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Functional and ecosystem service differences between tree species: implications for tree species replacement

R. J. Mitchell[1] · R. L. Hewison[1] · R. K. Haghi[1] · A. H. J. Robertson[1] · A. M. Main[1] · I. J. Owen[1]

Abstract

Key message **Tree species differ in their functioning at the scale of an individual tree which will result in differences in ecosystem service provision. Replacement trees for diseased trees should take account of functional differences.**

Abstract Globally tree species composition is changing due to species loss from pests and pathogens. The impact of this change on ecological functioning is rarely tested. Using six sites across the UK, with multiple tree species at each site, we test for functional differences between three species threatened by disease in the UK: *Quercus petraea*, *Q. robur* and *Fraxinus excelsior* and six other species: *Acer pseudoplatanus*, *Castanea sativa*, *Fagus sylvatica*, *Quercus cerris*, *Quercus rubra*, and *Tilia x europaea*, which have previously been suggested as ecological replacements. Differences between species were detected for all the variables measured: nitrogen mineralization, decomposition rate, total soil carbon and nitrogen, soil pH, soil temperature, and bark water holding capacity. Non-native *Quercus* species were only suitable replacements for native *Quercus*s for some of the functions measured but replicating native *Quercus*s functioning using a mixture of other species may be possible. The functioning of *F. excelsior* was different from most other tree species, suggesting that replicating its functioning with replacement tree species is difficult. The work highlighted that which species replaces diseased trees, even at the scale of single trees, will impact on the functions and ecosystem services provided.

Keywords Carbon sequestration · Ecosystem services · Ecological functions · Nutrient cycling · Temperature regulation · Tree diseases

Introduction

Trees are 'foundation' species (Boyd et al. 2013; Ellison 2005); individuals that define much of the structure of a community by creating locally stable conditions for other species, and by modulating and stabilizing fundamental ecosystem processes (Ellison 2005). As foundation species, trees influence many ecosystem functions such as primary production, soil formation, and nutrient cycling, and provide ecosystem services such as fibre, energy, carbon

sequestration, and climate regulation (Boyd et al. 2013; UK NEA 2011).

When forests of different tree species are compared, differences in their functioning can be detected. Forests, or areas within forests, dominated by different tree species have been shown to differ in their soil organic matter content (Cha et al. 2019), leaf litter decomposition rates (Albers et al. 2004; Berger et al. 2015), leaf litter chemistry (Reich et al. 2005; Ukonmaanaho et al. 2008), soil chemistry (Bonifacio et al. 2015; Cools et al. 2014; Langenbruch et al. 2012; Lorenz et al. 2004; Marcos et al. 2010), soil carbon storage (Oulehle et al. 2016; Vesterdal et al. 2012), and soil pH (Augusto et al. 1998). Trees not only occur in forests but also as isolated trees outside forests in parks, gardens, and hedgerows. In Britain, there is estimated to be a total canopy cover of 97, 000 hectares associated with lone trees (National Forest Inventory 2017). Whether differences between tree species in ecosystem functioning can be detected at an individual tree level is unknown.

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Understanding differences in function between tree species is crucial at this time of rapid change in tree species composition due to the recent increase in the number of pests and pathogens having catastrophic impacts on tree species (Boyd et al. 2013). For example, chestnut blight by *Cryphonectria parasitica* has caused the near complete loss of *Castanea dentata* in North America (Jacobs 2007), Dutch elm disease has caused a similar loss of *Ulmus* spp. in Europe and North America (Potter et al. 2011), and several species of *Pinus* spp. around the world are now threatened with the fungus *Gibberella circinata* which causes pine pitch canker (Wingfield et al. 2008). In the UK, in common with most of mainland Europe, *Fraxinus excelsior* is dying due to the ascomycete *Hymenoscyphus fraxineus* (Kjær et al. 2012; Baral et al. 2014), and *Quercus robur* and *Q. petraea* are declining due to Acute Oak Decline (Denman et al. 2014), Chronic Oak Decline (Denman and Webber 2009), Oak Processionary Moth (Tomlinson et al. 2015), and a variety of powdery mildews (Lonsdale 2015). *Fraxinus excelsior* and *Quercus robur/petrea* are the UK's most common and second most common non-woodland trees (Forestry Commission 2003).

A rapid loss of trees due to disease and increases in dead organic matter have been shown to cause changes in functioning at the forest scale (Hicke et al. 2012). In the longer term, changes in functioning following widespread death of a tree species will be determined by which tree species, if any, replaces the diseased one. Lovett et al. (2010) studied the impacts of 60 years of decline in *Fagus grandifolia* caused by the beech bark disease. *F. grandifolia* was replaced by *Acer saccharum* and the change in species composition resulted in increased litter decomposition, decreased soil C:N ratio, and an increase in extractable nitrate in the soil and nitrate in the soil solution. Hill et al. (2019) modelled differences in ecosystem properties between *F. excelsior* and other tree species which might replace *F. excelsior* based on tree traits. They showed that in some areas of Britain, provision of ash-associated traits, and hence related ecosystem properties, could be reduced by over 50% if all ash is lost. However, compensatory growth by other species could halve this impact in the longer term.

In some instances which tree species replaces a diseased tree will be determined by natural successional processes, but in other cases, it will be determined by human intervention. When alternative tree species for replacing diseased species are discussed, it is usually with respect to their suitability for commercial forestry or aesthetic value, rather than their similarity in ecological functioning to the diseased species. No tree species will completely replicate the functioning of another species. However, it is important to consider the change in functioning that will occur when one tree species replaces another and, if the objective is to maintain the existing ecosystem functioning as far as possible, then it is important to know which tree species will facilitate this.

Here, we test if there are functional differences between trees species; specifically, in nitrogen mineralization and decomposition rate, total soil carbon and nitrogen, soil pH, soil temperature, and bark moisture holding capacity. This is a far wider range of functions than is usually assessed at one time and uniquely assesses differences between individual trees outside woodlands. We assessed these functions for the British oak species *Quercus petraea* and *Q. robur* and *Fraxinus excelsior* and six other tree species: *Acer pseudoplatanus*, *Castanea sativa*, *Fagus sylvatica*, *Quercus cerris*, *Quercus rubra*, and *Tilia x europaea* which have previously been suggested as replacement tree species for *F. excelsior* and/or *Q. petraea/robur* (Mitchell et al. 2014, 2019). We test the following hypotheses. (1) There are differences between tree species in their functions at the scale of the individual tree. (2) *Fraxinus excelsior* is significantly different in the functions which it provides compared to the other tree species tested; Mitchell et al. (2014) and Mitchell et al. (2016) suggested that replicating the functioning of *F. excelsior* using these other tree species is problematic as its functioning is very different. (3) The UK native oak species, *Q. petraea* and *Q. robur,* are significantly different in their functioning to *C. sativa*, *F. sylvatica,* and *T. x europaea*. This tests the results of Mitchell et al. (2019) who propose that the functioning of *Q. petraea/robur* is similar to that of these other replacement tree species. (4) The two non-native oak species, *Q. cerris* and *Q. rubra*, are significantly different in their functioning compared native oaks.

Method

Site selection

Six sites were selected across the UK that were previously old country houses with large formal gardens and parklands and are now national arboreta and gardens. The sites were: the National Trust gardens at Knightshayes Court (England) and Bodnant and Dinefwr (Wales), the national arboretum at Westonbirt (England), the National Trust for Scotland's garden at Crathes Castle, and the Mount Stuart garden (Scotland) (Fig. 1, see Table S1 for details of location, ownership, size, aspect, altitude, soil type, and climate). Due to former historical management, these sites had a selection of old, often more than 150-year-old, trees. The sites were chosen to have as many as possible of the following species: *Acer pseudoplatanus*, *Castanea sativa*, *Fagus sylvatica*, *Fraxinus excelsior*, *Quercus cerris*, *Quercus petraea*, *Quercus robur*, *Quercus rubra,* and *Tilia x europaea*. In total, 230 trees were recorded, with 35–40 trees recorded at each site (Table 1).
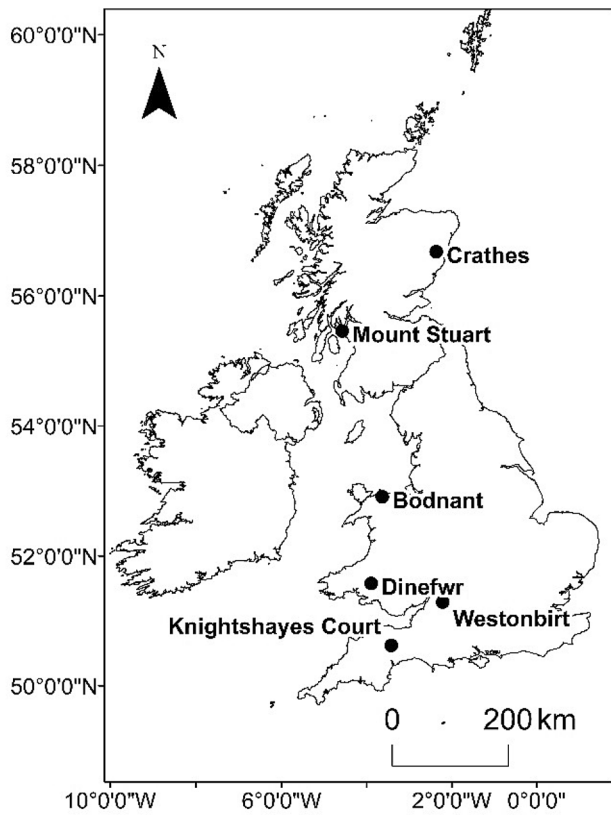
Fig. 1 Location of sites (see Table S1 for further details of site locations)

The assumption was made that differences between tree species within a site in the soil conditions were due to modifications of the environment made by the tree. We acknowledge that in natural experiments such as this, there is no true control and we cannot prove that the starting conditions prior to tree planting were identical between trees within sites c150 years ago. However (a) planting location was based on aesthetic value within the gardens not on best growing

conditions/soil type for productive forestry, thus reducing the likelihood that particular tree species were planted on particular soil types and (b) we used Fourier-transform infrared (FTIR) spectral analysis of the soil (see below) to check that there were no statistically significant differences in the mineral composition of the soil between tree species within sites, providing further indication that the starting conditions of the soil were similar. While this mineralogy may change on geological timescales, it is unlikely to change within the timeframe of the trees studied here.

Tree size

Tree size was recorded as a surrogate for tree age and, hence, the length of time the trees had been influencing the surrounding environment. For each tree, its diameter at breast height (DBH, 1.3 m) was measured and the height of the tree measured using a clinometer (Suunto Opti Height Meter Clinometer PM-5). Tree volume was then calculated as the volume of a cone based on the DBH and height measurements of each tree.

Soil collection and analysis

Eight soil samples were taken per tree (diameter 25 mm, depth 100 mm) about 2 m from the trunk and evenly spaced around the tree. The samples were bulked per tree and kept cool until they were processed. On return to the lab, each soil sample was homogenized and spilt in half. One half was passed through a 5 mm sieve and analysed for mineralized nitrogen following the method in Allen (1989). The other half was air dried at 30 °C and passed through a 2 mm sieve and the following analyses performed. Soil pH was measured in both water and $CaCl_2$. A 15 g soil sample was added to 45 ml water to assess $pH(H_2O)$ and 5 mls of 0.1 M $CaCl_2$ were added to the above slurry to measure $pH(CaCl_2)$, methods follow McLean (1982). A sub-sample of the 2 mm

Table 1 The number of trees of each species sampled at each site

Tree species	Sites						Total
	Bodnant	Crathes	Dinefwr	Knightsh-ayes Court	Mount Stuart	Westonbirt	
Acer pseudoplatanus	6	5	6	4	6	5	32
Castanea sativa	4		6	4	5	5	24
Fagus sylvatica	5	8	6	5	6	5	35
Fraxinus excelsior	4	6	7	5	5	5	32
Quercus cerris				7	2	5	14
Quercus petraea	8	5					13
Quercus robur	3	6	7	6	6	6	34
Quercus rubra	5			4	2	4	15
Tilia x europaea	5	5	5	5	6	5	31
Total	40	35	37	40	38	40	230

sieved soil was ball milled (MM22 Mixer Mill, Retsch) and analysed for total C and N following the method in Pella and Colombo ([1973]).

FTIR was used to provide an overall measure of soil quality differences. Spectral measurements were carried out on the ball milled soil samples using a Bruker Vertex 70 FTIR spectrometer (Bruker, Ettlingen, Germany) fitted with a potassium bromide (KBr) beam splitter. A Diamond Attenuated Total Reflectance (DATR) sampling accessory, with a single reflectance system, was used to produce ''transmission-like'' spectra. Samples were placed directly on a DATR/KRS-5 crystal, and a flat tip powder press was used to achieve even distribution and contact. The FTIR spectra were recorded in the working range from 4000 to 400 cm^{-1} (resolution of 4 cm^{-1}) by averaging 128 scans for each sample. A correction was made to the ATR spectra to allow for differences in depth of beam penetration at different wavelengths, using the OPUS software (Bruker, Ettlingen, Germany, version 7.2). The spectra were also baseline corrected.

Decomposition

Decomposition was studied by burying at each tree a source of lignin and cellulose: filter papers and wooden sticks. A standard source of artificial 'litter' was used rather than individual tree litter to (a) make it comparable between individual trees and (b) to avoid moving leaf litter and hence potentially tree diseases between sites; *Hymenoscyphus fraxineus* grows on the leaf litter of *F. excelsior* (Gross et al. [2014]). Four filter papers were weighed and placed inside a single bag made of 300 micron nylon mesh. The wooden sticks (manufactured and sold as lollipop sticks) were sorted to ensure uniform colour and appearance and weighed. One stick and one bag containing the four filter papers were buried 3 m south of each tree. The sticks and bags were buried in April/May 2018 and removed in September/October 2018. On return to the lab, the sticks and filter papers were dried, cleaned, and reweighed to calculate mass loss and the decomposition rate K.

Soil temperature

Soil temperature was measured every hour using i-Button miniature temperature loggers (DS1922L, Maxim Integrated, San Jose, CA, USA) placed just under the soil surface next to the decomposition experiment, i.e., 3 m south of the tree. The i-Buttons were collected in at the same time as the decomposition experiment, with data available from 18th May 2018 to 10th September 2018 for all trees under which i-Buttons were placed. Due to limited resources, i-Buttons were only placed under half of the trees, evenly distributed across sites and tree species. The average daily temperature was calculated.

Bark water holding

A small bark sample was taken from each tree. On return to the lab, the sample was air dried at 30 °C and any epiphytes and surface debris removed with a small wire brush. The bark was cut into small chunks of c. 5 mm × 5 mm × 5 mm and weighed. The bark volume was calculated by placing the bark chunks into a measuring cylinder and measuring the water required to fill the cylinder to 10 ml using an automatic dispensing pipette (Rainin EDP Plus). The bark was then left in the water for 24 h, mopped dry with a tissue before being reweighed to enable the water holding capacity of the bark to be calculated as the difference between the wet mass and the dry mass divided by the volume of the bark (Ellis et al. [2015]).

Data analysis

The FTIR spectra were pre-processed using the second Savitzy–Golay derivative, to better discriminate the difference between the species and locations. Applying this derivative to the spectra helped to remove the baseline offset and to overcome the overlap between peaks. The spectra were then divided into two data sets: 'mineral' and 'organic'. The spectral ranges 387–1199 cm^{-1} were classified as 'mineral' as they most closely relate to functional groups present within the mineral soil. Polysaccharide bands also occur in this region but only in peat soils, which were not present in this study. The higher spectral ranges above 1800 have some relation to mineralogy, but the lower bands are those most consistently related to mineralogy. These 'mineral' spectra are unlikely to have been influenced by the tree species as they represent underlying geology and, thus, provide some indication of whether the soil was similar under the tree species prior to planting. The 'mineral spectra' data were analysed by MANOVA using the "adonis" package within Vegan (Oksanen et al. [2019]) in the R software version 3.6.2 (R Core Team [2018]) to test for differences between tree species within each site. Pairwise comparisons between tree species were made using the function pairwise.adonis using the Bonferroni correction for multiple tests. The FTIR spectral range 1200–1800 cm^{-1} was classified as 'organic' as this is most closely related to the functional groups present within the soil organic matter. Carbonate bands will also occur in this region, and could, significantly, interfere with the organic matter bands, but were not detectable in any of the soils sampled in this project. Principal Component Analysis (PCA) was used to provide a qualitative discrimination analysis of 'organic' spectra. All the PCA analysis and pre-processing were performed using the Unscrambler® X 10.5 (Camo Software, Oslo, Norway). Differences in organic spectra composition between trees, sites, and their interaction were tested by MANOVA analysis as detailed above.

We used linear mixed-effects models to test the relationship between tree species, tree volume, and measures of soil chemistry, decomposition, and bark water holding capacity using the lmerTest package (Kuznetsova et al. 2017) in R version 3.6.2 (R Core Team 2018). Tree species was included in the model as a fixed effect, tree volume as a continuous variable, and site as a random effect to take account of differences between sites in climate and soil type. ANOVA type III tables and Satterthwaite methods for denominator degrees of freedom were used for F tests. To meet the assumptions of normality for the residuals, the percentage data (total nitrogen and carbon) were log transformed and decomposition rate K was square-root transformed. Tukey's pair-wise comparisons were used to determine differences between pairs of tree species and P values were adjusted using the Tukey correction method for multiple tests (Lenth 2019).

The average daily soil temperature was analysed using nlme in R (Pinheiro et al. 2018) to perform a REML analysis with site and tree included as random effects, tree volume included as a continuous variable as above, and the autocorrelation structure corAR1 used to take account of the repeated measures at each tree.

A comparison of tree species across all functions (nitrogen mineralization, decomposition rate, total soil carbon and nitrogen, soil pH, soil temperature, and bark water holding capacity) was carried out using a partial redundancy analysis (partial RDA) in which site was included as a co-variate using CANOCO v5.12 (Ter Braak and Smilauer 2012).

Results

FTIR: mineral spectra

Manova analyses of the spectra most closely related to the mineral component of the soil showed no significant differences between tree species within sites; thus, providing no evidence that the starting conditions differed between tree species within sites.

FTIR: soil organic matter

The first two principal components from the PCA of the FTIR explained 81% of the total variance in the FTIR. The samples showed some separation by site along Axis 2 (Fig. 2a). Samples from Crathes and Mount Stuart were towards the negative end of Axis 2, while samples from Bodnant and Dinefwr were towards the positive end of Axis 2. *A. pseudoplatanus*, *Q. cerris*, *Q. rubra,* and *T. x europaea* were clustered at the positive end of the first axis, and *Q. petraea* occurred towards the negative end of
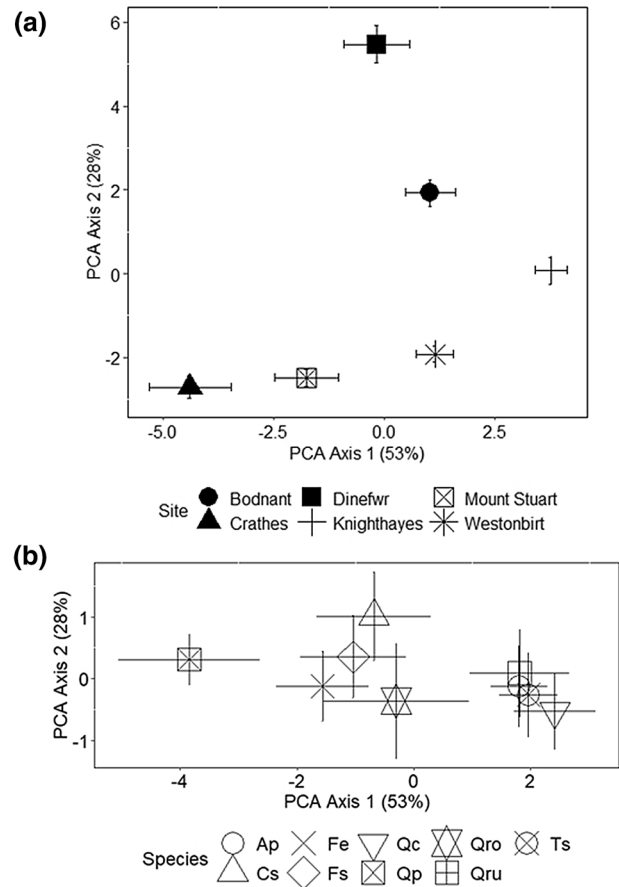

Fig. 2 PCA results from analysis of pre-processed FTIR spectra in the range 1800–1200 cm^{-1} with **a** samples coded by site and **b** samples coded by tree species Ap, *Acer pseudoplatanus;* Cs, *Castanea sativa*; Fe, *Fraxinus excelsior*; Fs, *Fagus sylvatica*; Qc, *Quercus cerris*; Qp, *Quercus petraea*; Qro, *Quercus robur*; Qru, *Quercus rubra*; Ts, *Tilia x europaea*. For clarity, the mean position $\pm$ 1SE are shown

the first axis, with the other species in the middle of the first axis. For some tree species, the samples were more closely clustered (smaller error bars Fig. 2b, *A. pseudoplatanus, Q. cerris,* and *T. x europaea*), while samples for the remaining tree species were more dispersed (larger error bars). Species which have samples which cluster more tightly would appear to show less influence of location and, therefore, have a greater influence on the nature of the soil organic matter.

Manova analysis of the FTIR spectra relating to soil organic matter showed significant differences between tree species ($F_{8,186} = 1.7$, $p < 0.05$) and sites ($F_{5,186} = 26.6$, $p < 0.001$) as well as a significant interaction between tree species and site ($F_{30,186} = 1.7$, $p < 0.01$). However, the pairwise comparisons showed no differences between individual pairs of tree species once multiple tests were taken account of.

Tree size

There were significant differences between tree species in their height ($F_{8,215} = 14.7$, $p < 0.001$) and DBH ($F_{8,217} = 9.0$, $p < 0.001$) which lead to a corresponding difference in tree volume ($F_{8,217} = 8.13$, $p < 0.001$) which declined in the order *Q. cerris, Q. robur, F. sylvatica, C. sativa, Q. petraea, F. excelsior, T. x europaea, A. pseudoplatanus, and Q. rubra* (Fig. 3a). As tree size could be driving differences in functions, it was included in all future analyses and taken account of before assessing the significance of tree species on any of the variables measured.

Decomposition

The decomposition rate of the filter papers was significantly different between tree species ($F_{8,200} = 5.2$, $p < 0.001$, Fig. 3b), but there was no effect of tree volume. Tree species had no effect on the decomposition rate of the sticks. Pairwise comparisons showed that *F. excelsior* had significantly faster decomposition than *F. sylvatica* and three of the four *Quercus* species (Fig. 3b). In addition, decomposition was significantly faster under *A. pseudoplatanus, C. sativa,* and *T. x europaea* than under *F. sylvatica.*

Soil temperature

There was a significant difference between tree species in the average daily soil temperature ($df = 8$, maximum likelihood ratio = 16.1, $p < 0.05$) (Fig. 3c). Pairwise comparisons showed that the soil was significantly cooler under *F. sylvatica* than *A. pseudoplatanus.*

Bark water holding capacity

The water holding capacity of the bark differed between tree species ($F_{8,216} = 15.7$, $p < 0.001$, Fig. 3d), but was not influence by tree volume. The water holding capacity of *C. sativa* was significantly greater than all the other tree species (Fig. 3d) and the water holding capacity of *T. x europaea* was greater than *F. excelsior* and the four *Quercus* species.

Fig. 3 Boxplots for nine tree species of **a** tree volume, **b** decomposition rate of filter papers, **c** average daily soil temperature, and **d** bark water holding capacity. Box plots show the median, the 25th and 75th percentiles and whiskers (defined as the largest (or smallest) value no further than 1.5×the interquartile range). Data beyond the end of the whiskers are plotted individually. Ap, *Acer pseudoplatanus*; Cs, *Castanea sativa*; Fe, *Fraxinus excelsior*; Fs, *Fagus sylvatica*; Qc, *Quercus cerris*; Qp, *Quercus petraea*; Qro, *Quercus robur*; Qru, *Quercus rubra;* Ts, *Tilia x europaea*. Letters indicate significant differences between pairs of tree species as assessed by Tukey's pair-wise comparisons
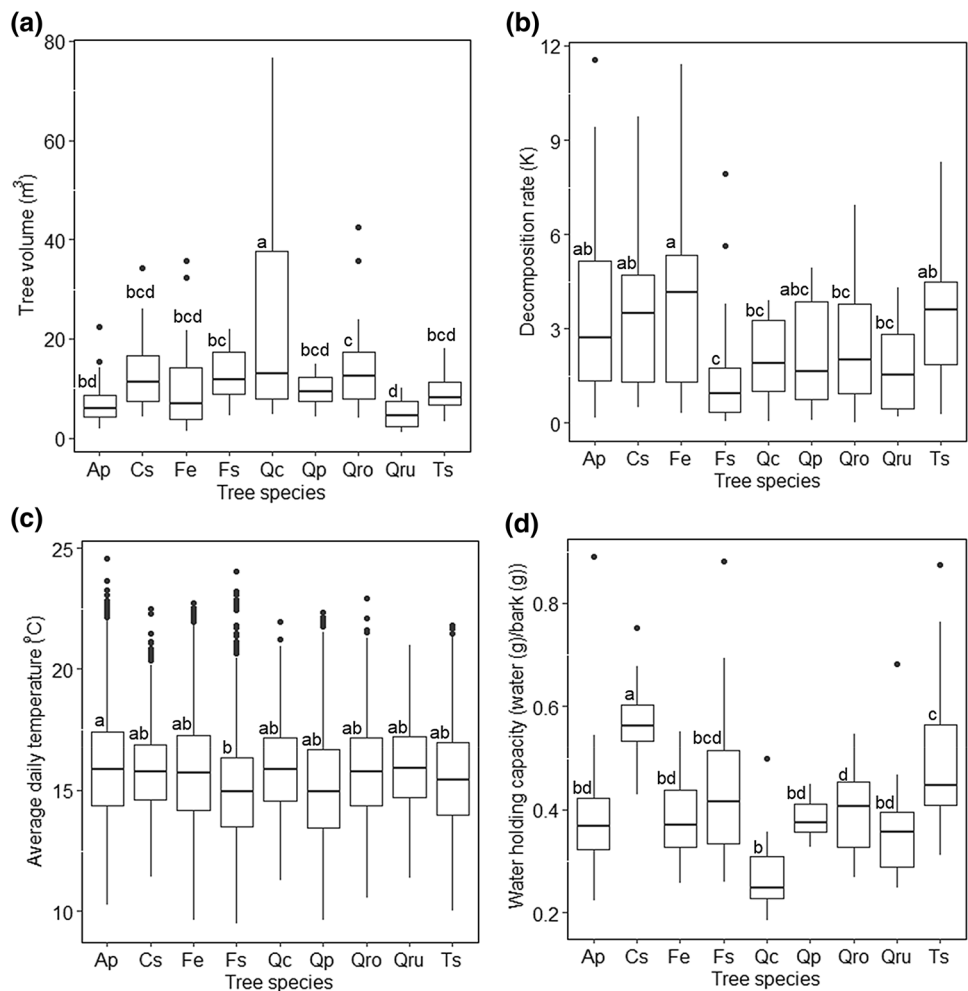
In addition, the water holding capacity of *Q. robur* was significantly greater than that of *Q. cerris*.

Soil chemistry

There were significant differences between tree species in total soil carbon ($F_{8,216} = 2.39$, $p < 0.05$), total soil nitrogen ($F_{8,216} = 2.47$, $p < 0.05$), soil pH ($F_{8,215} = 28.1$, $p < 0.001$), and mineralization rates ($F_{8,217} = 3.15$, $p < 0.01$) (Fig. 4). There was no effect of tree volume on any of the above soil characteristics. Only the results for soil pH in water are presented as the results for $CaCl_2$ were similar. Total soil carbon was significantly lower under *A. pseudoplatanus* than under *F. excelsior* and *Q. petraea* (Fig. 4a). Total soil nitrogen was significantly higher under *F. excelsior* than under *Q. cerris* (Fig. 4b). *A. pseudoplatanus, F. excelsior,* and *T. x europaea* all had more alkaline soil than the other six tree species, and there was no difference in soil pH between these three tree species (Fig. 4c). In addition, *Q. robur* had more alkaline soils than *C. sativa, F. sylvatica,* and both non-native

Quercus species. Nitrogen mineralization was significantly higher under *F. excelsior* than under *F. sylvatica* (Fig. 4d).

Analysis across multiple functions

The partial RDA analysis (Fig. 5) illustrates the similarity between tree species across multiple functions simultaneously with the first axis explaining 31% of the variation and the second axis 17%. *F. excelsior* was shown to be at one end of the gradient along the first axis with more alkaline soil, faster decomposition, higher soil temperatures, greater soil nitrogen, and faster nitrogen mineralization than the other tree species. *A. pseudoplatanus* and *T. x europaea* were the tree species closest to *F. excelsior* along this axis, indicating their similarity in terms of these functions. At the other end of the first axis from *F. excelsior* were *Q. cerris*, *Q. rubra,* and *F. sylvatica* with more acid soils, slower decomposition, lower soil temperatures, lower soil nitrogen, and slower nitrogen mineralization. The two native *Quercus* species were in the middle of this gradient. *C. sativa* occurred at the positive end of the second axis which was correlated

Fig. 4 Boxplots of soil properties under nine tree species: **a** total carbon, **b** total nitrogen, **c** pH, and **d** nitrogen mineralization. Box plots show the median, the 25th and 75th percentiles and whiskers (defined as the largest (or smallest) value no further than 1.5 × the interquartile range). Data beyond the end of the whiskers are plotted individually. Ap, *Acer pseudoplatanus*; Cs, *Castanea sativa;* Fe, *Fraxinus excelsior*; Fs, *Fagus sylvatica*; Qc, *Quercus cerris*; Qp, *Quercus petraea*; Qro, *Quercus robur*; Qru, *Quercus rubra*; Ts, *Tilia x europaea*. Letters indicate significant differences between pairs of tree species as assessed by Tukey's pair-wise comparisons
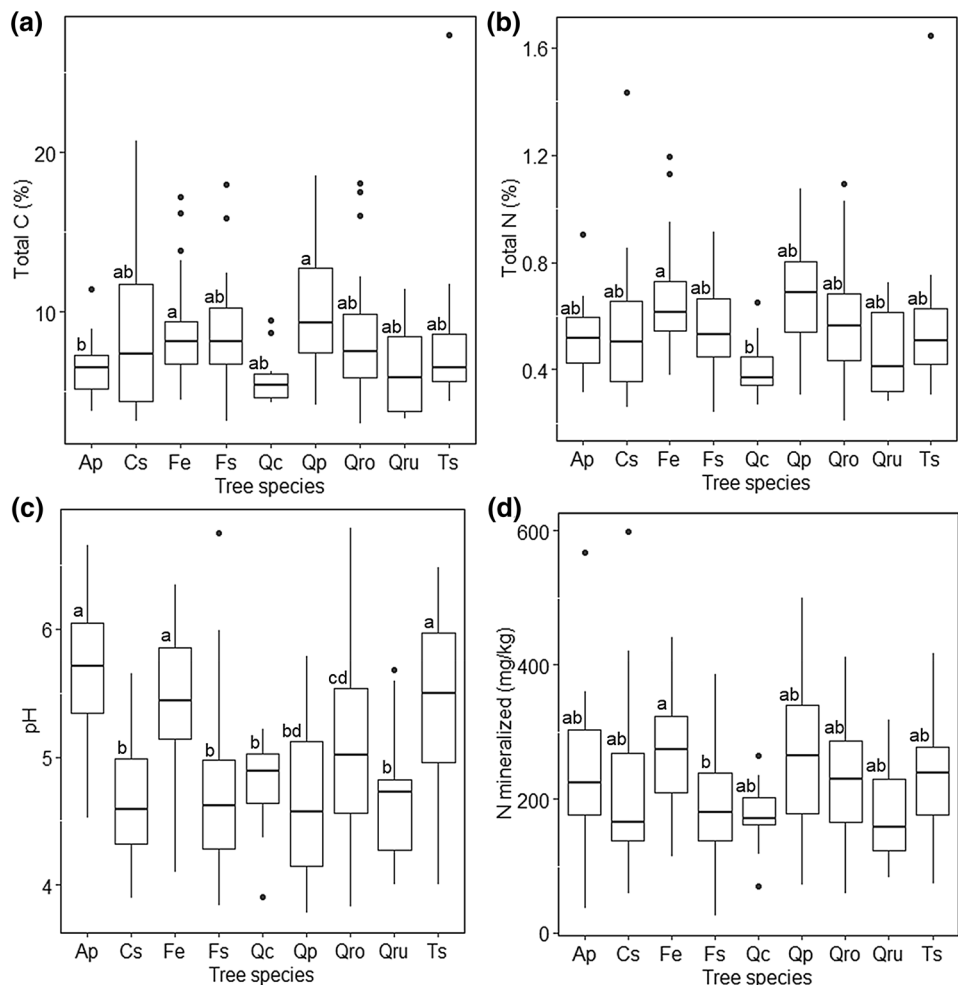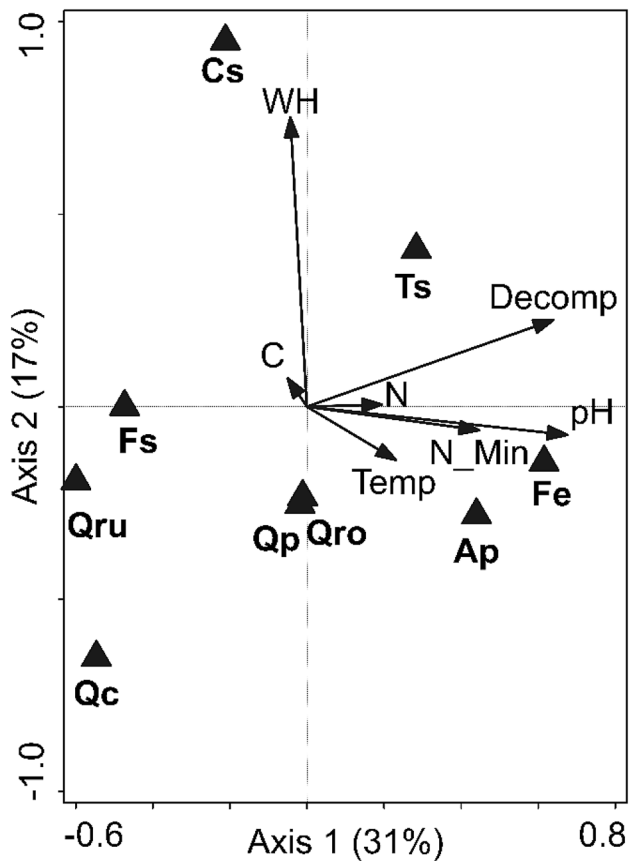
Fig. 5 Ordination diagram from partial RDA of nine tree species (centroids shown) and eight functions (arrows). Ap, *Acer pseudoplatanus*; Cs, *Castanea sativa*; Fe, *Fraxinus excelsior*; Fs, *Fagus sylvatica*; Qc, *Quercus cerris*; Qp, *Quercus petraea*; Qro, *Quercus robur;* Qru, *Quercus rubra*; Ts, *Tilia x europaea*. C, total soil carbon; Decomp, decomposition rate; N, total soil nitrogen; N_min, nitrogen mineralization; pH, soil pH; Temp, average daily soil temperature; WH, bark water holding capacity

with increasing bark water holding capacity and to a lesser extent increasing soil carbon. The other tree species, except for *T. x europaea,* occurred towards the negative end of this gradient.

Discussion

The functions and services provided by trees are usually assessed as the difference between trees versus no trees (e.g., Morakinyo et al. 2018), rarely are differences between tree species assessed as they were here (but see Cameron and Blanusa (2016) and Hill et al. (2019)). This work has confirmed Hypothesis 1: detecting functional differences between tree species at the scale of the individual tree. These functional differences will result in differences in ecosystem services (UK NEA 2011). Thus, when trees outside woodlands, in addition to woodland trees, are replaced, it

is important to consider how a change in tree species will impact on the functions and services provided (Hill et al. 2019).

Impacts of different tree species on functions and services

While no final ecosystem services were measured directly, the variables measured contribute to final ecosystem services (UK NEA 2011). Decomposition, soil N, pH, and nitrogen mineralization are a direct measure of the supporting service nutrient cycling which links to the final provisioning ecosystem service of standing vegetation. Soil temperature, soil C, and bark water holding capacity are functions which contribute to regulating services (UK NEA 2011). While acknowledging that other functions, in addition to the ones studied here, will also influence the delivery of these final ecosystem services, this study provides an indication of how functions and, hence, some ecosystem services differ between species.

Total soil C is a measure of soil carbon sequestration which contributes to climate regulation. Increasing tree cover is generally viewed as a measured to increase carbon sequestration (Bastin et al. 2019); differences between tree species in the carbon sequestrated in the soil are less well studied, but have been shown to depend on the mycorrhizal association of the tree species: more soil carbon is stored in ecosystems dominated by ectomycorrhizal associations than in ecosystems dominated by arbuscular mycorrhizal associations (Averill et al. 2014). This work clearly shows that tree species will influence carbon sequestration, and if the objective is to reduce climate change via soil carbon sequestration, then consideration should be given as to which tree species are planted.

Trees have long been known to aid temperature regulation and, hence, contribute to the ecosystem service of climate regulation by 'protecting soils, animals, and humans from extremes of temperature' (UK NEA 2011), particularly in urban situations where they are valued for this service (Morakinyo et al. 2018; Soto et al. 2018). Both soil temperature and bark water holding capacity are related to temperature regulation, with soil temperature reflecting the shade cast by the tree and the water holding capacity of the bark influencing the cooling of the air temperature. Soil temperature was lower and water holding capacity higher for *C. sativa* and *F. sylvatica* than most other tree species suggesting that, of the species studied, these species will keep the environment cooler and provide greater temperature regulation as the climate warms than the others. Trees with high bark water holding capacity will also reduce the amount of water which rapidly reaches the soil (Crockford and Richardson 2000; Van Stan et al. 2016) contributing to the hazard regulating service of flood control.

Suitability as replacement tree species for ash or oak

The similarity of other trees to *F. excelsior, Q. robur,* and *Q. petraea* may either be assessed across multiple functions simultaneously, based on the distance between tree species within the ordination diagram (Fig. 5) or with respect to whether there were significant differences between tree species in individual functions. When identifying replacement tree species, which method is most appropriate depends on whether the delivery of a particular function/service should be prioritized. For instance, temperature regulation is likely to be important in urban situations, whereas soil carbon storage may be more important in rural situations.

This study largely confirms Hypothesis 2 that *F. excelsior* is significantly different in terms of its functioning from many other tree species that might replace it. Across all functions, combined *F. excelsior* is at the furthest positive end of the Axis 1 in Fig. 5, with rapid decomposition and nitrogen mineralization, high soil N, soil pH, and soil temperature and low soil carbon. While the results from pairwise tests should be used with caution, assessment of the functions individually shows that *F. excelsior* is different from *C. sativa, F. sylvatica, Q. rubra, Q. cerris,* and *Q. robur* for 2 or 3 of the variables (Figs. 3 and 4). *F. excelsior* was only different for one variable for *A. pseudoplatanus* (soil C), *Q. petraea* (soil pH), and *T. x europaea* (bark watering holding capacity). While *A. pseudoplatanus* and *T. x europaea* have previously been suggested as being similar to *F. excelsior* in terms of its functioning, *Q. petraea* has been previously suggested as being very different (Mitchell et al. 2016).

With respect to Hypothesis 3, that the functioning of the native oaks is different from *F. sylvatica, T. x europaea,* and *C. sativa,* the results suggest that *F. sylvatica* has similar functioning to *Q. petraea/robur* with none of the functions measured differing between *Q. petraea* and *F. sylvatica,* and *Q. robur* only differing from *F. sylvatica* in terms of having more alkaline soil. *C. sativa* and *T. x europaea* differ from the native oaks in terms of having greater bark water holding capacity and different soil pH with *T. x europaea* being more alkaline and *C. sativa* being more acidic. However, these species did not differ in their functioning compared to native oaks with respect to the other variables related to nutrient cycling (decomposition, nitrogen mineralization, and soil nitrogen).

Previous studies have identified a lack of information available about the ecological suitability of non-native tree species to replace native tree species (Ennos et al. 2019; Mitchell et al. 2014, 2016, 2019). Utilizing botanic gardens and arboreta which contain a mix of native and non-native species, often of considerable age, allows us to fill this knowledge gap. There are a few differences between the different *Quercus* species in the functions measured (Hypothesis 4). The native species *Q. robur* has more alkaline soil than the two non-native species and greater bark water holding capacity (*Q. cerris*), while *Q. petraea* does not differ from either of the two non-native *Quercus* species. This suggests the possibility of using non-native *Quercus* species to replicate the functions of the native *Quercus*, depending on the relative importance of soil pH and bark water holding capacity versus the other functions measured.

Other tree species may have functions even more similar to *F. excelsior*, *Q. petraea,* or *Q. robur* than those measured here. The tree species selected here were chosen either, because they currently occur in forests containing *F. excelsior* or *Q. petraea/robur* and, hence, may grow to fill the gaps created by tree death, or they are non-native species known to occur on site types with the same climatic and soil conditions where *F. excelsior*, *Q. petraea/robur* occur and, hence, may be suitable replacement species (Mitchell et al. 2014, 2019). In addition, we were limited by the availability of tree species at the sites. Non-native *Fraxinus* species, *Juglans nigra* and *J. regia,* are also being discussed as potential replacements for *F. excelsior*, but were not assessed as they were not present in sufficient numbers at the sites.

The similarity of tree species to *F. excelsior*, *Q. petraea,* or *Q. robur* may also need to be assessed against other factors such as successional stage, tree life span, and the biodiversity supported in addition to functioning, before deciding on the most suitable replacement species (Mitchell et al. 2014, 2016, 2017, 2019). Successional stage and the variables measured here appear to be correlated. The earlier successional species, or comparatively shorted lived species, *F. excelsior, A. pseudoplatanus,* and *T. x europaea* (Grime et al. 1996; Thomas 2016) are all towards the positive end of the first axis in Fig. 5 and correlated with faster decomposition and nitrogen mineralization and higher soil temperature, soil N, and soil pH. In contrast, those species at the negative end of first axis in Fig. 5 (*Quercus species, F. sylvatica,* and *C. sativa*) are known to be later successional or climax canopy tree species (Grime et al. 1996; Jones 1959; Packham et al. 2012). The hypothesis that tree species that occur in European forests at a similar successional stage are similar to each other in terms of their functioning should be tested further, as this could aid identification of suitable replacement tree species.

Conclusion

Although this work focuses on replacement trees for three species under threat in the UK, it has wider relevance for all situations where diseased trees are being replaced by other species. First, trees with more 'extreme' ecological functions (in this example *F. excelsior*) may be more difficult

to replace in terms of functioning than trees with more 'average' functioning such as *Q. petraea/robur*. Second, non-native species of the same genera as the diseased tree species may only be similar to the diseased tree in some but not all of its functions and may not necessarily be a suitable replacement depending on the particular function/service to be prioritized. Third, although trees are renown for providing many ecosystem services (UK NEA 2011) not all tree species are equal with respect to the functions and ecosystem services which they provide. As reported by Cameron and Blanusa (2016), who studied service provision by trees in an urban environment, 'the devil is in the detail' of which tree species are planted. Even at the scale of isolated, non-woodland trees, differences between tree species in the functions and services provided were discovered. Those designing grant schemes for tree planting, advising on replacement trees post disease out-breaks, and planting the trees need to think carefully about which tree species which they select, not just within woodlands but also as isolated trees, as they will differ in the functions they provide and, hence, the ecosystem services which we receive from them.

Compliance with ethical standards

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