The biodiversity of conifer dominated forest at different stages of transformation towards irregular high forest

Butterfly Conservation Report Number S22-03

Patrick Cook[1], Dan Alder[2], Lisbeth Hordley[1], Stuart Newson[3], David Pengelly[4]

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[1] Butterfly Conservation, Manor Yard, East Lulworth, Wareham, Dorset, BH20 5QP

[2] Independent Ecologist, 12 Elm Close, Motcombe, Shaftesbury, Dorset, SP7 9HN

[3] British Trust for Ornithology, The Nunnery, Thetford, Norfolk, IP24 2PU

[4] Consultant Forester, SelectFor Ltd, Barrow Hill House, Wood Lane, Stalbridge, Dorset, DT10 2QZ

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Summary

- Commercial, conifer dominated forestry is a major land use in the UK and an important sector for the provision of timber. There is a growing interest in alternative forestry techniques such as irregular silviculture.
- Adoption of irregular silviculture is limited in the UK, but conifer dominated stands can be found at varying stages of transformation towards irregular structures.
- We examined the response of plants, spiders, moths, bats and birds in conifer dominated stands managed under irregular silviculture principles at the Stourhead (Western) Estate and National Trust Stourhead Estate.
- We document the biodiversity found at Stourhead and specifically tested (1) the influence of habitat structure within stands on biodiversity and (2) the response of biodiversity to three irregular forest development stand stages at different stages along the continuum of transformation.
- The Stage 2 and Stage 3 stands at Stourhead were characterised by a lower basal area than typical commercial, conifer stands in the UK, and the Stage 3 stand contained a greater habitat structural diversity and a higher component of broadleaved canopy trees.
- There was a surprising level of biodiversity at Stourhead, despite the conifer dominated nature of the stands and plantation origins on grassland. A total of 128 plants, 248 moths (27% of larger moths associated with woodland), 13 bats (76% of all UK resident species) and 26 birds species were recorded. This included a limited selection of scarcer species such as Waved Carpet moth or species of conservation concern such as Marsh Tit.

- Four habitat structural features were particularly important for increasing biodiversity.
- (1) Higher canopy cover of broadleaved trees was an important habitat feature for broadleaved tree feeding moths and three bat species.
- (2) Lower basal area (on a scale of 10-60 m^2ha), which increases habitat complexity, promoted higher plant and bird diversity.
- (3) Maintaining a variable canopy with patchy openness is important. Certain groups like bats responded to more open conditions whereas moths were associated with more closed conditions.
- (4) Greater quantities of deadwood promoted activity of Common and Soprano Pipistrelle.
- The Stage 3 and Stage 1 stands displayed higher biodiversity than the Stage 2, although patterns were often inconsistent. This reflects the (1) overlapping habitat structures found across the stand stages, (2) the most developed stand requires a further 30 years until reaching equilibrium along the transformation continuum, (3) the Stage 1 stand displaying higher structural diversity than expected in the idealised model and the Stage 2 stands and (4) factors external to the stand such as surrounding landscape habitats influencing what was recorded within a stand.

Contents

1. Glossary

The following technical terms are used throughout the report. Here we provide a definition for context of how they have been applied throughout the report.

Abundance- the number of a species found in an area.
Association- a relationship (positive or negative) between two measured variables.
Basal Area- the cross-sectional area of a tree at breast height (1.3 m), generally expressed in m^2 per hectare. Indicates growing stock density.
Bat activity- activity here represents usage of an area, which will be a combination of species abundance, and time spent in the area**.**
Diameter at Breast Height (DBH)- the diameter of a tree as measured at breast height (1.3 m), expressed in metres.
Ecosystem Service- a service provided by a forest that is important to humans. For instance the provision of timber or storage of carbon.
Foodplant- the plant a moth will feed on when in the caterpillar stage.
Frugivore/Granivore- a species that feeds on fruit and seeds.
Guild- a group of species that exploit a resource in a related way. For instance birds that feed on insects or moths that feed on broadleaved trees.
Insectivorous- a species that feeds on insects.
Larva/e- the caterpillar of a moth species. This stage is predominately focused on feeding.
Significant- this relates to statistics. If a result is statistically significant it is not likely to occur randomly.
Species Aggregation/Pair- A group of species that cannot be identified to species level reliably in the field and hence are aggregated.
Species Diversity- the number of species found in an area and their abundance relative to each other. A high value of diversity indicates a site with abundance more evenly spread across species.
Species Richness- the number of species found in a particular location.

2. Introduction

Forests ecosystems are globally important for biodiversity and ecosystem services (FAO & UNEP, 2020). The response of biodiversity to forest management is often highly context dependent, varying between species according to habitat preferences (Paillet *et al*., 2010; Boch *et al*., 2013; Gossner *et al*., 2014; Kirby *et al*., 2017; Kaufmann *et al*., 2018), the history of management within asavill stand and previous land use legacies (Motzkin *et al*., 1999; Dupouey *et al*., 2002; Hermy & Verheyan, 2007; Ellis *et al*., 2021).

Forests in the United Kingdom (UK) have a long history of management, primarily through coppicing to produce poles and timber (Rackham, 2015; Kirby *et al*., 2017). After the First World War (1914-1918) the demand for timber increased, which led to the formation of the Forestry Commission in 1919 and planting of thousands of hectares of commercial, plantation forestry (Gambles, 2019). Fast growing, non-native soft-wood conifers, such as Sitka spruce *Picea sitchensis* and Douglas fir *Pseudotsuga menziesii*, were selected to establish new plantations across a range of sites (Savill, 2015). Currently, conifer woodland, including native pinewoods *Pinus sylvestris,* covers 1,308,000 ha representing an important source of economic revenue (Forest Research, 2021).

Commercial, conifer dominated, forests have a legacy of even-aged structure in the UK due to management using clear-fell and replant. Cohorts of trees are harvested in coupes of varying size, during the stem exclusion phase, on a rotation of approximately 30-60 years for conifers (Mason *et al*, 1999; Mason, 2000). Post-harvesting, felled areas are restocked at high densities, creating homogeneous, even aged stands, often comprised of a single species (Fedrowitz *et al*., 2014). Once stands are established little light reaches the forest floor, limiting the development of an understorey (Mason, 2000). The technique has been criticised for the high levels of disturbance which can have negative impacts on biodiversity and ecosystem services (Pawson *et al*., 2006; Kuuluvainen, 2009; Harrison *et al*., 2010), although species that require open, sunny conditions, such as Woodlark or Pearl-bordered Fritillary, benefit from the open spaces created within a forest complex (Eycott *et al*., 2007; Clarke *et al*., 2011).

There is a growing interest in alternative silvicultural techniques, such as continuous cover forestry (CCF), which whilst widely implemented across continental Europe, have been adopted on a limited scale in the UK (Wilson, 2013; Puettmann *et al*., 2015). Within CCF is irregular silviculture (Pommerening & Murphy, 2004; Susse *et al*., 2011) which involves the selective removal of individual trees or small group felling (Sanchez, 2017). Interest in such techniques are driven by the need to create more resilient, sustainable forests, including economically, in the face of climate change and the resultant negative impacts this has on forests.

The primary aim of the technique is to promote diameter growth in retained trees, with a focus on maximising increment on trees with higher timber attributes, to the point at which they reach their maximum increment value. Stand stocking is held at a level that facilitates regeneration, resulting in vertical structural development. This system of forestry ensures a permanently irregular canopy, with spatially dispersed tree stocking levels. Increased light to the forest floor promotes sporadic natural regeneration of trees, and the development of a varied understorey (Susse *et al*., 2011; Muscolo *et al*., 2014; Fig. 1). Over time, with lower than standard tree growing stocks, stand heterogeneity and vertical structural diversity increase, which alongside the promotion of mixed stands of conifer and broadleaved tree species, is expected to increase biodiversity at varying spatial scales (Schall *et al*., 2018; Huuskonen *et al*., 2021).


Figure 1. An example of an irregular high forest stand.

It is increasingly recognised that commercial forests should deliver multi-functional benefits, beyond timber production, including ecosystem services, greater resilience to climate change and the provision of habitat for biodiversity (Gustafsson *et al*., 2012; Peura *et al*., 2018; Forestry Commission, 2020; Gustafsson *et al*., 2020). It is expected that the greater environmental stability provided by irregular silviculture will benefit species associated with mature forests and small-scale disturbances (Hyvaerinen *et al*., 2006; Kim *et al*., 2021). For instance the greater flexibility of irregular silviculture allows the retention of trees with valuable ecological characteristics, such as veteran trees with associated microhabitats (Larrieu *et al*., 2018). Forest biodiversity continues to decline, particularly forest specialist species, with both intensification and under-management of forests a contributing factor in this decline (DEFRA, 2020; Reid *et al*., 2021). Reversing biodiversity loss in forest ecosystems is important and the commercial forestry sector, a key stakeholder in the UK, has an important role to play in this process (Harris, 2020).

Limited evidence regarding the impacts of irregular silviculture on biodiversity have been gathered from the UK, including lowland broadleaved (Alder *et al*., 2018; Alder *et al*., 2021) and upland conifer forests (Calladine *et al*., 2015; Calladine *et al*., 2017). There is a requirement for more evidence from lowland, conifer dominated stands and stands of differing stages of transformation and therefore structural diversity. The Stourhead (Western) Estate and National Trust Stourhead Estate lie on the border between Wiltshire and Somerset in southern England. Both estates have commercial, conifer dominated forestry, at varying stages of transformation under irregular silviculture, making them an ideal site to study the influence of management on woodland biodiversity.

To address the gap in the research we investigated the response of biodiversity at multiple taxonomic levels, to management under irregular silvicultural principles in a lowland, conifer dominated commercial forest. We studied stands at three stages of transformation, towards irregular high forest. Taxonomic groups selected are plants, moths, spiders, bats and birds as they are important for woodland ecological processes and respond to management (Merckx *et al*., 2012; Boch *et al*., 2013; Alder *et al*., 2021). Here, we specifically tested (1) the influence of habitat structural variables on species richness, abundance and diversity and (2) whether species richness, abundance and diversity (overall and at a guild level) differ amongst stands at different stages of transformation to irregular.

2. Methods

The study was undertaken in three blocks of commercial, conifer woodland on the Stourhead (Western) Estate (SWE) and National Trust (NT) Stourhead Estate in southern England (51°06'46.1"N 2°21'32.2"W; 141 m - 239 m a.s.l; Fig. 2). The stands investigated represent three stages of transformation towards irregular high forest. (Fig. 3; Fig. 4). Locations of each stand development stage were exclusive to

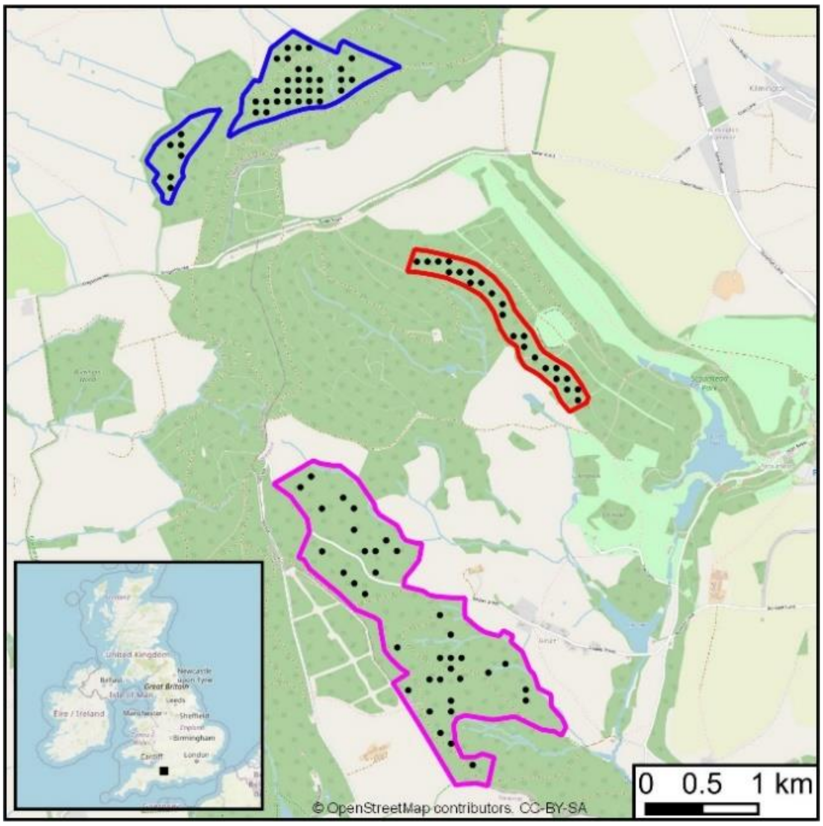

Figure 2. Location of the study site in southern England. Stands surveyed in this study are outlined. Polygons with a red outline represent the Preparatory Stage stands (Stage 1), dark blue outline represents the Regeneration Initiation stands (Stage 2) and purple outline represents the Structural Development stands (Stage 3). Black dots represent the location of sample plots to survey the selected taxonomic groups. © OpenStreetMap contributors CC BY-SA.

separate geographical areas and therefore genuine replication across the forest was not possible. The Estate had adopted an innovative silvicultural approach since the early 20th C and began a more formal transition towards permanently irregular structures in 1997. Stands can be found at varying points along a continuum from having relatively regular (even-aged) to irregular (mixed-age and species) structure. Some stands contain a limited proportion of broadleaved trees, dependent on the stand history rather than transformation stage. Variation in percentage cover of broadleaved trees varied in accordance with retention of stand elements after first rotation afforested stands were felled and replaced by current stand elements. Stands progress from Stage 1 (Preparatory Stage, PS), through Stage 2 (Regeneration Initiation Stage, RIS) to finally Stage 3 (Structural Development Stage, SDS). At the end of Stage 3 stand structure stabilises around an equilibrium.

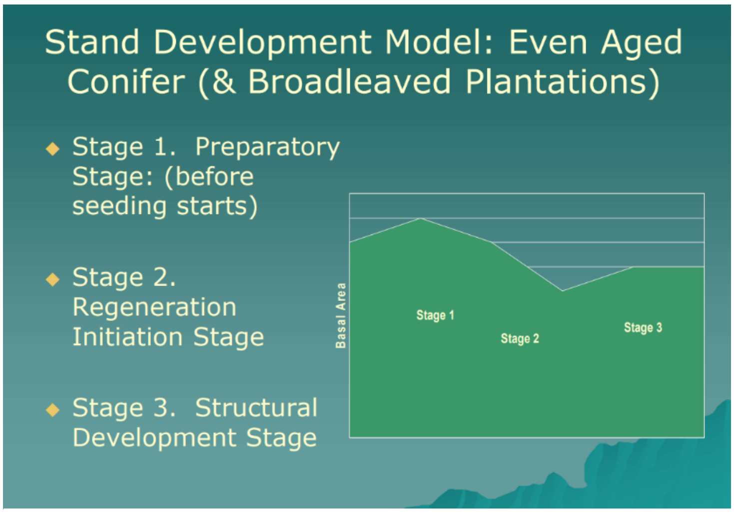

Figure 3. Stand development model for even aged conifer and broadleaved plantations in transformation towards irregular high forest. Chart provided by Andy Poore.

Stage 1: Preparatory Stage (PS)

Stands considered in Phase 1 for this project were at National Trust Park Hill, which has an underlying geology of Greensand and Gault clay. The site was part of a former deer park that remained as grassland and scrub until planting with conifers and broadleaved trees by the year 1800. Currently the stand is comprised primarily of Douglas Fir, Western Hemlock and Sitka Spruce. The northern end of the stand is largely without an understorey whereas the southern end which is on a steeper southwest facing slope contains a bramble and grass understorey. The presence of an understorey is not typical of Stage 1 stands which limits some conclusions from this study regarding this stand. The stand is relatively narrow, bordered by a greater amount of broadleaved woodland and grassland than other stands included in the study. Stands are at the beginning of transformation along the transformation continuum; in total the process of reaching equilibrium is estimated at 80 years. Silvicultural objectives of the stand include;

- Achieve stand stability by early thinning and then maintaining stand volumes near to even-aged levels.

- Avoid imposing regular spatial distributions and promote clumpy spatial distribution.
- Improve phenotypes by the intensive removal of stems with negative characteristics.
- Promote species diversity by ensuring that secondary and minor species are maintained within the stand.

Stage 2: Regeneration Initiation Stage (RIS)

Stands considered in Phase 2 for this project were at Kingswood Warren, which has an underlying geology of Greensand. The site has a complex history with wood pasture present until a major clearance in the 19th century and planting with conifers in the 1930's. Subsequently the site was managed with clearance and re-stocking, which removed any remaining semi-natural tree and shrub communities. The site is comprised primarily of Douglas Fir, with a developing understorey primarily of bramble. The stand is relatively broad on a gentle northwest facing slope with wide rides, bordered by farmland to the north. Tree regeneration is sporadic throughout the stand and some supplementary planting to diversify the mix is taking place. Stands are approximately 35% of the way along the transformation continuum with approximately another 50 years required to reach equilibrium. Silvicultural objectives of the stand include;

- Reduce stand volume/ basal area below the long-term target to initiate regeneration.
- Maintain intensive removal of stems with negative characteristics.
- Maintain secondary and minor species and other differentiated stand elements.

Stage 3: Structural Development Stage (SDS)

Stands considered in Phase 3 for this project were at Dropping Gutter, Castle Wood, Shootershill Copse and Gasper Common, with a north-eastern and south facing orientation, and underlying geology of Greensand. The area was a mix of common land and existing woodland before planting in the 18th and 19th centuries. Dominant conifer species include Douglas Fir, Sitka Spruce, Western Hemlock and Western Red Cedar alongside limited broadleaf elements particularly Alder and Oaks. Stage 3 stands displayed a lot of variation with some plots structurally diverse with mixed species (e.g. Dropping Gutter) and others less so (e.g. Shootershill Copse). Broadleaved elements varied greatly across the stands, being particularly frequent along streamside's and on wetter areas of ground. Surrounding the stand is primarily other conifer woodland and farmland although the site is fringed by ancient semi-natural woodland and plantation on ancient woodland in the northeast. Stands began transformation in 1997 and are approximately 60% of the way along the transformation continuum with around another 30 years required to reach equilibrium. Silvicultural objectives of the stand include;

- Allow stand volume to increase towards target volume/ basal area.
- Develop full structural and species diversification. Move towards long-term targets for size-class distribution.
- Relate stand structure to increment to guide structural development.

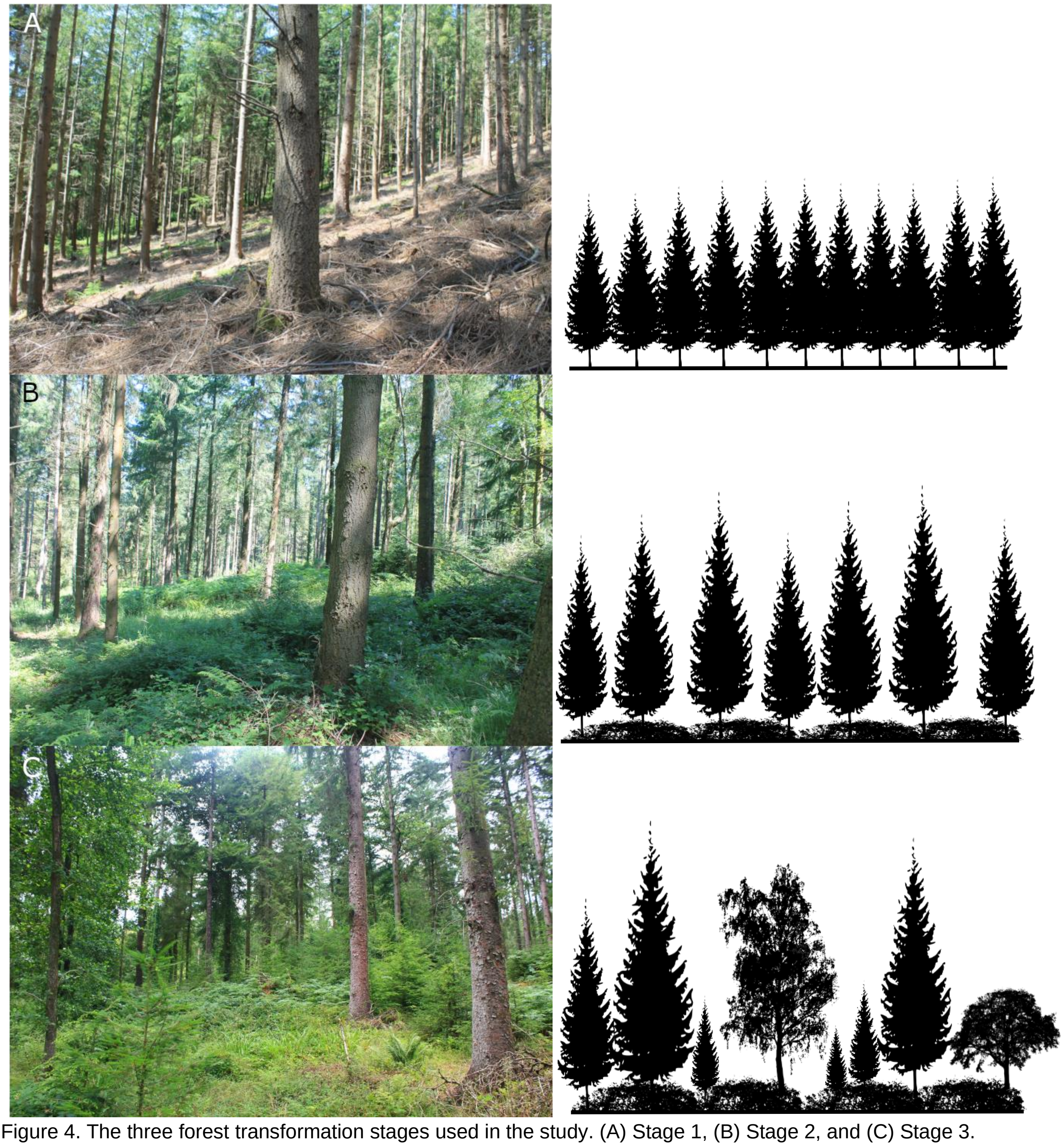

Figure 4. The three forest transformation stages used in the study. (A) Stage 1, (B) Stage 2, and (C) Stage 3.

Sampling of Taxonomic Groups and Statistical Analysis

A complete description of the methods used to survey taxonomic groups and statistical analysis are provided in Appendix 1. Habitat structural measurements were conducted in 30 m plots across the three stand stages in 2019 and 2021. Species groups surveyed included plants, moths, spider webs, birds and bats. For each species and species group we determined associations with particular habitat features and examined the following species metrics (species richness, species abundance and species diversity) making pairwise comparisons amongst the three stand stages.

3. Results

Biodiversity at Stourhead

A total of 415 species across all taxonomic groups and stand stages were recorded, with moth species making up 60% of the total number of species, followed by plants, bats and birds respectively (Table 1). A full species list for each group broken down by stand stage can be found in Appendices 2-5.

Table 1. Species richness and abundance/registrations (in brackets) where relevant of each taxonomic group across the stand stages. Moth species richness totals exclude aggregated species groups. Results presented in this table do not take account of sampling effort.

Taxonomic Group	Stage 1	Stage 2	Stage 3	All Stand Stages
Plants	52	86	109	128
Moths	171 (2867)	184 (3722)	175 (3575)	248 (10164)
Bats	11 (878)	12 (1344)	13 (3718)	13 (5940)
Birds	N/A	22 (125)	25 (278)	26 (403)

Habitat Structure across the Development Stage Stands

There were 14 significant differences in habitat structural variables between the stand stages for basal area, average DBH, number of tree species, stems ≥ 7.5 cm DBH, percentage broadleaved canopy and complexity score (Table 2, full results in Appendix 6).

Table 2. Habitat differences across stand stages in 2019 and 2021. Median values and interquartile range in parenthesis and results for mixed effect model. Significant differences between stands are highlighted in bold. The + and – sign indicate higher or lower and the number refers to the comparison stand. For instance a +3 under the column Stage 1 for basal area indicates higher basal area in Stage 1 than Stage 3.

Habitat Variable	Stage 1	Stage 2	Stage 3
2019			

Basal area	**38(6), +3**	29(5)	**24(9), -1**
Average DBH	47(13)	37(8)	47(25)
Number of tree species	3(2)	**2(1), -3**	**6(3), +2**
Stems 7.5cm DBH	**15(10) -2**	**30(9), +1, +3**	**11(7), -2**
Percentage broadleaved canopy	0(0)	**0(6), -3**	**0(43), +2**
Fallen deadwood	0(1)	2(6)	2(5)
Deadwood snags	0(1)	1(3)	0(3)
Canopy openness	10(7)	9(4)	24(15)
Complexity score	4(2)	**3(0), -3**	**6(3), +2**
2021			
Basal area	**38(8), +3**	**32(4), +3**	**22(8), -1, -2**
Average DBH	51(12)	**39(6), -3**	**53(22), +2**
Number of tree species	4(2)	4(1)	6(3)
Stems 7.5cm DBH	**15(7), -2**	**28(4), +1, +3**	**10(6), -2**
Percentage broadleaved canopy	**0(0), -3**	**0(21), -3**	**0(50), +1,+2**
Fallen deadwood	0(2)	2(4)	3(8)
Deadwood snags	0(1)	0(1)	0(2)
Canopy openness	12(6)	13(5)	24(20)
Complexity score	4(1)	**3(0), -3**	**6(2), +2**

Biodiversity and Habitat Features of Importance

This project identified ten key habitat associations (Table 3). Four of these features (lower basal area, broadleaved tree cover, amount of deadwood and variable canopy openness) were apparent across multiple species/groups and can be considered important for promoting biodiversity in conifer dominated stands.

Table 3. Statistically significant results between species or species groups and habitat feature. The direction of the relationship between the two variables is described as positive or negative (e.g. plant species diversity decreases at higher basal area). For statistical significance levels a * indicates a significant p value <0.05, ** highly significant p value <0.01, and *** very highly significant p value <0.001.

Group	Habitat Feature	Relationship	Significance
Plants			
Plant species diversity	Basal area	Negative	**
Woodland generalist species richness	Percentage broadleaved canopy	Positive	***
Moths			
Total moth species richness	Canopy openness	Negative	**
Total moth abundance	Canopy openness	Negative	*
Total moth species diversity	Canopy openness	Negative	***
Woodland moth species richness	Canopy openness	Negative	**
Woodland moth abundance	Canopy openness	Negative	**
Broadleaved feeding moth species richness	Complexity score	Positive	**

Broadleaved feeding moth abundance	Distance to broadleaved	Positive	***
Broadleaved feeding moth abundance	Percentage broadleaved canopy	Positive	***
Conifer feeding moth species richness	Basal area	Positive	**
Conifer feeding moth abundance	Distance to broadleaved	Positive	***
Spiders			
Number of spider webs	Bramble	Positive	**
Number of spider webs	Brash	Positive	**
Bats			
Soprano Pipistrelle	Average DBH	Positive	**
Soprano Pipistrelle	Canopy openness	Positive	***
Common Pipistrelle	Canopy openness	Positive	***
Serotine	Canopy openness	Positive	*
Soprano Pipistrelle	Deadwood snags	Positive	*
Common Pipistrelle	Fallen deadwood	Positive	**
Brandt's/Whiskered	Percentage broadleaved canopy	Positive	***
Birds			
Bird species diversity	Basal area	Negative	**

Biodiversity in Stand Development Stages

We found 20 species/species group variables displayed a statistical difference between the stands (Table 4, full summary in Appendix 7).

Table 4. Statistically significant pairwise results amongst the three stand stages. The + and – sign indicate higher or lower and the number refers to the comparison stand. For instance a +2 under the column Stage 1 for total moth abundance indicates higher moth abundance in Stage 1 than Stage 2.

Species/Group Variable	Stage 1	Stage 2	Stage 3
Moths			
Total abundance	+2	-1	
Total abundance	+3		-1
Total species diversity	+2	-1	
Total species diversity	+3		-1
Woodland guild abundance	+3		-1
Broadleaf guild species richness	+2	-1	
Broadleaf guild abundance	+2	-1	
Broadleaf guild abundance		-3	+2
Conifer guild species richness	+2	-1	
Conifer guild species richness	+3		-1
Conifer guild abundance	+2	-1	
Conifer guild abundance	+3		-1
Conifer guild abundance		-3	+2
Grassland guild species richness	+3		-1
Grassland guild species richness		+3	-2
Spiders			
Number of webs	+2	-1	
Number of webs		-3	+2

Birds		
Woodland generalist species richness	-3	+2
Woodland specialist species richness	-3	+2
Invertebrate guild species richness	-3	+2

4. Discussion

Biodiversity at Stourhead

Interpreting species totals is dependent on a range of factors such as the length of the survey period, area of the stand (larger in Stage 3 and 2 than Stage 1) and latitude of the site. The number of species recorded at Stourhead does however indicate that plantation on former grassland, with a much lower basal area than standard in the forestry industry, can support surprising levels of biodiversity, particularly mobile species.

The plant community reflects the underlying geology of the site and the site history. A number of ancient woodland indicator species for south-west England were recorded including Wood-sorrel *Oxalis acetosella* and Yellow Pimpernel *Lysimachia nemorum*. Prior land uses before afforestation with conifers still had an influence on current plant communities (Dupouey *et al*., 2002; Watts *et al*., 2020). For instance acidic associated species like Ling Heather *Calluna vulgaris* were present in areas of former common land.

A total of 248 moth species of 10,164 individuals were recorded at Stourhead, including 27% of larger moths associated with woodland in the UK (Cook *et al*., 2022). This is lower than a study on the Rushmore Estate, 20 miles to the east on Cranborne Chase, where irregular high forest stands are also present (Alder *et al*., 2018), and a total of 486 moth species of 30,757 individuals were recorded (Sterling, 2017). However, the Rushmore study was based on a large, actively-managed ancient semi-natural woodland on a very different site-type and the total at Rushmore would be expected to be higher. The surveys at Rushmore were also conducted over a long time period (June to August), compared to a two-week window at Stourhead, and used more powerful light traps which would also increase the numbers of species and individuals recorded. At Rushmore it was found that the abundance of scarcer woodland species was highest in the irregular stand. At Stourhead we recorded fewer localised species, as to be expected in conifer dominated stands, but this included the scarce Waved Carpet (Fig. 5). This

Figure 5. Waved Carpet moth. Photo Phil Sterling.

moth is a species of former conservation concern, likely associated with alder rich streamside's found on the site, indicating the importance of a broadleaved element for biodiversity within conifer stands. We also recorded a few other localised moth species, for instance *Assara terebrella*, but recorded moth species were generally widespread. Many widespread moth species are undergoing rapid declines (Fox *et al*., 2021), so supporting these species through higher quality commercial forest stands is still important and valuable.

The total of 13 bat species, 76% of all known UK resident species, is impressive and indicates that the site supports a good bat fauna, comparable to the number of species recorded at Rushmore (Alder *et al*., 2021). Barbastelle, a bat species listed as near-threatened globally on the IUCN Red List, was the fifth most active bat in the study with 243 registrations (Fig. 6). No association with stand type was detected in this study but at Rushmore this species was found to have a higher level of occupancy in irregular stands compared to limited intervention and coppice stands (Alder *et al*., 2021).

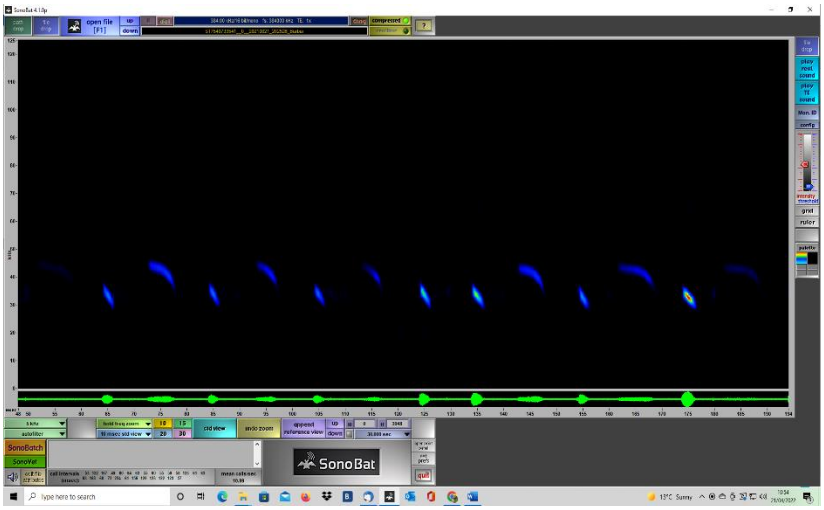

Figure 6. Audio recording of a Barbastelle at Stourhead.

The total number of bird species (26) was lower than at Rushmore where 38 species were recorded. Two red listed Birds of Conservation Concern were recorded, the Marsh Tit and Spotted Flycatcher. Both species were recorded in too low numbers to be able to understand any relationship to habitat structure, but the former was found at particularly high densities in irregular high forest stands at Rushmore (Alder *et al*., 2018). As stand development continues towards equilibrium at Stourhead the species could potentially increase within the stands.

Habitat Structure across the Development Stage Stands

The basal area of the stands decreased from Stage 1 to Stage 3, which differs slightly from the idealised model presented in Figure 3, where the basal area is expected to increase slightly in Stage 3 from Stage 2. This reflects two factors, (1) the requirement to remove diseased larch and ash trees infected with *Phytophthora ramorum* and Ash

Dieback *Hymenoscyphus fraxineus* respectively and (2) the current stage in the selection felling cycle. The Stage 3 stand displayed the highest degree of habitat complexity, with the lowest in Stage 2 as the Stage 2 stands were characterised by a high number of stems and relatively low overall diversity.

Lower basal areas are important in facilitating this higher complexity as it allows the development of an understorey. The Stage 3 stands at Stourhead displayed a more developed understorey, comprised of bracken, bramble and tree regeneration, primarily Western Hemlock. The presence of an understorey, particularly tree regeneration, was limited in the Stage 1 and Stage 2 stands in comparison, except for some stands at the southern end of the former.

The Stage 3 stands also displayed a greater habitat structural variability, which often encompassed the variation found in the Stage 1 and Stage 2 stands. The variability in habitat structures in the Stage 3 stand is critical to the provision of habitat for biodiversity in woodlands. For instance the average tree DBH, canopy openness, broadleaved canopy cover and number of tree species all displayed more variation in Stage 3 stands. A limited component of broadleaved trees within conifer stands, as displayed in the Stage 3 stand, is important for biodiversity as they can support a wider range of native species than introduced conifer species. For instance 129 species of larger moth feed on oaks and 55 on Common Alder, whereas only six species feed on Douglas Fir, two on Western Hemlock and 13 on Sitka Spruce. Differences between the stages and further development of features of interest (lower basal area, broadleaved component, deadwood and varied canopy openness) will likely expand further as they progress towards equilibrium.

Biodiversity and Habitat Features of Importance

Basal area has previously been found to be important for influencing both moths and birds (Fuentes-Montemayor *et al*., 2012; Lintott *et al*., 2014; Felton *et al*. 2021). We found both plant diversity and bird diversity increased at lower basal areas (10-60 m^{2}ha)(Fig. 7). Lower basal area within a stand creates more open conditions, allowing light to reach the forest floor, promoting the development of an

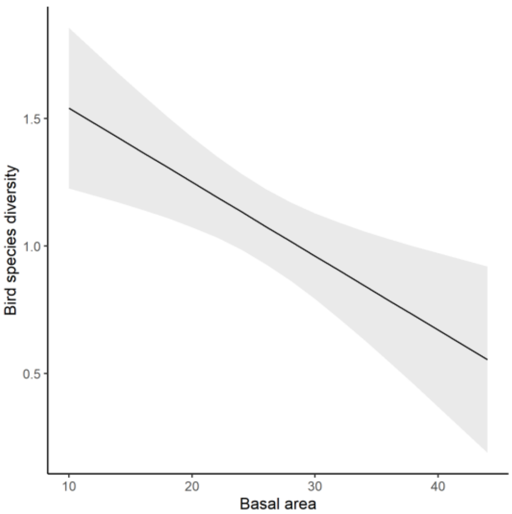

Figure 7. Relationship between bird diversity and basal area. Bird diversity was higher when basal area was lower (10-48 m^{2}ha).

understorey which results in greater habitat complexity. This creates a wider range of habitat opportunities for species to occupy. For instance the understorey at Stourhead included bramble, which was found to be positively associated with the number of spider webs. The developing understorey is also important as a structural feature for summer migrant birds, like Blackcap, which at the Rushmore Estate had a higher density in irregular stands (Alder *et al*., 2018).

Higher broadleaved tree canopy cover was also important for promoting biodiversity, across plants, moths and bats. Given the importance of broadleaved trees for maintaining and supporting native biodiversity in woodlands (Felton *et al*., 2021) these results are not surprising, but indicate the importance of a broadleaved element within conifer dominated stands for biodiversity. For instance we found the abundance of broadleaved tree feeding moths was higher in areas with higher levels of broadleaved tree cover, due to the greater availability of suitable foodplant resources during the larval feeding stage. This study also found a positive relationship between Brandt's/Whiskered bat and broadleaved canopy (Fig. 8). This supports findings from other studies in the UK, that have shown a positive association between the activity of this species and broadleaved woodland (Border *et al*. 2017).

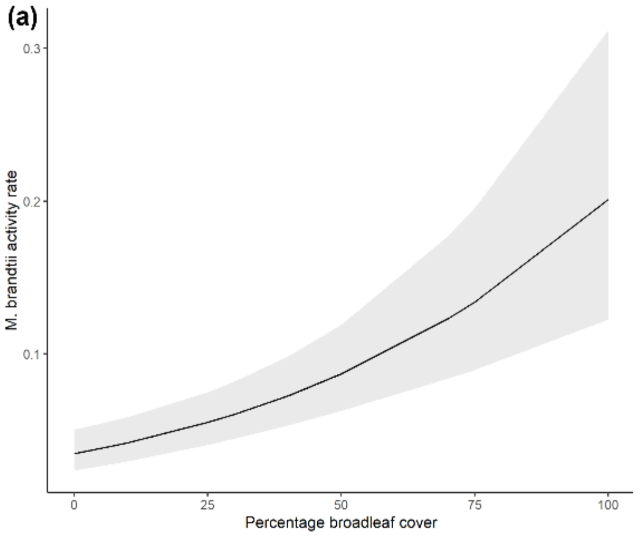

Figure 8. Positive relationship between activity of Brandt's Whiskered bat and broadleaved canopy cover.

Variable levels of canopy openness, most prevalent in the Stage 3 stands also promoted biodiversity. Three bat species (Common Pipistrelle, Soprano Pipistrelle and Brandt's/Whiskered) all displayed a positive relationship with canopy openness, which promotes cover of bramble, bracken and tree regeneration. This is in accordance with previously documented preferences of these species being habitat edge foragers (Muller *et al*., 2013; Alder *et al*. 2021). In contrast moths were more associated with lower canopy openness within the wider forest complex, which agrees with previous findings documenting a distinct moth community in closed canopy native woodland (Merckx *et al*., 2012). This indicates the value of maintaining patchy openings within the canopy, best supported by structurally developed irregular woodland, to deliver habitat for species groups with differing canopy cover requirements.

Both Soprano and Common Pipistrelle bat activity increased with the amount of deadwood available. Deadwood has previously been found to be an important resource for a wide range of species, including bats (Sandström *et al*., 2019), due to the opportunities it presents for roosting and foraging on emergent deadwood invertebrates (Tillon *et al*., 2016; Basile *et al*., 2020; Alder *et al*., 2021). Promoting higher levels of deadwood should be a biodiversity objective of any woodland both for bats and for other groups not included in this study, such as deadwood specialist invertebrates.

Biodiversity in Stand Development Stages

The Stage 3 and Stage 1 stands generally supported more biodiversity than the Stage 2, although patterns were often not consistent. This isn't particularly surprising as stands are still relatively early in the transformation process, with the most developed stands approximately 60% of the way along the transformation continuum. This may have precluded the detection of any differences, with overlap in habitat structural features still common across the stand types. A limitation of our experiment was that genuine replication wasn't possible across the site, as each stand transformation was found in one location. This may also have prevented the detection of any differences between the three transformation stages.

The Stage 1 stand, which appeared to perform comparatively to the Stage 3 stands in biodiversity comparisons, was influenced by a number of internal and external stand factors, which likely influenced this result. The selected Stage 1 stand at Park Hill did not fit the idealised stand development model and actually displayed more variation than the Stage 2 stand. This was largely due to the previously mentioned plots at the southern end of the stand that had a relatively developed bramble understorey, creating greater diversity for biodiversity. This feature is not typical of Stage 1 stands in the idealised model and means that we see greater diversity in the selected Stage 1 stand than expected. External factors such as the relatively narrow shape of the stand, surrounded by a greater amount of broadleaved woodland and grassland, also likely influenced the result, especially when surveying relatively mobile species like moths and bats. For instance of the 171 moth species recorded in the Stage 1 stand, 17.5% feed solely on broadleaved trees as a larva, despite the limited availability of this resource in the Stage 1 stand. Surrounding habitat in the landscape and habitat configuration have previously been found to influence forest biodiversity in other studies, including moths and bats (Fuentes-Montemayor *et al*., 2013; Merckx *et al*., 2019).

5. Conclusions

Commercial conifer dominated stands, with a lower basal area in the main canopy than standard in the forestry industry, supplemented by a developing understorey, and managed on a trajectory leading to permanently irregular structures, can support a surprising level of biodiversity. At the stands at Stourhead this is best exemplified by the number of woodland associated moths species and bat species recorded in the project. The findings of this research indicate a number of habitat structural variables are important for promoting biodiversity in commercial forests, whereby changes can be implemented within the economic and physical constraints of a site. Important habitat features include (1) lower basal area, (2) higher broadleaved canopy cover, (3) varied canopy cover and (4) higher deadwood levels. These features provide greater diversity both structurally and in terms of species mix within forest stands. Scaled up at the extent of land area currently covered by conifer plantations in the UK, this could make an important contribution to supporting biodiversity in the wider countryside.

The Stage 3 and Stage 1 stands generally displayed higher biodiversity than Stage 2, although patterns were often inconsistent. Given these stands are in the early stages of transformation this is not surprising. The surprising performance of the Stage 1 stands is influenced by internal stand dynamics such as a few relatively diverse plots, which means the stand does not fit the idealised Stage 1 stand development phase. External stand dynamics such as greater surrounding levels of broadleaved woodland probably also influenced the biodiversity recorded in this stand. As the stands continue to develop towards equilibrium in 30-50 years' time, and key habitat features of importance for biodiversity identified in this report (lower basal area, broadleaved canopy cover, deadwood and varied canopy openness) develop further, differences amongst the stand stages may become more apparent.

The research conducted here has begun to address the biodiversity value of conifer woodlands in transformation to irregular high forest. Further research is required at Stourhead when stands reach equilibrium, particularly the areas currently defined as Stage 3. Ideally this would include genuine replication across multiple sites to better account for different landscape characteristics and more detailed study of understorey parameters. The inclusion of other, less mobile species groups would also be valuable for understanding how different taxonomic groups respond as conifer stands progress through the transformation process.

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Appendices

Appendix 1- Full survey and statistical method details

Sampling of taxonomic groups

A total of 95, 30 m diameter, sample plots were randomly selected across the three treatments, 36 in Stage 3, 36 in Stage 2 and 23 in Stage 1. All sample plots were located a minimum distance of 30 m from the nearest major forest edge (defined as an agricultural boundary, a major ride > 8 m wide or a road), with each plot a minimum of 60 m from the next nearest plot. At each plot we undertook measurements of habitat structure, plants, spider webs and moths. Of the 95 plots, 32 were surveyed for bats, with two visits per plot. Bird surveys were restricted to the Stage 2 and Stage 3 stands.

Habitat Measures

Habitats measures were adapted from Khanaposhtani *et al*. (2012) and Alder *et al*. (2018). At each 30 m sample plot the following habitat measurements were gathered in July 2019 and 2021.

- Basal area was calculated by conducting a 360° sweep from the plot centre, with a basal factor of 2 and a minimum of ten trees, in the relascope MOTI application (Rosset *et al*., 2015).
- Diameter at breast height (DBH) was measured for the five largest trees.
- Number of stems ≥ 7.5 cm DBH.
- Number of tree species.
- Distance to nearest canopy or sub-canopy broadleaf tree.
- Percentage broadleaved canopy cover.
- Length of fallen deadwood > 1m in length and > 20 cm in diameter.
- Frequency of deadwood snags > 1m in length and > 10 cm in diameter.
- Percentage canopy openness using a spherical convex mirror densiometer.

- Percentage cover of dominant ground layer (0-1 m) vegetation.

The forest structure was divided into five categories for data collection; canopy, subcanopy, tall understorey (2.5-6 m), low shrub (1-2.5 m) and ground/field layer (0-1 m). We calculated cover for dominant field layer species using the DOMIN scale (Kent, 2011). Four percentage categories (0-10%, 11-20%, 21-50% and >50%) were used to estimate the tree cover of the canopy, sub-canopy, tall understorey and shrub layer with scores later converted to a 1-4 scale to calculate habitat complexity scores. Scores for the four categories were merged to calculate an overall habitat complexity score with high classified as ≥ 5 and low as <5.

Plants

Plant species were identified to the highest taxonomic level feasible between July and October 2021 (Stace, 2019). Closely-related species were aggregated where identification to species level in the field is not possible. Cover for each plant species was estimated within the 30 m plot using the DOMIN scale.

Moths

Moths were sampled using 6 W actinic light traps in July 2019 and 2021 (Fig. A1). Plots were located 60 m apart to reduce the effect of light interference (Merckx & Slade, 2014). Light traps contained a solar switch to turn on at dusk and off at dawn. Traps were sealed at dawn and processed shortly after, recording species to the highest taxonomic level possible. We did not conduct genitalia dissection for species where identification in the field is not feasible. Aggregated species pairs were not included in the analysis.

Figure A1. A 6W actinic light set up at a sample plot to survey adult moths.

Spider Webs

A novel method was used to assess spider webs in July 2021. At each sample location a 1m^3 plot was sprayed with water from a knapsack sprayer on fine mist mode. The location of the plot was 1 m from the centre of the sample location and determined based on a random compass bearing. After spraying, the number of sheet, orb and scaffold webs were subsequently counted. Presence or absence of key habitat features in the plot were recorded including cover of bare ground, bracken, bramble, brash, grass, large trees and small trees.

Figure A2.. Set up of a plot for surveying spider webs.

Bats

Bats were surveyed acoustically in 2021, with one night between the 10th and 17th of August and a second night between the 18th and 26th August 2021, using four Song Meter SM3Bat recorders (Wildlife Acoustics Inc, 2021). In any individual night of recording, SM3Bat's were placed in each of the three treatments. Surveys were conducted on nights without rain, wind speeds below force 4 on the Beaufort Scale and temperatures above 7°C (Froidevaux *et al*., 2014). Microphones were pole-mounted at a height of 3.0 m and a minimum of 1.5 m from dense vegetation (Alder *al*., 2021).

The bat detectors were set to record with a sample rate of 384 kHz and to use a high pass filter of 8 kHz which defined the lower threshold of the frequencies of interest for the triggering mechanism. Recording was set to continue until no trigger is detected for a 2 second period up to a maximum of 5 seconds. Detectors were deployed before sunset and detectors set to switch on and record 15 minutes after sunset until 15 minutes before sunrise the following day (Froidevaux *et al*., 2014). A trigger threshold of 12 dB was set, with a 8 kHz pass filter, with a recording continued until there was no trigger for a 2.0 second period (Newson *et al*., 2015). Each triggered event was categorised as a pass for each species. A first analysis of bat recordings was carried out using a classifier that was built to support the BTO Acoustic Pipeline (http://bto.org/pipeline).

Following recommendations by Barré *et al*. (2019), identifications with a probability of less than 0.5 (50%) were not considered further. For the remaining recordings, verification of species identification was carried out through the manual checking of spectrograms using software SonoBat 4.1 (http://sonobat.com/) which was used as an independent check of the original species identities assigned by classifier. This was carried out for recordings of all species, except for common pipistrelles where a sample of c.20% was manually checked to confirm identification.

Criteria for distinguishing *Myotis mystacinus* and *Myotis brandtii* are very subtle and poorly defined. Because these two species are extremely difficult to distinguish acoustically, as are *Plecotus auritus and P. austriacus* we treat these species here as species pairs respectively.

Bird Surveys

Transects were utilised rather than point counts to avoid issues with spatial autocorrelation, as plots could not be located more than 60 m apart without reducing the sample size. Birds were surveyed using a transect design adapted from Bibby *et al*. (2000). On each visit the observer covered the entire plot systematically by a series of transects, recording birds up to a distance of 50m (Bibby *et al*., 2000). Transects were repeated three times in the spring, once each in the months of April (12th-14th), May (10th-12th) and June (7th-9th) to ensure adequate coverage of both early season breeding species and late season breeding species which includes migratory species such as Spotted Flycatcher. Transect routes were designed to ensure coverage, within 100 m of the entire sampled area. Bird surveys were carried out between 05:30 and 11:00 in the morning, with birds identified both visually and acoustically. For each registration we recorded the location and species. Species that were observed flying over the survey area were not included in the analysis and birds observed flying from or to a static position were recorded from where they were seen to take off or land. Species found greater than 50 m from a plot were removed from the analysis to reduce bias from plots which are more isolated having higher species richness.

Species guilds

To investigate how different types of species responded to the different stand stages and habitat variables, we grouped species into guilds based on their habitat association or diet. Plants species were grouped into two guild categories, based on expert opinion and the ancient woodland vascular plant list (Rose, 1999). The first was broad plant category e.g. broadleaved tree and secondly whether they are a woodland specialist or woodland generalist. Moths were classed into two categories based on habitat use, and two categories based on diet. Species were classed as using predominately woodland or grassland habitat and classed as (larvae) feeding on broadleaf or coniferous host plants

(Cook *et al*., 2022). For birds, species were classed based on their habitat association as either a woodland generalist or specialist, using the Defra woodland bird indicator (DEFRA, 2020). Bird species were also categorised into two dietary groups, either a frugivore (feeding on seeds or fruit), or an invertivore (feeding on invertebrates) based on a species' dominant diet from (Wilman *et al*., 2014).

Covariates

To understand how biodiversity was affected by forestry management, we accounted for known drivers of species richness, abundance and diversity. In addition to the habitat structural measurements we measured the distance to the nearest major edge (agricultural boundary, major ride > 8 m wide or road), aspect, and elevation. Furthermore, to account for the impact of weather on the number and abundance of moth species caught in traps, we also measured the minimum temperature, cloud cover, and moon cycle at each plot for each trapping night. For birds, we calculated the average distance at each site between each bird sighting and the nearest plot to account for more isolated plots having greater species richness and abundance.

Statistical analysis

Firstly, we calculated the total species richness forplants, moths, bats, and birds. For spiders, we calculated the number of webs at each plot. Total abundance was calculated as the total number of individuals at each plot for moths and the total cover at each plot for plants. For bats, we calculated an activity rate as the proportions of 10-minute periods during a night, within which the bat species was recorded at least once. Four species did not occur frequently enough and were removed from the activity analysis (Leisler's *Nyctalus leisleri*, Nathusius's Pipistrelle *Pipistrellus nathusii*, Greater Horseshoe *Rhinolophus ferrumequinum*, and Lesser Horseshoe *Rhinolophus hipposideros*). We did not have sufficient data for birds to look at total abundance alone. Finally, we calculated a species diversity index (Shannon Diversity) for plants, moths, and birds, which combines the number of species within a site with the relative abundance/cover of each species.

To understand how the three stand development stages (PS, RIS, and SDS) influenced biodiversity, we composed mixed effects models with each biodiversity measure (species richness and total abundance/cover both overall and for each guild, species diversity, and each bat species' occupancy rate) as our response variable, stand stage as our explanatory variable, and sub-compartment as a random effect to account for similarities within sub-compartments. Year was also included as a random effect for moths, visit was included for bats, and month was included for plants. Covariates included were as follows: average distance to plot, distance to edge and aspect (birds), minimum temperature, cloud cover, moon cycle, distance to edge and distance to broadleaf (moths), and distance to edge (bats). Count data (species richness) were analysed with a Generalised Linear Mixed Model (GLMM) with Poisson distribution, unless underdispersion was detected and a Generalized Poisson was used instead. Abundance data were analysed using a negative binomial distribution to handle overdispersion, and species diversity was analysed using Linear Mixed Models (LMMs). All continuous variables were standardised to zero mean and one standard deviation. We checked for collinearity between explanatory variables prior to running our model (all $r<0.7$) and we calculated variance inflation factors (VIFs) from the fully specified model. Model assumptions (including overdispersion) were verified using the DHARMa R package. We generated all possible model combinations using the dredge function from the MuMIn R package and restricted our model set such that stand stage was included in all models, as this was our variable of interest. We identified a top model set containing models with $\Delta AIC<6$ and selected the most parsimonious model as the one having the fewest number of predictors. Tukey's post hoc multiple comparison tests were used to investigate pairwise differences between the three stand stages.

To analyse the influence of habitat variables on biodiversity, we fitted further GLMMs and LMMs with habitat measures as our explanatory variables. We selected five habitat variables: basal area, average DBH, complexity score, canopy openness, and percentage broadleaved canopy. We also investigated the impact of fallen deadwood and deadwood snags on bats and birds. For spiders, we investigated the impact of presence/absence of bracken, bramble, leaf litter, moss, grass, brash, tree regeneration and large trees. We fitted the same distributions as mentioned above, including the same random effects and covariates. All continuous variables were standardised to zero mean and one standard deviation. We checked for collinearity between explanatory variables prior to running our model (all $r<0.7$) and we calculated variance inflation factors (VIFs) from the fully specified model. Model assumptions (including overdispersion) were verified using the DHARMa R package. We generated all possible model combinations using the dredge function from the MuMIn R package and identified a top model set containing models with $\Delta AIC<6$. We averaged the top model set to obtain coefficients to plot the results between covariates and predicted values of species richness, abundance, or diversity.

Appendix 2. Plant species recorded across the three stand stages. Average DOMIN score is displayed for each species.

Scientific Name	Common Name	Stage 1	Stage 2	Stage 3
Abies species	Fir species			4
Acer platanoides	Norway Maple			1
Acer pseudoplatanus	Sycamore			5
Agrostis canina	Velvet Bent		4	4
Agrostis capillaris	Common Bent			4
Agrostis capillaris / vinealis	Common / Brown Bent	2	4	2
Alnus glutinosa	Alder			5
Alnus incana	Grey Alder			5
Anthoxanthum odoratum	Sweet Vernal Grass		2	1
Arctium minus	Lesser Burdock			1
Athyrium filix-femina	Lady Fern	1	2	1
Atrichum undulatum				2
Betula pubescens	Downy Birch	2	2	3
Blechnum spicant	Hard Fern	4	2	1
Brachypodium sylvaticum	False Brome		3	2
Calamagrostis epigejos	Wood Small Reed		2	
Calluna vulgaris	Ling	2	2	
Calypogeia fissa				2
Campylopus pyriformis		3		3
Cardamine flexuosa	Wavy Bitter-cress			3
Carex laevigata	Smooth Stalked Sedge	1	2	
Carex pendula	Pendulous Sedge	2	3	3
Carex pilulifera	Pill Sedge	2	2	1
Carex remota	Remote Sedge	3	2	2
Carex sylvatica	Wood Sedge	1	2	2
Castanea sativa	Sweet Chestnut	4		9
Ceratocapnos claviculata	Climbing Corydalis			2
Chamaerion angustifolium	Rosebay Willowherb		1	
Chrysosplenium oppositifolium	Opposite-leaved Golden-saxifrage		3	4
Circaea lutetiana	Enchanter's Nightshade	2	1	2
Cirsium palustre	Marsh Thistle		1	2
Cirsium vulgaris	Spear Thistle			1
Corylus avellana	Hazel		1	1
Crataegus monogyna	Hawthorn		2	1
Deschampsia cesptiosa	Tufted Hair-grass		2	2
Deschampsia flexuosa	Wavy Hair-grass		2	3
Dicranella heteromalla		3		
Dicranum scoparium		2	1	2
Digitalis purpurea	Foxglove	2	1	2
Dryopteris dilatata	Broad Buckler-fern			6
Dryopteris affinis agg	Scaly Male Fern	2	2	2
Dryopteris carthusiana	Narrow Buckler-fern			1
Broad Buckler-fern	Dryopteris filix-mas	5	3	5

Elymus caninus	Bearded Couch		2	
Epilobium agg	Willowherb species	2	1	2
Equisetum sylvaticum	Wood Horsetail		1	
Equisetum telmateia	Great Horsetail		3	8
Eurhynchium striatum		2	3	3
Fagus sylvatica	Beech	1	1	2
Festuca gigantea	Giant Fescue		1	1
Fraxinus excelsior	Ash		2	3
Galeopsis tatrahit agg	Common Hemp-nettle			2
Galium aparine	Cleavers			2
Galium palustre	Marsh Bedstraw		2	2
Galium saxatile	Heath Bedstraw		2	2
Geranium robertianum	Herb Robert	3	2	2
Geum urbanum	Wood Avens			2
Glyceria fluitans	Floating Sweet-grass	3	3	
Hedera helix	Ivy		1	2
Holcus lanatus	Yorkshire Fog	2	4	4
Holcus mollis	Creeping Soft-grass	2	4	4
Hookeria lucens				2
Hyacinthoides non-scripta	Bluebell			4
Hypericum pulchrum	Slender St John's-wort		1	3
Hypericum tetrapterum	Square Stalked St John's-wort		1	
Hypnum cupressiforme / jutlandicum		5	4	5
Hypnum jutlandicum				4
Ilex aquifolium	Holly	2	2	3
Juncus effusus	Soft Rush	3	2	3
Kindbergia praelonga		4	3	4
Lamiastrum galeobdolon	Yellow Archangel			2
Lapsana communis	Nipplewort			2
Larix species	Larch species			5
Lonicera periclymenum	Honeysuckle		2	3
Lophocolea bidentata		2	2	2
Lotus pedunculatus	Marsh Bird's-foot-trefoil		1	
Luzula pilosa	Hairy Wood-rush	2	2	2
Luzula sylvatica	Greater Wood-rush			5
Lysimachia nemorum	Yellow Pimpernel	1	2	2
Mentha aquatica	Water Mint		2	4
Mnium hornum		2	2	2
Oxalis acetosella	Wood Sorrel	3	3	3
Pellia epiphylla				3
Phalaris arundinacea	Reed Canary-grass			2
Picea abies	Norway Spruce			4
Picea sitchensis	Sitka Spruce	3	5	4
Plagiochila asplenioides			1	
Plagiothecium undulatum		2	2	2
Pleurozium schreberi				2
Polytrichastrum formosum		3	3	2

Potentilla anglica	Trailing Tormentil		2	1
Prunella vulgaris	Selfheal	1		2
Pseudoscleropodium purum		3		3
Pseudotsuga menziesii	Douglas Fir	7	6	6
Pteridium aquilinum	Bracken	5	4	6
Quercus robur	Pedunculate Oak		1	5
Ranunculus repens	Creeping Buttercup		2	2
Rhododendron ponticum	Rhododendron	2		1
Rhytidiadelphus loreus		3	3	4
Rhytidiadelphus squarrosus			3	
Rhytidiadelphus triquetris				2
Rubus fruticosus agg	Bramble	6	7	5
Rubus idaeus	Wild Raspberry	2	2	3
Rumex acetosa	Common Sorrel			1
Rumex acetosella	Sheep's Sorrel	2		1
Rumex sanguineus	Wood Dock		2	2
Salix cinerea	Grey Willow			3
Scrophularia auriculata	Water Figwort		1	
Scrophularia nodosa	Common Figwort		2	
Silene dioica	Red Campion	1		2
Solanum dulcamara	Woody Nightshade			1
Sorbus aucuparia	Rowan	1	2	1
Sphagnum squarrosum			3	2
Stachys sylvatica	Hedge Woundwort		1	2
Stellaria holostea	Greater Stitchwort		1	3
Stellaria uliginosa	Bog Stitchwort		2	
Taxus baccata			1	
Teucrium scorodonia	Wood Sage		2	
Thuidium tamariscinum		3	5	4
Thuja plicata	Western Red Cedar	3	1	2
Tsuga heterophylla	Western Hemlock	4	2	5
Ulex europaeus	Common Gorse			1
Ulex gallii	Western Gorse		1	
Urtica dioica	Stinging Nettle	1	2	4
Vaccinium myrtillus	Bilberry		1	
Veronica montana	Wood Speedwell		2	2
Viola riviniana	Common Dog Violet		2	2

Appendix 3- Recorded moth species with abundance per stand stage.

ABH number	Scientific Name	Common Name	Stage 1	Stage 2	Stage 3
3.001	*Triodia sylvina*	Orange Swift			1
3.004	*Phymatopus hecta*	Gold Swift		1	1
12.012	*Triaxomera parasitella*			1	
12.033	*Tinea trinotella*		1		
16.001	*Yponomeuta evonymella*	Bird-cherry Ermine	6	5	14
16.005	*Yponomeuta rorrella*	Willow Ermine			1

16.020	*Paraswammerdamia nebulella*		1		
17.003	*Ypsolopha dentella*	Honeysuckle Moth		1	
17.010	*Ypsolopha parenthesella*		1	2	2
18.001	*Plutella xylostella*	Diamond-back Moth		1	3
18.003	*Plutella porrectella*			1	
19.010	*Digitivalva pulicariae*				1
20.011	*Argyresthia brockeella*		1		1
20.012	*Argyresthia goedartella*		3		3
28.010	*Hofmannophila pseudospretella*	Brown House-moth	1		
28.014	*Crassa unitella*		2		2
31.001	*Carcina quercana*		4	4	
32.031	*Agonopterix alstromeriana*			1	
32.036	*Depressaria radiella*	Parsnip Moth		1	
35.010	*Aproaerema anthyllidella*		1	1	2
35.028	*Brachmia blandella*		7		
35.031	*Helcystogramma rufescens*		2	2	
35.064	*Argolamprotes micella*		4	1	3
41.002	*Blastobasis adustella*		59	24	136
42.002	*Stathmopoda pedella*				1
45.043	*Adaina microdactyla*	Hemp-agrimony Plume		2	
49.001	*Olindia schumacherana*				1
49.004	*Ditula angustiorana*	Red-barred Tortrix		1	2
49.005	*Epagoge grotiana*		2	6	1
49.013	*Archips podana*	Large Fruit-tree Tortrix		1	2
49.021	*Ptycholomoides aeriferana*				1
49.023	*Pandemis cinnamomeana*		2	1	3
49.025	*Pandemis cerasana*			1	
49.026	*Pandemis heparana*		1	2	
49.029	*Lozotaenia forsterana*			1	2
49.038	*Clepsis consimilana*			1	1
49.047	*Eana incanana*		3		
49.062	*Acleris forsskaleana*				1
49.066	*Acleris laterana*		2		2
49.071	*Acleris emargana*			1	
49.091	*Pseudargyrotoza conwagana*		2		
49.104	*Gynnidomorpha luridana*			1	
49.109	*Agapeta hamana*		1	1	1
49.110	*Agapeta zoegana*				1
49.128	*Aethes rubigana*			1	
49.133	*Cochylis nana*		1		
49.151	*Apotomis capreana*			1	
49.157	*Hedya pruniana*			1	
49.166	*Celypha lacunana*		5	21	11
49.194	*Bactra lancealana*			3	3
49.214	*Ancylis badiana*			2	
49.223	*Rhopobota naevana*	Holly Tortrix	6		2

49.238	*Epinotia cruciana*	Willow Tortrix		1	
49.259	*Zeiraphera ratzeburgiana*		1	8	2
49.265	*Eucosma cana*		1	2	1
49.269	*Eucosma campoliliana*		1		
49.279	*Gypsonoma dealbana*		1	1	4
49.294	*Notocelia uddmanniana*	Bramble Shoot Moth	15	16	28
49.338	*Cydia pomonella*	Codling Moth	1		
49.341	*Cydia splendana*		2	2	10
49.367	*Pammene fasciana*				1
49.376	*Pammene aurita*		1		
62.001	*Aphomia sociella*	Bee Moth	8		4
62.025	*Dioryctria sylvestrella*				1
62.028	*Dioryctria abietella*		2		
62.035	*Acrobasis advenella*			1	
62.047	*Assara terebrella*		1		
62.058	*Phycitodes binaevella*				1
63.006	*Pyrausta aurata*		1		
63.007	*Pyrausta purpuralis*		1	3	2
63.017	*Anania lancealis*		5	36	3
63.018	*Anania coronata*		1	1	2
63.022	*Anania crocealis*			6	1
63.025	*Anania hortulata*	Small Magpie	3	10	5
63.031	*Udea ferrugalis*	Rusty-dot Pearl	1		
63.033	*Udea lutealis*			1	
63.034	*Udea prunalis*		10	5	13
63.037	*Udea olivalis*		4	5	5
63.038	*Pleuroptya ruralis*	Mother of Pearl	65	116	117
63.060	*Evergestis pallidata*		12	31	47
63.063	*Scoparia basistrigalis*			4	4
63.064	*Scoparia ambigualis*		47	112	53
63.065	*Scoparia ancipitella*		41	34	33
63.066	*Scoparia pyralella*		2		
63.067	*Eudonia lacustrata*		107	131	131
63.072	*Eudonia delunella*		13	6	10
63.073	*Eudonia truncicolella*		1	1	3
63.074	*Eudonia mercurella*		145	181	100
63.077	*Chilo phragmitella*				1
63.079	*Calamotropha paludella*			2	
63.080	*Chrysoteuchia culmella*	Garden Grass-veneer	13	24	39
63.089	*Agriphila tristella*		11	34	13
63.092	*Agriphila selasella*		1	2	
63.093	*Agriphila straminella*		218	267	411
63.099	*Catoptria pinella*		7	1	
63.102	*Catoptria falsella*				1
63.114	*Elophila nymphaeata*	Brown China-mark		3	1
63.117	*Parapoynx stratiotata*	Ringed China-mark	1		
65.001	*Falcaria lacertinaria*	Scalloped Hook-tip	15	12	3

65.002	*Watsonalla binaria*	Oak Hook-tip	1		1
65.003	*Watsonalla cultraria*	Barred Hook-tip		1	1
65.005	*Drepana falcataria*	Pebble Hook-tip	3	1	2
65.007	*Cilix glaucata*	Chinese Character		2	
65.008	*Thyatira batis*	Peach Blossom	10	9	15
65.009	*Habrosyne pyritoides*	Buff Arches	20	48	51
65.013	*Ochropacha duplaris*	Common Lutestring	7	10	3
66.010	*Euthrix potatoria*	Drinker	85	256	90
69.003	*Laothoe populi*	Poplar Hawk-moth	9	15	8
69.006	*Sphinx ligustri*	Privet Hawk-moth			1
69.007	*Sphinx pinastri*	Pine Hawk-moth	3	10	4
69.016	*Deilephila elpenor*	Elephant Hawk-moth	18	15	8
70.011	*Idaea dimidiata*	Single-dotted Wave	4	14	16
70.013	*Idaea biselata*	Small Fan-footed Wave	53	101	78
70.016	*Idaea aversata*	Riband Wave	69	61	61
70.029	*Timandra comae*	Blood-Vein	1	3	
70.031	*Cyclophora annularia*	Mocha		2	2
70.036	*Cyclophora punctaria*	Maiden's Blush		1	2
70.037	*Cyclophora linearia*	Clay Triple-lines	1	2	
70.045	*Scotopteryx chenopodiata*	Shaded Broad-bar		2	1
70.049	*Xanthorhoe fluctuata*	Garden Carpet		1	
70.051	*Xanthorhoe spadicearia*	Red Twin-spot Carpet	5	10	6
70.053	*Xanthorhoe designata*	Flame Carpet	1		
70.054	*Xanthorhoe montanata*	Silver-ground Carpet		1	
70.059	*Camptogramma bilineata*	Yellow Shell	2	2	1
70.061	*Epirrhoe alternata*	Common Carpet	7	30	9
70.064	*Euphyia biangulata*	Cloaked Carpet		1	6
70.065	*Euphyia unangulata*	Sharp-angled Carpet			1
70.068	*Mesoleuca albicillata*	Beautiful Carpet	1	1	
70.074	*Hydriomena furcata*	July Highflier	19	79	23
70.079	*Thera britannica*	Spruce Carpet	15	21	4
70.081	*Thera obeliscata*	Grey Pine Carpet	4	10	3
70.087	*Cosmorhoe ocellata*	Purple Bar	1		
70.089	*Eulithis prunata*	Phoenix	18	7	20
70.093	*Gandaritis pyraliata*	Barred Straw		1	
70.094	*Ecliptopera silaceata*	Small Phoenix	26	94	49
70.097	*Dysstroma truncata*	Common Marbled Carpet		1	
70.098	*Dysstroma citrata*	Dark Marbled Carpet	3	9	5
70.100	*Colostygia pectinataria*	Green Carpet	1		
70.104	*Lampropteryx otregiata*	Devon Carpet			1
70.112	*Euchoeca nebulata*	Dingy Shell	5	3	19
70.113	*Hydrelia sylvata*	Waved Carpet	4	5	12
70.114	*Hydrelia flammeolaria*	Small Yellow Wave	1	7	1
70.121	*Hydria undulata*	Scallop Shell	2	2	
70.123	*Triphosa dubitata*	Tissue	1	3	
70.127	*Horisme tersata*	The Fern		1	

70.128	*Melanthia procellata*	Pretty Chalk Carpet	1		
70.131	*Mesotype didymata*	Twin-spot Carpet			1
70.132	*Perizoma affinitata*	Rivulet	1	3	
70.133	*Perizoma alchemillata*	Small Rivulet	1	4	2
70.138	*Perizoma flavofasciata*	Sandy Carpet	4		
70.141	*Gymnoscelis rufifasciata*	Double-striped Pug		2	1
70.142	*Chloroclystis v-ata*	V-Pug	3	10	8
70.147	*Eupithecia tenuiata*	Slender Pug	1		1
70.151	*Eupithecia pulchellata*	Foxglove Pug	4	4	6
70.207	*Lomaspilis marginata*	Clouded Border	30	37	21
70.208	*Ligdia adustata*	Scorched Carpet			1
70.212	*Macaria alternata*	Sharp-angled Peacock			2
70.214	*Macaria liturata*	Tawny-barred Angle	118	42	41
70.222	*Petrophora chlorosata*	Brown Silver-line			1
70.226	*Opisthograptis luteolata*	Brimstone Moth	2	3	3
70.227	*Epione repandaria*	Bordered Beauty		2	2
70.233	*Ennomos quercinaria*	August Thorn			1
70.237	*Selenia dentaria*	Early Thorn	28	32	45
70.239	*Selenia tetralunaria*	Purple Thorn	5	7	17
70.241	*Crocallis elinguaria*	Scalloped Oak	20	23	19
70.243	*Ourapteryx sambucaria*	Swallow-tailed Moth		3	7
70.252	*Biston betularia*	Peppered Moth	2	2	
70.258	*Peribatodes rhomboidaria*	Willow Beauty	21	35	30
70.264	*Deileptenia ribeata*	Satin Beauty	44	48	126
70.265	*Alcis repandata*	Mottled Beauty	36	35	46
70.271	*Ectropis sp.*	Engrailed	92	74	223
70.277	*Cabera pusaria*	Common White Wave	14	16	18
70.278	*Cabera exanthemata*	Common Wave	5	18	8
70.280	*Lomographa temerata*	Clouded Silver		1	
70.283	*Campaea margaritaria*	Light Emerald	14	10	30
70.284	*Hylaea fasciaria*	Barred Red	10	2	1
70.288	*Cleorodes lichenaria*	Brussels Lace	1	3	
70.299	*Geometra papilionaria*	Large Emerald	9	4	16
70.305	*Hemithea aestivaria*	Common Emerald	1	5	1
71.009	*Stauropus fagi*	Lobster Moth	2	2	2
71.012	*Notodonta dromedarius*	Iron Prominent	2	1	2
71.013	*Notodonta ziczac*	Pebble Prominent	3	2	1
71.018	*Pheosia gnoma*	Lesser Swallow Prominent	3		
71.020	*Pterostoma palpina*	Pale Prominent	2	2	3
71.021	*Ptilodon capucina*	Coxcomb Prominent	29	12	34
71.025	*Phalera bucephala*	Buff-tip	25	24	25
72.001	*Scoliopteryx libatrix*	Herald	1	1	
72.002	*Rivula sericealis*	Straw Dot	2	35	5
72.003	*Hypena proboscidalis*	Snout	5	9	16
72.007	*Hypena crassalis*	Beautiful Snout	1		1
72.010	*Lymantria monacha*	Black Arches	43	71	65

72.013	*Euproctis similis*	Yellow-tail		1	2
72.019	*Spilosoma lutea*	Buff Ermine	10	25	19
72.024	*Phragmatobia fuliginosa*	Ruby Tiger	9	19	19
72.026	*Arctia caja*	Garden Tiger		1	
72.035	*Miltochrista miniata*	Rosy Footman	118	136	154
72.036	*Nudaria mundana*	Muslin Footman			1
72.041	*Lithosia quadra*	Four-spotted Footman	14	3	3
72.043	*Eilema depressa*	Buff Footman	155	292	158
72.044	*Eilema griseola*	Dingy Footman	58	64	131
72.045	*Eilema lurideola*	Common Footman	56	79	86
72.046	*Eilema complana*	Scarce Footman	8	6	2
72.053	*Herminia tarsipennalis*	Fan-foot	4	8	14
72.055	*Herminia grisealis*	Small Fan-foot	7	8	11
72.061	*Schrankia costaestrigalis*	Pinion-streaked Snout	17	30	23
72.063	*Lygephila pastinum*	Blackneck		1	1
72.069	*Laspeyria flexula*	Beautiful Hook-tip	10	24	8
73.001	*Abrostola tripartita*	Spectacle	2		
73.012	*Diachrysia chrysitis*	Burnished Brass		3	2
73.015	*Autographa gamma*	Silver Y		1	1
73.016	*Autographa pulchrina*	Beautiful Golden Y		1	
73.017	*Autographa jota*	Plain Golden Y	3	3	6
73.024	*Deltote pygarga*	Marbled White Spot	8	37	25
73.032	*Colocasia coryli*	Nut-tree Tussock	5	3	7
73.045	*Acronicta rumicis*	Knot Grass	9	3	
73.047	*Craniophora ligustri*	Coronet	4		2
73.062	*Amphipyra pyramidea*	Copper Underwing			1
73.063	*Amphipyra berbera*	Svensson's Copper Underwing	1	7	1
73.064	*Amphipyra tragopoginis*	Mouse Moth	4		2
73.114	*Euplexia lucipara*	Small Angle Shades	1	5	1
73.141	*Archanara dissoluta*	Brown-veined Wainscot		1	
73.144	*Denticucullus pygmina*	Small Wainscot	1	5	12
73.147	*Photedes minima*	Small Dotted Buff	4	2	6
73.160	*Apamea scolopacina*	Slender Brindle	7	27	7
73.162	*Apamea monoglypha*	Dark Arches	13	15	5
73.216	*Cosmia trapezina*	Dun-bar	14	21	9
73.261	*Polia nebulosa*	Grey Arches	1	2	
73.267	*Lacanobia oleracea*	Bright-line Brown-eye	1	1	1
73.291	*Mythimna pallens*	Common Wainscot		1	
73.293	*Mythimna impura*	Smoky Wainscot	21	23	15
73.298	*Mythimna ferrago*	Clay	1	3	1
73.317	*Agrotis exclamationis*	Heart and Dart	6		2
73.325	*Agrotis puta*	Shuttle-shaped Dart	1		1
73.327	*Agrotis ipsilon*	Dark Sword-grass	1	1	1
73.328	*Axylia putris*	Flame		4	2
73.329	*Ochropleura plecta*	Flame Shoulder	4	4	
73.332	*Diarsia brunnea*	Purple Clay	7	4	9

73.338	*Lycophotia porphyrea*	True Lover's Knot		1	
73.342	*Noctua pronuba*	Large Yellow Underwing	137	56	31
73.343	*Noctua fimbriata*	Broad-bordered Yellow Underwing	3		
73.345	*Noctua comes*	Lesser Yellow Underwing	15	2	2
73.346	*Noctua interjecta*	Least Yellow Underwing	4	2	
73.347	*Noctua janthina*	Langmaid's Yellow Underwing			1
73.348	*Noctua janthe*	Lesser Broad-bordered Yellow Underwing	12	12	10
73.357	*Xestia xanthographa*	Square-spot Rustic	1		
73.361	*Xestia triangulum*	Double Square-spot	3	4	12
74.002	*Meganola albula*	Kent Black Arches			2
74.009	*Nycteola revayana*	Oak Nycteoline	1		
	Acronicta sp.	Grey/Dark Dagger sp.	1	4	1
	Agonopterix heracliana sp.		1	3	1
	Cnephasia sp.		24	34	41
	Coleophora sp.			3	5
	Hoplodrina sp.	Uncertain/Rustic sp.	92	61	50
	Mesapamea sp.	Common/Lesser Common Rustic sp.	244	192	175
	Oegoconia quadripuncta sp.			1	
	Oligia sp.	Marbled Minor sp.	7	6	2
	Phyllonorycter sp.			1	
	Scoparia sp.		12	19	11
	Spilonota sp.			1	

Appendix 4- Recorded bat species with number of registrations per stand stage.

Scientific Name	**Common Name**	**Stage 1**	**Stage 2**	**Stage 3**
Barbastella barbastellus	Barbastelle	84	4	155
Eptesicus serotinus	Serotine	9	5	51
Myotis daubentonii	Daubenton's bat	27	6	30
Myotis mystacinus/brandtii	Whiskered/Brandt's bat	28	24	560
Myotis nattereri	Natterer's bat	25	25	32
Nyctalus leisleri	Leisler's bat	1	1	2
Nyctalus noctula	Common noctule	178	81	323
Pipistrellus nathusii	Nathusius' pipistrelle			2
Pipistrellus pipistrellus	Common pipistrelle	68	902	1516
Pipistrellus pygmaeus	Soprano pipistrelle	402	260	931
Plecotus auritus	Brown long-eared bat	55	29	114
Rhinolophus ferrumequinum	Greater horseshoe bat		3	1
Rhinolophus hipposideros	Lesser horseshoe bat	1	4	1

Appendix 5- Recorded bird species with number of registrations per stand stage.

Scientific Name	Common Name	Stage 2	Stage 3
Accipiter gentilis	Goshawk	2	4
Aegithalos caudatus	Long-tailed Tit		2
Carduelis spinus	Siskin	3	1
Certhia familiaris	Treecreeper	2	15
Columba oenas	Stock Dove	1	1
Columba palumbus	Woodpigeon	10	14
Dendrocopos major	Great Spotted Woodpecker	1	3
Erithacus rubecula	Robin	9	23
Fringilla coelebs	Chaffinch	9	11
Garrulus glandarius	Jay	1	4
Muscicapa striata	Spotted Flycatcher	1	2
Parus ater	Coal Tit	9	16
Parus caeruleus	Blue Tit	1	8
Parus major	Great Tit	1	7
Parus palustris	Marsh Tit		6
Phylloscopus collybita	Chiffchaff	5	21
Phylloscopus trochilus	Willow Warbler	2	
Prunella modularis	Dunnock	1	6
Pyrrhula pyrrhula	Bullfinch		1
Regulus ignicapilla	Firecrest	1	8
Regulus regulus	Goldcrest	15	15
Sitta europaea	Nuthatch		1
Sylvia atricapilla	Blackcap	7	17
Troglodytes troglodytes	Wren	41	74
Turdus merula	Blackbird	2	13
Turdus philomelos	Song Thrush	1	5

Appendix 6- Differences in habitat structural variables amongst the stand types in 2019 and 2021. Significant p values are highlighted in bold. * refers to significant results with a p value <0.05, ** highly significant <0.01, and *** very highly significant <0.001.

Habitat Variable	Stand Comparison	Estimate	Standard Error	P value
2019				
Average DBH	2 - 1	-0.305	0.147	0.260
Average DBH	3 - 1	-0.018	0.145	1.000
Average DBH	3 - 2	0.287	0.115	0.101
Basal area	2 - 1	-0.273	0.116	0.153
Basal area	3 - 1	-0.543	0.123	**<0.001*** **
Basal area	3 - 2	-0.27	0.107	0.103
Canopy openness	2 - 1	-0.17	0.415	0.998
Canopy openness	3 - 1	0.526	0.416	0.775
Canopy openness	3 - 2	0.696	0.338	0.275
Complexity score	2 - 1	-0.088	0.067	0.742
Complexity score	3 - 1	0.16	0.067	0.137
Complexity score	3 - 2	0.248	0.054	**<0.001*** **
Deadwood snags	2 - 1	-0.097	0.544	1.000
Deadwood snags	3 - 1	-0.433	0.545	0.962
Deadwood snags	3 - 2	-0.336	0.443	0.969
Fallen deadwood	2 - 1	0.666	0.975	0.981
Fallen deadwood	3 - 1	0.595	0.983	0.989
Fallen deadwood	3 - 2	-0.071	0.805	1.000
Number of stems	2 - 1	0.68	0.239	**0.039***
Number of stems	3 - 1	-0.362	0.246	0.622
Number of stems	3 - 2	-1.042	0.189	**<0.001*** **
Number of tree species	2 - 1	-0.896	1.074	0.951
Number of tree species	3 - 1	1.718	1.054	0.526
Number of tree species	3 - 2	2.615	0.83	**0.016***
Percentage broadleaf canopy	2 - 1	-0.343	0.601	0.989
Percentage broadleaf canopy	3 - 1	1.169	0.546	0.202
Percentage broadleaf canopy	3 - 2	1.512	0.415	**0.002****
2021				
Average DBH	2 - 1	-0.28	0.137	0.272
Average DBH	3 - 1	0.077	0.128	0.988
Average DBH	3 - 2	0.356	0.094	**0.002****
Basal area	2 - 1	-0.163	0.103	0.572
Basal area	3 - 1	-0.51	0.099	**<0.001*** **
Basal area	3 - 2	-0.347	0.078	**<0.001*** **
Canopy openness	2 - 1	0.283	0.375	0.969
Canopy openness	3 - 1	0.514	0.353	0.655
Canopy openness	3 - 2	0.231	0.266	0.944

Complexity score	2 - 1	-0.083	0.06	0.709
Complexity score	3 - 1	0.153	0.057	0.064
Complexity score	3 - 2	0.236	0.043	**<0.001*** **
Deadwood snags	2 - 1	-0.008	0.491	1.000
Deadwood snags	3 - 1	0.469	0.462	0.897
Deadwood snags	3 - 2	0.477	0.348	0.711
Fallen deadwood	2 - 1	0.57	0.874	0.984
Fallen deadwood	3 - 1	1.628	0.824	0.322
Fallen deadwood	3 - 2	1.058	0.624	0.495
Number of stems	2 - 1	0.696	0.229	**0.021***
Number of stems	3 - 1	-0.045	0.215	1.000
Number of stems	3 - 2	-0.741	0.154	**<0.001*** **
Number of tree species	2 - 1	-0.111	1.001	1.000
Number of tree species	3 - 1	1.451	0.935	0.58
Number of tree species	3 - 2	1.562	0.689	0.174
Percentage broadleaf canopy	2 - 1	0.172	0.567	0.999
Percentage broadleaf canopy	3 - 1	1.597	0.533	**0.022***
Percentage broadleaf canopy	3 - 2	1.424	0.371	**0.001****

Appendix 7- Differences in taxonomic responses amongst the stand types. Significant p values are highlighted in bold. * refers to significant results with a p value <0.05, ** highly significant <0.01, and *** very highly significant <0.001.

Taxonomic Group (includes species and guilds)	**Stand Comparison**	**Estimate**	**Standard Error**	**P value**
Moths				
Total species richness	2 - 1	-0.154	0.089	0.194
	3 - 1	-0.181	0.084	0.079
	3 - 2	-0.028	0.065	0.905
Broadleaved species richness	2 - 1	-0.266	0.107	**0.034***
	3 - 1	-0.135	0.101	0.374
	3 - 2	0.131	0.084	0.258
Conifer species richness	2 - 1	-0.304	0.113	**0.020***
	3 - 1	-0.291	0.114	**0.029***
	3 - 2	0.013	0.106	0.992
Grassland species richness	2 - 1	-0.035	0.073	0.881
	3 - 1	-0.219	0.077	**0.012***
	3 - 2	-0.184	0.069	**0.020***
Woodland species richness	2 - 1	-0.147	0.089	0.222
	3 - 1	-0.158	0.085	0.148
	3 - 2	-0.01	0.066	0.986
Total abundance	2 - 1	-0.203	0.077	**0.024***
	3 - 1	-0.183	0.076	**0.042***
	3 - 2	0.019	0.067	0.956

Broadleaved abundance	2 - 1	-0.474	0.143	**0.003****
	3 - 1	-0.105	0.136	0.716
	3 - 2	0.368	0.111	**0.003****
Conifer abundance	2 - 1	-0.914	0.021	**<0.001*****
	3 - 1	-0.267	0.021	**<0.001*****
	3 - 2	0.646	0.03	**<0.001*****
Grassland abundance	2 - 1	0.056	0.141	0.916
	3 - 1	-0.094	0.135	0.763
	3 - 2	-0.15	0.109	0.352
Woodland abundance	2 - 1	-0.212	0.095	0.066
	3 - 1	-0.217	0.087	**0.032***
	3 - 2	-0.005	0.079	0.998
Species diversity	2 - 1	-0.246	0.057	**<0.001*****
	3 - 1	-0.286	0.058	**<0.001*****
	3 - 2	-0.04	0.05	0.700
Spiders				
Number of webs	2 - 1	-1.028	0.295	**0.001*****
	3 - 1	-0.255	0.273	0.618
	3 - 2	0.773	0.272	**0.012***
Bats				
Total species richness	2 - 1	-0.168	0.122	0.355
	3 - 1	-0.009	0.125	0.997
	3 - 2	0.159	0.114	0.348
Barbastelle Activity Rate	2 - 1	-1.039	0.741	0.334
	3 - 1	-0.297	0.513	0.829
	3 - 2	0.743	0.665	0.498
Brown Long-Eared Activity Rate	2 - 1	-0.291	0.284	0.562
	3 - 1	0.291	0.26	0.503
	3 - 2	0.581	0.265	0.072
Common Pipistrelle Activity Rate	2 - 1	0.584	0.663	0.648
	3 - 1	0.978	0.629	0.260
	3 - 2	0.395	0.449	0.648
Daubenton’s Activity Rate	2 - 1	-0.527	0.521	0.568
	3 - 1	-0.316	0.441	0.752
	3 - 2	0.211	0.538	0.918
Natterer’s Activity Rate	2 - 1	0.396	0.321	0.433
	3 - 1	0.287	0.342	0.678
	3 - 2	-0.109	0.32	0.938
Noctule Activity Rate	2 - 1	-0.165	0.279	0.824
	3 - 1	0.352	0.25	0.337
	3 - 2	0.517	0.246	0.090
Serotine Activity Rate	2 - 1	0.13	0.621	0.975
	3 - 1	0.45	0.41	0.508
	3 - 2	0.319	0.542	0.822
Soprano Pipistrelle Activity Rate	2 - 1	-0.484	0.695	0.762
	3 - 1	-0.071	0.655	0.993
	3 - 2	0.413	0.485	0.666

Whiskered/Brandt’s Activity Rate	2 - 1	-0.266	0.674	0.917
	3 - 1	0.814	0.626	0.392
	3 - 2	1.081	0.513	0.087
Birds				
Total species richness	3 - 2	0.215	0.177	0.225
Generalist species richness	3 - 2	0.534	0.183	**0.004****
Specialist species richness	3 - 2	0.451	0.192	**0.019***
Invertebrate species richness	3 - 2	0.36	0.174	**0.038***
Seed/fruit species richness	3 - 2	-0.294	0.372	0.429
Species diversity	3 - 2	0.293	0.173	0.091

Who we are

Butterfly Conservation is the UK charity dedicated to saving butterflies and moths.

Why butterflies and moths matter

Butterflies and moths are important parts of the ecosystem. They are beautiful and inspirational and people enjoy seeing them in their gardens and the countryside. They are sensitive to change and their fortunes help us assess the health of our environment. Two-thirds of butterfly and moth species are in decline. This is a warning that cannot be ignored.

What we do

Butterfly Conservation maintains and enhances landscapes for butterflies and moths. We provide advice to landowners and managers on how to conserve and restore habitats. We gather extensive butterfly and moth data and conduct research to provide the scientific evidence that underpins our work. We have an established record of reversing declines. We run programmes for more than 100 threatened species and are involved in conserving hundreds of sites and reserves. We rely on donations, membershi1 and grants to fund our work.

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