System Report: Wood Pasture and Parkland in the UK

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1 Context

The AGFORWARD research project (January 2014-December 2017), funded by the European Commission, is promoting agroforestry practices in Europe that will advance sustainable rural development. The project has four objectives:

1. to understand the context and extent of agroforestry in Europe,
2. to identify, develop and field-test innovations (through participatory research) to improve the benefits and viability of agroforestry systems in Europe,
3. to evaluate innovative agroforestry designs and practices at a field-, farm- and landscape scale, and
4. to promote the wider adoption of appropriate agroforestry systems in Europe through policy development and dissemination.

This report contributes to the second objective and specifically Deliverable 2.4 which aims to provide a "report describing the components, structure, ecosystem services, and economic value of selected high cultural and natural value agroforestry systems across Europe". The data included in this report will also inform the modelling activities being developed related to Objective 3.

This report provides some general background on wood pastures and parklands in the UK. It then focuses on some specific research to develop and apply a management tool for wood pastures. A substantial part of this report was completed by Alicia Bernal Lopez as part of her MSc thesis at Cranfield University in 2015 (Bernal Lopez 2015).

2 Wood pastures and parkland in the UK

In the UK, wood pastures and parklands are defined as open woodlands comprising scattered trees with a rich understory of grassland or heathland (Table 1). Maddock (2011) reports that they are often found in a mosaic landscape including extensive open and woody areas. They have often been created from long-term human interaction for example hunting grounds and wooded commons (Fay 2004).

Wood pasture and parkland systems occur throughout the UK. There are no reliable statistics on the extent of wood pasture and parkland. The UK Biodiversity Steering Group reports an area of 10,000 to 20,000 ha in "working condition" (Maddock 2011). Plieninger et al. (2015) using the European LUCAS dataset estimated that wood pasture covered about 3.3% of the surveyed area equivalent to about 800,000 ha. Wood pasture includes landscape-scale sites such the New Forest and Epping Forest in England through to smaller field-scale areas. Management practices in wood-pasture typically include grazing, often by cattle, and the pollarding and coppicing of trees to obtain charcoal and wood. Pollarding can also help produce micro-habitats for lichens and saproxylic species (Maddock 2011; Fay 2004).

Wood pastures are valued for their biodiversity with a particular focus on large invertebrates. Red listed species include the stag beetle (*Lucanus cervus*) that lives in crevices and the dead wood of veteran trees. Hence veteran trees are a key feature of most wood pastures and the loss of veteran trees is a particular concern. Hence efforts are sometimes made to clear the areas surrounding veteran trees to reduce competition.

Table 1. General description of wood pastures and parkland in the UK

General description of system	
Name of group	Wood Pasture and Parkland in the UK
Contact	Paul Burgess
Work-package	2: High Nature and Cultural Value Agroforestry
Geographical extent	Wood pastures and parklands exist throughout the UK including England (e.g. New Forest, Epping Forest), Wales (e.g. Dinefwr Park in Carmarthenshire), Scotland (e.g. Glen Finglas), and Northern Ireland (e.g. Crom's Parkland in County Fermanagh)
Estimated area	Maddock (2011) reported an area of 10,000 to 20,000 ha in working condition. Plieninger et al (2015) using the LUCAS dataset estimated a total wood pasture area in the UK of 799,800 ha, equivalent to 3.3% of the area.
Typical soil types	Wood pastures exist on most soil types that occur in the UK
Description	Wood pastures and parklands are open woodlands comprising scattered trees with a rich understory of grassland or heathland (Maddock 2011)
Tree species	UK wood pastures and parkland species include oak (*Quercus robur* and *petraea*), beech (*Fagus sylvatica*), alder (*Alnus glutinosa*), birch (*Betula* species), hazel (*Corylus avellana*) and sweet chestnut (*Castanea sativa*). Scots pine (*Pinus sylvestris*) is typical in parts of Scotland (Maddock, 2011)
Tree products	Fuelwood
Understorey species	Various including small trees and shrubs, grass, and herbaceous species like brambles
Understorey products	Ad-hoc non-commercial harvesting of blackberries and mushrooms.
Animal species	Conservation efforts in wood pastures tend to use cattle rather than sheep. Sheep, cattle and domesticated deer are used in parklands.
Animal products	Breeding livestock and meat products
Regulating services	Quine at al. (2012) highlight the regulating services provided by trees. For example trees can moderate the microclimate reducing the temperature fluctuations experienced by people, livestock, vegetation and soil fauna. Trees can sequester carbon primarily as wood biomass, help moderate the runoff of water and thereby contribute to flood control, and help reduce noise and atmospheric pollution.
Habitat services and biodiversity	Wood pastures and parklands are valued for their biodiversity including deer, butterflies, lichens, fungi, and saproxylic invertebrates such as spiders and beetles (Maddock 2011; Fay 2004). A mosaic of grassland and woodland habitats can also encourage wild pollinators such as bees (Mallinger et al. 2016). Wood pastures can favour birds such as woodpeckers and bats which can roost in crevices and hollows. Long established closed herds of deer and livestock are often associated with wood pastures (Maddock 2011).
Cultural services	Wood pastures and parklands in the UK provide a wide range of "cultural" or "information" services such as providing a pleasant environment to exercise, to walk a dog, education, and landscape appreciation (Agbenyega et al. 2009).

In some cases (Barwick & Powers 2000) the current number of ancient veteran tree has been considered too low and techniques can be applied to “age” young trees. Eventually even long-term trees such as oak will die and hence it is necessary to ensure the continuity of the tree population. Unfortunately it is not easy to determine what a sustainable population of trees might look like.

There is little literature about the economics of mature wood pasture and parklands in the UK. Dagley et al. (2014) provide a description about the costs of invisible fencing within a wood pasture. Estimates have been made of the revenue and costs associated with new silvopastoral systems. Bullock et al (1994) investigated the establishment of widely-spaced ash on grassland with lowland sheep. The analysis assumed that stocking levels could be maintained close to grassland without trees, but the tree establishment costs were only partly offset by future timber revenues and available subsidies. The driving argument for integrating trees with livestock system is therefore often based on additional benefits such as landscape enhancement, sport, shelter, reduced energy expenditure by livestock, or enhanced conservation (Bullock et al. 1994). Burgess et al. (2000) predicted the revenue and costs of establishing a parkland system near Bedford (over a 60 year rotation) relative to continued livestock production and conventional woodland. The parkland system was assumed to maintain similar returns as continued livestock production, but the cost of tree establishment and protection was not fully covered by grants and anticipated timber and fuelwood revenue. However it was a more cost effective way of establishing a landscape with trees than conventional woodland. There were also significant cultural benefits (Agbenyega et al. 2009).

Upson and Burgess (2014) described the results of an initial stakeholder meeting held in 2014 focused on wood pasture and parkland in the UK. The participants of this meeting highlighted the importance of wood pasture in terms of its biodiversity and provision of wildlife habitats. The resilience of wood pastures, their commercial availability and tools for grazing management were highlighted as areas of interest.

Later Upson and Burgess (2015) identified three possible objectives for future research on wood pastures within the UK component of the AGFORWARD project. These were: 1) to develop a web-based platform to allow farmers to interrogate GPS data from cattle collars, 2) perform a simple cost benefit analysis of the invisible fencing system, and 3) develop and apply a management tool for assessing the impact of grazing and tree management. The focus of the remainder of this report is on the third objective.

3 Models of wood pasture creation and maintenance

3.1 Wood pasture as a dynamic system

As indicated above this report focuses a management tool to evaluate the sustainability of wood pasture systems. There are competing arguments as to the “natural state” of woodlands in lowland Europe. Some like Birks (2005) argue than pollen analysis suggests that the key ecosystem in many parts of lowland Europe was “high forest”. By contrast Vera (2000) used pollen samples to argue that the original landscape was a mosaic of shifting grassland, scrub, closed woodland, and open canopy woodland (Figure 1). He argued that large herbivores would prevent the regeneration of trees (Grove phase) contributing to it openning up (Break-up phase), resulting in a open parkland (Park phase). The grassland would then be invaded by shrubs (Scrub phase) which would provide safe niches for the trees to regenerate and grow into a close-canopy forest again (Grove phase). In this system, tree regeneration can take place in parkland environments, whereas regeration in “high forest” ecosystems primarily occurs in gaps caused by tree death and wind-blow (Kirby 2003). Vera’s hypothesis is of interest because it suggests that the “natural state” of the ecosystem may be a mosaic of wood pasture and parkland systems. However Kirby (2003) explains that most wood pasture conservation does not seek to recreate “primeval” wood-pasture, but rather a cultural landscape from the last 3000 years.

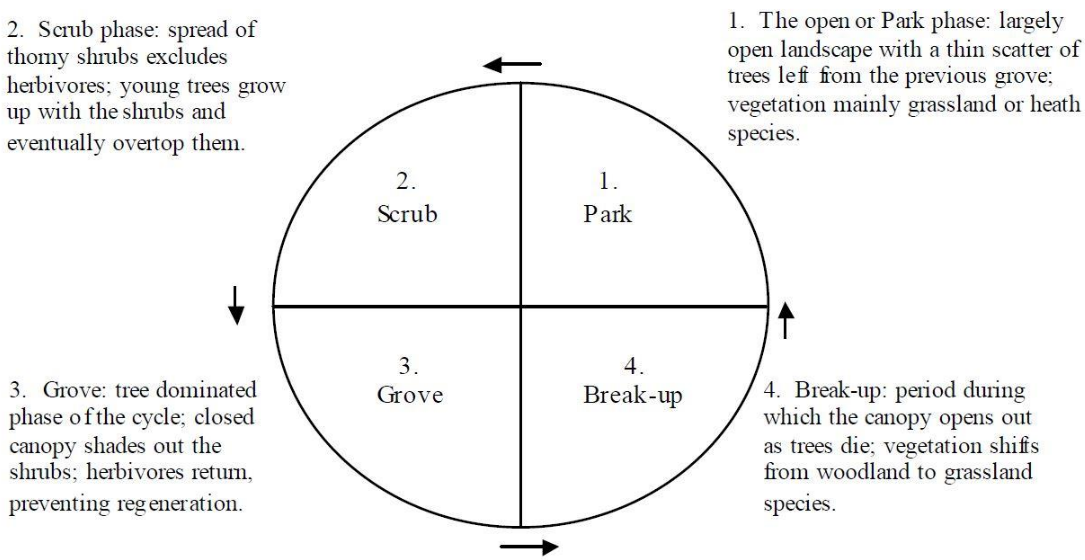


Figure 1. Vera's model, consisting of four phases of vegetation structure: open park, scrub, grove, and “break-up” stages. The “Break-up” stage was added to represent the transition from woodland grove back to open habitats (Kirby 2003).

Many of the wood pasture and parkland areas considered of value in the UK show evidence of grazing and pollarding. However during the last 200 years, the extent of pollarding and grazing has reduced. These changes mean that many wood-pastures have disappeared, transformed into dense-canopy woodland and scrubby habitats which are often assumed to be less diverse than wood pastures (J. Dagley, per communication, 18 June 2015). There is also a greater mortality of the veteran trees, partly attributed to mechanical breaks caused by the inability of the tree to support a large crown (Fay 2004).

In response to an increased interest in the ecological, cultural and recreational value of wood pasture (Maddock 2011), conservation organisations and other groups have developed restoration plans to preserve the ancient trees, open up the canopy and remove understorey trees. However the appropriate amount of canopy openness is uncertain. Kirby (2003) argues that wood pastures are more open than they used to be, citing that there are less young and intermediate aged trees than there should be according to the number of ancient trees present. It is clear that tree regeneration is necessary, yet the best way to achieve it is not known. A deeper understanding of how regeneration works on wood pastures and on the current state of the tree populations needs to be achieved to adapt the restoration plans to the real necessities of the sites.

3.2 **What is a sustainable tree population?**

The diagnosis of a "sustainable tree population" depends on balancing the "target ecosystem" for a specific location and the "current state and historical trajectory" (Hobbs and Norton 1996). The target ecosystem is effectively a mental picture of the desired ecosystem. The description of the "current state and historical trajectory" provides valuable information about the likely evolution of the ecosystem and about the elements that are influencing and constraining it.

A widely-used method to assess the tree population dynamics is the distribution of tree sizes (Condit et al. 1998). This is done by sorting the trees into cohorts according to, for example, their diameter or height, and counting the number of trees in each cohort. The selected tree size parameter is considered as a proxy of the tree age, and populations with a large number of trees in the young cohorts are considered to be more stable whilst those with few or no young individuals are considered as being in declining populations (Condit et al. 1998). Although the assumption that tree sizes are a useful proxy for tree age has been questioned (Silvertown and Charlesworth 2001; Saura et al. 2011), others consider that it still is a useful indicator of the regeneration process and conservation status (LeDuc and Havill 1998).

One weakness of the tree population methodology is that it fails to take into account the growth and survival rates of the species. Plant growth varies between individuals in the same population and during the lifetime of an individual (Silvertown and Charlesworth 2011). Trees often go through a period of reduced growth, when subjected to adverse conditions or strong competition, before resuming higher rates of growth when restraints are removed. Studies of the tree rings of pollarded oak trees show period of reduced growth following pollarding, followed by increased growth due to the higher availability of light (Rozas 2004). Building on the above, Kirby (2014) built a model to simulate the structure of a sustainable oak population in an oak parkland. This model can be used as a reference to compare the actual oak age structure of the parkland and hence to predict the likely evolution of the oak population.

This report describes the use of Kirby's model in relation to the key tree species at Epping Forest. The aim of the study is to determine the effects the restoration had and is having on the wood pasture and to evaluate the stability of the tree population. To achieve this aim, we developed the following objectives:

1. To determine the differences in tree layer structure and composition, and understory diversity and ground cover between restored, unrestored and secondary wood pasture areas.
2. To assess the differences on the density and size structures between the key tree species.
3. To estimate the age of the oaks, beech, hornbeam and holly populations.
4. To model the age structures the tree populations should have to maintain an stable number of trees in their oldest cohort through the adaptation of Kirby's model (2014)
5. To compare the predicted evolution in tree populations for the actual conditions and modelled age structures.
6. To predict the effect of the restoration on the ecosystem dynamics, including the tree layer and understory.

4 Methodology

4.1 Epping Forest

Epping (originally Waltham) Forest was a royal hunting ground comprising a medieval forest currently located in Essex and Greater London (Table 2). It was originally managed as a wood-pasture commons with different parties having different rights. The king had the right to keep and hunt deer, landowners may own the land but not the hunting rights, and commoners had the right to pollard the trees for firewood and to graze livestock. It is these common rights which led to the wood pasture features of a low density of pollarded trees within a matrix of grassland (Rackham 2006). In the nineteenth century, increasing urbanisation and the use of coal rather than wood, led to a decline in the practice of pollarding and commons grazing. Encroachment onto the forest was prevented in 1878, by the Epping Forest Act, which ensured that the forest as an 'an open space for the recreation and enjoyment of the public'.

Today Epping Forest covers over 2,450 ha and it is managed by the City of London Corporation (2015). Most of it is covered by ancient and secondary wood pasture of hornbeam (*Carpinus betulus*), beech (*Fagus sylvatica*) and pedunculated oak (*Quercus robur*) which used to be pollarded until 1876. Parts of the forest are Sites of Special Scientific Interest (SSSI) and Special Areas of Conservation (SAC). As part of the site management plan, some areas of Epping have started to be restored. In the early 1990s, ancient trees started to be pollarded again and in 1995 maiden trees were introduced to the cycle (JNCC 2011). The project is still in progress, being extended to a greater area each year. The management plan also includes the reintroduction of cattle, using an innovative invisible fencing system to control the area they can access. There are already some signals of the effect the cows are having on the area, such as the dispersal of the lousewort (*Pedicularis sylvatica*) (Site manager, personal correspondence 18 June 2015). However, the number of cows and time they have been allowed to graze on field have been considered too low to study their impact on the site.

Table 2. Description of Epping Forest

Site characteristics	
Description of forest	Epping Forest is in the south-east of England, in the counties of Essex and Greater London. It was designated as a Site of Special Scientific Interest on 1981 and as a Special Conservation Area on 2005. The Special Conservation Area covers 1605 ha
Area: Co-ordinates:	2400 ha The centre of the conservation area is 51°38'39'' N and 00°01'21' E.
Soil characteristics	
Soil type Soil depth Soil texture	Eutric luvic planosol 100 cm is a typical UK for the Wickham soil series (NSRI, 2015a, 2015b) Fine loam
Tree characteristics	
Tree species	70% of Epping Forest is covered by broad-leaved deciduous forest. The majority of it could be classified as ancient, semi-natural woodland, and it is abundant in veteran beech (*Fagus sylvatica*), oak (*Quercus robur* and *petraea*) and hornbeam (*Carpinus betulus*) pollards. The understory is mostly covered by holly, sometimes accompanied by yew (*Taxus*) (JNCC, 2011)
Tree density	Typically 30-60 trees ha^{-1} (Hornbeam) and 30-50 trees ha^{-1} (Beech)

Tree protection	None
Understorey characteristics	
Species Coverage	An important feature of Epping Forest are unimproved acid grasslands, which cover approximately 20% of the area; and dry and wet heathlands, which are considered as qualifying habitats for the designation of the site as a Special Area of Conservation. The Forest also includes inland water bodies. Ponds, bogs and fens are present in the area. Complete, but shade dependent
Livestock characteristics	
Species Stocking density	Red polls and Longhorn cattle Variable
Management	
History	Epping Forest is a remnant of the Royal Forest of Essex. It used to be managed as a wood-pasture which the commoners used to graze their cattle, dig gravel and extract wood, usually through pollarding. This site is renowned for its high concentration of old veteran pollards. During the 19^{th} century these traditional practices progressively fell out of practice and were definitely ceased in 1878 under the Epping Forest Act, which gave the jurisdiction of the forest to the City of London Corporation to manage the place for recreation. Nonetheless the necessity to reinstall these practices was issued recently, and in 1998 a new management strategy to restore the wood-pasture was approved. The pollarded cycle re-started in the early 1990 and in 1995 new maiden trees were introduced to the cycle. Similarly, cattle grazing is being re-introduced to the site, through an innovative invisible fencing system.
Biodiversity	The wood pasture areas support rich fungi, epiphyte and invertebrate communities, which include many rare species such as the moss *Zygodon fosteri*, or the saproxylic *Lucanus cervus*. Bird's biodiversity on is also high, and includes 48 breeding species. Fine-leaved grasses dominate the unimproved grasslands, and include a wide variety of species. The ponds and bogs are pools of biodiversity, and provide a habitat for rare flora and fauna.
Threats	The cessation of traditional management practices such as coppicing, pollarding and grazing, has affected the forest structure and there had been a decline in the epiphytic population. This community is starting to recover, thanks to the reintroduction of the pollarding cycle and the reduction of pollutant emissions. The status of the grassland areas had declined due to shrub encroachment and tree recruitment, but new conservation practices are reversing this change.

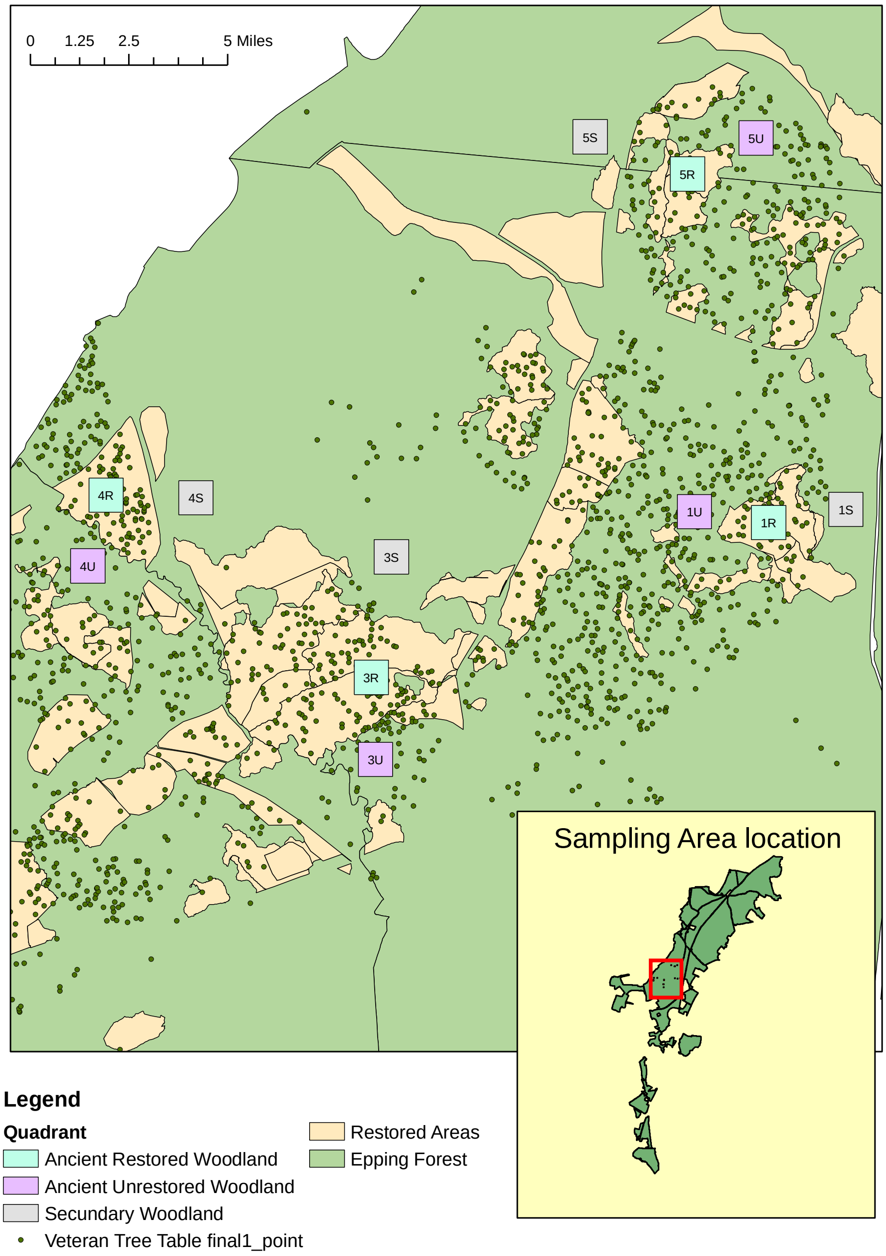
4.2 Experimental area

The field measurements were taken from the Fair Meadow area of Epping Forest. Prior to the site selection, the woodland area was classified according to its historical and current managements. The classification was based on a GIS layer provided by the site manager. Three classes of woodland were differentiated (Table 3).

Table 3. Description of the experimental treatments and the measurements

Description of experimental treatments		
Area	Epping Forest	
Treatment 1: Ancient restored wood pasture		Areas with veteran trees and which had recently been restored. This woodland had recently been opened up and its trees had been re-pollarded.
Treatment 2: Ancient unrestored wood pasture		Areas which used to be pollarded in the past but where no management has been undertaken in the last few decades.
Treatment 3: Secondary Wood pasture		Areas with no past pollarding records and no current management either. Prior to the site visit, it was assumed that veteran trees were absent or barely present on these areas.

Map of system	



Location of the sampling parcels at Epping Forest

Climate characteristics	
Mean monthly temperature	10.7°C
Mean annual precipitation	704 mm
Details of weather station	Hampsted (1981-2010; 137 m amsl; 19 km from Epping) http://www.metoffice.gov.uk/public/weather/climate/u10jbtxsb

Soil type	Epping is a lowland area. The geology is varied, including neutral to acidic clays and sands in the south.
Soil depth	Not determined
Soil texture	Not determined

4.3 Field measurements

The sampling sites were chosen using an aerial image, in which each of the three classes was mapped. Areas where the three wood pasture classes lied next to each other were identified and then the plots were drawn on them, trying to avoid the borders between the different classes (Table 3). The objective was to select adjacent plots of the three treatments to minimise the effects of differences in local ecology. The coordinates of these pre-designed parcels were taken, and used to localize the parcels on field with a Trimble GPS. To increase the accuracy of the survey, the parcels were redefined on field using a 50 m tape measure and a compass. The followed methodology is described in Appendix A.

Floristic data were collected in 12 parcels measuring 50 m x 50 m (as used for woodland classification in the National Vegetation Classification (NVC). Species and girth at a breast height of 1.3 m were surveyed in all the trees higher than 1.3 m in each parcel. Inside each parcel, five 4 m x 4 m plots were set to assess the field and shrub layer diversity, using the cover-abundance method and a Braun-Blanquet scale (Table 4). These were located on the centre and at mid-length of each semi-diagonal of the parcel. The number of seedlings (trees shorter than 1.3 m), their species and their height were recorded on a 1 m x 1 m square inside each 4 m x 4 m plot.

Table 4. Equivalence between Braun-Blanquet values and the percentages of cover-abundance they represent. The midpoint cover was the value used to convert the Braun-Blanquet value into a percentage.

Braun-Blanquet scale	Range of cover (%)	Midpoint of cover-range (%)
5	75-100	87.5
4	50-75	62.5
3	25-50	37.5
2	5-25	15.0
1	1-5	2.5
+	<1	0.1

4.4 Data analysis

Construction of population size-structures

The collected data were entered onto a spreadsheet and the tree girths were converted into diameter, assuming their stems were perfectly cylindrical (Equation 1).

$$dbh = \text{Girth}/\ \pi \qquad \text{Equation 1}$$

The trees were then sorted out into size classes of the same *dbh*. This range of each class was determined by dividing the greatest *dbh* (118 cm corresponding to a hornbeam) into 11 equal classes of 12 cm.

Parcel characteristics

In each parcel, the basal area and number of individuals of each tree species was calculated, as well as their overall values for all species and the tree diversity. Equation 2 shows the basal area (*BA*) calculation for each species, *s*, at each parcel *k*, where n_s is the number of trees of the species.

$$BA_{k_s} = \sum_{i=1}^{n_s} \pi\,(dbh_i/2)^2 \qquad \text{Equation 2}$$

Total parcel basal area was calculated as the sum of each species basal area on the parcel.

$$BA_k = \sum_{i=1}^{s} BA_i \qquad \text{Equation 3}$$

Understorey diversity

The understorey data was arranged into a matrix of 60 samples x 24 species containing the cover-abundance measurements as percentages. The conversion of the cover-abundance into percentages was performed assigning to each of the Braun-Blanquet categories their corresponding mid-range percentage (Table 4). The proportion of bare soil in each quadrant was inferred from the proportion of soil covered by the species. Species richness and Shannon-Wiener diversity index were calculated for all the samples and then averaged for each 50 m x 50 m parcel. Shannon-Weaver diversity index provides a measurement of the sample diversity from the log proportion each species represents on it (Equation 4).

$$H' = -\sum_{i=1}^{s} p_i \ln p_i \qquad \text{Equation 4}$$

Key species regeneration

In order to study the regeneration of the oak, beech, hornbeam and holly trees, the seedlings heights were sorted into three categories, <10 cm, 10-15 cm and >15 cm tall. The number of seedlings of each species and height category was counted in each parcel, summing the number of seedlings of each category at each of the 1 m x 1 m subplots.

Statistical analysis

All the analysis were performed using R (R DevelopmentCore Team 2015). The statistical level of significance was of 0.05 in all the tests. Count data variables cannot be modelled using ANOVA because their variance tends to increase with their means, and their errors are hardly ever normally distributed (Crawley 2005). Hence, all the variables expressing counts included in this study were analysed using Kruskal-Wallis non-parametric tests, which are able to handle rank as well as count data (McDonald 2014). This was important to model tree distributions and regeneration, as tree *dbh* and seedling heights were previously sorted into classes.

The patterns driving the tree size distributions were studied running several Kruskal-Wallis tests against the null hypothesis that there was no difference on the mean rank number of trees across different groups of wood pasture type, *dbh* class, species and all of their second and third order interactions. Similarly, seven tests were run to test the existence of significant differences between the number of seedlings and their height between species, wood pasture types and the interaction of three. The analysis of density and diversity at each parcel required one test for each, in which their variation with wood pasture type was checked.

Parcel characteristics

The variance between the basal area recorded at each parcel was examined using the ‘aov’ function implemented on the R-stats package (R DevelopmentCore Team 2015). To avoid the extra component of variance introduced by the location of the parcels from interfering on the analysis, the variable site was included as an error strata on the ANOVA.

The same analysis was applied to both classes of species dominances at each parcel and to the Shannon indexes and species cover at each understory plot. As all of these were proportion data, they were first arc-sine transformed into normally distributed data (Crawley 2005). This was mostly successful, but some remaining signs of non-normality were noted in the residuals values resulting from the model of the Shannon indexes, probably owing to the considerable amount of zero values contained in the dataset. The analysis of the understory data included the quadrant as an error strata as well as the site. To compare the differences among the categories inside each factor (-species and wood pasture type-), Tukey's Honest Significant Difference test was performed using the HSD.test function on the Agricolae R package (Mendiburu 2014). The proportion of bare ground at each quadrant was modelled with an ANOVA.

4.5 Tree age estimation

The ages of the oak, hornbeam, beech and holly trees were estimated following White´s methodology (1998). In this method, tree age is assessed subtracting its core area to its current basal area (Equation 5).

$$Core\ Age + \frac{\left(\frac{dbh}{2}\right)^2 * PI - Core\ Basal\ Area}{Area\ of\ the\ Outer\ Core\ Ring} \qquad \text{Equation 5}$$

Different sets of core age, basal area and outer ring area estimates are provided by White according to the growth conditions of the trees. As information about the structure of the wood pasture when these stands grew was not available, we used the "woodland boundary pollard or open woodland" parameters for the oaks, and the "inside woodland" parameters for the beech and holly trees, owning to the distances observed between trees. Hornbeams had not been included in White's study, so beech parameters were used again (Table 4), as it was assumed that the growth rate of both species in this location would be similar (Table 5).

Table 5. Equations used to relate tree size (cm) to tree age (years)

Tree species	Equation	
Oak	$100 + \frac{\left(\frac{dbh}{2}\right)^2 * PI - 2848}{76{,}6}$	Equation 6
Beech and hornbeam	$120 + \frac{\left(\frac{dbh}{2}\right)^2 * PI - 4072}{67{,}6}$	Equation 7
Holly	$60 + \frac{\left(\frac{\mathrm{dbh}}{2}\right)^2 * \mathrm{PI} - 1810}{59{,}8}$	Equation 8

4.6 Kirby's "sustainable" population tree model

In order to assess the sustainability of the wood pasture structure according to the data recorded on field, a model representing a stable population structure was constructed for each species. This model was based on a model Kirby´s (2014) devised for oak wood-pastures. It calculates the number of trees the species should have on each cohort to maintain an even population on its oldest cohort. The inputs of the model are the time length of the cohorts or time lapse between regeneration episodes, the average loss rate of trees, and the target density of ancient tress. The number of trees the population should have in one cohort *i* is calculated from the annual mortality rate (t); *l*, the cohort´s length; and N_i the number of trees on the immediately older cohort

$$N_{i-1} = {N_i}/{(1-t)^l} \quad \text{Equation 9}$$

The process followed to adapt the model to Epping Forest key species is illustrated in Figure 2.

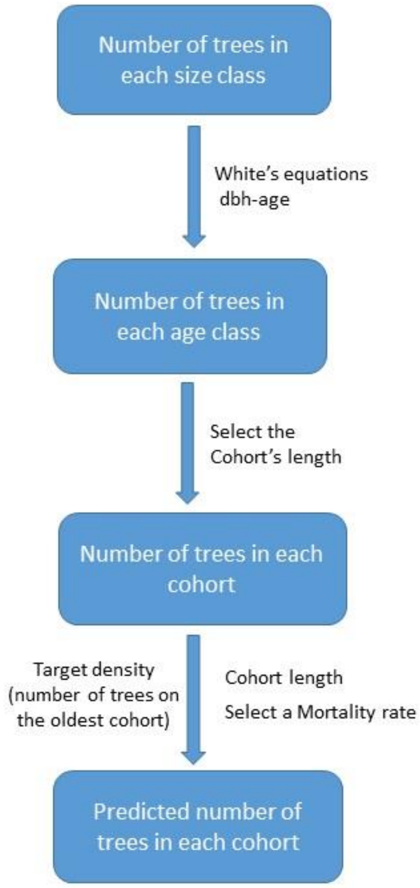


Figure 2. Process to build the stable age distributions. The tree size structures were converted into age structures using White equations and sorting the trees according to the cohort lengths. Then, the number of trees in the oldest cohort was used as the target density of the model. This combined with the mortality rate and the cohort length was used to estimate the number of trees that the population should have in each cohort.

The oak model was run using the same parameters as used by Kirby i.e. 100 years cohorts and annual loss rates of 0.7% for trees younger than 300 years and 0.4% for older trees. The target density was the number of trees in the oldest cohort (200-300 years), considering all the measured parcels together. Only one tree, of 205 years, was in this class, but its size did not differed much from that of some of the other oaks sorted into the next cohort. Probably all these trees were on the verge between 100 and 200 years old, so it was decided to include this oak in the 100-200 years old class.

There are few or no references in the scientific literature about the length between regeneration events for beech, hornbeam or holly. As beech starts producing flowers once they turn 50 years old (Packham et al. 2012) and its seedlings require the occurrence of small canopy gaps to growth, beech was allocated 70 years-old cohorts. The same age cohorts were assigned to hornbeam, which starts producing seeds after 30 years (Savill 2013) but may require bigger gaps to regenerate (unpublished data in Szwagrzyk et al. 2012). The first fruits appear on the hollies as young as 20 years, so they were assigned 50 years cohorts. The choice of cohort ages is explained in more detail in Appendix B.

The annual loss rate of trees was inferred from the mortality model devised by Holzwarth et al. (2013) for a near-natural mixed forest stand of beech, hornbeam and ash in Central Germany. Average values of annual mortalities for each cohort of beech and hornbeam were estimated calculating the area under the curve of the annual loss rate, then dividing it by the DBH range of the cohorts (Figure 3).

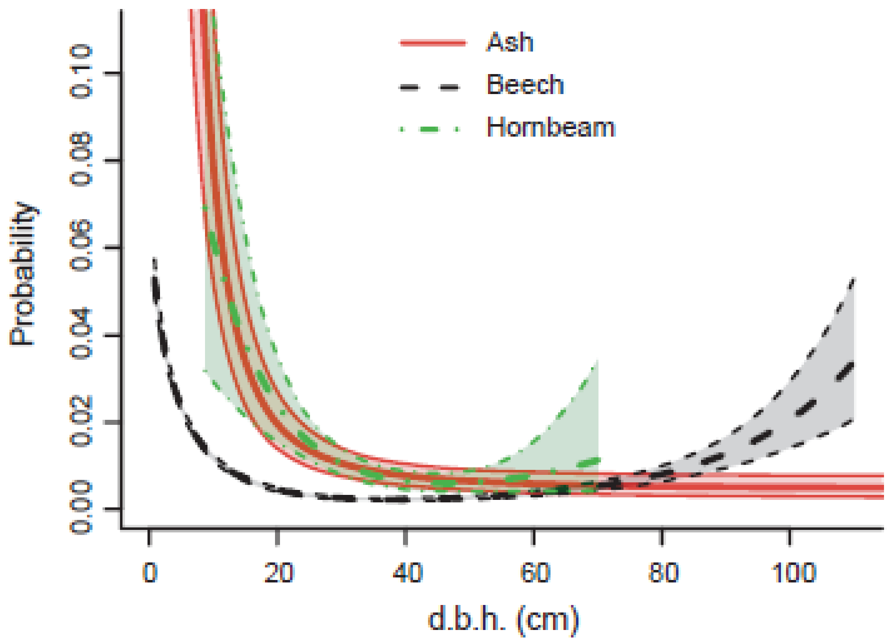


Figure 3. Holzwarth et al. (2013) modelled annual mortality probability over dbh (cm) for ash, beech and hornbeam. The thick lines represent the median estimate and the thin lines and shaded area the 95% confidence interval.

Due to the lack of scientific references, loss rates for holly cohorts were assumed to be similar to beech. The target density of old trees was the number of trees in the oldest cohort, which for beech was 3 for beech and 2 for hornbeam (Table 6). All the holly trees belong to the same and youngest cohort, so this species was not modelled.

Table 6. Cohort lengths, target density and annual mortality rate per cohort and species

Species k	Cohort length (years)	Target density	Annual mortality rate		
			1st cohort	2nd cohort	3rd cohort
Oak	100	52	0.7	0.7	0.7
Beech	70	2	1.8	0.9	1.6
Hornbeam	70	1	4	2	3
Holly	50	-	1.8	0.9	1.6

In order to assess the relative weight each of the input parameters have in the model, four additional age structures were generated for beech and hornbeam changing the mortality rates and cohort lengths (Table 7).

Table 7 Model names and parameters.

Model	Cohort length	Mortality rates
Original model (OM)	70	Calculated for each cohort (Table 6)
Equal Mortality Rate model (EMR)	70	0.007, equal to all species and cohorts
Reduced Mortality Rate model (RMR)	70	90% of the original mortality rate of each cohort
Equal Cohort Lengths model (ECL)	100	Recalculated mortality rate for 100 year cohorts
Equal Model (EQ)	100	0.007, equal to all species and cohorts

5 Results

The method of statistical analysis varies with the type of data. While normal distributions were fully described with their means and standard deviation, the median and the mad values were necessary to describe non-normal distributions resulting from count data. In certain cases jitter plots and boxplots were more illustrative than the numeric values. A short explanation of how these should be interpreted is included in Appendix C.

5.1 Population size structures

The number of trees at Epping varied across *dbh* size classes ($p<0.001$) and tree species ($P<0.001$) but not wood pasture type ($p=0.41$). However there were interactions between each of the combinations of *dbh* class, species, and wood pasture type, and high level interaction between all three explanatory variables (Table 8). The main effect of species was that the number of beech and holly trees was greater than for oak and hornbeam (Table 9).

Table 8. Analysis of the effects of *dbh* class, species, wood pasture type and their interactions on the number of trees per parcel (0.25 ha) in Epping Forest

Explanatory variables	Df	p-values
Dbh class	10	< 0.001
Species	3	< 0.001
Wood pasture type	2	0.41
Dbh class x species	43	< 0.001
Dbh class x wood pasture type	32	< 0.001
Species x wood pasture type	11	0.0003
Dbh class x species x wood pasture type	131	< 0.001

Table 9. Tree counts on different species per 0.25 ha per *dbh* class (n = 132). The last column is the averaged count resulting from the aggregation of the *dbh* classes (n = 12)

Species	Mean ± sd	Median ± mad	Averaged mean ± sd
Oak	$1^{a} \pm 1$	0 ± 0	11.4 ± 5
Beech	$2^{b} \pm 6$	0 ± 0	21.8 ± 55
Hornbeam	$3.1^{a} \pm 10$	1 ± 1	35 ± 31
Holly	$8.6^{b} \pm 33$	0 ± 0	94.9 ± 91

Tree-size distributions were positively skewed, so there were many trees with a small *dbh* and few trees of large *dbh* (Figure 4). There were similar large numbers of trees in the two narrowest *dbh* classes, similar numbers in the next three size classes (24 < *dbh* < 60 cm), and fewer trees with *dbh*s between 60 and 108 cm. There was only one tree with a *dbh* > 120 cm.

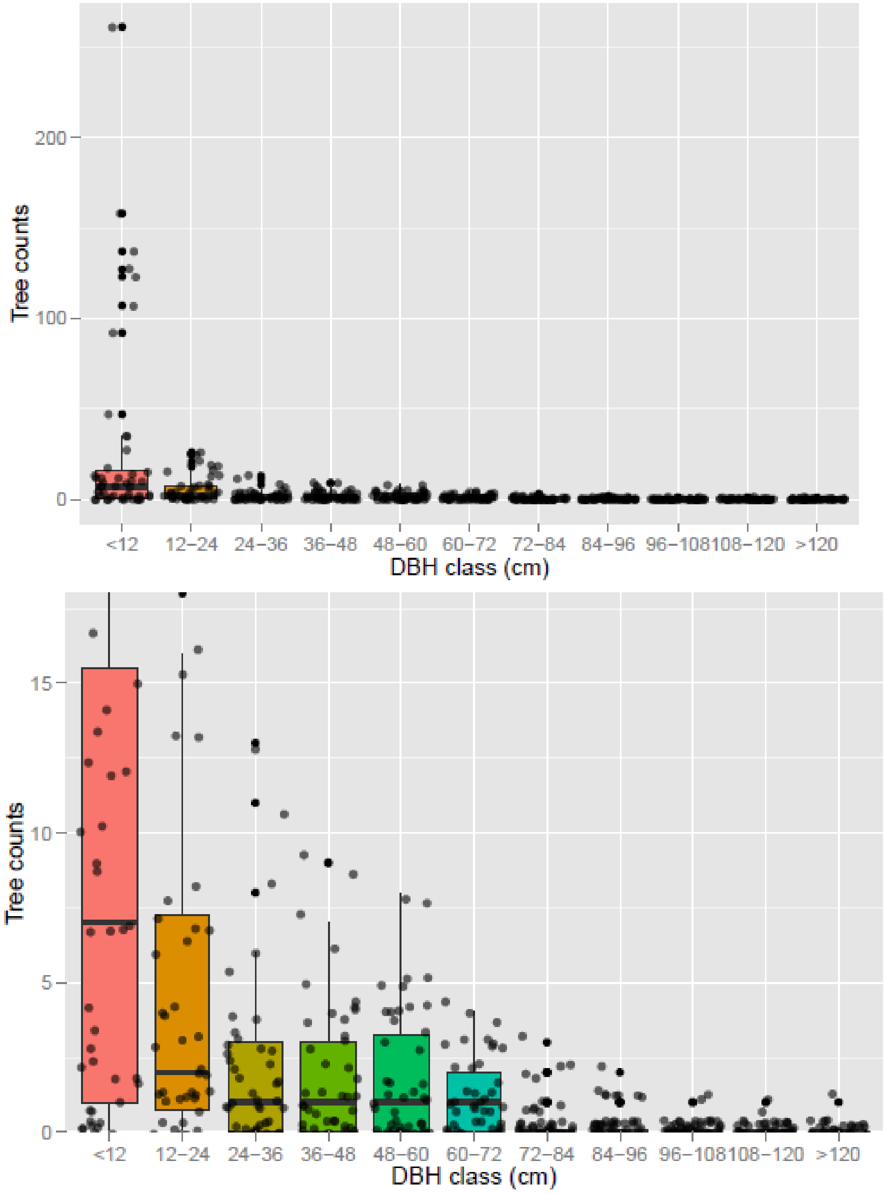


Figure 4. The overall number of trees within each *dbh* class declines as the *dbh* increases (n = 48). The lower figure is a snapshot of the upper one, which covers the whole range of measured values. Within each figure and *dbh* range, each point represents a measured value. The line within each box shows the median, and the box limits the upper and lower quartiles, while the whiskers show the interquartile range x 1.5.

There were significant interactions between species and *dbh* classes. The total count for oaks was low, but the oaks had a bell-shaped distribution of *dbh* with a large number between 36 and 72 cm (Figure 5). There were few or no trees larger than 96 cm. The *dbh* of the beech trees had an "inverse J" distribution, where there was a large number of narrow trees but similar numbers of medium-sized trees (Figure 5). Both the holly and hornbeam tree showed high levels of narrow trees, but whereas the widest holly trees had a *dbh* below 39 cm, the widest hornbeam was 118 cm.

a) Size distribution of oak trees

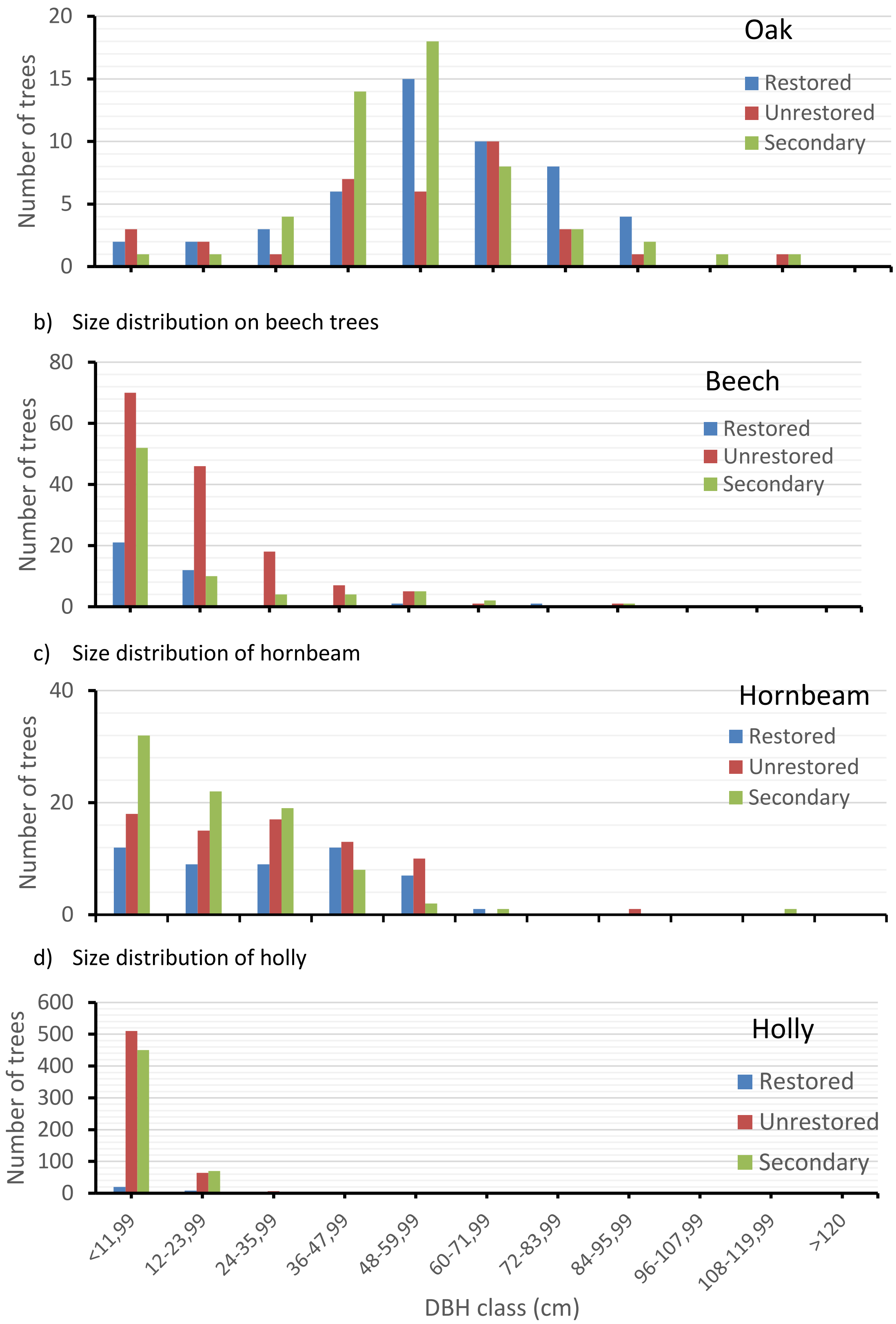


Figure 5. Distributions for each wood pasture type for a) oak, b) beech, c) hornbeam, and d) holly. Note that the vertical scales differ.

The distribution of trees (in terms of *dbh* classes) was similar between the three wood pasture types, although the unrestored area had a greater number of trees in the 24-36 cm class and the restored area had fewer trees in the smallest class (Figure 6). The individual species showed a similar response. Counts of hornbeam in unrestored areas were significantly different from that of the beech and holly on all the parcels, as well as from the count of oaks in unrestored areas. Beech and holly distributions were quite similar.

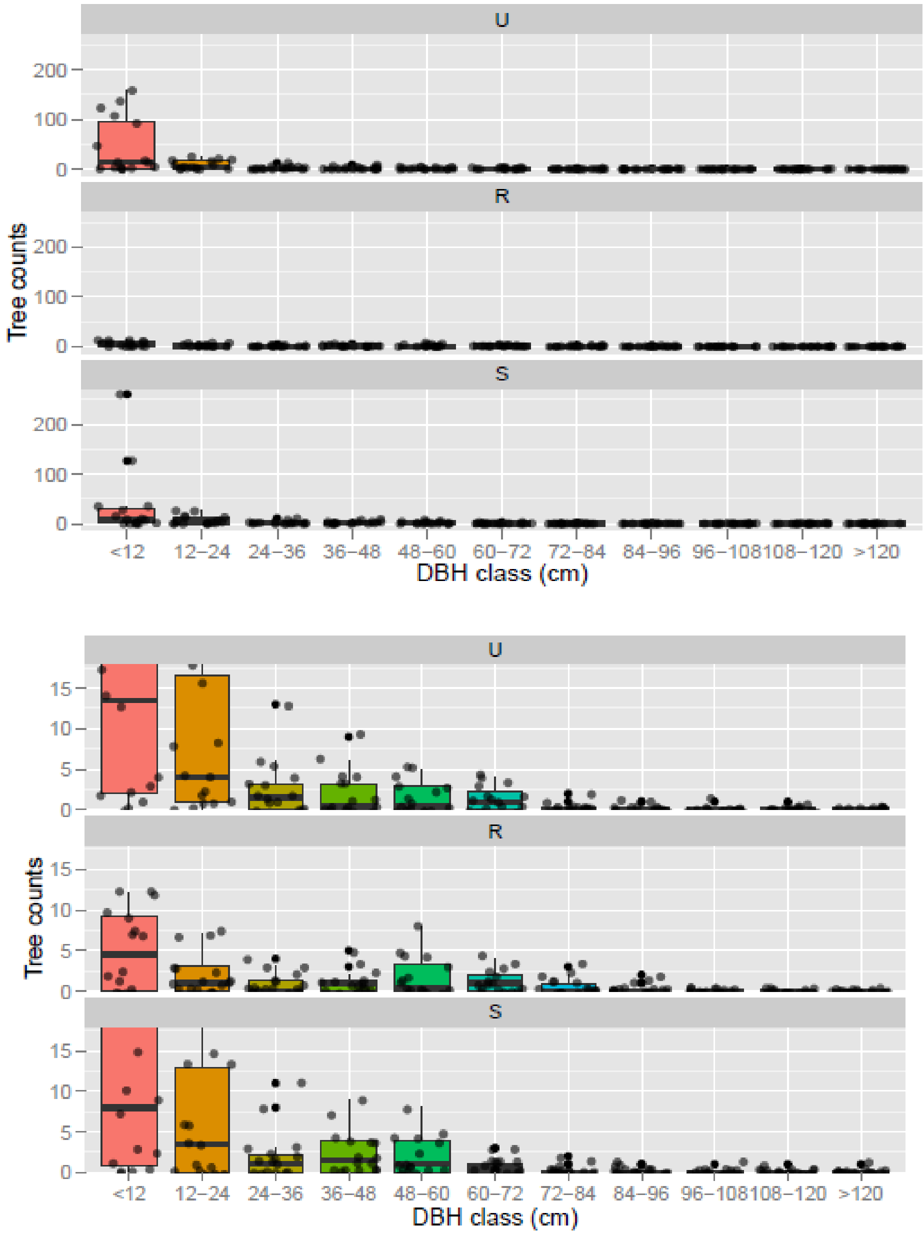


Figure 6. The count of trees per species in the unrestored (U), restored (R) and secondary (S) wood pasture in 11 *dbh* classes (n = 16)

Third order interactions

There was substantial variation in the tree counts between replicates which made it difficult to establish statistically significant differences. However some remarkable results were observed. For the two smallest diameter classes, holly trees were scarcer in restored areas than in the secondary and unrestored areas (Figure 7). There was also a lack of large beech trees beyond size class 4 (24-36 cm). Because there were few large trees of any species, there was no statistical difference in the species counts above size class 8 (> 84 cm).

5.2 Diversity, density and basal area

Tree diversity, density and basal area of the parcels was similar in the three wood pasture types (p>0.01, Table 10). However there were significant interactions between species and wood pasture type in terms of density and basal area (Table 10).

Table 10. Significance of the effect of wood pasture type, species, and interactions on density and basal area

Explanatory variables	df	p-values for density	p-values for basal area
Species	3	<0.001	<0.001
Wood pasture type	2	0.59	0.985
Species x wood pasture type	6	0.03	<0.001
Residuals	36		

The holly trees were dominant in the unrestored and secondary wood pasture but scarce in the restored areas. This caused the oak and hornbeam relative importance to be much smaller on the unrestored and secondary areas than in the restored ones, as their number and sizes are similar across all the wood pasture types (Figure 7).

Table 11. Mean basal area, density and diversity across the three wood pasture types

Parcel characteristic	*Mean*	*P value*
Basal area (m^2 ha^{-1})	26.13	0.89
Density (trees ha^{-1})	611	0.08
Diversity (species $(0.25\ ha)^{-1}$)	5	0.73

Table 12. The dominance of each species according to their basal area and density within each wood pasture type

Species	Dominance according to basal area (%)		
	Restored	Unrestored	Secondary
Oak	$0.52^{abcd} \pm 0.1$	$0.16^{d} \pm 0.0$	$0.28^{d} \pm 0.2$
Beech	$0.36^{cd} \pm 0.2$	$0.25^{d} \pm 0.2$	$0.33^{d} \pm 0.2$
Hornbeam	$0.82^{abc} \pm 0.1$	$0.42^{ab} \pm 0.2$	$0.51^{abcd} \pm 0.2$
Holly	$0.13^{d} \pm 0.2$	$0.92^{a} \pm 0.2$	$0.82^{ab} \pm 0.2$

Species	Dominance according to density (%)		
	Restored	Unrestored	Secondary
Oak	$0.84^{a} \pm 0.1$	$0.65^{ab} \pm 0.8$	$0.83^{a} \pm 0.1$
Beech	$0.19b^{cd} \pm 0.2$	$0.3b^{cd} \pm 0.3$	$0.26^{bcd} \pm 0.3$
Hornbeam	$0.51^{abc} \pm 0.1$	$0.64^{ab} \pm 0.1$	$0.61^{ab} \pm 0.2$
Holly	$0.32^{bcd} \pm 0.1$	$0.35^{bcd} \pm 0.1$	$0.3^{ab} \pm 0.1$

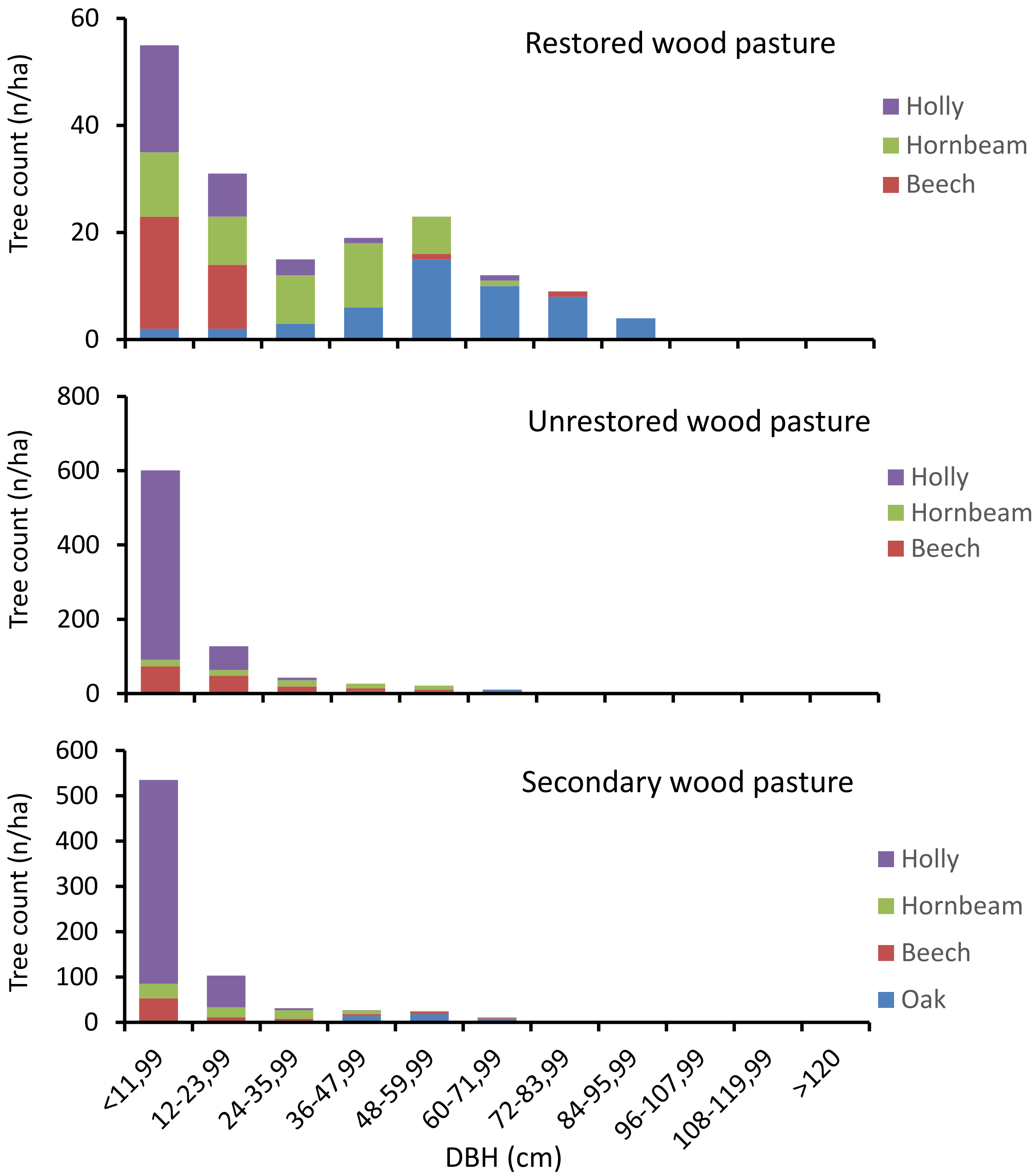


Figure 7. The cumulative count over 1 ha of oak, beech, hornbeam and holly trees in the unrestored (U), restored (R) and secondary (S) wood pasture. Note that the vertical axis have different scales

5.3 Understory diversity

The proportion of bare ground, the species richness, and the Shannon diversity index of the understory varied with the wood pasture type ($P < 0.01$). Bare ground, which was high in all wood pasture types, occupied a larger area in the secondary wood pasture than the restored wood pasture (Table 13). HSD tests did not indicate significant differences between the restored and unrestored areas, but with a bonferroni correction, the difference was significant, which corresponded with the impression received during the field visits. Shannon diversity index and species richness were greater in the restored areas than on the unrestored and secondary wood pasture (Table 14).

Table 13. Effect of wood pasture type on the proportion of bare ground (%) (n=20)

Wood pasture type	Mean ± sd	M (HSD)	M (bonferroni)
Restored	73.3 ± 32	a	a
Unrestored	90.5 ± 23	ab	b
Secondary	93.1 ± 16	b	b

Table 14. Effect of wood pasture type on the Shannon diversity indexes and species richness recorded on each 4 m x 4 m quadrat (n=20)

Wood pasture type	Shannon diversity Index	Species richness	
	Mean ± sd	Mean ± sd	Median ± mad
Restored	0.68[a] ± 0.5	4.9[a] ± 2	5 ± 1.5
Unrestored	0.29[b] ± 0.4	2.1[b] ± 2	2 ± 1.5
Secondary	0.23[b] ± 0.3	2[b] ± 1	2 ± 1.5

A higher Shannon index represents higher diversity, in terms of the relative proportion of the species. The species richness is the mean number of species.

There were significant wood pasture type and species effects and interactions on the proportion of understorey cover (Table 15). Bracken was the most common species, being abundant on the restored areas and present in the secondary and unrestored plots. It was followed by holly, moss, hornbeam and oak seedlings, where the cover did not differ between wood pasture types. The restored areas had the most diverse understory; 14 of the 24 recorded species in this wood pasture were not found on any of the other types. One of these species, the raspberry, was actually classified as the third more abundant species, reflecting the high percentage of bare soil on the secondary and unrestored wood pasture. The full list of species recorded is in Table 16.

Table 15. Significant of the effect of wood pasture type and species on the understory cover

Explanatory variables	*df*	*p-values*
Wood pasture type	2	<0.001
Species	23	<0.001
Species x wood pasture type	46	<0.001
Residuals	1349	

Table 16. Recorded understory species, ordered according to their abundance, on each wood pasture type. The colour represents species which appeared in more than one wood pasture type.

Restored wood pasture	Unrestored wood pasture	Secondary areas
Bracken (*Pteridium aquilinum* (L.) Kuhn) Bramble (*Rubus fruticosus* L.) Grass 2 (Poaceae L.) Holly (*Ilex aquifolium* L.) Hornbeam seedlings (*Carpinus betulus* L.) Moss Briophyta Oak seedlings (*Quercus petraea* (Matt.) Liebl) *Second Rubus species* Thistle 1 (Asteraceae Bercht. & J.Presl) Grass 1 (Poaceae L.) Honeysuckle (Lonicera L.) Ash seedlings (*Fraxinus excelsior* L.) Poplar seedlings (*Populus tremula* L.) Pinnate herb Beech seedlings (*Fagus sylvatica* L.) Grass 3 (Poaceae L.) Elder seedlings (*Sambucus nigra* L.) Hawthorn (*Crataegus monogyna* Jacq.) Ivy (*Hedera helix* L.) Slender rush (*Juncus tenuis* Willd) Thistle 2 (Asteraceae Bercht. & J.Presl) Unidentified	Holly Nettle (*Urtica dioica* L.) Bracken Hornbeam seedlings Honeysuckle Oak seedlings	Holly Hornbeam seedlings Oak seedlings Moss Bracken

Though the vegetation was identified to the species level whenever possible, some of the plants were identified only to the family level and two of the surveyed individuals (named pinnate and unidentified) were too young to even distinguish these.

5.4 Tree regeneration

The number of seedlings differed considerably between different species and height categories, but not between wood pasture types ($p > 0.05$). All the interactions studied were found to be significant (Table 17).

Table 17. Results from the analysis of variance (Kruskal Wallis) of tree regeneration.

Explanatory variables	df	p-values
Height	2	<0.01
Species	3	<0.01
Wood pasture type	2	0.27
Height x species	11	<0.001
Height x wood pasture type	8	0.04
Species x wood pasture type	11	<0.01
Height x species x wood pasture type	35	<0.01

Height and species of tree seedlings

Most seedlings were less than 10 cm tall and most of the seedlings were hornbeams (Table 18). There was substantial variations in the density of oak and hornbeam seedlings as reflected in the high standard deviations. By contrast the regeneration of beech and holly trees was minimal.

Table 18. Seedling density according to height (n = 240) and species (n = 180). Mean, standard deviation, median and mad values are given.

Height (cm)	Mean seedling density (m^{-2})	Median ± mad
<10	$166.6^{a} \pm 54.3$	0 ± 0
10-15	$26.6^{b} \pm 10.9$	0 ± 0
>15	$0.5^{c} \pm 1.7$	0 ± 0
Species	**Mean ± sd**	**Median ± mad**
Oak	$35.8^{ab} \pm 125.3$	0 ± 0
Beech	$0.1^{c} \pm 0.5$	0 ± 0
Hornbeam	$225.5^{a} \pm 617.8$	0 ± 0
Holly	$0.2^{bc} \pm 0.44$	0 ± 0

Most hornbeam seedlings were less than 10 cm, but there were small and similar numbers of 10-15 cm and > 15 cm height (Table 19). There were a number of oaks up to 15 cm tall. The number of beech and holly seedlings was low.

Table 19. Seedling density (number of seedlings m^{-2}) across different combinations of height categories and species. Mean and standard deviation are given.

Species	*Height (cm)*		
	<10	10-15	>15
Oak	$12.5^{ab} \pm 28.3$	$94.2^{ab} \pm 208$	$0.1^{cd} \pm 0.3$
Beech	$0.3^{bcd} \pm 0.9$	$0^{d} \pm 0$	$0^{d} \pm 0$
Hornbeam	$646.6^{a} \pm 960$	$11.6^{bcd} \pm 28.5$	$18.3^{bc} \pm 32.1$
Holly	$0.4^{bcd} \pm 0.7$	$0.1^{cd} \pm 0.3$	$0^{d} \pm 0$

5.5 Tree age

Using the equations described in Table 5, the distribution of tree ages were estimated (Table 20). Hornbeam showed the widest range of ages. The oldest oak tree was estimated to be 205 years old, and the oldest beech 152 years old. Each holly tree was estimated to be under 50 years.

Table 20. Tree distribution of each species according to their age

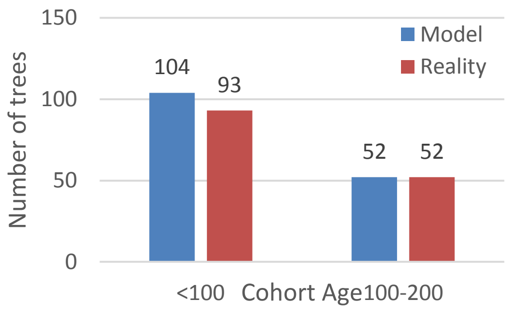
Age	Oak	Hornbeam	Beech	Holly
<30				366
30-40				742
40-50				7
50-60		108	54	
60-70	15	182	170	
70-80	22	50	15	
80-90	30	26	6	
90-100	26	21	7	
100-110	18	14	2	
110-120	14		1	
120-130	9	8		
130-140	2	2	1	
140-150	2		1	
150-160	4		1	
160-170	1			
170-180		1		
180-190	1			
190-200				
200-210	1			
>210		1		

Ages have been sorted into 10 years-classes. Note that the equations used have a lower limit to estimate tree ages, being unable to differentiate ages of oaks smaller than 70 years, hornbeams and beeches smaller than 60 and hollies younger than 30 years.

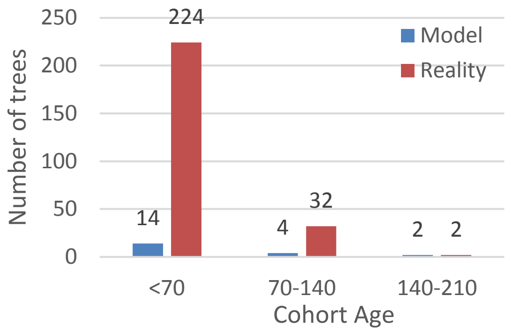
5.6 Comparison with a modelled sustainable population

The number of trees on each cohort needed to maintain the population stable, as predicted by Kirby's model, was compared with that observed in the field. The field population of oaks was similar to that predicted by the model, though there were 10% less trees in the young cohort (Figure 8). The number of beech trees in the field was substantially higher than predicted by the model. The number of hornbeam in the field aged 70-140 years was higher than that proposed for a stable population, but there were fewer at less than 70 years.

Oak			
Cohort	Model	Reality	Difference
<100	104	93	-11
100-200	52	52	



Beech			
Cohort	Model	Reality	Difference
<70	14	224	+210
70-140	4	32	+28
140-210	2	2	



Hornbeam			
Cohort	Model	Reality	Difference
<70	604	209	-395
70-140	34	108	+74
140-210	8	1	-7
210-280	1	1	

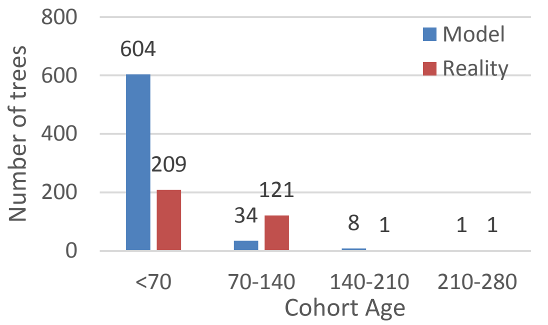


Figure 8. Comparison between tree number on each cohort according to the model (in blue) and the actual number of trees surveyed on field (in red), Results per three hectares.

Making assumptions about mortality rates, it is possible to predict the future distribution of the trees at Epping was predicted applying the model (Table 21). The number of trees within any cohort declines with time. According to the model, nine of the oak trees (which are currently 200 years old) will reach more than 400 years, which is regarded as the age of the oldest oak cohort in Britain (Kirby 2014). Because the current population of young beech trees is high, the population of old beech trees is predicted to increase. By contrast the number of mature hornbeams is predicted to increase in the next 70 years and then decline.

Table 21. Predicted number of oaks, beech, and hornbeam in the future according to the current population

Oak population	Present: (2015)	2115	2215	2315
<100	93			
100-200	52	46		
200-300		26	23	
300-400			13	12
>400				9
Beech population	Present: (2015)	2085	2155	2225
<70	224			
70-140	32	61		
140-210	2	17	32	
210-280		1	5	10
Hornbeam population	Present: (2015)	2085	2155	2225
<70	209			
70-140	121	12		
140-210	1	29	3	
210-280	1	0	3	0

Sensitivity of the model

The results from the model are sensitive to relatively small modifications of the input parameters (Table 22). For instance, a 10% reduction in the mortality rate (as used in the Reduced Mortality Rate (RMR) model) decreased the number in the youngest cohort of beech trees by 20% and the youngest cohort for hornbeam by 48%. This is as a result of the multiplicative effect of mortality.

Table 22. Comparison of the tree populations within a given cohort within the Original model (OM), a reduced mortality model (RMR), an equal mortality model (EMR), a model assuming equal cohort lengths (ECL), and an equal model (EM) assuming a consistent mortality rate.

Beech					
Model/ Cohort	OM	RMR	EMR	ECL	EM
1	14	11	5	90	24
2	4	4	3	26	12
3	2	2	2	6	6
Hornbeam					
Model/ Cohort	OM	RMR	EMR	ECL	EM
1	604	315	5	2449	8
2	35	24	3	159	4
3	9	7	2	21	2
4	1	1	1	1	1

Note: OM uses 70-year cohorts with different mortality rates. The Reduced Mortality Model (RMR) uses the same input parameters but the mortality rates are 10% smaller than on the OM. The Equal Mortality Model applies a 0.7% mortality rates to all its 70-years cohorts. The Equal Cohort Length adapts the original mortality rates to 100 year-cohorts. The Equal model applies the same mortality rate of 0.7% to each of its 100-year cohort.

Expanding the cohorts from 70 to 100 years, as in the Equal Cohort Length (ECL) scenario increased the required number of trees on the younger cohorts. For hornbeam this increase was of 305%, 354% and 133% in the first or youngest, second and third cohorts respectively. A comparison of the outcomes of Equal Mortality Rate and Equal Model, which differ only in terms of the cohort's length, illustrate the effect of this length on the cohort structure (Figure 9). Finally it is worth noticing that the prediction would have been totally different if all the species had been modelled using the same parameters, as in the Equal Model.

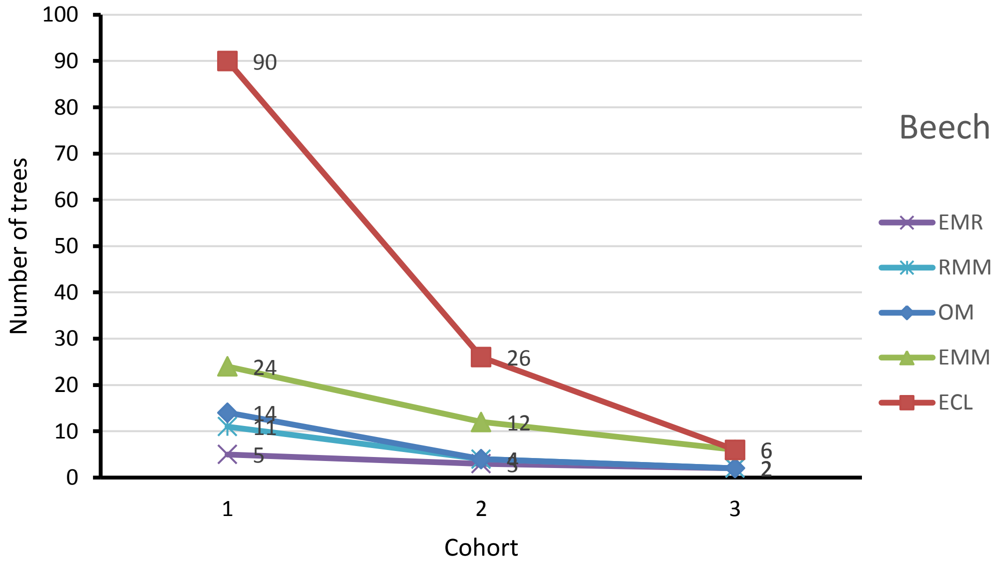


Figure 9. Representation of the beech structures generated by different models

6 Discussion

6.1 Restoration effects

The effect of woodland management can be described in terms of its impact on mature trees and the understory including seedlings.

In the tree layer, the most notable effect of restoration was the reduction in holly trees. This was a result of the restoration plan, because mature holly trees are not considered a desirable feature of wood pastures. Nonetheless, holly is a useful food source for small mammals and birds which feed from its berries during winter. As most of the holly trees belonged to the two smallest size classes (Figure 5), their clearance from restored areas significantly reduced the number of small trees, and increased the relative importance of other species (Figure 7).

The understory varied with wood pasture type. The restored areas had a more open canopy and a more diverse understorey compared to unrestored wood pasture and secondary woodland (where bare ground was the dominant cover). The species richness was approximately four times greater on the restored area (Table 16).

Despite the above, tree regeneration was not significant better in the restored areas than the unrestored wood pasture and secondary woodland. This could partly be attributed to the dominance of bracken in open areas. Bracken is highly competitive in full light conditions and once established it produces a heavy shade and releases allopathic substances. This can prevent the growth of the tree seedlings (Rhone-Poulenc 1990; Humphrey & Swaine 1997; Mountford et al. 2006) and other understory species (Rhone-Poulenc 1990). In fact dense bracken stands can reduce biodiversity, and has been reported as problematic in other wood-pastures (Barwick & Powers 2000).

Figure 10. Dense bracken stand on a restored parcel

6.2 Tree age estimation

This study suggests that many of the mature oak and hornbeam populations established around 200 years ago, the beech trees seemed to have established about 160 years ago, and the holly trees about 50 years ago. The accuracy of these estimates are dependent on the assumed relationship between tree age and diameter, which can vary with tree and temporal changes (i.e. Silvertown & Charlesworth 2001; Fritts 1976; White 1998). For example Rozas (2003) reported that oaks in the a single area with similar diameters (50-60 cm) could vary by 200 years in age.

Ideally, tree ages should have been estimated through regressions built with *dbh*-age data of the site, but this was not available. An estimation of the age of 16 oaks through core sampling (Najeeb 2013) was obtained on August but the data covered a limited size range and was not linked to the tree diameters. Therefore, our estimation was based on White's equations (1998) which were devised using data from UK trees and account for the reduction of tree growth with age. These equations were built with the purpose of estimating the age of ancient trees, and they were not able to provide an accurate estimation for trees which had not reached maturity. However our results for small oak and beech trees did not differed much from estimations from other studies Rozas (2003). Hornbeam age estimates might not be precise, as they were assumed to grow at the same rate as beech and no data was available to check the goodness of this approximation.

Another cause of uncertainty related with White’s equations was that the origin of the wood pasture was not known. A comparison of the equation results with the core sampling suggests that the ages might have been underestimated, perhaps because the veteran trees were subjected to a pollarding cycle which could have reduced their growth (S. Perry, personal communication, July 2015). Nevertheless, both estimations agreed on the 100 years resolution so it was concluded that the accuracy of the age estimates was enough for the purposes of this study.

6.3 Sustainability of the tree populations

Suitability and applicability of the model

The stability of the populations was studied through Kirby’s model, which provided results that matched those of the oak population. A key strength of the model is that it is simple to apply, as it requires only three input parameters.

This model was designed to provide a reference to identify the number of trees in each cohort that are required to maintain the numbers in a mature cohort. Whilst its interpretation is easy -if the number of trees given is smaller to the one present, the number of trees on the oldest cohort is bound to decrease – it is also limited, as the model is not concerned with the plausibility of this number occurring or goodness of the structure it generates. It may be the case that there is not enough space left for the next cohort to stablish, or it could also happen that the selected number of trees in the oldest cohort was too small to provide a habitat for the saproxylic species. The model does not provide insights about the factors constraining tree establishment or the ideal tree density; this depends on the site manager.

A limitation of the model is that it assumes that population dynamics will not change over time i.e. it does not include the effect of competition or tree density as a driver of the population dynamics. In practice, tree populations can vary annually due to highly stochastic nature of canopy disturbances and the creation of open spaces. This limitation is partly lessened by the fact that the model is run over long lapses of time- the tree cohorts- in which the randomness is somehow diluted.

Fit of the input parameters

The model is very sensitive to small changes on the input parameters, as the comparison in section 4.3 showed. Both tree mortality and cohort length are complex attributes which depend on many highly stochastic and site-specific variables which require long-term studies (Holzwarth et al. 2013). In fact, a difficulty we faced when applying the model to the studied species was that these inputs were not directly available on the scientific literature.

This puts into question the robustness of the model predictions, because the selected parameters may not have corresponded to the reality of Epping Forest. For example, beech and hornbeam tree mortality rates were taken from a study carried out in Thuringia, Germany, and, while they could be considered more detailed than the oak mortality rate- which was the same for the first 300 years of life-, their applicability for Epping Forest is not clear. The authors of the study, (Holzwarth et al. 2013) caution against their veracity outside their study area and the results from running the different models suggest that these mortality rates were indeed too high for the hornbeams at Epping forest.

The cohort's lengths were estimated from related information about the silviculture and dynamics of the species, and seemed to be too short for the beech population, which had a better fit to the model with 100 years cohorts. Hornbeam presented a better fit when modelled with the 70 years-cohorts, which highlights the differences between the two species dynamics.

The target density was selected as the number of trees on the oldest cohort, which, as already commented, might not have corresponded to the ideal density for the ecosystem. The trees were sorted into the separate cohorts according to their ages, which are a continuous attribute. This could have caused some trees closed in age to be artificially separated, as it happened with the oaks (Section 4.6.) so it was necessary to revise the tree sorting. A similar issue on the applied methodology occurs with seedlings and trees, which are studied separately but represent a continuum in the population and should not be regarded independently.

Predicted evolution of tree populations

The current oak population matched the model prediction, suggested that the number of 100-200 year old trees will only decrease slightly from 52 to 46 in the next century. The model also predicts that in 300 years, there will be 3 oaks per hectare that are over 400 years; a density of veteran oaks enough by itself to provide a continuous habitat for the saproxylic species according to Kirby (2014). On the other hand, the size structures revealed a deficiency of small trees (Figure 5), linked to a lack of recruitment. Whether or not this is considered as an indicator of the population decline in the future depends on the time scale used in the analysis. If we assume, as in the model, that the oak regeneration is mostly episodic and happens on a 100 year basis, the stability of the oak population is no cause of concern but if we considered that oak regeneration should happen in a more continuous cycle its stability could be questioned.

The model did not match the current beech populations, suggesting that the currently high beech population is likely to increase further and in its age range. This is in line with its size distribution, which is proper of a population with a continuous recruitment (Mountford et al. 1999). On the other hand, there were almost no beech seedlings, but this cannot be taken as an irrefutable indicator of the population evolution because this species, as oak and hornbeam, exhibits a masting pattern, meaning that they produce massive quantities of seeds every 5 or 10 years and almost no seeds in between (Silvertown & Charlesworth 2001). In addition beech seedling sprouting are subjected to the occurrence of damp conditions (Packham et al. 2012) that may not have happened this year.

Hornbeam populations followed an unstable pattern, increasing and decreasing subsequently over time. Even though the number of hornbeams decreased with increasing size, the size distribution was different from the negative pattern of the beech (Figure 5) perhaps indicating that recruitment was low in some periods. Hornbeam seedlings were quite numerous, as it was a mast year, but most of them were small (Figure 11).

Figure 11. Hornbeam and oak seedlings on an unrestored parcel. Note the quantity and small size of most of the hornbeam seedlings in comparison with the oaks.

6.4 Succession

Until this point each of the species trend has been discussed independently, however, in reality their evolutions are linked to each other. The interaction between the species and individual trees is a key driver of the ecosystem dynamics and its likely succession.

The current state of the unrestored areas and the size distributions of the species suggest that once the management stopped the canopy was rapidly covered. Oak, which seedlings have the highest light requirements (LeDuc & Havill 1998; Petritan et al. 2014) decreased its recruitment, whereas the new conditions benefited holly and beech, which are regarded as two of the most shade-tolerant European species. Hornbeam was still able to recruit on the small canopy gaps but it might be outcompeted by beech in the future because beech top height is greater than the hornbeam's (Packham et al. 2012; Szwagrzyk et al. 2012).

These observations may support the hypothesis that the overall density of trees is too great to preserve the mixture of the three species, so that even if the model (Figure 8) predicted that the oak population would be stable in the next 100 years this species might eventually be suppressed by the tree competition. The future model predictions (Table 21) also suggest that the density of trees is high, as the number of the veteran oaks alone was enough to support the invertebrate saproxylic community. Due to the removal of holly trees on the restored areas beech predominance might decrease, as oak and hornbeam will be more benefited from the higher light availability (Szwagrzyk et al. 2012; Petritan et al. 2014).

Another aspect of the restoration worth mentioning is the imminent reintroduction of livestock grazing. This could have different effects on the ecosystem: on the one hand, cattle might alter the vegetation community contributing to the dispersal of some species, as has already happened in other areas of Epping with the lousewort, and enhancing the presence or absence or other species through their selective diet. Barwick and Powers (2000) recommend to use livestock as a method to control bracken and Mountford et al. (1999) suggest that grazing prevented hollies from expanding at Denny Wood. On the other hand, livestock might limit tree recruitment, especially of the oaks, which the cattle selectively browse (Von Lüpke 1998). However the grazing pressure on Epping is not expected to be high enough to cause any significant damages on the trees.

6.5 Conclusions

This project has investigated the effect of restoration on wood pasture at Epping Forest. No differences between the wood pasture types were found on the tree layer, apart from a lower abundance of holly trees, which had been removed by the restoration works.

The understory already showed signs of improvement on the restored areas, both in terms of diversity and ground cover. Bracken may be hampering tree regeneration in these areas, so it is recommended that bracken control is included in the restoration plan.

The Kirby model was useful as a reference to estimate the likely evolution of the tree populations even though its predictions for beech and hornbeam might not be robust. The oak population seemed to be stable, and followed well the predictions made by the model. However their regeneration should be watched carefully because the light conditions their seedlings require to grow do not happen in unmanaged areas where the density is too high. The beech population is predicted to increase in age and number, whilst the hornbeam population seems unstable according to the model.

7 Recommendations

Epping Forest primary owns its designation as a Special Area of Conservation to the presence of "Atlantic acidophilus beech forest" traditionally managed as wood-pasture, which provide a habitat for declining epiphytes communities, fungi and rare saproxylic invertebrates (JNCC 2011). The management of this area should therefore seek to preserve and enhance wood-pasture and the biodiversity it holds.

The restoration of the wood pasture is promoting biodiversity and will potentially enhance tree recruitment and benefit the population of oak and hornbeam trees relative to beech and holly trees. On the basis of these results, it is recommended that the extent of restoration is increased, whilst also preserving areas of unrestored wood pasture and secondary woodland. By definition (Maddock 2011) wood pastures are a mosaic of open and closed spaces. It is precisely the combination between different areas which makes Epping Forest ecologically and aesthetically special.

It is recommended that bracken is controlled to encourage tree recruitment, whilst recognising that it can be a habitat for specialized wildlife and pioneers species (Pakeman and Marrs 1992 in Humphrey and Swain 1997). Bracken control could be partly tackled by cattle grazing, provided that the number of animals and timing was carefully considered, as an excessive grazing pressure can limit tree regeneration (Humphrey & Swaine 1997; Mountford et al. 1999). Low grazing can enhance biodiversity of the ecosystem, as it will enhance spatial heterogeneity through the animals' depositions and selective grazing.

As Puettmann et al. (2009) stated "ecosystems are never in equilibrium". Wood-pastures are no exception, and traditionally tree recruitment on these landscapes has been associated with shrub encroachment (Varga & Molnar 2014). The restoration should not aim to establish static landscapes (Brown 2009), but rather allow some small-scale changes and recreate a balance between open and closed spaces that used to be achieved in the past through constant management. Wood pastures are and have been intrinsically linked to humankind and hold an immense wealth of socio-cultural values, which should not be loss. The reintroduction of pollarding and grazing contributes to preserve part of these at the same time they enhance biodiversity and help to attract visitors to the site.

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Appendix A. Survey protocol

The purpose of this appendix is to describe the methodology followed to perform the field work. The materials used were:

GPS Trimble 2 Tape measures of 50 m 8 Tent pegs 20 Bamboo sticks 220 m of cord One 1 m x 1 m plot Warning tape	Point-sample markers A mallet A clipboard, filed templates and pens A camera Aerial image with localized parcels Chalk

The protocol followed was:

1. Using the GPS and on-desk selected coordinates, walk to the location of the predefine-parcel. Localize centre point and mark it with a point-sample marker
2. Using GPS and the tape measure walk 25m north from the centre point. Mark this point with a point-sample marker. Leave the tape measure forming a line between the two points
3. Define a perpendicular line to that line using the tape measures to draw a 3:4:5 triangle
4. Walk 25m on this direction and mark the point with a tent peg. This will be the first corner (north east) of the 50x50 quadrant
5. Write down the GPS coordinates of the first corner
6. Repeat operation on the contrary direction. Set a tent peg on the second or (North west) corner
7. Repeat steps 2-6, setting the other 2 corners
8. Set the cord around the tent pegs, defining the borders of the parcel
9. If the cord is not visible enough, add some brightly coloured adhesive to the cord
10. Take a photograph of the parcel
11. Carry out the inventory of the 50x50m2 quadrant, starting on the NE corner and move along towards the W until the NW corner is reached. Then take a step back and move along the E. Repeat until all the trees are surveyed. On each tree:
    - Identify species
    - Identify pollarded and health status
    - Measure girth at DBH
    - Write all of these down on the field template and mark the tree with chalk
12. With the tape measure, localize and mark (using point-sample marker) the middle point of each the semi diagonal of the parcel.
13. Look for the nearest tree of each species hornbeam, oak and beech and measure their canopy using the tape measure. Measure it along two diagonals.
14. Build the 4 m x 4 m quadrants taking the semi diagonal middle points as centre. To build the parcels, repeat steps 2-9 but using 4 m length
15. Perform the 4 x 4 m^2 parcel inventories.
    - Identify species and estimate their cover abundance using Braun-Blanquet scale.
    - Inside the 4 m x 4 m randomly place the 1 m x 1 m plot and identify and count the tree seedlings.

Appendix B. Justification of the choice cohorts lengths

The cohort length is not an attribute of tree populations that has been widely included in the scientific literature. Therefore, their value for the studied species was inferred from information about their botany.

Beech tree lifespan ranges between 150-300 years, but they may reach 500 years, especially when pollarded. Once they turn 50 years old the trees starts producing flowers. The beech saplings are extremely shade tolerant and can linger during years with very few light, waiting for the canopy to open up to growth. Beech regeneration has been reported as continuous in continental European forests (Packham et al. 2012) but in England it's regarded as unreliable (Mountford et al. 1999). The reason for this could be that beech seeds need to have been covered by a film of water before they can sprout, and do not grow well on open conditions neither so their regeneration could be subjected to constraints (Packham et al. 2012). Beech were assigned 70 year-cohorts in regards of the flowering age -50 years- and adding a 20 years margin for an effective regeneration episode to occur.

The same cohort's length was applied top hornbeams, which have a shorter lifespan- 150 years on average, which are often surpassed by pollarded trees that life for centuries- and start producing flowers earlier as well –once they reach 30 years- but which require bigger canopy gaps than beech to regenerate because they have a lower tolerance to shade conditions (Szwagrzyk et al. 2012). As holly trees are highly shade tolerant and they produce the first flowers with 20 years and reach their top production with 40 years (Watson Featherstone 2015), they were assigned 50 years-cohorts.

Appendix C. Presentation of the results from statistical analysis

The results from the statistical analysis differ on the way they are presented, owning to the type of data they represent (Davenport 2013). Normal distributions are described with tables containing their means and standard deviation. Non-normal distributions such as tree and seedlings counts are not fully described by their mean. In these cases the median (that is, middle range value of the distribution) and the median absolute deviation (mad) were included on the tables. The mad, which is also called the absolute deviation around the median is calculated as "the median of the absolute values of the residuals from the data's median's" (Davenport 2013):
$MAD = Median\left(|x_i - median_j(x_j)|\right)$ wherex_i, x_j, .. are the values from our data.

In other cases non-normal distributed are described graphically, using boxplots over jitter plots. Boxplots display boxes, showing the interquartile range, which contains half the observations made. The median is the line inside each box and the whiskers, that is, the vertical lines outside the boxes, represent 1.5 times the interquartile range. The points beyond the whiskers are outliers.
The jitter plot is a scatter plot in which some random noise is added in order to display the observations which are overlapping each other.

Appendix D. Species and wood pasture type interaction

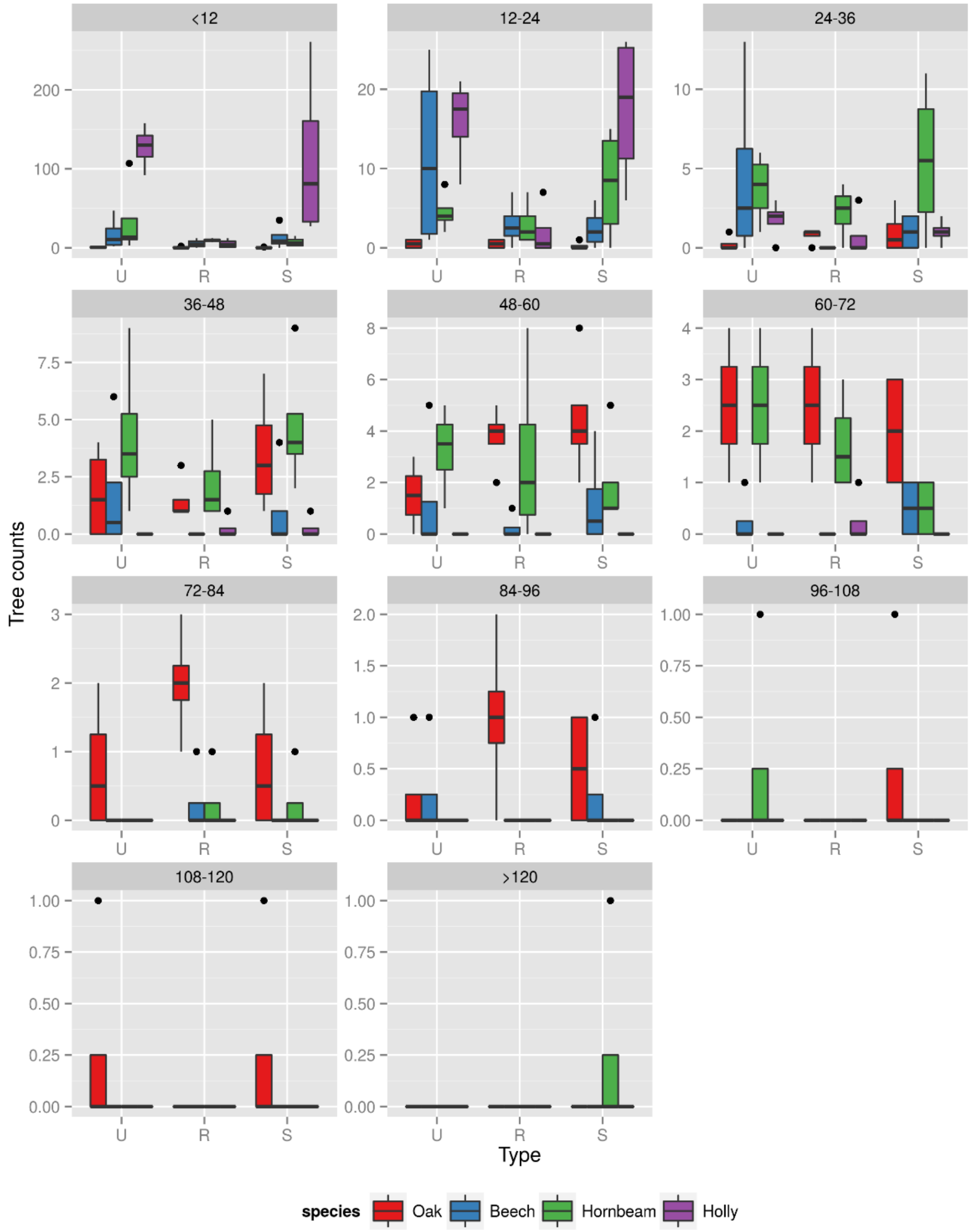

Figure 12. The count of trees per dbh class in the unrestored (U), restored (R) and secondary (S) wood pasture in oak (red), beech (blue), hornbeam (green) and holly (purple). The counts are presented per dbh class, so that each graph displays the tree counts of a particular dbh class in each species and in each wood pasture type. Note that the graphs differ on the scale of the vertical axis. Note: This figure displays the interaction between species and wood pasture type on the tree counts. The test is run with 44 observations per species and type, that is one for each dbh type (11 in total) and one for each replicate (4 in total). The data was not aggregated per dbh type as it is for site because this would reduce the test power.