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Predisposition of forests to biotic disturbance: Predicting the distribution of Acute Oak Decline using environmental factors

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ABSTRACT

In the UK, Acute Oak Decline (AOD) has caused much concern, due to its distinctive symptoms and its potential to impact oak species that form the largest component of native broadleaf woodland. Decline complexes involve multiple biotic and abiotic factors, which combine to reduce host vigor. In order to investigate forest decline, it is necessary to take a systems approach by considering biotic agents and their interactions with environmental factors, as unfavorable conditions may predispose host trees to pests and diseases. AOD affected trees have lesions in the phloem caused by necrogenic bacteria associated with galleries of the two-spotted oak buprestid (*Agrilus biguttatus*). Here, we test the extent to which AOD is influenced by environmental predisposition factors traditionally associated with oak decline. These are often factors that reduce water availability. During 2013 and 2014 extensive surveys were undertaken, which systematically visited oak woodlands across England and Wales. These locations were used in conjunction with reports from landowners, which have been collected from 2006 onwards. In total 544 locations have been used to assess relationships with soil type, climatic factors and pollutant deposition, notably atmospheric nitrogen, using logistic regression models. The resulting model has been used to produce a detailed risk map for England and Wales and predictions have been validated using the locations of an independent dataset of *A. biguttatus* sightings collected by entomologists. This spatial study re-emphasises the importance of predisposition factors in decline syndromes and suggests avenues for future management and mitigation.

1. Introduction

The combined threats posed by disturbance and environmental change will have large, often detrimental, impacts on temperate forests (Boyd et al., 2013; Cohen et al., 2016; Kautz et al., 2017). Disturbance processes such as disease, insect attack or fire are being complicated by largescale long term changes to the environment, which will impact both individual tree species and whole ecosystems (Millar and Stephenson, 2015; Pautasso et al., 2015; Trumbore et al., 2015). Due to the different processes and scales involved, environmental effects and biotic disturbance could be considered independent topics, but this represents a false dichotomy. In order to understand tree health and mortality it is important to take a systems approach, viewing forest health holistically to include both the proximate and the ultimate drivers (Anderegg et al., 2015; Desprez-Loustau et al., 2006; Jactel et al., 2012; Oliva et al., 2014). Traditional descriptions of forest decline achieve this goal. Decline may involve a wide range of factors, both abiotic and biotic, that reduce host vigour. The process of decline begins with predisposition factors, which weaken host resilience and render it susceptible to the damaging effects of biotic agents leading to tree mortality (Manion and Lachance, 1992).

In Great Britain, Acute Oak Decline (AOD) has been described as a specific condition within the wider oak decline complex (Denman et al., 2014). AOD has caused much concern amongst landowners regarding tree survival and vigour. AOD symptoms comprise of stem lesions and larval galleries formed by *Agrilus biguttatus* Fab.; both of which disrupt the vascular system (Brown et al., 2017a; Denman et al., 2014), leading to reduced health and increased mortality (Brown et al., 2016). Isolations from lesion edges have consistently identified bacterial species (Denman et al., 2016), which have necrogenic activity (Denman et al., in press). Considering that the largest component of native broadleaf woodlands in Britain is oak, *Quercus robur* (Matt.) Leibl. and *Q. petraea* L. (Brewer and Ditchburn, 2014), and that AOD affected woodland covers approximately one third of England and Wales (Brown et al.,

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2017b), much is at stake. The broader concept of oak decline has been reported in Europe's forests for hundreds of years and has been linked to a wide range of biotic and abiotic factors. Commonly cited biotic agents implicated in this complex include insect defoliators, bark and phloem borers, and root decay fungi (Thomas, 2008; Thomas et al., 2002). It has been hypothesised that AOD forms a sub-set of factors within the wider oak decline complex and here we examine how AOD is influenced by environmental predisposition factors.

Predisposition to oak decline is most frequently linked to factors that influence water availability. Plant growth can be limited by both a lack of water or an excess of it. Drought limits carbon assimilation (photosynthesis) by triggering stomatal closure and disrupts the vascular system. The hydraulic conductivity of the xylem is interrupted by air pockets (embolism) and reduced turgor in the phloem cells impairs the transport of sugars. These effects lead to depletion of stored carbon reserves and, potentially, to tree death due to carbon starvation (Allen et al., 2010; McDowell et al., 2008).

Oak, especially *Q. petraea*, is thought to be more drought tolerant than other European tree species, although its growth is optimal in moist nutrient rich conditions (Lévesque et al., 2016; Lévy et al., 1992). Assessments of the impact of climate on oak in Great Britain suggest that yield potential is reduced in the drought prone lowlands of southern England. It is thought that this effect will be accentuated under projections of future climates, although yield is likely to increase in upland areas (Petr et al., 2014; Sáenz-Romero et al., 2016). Waterlogged soils are also detrimental to tree roots, which are unable to respire in hypoxic conditions. Again, both tree species are affected by waterlogged conditions, although in this case *Q. robur* is more tolerant (Parelle et al., 2006; Vincke and Delvaux, 2005).

The availability of water to tree roots is greatly influenced by soil type (Thomas, 2008). Coarse, shallow or sandy soils have limited moisture-holding capacity, leading to water shortage during periods of low rainfall. Clay soils are both prone to moisture deficits in the summer and water logging in high rainfall periods. As such, heavy clay soil is thought to be unsuitable for oak (Vincke and Delvaux, 2005).

Air pollutants were originally described as a predisposing factor (Manion and Lachance, 1992), but have not been considered as major contributors to oak decline (Thomas et al., 2002). However, more recently linkages between plant predisposition and pollutants have been recognised. For example, critical loads for inorganic nitrogen deposition were exceeded on more than a third of European forest monitoring plots ($>$ 200 plots), with both soil and tree foliar nitrogen levels elevated within these plots (Michel and Seidling, 2015). High foliar nitrogen levels benefit phytophagous insects by enhancing palatability and reducing host defences, rendering the tree more susceptible to attack (Eatough Jones et al., 2008; Pitman et al., 2010). Elevated nitrogen and sulphur deposition can also have indirect negative effects through imbalances in tree nutrition (Braun et al., 2010; Jonard et al., 2015; Waldner et al., 2015).

AOD affected woodlands are found in southern Great Britain, where they occur with a similar distribution to entomologists' sightings of *A. biguttatus* (Brown et al., 2015). *Agrilus biguttatus* is a thermophilic species (Reed et al., 2017), however the impact of its temperature requirements on its distribution are not yet understood. Similarly, the effect of environmental predisposition on the AOD distribution needs to be documented and assessed. Data collected during the two systematic surveys for AOD, along with the extensive landowner reports (Brown et al., 2017b), provide ideal resources to examine the relationship between affected locations and environmental factors. These analyses will begin to reveal whether AOD fits the traditional decline model where occurrence is influenced by predisposition factors.

2. Methods

Location data for AOD occurrences was available through three sources: Unstructured landowner reports; a 2013 survey across England and Wales; and a 2014 survey that focused survey effort to describe the boundaries of the AOD affected area. All locations were used to extract values for environmental variables from selected spatial datasets (detailed below).

2.1. Landowner reports

The Forestry Commission Tree Health Diagnostic and Advisory Service (THDAS) has documented reports of AOD symptoms since April 2006. In March 2015, this dataset contained 207 locations that were confirmed positive for AOD and 48 locations had declining oak without AOD. The THDAS data comprised of reports received from the concerned members of the public and landowners. The data were unstructured and the product of ad-hoc sampling effort where detections are reported at times and locations that are convenient and when the reporter has both knowledge and concern about the presence of AOD, so this is likely to include sampling bias (Isaac and Pocock, 2015).

2.2. Survey data

An initial systematic survey across England and Wales was conducted by Forest Research staff between August and September 2013. Sites were selected for survey in two stages firstly 120 hectads (10 km × 10 km squares) were chosen at random and then a specific woodland was chosen within each of these locations. The two stage stratification was necessary because oak abundance data from the National Inventory of Woodland and Trees (NIWT) was available at hectad resolution (Forestry Comission, 2003). Site selection was stratified to reflect the extent and distribution of oak woodland. The survey area was divided into 50 km × 50 km grid squares. In each 50 km grid cell ($n = 81$) at least one hectad was selected, this was the one with the greatest number of NIWT sites containing oak. A second hectad was selected in grid squares with the most oak woodland ($n = 39$). The final survey obtained permission to visit woodland in 117 hectads, in each one survey teams travelled to a specific woodland. In 13 cases AOD was detected more than 100 m from the original site and in these cases the positive detection was recorded as an additional data point.

A second survey, was conducted between August and September 2014, this was conducted across a reduced area close to confirmed AOD sites. The aim was to use the limited survey resource to best determine the extent of the known AOD distribution. The survey selected sites within a buffer of 75 km, which represented the maximum nearest-neighbour distance between known positive sites. Again, the survey was stratified within the 50 km grid squares and reflected oak abundance. For the second survey improved oak abundance data was available from the National Forest Inventory (NFI) (Forestry Commission, 2011). Within each 50 km square sites were selected in five 10 km by 10 km hectads for survey. If only part of the 50 km strata was covered by land within the buffer region the number of survey squares was reduced, so that the number of survey sites was proportional to the land area. In total the second round of survey selected 198 squares, however as 38 already contained AOD positive sites (when the survey was designed in March 2014) only 160 were visited for survey. Hectads identified as already AOD positive were retained as a sub-sample at the same intensity as the surveyed squares. This had the effect of enabling a larger survey at no extra cost. The final survey visited 158 hectads, in one case AOD was detected more than 100 m from the surveyed site so this was recorded as an additional location. By March 2015 the 198 selected squares contained 62 THDAS positive locations, 11 THDAS negative locations, and 21 negative locations from the 2013 survey.

In both surveys, the NFI database was used to identify oak woodland to visit. Where permission to access a site was not received, a substitute site on publicly accessible land was used. These sites were typically owned by The Woodland Trust, National Trust, Wildlife Trusts, Forestry Commission and local councils.

The systematic surveys recorded the presence and absence of the