old chalkland villages of the previous occupiers became neglected (Green 2000).

Rushmore lay at the heart of Cranborne Chase an area which despite clearance over much of the surrounding chalk landscape remained largely wooded (Allen & Gardiner 2009). The Chase was to become an important hunting preserve, established by Saxon charters under the Lordship of Bictric son of Algar (Hawkins 1980). Following the Norman Conquest of 1066 AD, the Chase transferred to Matilda of Flanders, the wife of William the Conqueror (Crittall 1959). Although not established as a Royal Hunting Forest its status as a Chase meant that it was subject to similar forest laws with rights given to those who owned and managed the land with the Chase court held twice-yearly at the village of Cranborne, Dorset (Hawkins 1980). The system was two-tiered with an overall Chase ownership covering the outer perambulation which extended for 800,000 acres (323,748 ha) and individual Barons who were awarded tenancy of estates with a peasant workforce who lived and worked on the land which followed the feudal system that operated in Medieval England (Crittall 1959). Over many centuries ownership of the Chase changed and included Royalty from King John who became the Earl of Gloucester at the end of the 12th century, until King James 1st in the early 17th century (Barker 2006).

Throughout the medieval period until the early 19th century common rights existed over the woodland. There were areas of enclosed coppice that were protected from grazing to ensure the regrowth of trees and also more open wood pasture with rights to firewood ‘wood bote’ and rights to graze livestock, which often blurred the distinction between woodland and grassland in some areas at the edges of Rushmore (Poore 2016). There were rights to graze some of the coppices once the regrowth had attained a certain height and as with the other rights would have been subject to close regulation (Peterken 1981). The Chase as a regulated land-use helped to preserve the woodland character so that by the 15th century underwood managed as coppice was well established as a silvicultural system across most of the woodlands. To uphold the forest laws and resolve disputes a number of Chase officials were employed as wood wardens, foresters, keepers and rangers, (Figure 16), who often dealt with issues around the protection of ‘beasts of the Chase’ especially deer, protection of the ‘vert’ or vegetation in and on which the deer lived, and husbandry of the land (Hawkins 1980). For instance, in Rushmore in 1554, fines were imposed for allowing un-ringed pigs to pannage in the Chase wood, and coppice being left un-cut past its usual harvest time was also met with punishment meted out by the Cranborne Manor court. However, fines were the most commonly used punishment as it raised revenue for the Chase owner and ultimately the Monarchy (Crittall 1959).

Figure 16. An engraving from 1857 of a Cranborne Chase Keeper in his protective forest night dress, cutlass and staff, Rushmore 1815. Salisbury Museum© Salisbury Museum /Bridgeman Images

Extensively managed coppice woodland at Rushmore was well developed by the 14th century; records in the 14th and 15th century show an elaborate system of strictly controlled, temporary, ‘dead’ hedging being used to protect recently cut coppice from browsing. National statutes covered this practice and in 1483 AD a law was passed which increased the maximum period of enclosure from 3 to 7 years (Poore 2016). Coppice was sold by the acre with an additional area given to provide material for the hedge and a contra payment ‘by the perch’ to the purchaser for the construction of the hedge. The Chase map of Aldwell 1618 AD shows extensive, named coppices across much of the woodland at Rushmore. In a survey of 15 coppices here in 1547 AD the current years of growth varied from 1 to 28 years with 6 in the 20’s. The coupe size ranged from 8 to 24 acres (3.2 to 9.7 hectares) that would have produced material largely for firewood. It appears that long rotations were the norm until after 1829 AD following disenfranchisement (abolition) of the Chase rights (Hawkins 1980). The long rotations and restrictive environment also suggest that little conscious effort would have been made to alter the species composition of the underwood (Poore 2016). However, Rushmore became an important area for the coppice industry in the 19th century with many woodland compartments being planted with hazel to meet with the burgeoning demand for hurdles for the folding (penning in) of sheep on the chalk downs and water meadows around the many chalk streams of the area (Hawkins 1980).

Wooded commons (wood pasture) of Rushmore which later developed into woodland existed at Farnham Common and the adjacent Tollard Green. Despite the disenfranchisement of the Chase Rights in 1829 much of the woodland at Rushmore survived, more so than on other estates within Cranborne Chase. Common grazing rights had been removed from most of the Wiltshire woods of the Chase in 1794 and in Dorset in 1796 and 1852. In the 19th century Bridmore Green and Farnham Common Wood were planted with hazel and Old Hewitts was cleared. Only Tollard Green survived as grazed woodland into the 20th century (Poore 2016). The Rushmore woodlands at the beginning of the 19th century were dominated by hazel and birch underwood while high forest stands dominated by ash and oak were a rarity; this situation had probably existed for centuries previously. After disenfranchisement coppice management intensified and Rushmore became one of the principal centres of the hazel underwood trades which served the wood trade across Wessex; Dorset, Wiltshire and Hampshire (Colebourn 1983). This remained the case up to the 1950’s and underwood auctions continued until the early 1970’s. The main products were hurdles for sheep folding, and spars for thatching ricks and houses (Poore 2016, Hawkins 1980). Today (2022) hurdle making continues with a single hurdle-maker providing hurdles for garden screens and ornamental fences, (Figure 17). There are several stands of pure Birch *Betula pendula/pubescens* coppice cut on short rotation for use as horse jumps, revetments for riverbank restoration and besom brooms (Figure 18); sales of the latter have increased since the Harry Potter films!

Figure 17. Don Taylor, Hurdle-Maker constructs a hazel hurdle from the coppice he has recently cut, a process followed by successive generations of coppice-workers for at least 500 years in the Chase woods. Rushmore, Wiltshire, April 2014.

Figure 18. Produce from an area of pure Birch *Betula spp* coppice cut on a 3–4-year rotation stacked awaiting collection for use as horse jumps and revetments for river bank restoration. March 2014.

2.1.3 Silvicultural Description of the Study Area

Following the national trend in the 20th century there was a steady decline at Rushmore of coppice management up to World War One and a rapid decline thereafter (Poore 2016). Around 150 acres (60 ha) was sold annually up to 1913 (indicating an on-rotation (cutting every c.7 years), area of 1200 to 1400 acres (485 to 566 ha)), 40 acres (19 ha) in 1946 and less than 10 acres (4 ha) when the underwood auctions ceased in the mid 1970's. With the decline in coppicing after the Second World War, there was some conversion of coppice woodland to conifers and more locally to beech. By the mid-1980's, however, over half of the Estate's 2000 acres (800 ha) of woodland remained as neglected coppice woodland with a direct link to the woodland area which had attracted the attention of the Saxon Rulers (Poore 2016). Because of this continuity and despite cessation of active management, Cranborne Chase's ancient semi-natural woodland with its long history of coppice management became recognised as being of great importance for nature conservation (NCC 1989). It contains the largest block of semi-natural woodland suitable for restoration to coppice management in southern Britain (NCC 1989). Potentially it could support sustainable populations of a range of woodland plants, woodland birds including garden warbler *Sylvia borin* and insects, such as fritillary butterflies, and mammals, including bats *Chiroptera* and hazel dormouse *Muscardinus avellenarius*, which are reliant on structurally varied habitat, which has become increasingly reduced and fragmented negatively affecting their conservation (NCC 1989, Bright and Morris 1996). In 2009 the Cranborne Chase woods became one of four ancient woodland priority areas in south-west England identified by the Forestry Commission as robust, permeable networks of existing woodland habitats with the potential for expansion, and to link areas of suitable habitat that are otherwise fragmented (CCandWWD AONB 2019). Between 1991 and 2009 the Rushmore Estate and Natural England, with assistance from the Forestry Commission, were engaged on a major project to restore underwood stands for coppice where appropriate. Across the remaining native woodland area, the aim has been to promote the development of semi-natural high forest, particularly using irregular high forest (Poore 2016). There are 442 ha of ancient semi-natural woodland on the Rushmore Estate with a common history, mostly from coppice and some areas of former common land which were planted or reverted to woodland (Poore 2016). The transformation of some of the semi-natural woodland to an Irregular high forest began in the 1980's and continues to the present day with various stands in different stages of development, while in-rotation coppice of hazel and pure birch stands remains actively managed (Table 2, and Figure 19 and Figure 20). Transitional high forest are stands undergoing the first stages of transformation towards Irregular (typically with their first or second silvicultural intervention within the preceding 5 – 8 years) and are typically derived from even-aged high forest, overstood neglected coppice or limited intervention stands (Poore 2016). The latter are stands with a mix of undermanagement from former coppice or high forest and have typically not been managed for at least 50 years in the case of coppice or 30 years for high forest (Poore 2016).

Table 2. Summary of ancient semi-natural broadleaved woodland and current silvicultural management at Rushmore used in the study.

Woodland type *UK Priority Habitat**	**Silvicultural Management**	**Area (ha)**	**% Broadleaf Wood**	**% SSSI Area**
Ancient Semi-Natural Broadleaved Woodland	Irregular High Forest	137.1	31	25.2
	Transitional High Forest	97.4	22	26.6
	Limited intervention	102	23	16.5
	Coppice	106.1**	24	23.5
Total		442.6	100	91.8

* Habitat of principal importance in United Kingdom s41 Natural Environment and Rural Communities Act 2006 (JNCC 2011).

** 84.3 ha of hazel dominated and 21.9 ha of birch dominated coppice

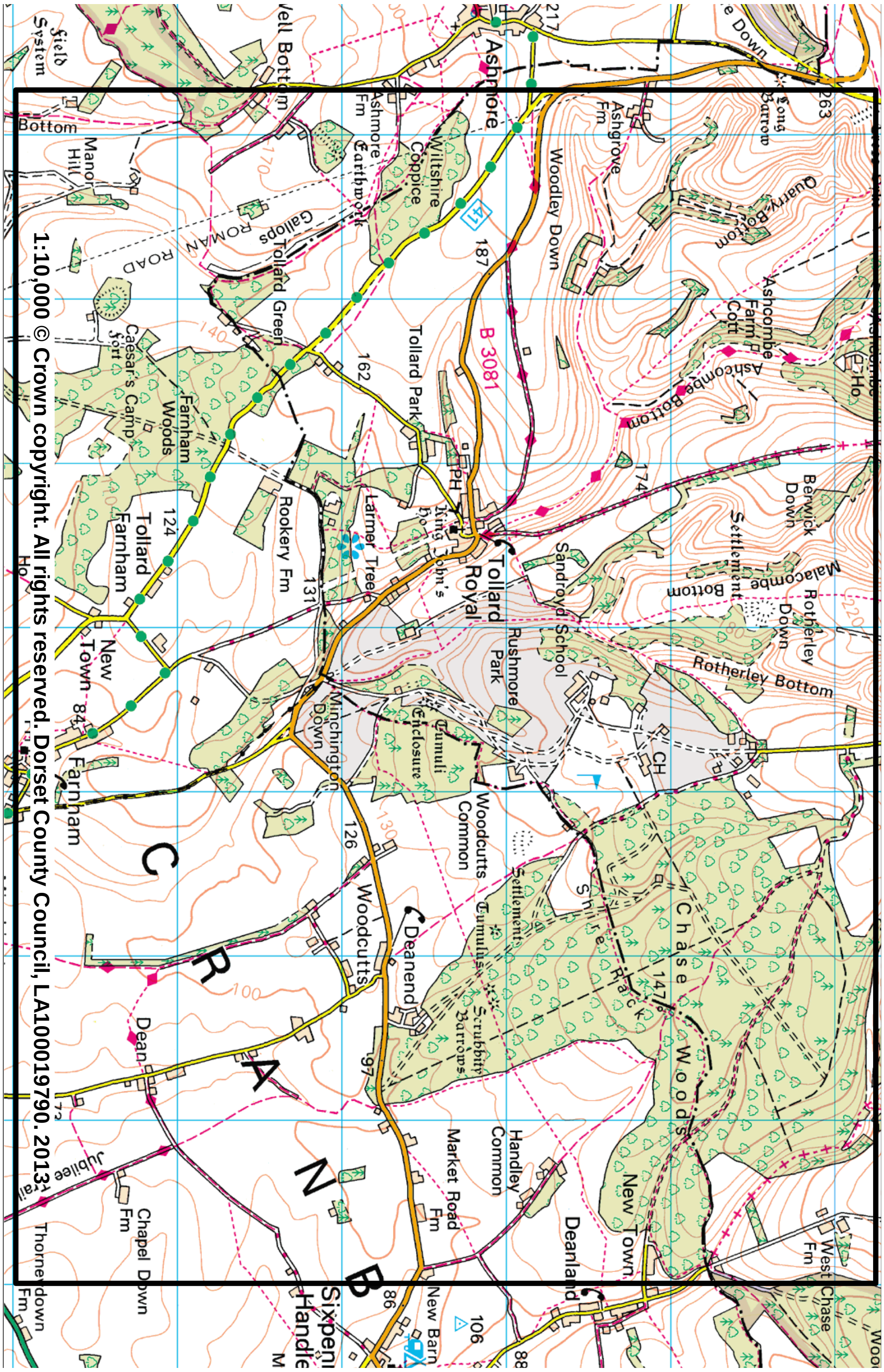
1:10,000 © Crown copyright. All rights reserved. Dorset County Council, LA100019790. 2013

Figure 19. The Cranborne Chase woodlands.

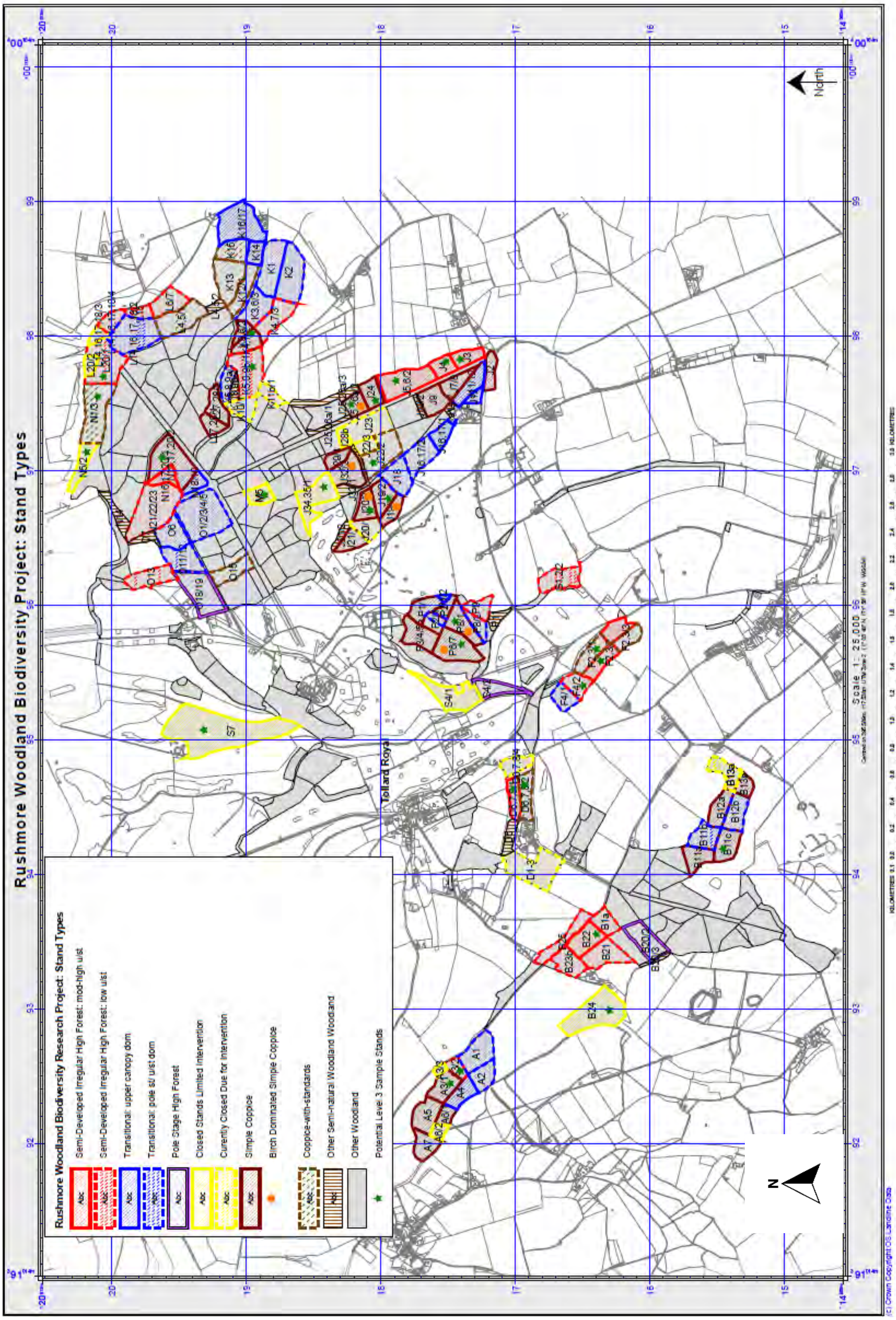

Figure 20. Ancient woodland locations used in the study across the Rushmore Estate Tollard Royal, Wiltshire 2014 -2016; stand descriptions are given.

2.1.4 Conservation Rationale for Cranborne Chase Woods

The intrinsic value of the Rushmore woodland which forms the basis of this study are recognised through statutory landscape and nature conservation designations. As such these influence the aims and objectives of the management of the woodland. The aims and objectives for land management reflect the UK government policies e.g., The 25 Year Environment Plan (DEFRA 2018), to promote sustainability across all sectors including forestry with biodiversity conservation as a primary objective. At a landscape scale the Cranborne Chase and West Wiltshire Downland Area of Outstanding Natural Beauty within which the Rushmore woodlands sits outlines the following objectives for the Cranborne Chase woodlands in general terms through the AONB management plan (2019-2024):

- The landscape character, tranquillity and special qualities of the AONB and its settings are conserved and enhanced.
- Sustainable ecological networks are established and maintained across the AONB.
- Farmers, foresters, game and fishery managers actively assist in conserving and enhancing the landscape and environment of the AONB through their business operations.
- Local communities benefit from a sustainable rural economy, based on the resources of the AONB, that also conserves and enhances its landscape character and special qualities.

The United Kingdom Forestry Standard (UKFS) promotes the sustainable adoption of best practice in forestry to enable the UK government to comply with international obligations and treaties around the following criteria (Forestry Commission 2017):

- Maintenance and appropriate enhancement of forest resources and their contribution to global carbon cycles.
- Maintenance of forest ecosystem health and vitality.
- Maintenance and encouragement of productive functions of forests (wood and non-wood).

- Maintenance, conservation and appropriate enhancement of biological diversity in forest ecosystems.
- Maintenance and appropriate enhancement of protective functions in forest management (notably soil and water).

All forest managers and practitioners in the UK are expected to meet the UKFS requirements and the authorities will assess applications for forestry proposals (felling licence and woodland grant applications) against these standards before giving permission and offering grant aid (Forestry Commission 2017). The requirement for an approved management plan is embedded within this approach to satisfy the statutory agencies i.e., Forestry Commission and Natural England who will be consulted and comment before approval. For Rushmore the woodland management objectives for the ancient semi-natural woodlands have been established by Poore (2016), as follows:

Objectives

1. To maintain the scenic, historic and scientific interest of the outstanding landscape and preserve its character in accordance with the undertakings as amplified in the Rushmore Heritage Landscape Management Plan.
2. To conserve, and where appropriate enhance, those wildlife habitats identified as being of significance in consultation with Natural England as appropriate.
3. To create a structure across the Woodland Estate which maintains positive cash flows as far as possible through reducing costs and which seeks, in the long term, to maximise the production of quality sawlogs and where appropriate, larger dimension timber.
4. To create a forest structure and composition which will be resilient to biotic and climatic threats.
5. To manage the forest with due regard to the UK Forestry Standard.
6. To protect features of historic and archaeological interest and their settings in consultation with Historic England as appropriate.
7. To provide reasonable public access for walkers and riders.

OBJECTIVES

Silviculture

a) Stand improvement shall be given the highest priority where it does not conflict with other objectives. Aim for a structure that maximises diameter growth of the best individuals whilst maintaining stability and timber quality.

b) Aim to create mixtures with one main species and one to three secondary species.

c) Aim to reduce re-stocking costs by avoiding clear-felling and promoting a structure which promotes natural regeneration of the preferred species.

d) Aim to produce high quality sawlogs of species appropriate to the site.

e) Aim to market directly to the processor/ end-user wherever possible.

Nature Conservation

- Maintain and, where appropriate enhance, biodiversity and take regard of nationally and locally important species and habitats.

- Manage stands within Cranborne Chase and Rotherley Downs SSSIs in consultation with Natural England.

- Ancient Semi-natural Woodlands: achieve a range of habitat types and degrees of habitat dynamism by:
  - maintaining a network of open habitats in rides and glades and areas of ‘open high forest’.
  - managing a significant proportion of stands for underwood production on a short rotation

  - promoting the development of diverse, high forest stands as Continuous Cover High Forest using a selection system, with some supplementary planting where appropriate.
  - maintaining a network of stands in which silvicultural development is not directed and where old growth characteristics are encouraged.

- Deadwood:
  - to provide both standing and fallen deadwood habitats throughout the woodland, where this does not conflict with the safety of the public or forestry workers or the health of the woodland.
  - to aim to accumulate deadwood on key sites so that 10-20 cubic metres per hectare of standing and fallen deadwood are present or 5-10% of standing volume. Emphasis will be placed on conservation of standing deadwood and large-diameter sections of fallen deadwood.
  - to safeguard deadwood habitats by avoiding drastic changes in conditions through the use of Continuous Cover Forest management

2.2 Overview of the Research

2.2.1 Aims and Objectives

A primary ambition for this study has been to address the paucity of information around the introduction of Irregular high forest in Britain (Mason *et al*. 2022). Against a backdrop of building resilience in which woodlands are increasingly being managed for adaptation to changes in climate and tree pests and diseases (Read *et al*. 2009, Forestry Commission 2020), we require a more complete understanding of how variants in woodland management affect biodiversity when developing future woodland management practices (Fuller 2013). As the Rushmore estate woodlands are part of the Cranborne Chase SSSI, evidence for changing the way land management is undertaken as part of the SSSI reform being promoted under the UK governments 25-year environment plan, will contribute to improved understanding of adaptive management and future woodland policy (Natural England 2021). Diversification of woodland structure and allowing natural processes to lead the management response is seen as critically valuable (Natural England 2021, Forestry Commission 2020). Both are principal drivers underpinning the approach to management of transformation of under-managed woodland to an irregular high forest at Rushmore (Poore 2016). Structural attributes of temperate broadleaf woodland influence a range of species of conservation interest, plants, woodland birds and bats (Peterken 1996, Quine *et al*. 2007, Bouvet *et al*. 2016). Therefore, understanding how structure varies between and within silvicultural management types was fundamental to this research as much as how species responded to it. This study also aims to demonstrate how different taxonomic groups respond to stands undergoing silvicultural treatment where the economic and ecological returns may be reconciled (Aggestam *et al*. 2020). In Europe balancing economics with nature conservation has been fraught with challenges where a more constrained criteria around governance and certification has led to a reduction in forest structural diversity at a landscape scale (Kuuluvainen *et al*. 2019).

The scale and configuration of the woodlands at the Rushmore estate were especially conducive to scientific study because different silvicultural treatments were intermixed (see Figure 20). As such spatial bias could be more easily considered and addressed during analysis as sampling locations were geographically represented across the study area and stratification of silvicultural management was therefore straightforward to achieve (Kent 2012).

The research objectives were:

1) To examine the structural habitat characteristics of vegetation within the study woodlands and identify how any variations relate to stand management.

2) To examine the woodland flora community composition and richness using phytosociological groups and relate these to the structural habitat characteristics across the following stand management types; coppice, Irregular and limited intervention.

3) To identify patterns of bird community composition and abundance in spring and winter across different woodland management regimes of the broadleaf woodland

mosaic (i.e., between areas of coppiced woodlands, irregular high forest stands, transitional stands and limited intervention stands).

4) To identify the bat community composition present within each stand type and identify the relative patterns of activity for each species. Activity will be analysed using acoustic recognition, and to examine the habitat structural characteristics of those locations used by bats across the stands.

5) To use the results of 1-4 to produce recommendations and guidance to the forestry industry and statutory nature conservation bodies.

2.2.2 Study Design

The fundamental requirement of all the research described in this thesis was that as acomparison study across the different stand management types, it required sufficient plots from which to sample the habitat structures and different taxonomic groups.. A plot-based study within which all measures of both habitat and species are gathered gives greater detail and precision when investigating a species- habitat relationship (Bibby *et al*. 2000). A variable plot-based sampling method was employed (Figure 21), from where all measurements were collected to best capture the variability of habitat structures across the woodland and consequently be representative of each stand management type (Kent 2012, Bibby *et al*. 2000, Hansen and Hounihan 1998). A systematic sampling protocol was used stratified across the stand management types (Figure 22). Plots were placed at least 100 metres apart and 30 metres from the edges of each stand to reduce the effect of proximate habitats e.g., permanent rides (Kirby and Hall 2019, Bibby *et al* 2000). Within each plot all structural habitat measures were collected from circular plots and vascular plant data from within the 20mx20m quadrat. Point counts and Acoustic activity measures for birds and bats respectively were collected at the plot centre. Plot adapted from Hansen and Hounihan (1996). Site effects which may unduly influence the silvicultural treatment effects were accounted for by including each of the sample plots (sub-samples) within each stand unit as the overall sample. To overcome possible pseudoreplication as a result of plots being spatially autocorrelated (therefore non-independent samples), a stand unit number was incorporated into the analyses of the three taxonomic groups as a random factor (Davies and Gray 2015).

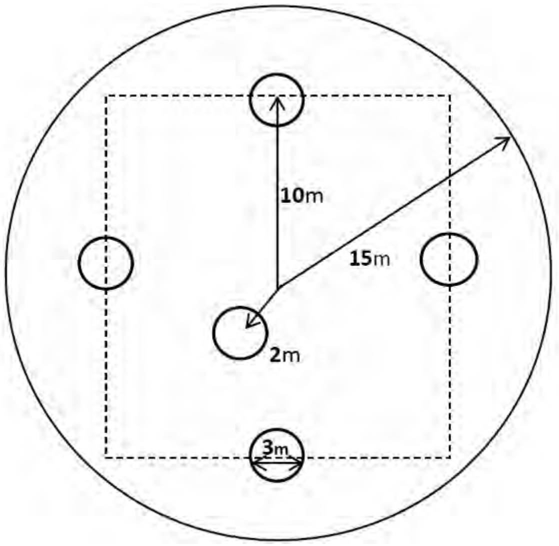

Figure 21. Variable plot layout as used in the study.

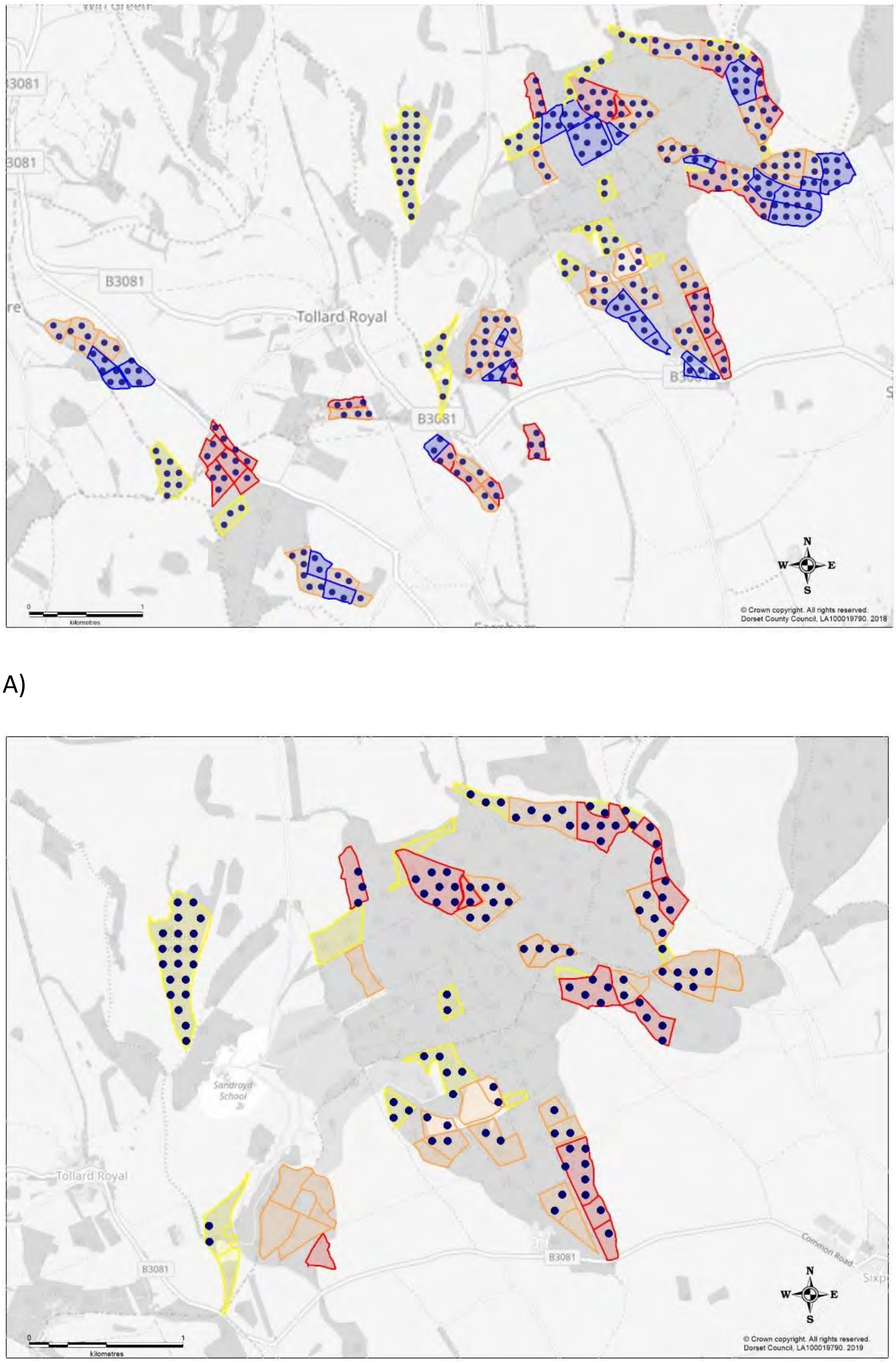

Figure 22. A) Locations of all study plots within each of four stand types using 310 sample plots for woodland birds and their habitat structural measures with a subset of 120 sample plots B) selected for sampling birds, bats, vascular plants, and moths for three stand types; key: yellow limited intervention, red Irregular high forest, orange coppice and blue transitional. Rushmore, Wiltshire.

The habitat structural measures selected represent the layers of the woodland canopy and understorey with the aim of exploring how these interact and reflect the stand interventions. The measures collected were used to provide an insight into the relative attributes of each stand type which in turn may be associated with the occurrence of the different species of birds and bats encountered. The presence of these attributes provides, in varying degrees, the functional resources required by these species in respect of foraging, nesting, roosting and dispersal (Fuller 2013, Carr *et al*. 2020). Similarly, the structure of the woodland affects the vascular plant community as woodland species responses vary according to light availability (Barkham 1992). Plot measures taken were as follows and measures of central tendency median and means plus ranges, standard deviation and coefficient of variance calculated as required for each.

Within the 30-metre diameter circular plot (707m^2);

- Basal Area m^2 /ha as a measure of biomass; using a factor of 2.25 a relascope sweep of 360^0 was taken using the android phone forest measurement application MOTI (Rosset *et al*. 2014). The camera is calibrated so that it reflects the BA factor and all stems >7.5cm diameter at breast height (dbh) within the sweep are counted as 'in' where they sit within the vertical lines shown.
- Number of the five largest canopy Oak *Quercus robur* and Ash *Fraxinus excelsior* in plot as measured by dbh.
- Count of all woody stems as a measure of tree density across 3 categories: Stems ha^{-1}. 1) >50cm , 2) 17.5 -50cm, 3) 7.5cm-17.5cm diameter at breast height.
- Estimate of Standing deadwood frequency for each of 4 dbh categories; 1) 3-7.5cm, 2) 7.5-30cm,3) >30cm. 4) For multi-branched dead trees >30cm the number of main branch points as an index of cover.
- Index of estimated fallen deadwood across 2 categories; 1) Length of fallen logs over 30cm diameter; 2) Volume in m^3 of coarse woody debris, fallen branchwood and cut scrub.
- Dbh in centimetres of the 5 largest trees regardless of species within the plot and their distances from the centre to the nearest 0.5 metre.
- The dominant % field layer in plot including seedlings ≤ 0.5m height using Domin values 1= few 2= several 3=many 4 = 4-10% 5 = 11-25% 6 = 26-33% 7= 34-50%

8 = 51-75% 9= 76-90% 10 = 91-100%.

Within the five circular 3 metre diameter sub-plots 4 were positioned at 10 metres from centre at each cardinal point N, E, S, W and 1 was positioned at 2 metres from centre of the main plot with its centre location derived from using a random compass bearing (7.1m^2);

- Number of saplings and coppice stems > 0.5m height from 5 sub plots extrapolated to whole plot at 10m from centre; 1) <3cm dbh, 2) > 3 - 7.5cm dbh.
- Understorey density at 4 sub-plots based on the compass cardinal points 10m from centre at 0.5, 1.5, 2.0m height bands. A measure of vegetation obscuring the chequerboard was estimated to the nearest 5%, against a 30cm x 15cm chequerboard, to derive a mean understorey density value per plot for each height for comparison between stand types (Figure 23).
- Canopy openness % calculated from the proportion of grid-squares on the mirror open to sky at 4 cardinal points 10m from centre measured using a convex mirror spherical densiometer (Lemmon 1956) to derive a mean value per plot to compare across stand types (Figure 23).

Hold instrument level, 12" - 18" in front of body and at elbow height, so that operator's head is just outside of grid area.

Assume four equi-spaced dots in each square of the grid and systematically count dots equivalent to quarter-square canopy openings.

Multiply the total count by 1.04 to obtain percent of overhead area **not occupied** by canopy. The difference between this and 100 is an estimation of overstory density in percent. (Assuming each dot to represent one percent is often accurate enough.)

Make four readings per location - facing North, East, South and West - record and average.

Robert E. Lemmon, FOREST DENSIOMETERS
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Figure 23. Chequer board as used to estimate woodland understorey density across a horizontal plane by moving it up or down a measuring pole. Three height bands were sampled 0.5 m, 1.5m and 2 m to look at variation in structure across the understorey strata. Spherical densiometer on right for measuring canopy cover.

2.2.3 Outline of the Research Chapters

The aim of the research at Rushmore were to compare stands undergoing transformation towards an irregular high forest silviculture against those traditionally managed as coppice and stands that had been under-managed for at least 50 years.

Using a plot-based stratified sampling approach the research focussed on vegetation structure and three taxonomic groups; woodland plants, woodland birds and bats. Multivariate community analysis using Principal Components Analysis was used to explore the relationships between woodland habitat structures and species in relation to stand management type and identify gradients along each axis which represent these. Non-Metric Multidimensional Scaling was used to look at Ancient Woodland Indicators of vascular plants. Generalised linear models and Generalised linear mixed models were used to compare species groups between stands with pairwise comparisons. Habitat associations were also explored using Generalised Additive Mixed Models. Multi-taxa studies of this type are unusual in UK woodlands and the results provide a unique contribution to our understanding of the dynamics of the habitats resulting from silvicultural interventions in ancient semi-natural woodland.

The following chapters 3, 4 and 5 relate to three peer-reviewed papers which have been accepted and published, and a final discussion chapter which draws together the main findings of the research, identifies where the study has given insight and where future research may be directed.

Chapter 3 introduces the wider study area across all 310 sample plots and uses multivariate analysis to give an over view of the vegetation communities and structural characteristics of the ancient semi-natural woodlands at Rushmore. The structural attributes of the different stand types were measured and compared and form the basis of the work on the vertebrate groups studied in subsequent chapters. It then focusses down onto the ancient woodland vascular plant community. Using a subset of 120 sample plots, Paper 1 demonstrates how woodland plants are influenced by silvicultural interventions using Generalised Linear Mixed Models with post-hoc pair-wise tests looking for differences in phytosociological groups of plants that indicate different environmental conditions in ancient woodland. A community analysis, was used to look at how ancient woodland indicator and coppice guild species of plants associated with woodland continuity and traditional coppice management respond to the effects of structures in the different silvicultural management types. Indicator species analysis uses a combination of abundance and occurrence at each plot and identified those ancient woodland plants which had the strongest affinity to a particular stand management type or types. The context of these findings is discussed in respect of woodland habitat structure and silvicultural management.

In Chapter 4, Paper 2 elucidates how woodland structure as driven by silvicultural management influences the woodland bird community. Using point counts across all 310 plots in both the breeding season and winter shows how the calculated densities of key woodland species including several of conservation concern, varied between stand management types and season using pairwise tests. Tests were undertaken to explore seasonal shifts when looking at niche breadth, and related birds to the structural attributes prevalent within each stand management type within a community analysis.

In chapter 5 Paper 3 demonstrates the differences in woodland bat activity across three stand management types and relate bat activity for each species to woodland structure. Using passive acoustic recordings across the breeding season and post breeding period two metrics of activity were developed for each sample plot; overall activity based on number of passes between sunset and sunrise and secondly the number of periods across each night at each plot where bat activity was detected.

In chapter 6, the final chapter considers the results of the three papers and introduces ideas for further analysis of congruence between the different taxonomic groups with the addition of moth data collected by other researchers from the same study area. It places the study in the wider context of woodland forest management policies and concludes by considering how irregular high forest management can contribute to biodiversity conservation. The chapter provides a synopsis of the main findings of the research and considers the ecological implications for the different groups along the main structural habitat gradients identified in the different stand management types. The chapter considers the implications of the research to woodland managers and recommendations for future work. The final section brings together the work in a general conclusion of the study and how both structural habitat characteristics and each group may serve as useful indicators of overall conservation management.

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Chapter 3 The structure and composition of the vegetation and its response to silviculture

3.1 Structural Characteristics of the ancient semi-natural woodlands

3.1.1 Introduction

Structural attributes of a woodland habitat, particularly woody growth features across the woodland strata, are known to significantly influence the communities of birds (Fuller *et al*. 2012), bats (Froidevaux *et al*. 2016) and vascular plants (Kirby *et al*. 2017). While physiognomy is important an understanding of the composition of vegetation can be especially valid when explaining the relative contributions made by different vegetation treatments (Rotenberry 1985, Fuller and Rothery 2013). Increasing structural heterogeneity in temperate woodland is known to contribute towards species diversity although the responses can differ depending upon a particular species requirement of resources (Heidrich *et al*. 2020). Indeed, contingent with this view is that the characteristics of vegetation shared between sites can vary in the fine-scale resources they may offer a particular species depending upon the structural state of the vegetation at a given time (Hewson *et al*. 2011). It is important to recognise the scale at which structural heterogeneity operates particularly because landscape context will influence processes around both succession and woodland disturbances as much as at the stand-level (Brūmelis *et al*. 2011). Despite this limitation, this study focusses on stand-level comparisons where there can be considerable variation both within and between stands undergoing different management treatments and where edge habitats and ecotonal variability is driven by the configuration of the stands (Dunning *et al*. 1992, McCollin 1998). The Rushmore woodlands have a common history and share similar tree composition throughout the estate (Poore 2016) typical of the Wooded Chalk Downland landscape character (LUC 2003). A primary focus of the study is to explore the structural characteristics of the ancient woodlands and elucidate some of the differences in these between the stand management types.

3.1.2 Methods

The first section of chapter 3 aims to provide an overview using descriptive methods. The structural attributes are therefore described for all 310 sampling plots representing four stand treatment types described in detail in Chapter 2. The dominant floristics, (those species contributing the most cover in each plot estimated by percentage), provide an overview of the ground layer characteristics, which are presented in a community analysis. Data collection and plot layout is explained in detail in Chapter 2.An analysis of variance (ANOVA) with pairwise comparisons across the four stand management types was used for each of the main habitat structural measures. Stand unit was included as a random factor to account for spatial autocorrelation (Davies and Gray 2015). Multivariate analysis with Spearman's Rank Correlation was used to explore the habitat structural and dominant floristic variables and a Principal Components Analysis (PCA) from the variables selected to identify the main habitat gradients across the wider woodland area represented by the four stand management types. The mean positions of the four main silvicultural treatments are shown in the PCA. The floristics are including in the PCA as supplementary variables to show how they relate to (but do not influence) the effects of the structural variables used to construct the gradient (Graffelman and Aluja-Banet 2003).

Following on from this exploratory and descriptive analysis, the publication shown at 3.2, Paper 1, Irregular silviculture and stand structural effects on the plant community in an ancient semi-natural woodland, specifically investigates the responses of the woodland flora to stand management (in a subset of 120 plots across three stand management types). The ground flora of ancient and semi-natural woodland is recognised as an intrinsically important taxonomic group which also contributes to the ecological functioning of the ancient woodland (Kirby 2020).

3.1.3 Results

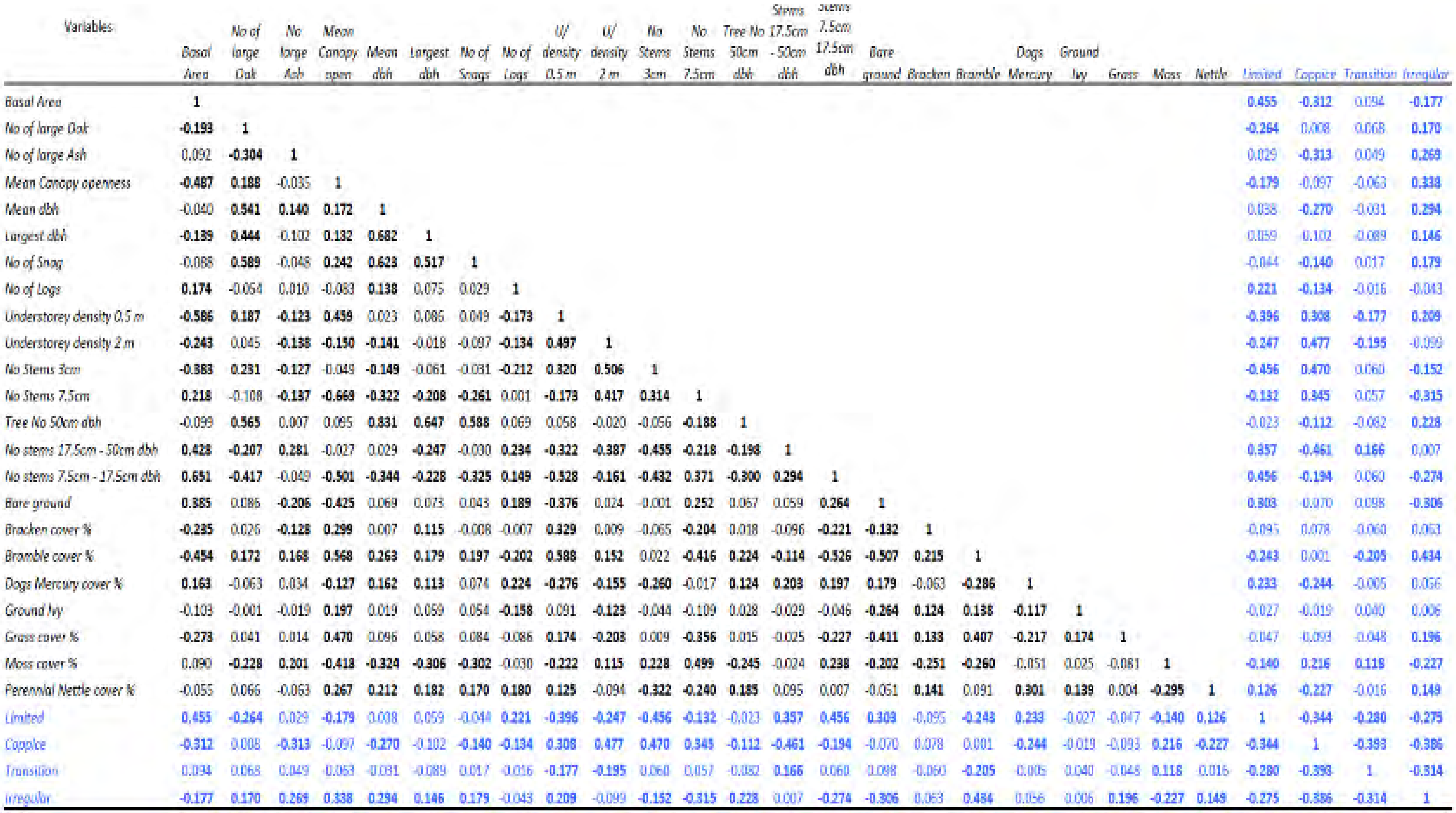
Structural Characteristics

A total of 17 habitat structural variables were compared across the four stand management types with significant differences detected in 12 of these and one which was near significant for canopy openness Table 3. Limited intervention woodland was characterised by increased woody biomass particularly for the number of tree stems 7.5 – 17.5cm dbh and was also reflected in higher basal area than for all other stand types. Canopy openness was significantly lower in limited intervention stands compared with Irregular. Limited intervention stands were much shadier, had more bare ground and less understorey density at 0.5m than coppice or Irregular stands. As canopy openness increased Bramble *Rubus fruticosus* cover showed a corresponding increase in Irregular stands particularly compared to all three other stand types. Correlation analysis identified several of the variables as being significantly positively correlated. (Table 4). The five stem dbh variables were pooled to give an overall stem density per plot. Six variables were therefore selected for showing the habitat gradients related to the stand types, (Figure 24). Two clear gradients emerged with cumulative variance of 67% captured for axis 1 and axis 2. Axis 1 revealed a gradient from low stem density to greater basal area and closed canopy. Along Axis 2 the gradient followed a pattern of higher understorey density at 2 m towards an open canopy but with larger trees.

Table 3. Median values of habitat structural variables measured across the four stand types; lower and upper quartiles in parenthesis and results of ANOVA tests for random effects (stand number) and fixed effects (stand type) Pairwise comparisons using Tukey's post-hoc test, for stands; C - coppice, I - Irregular, L - Limited intervention and T - Transitional; those in bold are highly significant P < 0.005.

Habitat Variable	Coppice (n 101)	Irregular (n 73)	Limited (n 61)	Transition (n 75)	Random	Fixed
Basal Area	18.0 (11-22) **L**	18.0 (15-22) **L**	29.0 (24 -33) T	22.0 (18-27) L	0.001	< 0.001
Canopy Openness	10.4 (8-19)	21.3 (14-29) L	9.9 (8-14) I	10.9 (8-21)	0.001	0.05
Mean dbh	36.0 (24-49) **I**	50.6 (44-56) **C**	42.8 (34-53)	39.4 (34- 50)	0.001	0.001
Largest dbh	61.0 (46-79)	71.0 (58-82)	67.0 (52-83)	62.0 (51-70)	0.02	0.07
No. Oak	1.0 (0-2)	1.0 (0-2)	0.0 (0- 0)	1.0 (0-2)	0.001	0.10
No. Ash	1.0 (0-2) I L	3.0 (2-4) C	2.0 (1-3) C	2.0 (1-4)	0.001	0.002
No. deadwood snags	8.0 (4-12)	13.0 (7-17)	8.0 (6-12)	8.0 (6-16)	0.001	0.07
Logs (m) per plot	0.0 (0-4) L	0.0 (0-4)	3.0 (0-8) C	1.0 (0-4)	0.001	0.02
Understorey density 0.5m	48.0 (25-85) **L** T	56.0 (19-75) **L** T	7.0 (3-22) **C I**	20.0 (11-36) I C	0.001	<0.001
Understorey density 2m	52.5 (30-76) **I L T**	23.8 (8-39) **C**	13.8 (5-28) **C**	17.5 (9-28) **C**	0.001	<0.001
No. stems ≤3 cm dbh	9.2 (5-18) **I L** T	2.8 (1-7) **C**	0.6 (0-2) **C**	5.4 (2-10) C	0.001	<0.001
No. stems 3-7.5 cm dbh	3.2 (1-7) **I L**	0.2 (0-1) **C**	0.8 (1-2) **C**	2.2 (0-4)	0.001	<0.001
No. trees 7.5-17.5 cm dbh	9.0 (1-39) **L**	9.0 (1-21) **L**	69.0 (43-88) **C I** T	21.0 (7-59) L	0.001	<0.001
No. trees 17.5-50 cm dbh	2.0 (0-4) **L** T	5.0 (2-7) L	11.0 (5-16) I **C**	7.0 (3-12) C	0.001	<0.001
No. trees ≥50cm dbh	1.0 (0-2)	2.0 (1-3) **C** T L	2.0 (1-3)	1.0 (1-2)	0.001	0.10
Bramble % cover	2.8 (0-19) **I**	30.0 (5-56) **C T L**	0.0 (0-4) **I**	0.0 0-7 **I**	0.001	<0.001
Bare ground %	8.4 (0-29) I	1.4 (0-12) **L**	26.0 (13-59) **I**	12.6 (6-35)	0.001	0.008

Table 4. Spearman’s Rank Correlation Coefficient values of main structural and floristic variables sampled across all four stand management types. Correlation coefficient values are shown between -1 negative correlation and 1 positive correlation values in bold are significant $P < 0.05$



Variables	Basal Area	No of large Oak	No large Ash	Mean Canopy open	Mean dbh	Largest dbh	No of Snags	No of Logs	U/ density 0.5 m	U/ density 2 m	No Stems 3cm	No Stems 7.5cm	Tree No 50cm dbh	Stems 17.5cm - 50cm dbh	Stems 7.5cm 17.5cm dbh	Bare ground	Bracken	Bramble	Dogs Mercury	Ground Ivy	Grass	Moss	Nettle	Limited	Coppice	Transition	Irregular
Basal Area	1																							**0.455**	**-0.312**	0.094	**-0.177**
No of large Oak	**-0.193**	1																						**-0.264**	0.008	0.068	**0.170**
No of large Ash	0.092	**-0.304**	1																					0.029	**-0.313**	0.049	**0.269**
Mean Canopy openness	**-0.487**	**0.188**	-0.035	1																				**-0.179**	-0.097	-0.063	**0.338**
Mean dbh	-0.040	**0.541**	**0.140**	**0.172**	1																			0.038	**-0.270**	-0.031	**0.294**
Largest dbh	**-0.139**	**0.444**	-0.102	**0.132**	**0.682**	1																		0.059	-0.102	-0.089	**0.146**
No of Snag	-0.088	**0.589**	-0.048	**0.242**	**0.623**	**0.517**	1																	-0.044	**-0.140**	0.017	**0.179**
No of Logs	**0.174**	-0.054	0.010	-0.083	**0.138**	0.075	0.029	1																**0.221**	**-0.134**	-0.016	-0.043
Understorey density 0.5 m	**-0.586**	**0.187**	**-0.123**	**0.459**	0.023	0.086	0.049	**-0.173**	1															**-0.396**	**0.308**	**-0.177**	**0.209**
Understorey density 2 m	**-0.243**	0.045	**-0.138**	**-0.150**	**-0.141**	-0.018	-0.097	**-0.134**	**0.497**	1														**-0.247**	**0.477**	**-0.195**	-0.099
No Stems 3cm	**-0.383**	**0.231**	**-0.127**	-0.049	**-0.149**	-0.061	-0.031	**-0.212**	**0.320**	**0.506**	1													**-0.456**	**0.470**	0.060	**-0.152**
No Stems 7.5cm	**0.218**	-0.108	**-0.137**	**-0.669**	**-0.322**	**-0.208**	**-0.261**	0.001	**-0.173**	**0.417**	**0.314**	1												**-0.132**	**0.345**	0.057	**-0.315**
Tree No 50cm dbh	-0.099	**0.565**	0.007	0.065	**0.831**	**0.647**	**0.588**	0.069	0.058	-0.020	-0.056	**-0.188**	1											-0.023	**-0.112**	-0.082	**0.228**
No stems 17.5cm - 50cm dbh	**0.428**	**-0.207**	**0.281**	-0.027	0.029	**-0.247**	-0.000	**0.234**	**-0.322**	**-0.387**	**-0.455**	**-0.218**	**-0.198**	1										**0.357**	**-0.461**	**0.166**	0.007
No stems 7.5cm - 17.5cm dbh	**0.651**	**-0.417**	-0.049	**-0.501**	**-0.344**	**-0.228**	**-0.325**	**0.149**	**-0.528**	**-0.161**	**-0.432**	**0.371**	**-0.300**	**0.294**	1									**0.456**	**-0.194**	0.060	**-0.274**
Bare ground	**0.385**	0.086	**-0.206**	**-0.425**	0.069	0.073	0.043	**0.189**	**-0.376**	0.024	-0.001	**0.252**	0.067	0.059	**0.264**	1								**0.303**	-0.070	0.098	**-0.306**
Bracken cover %	**-0.235**	0.026	**-0.128**	**0.299**	0.007	**0.115**	-0.008	-0.007	**0.329**	0.009	-0.065	**-0.204**	0.018	-0.096	**-0.221**	**-0.132**	1							-0.095	0.078	-0.060	0.063
Bramble cover %	**-0.454**	**0.172**	**0.168**	**0.568**	**0.263**	**0.179**	**0.197**	**-0.202**	**0.588**	**0.152**	0.022	**-0.416**	**0.224**	**-0.114**	**-0.526**	**-0.507**	**0.215**	1						**-0.243**	0.001	**-0.205**	**0.434**
Dogs Mercury cover %	**0.163**	-0.063	0.034	**-0.127**	**0.162**	**0.113**	0.074	**0.224**	**-0.276**	**-0.155**	**-0.260**	-0.017	**0.124**	**0.203**	**0.197**	**0.179**	-0.063	**-0.286**	1					**0.233**	**-0.244**	-0.005	0.056
Ground Ivy	-0.103	-0.001	-0.019	**0.197**	0.019	0.059	0.054	**-0.158**	0.091	**-0.123**	-0.044	-0.109	0.028	-0.029	-0.046	**-0.264**	**0.124**	**0.138**	**-0.117**	1				-0.027	-0.019	0.040	0.006
Grass cover %	**-0.273**	0.041	0.014	**0.470**	0.096	0.058	0.084	-0.086	**0.174**	**-0.203**	0.009	**-0.356**	0.015	-0.025	**-0.227**	**-0.411**	**0.133**	**0.407**	**-0.217**	**0.174**	1			-0.047	-0.093	-0.048	**0.196**
Moss cover %	0.090	**-0.228**	**0.201**	**-0.418**	**-0.324**	**-0.306**	**-0.302**	-0.030	**-0.222**	**0.115**	**0.228**	**0.499**	**-0.245**	-0.024	**0.238**	**-0.202**	**-0.251**	**-0.260**	-0.051	0.025	-0.081	1		**-0.140**	**0.216**	**0.118**	**-0.227**
Perennial Nettle cover %	-0.055	0.066	-0.063	**0.267**	**0.212**	**0.182**	**0.170**	**0.180**	**0.125**	-0.094	**-0.322**	**-0.240**	**0.185**	0.095	0.007	-0.051	**0.141**	0.091	**0.301**	**0.139**	0.004	**-0.295**	1	**0.126**	**-0.227**	-0.016	**0.149**
Limited	**0.455**	**-0.264**	0.029	**-0.179**	0.008	0.059	-0.044	**0.221**	**-0.396**	**-0.247**	**-0.456**	**-0.132**	-0.023	**0.357**	**0.456**	**0.309**	-0.095	**-0.243**	**0.233**	-0.027	-0.047	**-0.140**	**0.126**	1	**-0.344**	**-0.280**	**-0.275**
Coppice	**-0.312**	0.008	**-0.313**	-0.097	**-0.270**	-0.102	**-0.140**	**-0.134**	**0.308**	**0.477**	**0.470**	**0.345**	**-0.112**	**-0.461**	**-0.194**	-0.070	0.078	0.001	**-0.244**	-0.019	-0.093	**0.216**	**-0.227**	**-0.344**	1	**-0.393**	**-0.386**
Transition	0.094	0.068	0.049	-0.063	-0.031	-0.089	0.017	-0.016	**-0.177**	**-0.195**	0.060	0.057	-0.082	**0.166**	0.060	0.098	-0.060	**-0.205**	-0.005	0.040	-0.048	**0.118**	-0.016	**-0.280**	**-0.393**	1	**-0.314**
Irregular	**-0.177**	**0.170**	**0.269**	**0.338**	**0.294**	**0.146**	**0.179**	-0.043	**0.209**	-0.099	**-0.152**	**-0.315**	**0.228**	0.007	**-0.274**	**-0.306**	0.063	**0.484**	0.056	0.006	**0.196**	**-0.227**	**0.149**	**-0.275**	**-0.386**	**-0.314**	1

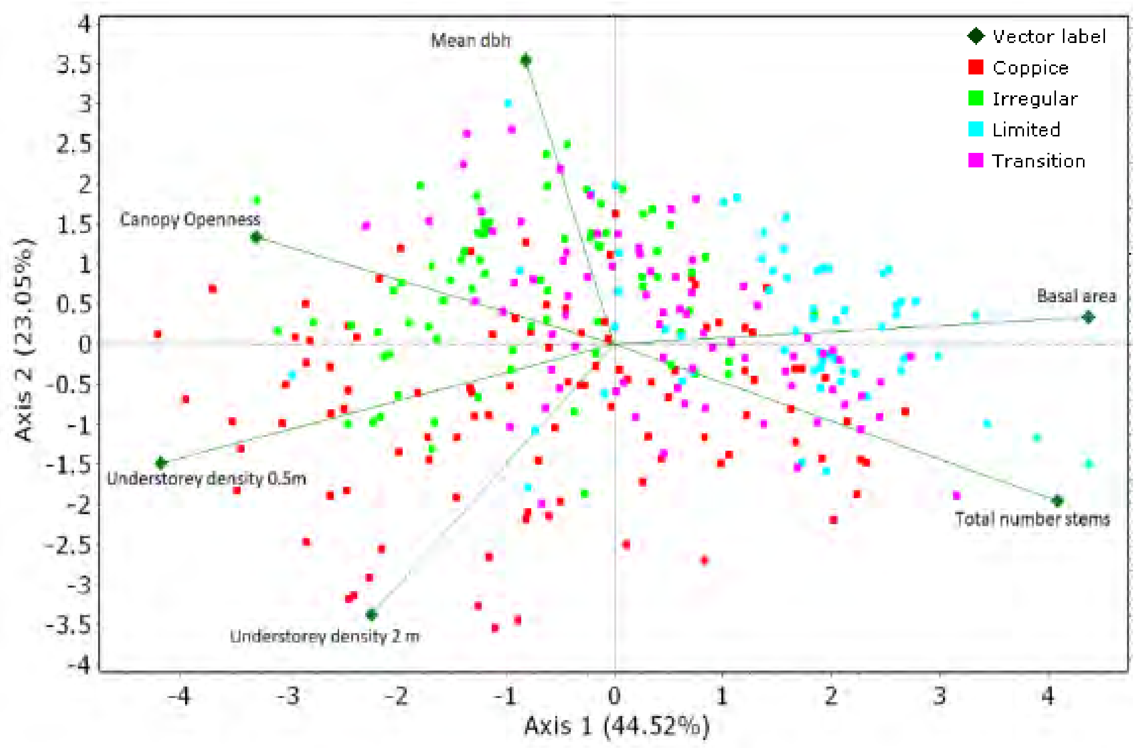


Figure 24. Principal Components Analysis ordination graph of habitat structural measures for the wider area of ancient semi natural woodland, Rushmore, Tollard Royal, Wiltshire. Stand management types are shown.

Dominant Floristic Cover

Seven floristic measures were identified which represent the most commonly occurring species by percentage cover (Figure 25). Factor scores (correlations) are given in Table 5. Shade tolerant Dog's Mercury was associated with higher basal area and closed canopy found in Limited intervention stands and Transition stands. The latter having reduced understorey is positioned mid-way in the ordination between Limited and Irregular stands. Conversely, grasses were positively associated with canopy openness and closely aligned with Irregular high forest stands. Higher stem density vector correlated with Bare ground and Moss yet the latter was most correlated with coppice and limited intervention on the gradient with higher stem numbers associated with each stand management.. Bracken *Pteridium aquilinum* and Ground Ivy *Glechoma hederacea* were both associated with Canopy openness while Perennial Nettle *Urtica dioica* and Bramble *Rubus fruticosus* were significant in this part of the gradient. As found in the pairwise tests from the

ANOVA, Bare ground was only significantly associated with Limited Intervention stands with a larger basal area and stem density.

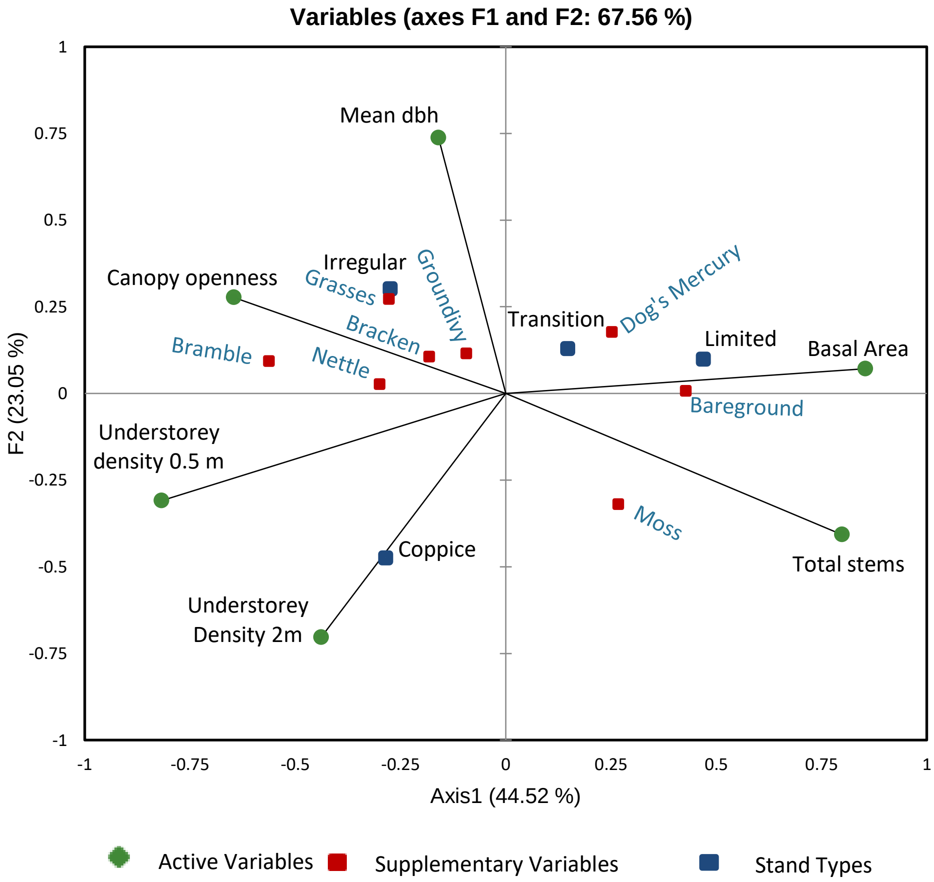


Figure 25. Principal Components Analysis ordination graph of habitat structural variables with correlations of floristic variables and bare ground for the wider woodland area of ancient seminatural woodland. Mean positions of the four stand types are shown. Rushmore, Tollard Royal, Wiltshire.

Examples of the four stand types are illustrated; (Figure 26) coppice, (Figure 27) Limited Intervention, (Figure 28) Irregular high forest and (Figure 29) Transitional.

Figure 26. Hazel coppice. Previous winters felling evident through open area and standard Oak; the adjacent dense understorey of regrown coppice stools can be clearly seen, (above). Preparing 'sails' (below) for a Hazel hurdle placed upright into the mould behind Don Taylor (Hurdle-maker) with binders woven through. Pole material prepared, ready to be worked. Chase Wood, Sixpenny Handley, Dorset March 2022

Figure 27. Limited intervention stand composed of Ash and overstood Hazel coppice last managed c.50 years previously; heavily shaded and higher basal area than other stands with evidence of self-thinning stems falling to the woodland floor. The ground flora is dominated by vernal species flowering and storing carbohydrate reserves in their bulbs before canopy leaf-burst. Tollard Royal, Wiltshire, April 2022.

Figure 28. Irregular stand with open canopy, mixed trees and variable, patchy understorey of Bramble, Hawthorn and Hazel interspersed with openness as shown by the emergent ground flora of vascular plants and grasses. Sixpenny Handley, Dorset April 2022.

Figure 29. Transition stands comprised of even-aged trees at pole-stage and not mature therefore requiring transformation to restructure age-classes and encourage natural regeneration; the first thinning has taken place the previous winter with Hazel understorey having been cut which can be seen resprouting. Further trees are marked to be felled to open the canopy. Tollard Royal, Wiltshire May 2014.

Table 5. Principal Component scores of significant habitat and floristic variables used in the community analysis across each of four stand types, Rushmore, Tollard Royal, Wiltshire. Values in bold are significant at P = 0.05.

Variable	F1	Variable	F2
BASAREA	**0.854**	Mean dbh	**0.738**
Total stems	**0.799**	*Irregular*	0.302
Limited	0.47	Mean Cano	0.277
Transition	0.147	*Transition*	0.129
Moss	0.097	Moss	0.116
Bare ground	0.037	*Limited*	0.099
Grass	0.012	Grass	0.098
Nettle	-0.019	BASAREA	0.071
Bramble	-0.028	Bracken	-0.012
Dogs Mercury	-0.056	Ground Ivy	-0.012
Bracken	-0.116	Bare ground	-0.025
Mean dbh	-0.16	Bramble	-0.033
Ground Ivy	-0.208	Nettle	-0.06
Irregular	-0.274	Dogs Mercury	-0.178
Coppice	-0.285	Dens 0.5m	-0.309
Dens 2m	-0.439	Total stems	-0.407
Mean Cano	**-0.646**	*Coppice*	-0.475
Dens 0.5m	**-0.817**	Dens 2m	**-0.703**

3.1.4 Discussion

The four silvicultural management types varied between the stands sampled and related to the habitat structural differences across the woodland strata. Stand interventions, particularly canopy opening influenced the characteristics of the understorey which appeared to respond proportionately to the varying levels of intervention. Transitional stand type in the initial phases of silvicultural management lacked understorey development and was therefore at an early stage in the successional phase of stand re-initiation (Harmer *et al*. 2010). Moreover, despite the removal of all of the understorey during this transformation stage the felling of canopy trees is undertaken gradually to avoid windthrow risk which can inhibit rapid regeneration associated with natural disturbances such as storm events (Kerr 1999, Kerr and Haufe 2011). Structurally Irregular high forest was similar to coppice in terms of basal area and understorey density at 0.5m height-band. However, there were clear differences with Irregular having lower overall stem number and lower understorey density at 2 m height-band as found in coppice that has grown from the 3rd year following cutting (Harmer and Howe 2003). It is likely that canopy openness in coppice was masked by the way it was measured below the understorey canopy. Stand management which retains some of the attributes of traditional coppice management and the associated flora and fauna are important to recognise for the conservation of biocultural heritage (Agnoletti *et al*. 2022). At Rushmore which was a centre of the coppice trade in the 19th century a proportion (12-15%) of the coppice woodland is likely to be retained because of its cultural and nature conservation significance (Poore 2016). A feature of the coppice system is the management of standard trees which were managed at a low density so as to avoid impeding the growth of the underwood which historically was most valuable (Harmer and Howe 2003). While Irregular silviculture focuses on managing canopy trees for timber it does so by creating openings and canopy gaps which while not directly analogous with coppice can give a similar appearance and set of conditions that are spatially heterogenous; notably varying age-classes of trees while encouraging understorey which helps in the natural regeneration of woody species as it acts as a 'nurse' to young tree seedlings (Kerr 1999). Understanding the structural characteristics of stands is important to meet with the multifunctional demands placed on woodlands by society and requires balancing economic objectives without compromising stand resilience and biodiversity interests (Aszalós *et al*. 2021).

Natural disturbances including extremes from drought impacts, increased or reduced rainfall and wind-speed in the future, could be increasingly more severe and unpredictable (Brang *et al*. 2014). Similarly, pest outbreaks can be exacerbated as forest vegetation is subjected to climatic extremes and ecosystem functioning is negatively altered (Hlásny *et al*. 2021). The impacts to biodiversity may include changes to an organism's behavioural patterns, niche separation and physiology while bringing together species which had not previously existed side by side (de Frenne *et al*. 2021). Structural heterogeneity associated with CCF and Irregular silviculture in particular may ameliorate such effects and is known to be an important driver of biodiversity conservation in temperate European forests (Kuuluvainen *et al*. 2021, Tinya *et al*. 2021). Uneven-aged management as a form of high forest silviculture may better replicate natural woodland dynamics than coppice but this must be caveated by acknowledging it is different as it relies on harvesting a crop and is where understanding the effects on a range of woodland species is important to guide future management trajectories (Kirby *et al*. 2017). Moreover, coppice abandonment is seen as a serious concern for conservation biologists as species declines are known to be associated with its demise (Müllerová *et al*. 2015). There is a focus on increasing ecological attributes in CCF management but these often focus on old growth features e.g., dead-wood with a lack of reference to scrub regeneration or successional dynamics (Gustafsson *et al*. 2020). Additionally, CCF management which produces a diverse tree and shrub species composition may be more sustainable in respect of reliance as a response to climate change effects (Tinya *et al*. 2020). High forest management has many variants and creating a range of structures which can include early successional scrub habitats using CCF and irregular high forest may address some of these concerns (Kirby *et al*. 2017, Calladine *et al*. 2017). Despite concerns over the loss of traditional forms of coppice management novel methods of stand management can create opportunities to develop structural attributes which are complementary for biodiversity and the ecological functioning required for sustainable woodland management (Dolman *et al*. 2017). Moreover, stand management can create ecological resources for a range of species much more rapidly than through natural stand dynamics (Kerr 1999, Quine *et al*. 2007, Peterken and Mountford 2017). As such the introduction of Irregular silviculture provides a unique opportunity for studying the effects on a range of taxa.

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3.2 Paper 1 Irregular silviculture and stand structural effects on the plant community in an ancient semi-natural woodland.

3.2.1 Background and Details of Authors Contributions

The following authors contributions are listed with their signatures.

Daniel Alder, Main Author 80%: Conceptualisation, Study design, Data collection of all habitat structural measures, Preparation of botanical data and statistical analysis, writing, responding to Journal Editor and two reviewer's comments and re-wrote text prior to resubmission.

D.C. Alder

Bryan Edwards: Field data collection of all botanical measures of vascular plants.

B.W. Edwards

Andrew Poore: Advice on silvicultural aspects and assistance with reviewer's comments from first submission.

Dr. John Norrey: Statistical advice on models.

Prof. Stuart Marsden: Conceptualisation, Study design, Supervision of data collection and preparation, Writing/Comments on text.

Forest Ecology and Management 527 (2023) 120622

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

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

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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 (Hermy, 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

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https://doi.org/10.1016/j.foreco.2022.120622
Received 4 May 2022; Received in revised form 18 October 2022; Accepted 31 October 2022

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 (opportunist 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 coppiuce layet (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 nonscripta*) that fall within

a)

b)

c)

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

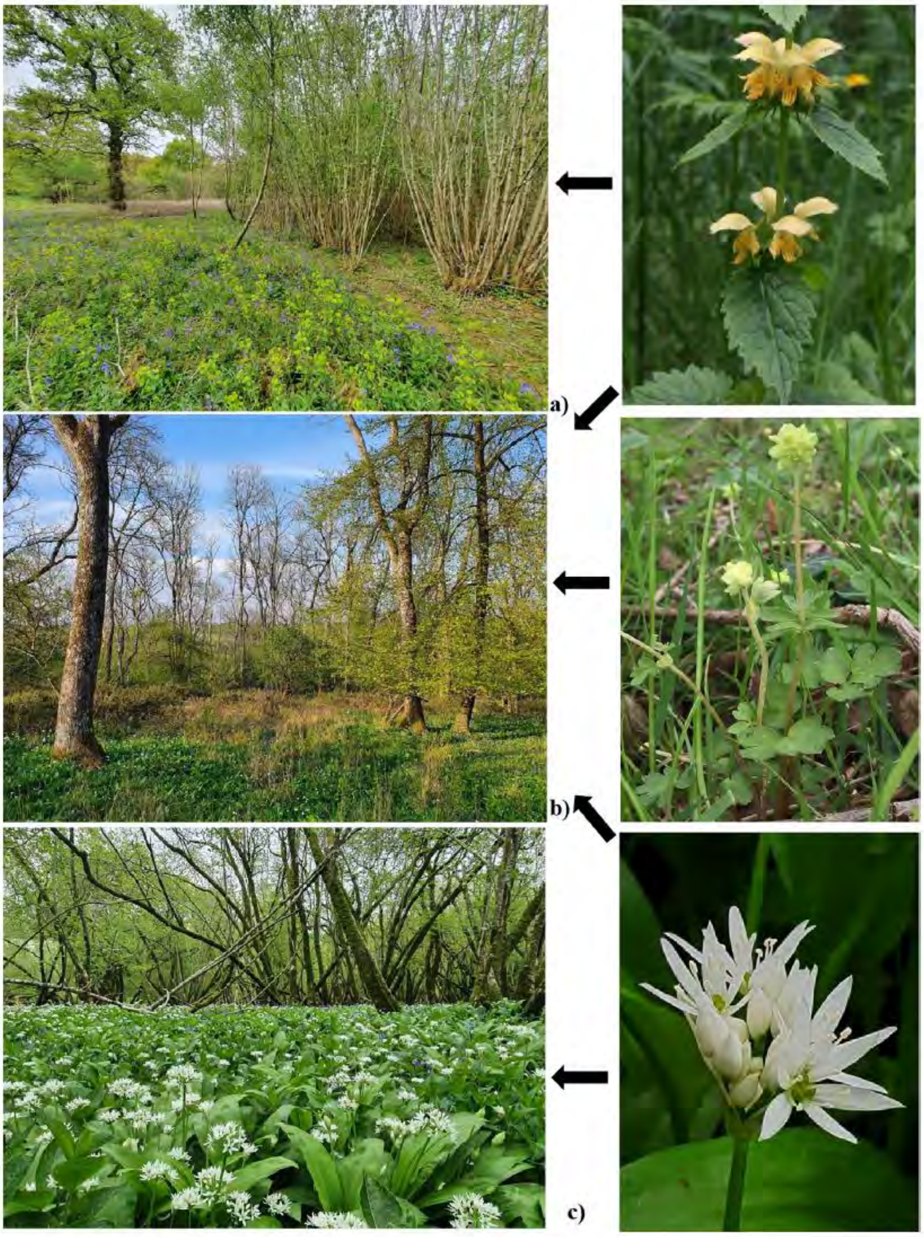


Fig. 2. Stand management types and examples of AWI plants associated with each (see Table 3 in results, arrows depict strongest association with a stand type in the examples), a) coppice with *Lamiastrum galeobdolon* in a diverse ground layer, mix of recently felled coppice and 7-year-old stems b) Irregular 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 m^2/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 m^2/ha^{-1}. Lower stocked areas still in transition can have a range of 10–16 m^2/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 m^2/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 be 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 subplot 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

(Dufrêne, & 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 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.

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

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*

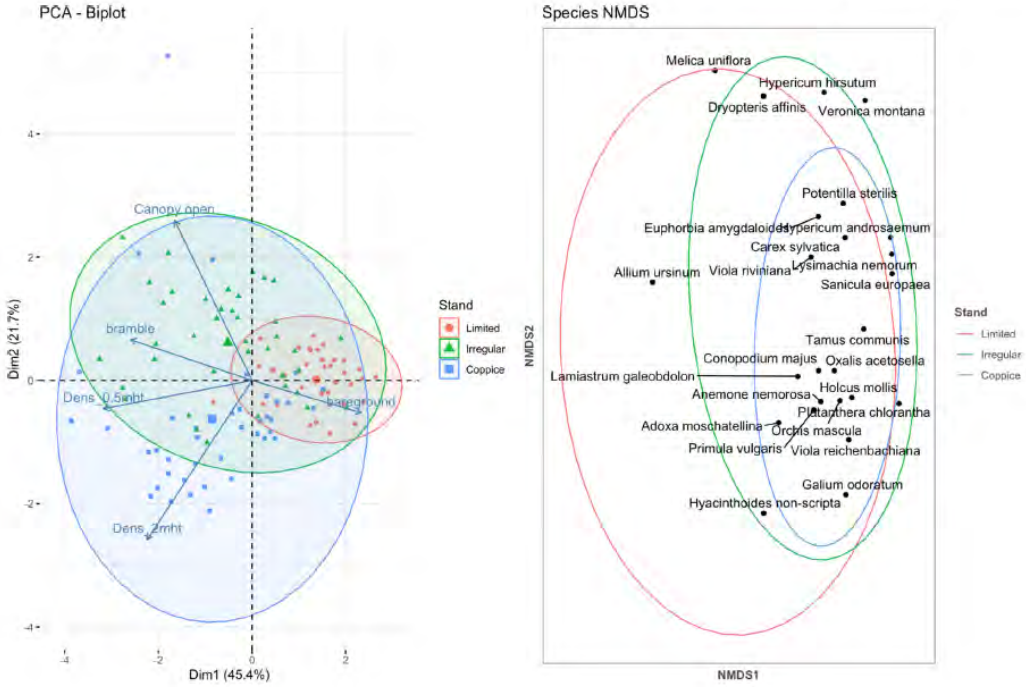
Indicator species analysis (ISA) identified 22 species with a significant association with a particular stand type or stand type pair (Table 3). These included nine of the twenty-five AWI species from four Coppice plant groups. The Spring vernal species were all included in both coppice and Irregular 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



3a) 3b)

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) L	16 (9 – 32) L	< 0.001
Ancient Woodland Indicators	2.5 (0 – 14) C	7.5 (1 – 13)	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	< 0.001
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 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 (Hédl 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

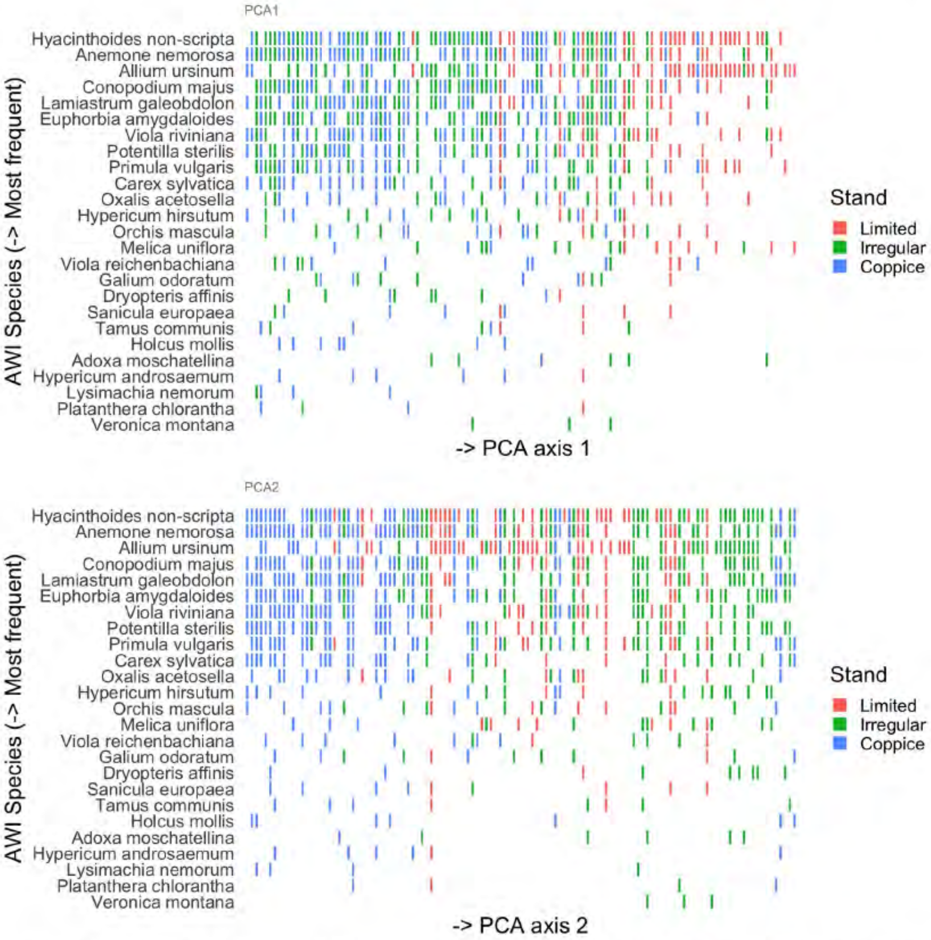


Fig. 4. Occurrence of ancient woodland plant species at each plot (n = 120; coloured by stand type) ordered along ordination axes 1 and 2 of the PCA.

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

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Table **S.1**. Measures using Domin score for ground flora % cover and conversion to mid-point value used in analysis.

Domin scores and % range		% Cover value equivalent
1		1.0
2		2.0
3		3.0
4	4-10%	7.5
5	11-25%	17.5
6	26-33%	29.0
7	34-50%	41.5
8	51-75%	62.5
9	76-90%	82.5
10	91-100%	95.0

Table **S.2** Vascular Plant Guilds (after Rackham, 2003, 2006) and other Vascular plants recorded at Rushmore. * Ancient woodland indicator plants, superscript letters refer to stand types where species was recorded; C – Coppice, I – Irregular , L – Limited intervention.

Spring perennial

*Anemone nemorosa** ^{CIL}
*Conopodium majus** ^{CIL}
*Hyacinthoides non-scripta** ^{CIL}
*Lamiastrum galeobdolon** ^{CIL}
*Orchis mascula** ^{CIL}
*Primula vulgaris** ^{CI}
*Stellaria holostea** ^{CI}

Summer Perennial

Brachypodium sylvaticum ^{CIL}
Dactylorhiza fuchsii ^{CL}
Deschampsia cespitosa ^{CIL}
*Holcus mollis** ^{C}
*Galium odoratum**^{CIL}
Listera ovata ^{CIL}
*Melica uniflora**^{CIL}
*Oxalis acetosella**^{CIL}
*Platanthera chlorantha**^{CIL}
Pteridium aquilinum ^{CIL}
*Sanicula europaea**^{CIL}
*Tamus communis**^{CIL}
*Viola reichenbachiana**^{CIL}
*Viola riviniana**^{CIL}

Mobile

Arctium sp.^{CI}
Arrhenatherum elatius ^{CI}
Circaea lutetiana ^{CIL}
Cirsium arvense ^{CIL}
Cirsium palustre ^{CI}
Cirsium vulgare ^{CI}
Epilobium montanum ^{CI}
Geum urbanum ^{CIL}
Stachys sylvatica ^{CI}
Senecio jacobaea ^{CI}
Taraxacum agg. ^{CIL}

Buried seed

Ajuga reptans ^{CI}
Angelica sylvestris ^{CI}
*Carex sylvatica**^{CIL}
Digitalis purpurea ^{C}
Dactylis glomerata ^{CI}
Eupatorium cannabinum ^{CI}
*Euphorbia amygdaloides** ^{CIL}
Ficaria verna ^{CIL}
Fragaria vesca ^{CI}
Galium aparine ^{CIL}
Geranium robertianum ^{CIL}
Glechoma hederacea ^{CIL}
Holcus lanatus ^{I}
*Hypericum androsaemum** ^{CL}
*Hypericum hirsutum** ^{CIL}
Hypericum perforatum ^{CL}
Hypericum pulchrum ^{C}
Juncus conglomeratus ^{C}
Juncus effusus ^{CI}
*Luzula pilosa** ^{C}
*Lysimachia nemorum** ^{CI}
Milium effusum ^{CIL}
*Moehringia trinervia** ^{IL}
Myosotis arvensis ^{C}
Poa trivialis ^{CIL}
*Potentilla sterilis** ^{CIL}
Ranunculus repens ^{I}
Rubus fruticosus agg.^{CIL}
Rumex sanguineus ^{CI}
Scrophularia nodosa ^{CI}
Silene dioica ^{IL}
Urtica dioica ^{CIL}
Valeriana officinalis ^{C}
Veronica chamaedrys ^{CIL}
Veronica montana ^{I}

Non Responsive

*Adoxa moschatellina** ^{CI}
*Allium ursinum** ^{CIL}
Arum maculatum ^{CIL}
Athyrium filix-femina ^{IL}
*Dryopteris affinis** ^{CIL}
Dryopteris dilatata ^{CIL}
Dryopteris filix-mas ^{CIL}
Mercurialis perennis ^{CIL}

Other Species Recorded

Agrostis capillaris ^{C}
Astragalus glycophyllos ^{C}
*Bromopsis ramosa** ^{I}
Carex flacca ^{C}
Clematis vitalba ^{CIL}
*Elymus caninus** ^{L}
Euonymus europaeus ^{CI}
*Festuca gigantea** ^{IL}
Lithospermum officinale ^{I}
*Polystichum setiferum** ^{I}
Primula veris ^{CI}
Solanum dulcamara ^{CL}
Veronica officinalis ^{CI}
Vicia sativa ^{C}
Vicia sepium ^{L}
Viola hirta ^{C}

Footnote: Data collection for vascular plants took place between May and July 2016.

Table **S.3**. Habitat variables across stand type. Median values and range in parenthesis and results for mixed effect model with stand number as random factor for difference across stand type. All measured variables were percentage data analysed using Linear mixed effects model with arcsine transformation. Significant difference between paired stands indicated by letter ($p < 0.05$), L – Limited, I – Irregular and C – Coppice, values show whether comparison was positive or negative.

Habitat Variable	**Limited**	**Irregular**	**Coppice**	**P**
Canopy openness	9.2 (7 -22) I	16.8 (7 - 40) L	9.4 (6 - 99)	0.038
Understorey density 0.5m	7.5 (0 - 81) IC	40 (3 - 100) L	54 (5 - 100) L	<0.001
Understorey density 2m	16.3 (0 - 53) C	21.3 (0 - 69) C	60.6 (0 - 100) IL	<0.001
Bramble	0.0 (0 - 6) I	29.1 (0 - 91) LC	3.6 (0 - 93) I	<0.001
Bare Ground	35.7 (0 - 93) IC	0 (0 - 91) L	8.4 (0 - 57) L	<0.001

Table **S.4.** Correlations between factor scores for PCA Axis 1 and 2 for AWI species

AWI Species	**Axis 1**	**Axis 2**
Anemone nemorosa	0.156	0.412
Conopodium majus	0.162	0.281
Hyacinthoides non-scripta	0.069	0.141
Lamiastrum galeobdolon	0.254	0.318
Orchis mascula	0.166	0.191
Primula vulgaris	-0.023	0.063
Galium odoratum	0.110	0.001
Holcus mollis	0.225	0.094
Melica uniflora	-0.091	-0.211
Oxalis acetosella	-0.015	0.094
Platanthera chlorantha	0.167	0.066
Sanicula europaea	-0.016	0.120
Tamus communis	0.083	0.094
Viola reichenbachiana	0.020	0.132
Viola riviniana	-0.005	0.430
Carex sylvatica	0.165	0.259
Euphorbia amygdaloides	0.210	0.314
Hypericum androsaemum	0.042	0.130
Hypericum hirsutum	0.147	0.080
Lysimachia nemorum	0.101	0.330
Potentilla sterilis	0.158	0.352
Veronica montana	0.036	-0.110
Adoxa moschatellina	-0.018	-0.109
Allium ursinum	-0.079	-0.272
Dryopteris affinis	0.219	-0.044

Chapter 4 Woodland Birds

4.1 Paper 2 Implications of transformation to irregular silviculture for woodland birds: A standwise comparison in an English broadleaf woodland

4.1.1 Background and Details of Authors Contributions

The following authors contributions are listed with their signatures.

Daniel Alder, Main Author: 90% Conceptualisation, Study design, Data collection of all field data on birds and habitat structural measures, Preparation of data and statistical analysis, writing, responding to Journal Editor and two reviewer's comments and re-wrote text prior to resubmission.

D. C. Alder

Prof. Robert Fuller – Advisor on analysis and comments on text

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Prof. Stuart Marsden – Principal Supervisor

Forest Ecology and Management 422 (2018) 69–78

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Implications of transformation to irregular silviculture for woodland birds: A stand wise comparison in an English broadleaf woodland

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ARTICLE INFO

Keywords:
Continuous cover forestry
Semi-natural woodland
Irregular silviculture
Stand management
Understorey characteristics
Woodland bird communities

ABSTRACT

Woodland birds in Britain have undergone significant long term declines since the late 1960s, associated in particular with changes in woodland structure in general, and loss of early successional vegetation. Irregular, continuous canopy broadleaf management is a form of selective logging, very recently adopted in UK that produces woodlands with open canopies and substantial mid- and understorey growth. We examined spring and late winter bird densities, estimated using distance sampling, at 310 points in irregular, transitional (that being managed towards irregular), limited intervention, and coppice stands within a large working broad-leaf woodland in lowland southern Britain. Almost all understorey and canopy vegetation measures differed significantly across stand types. Ten of 20 species had highest spring abundance in irregular woodland, five in coppice, three in transitional, and just two in limited intervention. In winter, 5–6 species preferred each of limited intervention, irregular and transitional, while no species preferred coppice. Densities differed little across seasons except in Paridae where abundances increased in late winter during which limited intervention stands were used more by this group. Birds generally occupied similar niche positions and had similar niche breadths across seasons. Compared to under-managed woodlands, irregular silviculture in UK's broadleaf woodlands is likely to enhance habitat quality for woodland birds, including several species of conservation concern e.g. marsh tit *Poecile palustris* which was twice as abundant in irregular stands as in any other stand type.

1. Introduction

Within the European forestry sector there is growing support for continuous cover forestry (CCF). These systems embrace a diversity of approaches but all seek to retain a continuous woodland cover, as opposed to large scale clear-felling (Mason et al., 1999; Mason, 2007). CCF systems, sometimes referred to as 'irregular forestry', are often advocated on the basis of having economic, ecosystem service and ecological advantages (Susse et al., 2011; Lõhmus et al., 2016; Pukkala et al., 2016). They form one strand of silvicultural alternatives to even-aged forestry which also include 'ecological forestry' or 'close-to-nature forestry' (Seymour & Hunter, 1999; Bürgi, 2015; Puettmann et al., 2015). All of these systems emphasise avoidance of clear-cutting, the use of mixtures of tree species, natural regeneration and small-scale structural variability (Puettmann et al., 2015). Improved understanding of the responses of biodiversity to a shift towards CCF from other systems such as clear-cutting and rotational coppicing (Harmer & Howe, 2003) have become increasingly important to forest managers (Puettmann et al., 2015; Quine et al., 2007). Using an 'irregular' selective felling system, canopy opening is patchy and can resemble natural woodland processes, with canopy gaps leading to localised seedling regeneration, while developing a continuum of tree and shrub ages from young thicket stage to mature trees in each stand (Susse et al., 2011). This structure is expected to create a different range of ecological resources to those present within clear-felling and coppice systems with consequent shifts in the composition of bird communities (Quine et al., 2007; Fuller et al., 2012). In Europe there have been few comparisons of bird communities in stands managed under CCF with those in stands managed under other regimes, though more data are available for North America (see for example Forsman et al., 2010). In beech dominated woodlands in the Belgian Ardenne, bird abundances were higher in uneven stands compared with even-aged (du Bus de Warnaffe and Deconchat, 2008). However, the effects of stand composition (conifer vs broadleaf) were more explicitly demonstrated where management for uneven-aged conifer did not enhance bird diversity. Understorey development from conifer stands undergoing CCF

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https://doi.org/10.1016/j.foreco.2018.04.004
Received 22 December 2017; Received in revised form 29 March 2018; Accepted 3 April 2018

management, important to several species of conservation concern, has highlighted the value of this management type in the UK (Calladine et al., 2015).

There is a more specific question concerning the wider adoption of new irregular forestry – can it assist in the recovery of declining woodland biodiversity? In the case of birds, several species of woodland birds in Britain have undergone striking contractions of range and decreases in abundance in recent decades. The species affected vary in taxonomy and ecology, though a disproportionately high number of long-distance migrants have declined (Hewson et al., 2007; Hewson & Noble, 2009; Fuller et al., 2013). There are several potential causes of these declines, one of which is reduction in habitat quality as a result of progressive shifts in woodland management that occurred during the 20th century (Fuller et al., 2007). Towards the end of that century much woodland had become heavily shaded, with associated reduction of understorey complexity, partly as a result of the demise of coppicing and partly due to canopy-closure in plantations within afforestation and existing broadleaf woodland (Hopkins & Kirby, 2007; Mason, 2007). Concurrently, numbers of deer also increased in Britain with similar consequences for woodland structure as lack of management (Gill & Fuller, 2007). These factors have led to interest in new regimes for woodland management that reflect both biodiversity concerns and which adapt to changes in woodland product demand (Fuller, 2013).

Britain lacks most of the specialist species dependent on late forest successional stages that can be found, for example, in eastern Europe and Fennoscandia where the conservation priority focuses mainly on retaining old forest stands (Wesołowski, 2005; Roberge et al., 2008). In Britain, however, the restoration of some form of woodland management including CCF Forestry, to unmanaged woods is widely regarded as potentially beneficial for conservation (Fuller et al., 2007). This reflects the fact that most unmanaged woodland does not consist of 'near natural' stands but is woodland that had formerly been harvested especially by a long tradition of coppicing (Buckley & Mills, 2015), and currently exists in a neglected often structurally homogenous condition (Peterken & Mountford, 2017; Mason, 2007). Therefore, woodland management, which we define here as sustainable harvesting of standing timber of varying age classes, may enhance habitat quality for a range of scarce and declining vertebrate and invertebrate species associated with early successional habitats; many of these species are ones that have been adapted to a very long history of human exploitation of British woodlands (Fuller, 2013; Hinsley et al., 2015). However, not all species may benefit from reintroducing coppicing, an example being marsh tit *Poecile palustris* (Broughton & Hinsley, 2015) and invertebrates that depend on features such as standing deadwood (Sterling & Hambler, 1988).

The results presented here provide, as far as we are aware, the first assessment of the responses of birds to CCF within temperate broadleaved stands in Europe. Our aim was to compare bird abundance and relevant vegetation attributes across four stand types in a large ancient semi-natural woodland: coppice; limited intervention (formerly managed, now neglected); irregular high forest; and transitional high forest. The latter consisted of stands undergoing initial management towards irregular. Having examined differences in habitat structure between these four broadleaf management types, we then compare bird densities both in spring and winter across stand types, and identify contrasts in habitat use across species and seasons.

2. Methods

2.1. Location and general description

The study was conducted on 442 ha broadleaf woodland and statutorily protected Site of Special Scientific Interest (SSSI) spread across nine contiguous blocks on the Rushmore Estate, in southern England (110–190 m a.s.l; 395724.26 E, 117963.15 N; Fig. 1). The principal National Vegetation Classifications (NVC) are W8 (ash-field maple) associated with base-rich soils with some W10 (oak-birch) on slightly acidic soils, that fall within the broad category of lowland mixed deciduous woodlands on fertile soil with several sub-categories around the former (Rodwell et al., 1991, B. Edwards *pers. comm.*, 2017). 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*. There are a significant number of veteran trees particularly of oak, ash and field maple along with whitebeam and 19th Century beech plantings (Poore, 2016).

2.2. Descriptions of stand types

The following broadleaf stand management types and prescriptions are described (A. Poore pers. comm. 2017; see Table 1 and Fig. 2).

'Limited intervention' stands were those with a closed canopy, high tree density, and limited understorey due to a long period (> 30 years) without formal silvicultural intervention. Some of the limited intervention stands have developed from open canopy high forest and have higher understorey densities.

'Coppice stands' have few canopy trees (< 10% canopy cover) and include both simple coppice and coppice with standards with up to 25% cover of standard trees. Coppice cycle lengths vary depending on uses with hazel dominated, (covering c.15 ha), cut every 8–12 years for hurdle fencing, thatching materials and bean poles. Birch coppice managed on two rotations of pure birch (c.19 ha) cut at 3–4 years for horse jumps or revetment faggots and the remaining 50 ha hazel-birch mix on 25–30 year cycles for wood fuel. (There was a broad representation of growth stages with a mean age of coppice during the study of 9.4 years (SD ± 6.7) with 0–5 years (n = 25), 6–9 years (n = 37), 10–15 (n = 21), years and 15–30 years (n = 18)). At each cutting the entire panel between 0.5 and 1.5 ha of underwood is removed leading to even-aged regrowth (Harmer & Howe, 2003).

'Irregular High Forest stands' (continuous cover forestry) have been transformed from unmanaged coppice or even-aged stands to a selective irregular management for at least 30 years. This involves selective removal of harvestable trees, and of weaker growing specimens along with cutting of the understorey to increase light levels reaching the woodland floor. The aim is to increase incremental growth of retained trees to enhance their silvicultural and economic value, promote natural regeneration of trees and shrubs and establish a range of tree age classes. Selection of the trees best adapted to site conditions (phenotypes) is a key objective (Susse et al, 2011). Stands with 'moderate stocking' have stand basal areas (> 7.5 cm dbh) in the range 17–24 m^2 ha^{-1} whilst those classified as 'low stocking' are in the range 10–16 m^2 ha^{-1}. Understorey stocking varies with past management and the effects of deer, and can be dense in places yet patchily distributed.

'Transitional High Forest' stands are intermediate between coppice and irregular High Forest and are developing towards irregular from former coppice or even-aged high forest. Transitional stands have undergone initial interventions within the previous 10–20 years but are yet to develop the range of irregular stand elements i.e. mixed age and height classes of trees and saplings but often with a developed understorey. They are variable with regard to both canopy and understorey density. However, they broadly separate into two categories depending on whether large trees or pole-stage trees form the canopy (Poore, 2016).

2.3. Data collection

A plot-based stratified sampling approach was used (Bibby et al., 1998; Kent, 2012) for 310 plots derived from grid coordinates

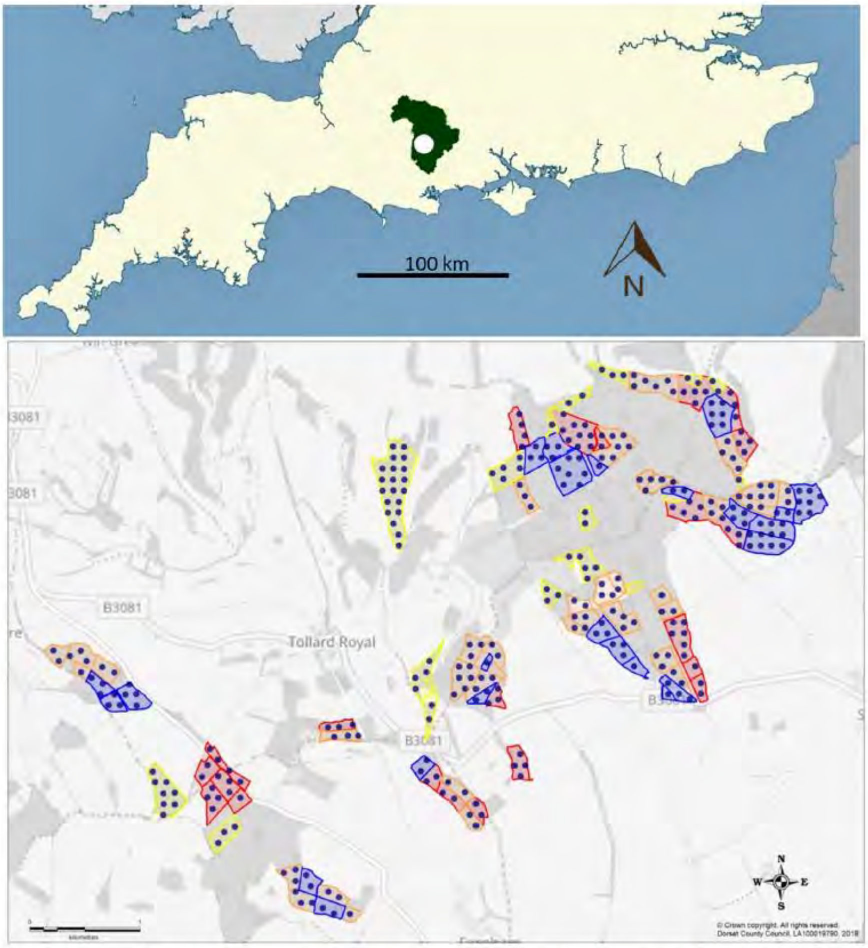

Fig. 1. Location of Cranborne Chase and study area, above, Dorset-Wiltshire border, southern England, UK. Sampling points below within stand types; orange – coppice, blue – transitional high forest, yellow -limited intervention, and red – irregular high forest. © Natural England copyright 2012. Contains Ordnance Survey data © Crown copyright and database right 2012. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Areas of semi-natural broadleaved woodland stand types within the Rushmore Estate and number of sample plots where habitat structural measures and bird community data were collected.

Woodland type	Stand Type	Area (ha)	% Broadleaf Wood	Number of Sample plots
Semi-Natural Broadleaved Woodland	Irregular High Forest	137.1	31	73
	Transitional High Forest	97.4	22	75
	Limited intervention	102	23	61
	Coppice	106.1[a]	24	101
Total		442.6	100	310

[a] Area in active rotation currently 85 ha.

generated in MapInfo version 12 (Pitney Bowes Ltd (2013)) representative of the four stand types. Plots were a minimum distance of 100 m apart to minimise duplication in counts of birds (Table 1). To reduce the influence of proximate habitats, plots were located a minimum distance of 30 m from stand edges (Bibby et al., 2000). Each plot consisted of a 30 m diameter circle (0.07 ha) with five subplots of 3 m diameter within each (four located at the cardinal points at 10 m radii (see Hansen & Hounihan, 1995) and one at 2 m off-centre along a random compass bearing.

Within 30 m plots, the following habitat measurements were made: number of trees > 50 cm dbh, number of woody stems (coppice and individual trees) of dbh 7.5-≤ 17.5 cm and 17.5-≤ 50 cm dbh, and the five trees with the largest dbh. These five were identified to species and mean dbh also calculated. At each 3 m subplot, the number of saplings and coppice stems < 3 cm, and > 3–7.5 cm dbh were counted if > 0.5 m tall. Percentage canopy openness was measured with a spherical convex mirror densiometer (Lemmon, 1956). Basal area ($m^2 ha^{-1}$) was measured at each plot centre using the relascope principle (Bitterlich, 1984) with each tree > 7.5 cm dbh counted in a 360° sweep at each

Fig. 2. Examples of stand types used in study shown clockwise from top left; limited intervention, coppice, transitional and irregular.

sample point centre. A minimum number of ten trees are required to give precision (Bitterlich, 1984). The relascope application MOTI was used (Rosset et al., 2014), calibrated for the basal area factor and camera in a Samsung Galaxy S2 smart-phone. To calculate understorey density, a percentage score of obscuration to the nearest 5% was estimated at each cardinal point using a 50 × 30 cm chequer board with 10 × 10 cm squares (Fuller & Henderson, 1992). Scores were taken at 0.5 m and 2.0 m above ground to assess variation at different levels. Dead trees and dead branches (snags) over 20 cm diameter were counted at each plot (Charman et al., 2010). Percentage means were calculated at each plot for bramble *Rubus fruticosus* cover and area of bare ground.

Bird occurrence and abundance was recorded using 5 min point counts (Bibby et al., 2000) at the 310 survey plots across three visit periods: early spring (28 April to 16 May 2014), late spring (21 May to 13 June 2014) and late winter (10 February to 12 March 2015). Counts started one hour after sunrise and completed by 09h30 for the spring visits, and 11h00 for winter visits. Counts took place during fine weather avoiding periods of persistent rain and wind (Bibby et al., 1998). The distance to each bird or group on first encounter was measured using a laser rangefinder and distances were estimated to singing/calling birds obscured by vegetation. Birds beyond 50 m of the plot centre were ignored, as were birds flying into or over the plot. Birds flying away were only recorded if they were believed to be 'within' the plot, and the distance to their original position could be measured (Buckland, 2006). All fieldwork was carried out by DA.

2.4. *Data analyses*

Given the spatial arrangement of woodland stands (Fig. 1), it is reasonable to expect some non-independence of sampled survey plots because they are nested within 53 stands. These stands have their own ecological signature, arising both from their geography and its effect on soil, isolation etc, but also through their history of management. The issue of pseudoreplication has received much attention from ecologists and statisticians (e.g. Hurlbert, 1984), with a great deal of debate as to how important the issue is, and how to best address it (Oksanen, 2001; Davies & Gray, 2015).

In an attempt to overcome the effect of non-independence in the across stand type habitat analysis, we "partialled out" the unwanted effect of stand number (the random effect; Davies & Gray, 2015). Differences in individual habitat measures were tested across stand type (the Fixed effect) using a generalised linear mixed model in package 'lme4' with Stand number (1–35) as a random factor. The significance of the fixed effect and random effect were calculated using the ANOVA in 'lmerTest', along with Tukey's post hoc pairwise comparisons across stand types.

In the bird density analysis, we did not consider stand number as a factor for two reasons. First, points were spaced 100 m apart and positioned in stands which themselves were often just 100–300 m long/wide and usually less than a few hundred metres from each other (Fig. 1). Second, numbers of survey points per stand were fairly even (mean = 5.7 ± 3.9 SD) with only five of the 53 stands having more than ten survey points. Any issue in pseudoreplication in the Distance analysis due to two visits to each survey point in the Summer are accounted for in the analysis by lumping data from the two visits to each point under 'effort = 2'.

To compare across stand types, density estimates (individuals km^{-2}), coefficients of variation (% SE) and 95% confidence limits were produced in DISTANCE version 6, (Thomas et al., 2010). Data were truncated removing the furthest 5% of bird records to minimise the influence of outliers in the model. Data were entered as groups with 'exact' distances to encounters, with encounters of flying birds removed. Detection functions for spring and winter were very different, reflecting both the profound changes in visual detectability caused by leaf-fall in the largely deciduous woodland, and changes in vocalisation patterns between breeding and non-breeding seasons. While covariates (see below) can be added to alter parameters in the detection function to account for variation in vegetation coverage across plots but within season, we thought it safer to conduct separate seasonal analyses as the actual family of detection model (e.g. Uniform, Half-normal) was likely to differ between spring and winter. The Multiple Covariate Distance Sampling (MCDS) engine was used with understorey density included as a covariate likely to influence detection probability (Marques et al., 2007). Density estimates for each species in each stand type were compared using ANOVA (seasons analysed separately) and significant differences between pairs of stand types identified with Tukey's range tests.

Principal components analysis (PCA) was used to condense the habitat variables onto two component axes/factors (Jolliffe, 2002) and centroids for stand type and each bird species plotted on these axes. The differences between mean 'niche positions' (coordinates of plots at which each bird species was recorded) on factors 1 and 2 in spring and winter were tested using Wilcoxon matched pairs tests. Niche widths of species on the two factor axes were calculated as the standard deviations of Factor 1 and 2 scores for 'positive' plots for each species. We then examined any widening or narrowing of habitat associations between seasons (Lloyd & Marsden, 2008).

3. Results

3.1. Habitat differences between stand types

Thirteen of the 17 vegetation habitat variables differed significantly across stand types (Table 2). Only dbh of largest tree, number of oak and dbh < 50 cm did not differ significantly between stands. There was a higher frequency of deadwood snags in irregular but this was not a significant fixed effect. Understorey densities were highest in coppice and irregular with coppice having markedly higher density at 2.0 m. Bramble cover was highest in irregular while the area of bare-ground was significant in limited intervention. Basal areas were lowest in both irregular and coppice compared to limited intervention and transitional stands. Canopy openness was much greater in irregular plots than in other stands.

3.2. Bird densities across stand types and season

Across the 310 points, we accumulated 4994 bird records of 38 species. We calculated density estimates for 16 resident species and four spring migrants (Table 3). Three from the 20 species went unrecorded in limited intervention stands, and two of the species were spring migrants (willow warbler *Phylloscopus trochilus* and garden warbler *Sylvia borin*). Six and five species had density estimates > 100 individuals km^{-2} in at least one stand type in spring and winter respectively. Blue tit *Cyanistes caeruleus* and wren *Troglodytes troglodytes* had estimates > 100 individuals km^{-2} in all stand types in spring, and blue tit and great tit *Parus major* in all stand types in Winter.

The mean variation in densities across stand types in spring (the percentage difference between pairs of stand wise densities) was 31.2% ± 23.0 (SD; n = 96). For winter, variation was 29.8% ± 20.8 (n = 96), these figures not differing significantly (W = 4640, p = 0.94). There were significant differences in across-stand densities for twelve species in spring and six in winter (Table 3). Ten species had highest spring density estimates in Irregular stands, with seven of these being significantly higher than in Low intervention stands, and three being significantly higher than in both transitional and coppice. Marsh tit *Poecile palustris* and all four summer warblers had significantly higher densities in irregular over limited intervention. Coppice had five species with highest spring densities, and these included three of the four migrant warblers. All five species occurred in densities within coppice that were significantly higher than in limited intervention, transitional, or both. There were far fewer significant differences in densities across stand types in winter. Irregular stands had higher densities of four species than coppice, limited intervention, or both, while transitional was significant compared to coppice for two species.

3.3. Habitat gradients and bird niche positions from ordination

PCA identified two woodland structural gradients which accounted for 44.3% of the variance within 15 original habitat variables (Fig. 3). Factor axis 1 represented a gradient from open canopy mainly oak woodland with scattered large trees (> 50 cm dbh) associated with irregular stands to more closed woodland with relatively high tree and stem density aligned closely to limited intervention stands. These denser woodlands were composed of small saplings and shoots (3–7 cm dbh), small to medium (7–17.5 cm dbh), and larger (17.5–50 cm) trees. Factor 2 was associated with greater understorey density at both 0.5 m and 2.0 m height and had high density of stems (< 3 cm dbh) associated with coppice stands. These variables are negatively correlated with high scores for medium-large diameter sized trees within limited intervention stands.

The majority of bird species were associated with either coppice-like plots (dense understorey; top-left quadrant of Fig. 3) or irregular-type plots (open canopy; bottom-left quadrant). Garden warbler and willow warbler were particularly associated with coppice, and treecreeper *Certhia familiaris*, blue tit and chaffinch with irregular-type stands. Woodpigeon *Columba palumbus* was the only species strongly associated with dense plots characteristic of limited intervention management.

Table 2

Median values of habitat variables measured across the four stand types; lower and upper quartiles in parenthesis and results of ANOVA tests for random effects (stand number) and fixed effects (stand type) Pairwise comparisons usingTukey's *post-hoc* test, for stands; C - coppice, I - Irregular, L - Limited intervention and T - Transitional; those in bold are highly significant P < 0.005.

Habitat Variable	Coppice (n 101)		Irregular (n 73)		Limited (n 61)		Transition (n 75)		Random	Fixed
Basal Area	18.0	(11–22) **L**	18.0	(15–22) **L**	29.0	(24–33) T	22.0	(18–27) L	0.001	< 0.001
Canopy Openness	10.4	(8–19)	21.3	(14–29) L	9.9	(8–14) I	10.9	(8–21)	0.001	0.05
Mean dbh	36.0	(24–49) **I**	50.6	(44–56) **C**	42.8	(34–53)	39.4	(34–50)	0.001	0.001
Largest dbh	61.0	(46–79)	71.0	(58–82)	67.0	(52–83)	62.0	(51–70)	0.02	0.07
No. Oak	1.0	(0–2)	1.0	(0–2)	0.0	(0–0)	1.0	(0–2)	0.001	0.10
No. Ash	1.0	(0–2) I L	3.0	(2–4) C	2.0	(1–3) C	2.0	(1–4)	0.001	0.002
No. deadwood snags	8.0	(4–12)	13.0	(7–17)	8.0	(6–12)	8.0	(6–16)	0.001	0.07
Logs (m) per plot	0.0	(0–4) L	0.0	(0–4)	3.0	(0–8) C	1.0	(0–4)	0.001	0.02
Understorey density 0.5 m	48.0	(25–85) **L** T	56.0	(19–75) **L** T	7.0	(3–22) **C I**	20.0	(11–36) I C	0.001	< 0.001
Understorey density 2 m	52.5	(30–76) **I L T**	23.8	(8–39) **C**	13.8	(5–28) **C**	17.5	(9–28) **C**	0.001	< 0.001
No. stems ≤ 3 cm dbh	9.2	(5–18) **I L** T	2.8	(1–7) **C**	0.6	(0–2) **C**	5.4	(2–10) C	0.001	< 0.001
No. stems 3–7.5 cm dbh	3.2	(1–7) **I L**	0.2	(0–1) **C**	0.8	(1–2) **C**	2.2	(0–4)	0.001	< 0.001
No. trees 7.5–17.5 cm dbh	9.0	(1–39) **L**	9.0	(1–21) **L**	69.0	(43–88) **C I** T	21.0	(7–59) L	0.001	< 0.001
No. trees 17.5–50 cm dbh	2.0	(0–4) **L** T	5.0	(2–7) L	11.0	(5–16) I **C**	7.0	(3–12) C	0.001	< 0.001
No. trees ≥ 50 cm dbh	1.0	(0–2)	2.0	(1–3) **C** T L	2.0	(1–3)	1.0	(1–2)	0.001	0.10
Bramble% cover	2.8	(0–19) **I**	30.0	(5–56) **C T L**	0.0	(0–4) **I**	0.0	0–7 **I**	0.001	< 0.001
Bare ground%	8.4	(0–29) I	1.4	(0–12) **L**	26.0	(13–59) **I**	12.6	(6–35)	0.001	0.008

Table 3

Density estimates (individuals km^{-2} ± CV), 95% confidence intervals and numbers of encounters for resident and spring migrant woodland birds by season and stand type. Results of Tukey's Range Test pairwise comparisons of density across stand types, where > indicates pairs differ at $P < 0.05$ and > > $P < 0.005$. Direction of sign denotes which density estimate is larger. C = coppice; I = irregular; L = limited intervention; T = transitional.

	Spring				Winter			
	Coppice	Irregular	Limited intervention	Transitional	Coppice	Irregular	Limited Intervention	Transitional
Woodpigeon *Columba palumbus*	60.1 ± 10 49–73(86) > I	32.4 ± 17 23–45(33)	74.2 ± 12 59–94(62) > I	66.0 ± 11 53–82(71) > I	17.0 ± 35 9–33(12)	20.0 ± 33 10–39(10)	38.1 ± 22 25–59(16)	47.2 ± 21 31–71(25) > C
Great spotted Woodpecker *Dendrocopos major*	10.4 ± 27 6–18(15)	12.7 ± 31 7–23(13)	7.1 ± 47 3–17(6)	9.2 ± 34 5–18(10)	5.4 ± 50 2–14(4)	19.0 ± 34 10–36(10)	22.8 ± 30 13–41(10)	16.2 ± 36 8–33(9)
Goldcrest *Regulus regulus*	25.9 ± 27 15–44(16)	27.2 ± 29 16–48 (12)	27.7 ± 32 15–51(10)	60.1 ± 19 42–87(28) > C I	48.8 ± 28 28–84(15)	68.8 ± 30 38–124(15)	93.3 ± 27 55–159(17)	47.9 ± 30 27–86(11)
Blue tit *Cyanistes caeruleus*	124.7 ± 12 99–158(66)	135.1 ± 13 115–175(51)	129.4 ± 15 96–174(40)	120.5 ± 14 92–158(48)	173.3 ± 10 142–211(74)	244.5 ± 9 206–290(74) > C	197.7 ± 13 153–255(50)	200.5 ± 11 161–249(64)
Great tit *Parus major*	92.4 ± 22 61–141(27)	115.2 ± 24 72–184(24)	128.9 ± 24 81–206(22)	86.4 ± 25 53–141(19)	155.9 ± 19 107–228(29)	182.1 ± 20 123–269(24)	236.0 ± 19 163–343(26)	194.2 ± 22 126–299(27)
Coal tit *Periparus ater*	22.5 ± 24 14–36(21)	27.0 ± 24 17–44(18)	9.2 ± 45 4–22(5)	17.1 ± 30 10–30(12)	17.3 ± 43 8–39(7)	59.3 ± 25 36–96(17)	62.6 ± 26 37–105(15)	66.1 ± 24 41–105(20) > C
Marsh tit *Poecile palustris*	65.1 ± 21 43–99(29)	122.8 ± 19 86–176(39) > C L T	53.8 ± 27 32–91(14)	34.9 ± 29 20–63(12)	63.1 ± 22 41–96(21)	76.4 ± 24 48–122(18)	86.3 ± 27 51–146(17)	68.4 ± 23 43–108(17)
Long-tailed Tit *Aegithilos caudatus*	66.0 ± 36 33–130(13) > L	56.5 ± 46 24–133(8) > L	0 0	33.5 ± 50 13–86(5) > L	77.7 ± 37 39–157(10)	65.7 ± 45 28–153(6)	78.7 ± 44 34–182(6)	41.6 ± 53 15–112(4)
Chiffchaff *Phylloscopus collybita*	98.4 ± 11 80–122(82) > > L T	82.5 ± 14 63–108(49) > L T	34.9 ± 23 23–55(17)	35.0 ± 21 23–52(22)				
Willow Warbler *Phylloscopus trochilus*	19.3 ± 62 7–64(10) > L	5.4 ± 89 1–25(2) > L	0 0	3.0 ± 113 0.5–16(1) > L				
Blackcap *Sylvia atricapilla*	101.1 ± 12 81–127(79) > L T	120.2 ± 13 94–154(67) > > L T	50.4 ± 21 33–77(23)	49.3 ± 19 34–71(29)				
Garden Warbler *Sylvia borin*	30.3 ± 20 21–45(38) > L T	18.9 ± 28 11–33(17) > L	0 0	7.4 ± 38 4–15(7) > L				
Nuthatch *Sitta europaea*	24.4 ± 32 9–32(16)	31.4 ± 35 16–61(16)	27.9 ± 37 14–57(17)	29.7 ± 33 16–56(17)	20.8 ± 23 13–33(16)	29.4 ± 24 18–47(16)	37.3 ± 21 25–56(17)	29.6 ± 23 19–47(17)
Treecreeper *Certhia familiaris*	9.4 ± 32 5–18(10)	30.2 ± 21 20–46(23) > C	25.6 ± 25 16–41(16)	21.1 ± 24 13–34(17)	20.4 ± 31 11–37(10)	48.9 ± 22 31–76(17)	34.4 ± 33 18–66(10)	24.6 ± 32 13–46(9)
Wren *Troglodytes troglodytes*	108.6 ± 8 92–128(121)	221.6 ± 6 195–252(176) > > C L	148.0 ± 8 126–172(96)	180.1 ± 8 154–211(151) > > C	77.9 ± 15 58–105(43)	163.5 ± 13 126–212(64) > > C > L	88.7 ± 19 62–128(29)	106.6 ± 18 74–153(44)
Blackbird *Turdus merula*	56.2 ± 10 46–68(78)	53.6 ± 12 43–68(53)	46.9 ± 14 36–62(38)	63.2 ± 11 51–79(66)	60.1 ± 16 44–83(36)	82.4 ± 19 56–121(35) > L	31.0 ± 28 18–54(11)	49.2 ± 21 33–74(22)
Song thrush *Turdus philomelos*	29.2 ± 15 22–39(41) > L	24.0 ± 19 17–35(24)	11.0 ± 36 6–22(9)	24.6 ± 18 17–35(26)	24.3 ± 24 15–39(19)	21.7 ± 27 13–37(12)	19.5 ± 31 11–36(9)	27.4 ± 23 18–43(16
Robin *Erithacus rubecula*	134.0 ± 9 112–161(109)	87.9 ± 13 68–114(51)	132.6 ± 12 106–167(61)	150.3 ± 10 125–182(92) > I	80.9 ± 13 62–105(54)	76.1 ± 15 56–103(36)	96.1 ± 14 73–127(38)	104.2 ± 11 83–131(52)
Dunnock *Prunella modularis*	51.8 ± 20 35–77(34)	61.9 ± 22 40–96(29)	20.9 ± 40 10–45(8)	26.3 ± 29 15–46(13)	67.3 ± 23 43–105(30)	107.6 ± 20 72–160(34) > L	15.1 ± 50 6–39(4)	57.0 ± 27 34–97(19)
Chaffinch *Fringilla coelebs*	16.1 ± 20 11–24(25)	29.8 ± 17 22–41(34)	25.3 ± 22 17–39(23)	19.7 ± 21 13–30(23)	26.7 ± 23 17–42(21)	25.2 ± 24 16–41(14)	23.7 ± 31 13–43(11)	35.8 ± 22 23–55(21)

There was no systematic pattern of seasonal niche position shifts across species (Fig. 4a; F1: $V = 64$, $p = 0.85$, $n = 16$; F2: $V = 51$, $p = 0.40$, $n = 16$). Five species 'shifted' to increasingly open woodland in winter - notably dunnock, already associated with open woodland, and wren associated with dense understorey. Great spotted woodpecker *Dendrocopos major* showed the greatest niche position shift, being associated with open woodland and dense understorey in spring and closed canopy plots (limited intervention) in winter. There was no significant increase or decrease in niche breadths between spring and winter (F1: $V = 35$, $p = 0.10$, $n = 16$ F2: $V = 38$, $p = 0.13$, $n = 16$) (Fig. 4b).

4. Discussion

4.1. Differences between stand types

There were clear differences between stand types in both bird communities and woodland structure. Unlike other stand types, irregular management was characterised by more open woodland with larger trees, developing understorey and an uneven mix of tree ages. Spring bird densities were highest or second highest in irregular for 15 of the 20 species examined. In contrast, limited intervention had the

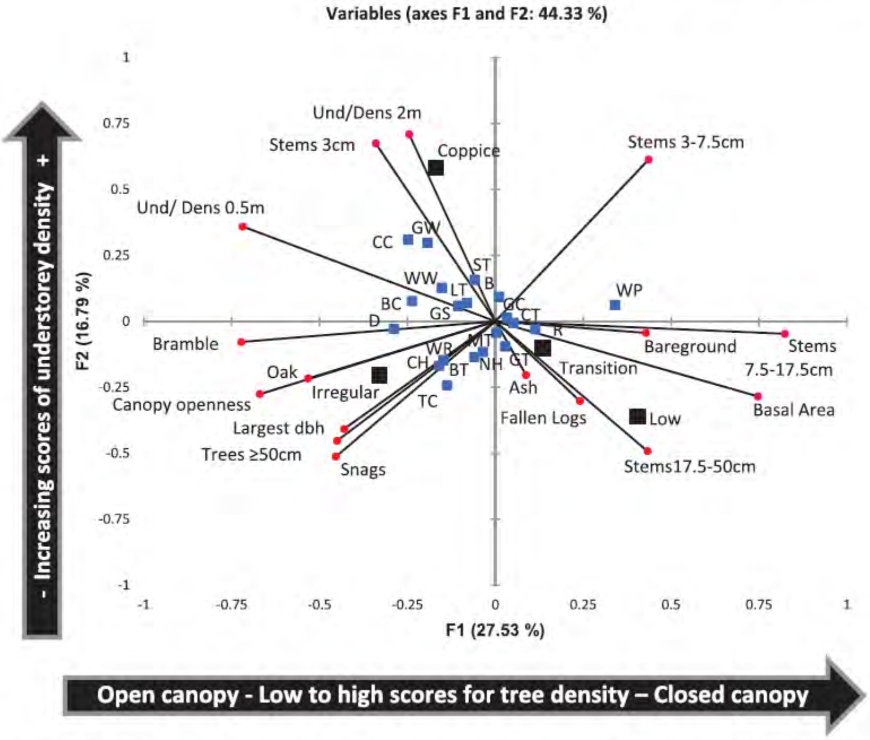

Fig. 3. Ordination of sample plots on PCA Factors 1 and 2 with vectors showing contribution of individual habitat variables. Ordinations show mean positions of stand management types and bird species during the spring. B – blackbird, BC – blackcap, BT – blue tit, CH – chaffinch, CC, chiffchaff, CT – coal tit, D – dunnock, GC – goldcrest, GS –great spotted woodpecker, GT – great tit, GW – garden warbler, LT – long-tailed tit, MT – marsh tit, NH – nuthatch, R – robin, ST – song thrush, TC – treecreeper, WP – woodpigeon, WR – wren, WW – willow warbler. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

lowest or second lowest spring densities for 14 of 20 species, with notably low abundances for species, such as the warblers, that require complex understorey structures. There were generally low numbers of warblers in transitional stands suggesting the understorey was insufficiently developed. As expected from previous studies in the UK, three of four summer migratory warbler species had highest densities in coppice (e.g. Fuller & Henderson, 1992; MacColl et al., 2014) but all had second highest densities in irregular stands with blackcap *Sylvia atricapilla* more abundant. In winter, for all species, the highest abundances occurred in irregular, transitional and limited intervention stands, although there were fewer differences in bird abundances between stand types than in spring.

Previous European studies of birds in CCF stands have generated mixed findings although importantly these are not in pure broadleaf woodlands as in our study. Working in spruce plantations in upland Britain, Calladine et al. (2015) found that most 'mature forest' bird species reached higher abundance in CCF than in rotational clear-fells. However, in Belgium, du Bus de Warnaffe and Deconchat (2008) reported that in beech and conifer forests, no clear differences in bird communities were evident between CCF and clear-cut systems. In North America, a meta-analysis by Forsman et al. (2010) found that silviculture creation of small gaps did not result in clear negative impacts on bird communities relative to unlogged forest.

4.2. Seasonal differences

There were fewer differences between bird densities across stand types in winter than in spring, presumably because resource use patterns differ in the former and latter (Fuller et al., 2012). In winter, many species, especially titmice, Paridae, nuthatch *Sitta europaea* and treecreeper become increasingly mobile, gleaning insect larvae from bark and buds in stands with higher tree density (Fuller, 1995). In our study, this group of birds associated least with coppice in winter. Previous studies have shown these resident species use a broader range of woodland habitats in winter (Bilcke, 1984). Although we did not look at demographic variation in our study it is known that several species differ in their seasonal responses to understorey age, coppice especially, depending on whether they are adults or juveniles (MacColl et al., 2014). Four species (blue tit, blackbird *Turdus merula*, wren and dunnock *Prunella modularis*) had significantly higher winter densities in irregular than in limited intervention stands. For those species associated with foraging close to the woodland floor, it seems likely that the denser understorey of irregular stands provides increased protection from predation risk and thermal variation (Holt et al., 2014). Although we found no statistically significant niche shifts from spring to winter for resident species, there were a few notable changes in habitat/niche use. Wren and dunnock were both significantly more abundant in irregular stands during the breeding season, and this association strengthened during the winter, presumably as they sought increased protection in the denser shrub-layer. Bramble *Rubus fruticosus* cover was significantly higher in irregular stands and contributed to the understorey density values at 0.5 m above ground which was strongly associated with this stand type in our study. Winter marsh tit densities were highest in limited intervention, although its density in irregular stands

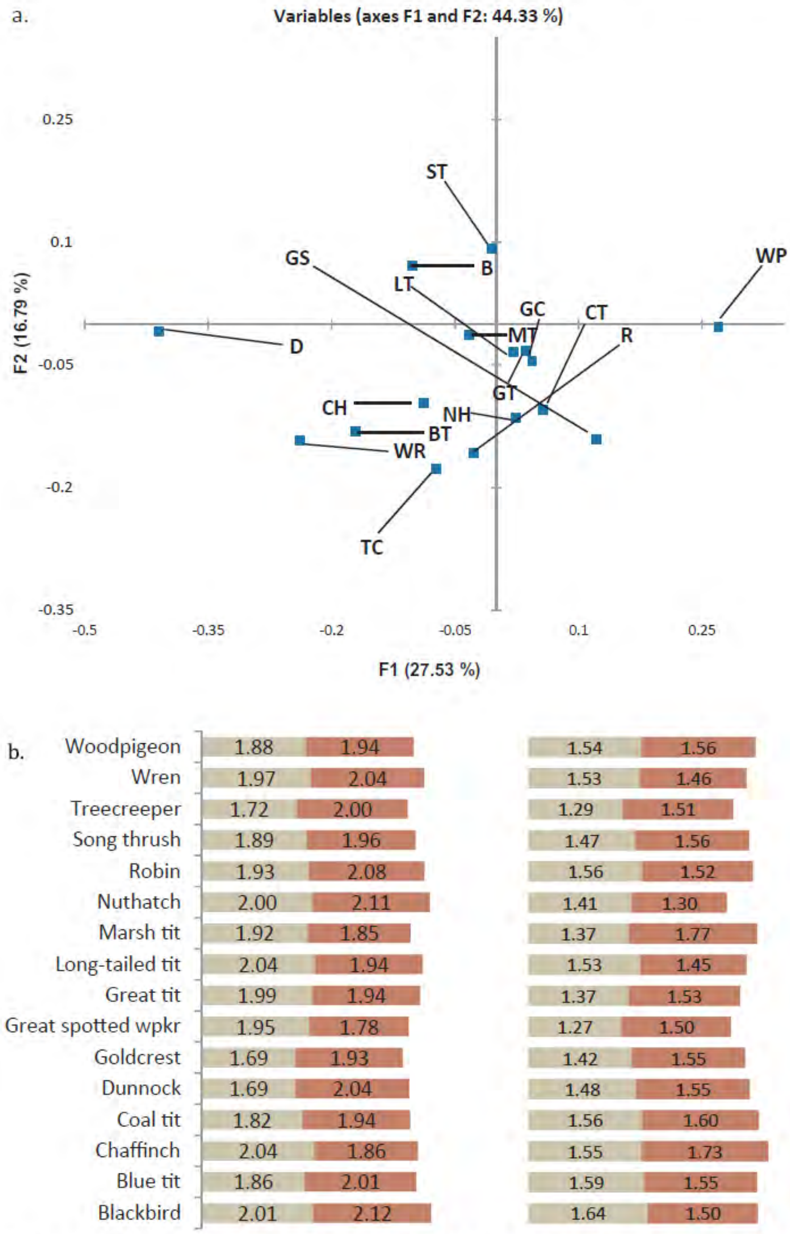

Fig. 4. Spring and winter niche characteristics for resident woodland birds. a. niche position shifts from spring (letter codes; see Fig. 3.) to Winter – (blue points); b. niche breadth changes from Spring to Winter on Factor 1 and Factor 2 scores left and right respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

were only a little lower, perhaps reflecting a widening of home range and differential use of habitats between the breeding and winter periods (Broughton et al., 2014). This is likely to be true of several species although there was little evidence of systematic movement of niches. Great spotted woodpecker was associated with open woodland during spring (see Calladine et al., 2015) and moved into stands with a greater abundance of fallen deadwood, closed canopy and higher basal area in winter.

4.3. Implications for woodland bird conservation

We are unaware of any similar research in lowland broadleaved woodland in Britain or Europe where stands have undergone a transformation to an irregular high-forest management system, a type of

CCF. Taken overall, the findings suggest that irregular forestry can provide suitable woodland habitats for a high proportion of bird species in lowland British woodland, especially in spring, and that for some species it may even provide preferred habitats. In combination with previous studies referred to above, our research suggests that CCF is likely to be either beneficial or neutral in terms of its effects on bird communities. However, two important caveats should be acknowledged. Firstly, the effects may be context dependent according to region, forest type and the exact stand types being compared. Secondly, some early successional bird species may prefer either coppice or young clear-fells which can provide larger areas of young-growth than are found with CCF (Calladine et al., 2015). For example, in our study we found tree pipit *Anthus trivialis* exclusively in recent clear-fell gaps outside of the stand types under question.

The value of coppicing to early successional birds and other species associated with dense understorey is well documented (Fuller & Warren, 1991; Fuller, 1992; MacColl et al., 2014) while it has a strong cultural association with many ancient semi-natural woods such as those found in Cranborne Chase (Rackham, 1990; A. Poore pers. comm., 2017). Other than government grant-funding targeted at sites of high nature conservation value, woodfuel production is likely to be the main economic driver sustaining coppice management (Fuller, 2013; Buckley & Mills, 2015). However, irregular stand management as a more widely economically viable system appears to provide resources for most woodland birds associated with both understorey and old growth here in southern England. Furthermore, proponents of CCF point out the multiple benefits it can offer in terms of meeting sustainability measures (Bürgi, 2015).

No single silvicultural system can provide the preferred habitat of all woodland birds. In practice, therefore, a conservation strategy that embraces a dynamic range of management interventions is desirable to enhance habitat heterogeneity and complexity at varying spatial and temporal scales (Fuller et al., 2007; 2012, MacColl et al., 2014). Irregular CCF forestry clearly has the potential to play an important role in developing this heterogeneity. However, there is a question about whether it can meet the requirements of all early successional species. In this respect, further work is needed to assess how varying gap sizes and canopy openings within different variants of CCF affect biodiversity (Puettmann et al., 2015).

Finally, the results of this study support the notion that in a British context, management of neglected woodland benefits the numbers of many woodland bird species. Both the irregular stands and the coppiced stands held higher densities of breeding birds than the limited intervention stands, typical of much neglected woodland in lowland Britain. Restoration of such stands to a structurally more complex state through opening up the canopy to stimulate the understorey would be beneficial and, if conducted on a sufficiently large scale, could potentially assist in the recovery of some woodland bird populations at a regional level. In this context, it is notable that the spring abundance of marsh tit in irregular stands was approximately twice that in the other stand types. Broughton and Hinsley (2015) cautioned that large scale management by coppicing could be detrimental to habitat quality for this species, but it appears that irregular stand management may benefit it, though more research is needed to draw firm conclusions. An integrated approach to forest management which incorporates stand-level targets to attain biodiversity attributes e.g. deadwood, as shown by Susse et al (2011) is an exciting option; particularly if it can be adapted to include measures that provide important functional resources used by woodland birds in the UK including those associated with understorey.

Acknowledgements

Andy Poore (Consultant Forest Manager) provided background information on stand management and suitable locations for the study. Ian Burt (Rushmore Estate), Rhiannon Rogers and Jon Corkill (Dorset Environmental Records Centre) helped with fieldwork and GIS support respectively. For access to the woodlands we are grateful to the Trustees of the Rushmore Estate and particularly support from the managing agents Philip Gready and Ruth Mason, along with the gamekeepers Andy Taylor and Robert Taylor and coppice woodman Don Taylor for their practical assistance. We are particularly grateful to Dr Annabel King for the recommendation and assistance given during the planning stages. The fieldwork was funded by the Golden Bottle Trust, Henry Hoare Charitable Trust and Forestry Commission (England). The study formed part of a multi-taxon study of the effects of transformation of broadleaf woodland overseen by Dr Phil Sterling (Dorset County Council) and Andy Poore. There are no declarations of conflicts of interests.

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Chapter 5 Bats

5.1 Paper 3 Irregular silviculture positively influences multiple bat species in a lowland temperate broadleaf woodland

5.1.1 Background and Details of Authors Contributions

The following authors contributions are listed with their signatures.

Daniel Alder, Main Author: 80% Conceptualisation, Study design, Data collection of all field data on bats and habitat structural measures, Preparation data and statistical analysis, writing, responding to Journal Editor and two reviewer's comments and re-wrote text prior to resubmission. D. C Alder

<u>Co-authors</u>

Mr A Poore: wrote text on silviculture and advised on silvicultural implications of results.

Dr. J D Norrey: provided advice and support with data analysis.

Dr S Newson: advisor on data collection, ran acoustic identification software. S Newson

Prof S Marsden: Main Supervisor.

Forest Ecology and Management 483 (2021) 118786

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Irregular silviculture positively influences multiple bat species in a lowland temperate broadleaf woodland

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ARTICLE INFO

Keywords:
Bat activity patterns
Occupancy
Structural heterogeneity
Habitat use
Stand type
Woodland management
Irregular high- forest
Retention silviculture
Continuous cover forestry

ABSTRACT

Changing economics in the 20th century led to losses and fragmentation of semi-natural woodland in Britain and to a reduction in active woodland management with many becoming increasingly neglected, even-aged and with closed canopy. Lack of woodland management is known to contribute to declines in some taxonomic groups, for example birds. However, the response of bats to changes in woodland structure are poorly understood. We compared two measures of bat activity, derived from static acoustic recorders across 120 sample plots in coppice, irregular high forest (uneven-aged, continuous cover) and limited intervention (under-managed, even-aged) management stands, within a large tract of ancient woodland in southern England. Bat species richness was highest in irregular high forest stands, and there were significant differences in occupancy rates for most bat species across stand management types. Coppice recorded low activity of several bat species and irregular high forest showed high occupancy rates, including for Barbastelle *Barbastella barbastellus*, which is IUCN listed as near threatened. The occupancy rates in stand management types differed for some bat species between mid- and late summer counts, suggesting seasonal variation in habitat use. Within stands, most bat species were associated with opened canopy, lower growing stocks and reduced densities of understorey, and to a lesser extent, with large-girthed trees and presence of deadwood snags. In some cases, species responded to a given habitat variable similarly across the three stand management types, whereas in others, the response differed among stand management types. For example, increased numbers of large-girthed trees benefitted a number of bat species within coppice where these were least common, but not in irregular stands. Irregular silviculture high forest appears to provide many of the structural attributes that positively influence occupancy of several woodland bat species, including *Barbastella barbastellus*.

1. Introduction

Developing strategies for forest and woodland resilience in the face of climate change and increasing exploitation of forest resources is seen as a global priority (Pastur et al. 2020, Brang et al. 2014, Bussotti et al. 2015, Thompson et al. 2009). Structural and functional change following intensive silvicultural interventions (e.g. clear felling) can compromise woodland resilience and reduce the range of ecosystem services woodlands and forests support at multiple scales (Felipe-Lucia et al. 2018). Simplification of forest habitats has led to losses of biodiversity (Lelli et al. 2019) and in turn is likely to have impacted upon the ecological functioning and economic productivity of forest systems (Liang et al. 2016). During the 20th Century, many European woodlands became structurally more homogeneous as a result of clear-fell silviculture followed by abandonment and the rise of plantations or neglect (Hopkins & Kirby 2007, Savill 2015, Russo et al. 2016). In Britain many semi-natural woods were heavily exploited during both World Wars then abandoned due to the economic demise of coppice management after the Second World War (Hopkins & Kirby 2007). Many ancient woodlands in Britain (those present since at least 1600AD; Spencer & Kirby 1992) had been subject to traditional management regimes, particularly coppicing, for>650 years (Rackham 1986). The structural homogenisation of these woodlands following abandonment and the widescale conversion to coniferous plantation transformed Britain's

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https://doi.org/10.1016/j.foreco.2020.118786
Received 5 August 2020; Received in revised form 6 November 2020; Accepted 8 November 2020

landscape during the 20th Century (Harmer et al. 2010) and ancient woodlands that were spared degradation are seen as relics of high historical/cultural (Rackham 2003) and nature conservation value (Fuller & Warren 1993). In these remaining semi-natural stands, however, there has been a long-term, natural process of structural change leading to increasing density of trees and declining density of underwood. Climate induced reduction in temperate forest health in Europe (Senf et al. 2018), and the ecological consequences of tree pests and pathogens e.g. *Hymenoscyphus fraxineus* on Ash, *Fraxinus excelsior*, are expected to increase in the absence of mitigation (Mitchell et al. 2014, Hill et al. 2019, Forestry Commission 2019).

Continuous cover forest management (CCF; Mason et al. 1999), is a relatively new woodland management system for the UK (Kerr 1999). Silvicultural management using CCF systems are likely to be important where adaptive responses to ecological change are essential (Wilson et al.2018). Irregular silviculture is one strand of CCF, which aims at permanently irregular high forest structures. It emphasises natural processes and seeks to develop complex habitat structures with a range of different size-classes of trees and an understorey partly comprised of tree saplings (Susse et al. 2011, Kerr 1999). This approach has been advocated because it provides a range of ecological benefits and ecosystem services (Pukkala 2016, Kerr 1999) while providing economic return (Lõhmus et al. 2016, Pastur et al. 2020). Using a stem-by-stem or group harvesting system, canopy opening is patchy and can resemble natural woodland processes (Bürgi 2015, Kuuluvainen 2009), with canopy gaps leading to localised seedling regeneration, while developing a continuum of tree and shrub ages from young thicket stage to mature trees in each stand (Sanchez 2017, Susse et al. 2011). Semi-natural stands are highly variable in the level and spatial distribution of their growing stock and in the spatial distribution of individual trees with high biodiversity or economic values (Susse et al. 2011). Unlike irregular silviculture, even-aged silviculture constrains within stand complexity (Puettmann et al. 2015, Sanchez 2017). Finally, Irregular Silviculture involves moderate change and provides benign environments for vulnerable stand elements such as standing deadwood (Sanchez 2017). Despite the potential of irregular management to support keystone species (Gustafsson et al. 2020, Basile et al. 2020), there remains a significant knowledge gap of the effects on biodiversity following its introduction within temperate forests (Storch et al. 2020). Recent research as part of our wider study has highlighted positive effects of irregular silviculture on woodland birds (Alder et al. 2018).

All 17 species of bats found in Britain use woodlands (Altringham 2003) and several, including *Barbastella barbastellus,* are reliant upon semi-natural broadleaf woodlands (Dietz et al. 2018, Zeale et al. 2012). Broadleaf woodland provides keystone resources on which many species depend (Mendes et al. 2017, Boughey et al. 2011). Bats are an important indicator of changes in the structure and function of managed temperate woodlands (Jones et al. 2009, Kalda et al. 2015) and provide important forest ecosystem services (Garin et al. 2019). The availability of insect prey (Tillon et al. 2018), the ability of bats to forage effectively (Müller et al. 2012, Adams et al. 2009), microhabitat features important for roost availability (Regnery et al. 2013, Tillon et al. 2015, Russo et al. 2016), and abundance of standing deadwood (Carr et al. 2019, Tillon et al. 2018, Dietz et al. 2018, Lučan et al. 2009, Russo et al. 2004), can influence bat abundance and are all affected by woodland management. Bat species within the same guild face competitive challenges that they must overcome in the way they respond to the often variable, complex vegetation structures of temperate woodland (Langridge et al. 2019, Denzinger & Schnitzler 2013). Partitioning of resources may be achieved through choice of prey, avoiding direct competition by feeding at different periods, selecting different habitat patches and through behavioural differences (Swift & Racey 1983).

While our knowledge of the habitat associations of European bats is good (Downs & Racey 2006, Tillon et al. 2018) we know little about the effects of different silvicultural management options across a range of broadleaf woodlands, and in particular as a result of manipulating high forest structures (Russo et al. 2016). Furthermore, caution has been urged over the restoration of traditional coppice management on *Plecotus auritus* (Murphy et al. 2012). Excessive levels of harvesting in high-forest stands are known to negatively affect bats (Tillon et al. 2018, Russo et al. 2016).

Studies in mixed broadleaf stands in western Europe have highlighted the positive influence on bats, in woodland managed sensitively to produce a varied structure (Jung et al. 2012) and through the introduction of innovative selective silviculture (Cistrone et al. 2015). Conversely, a comparison across even-aged, uneven-aged and unmanaged beech *Fagus sylvatica* forest by Schall et al. (2018) identified similar bat diversity. However, we are unaware of a direct comparison between management types in British woodlands that include irregular silviculture amongst the management options in ancient semi-natural broadleaf stands, and the effects on bats of creating diverse high forest structures. We compared a range of structural habitat measures across three management types and assessed bat species richness and activity of each species across coppice, limited intervention, and irregular high forest stands. We used two metrics of bat activity from acoustic recorders; (1) an encounter rate of number of passes through the night; (2) one reflecting the proportion of ten-minute periods during which each species was recorded at least once. We then looked within woodland stand management types to identify structural attributes influenced by woodland management and associated these with bat activity.

2. Methods

2.1. Study area and stand types

The study was conducted within 442 ha of semi-natural broadleaf woodland, mostly statutorily protected Site of Special Scientific Interest (SSSI), across two contiguous blocks on the Rushmore Estate, in southern England (110–190 m a.s.l; 395724.26 E, 117963.15 N; Fig. 1). The principal National Vegetation Classifications (NVC) are W8 (ash-field maple) associated with base-rich soils with some W10 (oak-birch) on slightly acidic soils, that fall within the broad category of lowland mixed deciduous woodland on fertile soil with several sub-categories around the former (Rodwell et al. 1998, B. Edwards *pers. comm.* 2019). 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*. There are a significant number of veteran trees, those identified as having biological and cultural importance (Read 2000); particularly of oak, ash and field maple and 19th Century beech *Fagus sylvatica* plantings (Alder et al. 2018, Poore 2016).

2.2. Descriptions of broadleaf stand types

We evaluated three broadleaf stand management types (A. Poore *pers. comm.* 2019; Fig. 2). Silviculture is either high forest with trees derived from seed on long felling rotations 50–200 years or coppice, referring to cyclical cutting of regenerated stems on short rotations (Harmer et al. 2010). We define woodland management as the harvesting of woody material and the stand as the silvicultural unit at which forest management was undertaken.

Limited intervention stands (43.4 ha) were those with a closed canopy, high tree density, and limited understorey due to a long period (>30 years) without formal silvicultural intervention. Some of the limited intervention stands developed from open canopy high forest and had higher understorey densities. Limited intervention stands originate from three starting points which were typical in lowland Britain following reductions in broadleaf management (Mason 2007).

Fig. 1. Location of study area within Cranborne Chase on the Dorset-Wiltshire border, southern Britain, UK. © Natural England copyright 2012. Contains Ordnance Survey data © Crown copyright and database right 2012.

- Stands which had a more varied structure when management ceased and where a somewhat more complex structure persists.
- Stands which had a more uniform coppice structure at the point of abandonment.
- Stands which came out of a wood pasture structure with less underwood but where some remnant scrub persists.

Coppice stands (59.0 ha) include both simple coppice and coppice with standards with up to 20% cover of upper canopy trees. However, effective underwood production requires a maximum cover of 10% upper canopy trees. Underwood cycle lengths vary with use: hazel dominated coppice cut every 8–12 years, birch coppice was managed on two rotations, with pure birch cut at 3–4 years and the remaining 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 ($n = 11$). 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 (52.9 ha) were transformed to high forest (tree recruitment into canopy) from unmanaged coppice or developing high forest stands to an irregular stand structure for at least 30 years. This involved selective removal of harvestable trees and of weaker growing specimens and cutting the understorey to increase light levels reaching the woodland floor. The aim was to increase incremental growth of retained trees to enhance their economic value, promote natural regeneration of trees and shrubs and establish a range of tree age classes. Stands with 'moderate stocking' have stand basal areas (>7.5 cm diameter at breast height, (dbh)) in the range 17–24 m^2 ha^{-1} whilst 'low stocking' are in the range 10–16 m^2 ha^{-1}. Understorey stocking was dense in places yet patchily distributed as influenced by management and the effects of deer browse. Species diversity was encouraged and individual trees with particular biodiversity values retained, including senescent and standing deadwood (Susse et al. 2011). A feature of irregular high forest stands at Rushmore was the high densities of retained deadwood and trees with cavities.

The coppice and irregular stand types in the south-west of our study were not chosen being unrepresentative of the age-classes of each; coppice here was mostly advanced in-cycle and the irregular was more recently transformed < 30 years ago.

2.3. Collection of acoustic data

Bats were sampled acoustically during the summer over two periods 24 June – 22 July and 31 July – 2 September 2015 using six Song Meter 3 (SM3) acoustic recorders fitted with a single omnidirectional microphone (Wildlife Acoustics Inc. USA). Microphones were pole-mounted at 3 m height to avoid reflected sounds from the ground, facing downwards at an angle of 45^0, and placed a minimum of 1.5 m from dense leafy growth to reduce reflection from vegetation (Müller et al. 2012).

Full spectrum audio using an 8 kHz high pass filter was used to reduce the chance of recording low frequency sounds not made by bats (Newson et al. 2015). SM3s were programmed to switch on 15 mins before sunset and off 15 mins after sunrise, and record throughout the night (Froidevaux et al. 2014) using a trigger threshold above 12 dB and recording set to continue until no trigger was detected for a 2.0 s period (Newson et al. 2015). Each triggered event was categorised as a bat pass for each species identified following Newson et al. (2015). We adopted a stratified sampling procedure with simultaneous recording made using two SM3 units in each of the three stand types, each sampling night (Humes et al. 1999) with each plot sampled twice across the two periods with a minimum interval of 3 weeks between each visit (Frey-Ehrenbold et al. 2013). Plots were located a minimum of 30 m from the edges of each stand to reduce the effects from proximate habitats (Humes et al. 1999). There were 40 sampling plots (a total 120 plots) in each stand type across 26 individual stands Fig. 3. Acoustic sampling was conducted on nights without rain, wind speeds below force 4 on the Beaufort scale and temperatures above 7 °C (Froidevaux et al. 2014).

2.4. Sound identification of bats

Bats were identified according to a two-step procedure following Newson et al. (2017) whereby recordings were firstly filtered through species classifiers built by one of us (SEN) using the software TADARIDA (Bas et al. 2017), which assigns bat calls to species. This automatically detects and extracts acoustic features of the recorded echolocation calls and classifies them to species using a Random Forest algorithm (Claireau et al. 2019). Manual verification (step 2) of all bat calls following TADARIDA was made using Sonobat 4.1 software (www.sonobat.com) producing 35,230 confirmed bat passes from 137,018 sound files. Of these, 10,992 bat passes were not assigned to species as manual verification could not be identified with confidence to species (Russ 2012). *Myotis mystacinus* and *M. brandtii*, and *Plecotus auritus* and *P. austriacus* are particularly difficult to identify acoustically, and were treated as species pairs, therefore *M. mystacinus / brandtii* and *P. auratus / austriacus* respectively (Starik et al. 2018). 'Guilds' for each species identified are used; SRE – short range echolocators, MRE – medium range echolocators, LRE – long range echolocators (adapted from Denzinger & Schnitzler (2013)).

Fig. 2. Examples of stand types sampled in the study from top to bottom: limited intervention, coppice and irregular high forest.

2.5. Habitat measures

At each sample plot measurements of woodland structure 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 (Alder et al. 2018).

Within 30 m plots and 3 m sub-plots, the following habitat measurements were made:

- ***Number of trees*/stems in each 30 m plot** > 50 cm dbh, number of woody stems (coppice and individual trees) of dbh 7.5–17.5 cm and 17.5–50 cm dbh, and the five trees with the largest dbh. These five were identified to species and mean dbh also calculated.
- At each 3 m subplot, the **number of saplings and coppice stems** < 3 cm, and > 3–7.5 cm dbh were counted if > 0.5 m tall.
- Percentage of ***canopy openness*** was measured at each 3 m sub-plot with a spherical convex mirror densiometer (Lemmon 1956).
- ***Growing stock density*** (basal area (m^2 ha-1)) was measured at each plot centre using the relascope principle (Bitterlich 1984) where each tree > 7.5 cm dbh is counted in a 360^0 sweep at each sample point centre. A minimum number of ten trees are required to give precision (Bitterlich 1984). The relascope application MOTI was used for this (Rosset et al. 2014), calibrated for the basal area factor and camera and was used in a Samsung Galaxy S2 smart-phone.
- To calculate ***understorey density***, a percentage score of obscuration to the nearest 5% was estimated at each cardinal point of the 30 m plot using a 50 × 30 cm chequer board with 10 × 10 cm squares (Alder et al. 2018).
- ***Standing deadwood***, dead trees and dead branches (snags) over 20 cm diameter (as a proxy for cavity availability (Paillet et al. 2018)) were counted around each 30 m plot centre (Charman et al. 2010)
- ***Length of fallen logs*** over 20 cm diameter were measured entirely within each 30 m plot (Lush et al. 2012).
- ***Percentage cover*** was calculated at within 30 m plot for dominant vegetation; bramble *Rubus fruticosus* cover, and area of bare ground.

All fieldwork was carried out by DA.

2.6. Data analyses

Structural habitat measures were compared across stand types using a mixed effect models and pairwise comparisons with stand number as a random factor to account for nestedness in samples within stands. Measured continuous variables were analysed using Linear mixed model using the package "nlme" (Pinheiro et al. 2020) or GLMM with a gamma distribution. Count data was analysed with a GLMM with Poisson distribution. For percentage data an arcsine transformation was applied to the data and analysed using a Linear Mixed effects Model (see table × in supplementary material).GLMM models were performed using the "LME4" package (Bates et al. 2015). Tukey's post-hoc multiple comparison tests were used to make comparisons across management stand types. Spearman's rank correlations (supplementary file S 4) were used to select habitat variables to include in bat habitat association models and to compare across and within stand types.

We calculated bat species richness at each plot in each survey period. We expressed bat activity across stand types and survey periods using two different metrics. First, 'overall encounter rates' were calculated as the mean number of bat passes per hour, to give an overall indication of activity during the sampling night. For encounter rate we excluded the first and last 30 min of each night, to avoid issues associated with high numbers of bats moving to and from roost sites (Wood et al. 2017). The second, 'occupancy or activity rates', was calculated as the proportions of 10-minute periods during a night, within which the bat species was recorded at least once. Using the proportion of 10-minute periods, which differed across nights of different length (in our study period it varied between 7.5 h and 10.5 h), allowed us to account for night length differences in our activity metric.

A GLMM with Poisson distribution was used to analyse species richness across stand types. A GLMM with a binomial distribution was used to analyse activity level (proportion of possible 10-minute periods each species was active per night) between the stand types. Because sampling plots were nested within woodland stands (n = 30) we included stand number as a random factor in all models (Zuur et al.

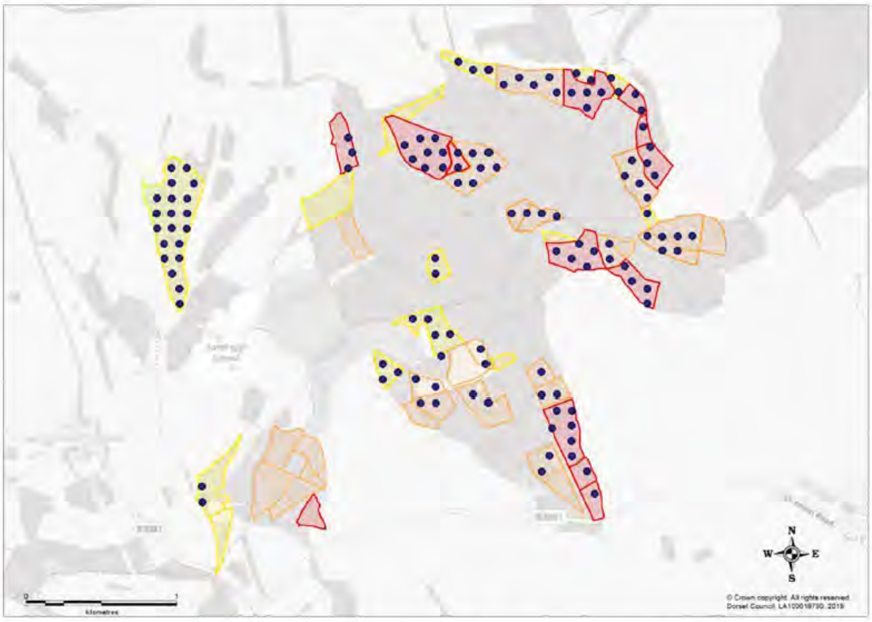


Fig. 3. Location of sample points within three stand management types; orange coppice, yellow limited intervention and red irregular. Average nearest plot distances within stand types was 117 m. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2009). Encounter rate data (mean number of bats per hour) being continuous and including zeros were analysed using a zero-inflated mixed effects model with a gamma distribution using the package 'glmmTMB' (Brooks et al. 2017). Models were run for each species with management stand type and an interaction with survey period and stand type as predictors.

To examine the effect of habitat variables on species activity within each habitat type separately, three GLMM's with binomial distribution were applied with canopy openness, general stem density, mean DBH and snag frequency as predictors. Habitat variables were based on gradients of openness, stem size and density and standing deadwood and selected by examining collinearity between all habitat variables collected. Model averaging using the package "MuMIn" (Barton, 2020) was used to identify the relative importance of each habitat variable on each species within the three stand types.

3. Results

3.1. Bat species data

Eleven bat species were identified (Table 1). *Pipistrellus pipistrellus* dominated the sample, making up 78% of records from 90% of plots. Three other species, *Barbastella barbastellus*, *P. pygmaeus* and *Myotis mystacinus/brandtii* all had>1,000 bat passes. *Myotis mystacinus/brandtii* group comprised 1,733 records and were recorded on 63% of plots. *P. nathusii* (22 records; <2% of plots) and *Nyctalus leisleri* (52 records; 14% of plots) were deemed too rare for further analysis. Species richness differed between irregular and coppice stand types with higher species richness in the irregular stands (Cop- Irr, estimate ± se, Z, p: −0.4 ± 0.1, −2.6, 0.03; see Supplementary file S 2). Seven of the nine species were more often recorded in the second survey period than the first. However, there were no significant differences across survey periods, or interaction between period and stand management type.

Table 1
Bat passes and percentage of occupied survey plots for eleven bat species recorded over two survey periods.

Bat Passes					% Plots used	
Species/Guild	Period one	Period two	All	% of total	Period one	Period two
Plecotus auritus/austriacus^{SRE}	63	187	250	0.7	28.3	31.7
Barbastella barbastellus^{SRE}	234	789	1023	2.9	40.0	37.5
Myotis nattereri^{SRE}	278	268	546	1.6	51.7	50.0
Pipistrellus pipistrellus ^{MRE}	9,881	17,660	27,541	78.0	89.2	90.8
Pipistrellus pygmaeus ^{MRE}	1,669	1,192	2,861	8.1	61.7	68.3
Pipistrellus nathusii^{MRE}	22	0	22	0.1	2.5	0.8
Myotis mystacinus/brandtii^{MRE}	715	1,018	1,733	4.9	63.3	62.5
Myotis daubentonii^{MRE}	147	316	463	1.3	42.5	49.2
Eptesicus serotinus^{LRE}	181	247	428	1.2	50.0	56.7
Nyctalus noctula^{LRE}	256	55	311	0.9	49.2	32.5
Nyctalus leisleri^{LRE}	21	31	52	0.2	19.2	9.2
Total	13,467	21,763	35,230	100	96	96

3.2. Bat activity metrics across stand management types

Although encounter rates and occupancy metrics were correlated (r = 0.73, n = 2160, p < 0.001, across all species / survey period /and plots), occupancy indicated more significant differences among stands or between survey periods (24 significant differences), than 'encounter rates' (10 significant differences). We describe our rationale for selection of each metric in the Discussion but here, we focus on the results of the latter (encounter rate results appear alongside occupancy rates in Supplementary file S1).

Activity for two of the three short-range echolocators was greatest in Irregular, for two of four MREs, and one of two LRE. We expand on differences in activity between species sharing similar traits in the discussion. Six of nine bat species (Fig. 4) had significantly greater occupancy in irregular high forest than in at least one of the other stand management types. *Eptesicus serotinus* and *P. auratus / austriacus* were most active compared to limited intervention; whereas *M. daubentonii*, *M. mystacinus / M. brandtii*, *P. pygmaeus* and *B. barbastellus* were encountered more than in Coppice (*P. pipistrellus* higher than in both). Only *M. nattereri*, was significantly more likely to be recorded in limited stand management type over both coppice and irregular high forest. The results highlight the generally low occupancy rates in coppice stands. *M. nattereri*, *P. pipistrellus* and *P. pygmaeus*, and *M. mystacinus/brandtii* selected limited intervention over coppice, with *E. serotinus* more common in coppice than limited intervention.

Six of nine species showed significantly different levels of occupancy of the stand management types between the survey period. Two taxa, *P. pipistrellus* and *M. mystacinus/brandtii*, increased usage during period 2 in one stand type (limited intervention and coppice respectively) over another stand type (irregular high forest and limited intervention), suggesting a change in habitat use within the study area according to season. In contrast *P. pygmaeus* and *N. noctula* used two stand types less in period 2, which along with the general lack of records from period 2

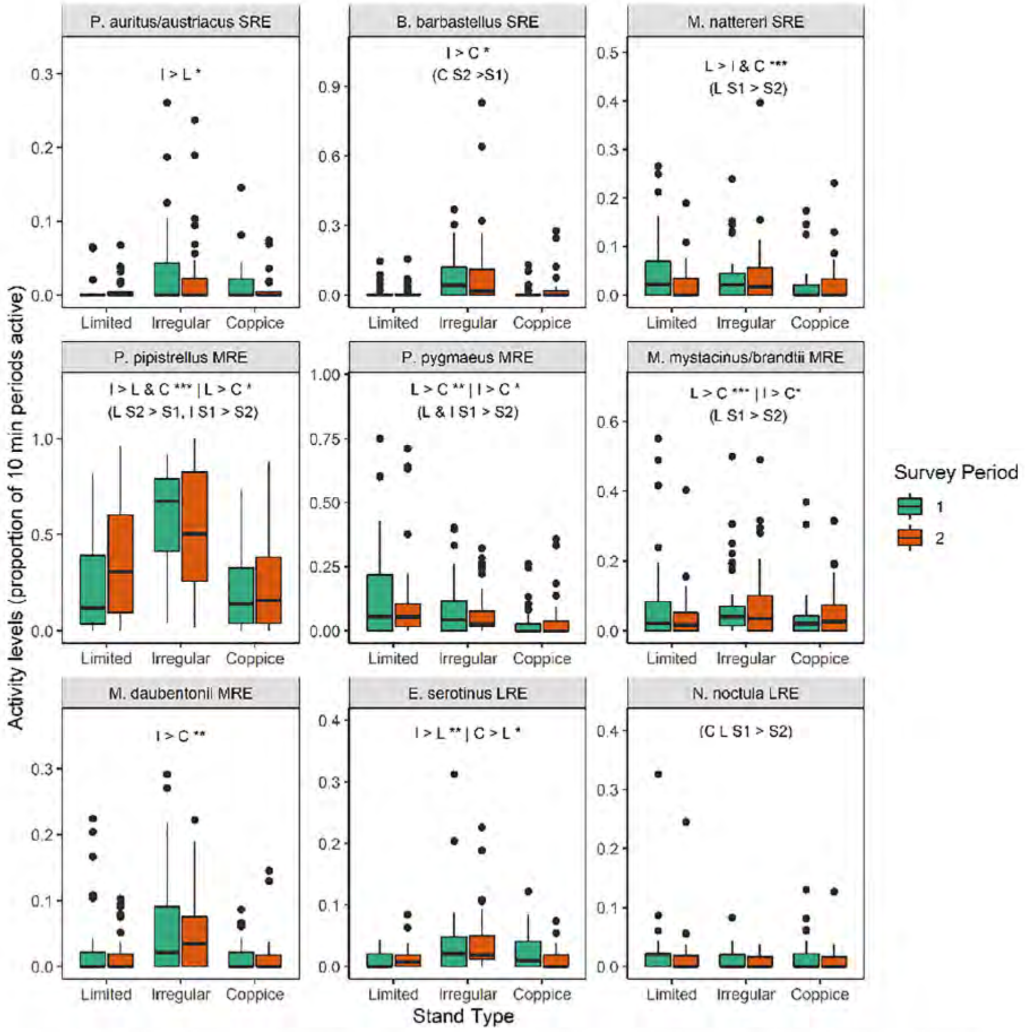


Fig. 4. Bat activity (proportion of possible 10-minute periods each species was active per night) as a measure of occupancy throughout the sample night. Where significant, management code I = Irregular, C = Coppice, L = Limited were combined with < (less than) or > (greater than) and * ($p < 0.05$), ** ($p < 0.01$), and *** ($p < 0.05$) to show significant difference in management type. For survey period and management type interactions that were significant (S1 = Survey period 1, S1 = Survey period 2) were combined with management codes (above) and < and > with asterisks (see above) to show direction of difference and significance level.

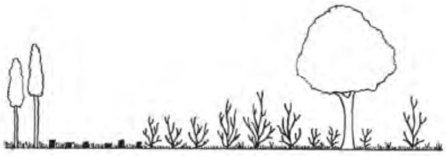
(Table 1) suggest a movement out of the study site post-breeding. *M. nattereri*, although preferring limited intervention stands overall, reduced its use of this stand management type in period 2, while *B. barbastellus* used coppice stands more in period 2.

3.3. Stand habitat characteristics

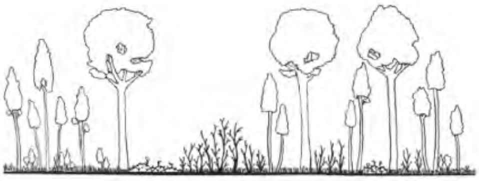
There were 19 habitat variables which showed significant differences in pairwise comparisons of stand management types (Supplementary file S 3). Fig. 5 shows a schematic of the three stand management types labelled with key habitat features.

3.4. Habitat associations

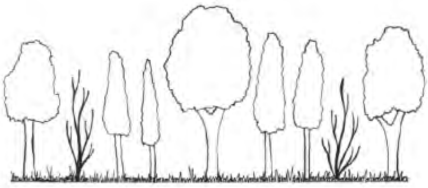
Of the four habitat variables considered (see Supplementary file S 4 correlations of all habitat variables), canopy openness was significantly associated with bat occupancy rates in eleven species/stand type cases (Fig. 6), stem density in six, and DBH and snags five each. In nine of the eleven cases, it was high values of canopy openness that were positively associated with bat occupancy rates, while in all six cases, low stem density was associated with high occupancy rates. In general, larger DBHs and frequent snags promoted bat occupancy (Fig. 6).



Coppice: low tree stocking, dense understorey or no understorey if recently cut; few large trees; heavy moss cover



Irregular High Forest: patchy open canopy, range of tree sizes including large trees; variable understorey with low, dense bramble cover; combines many characteristics of coppice and limited intervention



Limited Intervention: High tree stocking with high stem density; few oaks; closed canopy; sparse understorey and bare ground; high volume of fallen dead wood.

Fig. 5. Significant structural characteristics identified within each stand.

For some species, associations of occupancy with individual habitat measures was very similar across different stand management types. For example, *B. barbastellus* was strongly positively associated with the most open plots in all three stand management types, and *P. pygmaeus* generally negatively associated with stem density, regardless of stand type. The generalist/edge species *E. serotinus* had no significant associations with any of the habitat variables which was consistent across stand management types.

In other cases, species appeared to respond differently to the same habitat variable in different stand management types. So, there was a stronger likelihood of a species having a positive relationship with Mean DBH in the coppice, and to a lesser extent, limited intervention, than in irregular stands where Mean DBH was higher. Nevertheless, there were several differences in species-specific responses across stand management types. Several of these involve the closely related species *P. pipistrellus* and *P. pygmaeus* despite sharing similar morphological characteristics the two Pipistrelles exhibit differences in habitat use. *P. pygmaeus* used closed canopy more than *P.Pipistrellus* which is more of an edge species. In other cases, it may be that the rarity of a bat species in one or more of the stand management types is affecting models. – essentially the habitat is far from suitable in terms of that individual habitat measure so changing values as they appear across our plots is having little effect on overall suitability.

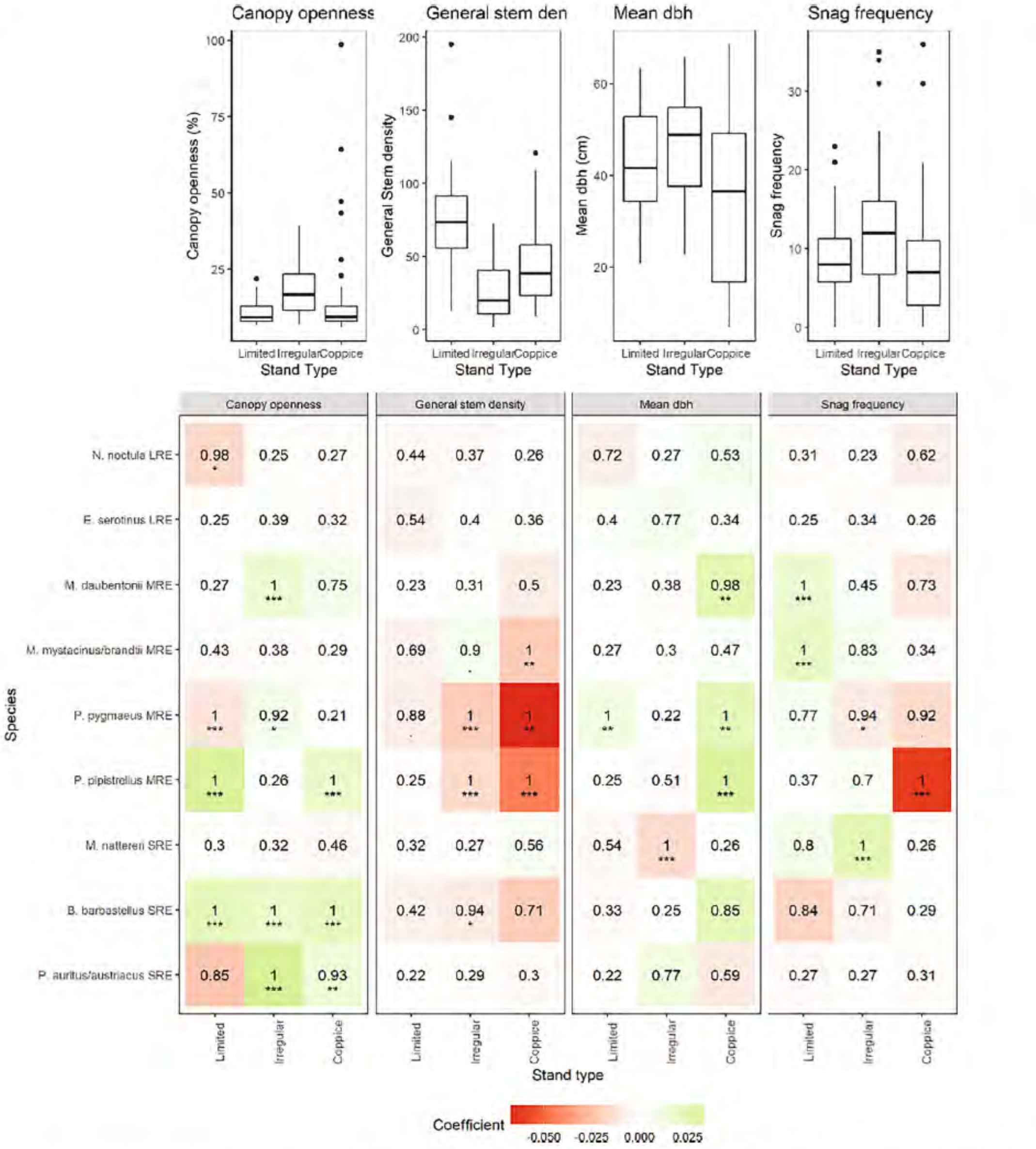
4. Discussion

4.1. Species response to stand management

We found clear differences in bat occupancy among three stand management types. Irregular high forest, had the highest species richness, and highest occupancy rates for most bat species, including the IUCN ‘near-threatened’ *B. barbastellus* (Piraccini et al. 2016). Activity across three foraging guilds was higher in irregular than in either coppice or limited intervention stands. Coppice had lower bat activity for four species, *B. barbastellus, E. serotinus, M. daubentonii*, and *P. pipistrellus* and lower species richness compared with irregular stands. This may reflect the coppice age structure sampled with 10% at 0–3 years. Four plots in closed-canopy coppice (c14 years) where no bats were recorded, suggested that short-range echolocating (SRE) species including *M. nattereri* avoided densest clutter (Rainho et al. 2010, Froidevaux et al. 2016, Arlettaz et al. 2001).

Broadleaf stands which have undergone thinning can positively influence bats (Blakey et al. 2016) although recent research found rarer species benefitted from non-intervention compared to managed stands (Carr et al. 2019). However, the choices of silviculture management available to forest managers are diverse, reflecting site conditions and past management histories (Adams et al. 2009, Langridge et al. 2019). Irregular silviculture is very different from even-aged management (Bürgi 2015, Lõhmus et al. 2016). Our study suggests variable retention of tree size classes, deadwood, understorey, open canopy and larger tree size associated with irregular seems to benefit multiple bat species across foraging guilds (Renner et al. 2018).

Structural complexity in irregular stands is likely to influence habitat quality for bats including accessibility to abundant invertebrate prey associated with denser low understorey (Starik et al. 2018, Tillon et al. 2018, Charbonnier et al. 2016, Plank et al. 2012, Adams et al. 2009). Differences in three-dimensional structure of vegetation influences the composition of bat species assemblages (Adams et al. 2009, Jung et al. 2012, Kirkpatrick et al. 2017). Work on woodland birds within our study area (Alder et al. 2018) indicated that irregular silviculture can provide several functional resources for species reliant on early successional growth and old growth features. Where woodland management constrains levels of decaying trees, the presence of keystone cavity makers like woodpeckers can be important (Remm & Lõhmus, 2011). Great Spotted Woodpecker *Dendrocopos major* had highest spring densities in irregular stands in our study area where deadwood snags were frequent



Species	Canopy openness Limited	Canopy openness Irregular	Canopy openness Coppice	General stem density Limited	General stem density Irregular	General stem density Coppice	Mean dbh Limited	Mean dbh Irregular	Mean dbh Coppice	Snag frequency Limited	Snag frequency Irregular	Snag frequency Coppice
N. noctula LRE	0.98 *	0.25	0.27	0.44	0.37	0.26	0.72	0.27	0.53	0.31	0.23	0.62
E. serotinus LRE	0.25	0.39	0.32	0.54	0.4	0.36	0.4	0.77	0.34	0.25	0.34	0.26
M. daubentonii MRE	0.27	1 ***	0.75	0.23	0.31	0.5	0.23	0.38	0.98 **	1 ***	0.45	0.73
M. mystacinus/brandtii MRE	0.43	0.38	0.29	0.69	0.9 .	1 **	0.27	0.3	0.47	1 ***	0.83	0.34
P. pygmaeus MRE	1 ***	0.92 *	0.21	0.88 .	1 ***	1 **	1 **	0.22	1 **	0.77	0.94 *	0.92
P. pipistrellus MRE	1 ***	0.26	1 ***	0.25	1 ***	1 ***	0.25	0.51	1 ***	0.37	0.7	1 ***
M. nattereri SRE	0.3	0.32	0.46	0.32	0.27	0.56	0.54	1 ***	0.26	0.8	1 ***	0.26
B. barbastellus SRE	1 ***	1 ***	1 ***	0.42	0.94 *	0.71	0.33	0.25	0.85	0.84	0.71	0.29
P. auritus/austriacus SRE	0.85	1 ***	0.93 **	0.22	0.29	0.3	0.22	0.77	0.59	0.27	0.27	0.31

Fig. 6. Habitat attributes across stands (upper) and bat species associations within each stand management type (lower) taken from a GLMM with binomial distribution and model averaging. The number shown in the individual panes are the sums of 'Akaike weights' over all models with Delta AICc < 6. The colour indicates the direction and strength of the fixed effect variable. Significance is indicated by * ($p < 0.05$), ** ($p < 0.01$), and *** ($p < 0.001$).

(Alder et al. 2018). Importantly, irregular silviculture creates benign conditions for retaining trees with special biodiversity features (Sanchez 2017).

B. barbastellus, a SRE, low-level foraging bat (Rainho et al. 2010, Plank et al. 2012, Denzinger & Schnitzler 2013), was significantly associated with more open canopy areas in all stand management types with highest occupancy in irregular high forest. Within coppice stands *B. barbastellus* was significantly associated with larger trees and strongly correlated to the presence of snags in all stand types (See Supplementary file S 3). Dead wood availability is important for *B. barbastellus* (Russo et al. 2004, Carr et al. 2019) because individuals frequently switch roosting locations (Russo et al. 2005). Their higher occupancy in irregular stands potentially reflects the abundance of retained deadwood (Görföl et al. 2019) and feeding habitat across patches of dense understorey (Zeale et al. 2012, Hill & Greenaway 2008). We found a negative association in limited intervention stands with deadwood snags; interestingly Tillon et al. (2016) did not identify a relationship between *B. barbastellus* and deadwood presence. Moreover, there may be thermophilic benefits for *B. barbastellus* utilising open and sheltered interiors of irregular stands (Carr et al. 2019, Dietz et al. 2018).

Eptesicus serotinus occupancy was higher also in irregular and coppice stands Accessible prey is possibly a key factor; *E. serotinus* is an adaptable forager (Catto et al. 1996) using forest interiors where structural heterogeneity enables manoeuvrability (Langridge et al. 2019, Plank et al. 2012). It is associated with deadwood (Tillon et al. 2016) and tree roost woodpecker cavities (Langridge et al. 2019).

Nyctalis noctula, a LRE (Langridge et al. 2019), was encountered across all stand types, most in limited intervention but not significantly. It was negatively associated with canopy openness in limited intervention stands in our habitat models. *N. noctula* uses open-space flight-lines above the woodland canopy over which it can hawk flying insects (Müller et al. 2013).

Several *Myotis* species are morphologically similar yet differ in echolocation, enabling each to exploit different vegetation structures (Siemers & Schnitzler 2004). *M. daubentonii*, an edge species (Müller et al. 2012), had highest occupancy in irregular high forest, significantly so over coppice and a positive association with canopy openness. Plank et al. (2012) found this species flew at ground level in uncluttered woodland which explains its low occupancy in coppice. Snag frequency within limited intervention stands was important, perhaps because open understorey enables *M. daubenonii* to exploit snags as roosts. The species is known to use cavity roosts which develop in humid conditions associated with closed-canopy woods (Boonman 2000).

M. mystacinus/brandtii stand-wise occupancy was highest within limited intervention followed by irregular high forest over coppice. Our models showed strong avoidance of highest stem densities typical of dense coppice and accords with a association with woodland edges (Müller et al. 2013). The species group utilises lower height stratum beneath canopy in accessible forest interiors, (Cel'uch & KRopil, 2008, Froidevaux et al. 2016). Despite high tree densities in limited intervention stands the open understorey enables the species to manoeuvre at heights below 10 m (Bačkor 2016).

M. nattereri with highest occupancy in limited intervention over coppice and irregular high forest suggest it is able to exploit a range of closed canopy environments including all but the densest clutter where it gleans arthropods from foliage (Swift & Racey 2002, Tillon et al. 2016). The negative relationship with mean dbh and positive with deadwood snags suggests avoidance of open habitats with larger trees. *N. nattereri* as a SRE exploits closed-canopy woods using very broadband echolocation to forage in cluttered conditions (Siemers & Schnitzler 2000, Müller et al. 2012, Plank et al. 2012).

Although recorded in our study area we did not identify *Myotis bechsteinii*. This species exploits tree canopies and can go undetected (Plank et al. 2012). *M. bechsteinii* is difficult to distinguish acoustically from other *Myotis* species (Russ 2012), particularly in cluttered woodlands. It is possible that recordings were missed during auditing.

Plecotus auritus/austriacus: was significantly associated with irregular stands compared with limited intervention stands, less so in coppice stands. *Plecotus auritus/austriacus* occupancy was positively associated with mean tree dbh in irregular stands. *P. auritus* is known to avoid wide gaps (Entwistle et al. 1996, Murphy et al. 2012) which may explain the negative association with mean dbh in coppice. We found *Plecotus spp* used coppice more than limited intervention. There have been concerns over the widespread reintroduction of coppice for *P. auritus* which appears to prefer well-developed understorey and more heterogenous canopy structure (Murphy et al. 2012). In the absence of natural disturbances, creating the desired understorey requires silvicultural intervention which we suggest irregular silviculture could satisfy (Mölder et al. 2019, Horak et al. 2014).

Both *Pipistrellus* species tended to avoid the cluttered environment in coppice reflecting their similar morphology as MRE (Nicholls & Racey 2006a, Carr et al. 2019). There was a positive habitat association with canopy openness in coppice and limited intervention stands for *P. pipistrellus* yet a negative association within limited intervention for *P. pygmaeus* which may reflect habitat partitioning (Nicholls & Racey 2006b, Davidson-Watts et al. 2006).

4.2. Conservation and research implications

Although *P. pipistrellus* and *P. pygmaeus* made up 86% of all bat passes, we recorded over 200 passes for nine species, at > 25% of plots. The proportion of ten-minute periods with at least one pass, provided a useful measure of intensity of habitat use through the night (Gorresen et al. 2008).

Most European bats can be recorded beneath tree canopy (Müller et al. 2012) although differences in canopy height and vegetation structure may affect detection probabilities across stand types (Gorresen et al. 2008). Except for *Plecotus* species, the difference in detection distance between extremes of recording in open environments and dense forest understorey is about 5-m or less (Barataud 2015). In practice, the difference in detection distance between stands is less because the influence of understorey heights and densities varies depending upon the growth stage.

We identified important associations between bat species and woodland structures, but these do not fully describe the complex needs of individual species (Langridge et al. 2019). Linking activity patterns of bats to three dimensional models of habitat complexity, (e.g. using LIDAR data), are exciting developments, particularly for the study of volant animals within complex forest habitats (Froidevaux et al. 2016, Russo et al. 2016, Renner et al. 2018). Despite including stand number as a random effect in models, we acknowledge habitat use across stand types will be blurred especially in ancient woodlands with intricate habitat mosaics (Hilmers et al. 2018).

Irregular silviculture in our study appeared to promote structural features which positively influence bat activity (Kusch et al. 2004, Wood et al. 2017, Starik et al. 2018). In managed temperate high-forests habitat complexity increases in stands under irregular silviculture (Jung et al. 2012, Gustafsson et al. 2020). Understorey density, at 0.5 m was similar between irregular and coppice yet considerably less in irregular at 2 m (Supplementary file S 3), and combined with a varied distribution of tree sizes and open canopy suggests irregular maybe more accessible to foraging bats across guilds which our results indicate (Adams et al. 2009, Titchenell et al. 2011, Wood et al. 2017).

Our study area within a complex patchwork reflects historical changes in woodlands over much of lowland Britain (Peterken 2015). Differences between irregular high forest and limited intervention here are less than is often encountered in managed high forest (Peterken & Mountford 2017). Coppice had low tree densities and reduced deadwood, typical of managed coppice (Harmer & Howe 2003, Buckley & Mills 2015, Buckley 2020), limiting roost availability. Irregular silviculture incorporates structural similarities of both young coppice and old growth stands and appears to cater for several species associated with each (Alder et al. 2018). Further research on habitat selection for rare bats like *B. barbastellus* will be beneficial, particularly elucidating knowledge of moth prey between stand management types including irregular high forest.

Transformation to heterogenous irregular high forest appears to enhance habitat quality for woodland bats (Tillon et al. 2018, Ketzler et al. 2018). Large trees provide important foraging resources including saproxylic invertebrates (Siitonen et al. 2015) and roosting features (Dietz et al. 2018). Structural diversity is likely to become an important ambition for forest managers (Forestry Commission 2019), which potentially establishes a range of resources benefitting woodland bats (Langridge et al. 2019, Tillon et al. 2015). The biodiversity value of successional gradients within temperate European forests is clear (Hilmers et al. 2018, Kuuluvainen 2009). Stand manipulation provides an opportunity to create dynamic, mixed structures, enhancing habitat quality for a range of species (Lelli et al. 2019, Dieler et al. 2017) including bats within temperate broadleaf woodland (Carr et al. 2019).

Non-intervention as the appropriate woodland management treatment for bat conservation may not be broadly applicable without an understanding of the structural characteristics required by bats, which is more useful to forest managers (Law et al. 2016, Langridge et al. 2019). Each woodland has its own historical signature reflecting past exploitation; many unmanaged woodlands today lack the mix of characteristics found in both old growth woodlands and in-cycle coppice (Amar et al. 2010, Peterken & Mountford 2017; Buckley, 2020). Interventions are often necessary to transform even-aged or neglected woodland to create such conditions (Ketzler et al. 2018, Law et al. 2016, Jung et al. 2012, Patriquin et al. 2003, Susse et al. 2011). Irregular silviculture in temperate woodlands may offer a sustainable and cost-effective option for the conservation of woodland biodiversity.

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.

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 throughout. Rhiannon Rogers and Jon Corkill of Dorset Environmental Records Centre helped with fieldwork and GIS support respectively. Dr Niamh McHugh made useful suggestions on data analyses. We are especially indebted to our funders, The Golden Bottle Trust and Henry Hoare Charitable Trust, and are grateful to Dr Annabel King for the recommendation. We acknowledge the generous support of Forestry Commission (England). Stuart Newson was supported by the BTO's Young Scientists' Programme. Freddie Poore kindly drew the stand type schematics.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2020.118786.

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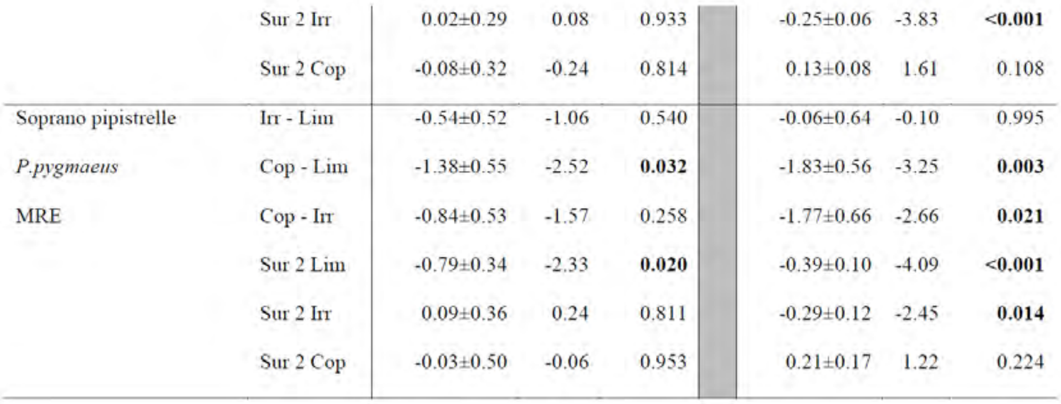
Supplementary Files

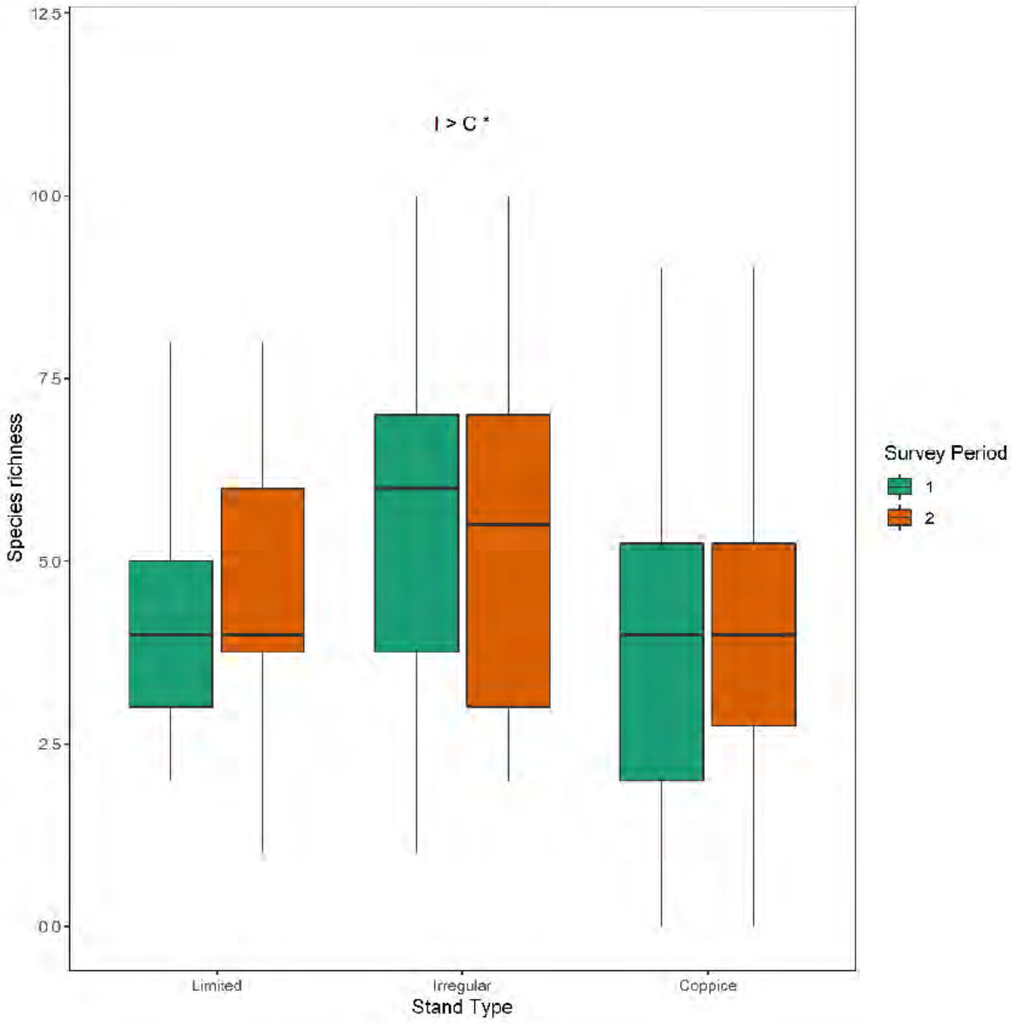
S 1. Pairwise comparisons for overall night encounter rate (mean bats per hour) and occupancy (proportion of 10 min periods in which the species was recorded per night) as a measure of activity across night at each stand types and between survey periods for nine bat species. P values in bold are significant. Zero inflated Generalized Linear Mixed Models with Gamma distribution were run using the package "glmmTMB" on the encounter rate. Activity levels were analysed using a GLMM with a binomial distribution using the package "LME4".

		Encounter Rates			**Activity Levels**		
Species	**Fixed effects**	**Estimate±SE**	**z/t**	**p**	**Estimate±SE**	**z/t**	**p**
Barbastelle	Irr - Lim	0.47±0.61	0.77	0.72	1.48±0.80	1.84	0.155
Barbastella barbastellus	Cop - Lim	0.03±0.67	0.05	1.000	-1.12±0.84	-1.34	0.370
SRE	Cop - Irr	-0.44±0.59	-0.74	0.740	-2.60±0.77	-3.37	**0.002**
	Sur 2 Lim	-0.05±0.52	0.515	0.931	0.05±0.27	0.19	0.851
	Sur 2 Irr	0.26±0.27	0.96	0.340	0.07±0.12	0.54	0.588
	Sur 2 Cop	0.004±0.47	0.01	0.994	0.65±0.25	2.57	**0.008**
Serotine	Irr - Lim	1.16±0.35	3.31	**0.003**	2.15±0.63	3.45	**0.002**
Eptesicus serotinus	Cop - Lim	0.28±0.35	0.82	0.690	1.83±0.67	2.71	**0.018**
LRE	Cop - Irr	-0.87±0.29	-3.05	**0.007**	-0.34±0.49	-0.68	0.773
	Sur 2 Lim	-0.13±0.28	-0.47	0.641	0.47±0.31	1.53	0.125
	Sur 2 Irr	-0.67±0.22	-3.00	**0.003**	-0.06±0.16	-0.38	0.703
	Sur 2 Cop	-0.44±0.24	-1.85	0.064	-0.46±0.24	-1.91	0.057
Daubenton's	Irr - Lim	0.004±0.35	0.01	1.000	0.62±0.59	1.04	0.550
Myotis daubentonii	Cop - Lim	-0.96±0.38	-2.52	**0.031**	-1.33±0.66	-2.00	0.110
MRE	Cop - Irr	-0.97±0.34	-2.85	**0.012**	-1.95±0.65	-3.00	**0.007**
	Sur 2 Lim	-0.82±0.33	-2.50	**0.012**	-0.33±0.21	-1.60	0.109

	Sur 2 Irr	-0.20±0.24	-0.82	0.412	-0.16±0.14	-1.10	0.273
	Sur 2 Cop	0.33±0.36	0.90	0.365	0.03±0.27	0.12	0.905
Whiskered/Brandt's	Irr - Lim	-0.29±0.50	-0.57	0.840	-0.55±0.43	-1.29	0.403
M. mystacinus/brandtii	Cop - Lim	0.97±0.50	-1.92	0.130	-1.63±0.42	-3.90	**<0.001**
MRE	Cop - Irr	-0.68±0.45	-1.52	0.280	-1.08±0.44	-2.47	**0.036**
	Sur 2 Lim	-1.11±0.39	-2.88	**0.004**	-0.64±0.14	-4.55	**<0.001**
	Sur 2 Irr	0.38±0.39	1.04	0.300	0.07±0.12	0.55	0.579
	Sur 2 Cop	0.72±0.42	1.72	0.086	0.40±0.15	2.65	**0.008**
Natterer's	Irr - Lim	-0.14±0.41	-0.340	0.940	-1.68±0.43	-3.90	**<0.001**
M. naterreri	Cop - Lim	-0.48±0.43	-1.13	0.500	-2.54±0.49	-5.22	**<0.001**
SRE	Cop - Irr	-0.34±0.44	-0.77	0.720	-0.86±0.50	-1.73	0.195
	Sur 2 Lim	-0.46±0.30	-1.52	0.127	-0.99±0.18	-5.49	**<0.001**
	Sur 2 Irr	0.30±0.32	0.94	0.350	0.08±0.16	0.51	0.610
	Sur 2 Cop	0.06±0.36	0.15	0.879	0.22±0.22	1.01	0.310
Noctule	Irr - Lim	-0.82±0.45	-1.81	0.170	-0.6±0.71	-0.84	0.670
Nyctalus noctula	Cop - Lim	-0.39±0.40	-0.98	0.590	0.52±0.61	0.85	0.670
LRE	Cop - Irr	0.43±0.39	1.09	0.520	1.12±0.73	1.55	0.270
	Sur 2 Lim	-0.008±0.31	-0.03	0.980	-0.45±0.22	-2.06	**0.039**
	Sur 2 Irr	-0.28±0.45	-0.63	0.527	-0.31±0.34	-0.92	0.356
	Sur 2 Cop	-0.32±0.39	-0.84	0.403	-0.72±0.27	-2.61	**0.009**
Brown long eared	Irr - Lim	0.56±0.54	1.03	0.550	2.58±0.99	2.61	**0.024**
Plecotus auratus/austriacus	Cop - Lim	-0.31±0.54	-0.57	0.830	1.77±1.01	1.75	0.183
SRE	Cop - Irr	-0.87±0.37	-2.33	**0.050**	-0.80±0.75	-1.08	0.523
	Sur 2 Lim	-0.21±0.53	-0.39	0.696	0.62±0.44	1.42	0.157
	Sur 2 Irr	-0.65±0.23	-2.81	**0.005**	-0.31±0.18	-1.67	0.094
	Sur 2 Cop	0.07±0.34	0.20	0.844	-0.41±0.29	-1.39	0.166
Common pipistrelle	Irr - Lim	1.07±0.49	2.20	**0.071**	2.82±0.45	6.31	**<0.001**
Pipistrellus pipistrellus	Cop - Lim	-0.78±0.48	-1.63	0.232	0.96±0.35	2.75	**0.016**
MRE	Cop - Irr	-1.85±0.46	-4.06	**<0.001**	-1.86±0.43	-4.31	**<0.001**
	Sur 2 Lim	0.32±0.33	0.97	0.330	0.60±0.07	8.06	**<0.001**



	Sur 2 Irr	0.02±0.29	0.08	0.933	-0.25±0.06	-3.83	**<0.001**
	Sur 2 Cop	-0.08±0.32	-0.24	0.814	0.13±0.08	1.61	0.108
Soprano pipistrelle	Irr - Lim	-0.54±0.52	-1.06	0.540	-0.06±0.64	-0.10	0.995
P.pygmaeus	Cop - Lim	-1.38±0.55	-2.52	**0.032**	-1.83±0.56	-3.25	**0.003**
MRE	Cop - Irr	-0.84±0.53	-1.57	0.258	-1.77±0.66	-2.66	**0.021**
	Sur 2 Lim	-0.79±0.34	-2.33	**0.020**	-0.39±0.10	-4.09	**<0.001**
	Sur 2 Irr	0.09±0.36	0.24	0.811	-0.29±0.12	-2.45	**0.014**
	Sur 2 Cop	-0.03±0.50	-0.06	0.953	0.21±0.17	1.22	0.224



S 2. Median ± Inter-quartile ranges of bat species richness by stand type and survey period.

S 3. Habitat difference across stand type. Median values and Interquartile range in parenthesis and results for mixed effect model with stand number as random factor for difference across stand type. Measured continuous variables were analysed using Linear mixed model [a] or GLMM with a gamma distribution [b]. Count data was analysed with a GLMM with Poisson distribution [c]. For percentage data an arcsine transformation was applied to the data and analysed using a Linear Mixed effects Model [d]. Significant difference between stands indicated by letter ($p < 0.05$), L – Limited, I – Irregular and C – Coppice

Habitat Variable	**Limited**	**Irregular**	**Coppice**	**P**
Basel Area [b]	**29.0 (9) IC**	**20.0 (7.5) L**	**16.5 (9) L**	**<0.001**
Canopy Openness [d]	**9.2 (5.1) I**	**16.8 (12.0) L**	**9.4 (4.7)**	**0.038**
Mean DBH [b]	**41.6 (18.5)**	**48.8 (17.2)**	**36.5 (32.5)**	**0.029**
Largest DBH [b]	70.0 (29.3)	62.5 (26.6)	56.0 (33.8)	0.553
No. Tree Species [c]	2.0 (1)	2.0 (0.3)	2.0(1)	0.755
No. Oak [c]	**0.0 (0) IC**	**1.0 (2) L**	**0.5 (1) L**	**<0.001**
No. Ash [c]	**2.0 (2)**	**3.0 (2) C**	**1.5 (3) I**	**0.048**
Snag Frequency [c]	**8.0 (5.5)**	**12.0 (9.3) C**	**7.0 (8.3) I**	**0.031**
Fallen Logs [c]	**5.0 (9.3) C**	**1.5 (5)**	**0 (3.3) L**	**<0.001**
Density 0.5m [d]	**7.5 (18.3) IC**	**40 (51.5) L**	**54 (52) L**	**<0.001**
Density 2m [d]	**16.3 (17.5) C**	**21.3 (19.4) C**	**60.6 (48.1) IL**	**<0.001**
Sapling 3cm [a]	**0.6 (1.7) C**	**2.1 (5.5) C**	**15.7 (20) IL**	**<0.001**
Sapling 3 - 7.5cm [a]	**0.8 (1.3) C**	**0.4 (3.1) C**	**4.0 (5.4) IL**	**<0.001**
Tree_50cm [c]	1.5 (1)	2.0 (2)	1.0 (2)	0.253
Tree.17.5_50cm [c]	**11.5 (11.5) IC**	**5 (7) LC**	**2 (3.3) IL**	**<0.001**
Tree.7.5.17.5cm [c]	72.5 (38)	18.0 (22.5)	9.0 (25.8)	0.073
All Stems [b]	**85.8 (40.3) IC**	**31.5 (25.4) L**	**42.0 (30) L**	**<0.001**
Bramble [d]	**0.0 (0) I**	**29.1 (55.7) LC**	**3.6 (20.9) I**	**<0.001**
Bare Ground [d]	**35.7 (51.7) IC**	**0 (15.1) L**	**8.4 (25.7) L**	**0.001**
Understory Age [c]	**50.0 (20) IC**	**9.0 (9.5) L**	**7.0(6.5) L**	**<0.001**

S 4. Spearman's correlation table for testing habitat variables and selection of those to use in bat activity and habitat association model: above probability with significance in bold and below ± correlation coefficient values.

Variables	Basal area	Canopy openness	Mean dbh	Number of Oak	Number of Ash	Snags frequency	Fallen logs	Understorey density 0.5m	Understorey density 2m	Sapling dbh 3cm	Sapling dbh 3-7.5cm	Tree dbh >50cm	Tree dbh 17.5_50cm	Tree dbh 7.5-17.5cm	All stems	Bramble	Bare-ground	Dog's mercury	Moss cover
Basal area	**0**	**0.000**	0.422	**0.011**	0.866	0.801	**< 0.0001**	**< 0.0001**	**< 0.0001**	**< 0.0001**	0.191	0.269	**< 0.0001**	**< 0.0001**	**< 0.0001**	**< 0.0001**	**< 0.0001**	**< 0.0001**	**0.000**
Canopy openness	**0.000**	**0**	0.246	**0.004**	0.706	**0.001**	**0.023**	**< 0.0001**	0.537	0.405	**< 0.0001**	0.598	0.822	**< 0.0001**	**< 0.0001**	**< 0.0001**	**< 0.0001**	**0.012**	**0.003**
Mean dbh	0.422	0.246	**0**	**< 0.0001**	**0.005**	**< 0.0001**	**0.004**	0.294	0.054	**0.002**	**0.023**	**< 0.0001**	0.188	0.098	**0.000**	0.066	0.927	**0.018**	0.148
Number of Oak	**0.011**	**0.004**	**< 0.0001**	**0**	0.062	**< 0.0001**	0.510	**0.004**	0.199	**0.031**	0.559	**< 0.0001**	**0.022**	**< 0.0001**	**< 0.0001**	**0.004**	0.108	**0.040**	0.814
Number of Ash	0.866	0.706	**0.005**	0.062	**0**	0.342	0.506	0.347	**0.022**	**0.007**	**0.047**	0.199	**0.010**	**0.022**	**0.000**	**0.002**	**0.003**	0.761	**0.016**
Snags frequency	0.801	**0.001**	**< 0.0001**	**< 0.0001**	0.342	**0**	0.479	0.897	0.070	0.097	0.071	**< 0.0001**	0.211	**0.040**	**0.000**	**0.003**	0.121	0.364	**0.044**
Fallen logs	**< 0.0001**	**0.023**	**0.004**	0.510	0.506	0.479	**0**	**0.000**	**0.050**	**0.002**	0.492	0.172	**0.000**	**0.001**	**0.010**	**< 0.0001**	**0.000**	**< 0.0001**	0.114
Understorey density 0.5m	**< 0.0001**	**< 0.0001**	0.294	**0.004**	0.347	0.897	**0.000**	**0**	**< 0.0001**	**< 0.0001**	0.566	0.838	**0.005**	**< 0.0001**	**< 0.0001**	**< 0.0001**	**< 0.0001**	**< 0.0001**	0.545
Understorey density 2m	**< 0.0001**	0.537	0.054	0.199	**0.022**	0.070	**0.050**	**< 0.0001**	**0**	**< 0.0001**	**< 0.0001**	0.633	**< 0.0001**	**< 0.0001**	0.113	**0.043**	0.735	**0.000**	**0.005**
Sapling dbh 3cm	**< 0.0001**	0.405	**0.002**	**0.031**	**0.007**	0.097	**0.002**	**< 0.0001**	**< 0.0001**	**0**	**< 0.0001**	0.099	**< 0.0001**	**< 0.0001**	0.100	0.230	0.225	**< 0.0001**	**0.000**
Sapling dbh 3-7.5cm	0.191	**< 0.0001**	**0.023**	0.559	**0.047**	0.071	0.492	0.566	**< 0.0001**	**< 0.0001**	**0**	0.459	**0.001**	0.507	0.054	**0.002**	0.062	0.548	**< 0.0001**
Tree dbh >50cm	0.269	0.598	**< 0.0001**	**< 0.0001**	0.199	**< 0.0001**	0.172	0.838	0.633	0.099	0.459	**0**	0.113	0.139	**0.003**	0.072	0.746	0.155	0.832
Tree dbh17.5_50cm	**< 0.0001**	0.822	0.188	**0.022**	**0.010**	0.211	**0.000**	**0.005**	**< 0.0001**	**< 0.0001**	**0.001**	0.113	**0**	**0.003**	**0.014**	0.621	**0.045**	**0.000**	**< 0.0001**
Tree dbh 7.5-17.5cm	**< 0.0001**	**< 0.0001**	0.098	**< 0.0001**	**0.022**	**0.040**	**0.001**	**< 0.0001**	**< 0.0001**	**< 0.0001**	0.507	0.139	**0.003**	**0**	**< 0.0001**	**< 0.0001**	**< 0.0001**	**< 0.0001**	0.298
All stems	**< 0.0001**	**< 0.0001**	**0.000**	**< 0.0001**	**0.000**	**0.000**	**0.010**	**< 0.0001**	0.113	0.100	0.054	**0.003**	**0.014**	**< 0.0001**	**0**	**< 0.0001**	**< 0.0001**	**0.001**	0.584
Bramble	**< 0.0001**	**< 0.0001**	0.066	**0.004**	**0.002**	**0.003**	**< 0.0001**	**< 0.0001**	**0.043**	0.230	**0.002**	0.072	0.621	**< 0.0001**	**< 0.0001**	**0**	**< 0.0001**	**< 0.0001**	0.891
Bareground	**< 0.0001**	**< 0.0001**	0.927	0.108	**0.003**	0.121	**0.000**	**< 0.0001**	0.735	0.225	0.062	0.746	**0.045**	**< 0.0001**	**< 0.0001**	**< 0.0001**	**0**	**0.002**	**< 0.0001**
Dog's mercury	**< 0.0001**	**0.012**	**0.018**	**0.040**	0.761	0.364	**< 0.0001**	**< 0.0001**	**0.000**	**< 0.0001**	0.548	0.155	**0.000**	**< 0.0001**	**0.001**	**< 0.0001**	**0.002**	**0**	0.542
Moss cover	**0.000**	**0.003**	0.148	0.814	**0.016**	**0.044**	0.114	0.545	**0.005**	**0.000**	**< 0.0001**	0.832	**< 0.0001**	0.298	0.584	0.891	**< 0.0001**	0.542	**0**

Variables	Basal area	Canopy openness	Mean dbh	Number of Oak	Number of Ash	Snags frequency	Fallen logs	Understorey density 0.5m	Understorey density 2m	Sapling dbh 3cm	Sapling dbh 3-7.5cm	Tree dbh >50cm	Tree dbh 17.5_50cm	Tree dbh 7.5-17.5cm	All stems	Bramble	Bare-ground	Dog's mercury	Moss cover
Basal area	**1.00**	**-0.33**	0.07	**-0.23**	0.02	0.02	**0.37**	**-0.65**	**-0.44**	**-0.57**	-0.12	-0.10	**0.62**	**0.65**	**0.55**	**-0.41**	**0.45**	**0.42**	**-0.32**
Canopy openness	**-0.33**	**1.00**	0.11	**0.26**	0.03	**0.30**	**-0.21**	**0.46**	-0.06	-0.08	**-0.52**	0.05	0.02	**-0.39**	**-0.48**	**0.59**	**-0.44**	**-0.23**	**-0.27**
Mean dbh	0.07	0.11	**1.00**	**0.44**	**0.26**	**0.61**	**0.26**	-0.10	-0.18	**-0.29**	**-0.21**	**0.83**	0.12	-0.15	**-0.33**	0.17	0.01	**0.22**	-0.13
Number of Oak	**-0.23**	**0.26**	**0.44**	**1.00**	-0.17	**0.46**	-0.06	**0.26**	0.12	**0.20**	0.05	**0.47**	**-0.21**	**-0.35**	**-0.39**	**0.26**	-0.15	**-0.19**	0.02
Number of Ash	0.02	0.03	**0.26**	-0.17	**1.00**	0.09	0.06	-0.09	**-0.21**	**-0.25**	**-0.18**	0.12	**0.23**	**-0.21**	**-0.34**	**0.28**	**-0.27**	-0.03	**0.22**
Snags frequency	0.02	**0.30**	**0.61**	**0.46**	0.09	**1.00**	0.07	-0.01	-0.17	-0.15	-0.17	**0.49**	0.11	**-0.19**	**-0.34**	**0.27**	-0.14	0.08	**-0.18**
Fallen logs	**0.37**	**-0.21**	**0.26**	-0.06	0.06	0.07	**1.00**	**-0.33**	**-0.18**	**-0.29**	0.06	0.13	**0.33**	**0.31**	**0.24**	**-0.38**	**0.32**	**0.47**	-0.14
Understorey density 0.5m	**-0.65**	**0.46**	-0.10	**0.26**	-0.09	-0.01	**-0.33**	**1.00**	**0.57**	**0.53**	-0.05	-0.02	**-0.25**	**-0.62**	**-0.49**	**0.60**	**-0.40**	**-0.54**	0.06
Understorey density 2m	**-0.44**	-0.06	-0.18	0.12	**-0.21**	-0.17	**-0.18**	**0.57**	**1.00**	**0.69**	**0.45**	-0.04	**-0.38**	**-0.37**	-0.15	**0.19**	-0.03	**-0.35**	**0.26**
Sapling dbh 3cm	**-0.57**	-0.08	**-0.29**	**0.20**	**-0.25**	-0.15	**-0.29**	**0.53**	**0.69**	**1.00**	**0.49**	-0.15	**-0.53**	**-0.47**	-0.15	0.11	-0.11	**-0.41**	**0.34**
Sapling dbh 3-7.5cm	-0.12	**-0.52**	**-0.21**	0.05	**-0.18**	-0.17	0.06	-0.05	**0.45**	**0.49**	**1.00**	-0.07	**-0.31**	0.06	0.18	**-0.28**	0.17	-0.06	**0.49**
Tree dbh >50cm	-0.10	0.05	**0.83**	**0.47**	0.12	**0.49**	0.13	-0.02	-0.04	-0.15	-0.07	**1.00**	-0.15	-0.14	**-0.27**	0.16	-0.03	0.13	-0.02
Tree dbh17.5_50cm	**0.62**	0.02	0.12	**-0.21**	**0.23**	0.11	**0.33**	**-0.25**	**-0.38**	**-0.53**	**-0.31**	-0.15	**1.00**	**0.27**	**0.22**	-0.05	**0.18**	**0.34**	**-0.37**
Tree dbh 7.5-17.5cm	**0.65**	**-0.39**	-0.15	**-0.35**	**-0.21**	**-0.19**	**0.31**	**-0.62**	**-0.37**	**-0.47**	0.06	-0.14	**0.27**	**1.00**	**0.88**	**-0.52**	**0.35**	**0.42**	-0.10
All stems	**0.55**	**-0.48**	**-0.33**	**-0.39**	**-0.34**	**-0.34**	**0.24**	**-0.49**	-0.15	-0.15	0.18	**-0.27**	**0.22**	**0.88**	**1.00**	**-0.59**	**0.42**	**0.31**	-0.05
Bramble	**-0.41**	**0.59**	0.17	**0.26**	**0.28**	**0.27**	**-0.38**	**0.60**	**0.19**	0.11	**-0.28**	0.16	-0.05	**-0.52**	**-0.59**	**1.00**	**-0.62**	**-0.46**	-0.01
Bareground	**0.45**	**-0.44**	0.01	-0.15	**-0.27**	-0.14	**0.32**	**-0.40**	-0.03	-0.11	0.17	-0.03	**0.18**	**0.35**	**0.42**	**-0.62**	**1.00**	**0.27**	**-0.42**
Dog's mercury	**0.42**	**-0.23**	**0.22**	**-0.19**	-0.03	0.08	**0.47**	**-0.54**	**-0.35**	**-0.41**	-0.06	0.13	**0.34**	**0.42**	**0.31**	**-0.46**	**0.27**	**1.00**	-0.06
Moss cover	**-0.32**	**-0.27**	-0.13	0.02	**0.22**	**-0.18**	-0.14	0.06	**0.26**	**0.34**	**0.49**	-0.02	**-0.37**	-0.10	-0.05	-0.01	**-0.42**	-0.06	**1.00**

Values in bold are different from 0 with a significance level alpha=0.05

Chapter 6 Discussion

6.1 Context of the research

The introduction of a novel continuous cover forestry using Irregular high forest management, into an ancient semi-natural woodland, presented a unique opportunity to understand the influence of structural changes across a range of taxonomic groups. It is timely given the increasing urgency for both foresters and nature conservationists to consider different options of forest and woodland management against a backdrop of climate change (Larsen *et al*. 2022). The demise of traditional coppice management across Europe raises concerns for the conservation of ancient woodlands and their inherent biocultural interests (Müllerová *et al.* 2015). A key question asks if there are alternative forms of silvicultural management which maintain coppice-associated species (Kirby *et al.* 2017). As demonstrated in this thesis, a lack of management has been linked with reduced structural heterogeneity and lower species richness and abundances in key woodland groups. Woodland resilience in response to climate change and new pest and disease outbreaks has been highlighted as a key challenge to forest management given the increasing and multiple demands being placed upon woodlands and their ability to sustain natural capital for the benefit of society (Stafford *et al.* 2021, Spencer and Field 2019). Importantly, woodland species which depend upon woodland functional resources, are vital to ecosystem functioning and woodland resilience (Spencer 2018). Continuous cover forestry, of which Irregular high forest is one silvicultural system, is being encouraged in Europe as it may mitigate risks from extremes in temperature and weather events, through diversification of stand structure and tree species composition (Vitkova and Dhubháin 2013, Tew *et al.* 2021). However, demonstrating the effects on biodiversity following transformation towards irregular structures in temperate forests remains a priority to inform ecologists and foresters alike (Kjučukov *et al*. 2022). This thesis has brought together forestry and ecology expertise and highlights some important findings from research undertaken in southern Britain. A primary aim for the study has been to address the paucity of information around the introduction of Irregular high forest in Britain (Mason *et al.* 2022). Moreover, understanding how structure varies between and within silvicultural management types; traditional coppiced woodlands,

recently established Irregular high forest stands, transitional high forest stands that are undergoing the initial stages of transformation towards Irregular structure, and limited intervention stands, those that had been unmanaged for at least 30 years, was fundamental to this research as much as how species responded to it.
The research objectives addressed were:

1) To examine the structural habitat characteristics of vegetation within the study woodlands and identify how any variations relate to stand management.

2) To examine the composition and richness of woodland flora community using phytosociological groups and relate these to the structural habitat characteristics across the following stand management types; coppice, Irregular and limited intervention.

3) To identify patterns of bird community composition and abundance in Spring and Winter across different woodland management regimes of the broadleaf woodland mosaic (i.e., between areas of coppiced woodlands, irregular high forest stands, transitional stands and limited intervention stands).

4) To identify the bat community composition, present within each stand type and identify the relative patterns of activity for each species. Activity was defined by analysis using acoustic recognition, and to examine the habitat structural characteristics of those locations used by bats across the stands.

5) To use the results of 1-4 to produce recommendations and guidance to the forestry and statutory nature conservation bodies.

Ancient semi-natural woodlands in Britain are valuable repositories of biological and cultural legacies in the landscape (Rackham 2003). They have an ‘ecological memory’ that retains evidence of past events including intensive human exploitation (Vellend *et al.* 2007, Kirby *et al.* 2022, Ogle *et al.* 2015). Yet, ancient woodlands are facing uncertainties as the climate changes and withdrawal of management alters the composition of their inherent species (Rackham 2008). Continuity of management is recognised as important when considering the nature conservation value of ancient woodland as much because of the cultural associations alongside the biological interests that arose (Dolman *et al.* 2017, Bergès and Dupouey 2021). Demands for sustainable timber resources are likely to increase and expectations for woodlands to provide multiple ecosystem services are accelerated as society looks to the natural world to adapt and mitigate the predicted worse-case scenarios of the human-induced ecological crisis (Hahn *et al*. 2021). While continuity of management is deemed important it remains unclear how ancient woodlands will respond to changes in silviculture practice (Fichtner and Härdtle 2021). Furthermore, uncertainties exist over climate effects on woodland vegetation from raised temperatures (thermophilisation) with some evidence of thermal buffering provided by tree canopy retention (Zellweger *et al.* 2020). The extent of woods and forests has been altered considerably since the last ice-age c.10,000 years BCE, much of which as a result of human activity and exploitation (Rackham 2003). Tree composition has changed and with a comparatively low number of tree species present in ancient seminatural woodlands in the UK, options available for their sustainable management in a rapidly changing climate requires careful consideration (Spencer and Field 2019). Moreover, throughout their history, the extent of ancient and semi-natural woodlands has varied according to changes in exploitation by people and livestock or abandonment; woodlands in many places have been temporally dynamic in how open or closed canopy they were (Barnes and Williamson 2015).

Many ancient broadleaf woodlands in lowland Britain and central and southern Europe have a long tradition of coppice management over many centuries (Buckley 2020). This created significant areas of young woody growth, cyclically felled on short rotations of between 7 and 25 years (Harmer and Howe 2003). Despite intensive management specialist woodland plant species associated with the periodic opening followed by rapid canopy closure thrived and distinct flora developed as a result (Decocq *et al*. 2005). Abandonment of coppice management has led to a reduction and loss of this community as a result of structural homogenisation through canopy closure and shading with only plants tolerant of such conditions, remaining (Kopecký *et al*. 2013). These structural changes are known to negatively affect several woodland birds, with species associated with the early to mid-successional stages of woody growth found in coppice cycle, declining as important nesting and foraging resources disappear (Fuller 1992). Ancient semi-natural broadleaf woodland is also important for all species of UK bats *Chiroptera* where foraging and roosting sites include a range of structural attributes including cavities, splits and woodpecker holes associated with old growth and deadwood and open canopy areas with woodland edge ecotones (Erasmy *et al.* 2021, Dietz *et al.* 2009). Further, Barbastelle bat *Barbastella barbastellus* a rare woodland specialist requires a combination of the above resources when selecting maternity roosts (Kortmann *et al*. 2018).

6.2 Synopsis of results

There were many striking variations identified between the stand management types with most habitat structural measures showing significant differences. Higher basal area and higher total stem counts were found in limited intervention stands, which lacked any understorey. These stands represent a time since last management of at least 30 years and some up to 50 years, which has led to a simplified structure and a closed canopy. The larger trees in this study were associated with Irregular stands where mean diameter at breast height (dBH) was most positively related. Large trees provide critical resources for woodland biodiversity (Lindenmayer *et al.* 2014). Both coppice and Irregular high forest being open canopy, exhibited different understorey characteristics compared with limited intervention stands and transitional stand management. The latter representing an intermediate stage following an initial silvicultural intervention after a long period, c.30 years, of neglect. While coppice and Irregular stands shared similar understorey characteristics at the lower 0.5 m level height, coppice was significantly positively associated with the 2 m height band compared with Irregular. This reflects the stages at which the coppice growth had reached when measured with only 10% at less than three years since cutting. Coppice management also requires a high stool density to be viable, with 1,200-2,000 stools ha^{-1} for hazel and produces a high number of growing shoots per stool when cut on a 7–10-year cycle compared to older stools, and those cut on longer rotations associated with high forest and under-managed stands (Harmer and Howe 2003). Conversion to high forest leads to a decrease in understorey regrowth, particularly for hazel, because of the relationship between the increasing number of canopy trees and the availability of light reaching the understorey (Howe 1995). However, Irregular high forest had a more open overstorey and was characterised by a lower basal area, which was comparable with that of coppice over the wider woodland area in this study. Bramble contributed to the higher values associated with understorey density at 0.5 m height band being most positively correlated with Irregular. Bramble is associated with canopy opening and can lead to a reduction of ground flora unless canopy closure occurs rapidly as in the case of coppice (Harmer *et al*. 2017). However, bramble was not negatively associated with the ground flora in this study although its presence is carefully monitored by the estate foresters, and interventions through cutting undertaken where it has suppressed tree regeneration (Poore 2016). Bramble is an important species providing cover for nesting birds and nectar sources for invertebrates (Fuller and Warren 1993).

For all groups studied, woodland birds, bats and vascular plants, species richness and abundance were associated with a more open canopy and developed understorey. These findings concur with those of Sebek *et al.* (2015) who identified similar patterns in bird and plant species responses following canopy opening in otherwise closed canopy woods. However, species richness *per se* may not reflect the conservation value of ancient woodlands as it includes species with a ubiquitous distribution that are often generalists (Hopkins and Kirby 2007, Fuller *et al.* 2007). All the species of conservation interest were positively associated towards increasingly open woodland and understorey, although some, including Barbastelle bat *Barbastella barbastellus*, with a Vulnerable conservation status in the United Kingdom and globally near-threatened (Mathews and Harrower 2020, Piraccini 2016), avoided the densest understorey (Alder *et al.* 2021). Marsh Tit *Poecile palustris*, a red listed bird of conservation concern (Stanbury *et al.* 2021), also positively responded in this way with exceptionally high densities in Irregular high forest (Alder *et al.* 2018). Marsh Tit requires cavities in trees in which to nest and suitable foraging resources within the canopy and understorey (Broughton *et al.* 2012). In this study both Marsh Tit and Barbastelle bat were most strongly associated with Irregular high forest stands with fewer but larger canopy trees and a higher proportion of standing deadwood than the other stand types (Alder *et al.* 2018, Alder *et al.* 2021). Woodland bat species richness was highest in Irregular high forest stands, where activity levels for six of nine bat species reached a maximum. Notably, this included the rarest species encountered, Barbastelle.

Stands with larger trees and their associated microhabitat features, deadwood snags and cavities are generally valuable to forest biodiversity especially those associated with old growth such as saproxylic invertebrates, lichens and fungi (Dieler *et al.* 2017). However, in lowland British woodlands early successional habitats typically associated with the coppice cycle are important for several taxa; birds, vascular plants and thermophilic invertebrates because of the varied and dynamic changes that rapidly occur over 7-10 years of a typical rotation (Fuller and Warren 1991). Several woodland bird species in our study were mainly associated with coppice e.g., Garden warbler *Sylvia borin* and Willow warbler *Phylloscopus trochilus* while avoiding open areas without dense understorey regardless of canopy cover. Irregular high forest provided some of their habitat requirements with second highest densities, being notably absent in the limited intervention stands where the structural resources which they rely on were absent (Alder *et al.* 2018). While those species associated with old growth features in mature trees e.g., Great spotted woodpecker *Dendrocopus major*, and Eurasian Treecreeper C*erthia familiaris*, were most abundant in Irregular high forest.

In some cases, species responded to a given habitat structural variable similarly across the three stand management types, whereas in others, the response differed among stand management types. For example, several bat species were significantly associated with larger diameter trees in coppice stands but not Irregular. This may be because in coppice, larger trees are at the lowest density and provide an increasingly important foraging and navigating resource for bats in this stand type (Langridge *et al.* 2019), or it may be that a particular species exhibited differential habitat segregation (Davidson-Watts *et al.* 2006). For bats, and quite likely other mobile vertebrates, changes in habitat use can vary according to location within a landscape matrix (Lintott *et al.* 2015). Habitat selection is scale dependent and detection of resource-use versus its availability can be localised when these resources e.g., foraging sites, are geographically restricted (Alder and Marsden 2010, Johnson 1980).

There were no significant differences detected in ancient woodland vascular plant abundances between coppice or Irregular stands (Alder *et al.* 2023). All are coppice-associated species with a long history of alignment with traditional coppice management (Rackham 2003). Ancient woodland vascular plants are indicators of woodland continuity yet exhibit varied phytosociological responses according to individual species adaptation to the amount of light they receive; different species responding according to their tolerance or avoidance of shade (Kirby 2021). Some, like Dog's Mercury *Mercurialis perennis,* are shade tolerators, identified as significantly so in this study while others such as Woodruff *Galium odoratum* are vernal species which emerge and flower during early spring before leaf-emergence on trees and shrubs (Decocq *et al.* 2005). Ancient Woodland Vascular Plant richness characterised the dependence of the light and dark phases being positive with an opening canopy and understorey, while negative in stands which are closed yet lack understorey (Alder *et al.* 2023). Coppice-associated plant communities are linked to a rapid and dynamic change following the rotational cutting of woody stems which is typically very 7-15 years, sometimes longer, although extending cutting cycles does alter plant communities towards increasing shade tolerance (Buckley 2020). Conversely, areas of woodland that become permanently open in which woody vegetation is constantly being removed e.g., by heavy browsing by deer *Cervidae* may lose the woodland plant community which is replaced by a grasses *Poacaea* and sedges *Cyperaceae* (Cooke and Farrell 2001). While there was no evidence in the study at Rushmore of significant deer impacts there were higher cover values detected for grasses in the Irregular stands.

6.3 Woodland Management Implications

Continuous cover forestry, of which Irregular high forest is one management system, promotes diverse stand structures which can help mitigate uncertain risks resulting from a less stable climate while promoting biodiversity (Tew *et al.* 2021, Pommerening and Murphy 2004, Kerr 1999). Most woodlands in Europe have been affected by human intervention with few uniquely natural stands, such as those of Białowieża, Poland, to act as a guide to natural stand dynamics and how these interact with woodland species

(Jaroszewicz *et al.* 2019). Moreover, there will be geographically distinctive woodlands throughout Europe which reflect a blend of historical use, soils, and climate (Krumm *et al.* 2020, Larsen *et al.* 2022). However, forest management when carefully considered at multiple scales has the potential for positive outcomes for biodiversity (Schulze *et al.* 2019). In this research at Rushmore, species-specific responses to woodland gradients varied considerably and although the results are likely to be similar to those found on a natural disturbance gradient within temperate woodlands, the difficulties in making assumptions of overall habitat conditions in dynamic structures are recognised. However, this research has shown how Irregular silviculture accommodated bats, birds and ancient woodland plants, and was significantly correlated with each of two gradients, (those which accounted for the most structural variation), in the multivariate analysis. These included a more open canopy with a mix of understorey densities and lower basal area. Compared with coppice and limited intervention stands, Irregular silviculture provided the broadest range of conditions along a wide ‘structural bandwidth’ that included both old growth and early successional habitat structures; important functional resources for woodland biodiversity (Hilmers *et al.* 2015). A knowledge of structural gradients and microhabitat features can be especially useful to guide woodland management alongside *a priori* evidence of the responses of different taxa to various environmental conditions (Paillet *et al.* 2018, Evans *et al.* 2019).

The dynamics of woodland vegetation are not immutable although the development of a more uneven-aged and vertically mixed structure can be very gradual, often taking hundreds of years in even-aged high forest in the absence of significant natural disturbances (Peterken and Mountford 2017). Stand management using Irregular high forest therefore presents an opportunity to rapidly create structural complexity and heterogeneity at varying spatial scales providing conditions for a range of woodland species in addition to sustainable exploitation of the timber resource (Quine et al. 2007, Kerr 1999). Woodland heterogeneity will become increasingly important as part of an adaptive response towards developing resilient woodlands (Muys *et al.* 2022). Targeted woodland management measures which lead to woodland structures like those identified in Irregular high forest in this study i.e., lower basal area, heterogeneous canopy cover and dynamic understorey regeneration have been shown to benefit specialist and threatened woodland birds, and highlights the value of structural complexity in woodland (Bellamy *et al.* 2022).

The European Forestry Institute (EFI) the representative Forestry organisation of thirty European member states, including the United Kingdom, has established the newer concept of 'Closer to Nature Forest Management' (Larsen *et al*. 2022) Using the most recent scientific research, (including work on woodland birds from this study (Alder *et al.* 2018)), the EFI defines the concept along the recommendation of seven principles for forest and woodland management (Larsen *et al*. 2022). All of which can be delivered through the adoption of Irregular high forest management.

The seven principles of Closer-to-Nature Forest Management are:

1. Retention of habitat trees, special habitats, and dead wood
2. Promoting native tree species as well as site adapted non-native species
3. Promoting natural tree regeneration
4. Partial harvests and promotion of stand structural heterogeneity
5. Promoting tree species mixtures and genetic diversity
6. Avoidance of intensive management operations
7. Supporting landscape heterogeneity and functioning

Irregular silviculture appears to provide a range of resources for different taxonomic groups reflecting the stand successional gradient with a comparatively broad 'structural bandwidth.' Integrating silvicultural interventions which represent a more heterogenous stand structure and tree species composition associated with continuous cover forestry are known to be important to a broad range of communities in temperate forests (Tinya *et al.* 2021). For those ancient woodland species associated with early successional and more open woodland, Irregular silviculture in this study retained suitable conditions, while also exhibiting old growth features notably larger trees and standing deadwood. Irregular silviculture, as has been demonstrated in this study, offers reasons for optimism.

6.4 Future research

Where a primary aim is to conserve a range of woodland species through retaining both early successional and old growth characteristics which are known to be lacking in many European ancient woodlands, care is required in selecting indicator species which are truly representative of a wider cohort (Oettel and Lapin 2021). Advancing knowledge of woodland structures and the way they correlate with a selection of relevant indicator species will be useful to inform forest managers (Lõhmus *et al*. 2015). Further research is suggested within Irregular high forest to include invertebrate groups e.g., Moths, and also Fungi, Bryophytes and Lichens as these are likely to exhibit contrasting responses to woodland management (Gerlach *et al.* 2013, Jokela *et al.* 2018). Ancient woodlands, however, vary considerably in Britain (Rodwell 1998) and environmental conditions correspondingly will be different and therefore selection of indicator species should reflect this (Goldberg *et al.* 2007). It is important to recognise that no single type of silviculture can cater for all species and wider landscape scale factors affect populations (Nilsson 2009).

Responses of different species to varying conditions along gradients requires further research from a range of sites before they can be more widely applicable as indicators; this should include looking at other metrics e.g., traits and phylogenetic diversity, which may further explain the relationships between an organism and habitat (Evans *et al.* 2019, Bełcik *et al.* 2020). A recommendation pertinent to this study is to undertake a traits-based analysis of the moth data from Rushmore to better interpret the associations with the structural gradients and to explore congruence with the different plant guilds that were identified (Alder *et al.* 2023). This should include an assessment of species similarity to check for patterns of community congruence in the way moth and plant communities (and the other vertebrate species) relate to each other within and between sites representing different habitat structures and silvicultural management types (Larrieu *et al.* 2019). An understanding of these trophic interactions can provide valuable insights into how species of conservation concern e.g., Barbastelle bat, is influenced by woodland management (Carr *et al.* 2020). Linking species diversity and key woodland indicator species with economic measures such as timber yield and incremental growth of timber trees will likely be necessary when accounting for the wider benefits of forestry management (see Susse *et al.* 2011). Moreover, identifying indicator species and associated biological communities will be important when considering the ecological functioning of woodlands and their resilience to meet with the various demands being placed upon them towards climate adaptation (Crane 2022). Natural capital value, carbon stocks, carbon sequestration, flood management, rewilding and human wellbeing are increasingly being recognised in environmental and forestry policy mechanisms (Dandy 2023). The asset value of UK woodlands was estimated to be £351.4 billion in 2020; while timber and wood fuel accounted for 3.6% of this figure or £12.6 billion (ONS 2022). In order to meet the broad range of objectives, the outcomes for biodiversity should be better understood alongside the silvicultural management types used (Asbeck *et al.* 2021).

Promoting stand structural characteristics with known associations for woodland species diversity across a forest successional gradient (Hilmers *et al*. 2018), is likely to meet the habitat requirements of a range of woodland species and taxonomic groups (Leidinger *et al.* 2020). Selecting a combination of habitat structural measures may be especially helpful to develop species diversity models as has been shown for forest plant communities (Gao *et al.* 2014). Further studies looking at the interaction with tree canopy and understorey structures and the way it modulates woodland plant communities are recommended in Irregular stands. Moreover, developing stand-level structural indicators of biodiversity may be more readily interpretable for foresters, rather than using indicator species, to guide forest management (Ćosović *et al*. 2020). The value of structural indicators of biodiversity requires further testing with a wider cohort of taxonomic groups, including the examples mentioned above, in different stand management types to assess their potential congruence and surrogacy. As found in this research species of conservation concern i.e., Marsh Tit, Barbastelle bat and ancient woodland plants appear to flourish in Irregular silviculture, although these do not fully account for the beta diversity found in ancient woodlands. Nevertheless, a blend of stand structural measurements and targeted monitoring of different taxon with known habitat associations e.g., ancient woodland specialists, may offer a pragmatic solution to foresters to help towards enhancing overall woodland biodiversity (Tinya *et al*. 2021).

Importantly, such measures must be readily interpretable on the ground, simple to integrate into forest management plans and contribute to conservation condition assessments for ancient woodlands (Lelli *et al.* 2019, Goldberg *et al.* 2015, Kraus and Krumm 2013, Ferris and Humphrey 1999).

6.6 References

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Appendices

Appendix 1 Glossary of terminology and abbreviations used

Ancient woods (or ancient forests) are those where there has been continuous woodland cover since a set threshold date, often around 1600 CE in Britain. These might, however, be on land that was open at some time before this date, so they are not necessarily primary. They have also usually been felled or manged at some time.

ASNW – ancient semi-natural woodland, British context to describe woodland present since 1600 CE. Used interchangeably with ancient woodland and ancient forest.

AWI – ancient woodland indicator species; pertinent to vascular plants in ancient semi-natural woodland used to assist with the classification of ancient woodland.

AWVP – ancient woodland vascular plant mostly synonymous with AWI but can include associated plants that form part of Rackham's coppice-guild

Block – woodland management unit area which may be comprised of several stands of different silvicultural type.

CCF – continuous cover forestry; a type of high forest silviculture based on retention of tree cover within a woodland. Continuous cover is an approach to forest management that is guided by four main principles:

1. managing the forest ecosystem rather than just the trees;
2. using natural processes as the basis for stand management;
3. working with site limitations;
4. creation of a diverse stand structure with a range of species.

As defined in Mason, B., Kerr, G. and Simpson, J. 1999) What is continuous cover forestry? Forestry Commission Information Note 29. Forestry Commission, Edinburgh.

Close to nature forestry – another term which is often used synonymously with CCF and avoids clear-cutting, uses natural forest processes, natural regeneration and harvesting selectively, while allowing non-native species planting for economic necessity, adding structural diversity and minimising use of artificial pesticides and fertilizers. As defined in Bürgi, M. 2015: "Close-to-nature forestry." In, Kirby K, Watkins C (eds) Europe's changing woods and forests: from wildwood to managed landscapes; Cabi Int, Oxfordshire, UK, CABI, Wallingford 107-115.

Closer to nature forest management – a framework and guiding principles of the management of forests and woods coined by the European Forestry Institute which aims to improve the conservation values and climate resilience of multifunctional, managed forests throughout Europe. As defined in Larsen, J.B., Angelstam, P., Bauhus, J., Carvalho, J.F., Diaci, J., Dobrowolska, D., Gazda, A., Gustafsson, L., Krumm, F., Knoke, T., Konczal, A., Kuuluvainen, T., Mason, B., Motta, R., Pötzelsberger, E., Rigling, A., Schuck, A., 2022. Closer-to-Nature Forest Management. From Science to Policy 12. European Forest Institute.

Coppice – the underwood silvicultural system of cyclical cutting of trees which regrow and are harvested on short rotations between 4 and 30 years across a compartment or coup. The resultant growth is therefore even-aged. Typically, single species but can be two or three species. See Harmer and Howe (2003).

Coup – a term describing the compartment or area of underwood which is under a coppice management system.

Forest – an area of trees and a term which in this thesis is interchangeable with woodland. It also refers to the medieval description of land which was subject to forest law related to hunting and had varying degrees of tree cover not always entirely wooded, e.g., The New Forest in Hampshire.

High forest – refers to canopy cover and relates to the system of silviculture which harvests canopy trees or overstorey but also refers to unmanaged woodland cover with a high forest canopy cover that has developed since last management often many decades earlier.

Intervention – a term used to describe a forestry action undertaken within a stand or entire woodland block.

Irregular or Irregular high forest - Irregular stands are those where felling and regeneration are continuous over the whole area of a stand and in general where single tree or group selection systems are being used.

Overstorey – another name for canopy relating to the timber tree cover or coppice which has become overstood from neglect and now forms the main canopy overhead.

Plantation - are areas where the majority of trees have been planted. The stands may be created within existing woodland or on previously open ground, and are often referred to as planted forests. The trees may be native to the area or introductions; they may be planted in large even-aged blocks or as wide-spaced individual stems Evans 2009). Evans, J. 2009). Sustainable silviculture and management. Planted forests: Uses, impacts and sustainability, 113-140.

Self-thinning – woody stems which are shaded and weakened that die off as part of the process of natural stand dynamics.

Silvicultural system - Defined by Matthews 1991) as:
‘the process by which crops constituting a forest are tended, removed, and replaced by new crops, resulting in the production of stands of distinctive form.’ Matthews, J. D. 1991. Silvicultural systems. Oxford University Press. 284pp.

Stand – a distinct silvicultural unit area of woodland within a block which may itself be sub-divided into compartments for management.

Stool – a living coppice stump from which successive growing shoots emerge following each cutting intervention which for hazel is on a 7-to-10-year rotation, and for birch on a 3 to 4 year rotation in the study.

SFM – sustainable forest management, which aims to maintain and enhance the economic, social and environmental values of all types of forests, for the benefit of future generations, adopted at the Earth Summit United Nations Conference on Environment and Development) in Rio de Janeiro in 1992.

UKFS – United Kingdom Forestry Standard sets out the guidelines to sustainable forestry management and is the governance towards certification in accordance with national and international obligations.

UKWAS – United Kingdom Woodland Assurance Scheme, a certification scheme to meet with the requirements of the UKFS.

Underwood – refers to the woodland produce derived from coppicing trees.

Wood - woodland and Forest are all used generally to describe tree-covered lands. Wood tends to be used where relatively small discrete areas of land are involved: woodland and forest are used for more extensive tracts.

Wood Pasture - refers to landscapes where grazing by domestic stock or deer has created or maintained a relatively open tree cover. This includes parks whose boundaries are often marked by walls or fences as well as less well-defined areas with scattered trees.