

Long-term exclosure of sheep-grazing from an ancient wood: Vegetation change after a sixty-year experiment

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Abstract

Question: An ancient woodland site with a long history of coppicing and heavy grazing was protected from domesticated stock in 1955. Results of a vegetation-monitoring experiment were subsequently published in 1983. This study followed up the original research to investigate whether observed trends were as predicted. These included a shift in tree species composition in favour of shade-tolerant species, beech (*Fagus sylvatica*) and rowan (*Sorbus aucuparia*), at the expense of light-demanding birch (*Betula* spp.) and oak (*Quercus petraea* agg.), and progress towards a typical woodland ground flora.

Location: Peak District National Park, United Kingdom.

Methods: The mixed oak–birch woodland was re-surveyed in 2011. Two enclosures (1955 and 1980s) and an unenclosed control area were investigated. Overstorey structure and composition was assessed by measuring canopy openness and the girths of all trees and saplings. Herb layer species composition was also recorded in 28 vegetation plots.

Results: We demonstrated a progressive decline in the number of mature oaks and birch in the old enclosure although they still regenerated successfully. Only a few individuals of beech and rowan appeared. Herb layer species composition differed between the subareas but since the 1980s, the temporal change in the old enclosure was negligible. The new enclosure followed a similar pattern in both canopy and herb layer as observed in the early years in the old enclosure. However, the control sub-area had no regeneration of woody species and limited ground flora.

Conclusions: After nearly 60 years, the replacement of light-demanding dominants by shade-tolerant trees was still limited, probably by low pH and stable light conditions. The findings are pertinent to the impacts of large herbivore grazing (domestic stock or wild) on woodland dynamics.

KEYWORDS

ecological succession, forest management, grazing intensity, herbaceous layer, long-term change, species diversity, temperate woodland, tree regeneration, vegetation monitoring

1 | INTRODUCTION

Many European landscapes have been shaped by impacts of grazing animals for millennia (Bakker and Londo, 1998), firstly by wild grazers and then by domestic stock. The impacts of large, grazing herbivores at landscape scale, of fluctuations between domestic and wild stock over time, and of protection of woods from grazing, are currently debated (e.g. Vera, 2000; Rotherham, 2013a; Plieninger et al., 2015). Relevance of this debate is further discussed in Appendix S1 of ESM.

Recent recognition of detrimental impacts of over-grazing by domestic stock on woodland regeneration led to conservation-oriented attempts to reduce stocking densities or completely eliminate grazing by larger herbivores from European temperate woodlands using fencing enclosures (e.g. Hester et al., 1996; Latham and Blackstock, 1998; Cooper and McCann, 2011; Newman et al., 2014). However, the roles of grazing herbivores in woodland dynamics remain contentious in conservation management (Pereira and Navarro, 2015).

Grazing impacts on tree regeneration vary with different tree life stages. Grazers may be vectors of seed dispersal and through soil disturbance create patches for seedling establishment. Seedling growth may be facilitated by reduced competition from ground vegetation. On the other hand, it may be reduced due to direct damage (Mitchell and Kirby, 1990; Hester et al., 1996; Perrin et al., 2006). Furthermore, different responses of tree species to herbivore impact have implications for woodland dynamics and exclusion of grazing may eventually lead to replacement of forest dominants. For example, in an enclosure experiment in oak-dominated woodland in North Wales, Linhart and Whelan (1980) observed increased regeneration of highly palatable and shade-tolerant sycamore (*Acer pseudoplatanus*) in fenced plots. Similarly, in a 20-year old enclosure in alder (*Alnus glutinosa*)-dominated wood in the same area, there was no alder regeneration but high densities of ash (*Fraxinus excelsior*) saplings were recorded (Latham and Blackstock, 1998).

Ground flora species composition is influenced by similar mechanisms leading to the increase in palatable species such as *Rubus fruticosus* and the decline of less-competitive, low-growing species (Latham and Blackstock, 1998; Perrin et al., 2011; Newman et al., 2014). Shifts in species composition are often accompanied by changes in species richness; frequently with an initial increase followed by decline as competitive species become dominant (Cooper and McCann, 2011; Perrin et al., 2011; Newman et al., 2014).

Yarncliff Wood, situated in the Peak District National Park, is an excellent example of semi-natural, South Pennine, oak-birch woodland (Clapham, 1969). The woodland is on rough boulder-strewn peri-glacial talus slopes and by the 1950s, was regarded as a characteristic presentation of such woodland with oak-dominated canopy, "naturally depauperate ground flora," and little regeneration of trees and shrubs. Surveys indicated that since at least 1852, there had been almost no tree or shrub regeneration (Pigott, 1983). In 1955, in order to investigate the significance of sheep-grazing on tree and shrub regeneration in the wood, an enclosure of 1.12 ha was erected around a part of the then open grazed woodland. One possibility considered was regeneration being blocked by extremely

unfavourable soil conditions and harsh climate. The experiment was one of the first of its kind, and therefore attracted the attention of local researchers who subsequently investigated aspects of woodland changes (Jarvis, 1960; Anderson, 1978). Following sheep exclusion the most detailed surveys up to the 1980s were led by Dr Donald Pigott. Details of the early research were described by Pigott (1983), and the major findings are summarised for the current study. In the first two years after sheep exclusion *Deschampsia flexuosa*, *Vaccinium vitis-idaea* and *Vaccinium myrtillus* quickly recovered. Within a year, *Deschampsia flexuosa* was outcompeted by *Vaccinium myrtillus* and *Pteridium aquilinum*. Other species, including woodland specialists such as *Luzula pilosa*, gradually started to appear. By 1981, there was successful recruitment of dominant trees, oak (*Quercus petraea* agg.) and birch (*Betula pendula*, *Betula pubescens* and hybrids) along with a few saplings of previously absent woody species, such as beech (*Fagus sylvatica*) and rowan (*Sorbus aucuparia*). Vegetation changes were accompanied by soil development, the humus layer becoming less compact, better structured and with enhanced moisture regime. Pigott (1983) concluded that absence of sheep-grazing was important in influencing both herb layer species composition and woody species recruitment and establishment. The present study aimed to determine whether the originally observed successional trends had continued along predicted pathways or had slowed, stopped, or changed direction. The specific focus was on tree regeneration and herb layer composition. An additional, adjacent area was enclosed in the early 1980s and surveyed to investigate whether the succession had been similar to that in the old enclosure. A small adjacent area remains unenclosed and allows observation of the still-grazed wood, albeit with reduced intensity since the 1980s.

Most research on animal enclosures focused on impacts of wild ungulates (Russell et al., 2001; Habeck and Schultz, 2015), and studies of domestic animals are rarer and often span under two decades (e.g. Linhart and Whelan, 1980; Latham and Blackstock, 1998; Cooper and McCann, 2011). In this paper, we evaluate the following hypotheses: (a) in the old enclosure protected for 56 years, light-demanding oak and birch will be gradually replaced by shade-tolerant beech and rowan; (b) ground flora composition will further develop towards shade-tolerant communities due to increased canopy shading and competition from regenerating trees; and (c) in the new (1980s) enclosure, changes in tree regeneration and ground flora will follow trajectories originally observed in the old (1955) enclosure. Preliminary results based on a subset of plots were published in Vild and Rotherham (2011).

2 | METHODS

2.1 | Study area

The study site is located in Yarncliff Wood (Padley Gorge; 53°18' N, 1°37' W) in the Peak District National Park, UK. In 1972, the area was designated a Site of Special Scientific Interest and

re-confirmed by the Nature Conservancy Council in 1986 (NCC, 1986). The ancient woodland grows in a narrow valley and is surrounded by moorland and young secondary birch-wood. The study site is located on the southeast-facing slope with elevation from 270 to 290 m a.s.l., on a bedrock of millstone grit with coarse sandstone often protruding above the soil surface as massive boulders. The soil is nutrient-poor with very low pH in the topsoil (3.1–3.7). The mean minimum January and maximum July temperatures are 1.9°C and 21.1°C, respectively, with mean annual rainfall of 835 mm (data obtained from nearby Sheffield [131 m a.s.l.] covering 1981 to 2010 [https://www.metoffice.gov.uk]). Sheep-grazing in this area was very intensive. From the 1930s to the 1970s, the average sheep numbers increased fourfold from 0.7 sheep ha⁻¹ to 2.07 sheep ha⁻¹ (Anderson and Yalden, 1981). More details are presented in Appendix S2 of the ESM.

The stand represents the *Quercus* spp.–*Betula* spp.–*Deschampsia flexuosa* woodland community (W16) (Rodwell, 1991) with the tree layer dominated by oak and birch. There is an admixture of rowan, beech and rarely holly (*Ilex aquifolium*) and hazel (*Corylus avellana*). Prior to enclosure in 1955, beech and holly were absent from the study area (Pigott, 1983). The understorey is composed mostly of species such as *Vaccinium myrtillus*, *Deschampsia flexuosa*, *Pteridium aquilinum*, *Dryopteris dilatata* or *Agrostis capillaris*, all characteristic of low-nutrient, acidic soils. There are three subareas with different sheep-grazing histories within the study site (see details in Figure 1).

2.2 | Data collection

The basis for our fieldwork was the paper by Pigott (1983) who investigated the area in 1959, 1961, 1965, 1970 and 1981. Specifically, in 1981, a complete census of all tree individuals was conducted and a 0.34-ha plot, with 80% located inside the enclosure, was mapped with the positions of individual trees noted. Tree height and girth at 1.3 m were measured. The herb layer was surveyed in six plots of 1 m × 1.5 m in the same years as for the trees but with unknown location.

To assess changes in woodland structure, in 2011, tree distribution was recorded in a subarea (0.34 ha) which corresponded to the area surveyed in 1981. Eighty percent of the area was in the old (1955) enclosure whilst the rest was initially unenclosed but became part of the new enclosure a few years after the 1981 survey. For all stems over 60 cm of height, girth was measured as a proxy for tree age because other methods such as coring would have caused unnecessary damage. Thanks to the detailed marked location of individual tree shoots by Pigott (1983), it was possible to identify individuals which appeared since the last survey. Stems noted as trees or saplings were measured 1.3 m above ground whilst individuals recorded as seedlings and newly-found individuals were measured 0.3 m above ground. This survey did not include the unenclosed subarea because it was not covered by the 1981 survey. Moreover, field observations clearly showed the absence of regeneration from the

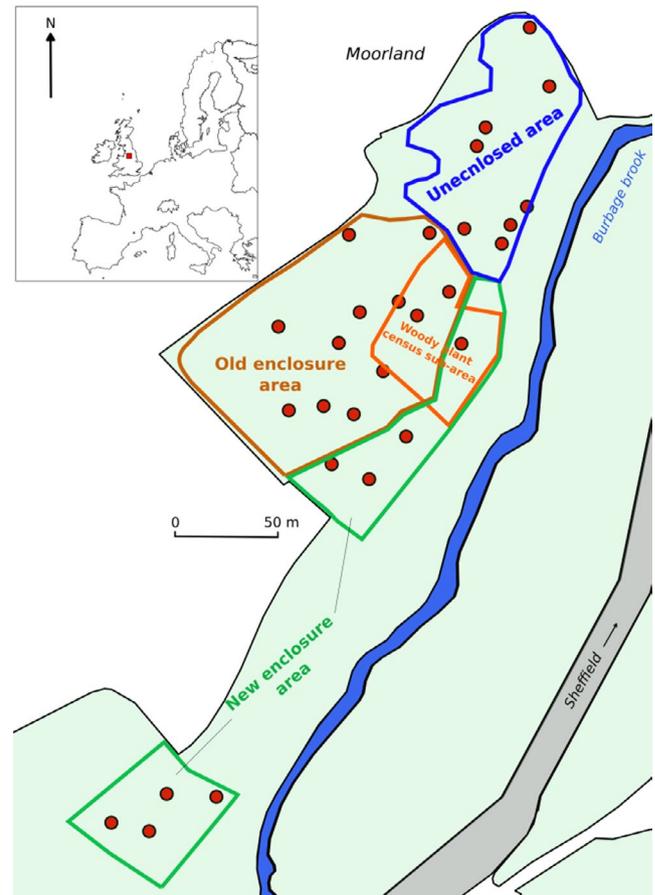


FIGURE 1 Map of the study area with study plots (red points). Three subareas with different grazing histories are marked. The grazed subarea (0.6 ha) is delimited by a blue line. The brown line delimits the subarea within the enclosure established in 1955 (1.1 ha) and the green line the subarea within the fence constructed in the early 1980s (0.5 ha). The orange line marks the subarea where a detailed woody plant survey was undertaken

unenclosed subarea with only old multi-stemmed oaks in the tree layer and scattered seedlings (Appendix S3 of the ESM).

Sampling of the herbaceous layer was done in June in 28 plots of 5 m × 5 m with plot coordinates randomly generated within specific subareas with similar environmental conditions: 12, nine, and seven plots were established in the old enclosure, new enclosure, and unenclosed control, respectively. The number of plots in each subarea was determined proportional to area and heterogeneity. All vascular plant species were recorded and cover abundance estimated using the nine-level Braun-Blanquet scale (Dengler et al., 2008). The nomenclature follows Stace (1997). Percentage cover of herb, shrub, and tree layers was estimated visually. Additionally, tree seedlings (below 60 cm height) were counted in each plot. Soil samples from four locations within a plot were taken from the upper 5 cm of the A horizon and pH was determined in distilled water from mixed samples. Understorey light availability was estimated using hemispherical photographs; four shots taken with a Nikon FC-E8 fish-eye lens 1 m above ground and analysed in the Gap Light Analyzer programme (Frazer et al., 1999).

2.3 | Data analyses

Differences in vegetation cover between plots in different subareas were assessed by the Kruskal–Wallis test followed by Dunn's post-hoc test for pairwise comparisons. *P* values were adjusted using Holm correction for multiple comparisons. Calculations were performed with R software, ver. 3.4.3 (R Core Team, 2017) with the *dunn.test* package (Dinno, 2017).

Permutational Multivariate Analysis of Variance (PERMANOVA; Anderson, 2001) was used to test differences in understorey species composition between subareas. We used a dissimilarity matrix calculated with the Bray–Curtis index from square-rooted percentage cover data first standardised by species maxima and then by sample totals (i.e. Wisconsin double standardisation). Significant results in PERMANOVA can indicate both directional changes and changes in species composition heterogeneity. It was intended to separate these components by testing for multivariate homogeneity of group dispersions (PERMDISP; Anderson et al., 2006) using the same dissimilarity matrix permutation settings as in PERMANOVA. These analyses were done with the *adonis* and *betadisp* functions from the *vegan* package (Oksanen et al., 2017). Species composition gradients were displayed by performing a non-metric multidimensional scaling (NMDS) on the same data matrix.

It was not possible to directly compare herb layer between 2011 and the historical survey data. The differences were therefore assessed from the species composition descriptions of Pigott (1983) and smaller studies in this area allowing sufficient comparison with the present state. Present contributions of individual species to driving differences in species composition between the subareas were identified by calculating species indicator values of all species using multi-level pattern analysis (De Cáceres et al., 2010) from the *indicspecies* package (De Cáceres and Legendre, 2009). The differences were compared by using the group-equalised phi coefficient on square-root-transformed cover data (Chytrý et al., 2002). Significance was tested through a randomisation test based on 999 permutations.

3 | RESULTS

3.1 | Tree regeneration

Oak was the most abundant tree in both old and new enclosures but the girth distributions differed substantially, with smaller girth classes less represented in the new enclosure (Figure 2). However, smaller girth classes of birch were more common in the new enclosure. Rowan and beech were represented in both enclosures with girths up to 80 cm found in the old enclosure but only up to 20 cm in the new.

3.2 | Understorey structure and soil pH

Neither the canopy openness nor estimated tree layer cover varied significantly between the subareas with different sheep-grazing

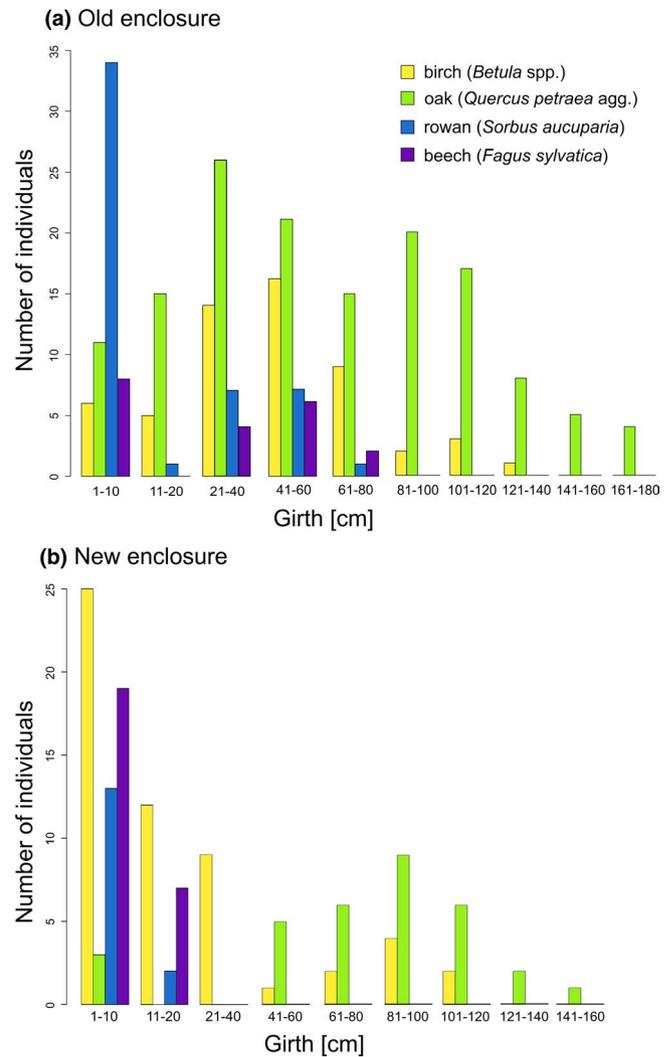


FIGURE 2 Distribution of girth values of stems of four most abundant tree species in the old (a) and new (b) enclosure. Birch and oak are light-demanding species whereas rowan and beech are able to tolerate shade. The unenclosed subarea was not included because regeneration was absent there

histories (Figure 3). Nevertheless, other vegetation layers showed marked differences (Figure 4); for example, with no shrub layer present in the unenclosed subarea, but about 15% average cover in the old enclosure, and around 8% in the new. The herb layer cover was also lowest in the unenclosed control and highest in the old enclosure. The moss layer had the opposite pattern, with highest cover in the unenclosed subarea. There were no significant differences in soil pH between subareas (Figure 3).

3.3 | Herbaceous layer species diversity and composition

The herbaceous species richness differed significantly (Kruskal–Wallis statistics: -3.64 ; $P = 0.001$) between subareas. It was highest in the new enclosure (14.3 species per plot on average) intermediate

in the unenclosed (12.6 species), and lowest in the old enclosure (10.6 species).

There were significant differences in species composition between subareas (PERMANOVA; $F = 7.82$, $P = 0.001$) and particular subarea pairs (PERMANOVA; unenclosed vs. new enclosure: $F = 8.55$, $P = 0.001$, unenclosed vs. old enclosure: $F = 11.10$, $P = 0.001$, new enclosure vs. old enclosure: $F = 4.63$, $P = 0.001$). However, some differences were in part attributable to species compositional heterogeneity between the subareas (PERMDISP; $F = 8.55$, $P = 0.001$). Only differences between the unenclosed control and the new enclosure were not attributed to compositional heterogeneity (PERMDISP; $F = 0.59$, $P = 0.434$) but there was a difference between the other pairs (PERMDISP; unenclosed vs. old enclosure: $F = 8.03$, $P = 0.001$, new enclosure vs. old enclosure: $F = 11.31$, $P = 0.001$).

Indicator species analysis and ordination analysis showed different species compositions in the subareas (Table 1, Figure 5), with the unenclosed control and the old enclosure at opposite ends of the species composition gradient. The unenclosed control

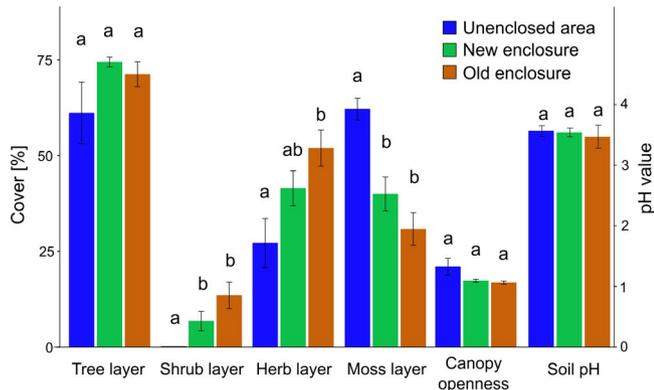


FIGURE 3 Comparison of estimated cover of vegetation layers, measured canopy openness and soil pH among subareas with a different history of sheep-grazing. The letters indicate differences between group pairs and bars show the standard error for each group

was characterised by light-demanding species common in open habitats and tolerant of disturbance (*Poa annua*, *Luzula campestris*, *Rumex acetosella*, *Agrostis capillaris* and *Galium saxatile*). On the other hand, species of woodlands and woodland clearings (*Corydalis claviculata*, *Carex pilulifera*, *Luzula pilosa*, *Oxalis acetosella*, *Rubus fruticosus* agg.), and tree seedlings or saplings, were typical of the enclosures. *Vaccinium myrtillus*, *Deschampsia flexuosa* and *Dryopteris dilatata* had the highest cover in the enclosures; *Vaccinium myrtillus* was dominant in the old enclosure, whilst *Deschampsia flexuosa* and *Dryopteris dilatata* had the highest cover in the new enclosure.

4 | DISCUSSION

This study documented vegetation succession in upland mixed birch–oak woodland free from domestic stock-grazing for almost 60 years. The work helped assess the natural development of vegetation at this site after enclosure in 1955 and followed up three decades of monitoring by Dr C.D. Pigott.

4.1 | Tree regeneration

Pigott (1983) predicted succession from light-demanding oak and birch to shade-tolerant beech and rowan. However, our results showed this successional change to be very slow, with only limited beech and rowan regeneration and persisting regeneration of oak and birch in the old enclosure. Oak seedlings probably benefitted from ambient low cover (< 10%) of *Rubus fruticosus* and *Pteridium aquilinum* which have been shown to inhibit tree regeneration in manipulation experiments (Humphrey and Swaine 1997; Petriřan et al., 2012).

Although the size structure of oak at the site suggests progressive decline in the old enclosure, its ability to continuously regenerate is striking. Whilst oak seedlings can establish in closed



FIGURE 4 The old enclosure (left) and the unenclosed part (right) with a fence separating these areas (middle). While the unenclosed area is characterised by heavily grazed turf with no shrub layer, abundant tree regeneration is visible in the protected area

Species name	Unenclosed	New enclosure	Old enclosure
<i>Poa annua</i>	86 (1.7 ± 0.4)	11 (0.2 ± 0.2)	0
<i>Rumex acetosella</i>	57 (1.4 ± 0.5)	0	0
<i>Luzula campestris</i>	71 (1.4 ± 0.4)	11 (0.2 ± 0.2)	8 (0.2 ± 0.2)
<i>Agrostis capillaris</i>	100 (11.6 ± 4.5)	100 (2.9 ± 0.7)	25 (0.4 ± 0.2)
<i>Galium saxatile</i>	100 (2.0 ± 0)	78 (1.6 ± 0.3)	17 (0.3 ± 0.2)
<i>Pteridium aquilinum</i>	86 (9.4 ± 5.3)	100 (2.1 ± 0.3)	50 (1.1 ± 0.4)
<i>Luzula pilosa</i>	57 (1.0 ± 0.4)	100 (2.1 ± 0.2)	50 (0.8 ± 0.3)
<i>Rubus fruticosus</i> agg.	0	67 (6.9 ± 4.0)	75 (3.0 ± 0.9)
<i>Vaccinium myrtillus</i>	100 (2.0 ± 0)	100 (11.9 ± 5.2)	100 (34.7 ± 2.8)
<i>Deschampsia flexuosa</i>	100 (3.6 ± 0.8)	100 (7.4 ± 1.5)	100 (2.9 ± 0.5)
<i>Dryopteris dilatata</i>	86 (1.6 ± 0.3)	100 (15.8 ± 5.6)	100 (10.5 ± 2.7)
<i>Corydalis claviculata</i>	86 (2.7 ± 1.0)	78 (1.7 ± 0.3)	92 (3.2 ± 0.7)
<i>Carex pilulifera</i>	0	44 (0.9 ± 0.4)	33 (0.4 ± 0.2)
<i>Oxalis acetosella</i>	0	44 (1.0 ± 0.4)	17 (0.4 ± 0.3)
<i>Carex caryophyllea</i>	29 (0.4 ± 0.2)	33 (0.4 ± 0.2)	0
<i>Anthoxanthum odoratum</i>	29 (0.7 ± 0.3)	22 (0.4 ± 0.3)	0
<i>Blechnum spicant</i>	14 (0.3 ± 0.3)	0	0
<i>Juncus conglomeratus</i>	14 (0.3 ± 0.3)	0	0
<i>Nardus stricta</i>	14 (0.1 ± 0.1)	0	0
<i>Solanum dulcamara</i>	14 (0.1 ± 0.1)	0	0
<i>Hypochaeris radicata</i>	0	11 (0.2 ± 0.2)	0
<i>Ajuga reptans</i>	0	0	8 (0.2 ± 0.2)
<i>Epilobium angustifolium</i>	0	0	8 (0.1 ± 0.1)
<i>Holcus lanatus</i>	0	0	8 (0.3 ± 0.3)
<i>Vaccinium vitis-idaea</i>	0	0	8 (0.2 ± 0.2)

TABLE 1 List of all herbaceous and sub-shrub species found in the study area

Note: Significant differences in the abundance in the subareas are presented in bold. Proportion of plot occurrences is given as percentages. Average cover values with standard error are given in brackets.

vegetation thanks to food storage in large cotyledons, due to high light requirements the species is often unable to reach the canopy layer of closed woodland (Jones, 1959; Linhart and Whelan, 1980; Perrin et al., 2006; Ligot et al., 2013). It is unclear why oak failed to regenerate in the new enclosure in spite of light conditions being similar to those in the old enclosure. Here, oak seedlings were numerous (Appendix S4 of the ESM) but only three exceeded 60 cm height. Seed predation by woodmice and voles (den Ouden et al., 2005) or stochastic events such as the irregularity of “mast years,” i.e. heavy crops of acorns (Jones, 1959), may have played a role. Also, in the absence of data on seedling age it may be that the seedlings established but simply grew very slowly.

Birch is also light-demanding and unable to produce established seedlings or reach maturity when light conditions are unfavourable (Mitchell, 1978; Rodwell, 1991; Atkinson, 1992). Unlike oak, birch has small seeds unable to penetrate the litter layer, currently much thicker in the enclosures than in the control. Shortly after establishment of the old enclosure, birch regenerated more successfully than oak but then declined quickly (Pigott, 1983). The abundant birch regeneration in the new enclosure was clearly a cohort established

soon after the fence was installed. This also explains why birch saplings are more abundant in the new enclosure than the old.

Compared to oak and birch, rowan has high shade tolerance and a high juvenile growth rate (Raspé et al., 2000; Myking et al., 2013). Rowan is a common component of this woodland type (Raspé et al., 2000) and whilst seedling recruitment can be higher in grazed plots (Hester et al., 1996), it benefits from protection from sheep-grazing (Linhart and Whelan, 1980; Latham and Blackstock, 1998). Its bird-dispersed seeds produce abundant saplings as observed in the study area. Interestingly, they were rare as larger size cohorts. This suggests either that spread was only a recent phenomenon or an unidentified factor had previously prevented sapling establishment.

Interestingly, even beech, abundant as a planted tree in the surrounding area and one of the most shade-tolerant European trees (Packham et al., 2012) struggles to establish in either enclosure. Studies from continental Europe suggest that in a woodland environment competition between oak and beech usually favours the latter (von Lüpke, 1998; Kuiters and Slim, 2002; Ligot et al., 2013; Annighöfer et al., 2015). At Yarncliff Wood there is only limited

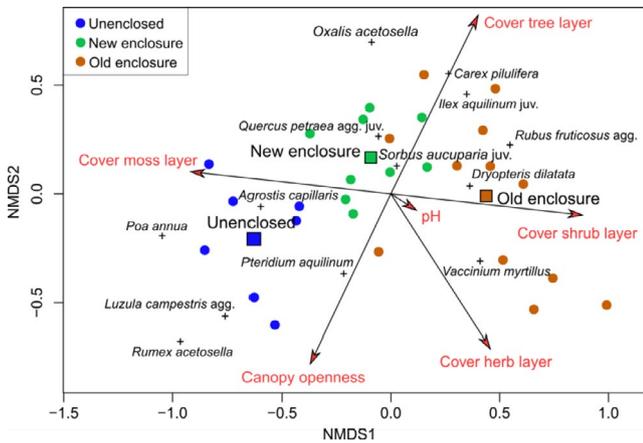


FIGURE 5 Ordination biplot of non-metric multidimensional scaling (NMDS) with plots and species. Circles and crosses show the position of plot and species, respectively. Squares indicate centroids of plot groups belonging to each of the subareas. Covers of vegetation layers, canopy openness and pH were passively projected to the NMDS diagram

evidence so far for the development trajectory predicted by Pigott (1983). Though beech is abundant, especially in the new enclosure, older specimens were rare. Native to mostly southeast England and probably historically ranging to the north but rather scarce there (Rackham, 2003), perhaps in this region beech is limited by late frosts and low summer temperatures (Packham et al., 2012). Poor soil can also disadvantage beech performance and mast years are strongly affected by weather so beech seedling recruitment can be sporadic. Nevertheless, gradual alleviation of soil conditions through litter accumulation in the ungrazed woodland (not measured) may lead to an eventual increase in beech dominance (Jones, 1959).

4.2 | Herbaceous vegetation

Herbaceous species composition is analogous to the composition of woody species in clear progression in the enclosures towards closed-canopy woodland and increased structural complexity. This is a common trend observed in other grazing exclosures in temperate woods and forests with formerly long grazing histories (Cooper and McCann, 2011; Perrin et al., 2011; Newman et al., 2014). However, species diversity was highest in the control subarea and lowest in the old enclosure due to the loss of numerous light-demanding species which is in line with data from other long-term enclosures (e.g. Latham and Blackstock, 1998; Cooper and McCann, 2011). The herb layer diversity in the new enclosure appears close to its expected peak with a mix of light-demanding species (e.g. *Agrostis capillaris* and *Galium saxatile*) and shade-tolerant woodland species. It is likely that over time, as in the old enclosure, increased shading from regenerating trees and shrubs and competition from other herbs will progressively reduce light-demanding species.

Soon after the experiment was established, there was a sharp increase in *Vaccinium myrtillus* cover and height (Pigott, 1983). In

her later survey, Anderson (1978) reported the average height of *Vaccinium myrtillus* to be 32 cm with a maximum of 44 cm in the old enclosure. The present study did not sample *Vaccinium myrtillus* heights but at some places field observations confirmed that it was higher than this in the old enclosure and covered approximately one third of the area. The high shade tolerance of *Vaccinium myrtillus* (Mäkipää, 1999) makes it an effective competitor with tree regeneration. It is assumed that the increased dominance of *Vaccinium myrtillus* combined with tree regeneration decreased woodland floor light levels and triggered declines in light-demanding species (Hester et al., 1991; Rodwell, 1991; Mäkipää, 1999), in spite of no differences in either tree layer cover or canopy openness.

Interestingly, in the old enclosure by 2011 the cover of highly palatable *Rubus fruticosus* had only reached a mean cover of 3%. Similar grazing exclosure studies elsewhere noted a rapid increase in *Rubus* cover (Linhart and Whelan, 1980; Kuiters and Slim, 2002; Harmer and Morgan, 2007). However, *Rubus* preference for open canopy (e.g. Balandier et al., 2013; Walter et al., 2016) may have slowed expansion at the study site. That *Rubus* cover in the old enclosure was only half that in the new enclosure suggests that it was limited by abundant, tall shoots of *Vaccinium myrtillus* in the former.

Vaccinium vitis-idaea increased rapidly in the late 1950s, but by 2011, it was recorded in only a single plot by the upper border of the woodland. *Deschampsia flexuosa* was not eliminated and remained frequent throughout. It occurred over most of the old enclosure but in low abundance, probably because of litter accumulation (Pigott, 1983). Of the species recorded in 1981, only *Epilobium angustifolium* had completely disappeared by 2011, suggesting that the community had reached a degree of relative stability by that time.

Some ferns are negatively affected by grazing exclusion (Perrin et al., 2011). *Pteridium aquilinum* together with *Vaccinium myrtillus* was reported to dominate the field layer since 1965 (Pigott, 1983), but it had decreased to only 2.1% in 2011. This was probably associated with increased herb layer competition. However, *Dryopteris dilatata* remained abundant, possibly due to its high shade tolerance (Rünk and Zobel, 2007).

Throughout other (unsampled) parts of the new enclosure, ongoing surveillance confirmed the presence of plants regarded as "indicators of ancient woodland" (Rotherham, 2011) and an obvious increase in flowering and seeding. These species included *Hyacinthoides non-scripta*, *Holcus mollis*, *Melampyrum pratense* and *Lonicera periclymenum*. Interestingly, none of these species was encountered in the core study areas sampled. This can be attributed to two causes: (a) soil conditions were not suitable for colonisation because of very low soil pH and "raw" mor humus (Rodwell, 1991); or (b) species were restricted due their slow colonisation rate (Bossuyt et al., 1999).

In contrast to the vascular plants, over the study period bryophytes declined in the enclosures. Still abundant in the open, unenclosed woodland and avoided by herbivores, they are able to exploit opportunities created by reduced competition from vascular plants (Mitchell and Kirby, 1990; Chollet et al., 2013; but see Latham and Blackstock, 1998).

4.3 | Methodological considerations

The value of the study lies in the exceptionally long study period covering 56 years. There are limitations in terms of wider interpretation of the findings. The area is relatively small and so the spatial context prevents truly independent replication and the plots are considered pseudo-replications. Whilst the subareas have comparable environmental conditions, the relationship between tree age and girth may be variable in sites with such extreme conditions (Anderson, 1978). Nevertheless, it is suggested that the described patterns are robust. A strong impact of previous long-term human usage in the Yarncliff Wood has shaped the current situation. The landscape before woodland enclosure and coppicing was grazed wood pasture, which was then enclosed and converted to coppicewood. This is therefore a strongly "eco-cultural" landscape (Rotherham, 2013b) and not "natural" per se. Predicting future developments needs to take account of the site history but also future fast-changing environmental conditions (Perring et al., 2018). Furthermore, it is important to keep in mind that enclosure experiments such as this one do not indicate how the vegetation would be without grazing but rather the process of recovery (Rooney and Waller, 2003).

5 | CONCLUSIONS

The differences between the enclosed (1955 and 1980s) and unenclosed (control) areas of the wood in terms of ground flora and tree or shrub regeneration have persisted for over 30 years. There has been a gradual change in tree species composition in the old enclosure, with declining dominance of light-demanding oak and birch, and increasing presence of shade-tolerant rowan and beech. However, the process was slower than predicted, especially considering the rapid initial change observed by Pigott (1983). Based on this description, it is concluded that changes in the ground flora of the old enclosure were negligible over the past 30 years, although there was a dramatic decline of one of the co-dominants, *Pteridium aquilinum*. Outside the enclosures tree recruitment was still almost totally prevented by sheep-grazing with the herb flora dominated by light-demanding and disturbance-tolerant species. Whilst this detailed study is from a single site, the findings are informative for the management of similar woodlands in Britain and Europe. In particular, they are relevant to current interests in the interactions between large grazing herbivores and woodland vegetation. The study provides evidence that the structure and vegetation composition in these woodlands has been largely shaped by historical grazing. Even though grazing intensity may be currently lower, it can effectively block ecological succession on sites with such harsh environmental conditions.

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AUTHOR CONTRIBUTIONS

IDR conceived the research idea; OV collected data and performed statistical analyses; both authors wrote the paper, discussed the results and commented on the manuscript.

DATA AVAILABILITY STATEMENT

Raw data are available at <https://doi.org/10.6084/m9.figshare.c.5058752>.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Appendix S1. Relevance to wider debates on woodland grazing

Appendix S2. Site history and grazing impact

Appendix S3. List of trees and shrubs

Appendix S4. Comparison of the number of tree seedlings

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