Historical maps confirm the accuracy of zero-inflated model predictions of ancient tree abundance in English wood-pastures.

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CONFLICT OF INTEREST

All authors declare there are no conflicts of interest associated with any of the work in this manuscript.

AUTHORS' CONTRIBUTIONS

VN conceived of the presented idea and performed the modelling and data analysis. TR, FG and NA verified the methods and provided input to the supervision of the project. NA assisted especially in establishing the methodology for the verification work. The initial draft was written by VN with final draft input from all authors.

DATA AVAILABILITY STATEMENT

Authors can confirm that all datasets mentioned in this manuscript can be found as open source datasets at the online locations referenced in the text, tables or figures. Data and code also available via figshare: https://doi.org/10.6084/m9.figshare.12942821.v1 (Nolan et al., 2021).

ABSTRACT

1. Ancient trees have important ecological, historical and social connections, and are a key source of dead and decaying wood, a globally declining resource. Wood-pastures, which combine livestock grazing, open spaces and scattered trees, are significant reservoirs of ancient trees, yet information about their true abundance within wood-pastures is limited. England has extensive databases of both ancient trees and wood-pasture habitat, providing a unique opportunity for the first large-scale, national case study to address this knowledge gap.

2. We investigated the relationship between the abundance of ancient trees in a large sample of English wood-pastures (5,571) and various unique environmental, historical and anthropogenic predictors, in order to identify wood-pastures with high numbers of undiscovered ancient trees. A major challenge in many modelling studies is obtaining independent data for model verification: here we introduce a novel model verification step using series of historic maps with detailed records of trees to validate our model predictions. This desk-based method enables rapid verification of model predictions using completely independent data across a large geographical area, without the need for, or limitations associated with, extensive field surveys.

3. Historic map verification estimates correlated well with model predictions of tree abundance. Model predictions suggest there are ~101,400 undiscovered ancient trees in all wood-pastures in England, around 10 times the total current number of ancient tree records. Important predictors of ancient tree abundance included wood-pasture area, distance to several features including cities, commons, historic Royal forests and Tudor deer parks, and different types of soil and land classes.

4. *Synthesis and Applications:* Historical maps and statistical models can be used in combination to produce accurate predictions of ancient tree abundance in wood-pastures, and inform future targeted surveys of wood-pasture habitat, with a focus on those deemed to have undiscovered ancient trees. This study provides support for improvements to conservation policy and protection measures for ancient trees and wood-pastures.

KEYWORDS

Ancient tree, Conservation, Historic maps, Ordnance survey, Species abundance, Wood-pasture, Zero-inflation

INTRODUCTION

Ancient trees (often referred to as ‘veteran trees’ or ‘large, old trees’) are found worldwide and are important ecological structures, in particular as a source of dead and decaying wood, in many ecosystems (Read, 2000; Siitonen, 2001; Butler et al., 2002). The ‘veteran’ characteristics that define an ancient tree, such as a hollowing trunk and branches, crevices and water-filled pools, enable them to act as ‘keystone elements’, supporting a wide range of saproxylic and non-saproxylic species, including fungi (Boddy, 2001), invertebrates (Speight, 1989), epiphytes (Read, 2000; Ranius et al., 2008) and larger vertebrates (Rasey, 2004; Ruczynski & Bogdanowicz, 2008). At a landscape scale, ancient trees provide ecosystem functions and have strong regulatory influences on local nutrient cycles and microclimate (Rubino & McCarthy, 2003; Lonsdale, 2013), but they are considered most important in terms of their contribution to the connectivity of deadwood habitat across the landscape, which is thought to be vital for the conservation and persistence of many endangered species (Lindman et al., 2020). Additionally, ancient trees are known for their cultural and historical ties, and can inform us of past land management and use, historical climate and changing social behaviours (Rackham, 1976, 1980; Read, 2000), as well as providing valuable tourism opportunities (Rackham, 1994; Lonsdale, 2013).

Wood-pastures, royal forests and historic parklands are habitats which often contain an abundance of ancient trees (Rackham, 1994; Hartel et al., 2013; 2018; Farjon, 2017). These also include deer parks, commons (land on which local people had some traditional shared grazing or harvesting rights), and chases (private hunting forests) (Rackham, 1976). These habitats, referred to here collectively as ‘wood-pasture’, usually combine livestock grazing with scattered trees either in maiden form or actively managed as pollards, where the tree is periodically cut to avoid livestock browsing, and the trunk and branches are removed for use as animal fodder, or for particular industrial purposes (Petit & Watkins, 2003). The resulting landscape is productive, open and relatively undisturbed by development or agriculture, providing an ideal environment for the development and persistence of ancient trees (Quelch, 2002; Hartel et al., 2018). Wood-pastures also more generally support high densities of rare flora and fauna (Rosenthal et al., 2012), and their conservation value is recognised throughout Europe (Dorresteijn et al., 2013; Hartel et al., 2018). Several studies have mapped European wood-pasture (Hartel et al., 2013; Plieninger et al., 2015), and it is estimated that it covers an area of ~203,000 km^2 (Plieninger et al., 2015).

Despite their importance, ancient trees are in global decline (Gibbons et al., 2008; Fischer et al., 2010), particularly due to the spread of disease and pests, urbanisation, and agricultural expansion (Read, 2000, ATF, 2005, 2011; Lindenmayer et al., 2012). In addition, there is a lack of tree planting and appropriate management to ensure the continuity and replacement of ancient tree populations and dead-wood habitats (Read, 2000). To add to this, wood-pasture is also considered an increasingly threatened habitat, particularly across Europe (Hartel & Plieninger, 2014; Forejt et al., 2017), where overgrazing, the decline of old trees, and land-use intensification and conversion are having major impacts (Kirby, 2015). Additionally, although the connection between wood-pasture and ancient trees is generally agreed upon, few studies, with the exception of Hartel et al. (2013; 2018) and Moga et al., (2016) in Romania, have investigated the true abundance or distribution of ancient trees within wood-pastures at an international or even a national scale. Further investigation and quantification of the links between ancient trees and wood-pasture at larger scales (i.e. across other regions, countries or continents), would enable more effective conservation and protection of ancient trees.

Compared to Europe and the rest of the world, both the number of ancient trees and the concentration of wood-pastures in the UK, and particularly in England, is extremely high (Rackham, 1994; Fay, 2004; Lonsdale, 2013). This is often attributed to the long history of continuous Royal and aristocratic land ownership and management of forests and parkland (Butler et al., 2002). Additionally, the UK has the most comprehensive ancient tree database in the world: the Ancient Tree Inventory (ATI). The ATI began as a citizen-science collaboration project in 2004 between the Woodland Trust (WT), the Ancient Tree Forum (ATF) and The Tree Register of the British Isles (TROBI), and over 200,000 ancient and other notable trees have been mapped since its beginning (Butler, 2014; Nolan et al., 2020). The extraordinary number of ancient trees recorded in the ATI presents a unique opportunity to investigate quantitatively the large-scale determinants of ancient tree abundance in wood-pastures, with the aim of identifying sites likely to contain undiscovered ancient trees across England.

The non-random, ‘ad-hoc’ recording method of the ATI means that the inventory is thought to be far from complete, and many more ancient trees in the UK, including those at risk from the many factors that threaten their survival, are likely to have gone unrecorded. This also means the ATI is likely to suffer from high levels of sampling bias, because certain geographical locations or time periods have been more extensively surveyed than others (Phillips et al., 2009; Mair & Ruete, 2016). We suspect that there are many partially or completely un-surveyed sites, including wood-pastures, that actually contain ancient trees; currently ~ 44 % of all ATI ancient trees are located in a wood-pasture, yet these wood-pastures represent only ~ 9 % of the total number of wood-pastures across England. The patchy recorded occurrence of ancient trees means that the data display a high level of zero-inflation (i.e. there are more wood-pastures with no trees than expected under standard statistical distributions), which presents a problem when trying to model tree abundance using conventional methods. Hence, in the present study we use zero-inflated (ZI) models to describe and predict abundance at the national scale.

The accuracy of large-scale spatial models of the distribution and abundance of organisms is best assessed by comparison with independent data collected in the field (Chatfield, 1995). However, such data are seldom available and model verification typically involves retaining one or more subsets of the original data as pseudo-independent 'test' data sets. In our study, we take advantage of the uniquely detailed mapping of trees in England over the past 200 years to perform a novel form of model verification using completely independent data on the location of the organisms we are attempting to model. We use of a series of historical Ordnance Survey maps with detailed records of trees across England, together with the National Tree Map (NTM) (Bluesky National Tree Map, 2015) which depicts the current location, extent and height of all trees above 3 m across England. By overlaying these maps across time, abundance estimates were obtained for a randomly selected sample of wood-pastures to verify model accuracy and predictive power.

Species distribution modelling (SDM) typically aims to determine the fundamental niche of a species using a combination of abiotic and biotic predictors (Phillips et al., 2006; Elith & Leathwick, 2009). Common predictors are usually based on either climate (e.g. temperature or precipitation), topography (e.g. elevation or slope) or habitat (e.g. vegetation cover) (Wisz et al., 2013; Hof et al., 2012; Barbet-Massin and Jetz, 2014). It is less common to model species using variables that reflect human and socio-cultural influences (Żmihorski et al., 2020), yet in the modern world the distributions of many species are at least in part determined by humans (Boivin et al., 2016). Modelling the distribution of ancient trees, which have strong human and historical links to the landscape, presents a unique opportunity in our study to explore the potential of including anthropogenic and historical predictors in SDMs to provide meaningful and accurate predictions of species locations. We aim to recognise the important role humans play in determining the contemporary niche of such a long-lived and economically/culturally important taxon: our models include a variety of unique predictors including those that capture anthropogenic influences and landscape history, something which is only possible because of the excellent data available for these predictors across the UK.

This study provides quantitative evidence for the drivers of the important relationship between ancient trees and wood-pastures in England, and highlights the international need to establish and expand ancient tree inventories such as the ATI. The study also highlights the high value of wood-pasture habitat, which is wide-spread across Europe, North America and other areas, in supporting populations of ancient trees. We hope our findings will assist with conservation efforts, both in the UK and worldwide, to locate and protect our ancient tree populations, and to ensure their survival into the future.

MATERIALS AND METHODS

Study area and ancient tree records

Data describing the distribution of 5571 mapped wood-pastures in England were obtained from Natural England (Wood Pasture and Parkland BAP Priority Habitat Inventory for England, accessed 04/12/17) (Fig. S1). The digitised wood-pasture polygons cover an area of ~2780 km^2 (see supplementary information for additional description). Ancient tree records in England were obtained from the ATI (Woodland Trust, accessed 17/12/18). In England, an ancient tree is defined generally as any tree that shows 'veteran' characteristics (e.g. hollow trunk, crown retrenchment, crevices and the presence of saproxylic organisms) (ATF, 2008), and that is older than most individuals of the same species (Nolan et al., 2020). The age of ancient trees is estimated based primarily on girth (as in White 1998), but also takes into account their environment and growing conditions. The ATI recording process requires volunteers to use the Woodland Trust's Ancient Tree Guide No. 4 (ATF, 2008) or their website (https://ati.woodlandtrust.org.uk/what-we-record-and-why/what-we-record/) to determine accurately whether a tree is ancient. In addition, approximate age-girth relationships are provided for the most common UK tree species (Woodland Trust 2008). Each record then receives a second visit from a trained Woodland Trust ancient tree verifier to check the tree before it is added officially to the ATI.

As a final step, the reliability and validity of each record in the ATI has previously been assessed by the Woodland Trust using a star rating system between one (least reliable) and five (most reliable) (Table S1) (Nolan et al., 2020). Consequently, we excluded all unverified (one or two star) records, and 185 records with incorrect or missing grid references. 10,450 records of ancient trees in England were retained, 4,582 (43.8%) of which fall within a wood-pasture polygon. Ancient tree abundance (number of ancient trees per wood-pasture) was subsequently calculated. Abundance ranged from 0 to 392, but was right-skewed with 5,092 (91.4%) wood-pastures containing no ancient tree records (Fig. S2) and only 479 (8.6%) wood-pastures containing records. Thus, the data showed severe zero-inflation (i.e. there were significantly more zeroes than expected when compared to a standard Poisson distribution) (Van den Broek test 1995: χ^2=14,356.69, df = 1, $p < 0.001$).

Predictor variables

A variety of sources was used to collect data on 21 characteristics for each wood-pasture (Table 1, Table S2). Wood-pasture area (km^2) was square-root transformed due to the large range of values and all 16 numeric predictors were z-transformed. A variety of anthropogenic factors were considered, including both the locations of towns (small settlements) and cities (large settlements), as defined by the UK Government (Table S2). There are many more towns across England (1,232) than cities (109), so both were included to assess their influence on ancient tree distributions within wood-pastures. We did not include interactions between environmental variables as predictors because we had no a-priori hypotheses about particular interactions, there was a very large number of possible interactions, and the models we created with just main effects already had high complexity. Effect size/direction and significance was assessed by z-tests of coefficients in a maximal model containing all predictors; we used a backward stepwise model-reduction approach, and likelihood ratio tests, to provide an alternative assessment of effect significance, the results of which were broadly similar and are reported in supplementary materials (Table S8).

Under-represented categories of the three categorical predictors (land classification, countryside type and soil type) across English wood-pastures were combined to aid model fitting (see Table S3 and S4 for more information). Two binomial predictors were used: whether the wood-pasture covered agricultural land or not (4,653 wood-pastures are on agricultural land) (see Table S5 for more information), and whether the wood-pasture covers land owned by the National Trust (NT). The NT is an environmental and heritage conservation charity and has the largest number of subscribing members of the public of any organisation across England, Wales and Northern Ireland. Since its foundation in 1895, the NT has acquired over 350 properties and 2470 km^2 of land, and there are 244 wood-pastures on NT land.

The minimum resolution possible at which to obtain the categoric predictors (including agricultural land) was 1-km^2, so the value (or average/ most common value if a wood-pasture covered multiple 1-km^2 grid squares) was extracted for each wood-pasture. As a result, many wood-pastures, which are recorded at a smaller resolution than the categoric predictors, fell within squares not necessarily designated as specific wood-pasture or parkland type habitat: some wood-pastures were assigned categories of land use based on squares whose primary designation was agricultural, urban or woodland. Nevertheless, including these land use predictors provides key information about the local environment and surroundings of the wood-pastures, which we believe could be important determinants of ancient tree distributions. Finally, due to the low prevalence of most ancient tree genera (Table S9) across the wood-pastures, we chose not to model tree genera/species separately. All data processing was carried out in ArcGIS (ESRI, 2011) and R (R Core Team, 2018).

Statistical modelling

Zero-inflated (ZI) models (Lambert, 1992) have been used effectively in ecology to model species data with excess zeroes and have been shown to be superior to equivalent Generalised Linear Models (GLMs) (Potts & Elith, 2006). This is because ZI models have two parts producing two sets of coefficients; a 'zero' logistic component modelling the probability of an observation being an excess zero, and a 'count' component generating the count estimates (see Lambert, 1992 or Welsh et al., 1996 for more information), and thus two different types of model predictions can be produced (Zeileis et al., 2008; Nolan et al., in prep). If all excess zeros are 'true absences' (arising from either unsuitability of the habitat or stochastic ecological processes) then the 'zero component' models causes of biological aggregation. If some or all excess zeroes arise from 'false absences' (arising from sampling, detection or misclassification errors), abundance predictions from the whole ZI model (hereafter known as 'model abundance' predictions) reflect the abundance that would be observed in the presence of the sampling error in the data. In this case, predictions produced purely from the 'count' component of the ZI model (hereafter known as 'true abundance' predictions), will typically be a better reflection of the true ecological or environmental processes that determine species abundance. As we suspect the excess zeroes arise primarily from the lack of sampling of wood-pastures, we assume here that the ZI 'zero' component will predominantly model the processes determining the likelihood that a wood-pasture has been sampled, whereas the 'count' component will model the ecological processes determining the suitability of the wood-pastures for ancient trees.

Ancient tree abundance data were modelled using two ZI models with different distributions: a zero-inflated Poisson model (ZIP) and a zero-inflated negative binomial (NB) model (ZINB), using the 'pscl' package in R (Zeileis et al., 2008) (see supplementary information for additional details). Fitting models using ancient tree density (taking into account wood-pasture area) was considered, but we concluded that using ZI models with wood-pasture area as a predictor would better deal with the issue of zero-inflation in our data. An additional benefit of ZI models is the ability to examine the coefficients from the zero-component, thereby gaining insight into potential predictors of excess zeroes; this is something which fitting a GLM using tree density as the dependent variable would not have allowed us to do. Comparative model fit to the data was assessed using Vuong's (1989) closeness test for non-nested models, likelihood ratio tests (package: 'lmtest': Zeileis & Hothorn, 2002), the significance of the Θ parameter, and visual analysis of hanging rootograms (package: 'countreg', Kleiber & Zeileis, 2016).

Model predictions from both the ZIP and ZINB models were produced using 10-fold cross validation; the data were split into 10 equal parts, with each subsample sequentially used as test data, and the other nine subsamples as the training data. Both 'true abundance' and 'model abundance' predictions were considered, as well as the predicted probabilities that each observation is an excess zero (i.e. the probability predictions from the 'zero' component only). Abundance predictions were evaluated against observed ancient tree abundance to assess each model's predictive power using Spearman's rank correlation coefficient (r_s) and root mean square log error (RMSLE). In addition, the probability of observing the data based on the predictions was calculated for each model; for every wood-pasture, a Poisson or NB probability distribution function was simulated based on the mean predicted count from the ZIP or ZINB model respectively. The natural log probability of obtaining the observed abundance under this simulated distribution was summed for all wood-pastures to produce an overall probability of obtaining the observed results. Following the evaluation of both model fit and model predictive power, only the best model (the ZINB model) then was chosen to undergo further verification using historical mapping.

Model verification

The ideal method for ecological model verification is the evaluation of predictions using an independent dataset, yet it is often time-consuming and costly to collect extra data from the field; here we propose a more efficient, novel method of verification using historic maps. Three map series were selected (Table S6), the first two of which are country-wide historic Ordnance Survey maps with detailed records of mature free-standing trees, designated as having a 'very high' or 'high' UK coverage respectively according to the EDINA Historic Digimap Service. The last map is the National Tree Map (NTM) (Bluesky National Tree Map, 2015), created using aerial photography, LIDAR data, and colour infrared imagery. The NTM is a digitised polygon-based dataset of the location, extent and height of all tree canopies over 3 m in height across England and Wales recorded as present in 2015, which is between 116-169 years after the date of the earliest map series we used. By overlaying all three map series (between 1846–2015) the persistence of individual trees can be traced over time to provide an estimate of current ancient tree abundance within wood-pastures.

All wood-pastures were then categorised into four groups based on the observed presence-absence of ancient trees and the predicted probability of being an excess ('false') zero converted into a binary variable (see supplementary information). Fifteen wood-pastures from each group were randomly selected resulting in 60 wood-pastures overall that underwent verification. Two volunteers from the Woodland Trust digitised all freestanding (i.e. non-woodland) trees within the wood-pasture polygon boundary for the first two map series by placing a single point in the middle of each Ordnance Survey tree symbol. Each of these symbols is taken to mean a mature, free-standing tree (at least ~75-100 years old) at the time of mapping (see https://maps.nls.uk/view/128076885). Only freestanding trees were selected rather than those in woodland patches as these usually were documented using a generic woodland symbol. The volunteers had no knowledge of the observed or predicted abundance of ancient trees for each wood-pasture.

NTM Canopy polygons containing a digitised tree from both the first and second Ordnance Survey map series were retained and considered to be ancient as they represented free-standing trees in 2015 which were probably already mature 116-169 years previously, meaning that they were at least 191 years old, and likely to be over 200 years old; the majority of trees reach the mature stage (prior to becoming ancient) by 100 years old (White, 1998). The abundance per wood-pasture of probable ancient trees was thus obtained, and we compared this value (using correlation) to the abundance predicted by the models, to verify those predictions. It is important to note that many species are only likely to reach ancient status sometime after the age of 200, and hence some of the trees assumed to be ancient from our mapping exercise may have been misclassified. Nevertheless, we assumed that trees which were recorded in all map sets were much more likely to be ancient than other trees alive today, and hence we believe the estimate derived from this analysis is a good proxy for true ancient tree abundance. We aimed to account for discrepancies and errors between the map series that may have occurred from either the original mapping methods or the digitising of the paper maps, by allowing an area of uncertainty around each historic tree. The verification process was therefore carried out for three different levels of accuracy using 1) the digitised tree point itself, 2) a 5-m buffer around the digitised tree and 3) a 10-m buffer around the digitised tree.

Verification abundance estimates were assessed against the ZINB model predictions (both 'true abundance' and 'model abundance') using Spearman's Rank correlation coefficient (r_s). Linear regression models were fitted in R, modelling the predictions in relation to the verification estimates for the 60 wood-pastures across the three different levels of accuracy (no buffer, 5-km and 10-km). These models were then used to predict total ancient tree abundance across a) all wood-pastures, b) wood-pastures currently containing ancient tree records and b) wood-pastures with no records.

RESULTS

Genera, size and form of ancient trees in wood-pastures

There were 4,582 ancient trees recorded in the ATI across all wood-pastures in England. Of these, the majority (59.5%) are Oaks (*Quercus* sp.) (Table S9). The next most frequent genus is Beech (*Fagus* sp.), comprising 10.7% of records, followed by Sweet Chestnut (*Castanea* sp.) with 8.6% of records. Although there are a total of 31 genera noted across all wood-pasture, 23 contribute less than 1% to the total number of ancient tree records. The mean measured girth of all trees across the wood-pastures was 5.09 m (lower quartile: 3.75 m, upper quartile: 6.39 m), with the majority recorded as being in maiden (free-standing, unmanaged) (43.0%) or pollard form (36.8%).

Model performance, parameter estimates and predictions

Abundance of ancient trees in wood-pastures in England was best modelled with a zero-inflated negative binomial (ZINB) model, which accounts for biological overdispersion as well as additional zero inflation. The ZINB model provided a more appropriate fit to the training data than an equivalent zero-inflated Poisson (ZIP) model, based on the Vuong AIC-corrected test ($z = -5.974$, $p < 0.001$) and the likelihood ratio test ($\chi^2 = 6{,}089.3$, $p < 0.001$). Additionally, the significant ϴ parameter in the ZINB model suggests overdispersion is present in the data, meaning the ZIP model is not appropriate to use with this dataset (Table S7). Visual analysis of hanging rootograms for each model suggest the ZIP model highly under-predicted wood-pastures with zero records and over-predicted wood-pastures with small numbers of records (less than 10) (Fig. 1).

The performance of the ZINB 'true abundance' predictions, based on the test data, was significantly better than that of the ZIP for all three evaluation metrics (predicted probability of obtaining results, r_s and RMSLE) (Fig. 2). There was no difference in the predictive power of 'model abundance' for two of the metrics (predicted probability of obtaining results and RMSLE) but ZINB 'model abundance' predictions correlated more strongly with original ancient tree abundance per wood-pasture than those from ZIP. Based on the best performing model (ZINB), the 'true abundance' predictions suggest that there are 13,848 ancient trees across all wood-pastures in England, which is over 3 times the total number already known (Table 2a).

Parameter estimates of the best-performing model (ZINB) suggest ancient tree abundance is most strongly influenced by the type of soil or land class within which the wood-pasture is situated (Fig. 3; Table S7), followed by a strong negative influence of length of minor roads per km^2 of wood-pasture and a positive effect of wood-pasture area. Increasing distance to the nearest city and nearest Royal forest, as well as decreasing distance to the nearest Tudor deer park or common, also have significant but slightly weaker influences on abundance (Table

S7). Ancient tree abundance is also significantly higher on National Trust and non-agricultural land (Table S7). The logistic parameter estimates from the ZINB model provide insight into the factors that influence the odds of a wood-pasture being an excess (‘false’) zero, which is most likely to arise because a wood-pasture has not been sampled and has undiscovered ancient trees. Such wood-pastures are more likely to be large, have a low coverage of forest or woodland and are on agricultural land. Nevertheless, it is soil type and land class that have the most influence on the probability that a wood-pasture is an excess (‘false’) zero (Table S7).

Model Verification

Verification estimates of ancient tree abundance across 60 selected wood-pastures ranged from 0 to 2,108 across the three levels of spatial accuracy, with mean values ranging from 20 (standard error = ± 4) (no buffer) to 202 (standard error = ± 43) (10-m buffer). All predictions correlated remarkably well with the verification estimates ($r_s > 0.5$), especially the ‘model abundance’ predictions, all of which produced strong correlations ($r_s > 0.7$). Predictions performed better as we allowed for greater levels of inaccuracy in the exact location of trees in the historic maps (i.e. as buffer size increased) (Table 2c).

Additionally, 100 % of wood-pastures categorised as true positives based on data partitioning (predicted to contain records when they actually do) and 13 out of 15 wood-pastures (87 %) categorised as false negatives (predicted to contain records but currently there are none) were verified as having ancient trees using the historic maps. Results for the other two categories were more ambiguous, with 8 out of 15 (53 %) ‘true negative’ wood-pastures (correctly predicted by the model to contain no records) and 9 out of 15 (60 %) ‘false positive’ wood-pastures (predicted to not contain records when there are some) having verified ancient trees.

Based on the linear regression models of the ZI model predictions and verification estimates, the total ‘true abundance’ estimates of ancient trees in English wood-pastures ranged from 101,402 (ZINB with no buffer) to 701,925 (ZINB with 10-m buffer) (Table 2b). It is most likely the true number falls closer to the lower, more conservative estimates from the ZINB model. This estimate is 22 times the number of ancient tree records currently in English wood-pastures, and almost 10 times the total number of ancient tree records in England.

DISCUSSION

Ancient trees are keystone organisms in the landscape, and it is important to understand where they are and how they might best be protected and managed for long-term conservation. The value of these trees in terms of their ability to support and facilitate the dispersal and survival of endangered saproxylic species, particularly in the face of our rapidly changing climate, is often underemphasised (Miklín et al., 2018; Lindman et al., 2020). It is crucial that future research focuses on understanding the distribution of large, old trees and their connectivity across the landscape, to better inform the conservation of their dependent species. Our study identified important environmental and anthropogenic factors that influence ancient tree abundance in English wood-pastures. As seen in previous studies (Moga et al., 2016; Hartel et al., 2018), wood-pasture area is a strong predictor of ancient tree abundance. This is to be expected, since larger areas by definition can contain more trees, but it may also be the result of historical management and land-ownership: many of the larger wood-pastures are either royal forests or former aristocratic estates, which have actively managed trees over the centuries in ways to continuously sustain and benefit from them (Quelch, 2002). Wood-pasture habitat is an important resource for the development and persistence of ancient tree populations, yet is not considered to be self-sustaining (Quelch, 2013). Constant, active management of both land and trees is needed in the form of sustainable grazing and continuation of traditional pollarding techniques (ATF, 2009; Lonsdale, 2013).

Abundance was also influenced by three anthropogenic factors, distance to a city, length of minor roads and agricultural land. In all cases, true ancient tree abundance is higher when further away from human activity. There are many threats to the future survival of ancient trees, especially agricultural intensification (Read, 2000; Fay, 2004; ATF, 2005) and urbanisation (Le Roux et al., 2014). It is important to mitigate these threats, and implement protection measures such as Tree Preservation Orders (TPOs) or scrub planting (Read, 2000; ATF, 2009) and policy changes (Lindenmayer et al., 2014). There are substantial efforts currently being undertaken by the IUCN to include the issue of the conservation of ancient trees in the post-2020 Aichi targets, and the European Union (EU) is being urged to include them in its post-2020 biodiversity strategy. There is also a push to establish an IUCN task force for ancient trees to encourage the EU to insert their conservation into the Natura 2000 plan. Studies like ours could provide important evidence testifying to the value of these trees across the landscape in order to support their inclusion in global conservation targets and policy.

Sampling bias is a common artefact in many large species databases (Phillips et al., 2009) and is thought to be present also in the ATI. Verification of the abundance estimates confirmed that the majority (almost 90%) of wood-pastures predicted to be false absences (i.e. wood-pastures that do contain undiscovered ancient trees) did in fact contain at least one ancient tree. Model coefficients from the 'zero' component of a ZI model provide insight into the factors that influence the probability of an excess zero (Lambert, 1992), and thus inform us about predictors of sampling bias in the ATI. One such factor is the occurrence of wood-pastures on agricultural land, or land not covered by ancient woodland or forests. Citizen-science recorders are known to favour interesting areas or species (Kramer-Schadt et al., 2013); for example we found ancient tree abundance to be much higher on NT land. Agricultural land is generally less appealing for ancient tree surveys, and is also is likely to be less accessible and have fewer public rights of way. As ancient trees on agricultural land are likely to be at increased risk of mortality from increasing field sizes, soil compaction, over-grazing and fertiliser applications (Read, 2000; Fay, 2004; ATF, 2005), these areas should be a priority for future surveys which aim to identify ancient trees in need of conservation intervention.

Historic maps are an incredibly useful source of information about past land use, management and socio-cultural factors, yet they are often undervalued in scientific research (Roper, 2003). In the UK the extensive collection of Ordnance Survey maps dating as far back as 1801 provides a unique, unrivalled source of historical landscape characterisation, and has been used successfully in geographical and ecological studies (Sutherland, 2012; Visser, 2014; Cowley et al., 1999). The high level of detail included in these maps, such as the specific locations of individual trees and different types of woodland patches, presents a rare opportunity to address ecological research questions such as ours, where we are using environmental, historical and anthropological factors to model a unique type of organism that can reach an age of several hundred, or even a 1000 years.

Abundance estimates from the verification work correlated highly with the model predictions, providing strong support for a) the predictive power of the model, b) the hypothesis that many wood-pastures are 'false absences' and actually do contain ancient trees and c) the benefits of historic maps for addressing landscape-scale scientific questions. The most conservative estimate of ancient tree abundance in English wood-pastures came from the initial raw models (13,848 trees), but when calibrated against the field data, the best model (the ZINB model) with the lowest level of uncertainty (no buffer) produced an estimate of 101,402 trees. Although at first glance this may seem an overestimate, as it represents a 2112 % increase on the known number of ancient trees in wood-pastures, it is not implausible. Because only 9% of wood-pastures contain 10,450 (43%) ATI ancient tree records, a figure close to 100,000 ancient trees (i.e. a 10 times increase) is possible, depending on the completeness of sampling across all wood-pastures. Other estimates of ancient tree totals have suggested figures close to nine million ancient or "veteran" trees (the latter being trees that are starting to show 'veteran' characteristics but are still younger than ancient trees) across the whole UK (Fay, 2004). Therefore, our value of ~100,000 in wood-pastures seems if anything conservative. Either way, our predictions highlight the fact that, even in the UK, where sampling is relatively good, most ancient trees in the landscape are yet to be recorded.

Limitations to the methodology and use of the historic maps

It is important to consider the accuracy of the Ordnance Survey maps used to verify our model predictions, especially as the early historic maps are thought to have the most inconsistencies (Harley, 1968; Visser, 2014) and there are likely to be a variety of caveats with using the historic maps, resulting in both under- and overestimation of ancient tree abundance. Our decision to map only free-standing ancient trees and exclude woodland patches is likely to have contributed to under-estimation of true abundance: although frequently less common, ancient trees can be found in woodland (Rackham, 1980). Additionally, inconsistencies and the misplacement of the historic tree symbols would also result in underestimation if the tree is still around today but did not fall within an NTM canopy polygon. This risk could be relatively high, particularly as there was no standardised key for the tree symbols in the first Ordnance Survey map. Alternatively, overestimation of abundance may have occurred where the locations of trees we recorded during verification actually reflected places in which more than one individual had been recorded over time. This may be one explanation for the discrepancy between the low model estimates of total abundance and the higher estimates produced when calibrated against the field data. For example, a mature tree recorded on an early map may have been felled and another immediately planted in its place. Although we deemed this unlikely to happen, given that the interval between any two map series was around 50-100 years, barely sufficient time for many species, especially free-standing Oaks, to reach maturity (White, 1998), it could have resulted in some immature or mature trees being labelled as ancient.

Finally, both under- and overestimation of abundance could have occurred owing to the interspecific differences in the age at which a tree reaches maturity and then becomes ancient (White, 1998; ATF, 2008; Lonsdale, 2013). By assuming that a mature or ancient tree, minimally 40 years old (White, 1989) in the first County series map, will now be at least 200 years old, this time period may be too long for the shorter-lived species to survive until the present day. Many fruit trees such as plum or pear, for example, will rarely reach 100 years old. Conversely, for some species such as Yew, which is generally only ancient after 800 years, this time period may not be long enough to classify it now as ancient. However, the majority of records were Oak and Ash, both of which often survive beyond 200 years, but are very likely to show ancient characteristics by this age or soon thereafter.

Despite the apparent high level of accuracy of our model predictions, validated using the historic mapping data, we should exercise caution when considering their precision (i.e. how realistic are our estimates of total tree abundance). Caveats related to the methodology used for the creation of the original historic maps means we should be careful in our interpretation of our estimates: total estimates of tree numbers from the verification exercise are more likely to represent 'relative' rather than 'absolute' abundance. We assume that trees recorded originally in the maps were mature or large (but not necessarily veteran or ancient), and therefore it is much more likely that trees are ancient today if they appear in the maps, than if they do not. But it is nevertheless likely that some trees classified as ancient were actually not yet old enough, whilst other mature trees which were not recorded on the historic maps have survived to this day and are now ancient. At the very least the historic mapping estimates are likely to be a good proxy for the true density of ancient trees on the ground: density of trees in the map is likely to be correlated with the true value (with some error) and can therefore provide a valid dataset for model verification. A precise estimate of current ancient tree density can really only be made by validating models with independent, ground-truthing surveys. However, the uncertainty regarding the precision of our population size estimate does not diminish the value of our conclusions about both the general abundance of ancient trees in wood pastures, and the environmental and human/historical factors which predict that abundance: these predictors are of obvious value to conservation planning.

We believe the potential use and benefits of historical maps for ecological studies is high, and we aim to draw attention to the possibilities that these often underused resources offer for research at a landscape scale. Our findings provide important insight into a key habitat for ancient trees, wood-pasture, that is present in many countries across the world, and is a crucial resource for the conservation of these trees. However, it is important to note that wood pasture is largely absent, or substantially differs in structure and form in many other areas, and this, combined with a much poorer documentation of the distribution of ancient trees in such areas, suggests that further work is required to understand the extent to which we can generalise our results globally. Nevertheless, we hope that our study will not only assist with the conservation and protection of valuable UK ancient trees and wood-pasture habitat, but that it also provides evidence for the high value of wood-pastures internationally to support ancient trees, and the urgent need for more large scale research into key environmental determinants and suitable locations for these trees.

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TABLES

Table 1. *The 21 variables describing wood-pasture characteristics used as predictors in statistical models of ancient tree abundance (see Table S2 for the source and date the data were accessed).*

Type	Predictor (unit)
Numeric	Wood-pasture area (km^2)
	Distance from nearest town center (km)
	Distance from nearest major city (km)
	Distance from a royal forest (km)
	Distance from a moated site (km)
	Distance from a medieval deer park (km)
	Distance from a Tudor deer park (km)
	Distance from a commons (km)
	Cover of ancient woodland (%)
	Cover of traditional orchard (%)
	Cover of forest or woodland (%)
	Cover of buildings (%)
	Distance from a major road (km)
	Length of minor roads per km^2 of wood-pasture (km)
	Mean altitude across wood-pasture (m)
	Distance from a water course (km)
Binomial	National Trust owned land
	Agricultural Land
Categoric	Type of countryside
	Most common soil type across wood-pasture
	Most common land classification

Table 2a. *Estimates of the abundance of ancient trees for the zero-inflated negative binomial model (ZINB) based on predictions from either the 'count' component of the ZI model ('true abundance') or the whole model ('model abundance). Three wood-pastures deemed to be outliers due to extreme predictions (all 10^{11} times greater than the next highest predicted abundances) were removed.* ***2b.*** *Estimates of abundance of ancient trees for the zero-inflated negative binomial model (ZINB) based on the historical verification estimates. Estimates were obtained across the three levels of accuracy (no buffer, 5-m buffer and 10-m buffer).* ***2c.*** *Spearman's rank correlations (r_s) between the predicted ancient tree abundance from the zero-inflated negative binomial model (ZINB), and the verification estimates for 60 selected wood-pastures in England. Coefficients are shown also across the three levels of accuracy, with p values representing test significance ($p < 0.05$:*, $p < 0.01$:**, $p < 0.001$:***).*

		Model Estimates (a)	**Verification Estimates (b)**			**Spearman's Rank Coefficient (r_s) (c)**		
			No buffer	5-m	10-m	No buffer	5-m	10-m
True abundance predictions *('count' component)*	All wood-pastures	13,848	101,402	368,411	701,925			
	Wood-pastures with records	7,118	29,900	108,649	207,021	0.553***	0.582***	0.594***
	Wood-pastures without records	6,729	71,516	259,836	495,067			
Model abundance predictions *('count' and 'zero' component)*	All wood-pastures	11,306	70,284	266,208	511,783			
	Wood-pastures with records	6,909	43,120	163,330	314,008	0.701***	0.710***	0.720***
	Wood-pastures without records	4,397	27,177	102,949	197,931			

FIGURES

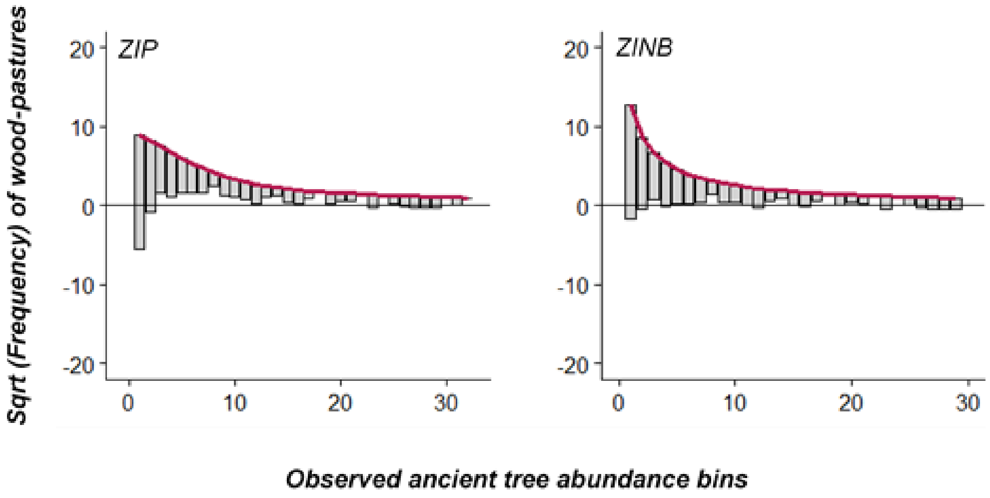

Fig 1. *Hanging rootograms to visualise the fit of the zero-inflated Poisson (ZIP) and negative binomial (ZINB) models to the ancient tree abundance data in English wood-pastures. The (square root) expected number of wood-pastures containing a certain ancient tree abundance is represented by the red line, and the observed number of wood-pastures by the grey bars. Therefore, bars that fall below a count frequency of zero are being under-predicted in a particular count bin, and bars that do not reach a count frequency of zero are being over-predicted by the model.*

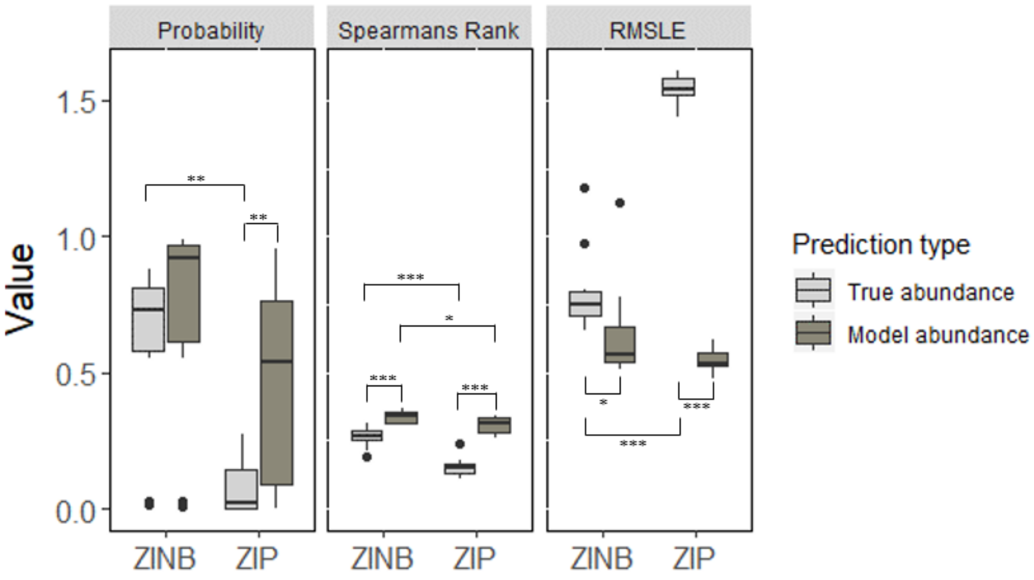

Fig 2. *Evaluation of abundance predictions from the zero-inflated Poisson (ZIP) and negative binomial model (ZINB). Two types of abundance predictions are evaluated: 'true abundance' predictions from the 'count' component of the ZI models and 'model abundance' predictions from the whole ZI model. Values shown represent the median, quartiles and range across all 10 cross-validation folds. See Materials and Methods for explanation of the evaluation metrics. Significance levels are represented by p < 0.05 = *, p < 0.01 = **, p < 0.001 = *** and were calculated using a two-samples Wilcoxon Rank Sum test.*

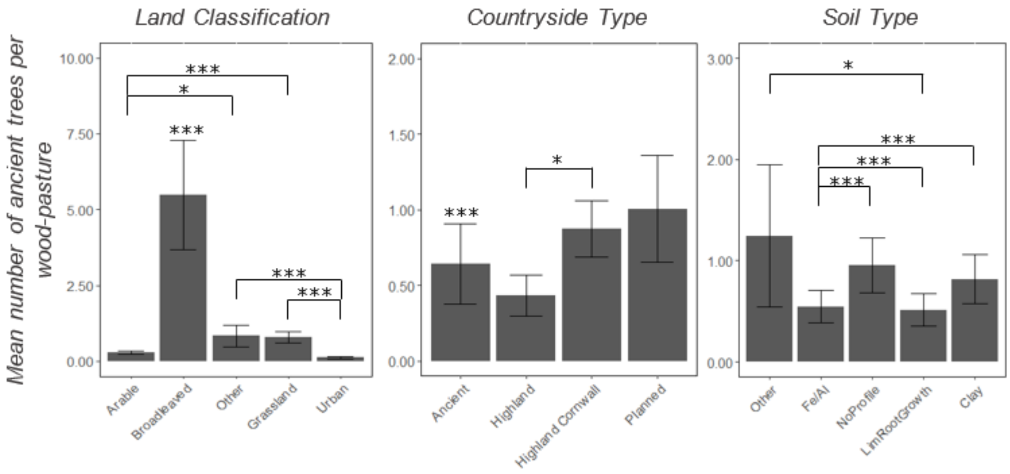

Fig 3. *Mean number of ancient trees per wood-pasture across each categorical predictor. Error bars = ± 1 SE. Significantly different categories are shown using brackets (Dunn's Test of Multiple Comparisons using Rank Sums: *** = p < 0.001, ** = p < 0.01, * = p < 0.05). Categories with no brackets associated with one or more * are significantly different from all other categories.*