Action Oak Knowledge Review

An assessment of the current evidence on oak health, identification of evidence gaps and prioritisation of research needs

May 2019

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Executive Summary

Oak is a much-loved and essential component of British landscapes in settings from woodlands to urban parks. There are concerns over its health and prospects for the future given a growing range of threats.

A knowledge review was commissioned to identify what is known and not known about oak health. In particular, the evidence relating to the two native oak species in the British landscape, *Quercus robur* and *Q. petraea*, the functions performed and threats faced, and the interactions with a range of social, economic and environmental factors. The aim is to provide a framework to prioritise future research on these native oak species in the UK.

Teams of authors, 41 in all from institutes in Britain and abroad, reviewed relevant published literature and consulted with stakeholders to ascertain the state of expert knowledge.

Findings are summarised in ten main chapters which focus on a particular topic (e.g. pests; diseases; monitoring), provide relevant sources and references, and identifiy specific gaps in the knowledge.

A panel of six senior scientists reviewed the findings, reflected on the broader knowledge requirements and incorporated them into a broad conceptual framework.

Six grand challenges emerged from the synthesis of the topics that provide a focus for future research, integrating the contribution of many disciplines. These are -:

1. *Securing long-term commitment - Tackle the dearth of long-term records through a renewed commitment to existing monitoring, trials and sustained commitment to exploration of new methods.*

2. *Understanding oak demography and its dynamics - Tackle the lack of understanding of demography, especially in non-woodland settings.*

3. *Uncovering the functioning of tree systems - Tackle the lack of holistic studies of oak health (and that of other tree species)*

4. *Profiling the threats - Tackle uncertainty over the magnitude of the future health problem from pests and diseases, those already in Britain and those yet to arrive, to understand the single and compound nature of threats.*

5. *Fostering management and engagement - Tackle the lack of management of (oak) woodlands and lack of engagement of owners and publics in tree health.*

6. *Establishing the nature of interactions and complexity - Tackle the inherently complex and uncertain nature of the health problems associated with oak.*

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1. Oak Health Knowledge Review – Introduction and Synthesis

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Introduction and scope of the Knowledge Review

Context

Oak (*Quercus robur* and *Q. petraea*) has a special place in the public consciousness, in British culture, and contributes to environmental stability, the woodland economy and biodiversity. It is the most common broadleaf tree species in Britain, supports more species and stores more carbon than any other native tree. In general oaks are regarded as robust and well adapted to a range of environmental conditions, but both these species are subject to a range of pests and diseases and are now facing many other pressures, such as increased air and soil pollutants, environmental pressures, and changing climate patterns with extreme weather events. Concern about the health of oaks has been heightened by people's memories of Dutch elm disease, and by the recent arrival of ash dieback emphasising the risks of new introductions. This report confirms that the concern about oak health is justified and proposes what could be done to obtain the knowledge necessary to address these issues.

The Action Oak public/private partnership is a new initiative to protect and improve the UK's oak trees – acknowledging their iconic and important role and responding to concerns over multiple threats to their health. The knowledge review was commissioned by Defra on behalf of the partnership to establish a baseline against which new knowledge is gained and proposals for new research are assessed.

Aim and scope of the review

The review aims to provide a clear, succinct assessment of the current evidence on oak health in all its dimensions and identify evidence gaps and priority research needs. The review addresses oak throughout the UK, in woodlands and other settings (e.g. hedgerows and as individual trees), both the existing cohort of oak trees (reflecting the historical legacies) and those of the future. It takes a broad perspective on oak health (encompassing current and foreseeable threats) and the drivers/factors shaping the UK's oak demography. This report provides a summary of the evidence and identifies the major gaps – so that further research and action can be initiated. It is not an exhaustive scientific literature review, more a 'state of the art' account of relevant information.

The initial audience for the review was senior stakeholders in the Action Oak (AO) partnership, and those responsible for shaping the framework for future research which may attract funding. The review has now been refined in the light of reviewers' comments and is being provided in this form so that it is available to a wide range of other stakeholders (including research funders, practitioners and other scientists).

Methods

Groups of experts were appointed to consider topics identified as key to oak health in preliminary discussions (Table 1.1). Each topic could easily have taken a full year's work for all involved, but in practice their findings were limited by the time available (5 months from initial request, 3 months from confirmation of approach) and the amount of information that could be collected. However, for each broad topic there was an element of systematic literature review, but also, importantly, an attempt to capture expert knowledge in non-peer reviewed articles and project reports, online sources and directly from practitioners; each chapter provides a listing of these evidence sources. In addition, the emerging findings from recent projects (such as the Defra Future Proofing Plant Health funded work on Acute Oak Decline and possible predisposing factors, a preliminary study of UK Oak genomics, the Tree Health and Plant Biosecurity Initiative funded project PuRpOsE investigating oak ecosystems and pests and diseases, and Woodland Heritage funded studies including dendrochronology, pathogenicity and metabolomics) were incorporated where possible.

The expert groups were asked to identify and assess the strength of evidence in relation to their particular topic, initially based on UK research, but broadening this search to other countries particularly where there were major gaps in the UK material. The strength of the evidence was summarised and recommendations for research priorities were made for each topic area. The editorial board drew on this material to identify broader knowledge gaps and to refine a conceptual framework (see below).

Groups were encouraged to adopt a consistent approach to establishing the weight of the evidence, and thus the knowledge gaps. Table 1.2 provides a commonly used four box model in environmental assessments which was adopted by many in this review.

Key terms – meanings

In the course of the review, it was apparent that some key terms were not consistently used, understood, or interpreted. Table 1.3 provides an explanation of how key concepts are understood in this summary and synthesis. There are several sources of data on the importance of oak drawn upon by chapter authors; emphasis may differ depending upon geographic focus and whether referring to oak in woodlands or elsewhere in the landscape. Table 1.4 provides a brief summary.

Summary of Chapter-specific findings

The chapter-specific findings are presented following this synthesis but the key messages are:

- The knowledge review confirmed the importance of environmental factors (notably climate and site properties) in impacting the health of oak either directly (e.g. strong winds and drought) or through predisposing trees to pests and diseases.
- Pests (both insect and mammalian) damage trees directly in a variety of ways, and some can also act as vectors for diseases.
- Many diseases are poorly understood and identification of causal organisms can be contentious; complex declines are being identified.
- Many pests and diseases which are not yet present in the UK could cause a significant additional threat to oak health.
- Much native biodiversity is associated with oak habitats and in some cases is completely reliant on them yet the functional importance of many species has yet to be understood.
- The post-glacial origins of the two UK native oak species are understood but protection of the genetic resource and performance of species and provenances has received little attention.
- Existing monitoring schemes provide helpful characterisation of the oak population but understanding demographic changes requires longer-term, consistent records and is

particularly scant for non-woodland trees. Long-term monitoring schemes themselves are under threat.

- Many woodlands remain unmanaged and there is considerable scope for engaging more owners, managers and publics in caring for oak.
- The focus of much woodland management has been on timber production and with an economic objective; objectives and techniques need to be expanded to encompass oak health.

Specific gaps were identified by the expert groups – ranging from some highly focussed requirements, e.g. diagnostics to confirm the identity of particular pests and pathogens, the need for specific trials of management methods, to the general e.g. the need for better data on many aspects of oak presence and health/condition across many settings.

The most compelling evidence needs are summarised in Table 1.5. Further detail can be found in the individual chapters. The Editorial Panel is, however, concerned that simply following these needs will result in a lost opportunity – as it will perpetuate past models of investigation that struggle to integrate evidence across disciplines and thereby fail to provide the necessary integrative solutions. We therefore also propose a synthesis that we consider provides a more promising framework.

Synthesis

The Editorial Panel review of the assembled topic material resulted in three general outcomes – a set of reflections on themes emerging; a potential conceptual framework for oak health; and six 'grand challenges' for future research.

Several recurrent themes emerged -:

- **General dearth of evidence** - despite the emblematic status of oak, it is notable how little we know about some key characteristics of the population of oak trees and their health status in Britain. For example, there is a need for better characterisation of the resource (demography and distribution) as well as condition; the status of non-woodland trees is particularly lacking. This includes the need to understand life cycles, proportions succumbing to different routes/forms of mortality, and how survivors get to be veterans. This was also the case for the reviews that were carried out in connection with ash dieback a few years ago.

- **Timescales** – the timescales over which some key processes operate are beyond those typically addressed by policy, by research programmes, or the careers of individual researchers. The interaction between current condition/observations and past (often undocumented) histories is particularly challenging to unravel. What are the echoes of historical activities and events and what are appropriate expectations around plant heath, ageing, senescence? Documenting of long-term change is rare and threatened by lack of commitment to long-term monitoring across a range of platforms (e.g. National Forest Inventory (NFI), Countryside Survey, Environmental Change Network (ECN) and the pan-European ICP Forests condition monitoring).

- **More than Oak** – a focus on oak has helped highlight needs for society to deal with other tree species and other tree diseases – for example, the monitoring of species across a range of landscape settings (individual trees, parkland, hedgerow, garden, street and woodlands), has sat awkwardly with departmental responsibilities and the motivations/focus of particular past surveys (e.g. NFI and Countryside Survey) and their contribution to current understanding. Lessons from this project could contribute to work on the impacts of ash dieback or alder death from *Phytophthora*, and vice versa.

- **Attention to detail** – current data does not provide sufficient resolution or detail to capture some characteristics thought to be key in understanding oak health as it occurs in other countries. For example, little is known about the distribution and relative proportion of pedunculate to sessile oak, the origin of trees (i.e. planted vs naturally regenerated trees; seed sources used if planted) or the extent and history of past management.

- **Prospects for new methods** – some new methods, including genomics, meta-barcoding, and remote-sensing, offer promise in increasing knowledge and diagnostics (e.g. understanding function, identity, change in status). However, they will require complementing with traditional methods, (e.g. in identification if the species are novel and there is no culture collection), investigations (e.g. to provide the material to be sampled, to provide the baseline characterisation), data (e.g. to ground truth remotely sensed imagery), and further work to develop broadly applicable tools from research methods.

- **Differing perspectives** – there are contrasting views/understandings around the dynamics of ageing/disease/deadwood provision – the desirability of stability versus dynamism - which might be summarised as “what is a healthy population?”. As we consider all native oaks in all settings, we must also consider the breadth of objectives relating to their management and utilisation.

- **Need for integrative studies and holistic approaches** – much of the summarised evidence was from narrow studies examining components of a complex situation on single, or just a few, sites, and for only a short period. However, much uncertainty is derived from the interactions between components (e.g. consumer preferences stimulating trade pathways which bring new organisms to threaten naïve hosts). A greater commitment (and encouragement through funding) of integrated studies, including those which address the social and economic systems as well as the natural systems are needed.

A conceptual framework for oak health

We initially used a conceptual model, which sought to emphasise the interactions. This was refined in light of the evidence and deliberations. In particular, we have sought to develop the traditional pest-host-environment model used by pathologists/entomologists, to capture the broader interactions with society, management and biodiversity and to note that these interactions change over time.

The model is presented in Figure 1.1 and the labelled interactions are explained further in the supporting table (Table 1.6). Each of the interactions (either singly or in combination) could be usefully studied further.

Grand challenges

Reflecting on the chapter specific needs, the broad themes, and the importance of interactions identified in the conceptual model – the Panel recommend the Action Oak partnership and other research funders focus on six grand challenges around which to seek to encourage research and build knowledge to secure the future for oak. The challenges emphasise the importance of breadth and depth of research needed, much of which should be approached in an interdisciplinary fashion; the challenges are summarised in the Table 1.7.

Conclusions

The Knowledge Review has uncovered a wealth of evidence across a wide range of topics. However, there are limitations on the current and future value of the existing evidence because of the way that long-term projects are often curtailed having met their initial objectives. Their potential to deliver on longer term problems is too often ignored and current funding models are not conducive to long term projects.

There is a dearth of evidence to answer questions relating to the extent of the problem of oak health in 2019, how the problems might change in coming years, and what solutions exist. There are exciting opportunities to address these gaps through the development of an integrative and applied research programme – targeted at six grand challenges.

This research should complement the incremental acquisition of knowledge, which may occur through narrower, discipline/topic specific studies. However, a step change in funding and commitment to long-term support is required if the potential is to be realised and the future of oak placed on a more secure knowledge footing.

Attention to oak in such a way could underpin a brighter future for all of Britain's trees. Many lessons learned in addressing the problems of an iconic tree species will be applicable and transferable to other important elements of the treescape.

Figure 1.1- Oak health conceptual framework

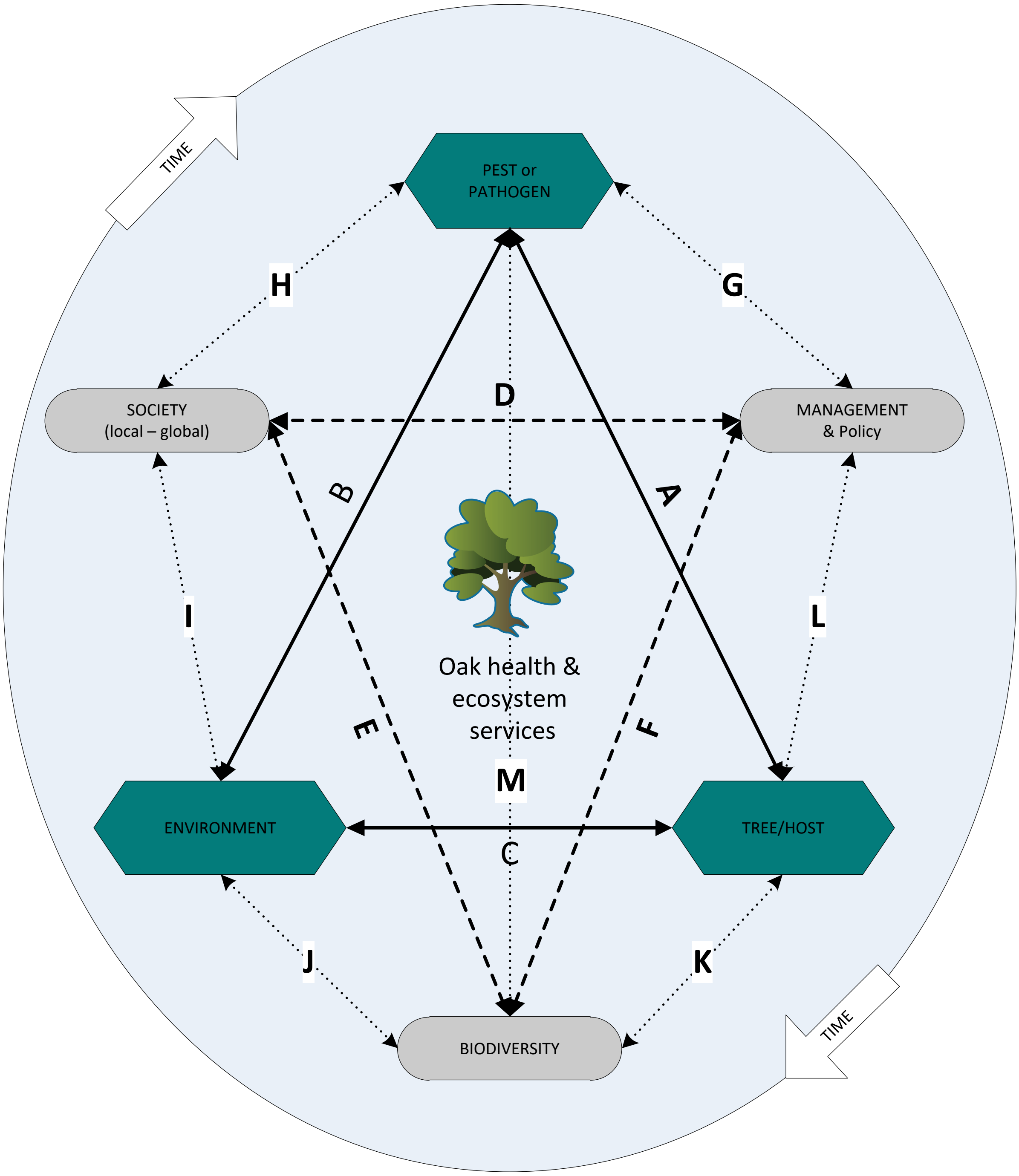

Table 1.1 Chapter structure of Knowledge Review

Topic chapters in Knowledge Review	**Relevance/potential contribution for defining and addressing the problem**
Environmental factors Pests and Diseases	What are the abiotic factors that affect oak health, in particular by predisposing trees to pests and diseases? What are the current and future pests and disease problems in the UK and how are they affected by environmental and other biotic drivers? Is there scope for remedial applications to reduce damaging environmental and pest and disease effects?
Biodiversity	What are the current status, composition and function of Britain's oak ecosystems? If oak populations do decline what are the consequential implications for other species and biodiversity more generally? To what extent might other components of the oak woodland systems, for example mycorrhizal diversity, help or hinder oak health?
Genetics	What genetic variation exists within British oak populations? Is it sufficient to allow for the emergence of resistance or tolerance and adaptation to the various threats that it is facing? How can we make best use of that variation?
Monitoring	What is the extent and condition of oak in Britain? Oak is widespread in both woodland and non-woodland situations in the UK, but how common are the two species (*Q. robur* and *Q. petraea*), what is the regional distribution, and the balance between woodland and non-woodland oaks? What are the characteristics of the oak demography and what is the current health status? How can change be detected so that appropriate action is taken now and into the future? What monitoring data are available to us about oak health and what systems might be put in place that will enable us to track changes in the oak population, including pests, diseases and other threats?
Engagement	How can more people get involved in taking care of British oaks whether through management, monitoring or other actions? How can knowledge, attitudes, beliefs and values be involved in changing behaviours and improving care of oaks? How might we translate findings into practical guidance for policy makers and land managers?
Management	The current oak population reflects past management practices or the lack of them, over various time scales, settings and environments. What management practices can contribute to oak health and which will be most suitable for managing woodland and non-woodland oaks in the future?

Table 1.2 Terminology relating to weight of evidence (after IPCC 4th Assessment and UK NEA)

	Amount of Evidence Lots	Little/None
Level of Agreement High	WELL ESTABLISHED	ESTABLISHED BUT INCOMPLETE
Low/None	COMPETING EXPLANATIONS *[or highly context specific]*	SPECULATIVE

Table 1.3 Glossary of terms

Term	**Working definition**
Health (in the context of tree health)	A broad and imprecise concept indicating "well-being": in practice, an absence of (atypical/excessive/unwanted) impacts of environmental stresses, pests and diseases, noting however that some of the wider aspects of ecosystem health depend on decay and decline in trees as part of a natural process.
Decline or decline	The generic term 'decline' refers to an imprecise description of "ill health" of populations (which could involve diminishing extent, population size, age class structure) or of individual trees (which could be a result of several stress factors). Decline (with a capital letter D) is used where a specific combination of biotic and abiotic factors appears to be leading to lack of vitality and mortality, rapidly as in Acute Oak Decline (AOD) or less markedly so as in Chronic Oak Decline (COD).
Mortality	Death of tree. Baseline mortality of trees (mainly driven by forest structure) may be exacerbated by a range of biotic and abiotic factors (*i.e.* premature death). Two fundamental hypotheses relate tree mortality to either hydraulic failure or carbon starvation (or both).
Predisposition	Effect of environmental (abiotic) factors which make trees more vulnerable to attacks and/or effects of pests and pathogens
Senescence	Ecological concept of ageing (e.g. leading to mortality and provision of new niches such as dead wood) loosely thought of as 'old-age' related – but which might be hastened by various stressors. [Note contrast with premature death]
Premature death	Early mortality (compared with 'typical' lifespans for climate and site) brought about by the impact of abiotic stresses and/or biotic impacts

Table 1.4 Summary of prominence of Oak in Britain: providing an answer to how much oak is not a trivial question because surveys differ in their approach, geographic focus and years in which they were undertaken.

Metric	**GB figure**	**Further detail**
How many oak? In woodlands	Approx 170mill [in 219 thousand hectares]	Of which 76% by number are in England; 13% in Scotland; 11% in Wales
How many oak? Outwith woodlands [strictly speaking in groups less than 0.5ha]	Approx 2.3 million [in 16 thousand hectares]	Of which 83% by number are in England; 5% in Scotland; 10% in Wales
What proportion of broadleaved stocked woodland?	17% of area of broadleaved woodland; 27% of volume of stocked broadleaved woodland; 9% of number of broadleaved trees in woodland	18% of area of broadleaved woodland in England; 19% in Wales; 9% in Scotland.
Rank in species of stocked broadleaved woodland?	1st in growing stock (volume) by species 2nd most frequent species in numbers after birch	In volume - 1st in England; 1st in Wales; 1st in Scotland In frequency - 1st in England; 1st in Wales; 2nd in Scotland

Sources

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Note: Chapter 7 provides description of the monitoring methods used to compile these reports. Figures for Northern Ireland were not available for summary in this way. Sources 1 and 2 are drawn upon in the Forestry Statistics reports produced annually by the Forestry Commission.

Table 1.5 Main chapter-specific knowledge gaps (paraphrased by the Editorial Panel); further explanation and other important areas for future research will be found in the relevant chapter.

Chapter Theme	Specific evidence needs [Note: selected highlights – see individual chapters for full listing of gaps]
Environmental factors	Examine site variability in soil properties, pollutants and compaction processes, and expand investigations to incorporate microbiome and particularly ectomycorrhizal aspects Establish experiments to investigate the impacts of nitrogen eutrophication and limited water availability on oak health Adapt and evolve existing environmental/growth models to examine the metabolic costs of oak defence mechanisms due to loss of foliage/root function
Pests	Examine the mechanisms and impacts of insect defoliation and cortical colonisation to understand their contribution in oak Declines (including Acute Oak Decline) Screen susceptibility of UK native oaks to new pest threats (including pathogen vectors), model populations in current and future climates, and develop surveillance methods (including those based on chemical ecology) combined with pathway analysis to detect invasive species Consider impacts of mammals on non-woodland trees via nutrient inputs, compaction, and loss of regeneration
Diseases	Build up organism-specific knowledge of biology (reproduction, dispersal, ecological constraints, especially with climate) and develop detection/ diagnostic methods for a range of priority pathogen species, both native and new threats. Develop epidemiological studies to establish correlations between environmental predisposition factors and disease occurrence; this may lead to functional hypotheses which can be experimentally challenged and to the identification of indicators to assist management recommendations. Monitor and assess genetic structures of pathogen populations to provide information about origins of diseases, dispersal and adaptation potential, which will underpin risk assessment and management.
Biodiversity	Evaluate the importance of non-woodland oak for ecological connectivity and habitat for oak-dependent biodiversity Establish means of ensuring a continuous supply of veteran trees and how to provide surrogates or alternatives for obligate and highly associated species where necessary. Broaden the examination of oak-dependent taxonomic groups and develop a more detailed understanding of the functional role of species within oak woodlands.

Genetics	Assess and protect genetic diversity in British oak populations. Analyse and expand provenance trials for both *Q. robur* and *Q. petraea* (including British and other European provenances) to understand local adaptation through key traits such as phenology, growth, and susceptibility to pests and pathogens; to provide a future resource for both traditional breeding and genomic studies; and to underpin guidelines for best use of genetic resources. Examine further developments in vegetative propagation and improved acorn storage (capitalising on mast years and avoiding risks e.g. pathogens on acorn imports) as a crucial resource for regeneration. Develop model systems where genetic architecture of key traits (e.g. disease resistance and tolerance) and approaches to selection can be examined using latest technologies.
Monitoring	Ensure the health of oak trees is monitored in forests, ideally aligned with international programmes. Establish a baseline of the current distribution, abundance and impact of priority diseases/pests of oak. Census open-grown (non-woodland) trees to determine and understand their distribution and demography. Develop remote-sensing methodologies, utilising field calibration and ground-truthing to ascertain potential for condition monitoring, and improve the use of citizen data (through e.g. identification guides, *ad-hoc* statistical analyses)
Engagement	Examine how values, attitudes and understandings can be used to encourage engagement to protect oak trees. Carry out a detailed stakeholder analysis to identify people, organisations and institutions which have a stake in oak health, and establish how the level of knowledge varies. Develop methods to target and mobilise passive owners/managers and other stakeholders to take action
Management	Explore the benefits of pre-emptive thinning to maintain/enhance health through reduction of competition and as disease prevention measures. Examine the interaction of environmental factors and management actions in affecting oak health, starting from the regeneration process. Expand the evidence review to consider the management of non-woodland trees, including ancient and veteran trees in all settings.

Table 1.6 Interactions contributing to oak health represented in the conceptual model

Link (as labelled on Fig. 1)	From	To	Examples of two-way interaction
A	Pest	Host	Cause of (contribution to) damage (e.g. via feeding activities) and mortality
A	Host	Pest	Mechanisms determining resistance and susceptibility
B	Environment	Pest	Influence of climatic conditions on population survival and growth
B	Pest	Environment	Contribution to nutrient cycling (e.g. insect frass) and compaction (e.g. mammal movements)
C	Environment	Host	Abiotic stresses (e.g. drought); may contribute to predisposition
C	Host	Environment	Influence of trees on microclimate, C and N cycling;
D	Society	Management	Acceptability of actions; demand for products/services; intervention through regulation/incentive
D	Management	Society	Actions to provide products and services; requests for support
E	Society	Biodiversity	Introduction of invasive, non-native species (INNS); disturbance of habitats and populations
E	Biodiversity	Society	Provision of ecosystem services; cultural value (e.g. wildlife, nature conservation)
F	Management	Biodiversity	Actions which enhance/deteriorate habitats; disturbance
F	Biodiversity	Management	Constraint to actions (associated with regulation); objective for management
G	Management	Pest	Implementation of control measures; population reduction
G	Pest	Management	Cause of challenge and expense; threat to objectives
H	Pest	Society	Loss of ecosystem services; cause of expenses; some health impacts
H	Society	Pest	Spread through pathways, trade, movement
I	Society	Environment	Impact on pollution (air, soil, water); anthropogenic forcing of climate change; locally, compaction
I	Environment	Society	Conditions for living; source of abiotic threats
J	Environment	Biodiversity	Climate influences on populations; provision of nutrients
J	Biodiversity	Environment	Nutrient cycling, contribution to microclimate
K	Biodiversity	Host	Symbiotic relationships; biomass consumption
K	Host	Biodiversity	Habitat; resource availability
L	Host	Management	Requirements for attention; limits to adaptation
L	Management	Host	Silviculture and genetics; adaptation
M	Biodiversity	Pests/pathogens	Oak environment (monospecific stands vs. heterogeneous landscape) and susceptibility to pests/diseases (including role of ecological cascades)
M	Pests/ pathogens	Biodiversity	Cascading effects of disease/insect damage on other taxa through oak health (oak as a foundation species)

Table 1.7 - Six grand challenges for oak health derived from the Knowledge Review

Six Grand Challenges	Description
1. Securing long term commitment	*Tackle the dearth of long-term records through a renewed commitment to existing monitoring, trials and sustained commitment to exploration of new methods.* Develop broad scale and site-specific in-depth investigations which continue through time and for which results are made available for future use (*i.e.* archived and open); recognise the contrasting prospects for reaction/cyclical action in tree-related studies (compared to e.g. agriculture). Encourage social and cultural change (*i.e.* broad-based commitment) to sustain effort and attention; refine policy and funding mechanisms. Explore the potential for new methods (eDNA, remote sensing) to fill gaps more efficiently than through traditional approaches.
2. Understanding demography and its dynamics	*Tackle the lack of understanding of demography, especially in non-woodland settings.* Make freely available the current knowledge of the oak demography in woodland and non-woodland situations. Refine the understanding of drivers such as historical events and economic pressures – and how these impact on cohorts (including health cohorts; proportions succumbing to different forms of mortality), senescence vs premature death. Explore the prospects for sudden change; incorporate evolutionary perspectives and increase attention to genetic/species composition.
3. Uncovering the functioning of tree systems	*Tackle the lack of holistic studies of oak health (and that of other tree species).* Consider the functioning of systems from within Tree (e.g. integrative genomics) to whole tree (e.g. ecophysiology) and woodland systems Integrate knowledge into functional (process-based) models enabling simulations under different scenarios and include what trees provide (e.g. ecosystem services) and support (e.g. biodiversity – profiled by function not simply identification, and explore cascading dependencies.

4. Profiling the Threats	*Tackle uncertainty over the magnitude of the future health problem from pests and diseases, those already in Britain and those yet to arrive, to understand the single and compound nature of threats.* Increase the study of present and future pests, diseases and environmental changes, and consequences of other drivers e.g. global pathways, to contribute to horizon scanning, risk management and triage.
5. Fostering management and engagement	*Tackle the lack of management of (oak) woodlands and lack of engagement of owners and publics in tree health.* Understand how to encourage greater (and sustained) engagement, and how this should be targeted (avoiding single/simple recipes) and prioritised. Support the application of new management, new scientific techniques, adaptive practice, and monitoring to learn from and share successes and failures.
6. Establishing the nature of interactions and complexity	*Tackle the inherently complex and uncertain nature of the health problems associated with oak.* Support greater effort and attention to understanding interactions between biotic/environmental/social factors (e.g. including legal e.g. health and safety as a driver); agricultural policies including policy incentives and regulation (e.g. deadwood; direct and indirect effects of land use policies)

2. Environmental factors stressing oak trees

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Introduction and scope of chapter

An oak tree can live for a long time and in doing so provides a habitat rich in biodiversity and many other ecosystem services. Oak ill-health arises when the metabolic cost of resisting a biological attack or compensation for abiotic damage cannot be met due to hydraulic failure or inadequate carbon and nutrient reserves. If the imbalance persists the tree may enter long term decline. This review addresses abiotic factors that predispose oaks to ecophysiological stress.

It is essential to identify environmental factors affecting the development of oak declines and understand how these impact biotic interactions that lead to deterioration of tree health and resilience. The scope of this chapter is to review what is known, not known and the gaps relating to the role of abiotic factors affecting oak health, predisposing trees to pests and diseases. This includes factors such as climate change, drought, soils, pollution, compaction (e.g. from recreation) and land use change. The main factors related to direct oak damage are also included.

The review methodology was selected to provide an understanding of the extent of research into abiotic factor effects on oak decline in the UK but also similar geographical areas, particularly research from France and Germany, which are considered as close analogues in terms of species composition of oak woodlands, climate, forest management objectives and policy. In addition, the annual and executive reports from the European ICP Intensive Forest Monitoring networks reporting on the conditions of European forests were reviewed.

The search aimed to capture a comprehensive sample of the relevant published literature and, in addition, unpublished literature and experience acquired by Forest Research staff through association with other research groups.

State of knowledge – UK

Literature relating to predisposition factors of oak decline in the UK
Reviewing the available published literature in relation to abiotic predisposition factors and oak decline in the UK highlighted key factors that are not well covered in the literature (see Figure 2.1 below). There was very little relevant research on the impact of compaction and recreation pressure or the impact of pollution (nitrogen or sulphur) on oak decline and health. In addition, only a few papers directly compared trees of differing health status in forest, parkland and shelterbelt woodland settings. The highest number of relevant published literature was relating oak decline to drought and soil conditions. The studies were also split according to the research and experimental approaches they have carried out (see Figure 2.2 below). The largest amount of studies, e.g. between 30-40 %, represents findings from those carrried out as “snap shots in time”, and dendrochonological and chronosequence approaches, while between 5 and 10% of the studies have carried out field and controlled environmental manipulation research or use data from short- and long-term monitoring.

Climate, water availabilities and oak response

Predisposition to oak decline is most frequently reported in terms of factors that influence water availability, both a lack and an excess of water, but there are not many studies presenting hard evidence of cause and effect relationships. However a dendrochronology study in Cheshire revealed a detrimental impact on oak growth through chronic water stress caused by anthropogenic abstraction [1]. Another example of effects of water deficiency was demonstrated when, extreme events, such as the persistent strong winds experienced through the summer of 1952 in SW England, imposed a high dehydration pressure and resulted in regional oak mortality [2,3]. Other dendrochronological studies have also revealed that the impact of drought is visible in significant reduction in radial growth [4], and a severe drought may result in a slow terminal decline [5]. For example, the onset of growth decline in the mid-1980s in Britain suggested that droughts in the summers of 1983/4 or the severe winters of 1984/5/6 may have acted as a trigger for the oak decline[6]. Thus, evidence of the mechanisms of cause and effect is lacking but comparative regional studies suggest that impacts of drivers of extreme growth tend to be localised rather than reflecting common climatic trends, revealing the importance of site-drivers and suitability [7].

Stand structure and species composition influence water storage and groundwater recharge in a forest ecosystem [8]. The proportion of annual rainfall reaching the forest soils under hardwoods (68%) is typically greater than that under conifers (54%) [9]. The difference reflects the aerodynamic roughness and height of the stand, size of the canopy, leaf area, bark surface roughness and branch architecture. The heavy canopy of a mature oak has higher canopy water interception (15 – 20% of annual rainfall) than light canopy species such as ash (11%). In addition, the proportion of annual rainfall reaching the soil as stem flow in rough barked species such as oak (<1%) is low compared to smooth barked species such as beech (5%) [10]. Thus, the structural morphology of oak contributes to reducing the rainfall reaching the soil surface and can be considered a drought factor, particularly in rainfall deficient years.

Drought impairs tree growth; however, temperate species are adapted to drought through an ability either to avoid or tolerate water stress. Within oak species, *Quercus petraea* is reported to be less sensitive to drought than both *Q. robur* [11] and *Q. rubra* [4], but is less drought tolerant than *Q. cerris* [12]. Temperate oak species maintain a relatively high rate of photosynthesis at low leaf water potentials and high vapour pressure deficits than co-occurring species of other genera. The xylem anatomy of oak is ring-porous, with large diameter, early-wood vessels allowing rapid sap movement when soil water is plentiful, and narrower, late-wood vessels that are more resistant to cavitation and sustain slow water movement during seasonal droughts [13]. Ring porous species typically allocate a greater proportion of lifetime resources to shoot growth at the expense of reproductive effort, and are less responsive to environmental variation than diffuse-porous species such as beech and sycamore [14]. Thus, ring porous species with large vessels are more vulnerable to water deficit effects such as cavitation (embolisms) and high temperatures and water shortages could cause physiological changes that amplify stress.

There is strong evidence for genetic control of the response to environmental variation in the timing of bud burst and leaf development in temperate broadleaf species [15]. Oak species respond to both temperature and photoperiod [16]. In the UK, oak bud burst is up to 7.5 days earlier in areas with high night-time light levels; both light pollution and the urban heat island effect are shown to be affecting oak phenology[17]. The Woodland Trust national phenology dataset reveals a consistent order between species; despite the geographic and inter-annual variation the initial date of bud burst for pedunculate oak is one week earlier than sessile oak. In contrast, leaf fall in both species coincide. Earlier bud burst predisposes the trees to more insect infestation. In addition, longer growing seasons increase water and nutrient demand by trees, which could make them more sensitive to environmental perturbation such as drought periods [139].

The accessibility of water in the soil profile affects root density, which varies with soil depth. The deep roots of oak [18] enable the trees to access deeper water sources and maintain relatively high predawn water potentials during periods of water stress [19]. This may result in greater depletion of soil water content under oak than other broadleaf tree species. One study [20] reports a reduction in root mass in the upper soil of drought-stressed young oak trees with a shift in the root distribution to lower soil depths. Root depth in young trees may also be affected by the nature of planting stock. Seed grown trees will naturally produce a tap root. In nursery grown trees this tap root is cut off in root pruning (in order to develop more radial roots) or in undercutting during harvesting, resulting in a significantly shallower root system [21]and loss of the leader tap root. This could make trees more vulnerable to wind damage and uprooting and less able to access very deep ground water in drought periods; greater sensitivity to water stress in root pruned planted oak seedlings compared to naturally grown seedlings has been reported in Slovenian forests [22]. Oak is already poorly represented in natural regeneration within woodlands [23], so further interventions may be necessary to encourage new saplings.

Mast seeding is the phenomenon of plant populations synchronising the production of abundant seed quantities, which exceed the average amount of seeds in a flowering year [29–31]. Changes in climatic conditions and N deposition could also affect the pattern and frequency of tree masting. Analysis in Great Britain showed a non-significant decrease in oak masting over the assessed periods, but the increase from 1996–2000 to 2002–2006 was significant ($p = 0.0038$) [32]. One study [33] also found that pedunculate and sessile oak in Great Britain did not show synchronised mast patterns. Juvenile oak grown under elevated CO_2 accumulated significantly greater leaf biomass, despite a CO_2-induced nitrogen deficiency [34], resulting in marked changes to the trees above/belowground biomass allocation, which also increases tree susceptibility to windthrow. Thus, a better understanding and experimental evidence of the environmental factors affecting nutrient allocation and seed production (including masting) would be beneficial for tree breeding and seed production, but also for management and improving the opportunity for natural regeneration.

The most recent spatial study in the UK [24] showed that Acute Oak Decline (AOD) occurrence is strongly correlated with environmental factors that have previously been associated with predisposition to forest decline [25]. Rainfall, air temperature (day degrees above 11.5^{o}C), elevation, nitrogen, sulphur and base cations deposition are significantly related to AOD occurrence in England and Wales. Previous studies that monitored AOD affected stands have identified variations in the rates of AOD progression between sites and shown that individual trees may be able to overcome infection and enter remission [24]. The rates of infection and remission also vary between years, which reflect annual variations in weather events not represented in long-term climate averages. Manion's Decline spiral model also identifies the importance of "inciting factors" or one-off events such as extreme drought or defoliation that may tip the balance for predisposed trees [25]. Thus, inclusion of both abiotic and biotic factors in future evaluations could provide better understanding and prioritisation of influencing factors on oak decline. Findings from such spatial studies need to be tested under site specific conditions in order to understand the small scale variability and relevance of each relevant predisposition factor.

Soils and oak response

Soil acidification, either naturally or through management or acid deposition, can have serious negative effects on the sustainability of forest ecosystems, in terms of production and vitality. Soil acidification can lead to phytotoxic levels of aluminium and may disturb or inhibit nutrient uptake, leading to deficiencies of some elements (e.g. Mg, K, Ca, P) or excesses of others (e.g. N) [102]. There is some evidence relating Al toxicity to fine root condition and function of conifer species in the UK [103] but not in Oak forest ecosystems. Provisional results from the Future Proofing Plant Health (FPPH) Oak Resilience project suggest that on specific soil types, Ca deficiency and Al toxicity in addition to P deficiency could contribute to changes in root biomass and morphology, and nutrient uptake of *Q. robur* (Vanguelova et al., in prep). Soil texture and organic matter are also important soil properties governing the water holding capacity, drainage and oxygen supply to tree roots and biota. Sandy soils with less organic matter are more prone to drought. Soil with high clay content and seasonal water table also increase tree predisposition to summer drought due to the shift of fine feeder roots into upper soil layers during high water tables in winter. Oak in the UK are predominately on soils with high clay content, which predispose them to increased summer drought stress.

Oaks could be also exposed to more unfavorable soil environments in parklands compared to woodland settings as the current evidence gathered through the FPPH Oak Resilience project investigating soil physical and chemical properties and tree responses suggests. Soil under oaks in parkland settings commonly have higher soil compaction and thus less water and oxygen provision, but also higher acidity, surface soil erosion and lower organic matter content compared to soil under oak in woodland settings (Vanguelova et al. in prep).

A study [24] investigated AOD occurrence and correlations with environmental factors including soil type and properties related to water drainage. They have not shown a significant influence of soil type and geology. The largest proportions of AOD positive locations (number AOD positive / total sites) were found on either soil rich in clay (58%), lowland gleys (50%) and shallow sandy Rendzinas (50%) compared with sites on brown earths (39%). On well-drained soils the proportion of AOD sites was smaller than on the seasonally waterlogged sites. Significant spatial trends were difficult to detect in the soil type data due to many soil sub-groups and a relatively small sample size. Thus, soil evaluation should be concentrated at a site and individual tree scale in order to capture small-scale variability, enabling assessment of the significance of soil condition with individual tree health status. Soil sampling design at such a scale could be stratified according to soil type [105] and assessment of water table depth, soil texture, rooting depth, stone content, organic matter, soil acidity as well as available nitrogen, phosphorous and base cations would be useful parameters to consider in assessment of site and tree health condition. Such local soil assessment will help guide site specific soil management prescriptions. For example, the impact of waterlogging can be reduced by improving site drainage and further influenced by species planting composition. Current research under the FPPH Oak Resilience project is undertaking detailed soil evaluation at more than ten sites comparing declining and healthy oaks.

The factors that affect the ectomycorrhizal (ECM) fungal communities in European oak stands within the ICP forest network, including the UK, have been studied as an overview, but not in the context of tree health condition[26]. Furthermore, the effect of important tree adaptation mechanisms to adverse environmental conditions such as changes in carbon allocation to belowground fine root biomass, root morphological traits and re-translocation of nutrients and how these are linked to the associated fungal and bacterial communities, considering tree health condition, need to be investigated to fully understand oak resilience. The effects of root associations, such as ectomycorrhizas and soil bacterial communities (for example, free-living nitrogen-fixing bacteria and other plant growth promoters), on the tree-soil feedback needs to be studied across trees of different health status. Important changes in root morphological traits such as fine root biomass, specific root length, number of roots tips, branching patterns with different tree health status have been indicated in preliminary results from the FPPH Oak Resilience project [27].

It is important to focus not only on the bulk soil but on the rhizosphere (soils attached to trees feeding fine roots) microbiome since these microbial communities interact with their host in a complex way and play a pivotal role in the tree functioning. They enhance tree disease resistance and nutrient uptake and therefore influence their growth, development and health. It is of the utmost importance to understand how these microbial communities are impacted by different factors and their role in the context of forest decline. Preliminary results suggest the bacterial and fungal communities of the rhizosphere are different in oaks with different health status (e.g. from healthy to chronically declining and to acutely declining trees), but proof of cause and effect is required [28]. Further studies will be needed to understand the ecological role of these bacterial and fungal consortia in tree health (see section 2.1 on oak health and functional diversity of ECM fungi in oak roots).

Fungal associations with tree roots are well known in their role as defensive mechanisms to toxic and stress effects caused by various biological and environmental factors. Root fungal networks aid water and nutrient uptake and often help the host plant to survive adverse conditions, and in exchange, the fungal symbiont is provided with access to carbohydrates. Quantifying the colonisation and diversity of ECM fungi on oaks of different health status will provide an indication of the role played by these organisms in oak resilience, the mechanisms used and the links between site conditions, rhizosphere microbial communities, root functions, tree nutrient status, tree metabolic signatures and long-term tree growth patterns. All this information is being collected during the current FPPH Oak Resilience (see also section below on ECM diversity in oak roots) and PuRpOsE projects, but requires full analysis and gap filling, and so will require further investment and time to bring to complete fruition.

Nitrogen deposition - direct and indirect impacts on oak trees
An increase in N deposition is likely to increase tree growth, with greatest effect where the soil organic layer C:N ratio is high, and the ecosystem is not N saturated (e.g. input of N is higher than N demand), and not deficient in other essential elements for example P. However, if rapid increase in growth should occur, it can lead to de-stabilisation because faster growth, leads to reduced investment in sturdy root formation and development, leading to root fragility and the risk of root loss and consequently the increased risk of drought stress [35] and windthrow. A study [36] found that repeated droughts increased foliar amino acid-N and soluble protein–N concentration, at the expense of structural N. The response to drought was greater in oak species growing in calcareous versus acid soil.

Higher N deposition than N uptake by the forest ecosystems can cause nutrient imbalance, resulting in crown discoloration associated with base cation, Mg and K deficiency, which lead to reduced growth rates, reduced crown densities and abnormal branching patterns. Nitrogen imbalances are also known to lead to a change in mycorrhizal communities, with a reduction in the numbers of large sporocarps (fruiting bodies) that appear to be particularly sensitive to NH_4^+. Reduction in sporocarps leads to lower spore load, which is part of the dispersal, spread and colonisation pathways of ECM. The more fastidious NH_4^+ mycorrhizas are replaced by those preferring rich N conditions, which tend to be those that are efficient at taking up phosphorous (P). Terrestrial P is already limited and Oaks are deficient in P across the UK and Europe. Phosphorous was shown to be the main limiting nutrient, driving nutrient imbalance of oaks even further [37]. In addition, increasing N deposition can cause increased litter production, flowering and fruiting which in turn can lead to reduced resources for reserve storage, important for future growth, and over the long term can lead to tree weakening. N accumulation as NH_4^+ or amino acids leads to increased sensitivity to abiotic and biotic stress and reduces frost hardiness associated with effects on late growth cessation and early bud burst, as young tissue is highly frost sensitive.

Increased nitrogen deposition in the UK has also been linked with impacts of increased insect damage to tree canopies but these relationships were mostly drawn for other tree species such as pines [38]. A study [39] reported increased insect damage on oak trees growing along motorways in the UK. The extent of defoliation was consistent with the measured profile of NO_2. Ongoing evaluation of oak crown condition from the FR Forest Condition database suggest likely negative links with nitrogen and sulphur deposition [24].

Biological activity in the canopy can alter fluxes of Dissolved Organic Carbon, N and P through the forest. The soil type determines the fate of these elements, which may be lost from sandy soils but retained in clay soil, moderating the long term impact of phytophagous insects on tree health [40].

Tree winter desiccation increases susceptibility to defoliation by leaf feeders and pathogen infection, although evidence is reported predominantly for beech and pine. Effects on oak should be determined. Due to their relatively high tannin content, oak foliage may be less susceptible to pest attacks than other tree species, such as beech, following N enrichment [41]. However, large and repeated infestations of caterpillars of *Tortrix viridana* and *Operophtera brumata* have been observed on long term oak monitoring plots in England and have impacted significantly on oak canopy condition. These defoliation events have increased litterfall and caused full defoliation, resulting in lammas growth in late spring; dendrochonological measurements showed oak growth was negatively affected [40]. The detrimental effects of defoliation were also evident in tree growth in other studies in England [42,43], where major attacks frequently build and dissipate over three year cycles [43–45].

N deposition has the potential to increase soil acidification though nitrification processes. Nitrate can leach out, if not consumed by the vegetation or microbial populations. Leaching has the potential to remove base cations, and reduce soil buffering capacity resulting in increased acidity [46]. Thus, in systems that cannot fully use N its deposition will cause N leaching and soil acidification.

N deposition affects the chemical composition of foliage through N and cation exchange and nitrification processes occurring in the canopy during the growing season; this changes the leaf litter chemistry and input of nutrients to the soil. Cellulose activity may be stimulated by increased N deposition. The level of lignins and phenol compounds, which can restrict fungal activity, together with decline in the activity of phenol oxidase leads to increased rates of decomposition. Overall mineralisation (*i.e.* decomposition of organic matter to plant available nutrients) tends to be increased by N deposition, potentially increasing nutrient availability. However, if N saturation occurs where N input is higher than N demand, this may impact negatively on litter decomposition and supply of nutrients [47] due to negative impact on microbial activity, changes in microbial and fungal communities and decrease in soil respiration rate [48].

Woodland canopies provide a rough three-dimensional surface and tend to intercept larger amounts of both dry and wet N deposition than smoother surfaces, e.g. grasslands. This is particularly the case for woodland edges, which experience the highest N deposition, especially where there is a local additional source of gaseous N, e.g. roads and / or intensive agricultural areas. Thus, there is often a gradient of N deposition declining from the woodland edge into the woodland [47,49]. Effects of N deposition can be both direct and indirect, and some are not easily distinguished from issues concerned with management, especially where this involves changing light levels e.g. thinning. Inappropriate or insufficient management and windthrow can simulate N effects and may result in very similar outcomes to N eutrophication (*i.e.* N excess), for example by enhancing grass growth. Woodlands surrounded by farmland and roads are most at risk from N eutrophication and invasion by 'casual' plants, because there is greater availability of seed sources for such plants, compared to remote areas that are surrounded by more semi-natural habitats. Woodlands near intensive livestock units are particularly at risk from ammonia deposition, which can be toxic to trees, ground flora and especially epiphytes [50]; this is especially so on acid soils. The type of N deposition could pose different risks to woodlands and are highlighted in Table 2.1.

N deposition is not believed to have a direct, major effect on tree growth in the UK. However, as illustrated above, the indirect effects are many and varied: N can affect woodlands through eutrophication and acidification, nutrient imbalances, and increased canopy insect infestation, and these changes are likely to predispose woodlands to these more highly deleterious indirect effects. Smaller fragmented oak woodlands near N emission sources are the most vulnerable. Factors like soils and climate can modify N deposition impacts. For example, soil type and the availability of other nutrients e.g. P and K, and any other growth influencing factors, will determine whether N deposition increases growth or leads to the accumulation of N in the foliage and soils. Climate could influence either via frost or drought, which can interact with N to exacerbate the impact of N deposition. More information on the dynamics of N and other base cation fluctuations and corresponding effects on oak resilience would be helpful in risk prediction modelling and development of management recommendations.

Literature relating to non-predisposition abiotic factors (extreme events, e.g. wind, fires, flooding) affecting oak health

Extreme weather events, such as damaging wind storms, fires and prolonged flooding could cause immediate mortality in trees. In comparison to most of Europe, the UK is subject to a severe wind climate, with strong winds being typically caused by the passage of North-Atlantic depressions over the British Isles. On average, about 150 depressions per year affect the UK, mostly in the north, and west regions during the winter months. Scotland is more commonly affected by the strongest winds compared to the other countries of the UK. It should be noted, however, that storm occurrence is a stochastic phenomenon, and considerable variability exists in terms of the timing, magnitude, and location of the strongest winds caused by these depressions[51]. In the UK, wind damage most commonly causes the anchorage provided by the root/soil system to fail, rather than the stems to break [52].

The degree of wind vulnerability of a stand of trees is determined by the complex interplay of a number of factors. These include: the geographical location of the stand, its exposure, and the topography and roughness of the surrounding area; the type of soil, and site preparation techniques (particularly in the case of a newly established stands), the management of the stand, especially with regards to thinning and the shape of the edge exposed to the prevailing wind; the size and form of the trees, and the species planted [51–54]. Forests in Britain have historically also been affected by catastrophic wind damage, most notably in the 1987 great storm when severe damage was recorded in southeast England [6]. The lessons learned from this storm and others in Europe during 1990 and 1999 were that uprooting was more common in planted than wild trees (see previous point about root pruning), but both breakages and uprooting were common among big, young, fast growing trees while ancient trees were less affected. Unhealthy looking trees were no more affected than healthy trees and the roots systems which were exposed were typically unexpectedly shallow [55]. Soil is the medium in which trees are anchored, and the interaction between different soil types and the root systems of trees is a pivotal trait in determining stability. The weight of the soil/root plate is the main component of tree resistance to uprooting during a windstorm [56], and the architecture of the root system will have a profound effect on the mass of the soil/root plate. Although oaks naturally develop a tap root system, which provides anchorage [57–59] the species have a high degree of root system plasticity, and root depth can be limited on surface and ground water gleys, owing to the seasonal fluctuations in the water table. The most favourable soils for root establishment are freely-draining brown earths, but rooting is typically restricted to 50 cm in surface and peaty gleys as a consequence of low oxygen supply due to waterlogging [51]. A study [60] estimated that an additional 15 cm in rooting depth increases tree resistance to falling over by about 25%, which emphasises the importance of healthy and deep root systems. Pedunculate oak has been shown to have higher liability to uprooting in storms compared to sessile oak, but fallen trees have similar survival after uprooting [55]. Associated root disease and fungal infections, particularly where the buttress roots are affected such as is the case with *Armillaria* but more specifically with *Gymnopus,* could also weaken the oak anchorage and make a tree more prone to wind damage.

Oaks in woodland settings are less prone to wind damage compared to single oaks in a parkland setting. In a hedgerow or shelterbelt, the vulnerability to wind damage will depend on the density and width, and the location with respect to prevailing wind direction. In general terms, an abrupt upwind edge affects the airflow over the canopy in a way that results in the edge trees being subject to large wind loading, and trees within the stand (typically at distances from the edge between 4 and 9 times the mean tree height) being at higher risk of wind damage. Studies [53] have shown that a tapered edge equal to half the mean tree height reduces wind loading on edge trees and mitigate the effect of the returning downward airflow on trees within the stand, which are often those most at risk of wind damage [51].

Deciduous species are leafless during the winter months, and while this reduces the drag of the canopy, it also increases the porosity of the stand, with deeper wind penetration. Forest Research (FR) began investigating the wind stability of different conifer forest species in the 1960s. Tree-pulling experiments provided data on the resistive capacity of different species in relation to site characteristics, soil types, rooting depths, and tree dimensions. Recently, broadleaf species were tested in Europe [61] and the data added to the ForestGALES database. This FR wind risk model [62]predicts tree anchorage under wind loading and suggests oaks are similar to beech and are classified as one of the most stable species across all main soil types.

State of knowledge – internationally

The Europe wide drought of 2003 significantly reduced growth across the Level 2 intensive monitoring plots. Norway spruce was severely affected but oak remained comparatively unchanged [63]. Tree-ring width in oak is less affected by summer droughts than pines [64] and beech [11]. Drought is reported to significantly reduce radial growth in the year of drought, and have long lasting growth reductions in larger oak trees [65]. Dendrochronological studies show water availability in early summer is the key growth limiting factor for oak on sandy soils in Germany [66]. Oak growth was resilient to periodic stagnating waterlogging on loamy soils. On rewetted peatland soils, many slow grown trees showed higher adaptive capacity compared with bigger previously dominant individuals, suggesting highly localised site-specific response to the extreme change in soil moisture.

Reports on the decline of European oak stands suggest that the factors responsible for deterioration in crown condition may include summer droughts [63,67–70], changes in precipitation, a combination of cycling between excess precipitation and summer droughts [67,70–75], cold winters and winter/spring frosts [63,75–77]. Drought impairs tree growth; however, temperate species are adapted to drought by an ability either to avoid or to tolerate water stress. A short term loss of crown condition, such as premature defoliation may be an adaptation to drought rather than a symptom of oak decline [78]. In Germany, a study [79] investigated signals of summer drought in oak crown condition. Oak lost crown condition in response to high temperature in the previous summer, however, in cool wet regions of Germany wet summers also led to high rates of defoliation. The impacts of P limitation has been linked with the development of poor crown condition on forests [80]. Others [37] identified an "alarming" deterioration in trends in foliar P concentration in oak across Europe linked to increased growth trends associated with high N deposition and increases in atmospheric CO_2.

An author [81] noted that oak root density was reduced on seasonally waterlogged sites and another [82] reported decreased oak root density in soil zones with low oxygen supply. The depleted rooting zone increased as a result of top soil compaction and reduced the ability of oak to draw water from depth during dry periods. A study [83] investigated the impact of soil compaction on oaks in Germany. They reported poor soil aeration was linked with low fine root density and both were associated with oak stands in decline. Tree root density, height and diameter at breast height have also been reported to be affected by the gas diffusivity of urban soils [84]. In a study of oak decline in Germany, fine root density of oak was not correlated with C, N or the C:N ratio below 4 cm [83]. Diseased stands tended to have higher base saturation and significantly higher pH than healthy stands. It has been suggested [85] oak trees may not take water directly from soil deeper than 1 m; however, soil water content at depth is a key predictor of site yield, suggesting it contributes to tree fitness and survival by maintaining favourable in-tree water potential. A review [86] suggests that under the climatic conditions of central Europe, the vertical root distribution of *Q. petraea* is more influenced by the availability of nutrients, especially nitrogen, than by the amount of plant-available soil water.

Soil properties influence site suitability for pathogens as well as host trees. A study [87] investigated distribution of *Gymnopus* (Syn. *Collybia*) *fusipes* across 30 oak plots in NE France and found *G. fusipes* was preferentially distributed on coarse textured soils and the detrimental impact on crown condition increased with soil sand content. However, others [22] observed significantly higher cations input from deposition (Ca+Mg+K) and significantly less dry and wet sulphur (S) deposition at AOD sites compared with healthy oak sites, suggesting that the AOD sites/soils may have better buffered soils and higher soil pH. The oak root pathogens, *Phytophthora* species, have mostly been found in clayed soils and not very acidic soil. Several studies have demonstrated the involvement of soil-borne species of the genus *Phytophthora* (class Oomycetes, kingdom Chromalveolata) in European oak decline, mostly on soils with pH >3.5 [88–91]. In general, *Phytophthora* are considered to be more aggressive at higher pH values [92]; a study [89] showed an increase in the production of sporangia in *P. quercina* with increasing soil pH. Local soil conditions may therefore have a strong impact on the pathogenicity of these microorganisms. Liming a former 45 to 50 year old sessile oak (*Quercus petraea*) coppice mixed with birch (*Betula pubescens*) and rowan (*Sorbus aucuparia*) on a poor acidic forest soil in the French Ardennes, resulted in an increase in soil pH and cation exchange capacity, and base saturation; a decrease of Al concentration in the soil and soil solution was also observed. A relative and maintained gain of radial increment of sessile oak, was observed immediately from the first year after treatments, suggesting this could be an ameliorating solution for oaks growing on poor nutrient soils [106].

N deposition has been linked to changes in insect activity, insect population densities, and within-community interactions [93], all of which could be potentially important for decline phenomena. Specifically, N deposition was suggested to increase the susceptibility of trees to damage by insects or pathogens [94,9538], and to decrease frost hardiness [78,96]. N excess, in combination with drought, possibly lead to reduced concentration of allelochemicals in the leaves of *Q. robur* [75,97]. In a recent experiment with North American oak species, leaf nitrogen and nitrate were significantly higher at the high pollution site than at the low pollution site, and foliar nitrate concentrations were positively correlated with the abundance of sucking insects, leaf rollers, and plutellids, suggesting a higher degree of insect-related damage associated with a higher level of N input [41]. On the other hand, a study from northern Germany investigating the nitrogen status of various oak stands affected by decline did not find large differences in N status of healthy compared with declining trees; it suggested that the actual outbreak of oak decline was due to other factors like frost, drought and insect attack [107].

Overall, both site and stand factors contribute to a tree's vulnerability to decline. Sites that are water logged in the winter, but also moisture deficient in the summer are most susceptible. Susceptible soils are either surface or ground water clays, which swell in the winter and shrink and crack in the summer, or coarse, shallow or sandy with limited moisture-holding capacity. These sites could generally support lower productivity stands, which are at greater risk for oak decline. Stand factors that are associated with decline include tree age, species composition and stocking. Mature trees from 70 to 90+ years are the most vulnerable. Trees in these older age classes have less capacity to counteract stresses and resume growth. Often the stands are crowded (overstocked) with large numbers of trees (excessive basal areas) that exacerbate moisture stress during drought periods. Stands composed of few species, particularly red oaks on poorer sites, are more susceptible.

Most literature describes oak decline as a complex phenomenon in which predisposing, inciting, and contributing factors interact simultaneously in a particular oak forest ecosystem [72,75,98–101]. High NH^{+}_{4} deposition coupled with reduced N uptake capacity in damaged oak stands resulted in high losses of nitrate and magnesium; however, some [102] suggest this is likely to be a consequence rather than the cause of oak decline in NW Germany.

The ICP Forest intensive monitoring program produces annual data on the condition of Europe's main tree species (including oak), which includes annual defoliation maps and the frequency of recorded damage types. Most recent evidence from the network[140] comparing sessile oak (*Q. petrea*) and pedunculate oak (*Q. robur*), growing in pure and mixed stands, suggests that over time, the effects of tree species diversity on crown defoliation shifted from negative to positive. This finding supports the stress gradient hypothesis, which predicts that interactions between species shifts from competition (negative effects) to facilitation (positive effects). Mixed stands will be less sensitive to drought as they can exploit a greater volume of soil for water and nutrients (laterally, vertically or over time) due to different and complementary root characteristics [141]. Thus, such detailed European datasets could be explored further to relate oak decline with abiotic and biotic factors.

2.1 Oak health and functional diversity of mycorrhizas

Introduction and scope of sub-chapter

Like most temperate forest trees, oaks do not have fine roots (i.e. "feeder" or "absorbing" roots) but have ectomycorrhizas instead. These trees do not interact directly with soil, instead tree interactions with soil nutrients, water and microbes are mediated by fungal tissues (i.e. mantle and Hartig net) that fully sheathe the surface of fine roots and grow in between their epidermal cells. To understand how oaks interact with soils regarding nutrient and water uptake, and protection from attackers, we need to understand their mycorrhizas. Therefore, this section focuses on the fungi that enter in symbiosis with the roots of oak to form ectomycorrhizas.

The filaments of one ectomycorrhizal (ECM) fungal individual typically cover a fine root, grow more or less extensively into the soil, cover neighbouring fine roots, and typically produce sexual reproductive structures (i.e. mushrooms, truffles or crusts) when conditions are favourable. These fungi compete for fine roots and obtain all their carbohydrates from them. Trees allocate up to 20% of their photosynthates to mycorrhizal fungi and in return, these fungi provide nearly all macronutrients, micronutrients and water needed by their tree hosts[108]. Fungal filaments are thinner, longer and able to produce a wider array of enzymes than fine root hairs. Thus, mycorrhizal fungi can use tree carbohydrates to fuel the soil mining, scavenging, uptake and translocation of scarce mineral nutrients such as N and P far more efficiently than trees themselves, determining seedling survival, tree growth and health[109].

The global increase in atmospheric CO_2 together with the cumulative effect of high N deposition has resulted in increased tree productivity, leading to higher nutrient demand by trees. When soil nutrient supply is not sufficient to meet the demands of faster growing trees, tree mineral nutrition deteriorates. This is the case for *Q. robur* and *Q. petraea* across Europe where these two oak species are showing alarming nutrient deficiencies[37]. Moreover, high N availability makes plants more susceptible to pathogens[110,111] while higher P availability is hypothesized to decrease plant susceptibility to pathogens[112].

Ecologists have moved beyond the black-box approach to soil processes; functional traits of mycorrhizas are now known to drive carbon (C) and N dynamics at global scales[113,114], but they are still rarely used in measures of forest condition[26]. At the interface between the soil and plant roots, ECM fungi are particularly susceptible to changes in the soil environment or in C allocation from the host[115] and these changes can impact tree performance.

Temperate oaks and ECM fungi in UK and Europe

Oaks can harbour diverse mycorrhizal communities and there is evidence that their associated ECM fungi are affected by biotic and abiotic factors, forest management practices and environmental change[116-119]. Tree diversity influences ECM richness in overmature plantations and ancient old-growth oak forests[117] and oak mycorrhizal communities can vary greatly between urban and forest trees[118]. Across Europe, including Britain, oak mycorrhizal richness and evenness have been shown to decline with decreasing soil pH and root density and increasing atmospheric N deposition, and there are shifts in dominant fungi showing different functional traits colonizing oak roots[116]. These changes in fungal richness and abundance affecting certain ECM functional groups with different capabilities with regard to storing C, taking up and translocating nutrients[120], can have important consequences for forest ecosystem stability and functioning with potential consequences in oak health and susceptibility to pests. Moreover, trees become naturally predisposed to decline when they are weakened by long-term environmental changes, for instance under reduced soil fertility or increased air pollution[121].

Fruitbody production by ECM fungi associated with oak is also altered by N pollution, some taxa (nitrophilic, inorganic N users) increase in numbers while other taxa (nitrophobic, usually organic N users) decrease or even disappear[122,123]. The latter can show some recovery in fruiting after a decrease in N pollution[124]. To our knowledge, there are no studies focusing specifically on analyses of oak mycorrhizal fungal reproductive phenology but, in general, fruitbody phenology is altered by climate change leading to an extended fruiting season[125].

Overall, we know very little about the link between functional diversity changes in ECM communities and oak health. Therefore, this represents a significant knowledge gap.

Key ECM fungi in temperate oak forests

Fungi forming ectomycorrhizas with oak across large geographical scales and that respond significantly to environmental factors (increasing in abundance, declining or that disappear) have the potential to be used as indicators of forest condition and/or oak health. For example, from intensive mycorrhizal surveys in oak roots and other dominant trees in Europe, including the UK[116,119], two mycorrhizal fungi, the oak milkcap (*Lactarius quietus*) and the yellowdrop milkcap (*L. camphoratus*) emerge as indicators for different environmental variables.

The oak milkcap is an oak specialist. It is the most abundant fungus in roots of oak across Europe and the UK and is specialized for uptake of labile N forms such as amino acids, ammonium and nitrate[126]. It increases in abundance with increasing N deposition and dominates in oak forests receiving more than 13 kg N/ha/year. It can be found in roots of healthy and declining oak[127,128].

The yellowdrop milkcap, also an oak specialist, is an indicator of relatively low N deposition sites (below 14 kg N/ha/yr). It is only abundant in areas below 10 kg N/ha/year and is not present at high N pollution levels. It has been found in asymptomatic *Q. ilex* trees (defoliation <30%) in Italy in higher frequencies than in declining trees[121].

Other key ECM fungi that associate with oak include *Scleroderma citrinum* (common earthball, generalist, indicator of high N pollution levels and low soil pH), *Russula parazurea* (powdery brittlegill, generalist, indicator of high N pollution levels and low soil pH), *Cortinarius anomalus* (webcap, decreases with increasing N pollution and soil NO_3 levels; hydrophobic mycorrhizas with proteolitic abilities[129,130]), and *Boletus reticulatus* (summer bolete, indicator of low N pollution levels; hydrophobic mycorrhizas with long distance soil exploration abilities[129,130]). Their effects on oak health merit further investigation.

ECM fungi and oak decline

Literature addressing the link between mycorrhizal communities and oak decline is scarce, only few studies are recent[128] and to the best of our knowledge, none of them address ECM communities from a functional perspective comparing healthy and declining trees. Some intriguing correlations between mycorrhizal diversity and oak decline have been demonstrated, but causality has not been tested experimentally. Tree decline is usually associated with reduced biomass and vitality of fine roots, reduced ECM tips and a significant change in community composition. Across temperate forest trees, strong shifts in fungal diversity are more commonly observed across gradients and experiments than changes in root colonisation which is typically nearly 100%. However, contrasting results have been obtained from studies comparing mycorrhizal communities (as biotic factors) between healthy and different levels of affected/declining oak trees [75]. These results range from reduced mycorrhizal colonization in oak trees showing severe decline in Poland[131] to a decrease of vital root tips but not in mycorrhizal colonization in declining *Q. robur* in Italy[132] and to a lower percentage of active mycorrhizal root tips in more defoliated trees in the Czech Republic probably due to the interacting effect or air pollution[133].

One study [127] found different dominant ECM morphotypes associated with declining compared to healthy *Q. robur* and *Q. petraea* trees in Hungary but some of their observations were site dependent so did not allow separation of ECM community effects from environmental effects. In a study of a coastal *Q.ilex* forest in Italy[121], the occurrence and distribution of some ECM morphotypes gave an indication of the severity of the decline and showed that declining trees had less morphotypes than asymptomatic ones. It was hypothesized that the ECM communities in healthy trees will be progressively replaced by less efficient fungi already colonizing the unhealthy trees. More recently, a study[134] did not find a significant relationship between *Phythopthora cinnamomi* and the proportion of non-vital and ECM tips; however, non-declining trees showed more *Russula* spp. Root vitality and ECM abundance were higher in non-declining trees in general; in non-infected trees, decline was mostly associated with losses in vital non-mycorrhizal tips, while in infected trees shifts in abundance were associated with losses in ECM root tips. Similarly, *Q. suber* decline was not found to impact ECM colonization but did effect community composition [135].

Management measures, particularly thinning have been attempted to ameliorate *Q. robur* decline in Italy by removing competition from other trees for water and nutrients [136,137]. However, declining trees showed even lower proportion of vital and ECM tips, compared with healthy trees after thinning.

Summary and priorities for new knowledge from review

1. **Improve understanding of soils and soil compaction at different scales and for the impact on oak health.**
   A major gap in research is an understanding of how variable soils are at different scales, including both around a tree and between trees at a single site and between woodlands at different sites. This would include analysis of soil compaction, soil texture and composition, soil chemistry, and water table depth on their impact on root form and function as the consequences for oak health and decline.

2. **Expand soil biology research (incorporating studies of microbiome, ectomycorrhizas fungi and soil fauna)**
   Research on soil biology, particularly microbial communities and ectomycorrhizal fungi, should be encouraged to understand the influence on tree root health and any corresponding impacts on the tree nutrient capacity and canopy vigour. In fact, it is unclear whether changes in ECM communities are causal factors of early stages of oak decline, or if they interact with or are the effect of other factors triggering the oak damage in the first place. It is therefore essential to understand the role that ECM communities play in the oak decline dynamics/complex. Therefore, research priorities should include:

   - Standardised and DNA-based belowground sampling of oak ECM communities across the continuum between healthy and affected trees.
   - Taxonomic and functional screening of ECM communities exploring the use of existing databases [138].
   - *In situ* soil chemistry, tree and environmental data available to analyse together with ECM community data.
   - Coverage of different geographical scales to avoid site-dependent effects.
   - Test cause-effect directionality in oak decline processes.
   - Incorporate ECM monitoring into forest monitoring.

3. **Long term monitoring and analysis of abiotic and biotic factors influencing oak health.**
   Another gap is an understanding of the linkages between environmental factors and the biotic and abiotic stressors and the relative importance of each to tree health. Such more holistic approaches would help prioritise influencing factors, distinguish causes and effects of diseases and tipping points for the health of trees to an unhealthy state. In addition to evaluation of large and long-term monitoring datasets for spatio-temporal relationships between environmental factors and oak decline, more controlled experiments are needed to determine clearly the cause effects relationships and the underlying mechanisms. Multivariate analysis will help to understand the relationships of single factors on each other and their contribution to oak declines.

4. **Evaluating difference in response, sensitivity and resilience of Oak trees in different setting**
   Response, sensitivity and resilience of oak trees growing in forest, parkland and shelterbelt woodland settings need to be quantified. This was highlighted as key gap in the existing

evidence base and is of paramount importance in guiding appropriate management actions to ameliorate oak decline in the UK.

5. **Identification of the metabolic cost of oak defence on tree yield and function.**
   A gap exists in the quantification of how abiotic and biotic factors (including pests and diseases) influence loss of tree yield due to defoliation and/or loss of root function. An understanding of the proportion of photosynthesis used up in response to infection and pest attack would inform decisions on the most appropriate measures to mitigate loss and maintain resilience.

6. **Understanding how to improve oak health.**
   There is a need to develop interventions to reduce the impact of stressors and to improve oak health. Such interventions need to incorporate temporal environmental changes and should also consider different scales from individual trees to woodlands to improve the future management of oaks in the UK.

Sources and assessment of knowledge

The following databases were searched: ISI Web of Knowledge (incl. ISI Web of Science and ISI Proceedings) and Google Scholar. All combinations of the search terms provided in Table 2.2 (see below) were used (where * denotes a wild card) in the following format: "(oak) AND (factor) AND (location)". The searches were repeated for France and Germany.

To be included in the review, the research must have been based in the UK, France or Germany, and investigated either pedunculate oak (*Quercus robur*) or sessile oak (*Q. petraea*). Searches of all online databases identified 388 potentially relevant titles in the UK. Of these, 25 were assessed as relevant at abstract-level screening. Some grey literature and research from other sources were also considered for the UK as relevant following full text screening. Searches in France and Germany for the main four factors produced a total of 175 and 197 papers, respectively, of which 12 and 15, respectively, were relevant. In addition, direct independent enquiry was made to European experts from about 26 countries, which returned additional published and grey literature from ~12 European countries.

In the literature there is inconsistency in the terminology used to describe oak decline/health/dieback. This is evidenced by a much higher hit rate when the keyword 'oak' was used rather than any specific terms such as 'oak decline' (Figure 2.3). So we have used all 4 terms (Oak, Oak condition, Oak decline, Oak health) in our Web of Science search.

Figure 2.1. Distribution of published relevant research in the UK across the main environmental factors, expressed as percentage of total number of publications consulted in this review.

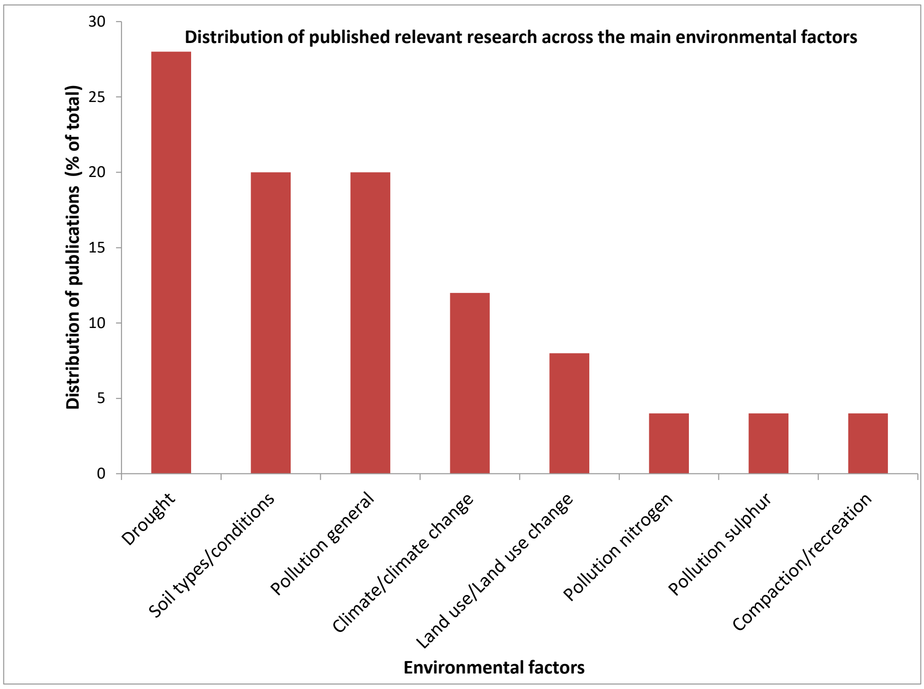

Figure 2.2 Distribution of published relevant studies in the UK across the main research and experimental approaches, expressed as percentage of total number of publications consulted in this review.

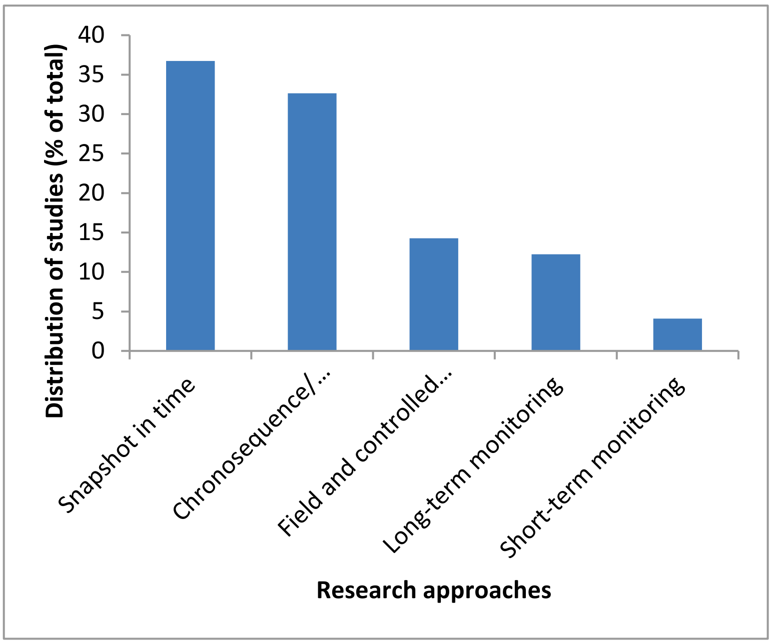

Figure 2.3 Number of publications (hits) on Web of Science using different search terms for oak decline.

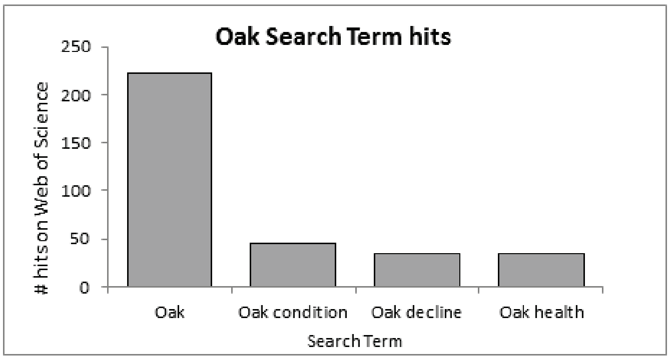

Table 2.1 Type and form of N deposition and associated risk areas

Type of N deposition	Form of N	Risk areas
Dry deposition Gaseous	NH_3	Woodlands in rural areas with elevated background concentration. Higher dry deposition is found close to point sources e.g. intensive livestock units.
	NOx	Woodlands close to combustion plants, and major roads and urban areas.
Wet deposition precipitation and occult (cloud, mist)	Ammonium (NH_4^+), Nitrate (NO_3^-), in varying proportions	The few woodlands at high altitudes will see orographic enhancement (larger volumes but lower concentrations) and occult deposition (higher concentrations)

Table 2.2 Search terms used in database

Oak search terms	Factor search terms	Factor search terms (cont.)	Location search terms
Oak	Climate	Human*	UK
Oak health	Climate change	Landuse	Germany
Oak decline	Global Warming	Landuse change	France
Oak condition	Drought	Urban	
	Moist*	Natur*	
	Soil	Greenspace	
	Sand	pH	
	Clay	Acidity	
	Pollution	Aluminium	
	Pollut*	Al toxicity	
	Nitr*	Heavy metals	
	Sul*	Texture	
	Compaction	Soil type	
	Compact*	Geology	
	Recreation	Nutrient*	

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3. Pest Threats to UK Oak Health

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Introduction and scope of chapter

Oak trees provide a food resource for many species of animal, of which insects are the most species-rich and abundant group. The majority of insects utilising oak trees remain at low population levels and are an integral part of the rich biodiversity of oak related ecosystems; biodiversity is considered in more detail in a later chapter. Oak trees are typically resilient to low levels of feeding damage, but insects which periodically build up high populations (outbreaks) can become damaging and are considered pests. The other main group of oak pests are grazing and browsing mammals. 'Primary' pests are those species which can attack healthy trees, whilst 'secondary' pests are those which develop on weakened hosts. All pests may contribute to host weakening, and in extreme cases, to host mortality. Fortunately, the insect pests of oak currently found in the UK rarely kill trees. Some, however, in interaction with other abiotic or biotic factors, are thought to contribute to widespread declines in oak health, including Acute Oak Decline (AOD).

The factors driving insect outbreaks are often complex and hard to predict. Important drivers of future pest status and damage to oak health will include climate change, forest management practices, and introductions of exotic insects through international trade. Climate change is expected to influence the life cycle and abundance of many forest insects, particularly through changes in temperature and rainfall patterns, and an increased frequency of extreme weather events[1]. These may act directly upon an insect; for example, warmer temperatures may increase its development rate, generation time or overwintering survival, or alter its distributional range. In turn, these changes might facilitate an increase in abundance, allow a pest to colonise novel hosts, or bring it into contact with new oak populations for the first time. Additionally, a changing climate is likely to act indirectly on pest impact by increasing host stress. Summers are likely to be warmer and drier, with an increased risk of severe drought, winters are likely to be wetter, increasing the risk of waterlogged soils, and extreme weather events such as storms and droughts are likely to become more frequent and damaging [1, 2], all of which may result in a larger pool of damaged and stressed hosts. Future changes in seasonal temperatures may also cause temporal shifts in host phenology, such as earlier bud burst, which may alter the synchrony of some insect-host relationships.

Non-native insects also pose a serious future threat to UK oak health. Internationally, many of the most damaging forest pests are accidentally introduced species that encounter 'naïve' hosts which lack co-evolved resistance against them. The impact which emerald ash borer *Agrilus planipennis* has had upon North American ash trees illustrates the unforeseen destruction which can arise when a previously minor pest encounters a novel host [3]. Introduced pests carrying damaging pathogens also pose a severe threat to naïve host trees, as does the development of novel pest-pathogen relationships. Typically, however, a lack of specific data on the ecology, population dynamics, and thermal biology of individual insect species, and of the susceptibility of UK native oak species *Quercus robur* and *Q. petraea* to introduced pests, makes it difficult to predict the severity of future risks to oak health. Although the general lifecycle parameters of many of these insects are known, very little robust data exists of the type needed to accurately predict the impacts of climate change upon native oak pests, or the success of an exotic species introduced into the UK.

The aim of this chapter is to identify invertebrate or vertebrate species which cause regular or significant damage to oak trees in the UK, or which may do so in the future, either as primary pests or in conjunction with other factors. This information may then be used to focus attention on the pests which appear to pose the greatest risk to oak health, and to identify where critical scientific knowledge is limited in terms of their ecology, their relationship with other risk factors or with the oak hosts themselves, and their projected future impact.

In Europe, oak trees have over 130 species of pest insect associated with them, the greatest of any broadleaf tree type assessed [4]. For the purposes of this review it is therefore necessary to distinguish between those species which cause limited or infrequent damage, from those which reduce oak health in a consistent or severe manner. The most significant pests of oaks in the UK and Europe are defoliating caterpillars and wood and bark boring beetles, and these are reviewed below in addition to the typically less damaging gall-forming insects, pests of acorns, and sap-sucking bugs and aphids. Table 3.1 summarises a selection of native and established insect pests of UK oak trees based on a broad literature review and enquiries to the Tree Health Advisory Service at Forest Research. Regarding vertebrate pests, the review focuses on the UK fauna of native and introduced mammalian herbivores. Finally, there are a large and perhaps unknoweable number of potentially invasive oak pests: insects which cause little damage in their native range, but which can become serious threats when introduced to naïve host trees. This review focuses on a few specific and pertinent examples to represent the wider threat faced from alien insect species, and these are summarised in Table 3.2.

State of knowledge – UK *(Native and established pests)*

Defoliating insects

Defoliators typically feed and develop on the leaves of healthy trees, so are considered primary pests. Deciduous trees are, however, highly tolerant of defoliation, and have been estimated to contain sufficient carbon reserves to replace their entire leaf canopies four times [5]. Average defoliation rates of broadleaves typically range from 5-35% [6], but few empirical studies have been conducted on the impacts of defoliation in the UK upon oak increment, vigour, survival, or fecundity. One UK study found that insecticide-sprayed *Q. robur* produced more acorns, but had the same annual growth as unsprayed trees [6]. The key native UK defoliators are early spring feeding caterpillars (Table 3.1), including winter moth *Operophtera brumata* and oak tortrix *Tortix viridana*, but outbreaks have tended to be localised and temporally limited. Both *Q. robur* and *Q. petraea* defoliated in early spring and summer are able to re-flush in the late summer with lammas growth, following the spring feeding damage.

Severe or repeated defoliation, due to sustained caterpillar outbreaks, may act as an ‘inciting’ factor and contribute to a general decline in tree health, by reducing carbohydrate assimilation and stored resources. This can render trees less tolerant of extreme weather events, because of a reduction in the fine-root growth needed to sustain water uptake in severe, prolonged summer droughts, and in the cold hardiness needed to tolerate severe frosts[7]. Defoliating caterpillars often feed in combination, with similar environmental drivers leading to increased abundance in multiple species, and they may also interact with the defoliation of late summer lammas growth by powdery mildew. Indeed defoliation by insects is often cited as a key contributory factor in oak decline in Europe, usually acting in association with environmental factors [8,9]. (See also chapter 2 on Environmental Factors regarding predisposition). Empirical studies in Europe and elsewhere have demonstrated such negative impacts of defoliation on growth and mortality rates; artificial defoliation of *Q. robur* in France was linked to growth reductions, reduced sapwood starch concentration, and increased mortality, especially in trees with severe powdery mildew infection [10]. Examination of the annual increment of *Q. robur* in east-central Russia after long-term monitoring found that increment loss was strongly linked to repeated insect defoliation, particularly from oak tortrix, gypsy moth (*Lymantria dispar*), and winter moth [11].

Elevated future temperatures may potentially lead to increased damage in the UK by some defoliators, by increasing the number of generations per year and altering their geographical distribution (Table 3.1). Conversely, there may be reduced populations of early spring defoliators, where the life cycle is linked to the spring budburst, if changing temperatures alter the synchrony between bud-burst and egg hatch. Greater mortality and reduced fitness in winter moth larvae has been demonstrated if hatching is asynchronous with budburst of *Q. robur*, mostly due to a rapid increase in condensed tannins in the foliage after budburst [12]. Host trees may well become more susceptible to attack under a warming climate; drought is often associated with defoliator outbreaks, when trees may become more attractive, defences are reduced, and leaf nutrient levels may be elevated [13]. Elevated temperatures may particularly benefit gypsy moth *Lymantria dispar* and nun moth *L. monacha*, both of which are currently restricted within southern England, and are highly polyphagous. At outbreak levels in Europe, these species cause widespread damage and mortality affecting a number of tree species, although most reports of nun moth damage relate to conifers. Their outbreak zone appears to lie to the south of the UK, but warmer summer temperatures are likely to push this zone northwards, with the UK becoming more climatically suitable [14]. Warm summer temperatures also favour outbreaks of the oak processionary moth *Thaumetopoea processionaea* (OPM), which causes considerable damage to oaks in Europe, and was accidentally introduced to England in 2005-6. Although this species has the potential to be a serious defoliator of oaks, the distribution is currently restricted to the London area and spread has been limited by nest removal and targeted insecticide application, motivated primarily by human health concerns. The irritating hairs of the caterpillars can cause serious allergic reaction in people and animals [15].

Wood and bark boring beetles

Most species of bark and wood boring beetles utilising oak trees in the UK are saprophagous, requiring moribund or dead tissue to breed in. Oak trees deploy a combination of physical and chemical defences against wood and bark boring insects [16], and although these are not as well understood as they are in conifers, they provide a robust barrier against pest attack. Consequently, the oak-boring insects currently present in the UK are all ‘secondary’ agents that may only develop on compromised hosts. Their actions may further reduce the vigour of weakened trees, and may eventually kill them, but to date no primary ‘tree-killing’ species threaten healthy oaks. In the UK, as worldwide, many oak pests fall within the Cerambycidae, Buprestidae, and Curculionidae (Scolytinae) (Table 3.1), the latter group comprising bark and ambrosia beetles.

Some Scolytinae can become damaging pests (often on conifers) when favourable conditions and susceptible hosts permit it, and a few aggressive species are able to overwhelm the defences of healthy hosts by mass-attacking individual trees. Many Scolytinae transport associated fungi, either symbiotically (ambrosia beetles) or inadvertently, and can become particularly damaging if the fungi are pathogenic. *Scolytus intricatus* is a bark beetle present in the UK that has been implicated in oak decline events in Europe [26, 38]. It is known to vector weakly pathogenic *Ophiostoma* fungi, and considered a potential vector of oak wilt, *Ceratocystis fagacearum* (an American pathogen not present in Europe). However, the true impact of the beetle or the pathogen is not well understood, and there are no known studies of its association with UK oak health. The ambrosia beetle *Xylosandrus germanus* has been recently introduced to the UK and is a highly polyphagous species. Amongst many confirmed hosts, it has been reported to attack weakened oak trees as well as fresh oak logs. It is still restricted in its UK distribution, to the far south of England, but is expected to spread widely [17]. Whether it will utilise weakened oak trees (e.g. those affected by AOD) is unknown, but it could potentially become another contributing factor in oak decline. Another fungus-vectoring beetle, pinhole borer *Platypus cylindrus,* is becoming a more prevalent pest in the UK, and has become increasingly damaging to cork oaks in Europe. Numbers are suggested to have increased following the 1987 great storm which left many damaged oak trees in southern Britain, and population levels are thought to have been subsequently supported by drought-stressed and decline-affected trees. The beetle is confined to stressed and dying, or recently dead hosts, tunnelling into the sapwood and later into the heartwood, damaging timber, whilst associated fungal symbionts cause staining. The beetle is a particular problem in timber destined for high quality products such as veneers [18].

Agrilus biguttatus, a buprestid thought to be native to the UK, is emerging as one of the most important secondary pests of oak trees in Europe. Several European authors have suggested *A. biguttatus* can kill trees that have been weakened by 'inciting' factors such as severe defoliation or water stress, but which otherwise might recover [8]. The perceived pest status of *A. biguttatus* in the UK has also increased due to its consistent association with AOD. The larval galleries of the beetle are almost always found adjacent to bacterial lesions when the bark is removed, and the beetle shares a notably similar distribution in southern and central England with that of AOD. Despite significant advances in the understanding of AOD, the precise role of the beetle in the syndrome, and its relationship with the characteristic bacterial component remain poorly understood [16]. As a secondary insect, it must utilise weakened oaks within a narrow physiological window before the tree dies and the inner bark becomes unusable, or else recovers and defends against the invading larvae. Indeed, AOD affected trees appear to regularly kill off *A. biguttatus* larvae, since the great majority of those destructively investigated exhibit larval galleries, but only 30% of them bear adult exit holes [19]. It seems likely that the beetle hastens the mortality of attacked trees when they are suitably weakened, but there are few empirical studies of the direct impact of phloem-mining beetles on tree health and mortality rates, and none on *A. biguttatus*. Numerous large-instar larvae may be able induce hydraulic failure in trees as the density of larval galleries increases, and damage to hydraulic conductivity may be locally exacerbated by a host wound response, as vessels are plugged adjacent to larval galleries [20, 21]. In a study in the US, experimentally phloem-girdled oaks died only if colonised by the related *A. bilineatus,* which shares a similar ecology to *A. biguttatus*, colonising weakened and dying oaks [22]. While the emerald ash borer *A. planipennis* has been shown to kill susceptible ash trees through xylem-girdling [23], its ecology is very different; it is an introduced species attacking naïve hosts.

An ongoing study seeks to determine whether *A. biguttatus* may be involved in the transmission of AOD bacteria between trees, for which there is no evidence to date. However, in field and lab experiments, AOD bacteria have been isolated from along larval *A. biguttatus* galleries, suggesting the larvae may have a role in within-tree bacterial spread [24]. The beetle may also be involved in AOD lesion formation; in the same study, lesion size was larger when larvae were present. This finding is also consistent with the view that *A. biguttatus* infestation causes fluid exudation as a defensive response in oak trees [8]. It is not known whether the feeding activities of the larvae enable endophytic 'AOD' bacteria to become pathogenic and create the lesions and this remains an important research gap. Conversely, the beetle may simply be taking advantage of trees already weakened by AOD. A more thorough understanding of the role of *A. biguttatus* in tree mortality, a determination of whether it is an essential component of AOD, and the nature of its interaction with the AOD bacteria, are urgently required to inform management efforts. Techniques for sensitive management, by promoting a robust host response, should also be considered.

Changing patterns of precipitation under climate change are expected to lead to an increased number of stressed hosts suitable for colonisation by secondary insect 'pests'. In combination with elevated summer temperatures which may reduce insect development times, increase survival rates, and lead to population increases, more frequent damage by secondary wood borers may occur. Elevated summer temperatures may also facilitate range expansions in wood and bark boring beetle species with restricted distributions, as these are often limited by summer heat availability [25]. *Scolytus intricatus, P. cylindrus, X. germanus* and *A. biguttatus* all currently have restricted ranges within the warmer parts of the UK and may expand into new areas as summer temperatures increase. Recently increased abundance and damage from each of these species has been reported in Europe [17, 18, 26–28] but only the thermal requirements of *A. biguttatus* are known [29]. These data are being utilised in AOD risk maps [30], but could be additionally used to model how the beetle distribution may expand under a warming climate. This is likely to be important if the beetle is an essential component of AOD, since the distribution of the syndrome would also change from its currently restricted distribution. A better understanding of how temperature affects the population dynamics and host ecology of the other species would similarly help in determining future risks posed by these beetles.

Sucking insects, gall wasps, root pests, and acorn pests

Insects of these groups are generally of lesser concern to oak health than defoliators or boring insects. Several hemipteran pests have been reported to cause damage to oaks (Table 3.1), but information on the true impacts of these species, particularly within the UK, is limited, reflecting their less damaging nature. The introduced oak bark phylloxera, *Moritziella corticalis*, has been reported to cause severe dieback of second year oak shoots, damaging young oak trees of up to ten years [31]; however, very little information exists on the biology of this species, and the impact on tree health seems limited. The oak scale *Kermes quercus* has been reported in high abundance when associated with oaks suffering dieback in the UK [32] and Hungary, but damage seems to be limited to compromised trees such as those planted on suboptimal soils [33, 34]. Root feeding by insects is well studied in agricultural systems but has been largely overlooked in forests. Of the below-ground herbivorous insects known to feed on tree roots, most are beetle larvae, particularly of the Curculionidae and Scarabaeidae families. Due to the cryptic nature of any damage, it is rarely recorded so the role of such feeding in tree health or as a predisposition factor in decline is unknown as, due to the cryptic nature, the damage is rarely recorded. Root herbivory by beetle larvae has been demonstrated to influence tree seedling mortality to a greater degree than defoliation, particularly under drought conditions [35].

Gall wasps (Cynipidae) of oaks are a well-studied group, with around 40 species causing galls on *Quercus* in the UK. Most of these, however, have alternating sexual and asexual generations, raising the number of gall 'causers' to over 70 [36]. Vigorously growing plant organs are preferentially selected [37], and the galls tend to have a negligible impact upon tree health. Both *Andricus quercuscalicis* (knopper gall wasp) and *A. kollari* (oak marble gall wasp) are introduced species, alternating sexual and asexual life stages on *Q. cerris* and *Q. robur* (or *Q. petraea*) respectively. This limits their local distribution to areas where *Q. cerris* is present, although both species are now widespread in Britain. *Andricus quercuscalicis* probably plays the more significant role in oak health as an acorn pest of *Q. robur*.

Acorn pests include both invertebrates and vertebrates; the majority of predispersal seed predators (when acorns are on the tree) are insects, whilst most important postdispersal predators are generalist vertebrates [38]. Key predispersal acorn pests in England include *A. quercuscalicis* and the native acorn weevil *Curculio glandium*, which vary in abundance and impact upon an acorn crop from year to year, according to the size of the crop in the previous year [39]. Together these two species may destroy between 30-90% of the acorn crop each year, with the proportion of acorns predated being typically lower in years when the crop was larger, due to predator satiation. Some vertebrates, including grey squirrels and jays, also remove acorns from the tree; whilst jays actually contribute to acorn dispersal and recruitment through caching activities, grey squirrels do not as they bite the embryo from the seed before caching to prevent germination. Vertebrates are estimated to predate less than 10% on average of an acorn crop during mast years, to over 70% in low years [38]. Postdispersal predation of acorns on the ground can also be high, varying by habitat and individual tree, and may involve deer, rabbits and wood mice. Overall, acorn loss is estimated to vary on an approximately 2 year cycle, from as high as 100% in poor years, to around 50% in high cropping years [38.] Recruitment of new oak seedlings may be linked to acorn production in some, but not all habitats, but evidence of reduced regeneration rates due to acorn predation is limited.

Mammals

Herbivores affect oak and oak ecosystems through at least 12 different processes: grazing and browsing foliage or shoots; bark stripping; antler rubbing; trampling; deposition of urine and dung; endo- and epi-zoochorous seed dispersal; seed caching and seed consumption; and rooting and dispersal of fungal spores. These effects vary amongst species. For any given species, however, these behaviours are unevenly distributed in space and time: dung and urine for example is not necessarily deposited in the same place or in proportionate amounts to grazing. This contributes to diversity and clustering of damage. To date most attention has focused on the effects of browsing and bark stripping and measures to deal with this are well established in forest practice. More recently attention has focussed on some of the other processes.

Effects of grazing and browsing on oak trees

Native UK oak shoots, foliage and seedlings are very palatable and readily consumed by deer and domestic herbivores [40, 41]. It is unclear how much reliance is placed in the UK on natural regeneration for the maintenance of oak in hedgerows and small woodlands. Deer have, however, increased in abundance and distribution in recent decades and many of the mature trees present in the landscape would not have been subject to such a high browsing pressure when they were seedlings. Shrubs and climbers, particularly thorny plants can facilitate regeneration of oak seedlings in a grazed environment [42, 43]. The introduced Muntjac deer, however, are able to penetrate thickets more easily than larger ungulates and it remains unclear how much oak natural regeneration will succeed where they occur without the provision of additional protection.

The negative effects of ungulate browsing on the growth and survival of young oaks are well established, including in the UK, although such damage is not regularly monitored or quantified [44]. Some recent evidence from a long-term exclusion study in the United States suggests, however, that the growth rate of mature trees is increased by deer, due to the effects of nutrient deposition through dung and urine [45]. There is also increasing awareness that some of the effects of ungulates are not quickly reversed following removal or control. International studies focusing on oak and other forest types suggest this can occur in a variety of ways: where grazing tolerant species can resist competition once grazing is removed; where the seed bank has shifted towards more grazing-tolerant and endo-zoochorous (dispersed via animal gut) species; where the forest age structure has changed as a result of tree recruitment failure; and through changing nutrient levels due to deer importing nutrients from neighbouring farmland [46–48]. Some of these effects have not been investigated in the context of the British lowland landscape.

Effects of grazing on soil and nutrients

By removing plant biomass, grazing removes some of the vegetation that would ultimately become senescent. Grazing reduced leaf litter biomass in an experimental study of oak saplings [49], and international studies involving oak forests showed a reduction in the depth of the litter or organic horizons [50, 51]. In spite of a reduction in litter, many international studies within oak woodlands indicate that soil nitrogen levels are increased by grazing, attributable to the deposition of dung and urine [50, 52–54], and some studies also find elevated levels of other nutrients as well (Ca, P and total carbon). In contrast, some studies examining oak and other forest types find no change in nutrient levels or report a decline [54–56].

Grazing can lead to soil compaction and reduced infiltration, as has been shown in international grassland and forest studies [57–62] and these changes are found to be less suitable for plant growth [59, 63]. Soil types differ in sensitivity to compaction: for example, in the UK soil moisture deficit has been shown to reduce sensitivity to compaction under grazing [64].

There are many examples in the international literature relating to oak forests and other ecosystems of spatial unevenness in grazing activity causing, or contributing to, high spatial heterogeneity in soil nutrients or structure with consequent effects on vegetation or soil fauna [65–68]. These effects can occur at varying spatial scales. Domestic ungulates can potentially cause high impacts around focal points such as water troughs or shade-bearing trees. There appears to be a lack of information on the potential impacts or stress imposed on isolated trees in pastures or woodland boundaries in the UK. There is mixed evidence as to the extent or speed of recovery when grazing is withdrawn and little evidence from the UK or relating to oak woodlands. Internationally, some studies suggest that nutrient levels remain elevated in the soil for decades or centuries following a period of forest clearance and grazing [69], whereas others point to recovery [70].

Bark stripping by grey squirrels

Bark stripping by grey squirrels is a serious concern for woodland owners in the UK and a major disincentive to investment in woodland establishment. Oak is one of the most susceptible species [71]. Young oak trees can be fenced to prevent deer damage, but this does not prevent squirrel attack. Squirrels obtain little nutritional benefit from bark stripping and the motives behind the behaviour are unclear. Previous investigations by FR have attempted to draw a link between seed supplies and the number of squirrels caught in cage traps in order to predict bark stripping damage. However, the amount of bark stripping proved to be too variable and did not reveal a clear association between damage and either seed supply or numbers trapped. Recent research investigated the hypothesis that bark stripping was motivated by a calcium deficiency [72, 73]. The results did not fully support the hypothesis but did not reject it either.

Evidence is now available from studies in Ireland and Scotland that an increasing pine marten population is associated with a decline in grey squirrels and a recovery of red squirrels ([74]; Sheehy 2018 pers. comm.). Research is currently underway, with two collaborative projects with the universities of Exeter and Aberdeen, to investigate some of the mechanisms and environmental factors involved. These projects are not, however, investigating how squirrel damage is affected by the arrival of the pine marten. The re-introduction projects in Wales and the proposed introduction in the Forest of Dean provide excellent opportunities to investigate the trends in damage and to establish how much squirrel control effort may still be needed following any re-establishment of the pine marten.

State of knowledge – internationally *(Potentially invasive pests)*

The resilience of healthy UK oaks to damage from native pests reflects a shared co-evolutionary history, wherein a range of host defences and strategies have developed to minimise pest impacts. However, rapid global change is likely to significantly affect oak health via two key mechanisms: climate change and the global movement of invasive organisms. The potential impacts of climate change have been discussed above. More immediately, the expansion of global trade has accelerated the rate of introduction of exotic forest pests and pathogens across the world. Introduced organisms are often only identified if they become damaging in the new area, and the robust defences of oak trees are likely to be effective against many or most oak-associated insects, even without a shared evolutionary history [75]. The scale of anthropogenic movement of potential pests and pathogens globally is, however, unprecedented and has led to numerous highly destructive introductions.

Introduced wood and bark boring beetles and their associated fungal symbionts probably pose the greatest risk to UK oaks, if specific resistance mechanisms are not present within the trees. For example, the introduction of the emerald ash borer *A. planipennis* into North America has caused the death of millions of susceptible but healthy ash trees [3]. It is conceivable that oak buprestids present as secondary pests in non-UK oak trees might become primary pests if they are accidentally introduced into the UK; *A. bilineatus* is a potential example (Table 3.2), although no impact has been recorded to date in Turkey where this species has been introduced. The fungal symbionts carried by novel wood and bark boring pests may also pose a severe threat to naïve trees. For example, a wilt fungus, *Raffaelea quercivora*, has caused the wide scale mortality of Japanese oak trees (see chapter 4), and is vectored by a wood boring beetle, *Platypus quercivorus* (Table 3.2). The susceptibility of UK oak species is not known, but the fungus has been identified from beetle galleries in wilt-killed *Q. robur* trees in Japan [76]. Native and established boring beetles may also become increasingly damaging by developing novel relationships with damaging pathogens. An historical example in the UK includes native elm scolytid beetles vectoring the introduced Dutch elm disease

Ceratoscystis ulmi fungus [77]. The UK native *Scolytus intricatus* is considered a potential vector of the highly pathogenic *C. fagacearum*, which causes wilt in North American oak trees.

The international status of some pests may also be useful in predicting future risks from species already present in the UK. *Platypus cylindrus,* for example, is emerging as a damaging pest of cork oaks *Q. suber* in southern Europe and North Africa. Although it is still a secondary pest in the UK, it has recently been shown to vector the highly damaging cork oak charcoal canker *Biscogniauxia mediterranea* [78], and in some areas, the beetle also appears to have become capable of mass attack and killing of apparently healthy trees [79]. Some defoliators also do significantly greater damage to oaks internationally (Table 3.2). As a highly damaging invasive species in North America, Gypsy moth has actually reduced the level of oak dominance in affected forests [80].The planting of more drought-tolerant provenances and species of oak in the UK may also introduce new insect pests. At least 9 species of cynipid gall wasp have invaded NW Europe following the widespread planting of *Q. cerris* beyond its native range [81].

Of the organisms introduced into British forests, the most destructive to date are fungal pathogens, some of which have caused landscape-scale changes. These include ash dieback (*Hymenoscyphus fraxineus*), *Phytophthora ramorum,* Dothistroma needle blight (*Dothistroma septosporum*), and Dutch elm disease (*C. ulmi*). To date, introduced pest insects have generally impacted UK tree health to a lesser degree, e.g. great spruce bark beetle (*Dendroctonus micans*), horse chestnut leaf miner (*Cameraria ohridella*), and Asian longhorn beetle (*Anoplophora glabripennis*). The difference in the severity of damage caused by fungal pathogens and insects may be partly due to the suitability of the UK climate for each group. Some pathogens such as *P. ramorum* have spread very effectively in damp, cool UK forest conditions, whereas the spread of Asian longhorn beetle was evidently limited in southern England due to a suboptimal climate. In particular, the relatively cool mean summer temperatures (compared to continental Europe and North America), appeared to retard the development, generation time, and opportunities for dispersal by flight [82].

There are an enormous number of oak-associated insects around the globe which could prove to be damaging pests in the UK if they were accidentally introduced. It is difficult to assess which species present a serious risk, particularly when no evidence is available on the suitability of *Q. robur* or *Q. petraea* as hosts, or on the effectiveness of the tree defences against those insects. We can make some assessment based on their present distribution and whether the climate of the UK appears compatible. Of the potentially invasive oak species listed in Table 3.2, those which appear likely to find current UK temperatures suboptimal are all suggested to be 'low' risks, since establishment success, development rate, and pest impact would be diminished. The risk rating is otherwise based on the amount of damage they have caused elsewhere, and qualified in the table. However, a more accurate assessment of risk, with greater certainty, would require good-quality empirical data on the thermal requirements of each of the species in Table 3.2. This would also enable predictions to be made regarding potential changes in risk under a warming climate. Robust data on the pathways by which these pests might be transported to the UK is also urgently required. Because the species listed in Table 3.2 are merely representative of the enormous global pool of oak-associated insects, rather than an exhaustive list, an assessment of the key pathways by which *Quercus* timber, live plants and wood products enter the UK (and Europe) would help inform this process and highlight the most important pest risks.

Assessment of knowledge

Regarding pest threats currently present in the UK, only two insect species have been considered here to present a medium or medium-high risk to UK oaks; OPM (also taking into account the risk to human health) and *A. biguttatus*. However, important knowledge limitations include the true impact of these species on tree health.

OPM is only recently established in the UK, and as a health risk has been subject to significant control measures within greater London; as a result, the potential impact on oak vigour is difficult to assess and remains speculative. As OPM continues to spread it is likely that populations will develop beyond the controlled areas. The health risks of working on OPM has limited research on it to date, and so the factors which might promote high population growth of this insect are not known. The potential in the UK for natural enemies to contribute to controlling OPM populations, or whether specific parasitoid enemies might be introduced to limit the risk of outbreaks, remains unclear.

The difficulties of working on *A. biguttatus* are different, but important knowledge gaps remain. As a cryptic and patchily-distributed species living within a robust and valuable amenity / timber tree, quantitative data regarding its impact on oak health and mortality is critically lacking. Understanding of the role of the beetle in AOD also remains unclear, with evidence either speculative or incomplete [24]. Evidence about the role of abiotic factors in predisposing trees to AOD is beginning to emerge [30], but the importance of defoliators such as OPM remains unknown.

Modelling the altered risk of pests in a changing climate requires detailed knowledge of species biology, population dynamics, and host relationships. Some species of defoliators may become more damaging; outbreaks of *E. chrysorrhoea*, *L. dispar, L. monacha, O. brumata,* and *T. processionea* have all been linked to warm temperatures, and generation time may be reduced in species not linked to budburst. The impact of wood and bark boring beetles may increase if changing precipitation patterns and more frequent severe weather events increase the availability of stressed host trees. Warmer summers may expand the currently restricted UK distributions of *A. angustulus, A. biguttatus, A. sulcicollis, P. cylindrus, S. intricatus and X. germanus.* Detailed information on biology and thermal requirements exists for *L. dispar* [83, 84] and *A. biguttatus* [29] but not for the other species listed here.

The quality of distribution and monitoring data for individual pest species (and their hosts – see chapter 7 on Monitoring), which may be used in predictive modelling, is also quite variable. Long-term population data for individual species and accurate estimates of distribution are important components of modelling the future impacts and spread of pest species. Rothamsted Research carries out long-term, UK-wide monitoring of night-flying moths and aphids, and surveying for *A. biguttatus* has been undertaken by the AOD research consortium. Some additional monitoring has also been carried out for OPM and gypsy moth since the establishment of these species in the UK. Other sources of population data on native and established insects include self-reporting systems such as Tree Alert and the National Biodiversity Network, but while valuable, these do not reflect a systematic assessment of pest abundance and impact across the UK oak resource. A comprehensive long-term monitoring program to identify changes in abundance and distribution of key oak pests, and for use as an early warning system against future invasive species would be invaluable for risk prediction and rapid reaction. This should be combined with improved monitoring of the oak population itself (see chapter 7 for further coverage).

There is a general lack of empirical studies on the impacts of pests on oak growth, vigour, and survival, particularly in the UK, which limits our understanding of their importance, and which will hamper predictive modelling under climate change. The body of evidence quantifying the impact of severe defoliation on host vigour seems established, but the link between defoliation and the decline of mature oaks remains more speculative and lacks empirical data. Many studies have quantified the impacts of gypsy moth on tree health, but these studies were carried out in North America, on different oak species, and in a different climate [85]. There are competing explanations as to the impact of wood and bark boring insects on oak health. The generally accepted theory that secondary insects further weaken or kill susceptible hosts is also largely anecdotal and lacking in empirical data. Theories of broadleaf host resistance mechanisms to wood and bark boring larvae also remain largely speculative, although a number of experimental studies have shed some light on host defences against the emerald ash borer [86, 87].

Information on the susceptibility of UK tree species to non-native pests is typically lacking in advance of an invasion. Research on the suitability of *Q. robur* / *Q. petraea* to key pest threats should be conducted (e.g. using freshly cut logs to mimic healthy hosts), alongside investigations of thermal biology. The identification of potentially invasive oak pests is typically based upon the damage that those insects have caused elsewhere, usually in their native range; on different oak species and in a different climate. Although this 'horizon scanning' is a practical approach, critical knowledge gaps exist in each case regarding the suitability of the UK climate and native oak species for their establishment and impact. Little known, or even undescribed insect species might prove highly damaging upon a naïve oak host, but the pathways by which *Quercus* plants, timber and products are transported into the UK from all over the world have not been fully assessed. Such data would help to narrow the search for the most potentially damaging pests (and pathogens) and could usefully be combined with an approach to make more use of sentinel trees for early identification of new threats [91].

Regarding vertebrate pests, the bark stripping activities of grey squirrels present a considerable (medium-high) risk to oak health in the UK. While the negative effects of deer browsing on young oaks in the UK are well established, there remain competing explanations as to the effects of grazing on soil and nutrient status. Whilst deer can be excluded from young regenerating trees by fencing, squirrels are much more difficult to manage, and the causes and hence mitigation of grey squirrel bark stripping remain unclear.

Summary and priorities for new knowledge from review

1. Native & established defoliators

- Determine the impact of defoliating insects in predisposing oak trees to decline. Can serious defoliation increase the susceptibility of oak to AOD?
- Identify the environmental conditions which may promote high OPM populations, increasing the risks of damaging defoliation and to human health.
- Clarify the effectiveness of natural enemies in controlling OPM populations and explore opportunities for introducing specific parasitoids for control.

2. Native and established wood and bark boring beetles

- Determine whether *Agrilus biguttatus* is an essential component of AOD and whether affected trees can better recover from AOD in the absence of the beetle.
- Determine the relationship of *A. biguttatus* with the bacterial lesions of AOD. Does the beetle facilitate lesion development, or is it taking advantage of weakly resistant tissue?
- Quantify the influence of *A. biguttatus* in the mortality of AOD affected trees (compared to the bacterial lesions). Determine whether the beetle is an appropriate focus for management of the disease and explore options to promote the health of the tree and reduce suitability for larval development.
- Assess the risk presented by UK bark-boring beetles as potential vectors of non-native oak pathogens, e.g. *Scolytus intricatus* and *Ceratocystis fagacearum.*

3. Potentially invasive pests of oak

- Identify key global pathways of *Quercus* products being transported into the UK, as part of a broad horizon scanning assessment of potentially invasive oak pests and pathogens. Determine which non-native species may present the greatest risk to UK oaks, and review the effectiveness of the biosecurity measures and monitoring/surveys in place for oak pests.
- Implement long-term monitoring program of current oak pest populations and explore use of sentinel trees as an early warning system against invasive species.
- Determine the climatic suitability of the UK for the most important non-native threats identified to oak health (e.g. *Agrilus bilineatus, Platypus quercivorus* and its associated wilt fungus *Raffaelea quercivora*).

- Determine the susceptibility of UK oak species to these key pests (e.g. the influence of *Q. robur* on larval growth rate and survival of *Platypus quercivorus*).

4. Potential impacts of climate change

- Utilise existing data on the thermal biology of *A. biguttatus* to model the likely impacts of climate change upon its life cycle and distribution. This will be particularly important if the beetle is an essential component of AOD, since the distribution of the disease would also be affected.
- Determine the impact of drought stress upon oak resistance mechanisms; explore how key wood & bark boring pests (native and invasive) may become more damaging to predisposed oak trees.
- Investigate natural variation in resistance mechanisms amongst different provenances of *Q. robur* and *Q. petraea.*

5. Grey squirrel bark stripping

- Determine the causes of bark stripping by grey squirrels, and the risk of damage through monitoring of squirrel populations, their food supply and the damage caused. Investigate the chemical and physical characteristics of the trees involved. As a specific follow-up to recent studies, use DNA sequencing to determine if oxalate – metabolising bacteria are present in the squirrel gut and whether this might contribute to bark-stripping behaviour.
- Investigate how grey squirrel damage to oak is affected by the arrival of the pine marten.

6. **Herbivore impacts on soils**

- Investigate the effects of nutrient inputs and trampling on pasture and hedgerow oak trees.
- Investigate the scale of nutrient inputs into woodlands from deer foraging in a farmland-woodland mosaic and whether these effects are reversible.

7. Oak recruitment and natural regeneration

- Establish the importance of natural regeneration in maintaining the population of hedgerow/ small woodland oaks, and whether protective measures are needed against deer and also insect pests of acorns.

Table 3.1 Native and established insect pests of oak trees in the UK

Species demonstrating significant or regular damage to oaks are included; selection of more minor oak pests is representative rather than exhaustive. Introduced species are marked *.

Risk Ratings represent an estimate of the damage potential of each insect species to oak tree health in the UK; based on published or observed evidence of impact.

Low - likely to have very little impact on tree health in the UK

Low-medium - typically having a small impact on tree health. Insects may be secondary pests and contribute to some reduction of host vigour, but other causal agents will be more important.

Medium - moderate damage to tree health may be expected, impairing growth and function of the tree. Affected hosts may recover, or suffer worsening health over the long term. Includes risks from invasive species which could become more aggressive pests on 'naïve' UK oak species.

Medium-high - insects contribute significant and noticeable damage that often, but not always, leads to the death of trees.

High - significant damage that usually leads to death of trees, often in a short time

Scientific name Common name	Taxonomic group	Ecology	Damage	Risk rating	Risk Qualifier	Potential for future risk elevation
Defoliators						
Thaumetopoea processionea * Oak processionary moth (OPM)	Lepidoptera: Thaumetopoeidae	Larvae feed gregariously on leaves in characteristic "processions". Recently introduced to the Greater London area and is spreading despite intensive eradication efforts.	Outbreaks can completely defoliate trees in Europe. Larvae have irritating hairs which present a severe public health threat. Economic impact from the costs of control.	Medium†	†Rating here refers to moderate risk to human health. Currently subject to control efforts in UK accordingly.	Outbreaks linked to warm temperatures. Distribution is expanding.
Euproctis chrysorrhoea Browntail moth	Lepidoptera: Erebidae	Larvae feed gregariously on leaves.	Periodic outbreaks can completely defoliate trees. Has been linked to oak decline events in Europe.	Low-Medium	Damage may become more severe in warmer summers.	Outbreaks linked to warm temperatures. Larvae have irritating hairs. Potential as predisposition factor in oak decline.
Lymantria dispar * Gypsy moth	Lepidoptera: Erebidae	Considered a key pest of *Q. petraea* & *Q. robur* in Europe. Formerly extinct in the UK but reintroduced. Restricted distribution within England.	Outbreaks may cause severe defoliation. Linked to oak decline events in Europe.	Low-Medium	Damage may become more severe in warmer summers. Low risk of outbreaks under current UK climatic conditions.	Outbreaks linked to warm temperatures. Distribution may expand under warmer climate. Potential as predisposition factor in oak decline.
Operophtera brumata Winter moth	Lepidoptera: Geometridae	Larvae hatch at budburst and feed on young leaves.	Outbreaks can cause severe defoliation, and reduce growth increment. Has been linked to oak decline events across Europe.	Low-Medium	Frequently encountered defoliator of UK oaks. Reflushing of leaves offsets damage. Repeated defoliation rarely kills mature trees.	Seems to benefit from warm temperatures. Climate change may alter synchrony of egg hatch and budburst, reducing damage.
Tortrix viridana Oak roller moth	Lepidoptera: Tortricidae	Leaf-feeding larvae, fold leaves for protection.	At outbreak levels can completely defoliate oak and impact growth, occasionally canopy die back. Implicated in oak decline and mortality events in the UK and across Europe.	Low-Medium	Frequently encountered local defoliator of UK oaks. Reflushing of leaves can offset damage. Repeated defoliation rarely kills mature trees but may contribute to declining health.	May benefit from other increasing stress factors upon hosts.

Scientific name **Common name**	**Taxonomic group**	**Ecology**	**Damage**	**Risk rating**	**Risk Qualifier**	**Potential for future risk elevation**
Acrobasis consociella Broad-barred Knot-horn	Lepidoptera: Pyralidae	Web-spinning, gregarious caterpillar.	Typically minor, leaves are skeletonised. May cause damage to nursery stock & young trees.	Low	Little serious damage.	
Caliroa annulipes Oak slug sawfly	Hymenoptera: Tenthredinidae	Gregarious larvae feed under leaves. Two generations per year.	Larvae skeletonise lower surface of leaf. Damage is rarely severe.	Low	Little serious damage.	
Dyseriocrania subpurpurella Common oak purple moth	Lepidoptera: Eriocraniidae	Micro-moth; larvae mine oak leaves.	Create distinctive 'blotch mine' in leaves.	Low	Little serious damage.	
Lymantria monacha * Nun moth	Lepidoptera: Erebidae	Larvae are polyphagous on wide range of conifers & broadleaves.	Outbreaks may cause severe defoliation, typically on conifers.	Low	Damage may become more severe in warmer summers. Low risk of outbreaks under current UK climatic conditions.	Increasing frequency of outbreaks in Europe, linked to warm temperatures. Larval hairs can be allergenic.
Phalera bucephala Buff tip moth	Lepidoptera: Notodontidae	Larvae polyphagous on broadleaves. Frequent reports to FR thought to be due to superficial resemblance to OPM.	Infrequently associated with Polish oak decline. Limited late season defoliation.	Low	Little serious damage.	
Phyllobius pyri Common leaf weevil	Coleoptera: Curculionidae	Leaf-feeding adults are polyphagous on broadleaves, larvae are root feeding.	Typically limited damage, though young trees are occasionally severely defoliated.	Low	Proximity of hosts to grass roots (larval food) increases populations in farm woodlands.	
Phyllonorycter messaniella * European oak leaf miner	Lepidoptera: Gracillariidae	Leaf-mining moth. Non-native; invasive from Europe.	Larvae mine oak leaves, causing blotching & distortions.	Low	More common & damaging on *Q. Ilex.*	
Phylloxera glabra Oak leaf phylloxera	Hemiptera: Phylloxeridae	Aphid-like insect with complex life cycle. Feed on leaves.	Leaf chlorosis & wilting may result in premature defoliation and impact on the vigour of young trees.	Low	Little serious damage.	Occasional, typically short lived outbreaks in Europe cause more chronic damage.
Thelaxes dryophila Common oak thelaxid	Hemiptera: Aphididae	Colonies form on the undersides of young leaves, flower and acorn stalks producing honeydew.	In high numbers, infestations can damage and kill young shoots, and which may reduce the vigour of young trees.	Low	Little serious damage.	Warmer future temperatures may lead to an increase in the number of generations per year.
Tuberculoides annulatus Common oak aphid	Hemiptera: Callaphididae	Aphids; feed on the underside of leaves.	Limited. Wilting & discolouration of leaves.	Low	Little serious damage.	Warmer future temperatures may lead to an increase in the number of generations per year.
Gall forming insects						
Andricus kollari * Oak marble gall wasp	Hymenoptera: Cynipidae	Requires both *Q. cerris* and *Q. robur* or *Q. petraea* for life cycle. Non-native: imported from eastern Mediterranean in the 1830s.	Produces autumn bud galls up to 28mm diameter. If abundant, galls may disfigure young trees.	Low	Little serious damage.	

Scientific name **Common name**	**Taxonomic group**	**Ecology**	**Damage**	**Risk rating**	**Risk Qualifier**	**Potential for future risk elevation**
Andricus quercusradicis Truffle gall wasp	Hymenoptera: Cynipidae	Large galls are produced on fine roots and knot galls on young stems and on the base of leaf stalks.	Galls kill leaves and young stems. Outbreaks have been associated with oak decline in Austria, with galls affecting up to 80% of young shoots on a tree.	Low	Little serious damage in UK.	
Cynips quercusfolii Cherry gall wasp	Hymenoptera: Cynipidae	Forms small galls on buds in spring, and larger "cherry-like" galls on the undersides of leaves in summer.	Minimal impact upon oak health.	Low	Little serious damage.	
Neuroterus quercusbaccarum Spangle gall	Hymenoptera: Cynipidae	Gall-forming wasp. Clusters of cone-shaped yellow galls on the underside of leaves, and "currant"-like galls on male flowers.	Galls have minimal impact.	Low	Little serious damage.	
Resseliella quercivora Oak gall midge	Diptera: Cecidomyiidae	Larvae develop on the cambium of young oaks following damage from woodpeckers (& occasionally bark beetles, dormice).	Causes necrotic cankers in the bark of young oak trees (named "oak cancer"); considered a pest in France.	Low	Little serious damage in UK.	
Wood & bark boring insects						
Agrilus biguttatus Two spotted oak buprestid	Coleoptera: Buprestidae	Larvae feed at the cambial interface of weakened hosts, preferentially on mature trees.	Linked to UK and European oak decline. Abundant larval galleries may cause considerable damage to vascular tissues. Closely associated with AOD in the UK; uncertain relationship with pathogenic AOD bacteria, and in the formation of necrotic lesions.	Medium-High	Nature of relationship with AOD bacteria remains unclear, but a distinctive association with the disease is apparent.	Present distribution is thermally restricted, expected to expand under climate change. Availability of declining oaks also expected to increase.
Agrilus angustulus Oak borer	Coleoptera: Buprestidae	Similar to *A. biguttatus* but tends to colonise upper stem, branches & twigs, or smaller hosts. *A. laticornis*, another native oak buprestid shares this niche.	Associated with oak decline in several European countries.	Low - Medium	Unknown association with AOD bacteria (also applies to *A. laticornis*).	UK distribution currently restricted to England and Wales. Potential for future spread.
Agrilus sulcicollis * European oak borer	Coleoptera: Buprestidae	Similar to *A. biguttatus* but tends to colonise upper stem, branches & twigs, or smaller hosts. Non-native: recent introduction from Europe, possibly in cut timber.	Implicated in oak decline in several European countries.	Low - Medium	Unknown association with AOD bacteria.	UK distribution currently very restricted with potential to spread. Potential interaction with AOD.

Scientific name **Common name**	**Taxonomic group**	**Ecology**	**Damage**	**Risk rating**	**Risk Qualifier**	**Potential for future risk elevation**
Platypus cylindrus Oak pinhole borer	Coleoptera: Platypodidae	Larvae colonise severely declined and recently dead trees / timber, feeding in the sapwood for the first year and then tunnelling into the timber. Vector a symbiotic ambrosia fungus for food.	Tunnelling activity damages logs/timber until moisture content is reduced. Staining around galleries by fungus. Associated with European oak declines, but does not directly kill hosts.	Low-Medium	Appears to be increasing in abundance & frequency, possibly due to increased host availability or warming climate.	Increasingly aggressive populations reported in parts of Europe and N. Africa. Could develop an association with pathogenic fungi; shown to vector charcoal canker in cork oaks.
Dryocoetes villosus Oak bark beetle	Coleoptera: Curculionidae, Scolytinae	Larvae develop on severely declined stems or on logs.	Secondary damage to severely weakened tissues.	Low	Little serious damage.	
Phymatodes testaceus Tan bark borer	Coleoptera: Cerambycidae	Feeds in the inner bark and sapwood of recently dead hosts or fresh cut logs. Polyphagous on broadleaves, with preference for *Quercus*.	Pest of tannery bark and felled timber. Minimal impact on live trees.	Low	Galleries do not penetrate deeply into timber.	
Scolytus intricatus European oak borer	Coleoptera: Curculionidae, Scolytinae	Confined to weakened hosts. Associated with European oak decline events.	May colonise and kill weakened oaks, and vectors fungi that are weak pathogens of oaks.	Low	Considered a potential vector of *Ceratocystis fagacearum*.	
Xylosandrus germanus * Black timber bark beetle	Coleoptera: Curculionidae, Scolytinae	Invasive ambrosia beetle, widespread across Europe, now in UK. Very polyphagous secondary pest of stressed hosts.	Typically limited to moribund hosts, but stressed trees can be attacked & timber damaged & stained.	Low	Not yet spread throughout UK Unknown potential for interaction with declining oak.	Previous damage linked to climatic stress of hosts.
Acorn pests						
Andricus quercuscalicis * Oak knopper gall wasp	Hymenoptera: Cynipidae	Requires both *Q. cerris* and *Q. robur* for alternating generations. Non-native: introduced from south-eastern Europe.	Galls abort acorn. Can attack up to 90% of acorn crop in some years. Can impact seed trade.	Low	No clear evidence of reduced fertility / regeneration. Requirement for *Q. cerris* presence.	
Curculio glandium Acorn weevil	Coleoptera: Curculionidae	Adults pierce and lay eggs in acorns. Larvae develop within, before emerging to pupate.	Damage to acorns, typically limited.	Low	No evidence of reduced regeneration despite considerable proportion of acorns affected.	
Cydia splendana Acorn moth	Lepidoptera: Tortricidae	Larvae develop within acorns, (& chestnuts) causing premature fruit fall.	Damage to acorns, limited.	Low	More economically important on chestnuts.	
Stem-feeding sucking insects						

Scientific name **Common name**	**Taxonomic group**	**Ecology**	**Damage**	**Risk rating**	**Risk Qualifier**	**Potential for future risk elevation**
Kermes quercus Oak scale	Hemiptera: Coccidae	Colonises the stem, can be abundant on poorly growing oak.	Can reduce vigour of poorly-growing pole stage trees. Has been linked to crown dieback in the UK and Hungary.	Low	Damage tends to be restricted to poorly-growing trees.	May benefit from increasing host availability.
Moritziella corticalis * Oak bark phylloxera	Hemiptera: Phylloxeridae	Colonises the bark of shoots from previous year(s). Introduced from Europe or N. America.	Can cause shoot dieback on young trees.	Low	Little information on impact, limited damage.	

Table 3.2 Non-native insects posing a potential future risk to oak health in the UK (potentially invasive pests).

Species demonstrating significant or regular damage to oaks within their current distribution are included, and selection is representative rather than exhaustive. Risk ratings are estimated as for Table 3.1. Species were selected from the UK Plant Health Risk Register[88], CABI Invasive Species Compendium[89], and EPPO Global Database[90].

Scientific name **Common name**	**Taxonomic group**	**Ecology**	**Damage**	**Risk rating**	**Risk Qualifier**	**Distribution**
Defoliators						
Ennomos subsignaria Elm spanworm	Lepidoptera: Geometridae	Occasional serious defoliator of N. American broadleaves including chestnut and various oaks (white oak spp. preferred).	Significant canopy damage causing growth loss and mortality during outbreaks.	Low-Medium	Polyphagous habit, likely to utilise UK oaks. Potential as predisposition factor in oak decline.	Eastern seaboard of N. America.
Lymantria mathura Pink gypsy moth	Lepidoptera: Erebidae	Polyphagous: feeds on flowers & leaves of broadleaves, esp. *Quercus*. Has broad climatic distribution.	Important defoliator within its range, outbreaks can be extensive, causing loss of vigour & leading to secondary pest attack.	Low-Medium	Polyphagous, including most Fagaceae tested, regardless of origin. Potential as predisposition factor in oak decline.	Russia, Siberia, China, Japan, Korea, Taiwan, Nepal, India.
Malacosoma disstria Forest tent caterpillar	Lepidoptera: Lasiocampidae	Major defoliator of broadleaves incl. *Quercus,* outbreaks may be extensive & last 3-4 years. Larvae spin webbing for protection.	Attacked trees generally survive complete defoliation, but growth reduction may be considerable.	Low-Medium	Widely distributed in N. America, representing broad thermal tolerance. Regional populations show host preferences, but all can utilise oaks.	USA, Canada.
Corythucha arcuata Oak Lace Bug	Heteroptera: Tingidae	Nymphs & adults pierce oak leaves during feeding causing chlorosis.	Feeding damage increases through summer & can cause leaf drop. May reduce growth & weaken trees in combination with other stress factors.	Low	Leaf function continues for most of summer even with heavy infestation. Impact on larger trees is limited.	USA & S. Canada, introduced into Italy, Switzerland, Turkey, Bulgaria, Croatia, Hungary, Serbia, Slovenia.
Malacosoma parallela Mountain ring silk moth	Lepidoptera: Lasiocampidae	Important polyphagous defoliator of broadleaves, larvae form a web nest.	Damages *Quercus, Prunus Malus*. Outbreaks often last 2 years.	Low	Outbreaks tend to occur in mountain forests, evidently a more cool-adapted species.	Central Asia: Turkey, Armenia, Kazakhstan, Iran, Kyrgyzstan, Syria, Tajikistan.
Wood & bark boring insects						
Agrilus bilineatus Two lined chestnut borer	Coleoptera, Buprestidae	North American buprestid, occupying a similar niche to *A. biguttatus* in several *Quercus* spp. Prefers weakened trees.	Can cause dieback and contribute to host mortality. Occasional nursery pest.	Medium	Unknown susceptibility of UK oak spp.Has attacked *Q. robur* planted in USA, but no known impact recorded in Turkey. Potential for interaction with AOD.	Eastern US & Canada. Introduced to Turkey.

Scientific name **Common name**	**Taxonomic group**	**Ecology**	**Damage**	**Risk rating**	**Risk Qualifier**	**Distribution**
Massicus raddei Oak longhorn beetle	Coleoptera: Cerambycidae	Affects a range of *Quercus* & *Castanea* spp. in North-East Asia. Pest of oaks in China.	Larval galleries within wood of oaks, leading to dieback of crown.	Medium	Unknown susceptibility of UK oak spp. Unclear whether mortality caused in native range. Potential for interaction with AOD.	Russia (far east), China, Korea, Japan, Taiwan, Vietnam.
Platypus quercivorus Oak ambrosia beetle	Coleoptera: Platypodidae	Wood boring ambrosia beetle which vectors *Raffaelea quercivora*, Japanese oak wilt disease. Capable of mass attacks. Many Fagaceae hosts.	Vectored fungus *R. quercivorus* causes widespread mortality of oaks in Japanese forests dominated by *Quercus mongolica* and *Q. serrata*. Direct damage to timber quality from boring activity.	Medium	Not all oaks are susceptible to the fungus; unknown suitability of UK oaks, but limited evidence suggests *Q. robur* may be susceptible.	Widely distributed in Asia, across temperate, subtropical and tropical climates.
Enaphalodes rufulus Red oak borer	Coleoptera: Cerambycidae	Larvae feed on living oak tissue. Preference for red oak spp. Occasional outbreaks.	Larval galleries in phloem & xylem causing economic damage to timber. Severe outbreaks linked with host mortality (in association with other stress factors).	Low - Medium	Preference for red oak spp., UK oak susceptibility unknown.	USA, Canada.
Pseudopityophthorus minutissimus Oak bark beetle	Coleoptera: Scolytinae	Potential vector of oak wilt, *Ceratocystis fagacearum.*	Adults inflict feeding wounds on stem, leaf, bud axils, through which they might transmit oak wilt. This causes wilting & dieback of foliage, and can kill trees within a few years.	Low-Medium	Oak wilt fungus is the primary concern; the beetle not a pest in own right. Unknown risk of UK native bark beetles as vectors. American white oaks more likely to recover than red oaks from the disease, although all spp. susceptible.	USA, Canada. Another N. American species, *P. pruinosus* is also a possible vector.
Agrilus auroguttatus Gold spotted oak borer	Coleoptera: Buprestidae	Larvae feed in the phloem of weakened oak hosts in native range, but attacks healthy naïve spp. where introduced. Preference for red oak spp.	Major impact, contributing to the mortality of naïve hosts in California since its introduction.	Low	Preference for red oak spp., UK oak susceptibility unknown. UK climate likely to be suboptimal, regulations in place to prevent import.	SW USA & Mexico.
Coraebus florentinus Oak burncow	Coleoptera, Buprestidae	Pest of oaks in Mediterranean region, prefers southern exposed, sun warmed branches.	Damage & dieback of branches, loss of vigour.	Low	Thermophilous species, damage greatest in Mediterranean countries.	European.
Euwallacea sp. (fornicatus) Polyphagous Shot Hole Borer	Coleoptera: Curculionidae, Scolytinae	Polyphagous ambrosia beetle, females vector *Fusarium* fungus as food source. Infests wide range of healthy host plants.	Vectors *Fusarium euwallaceae* which can cause wilt and dieback of hosts. Infests many oak spp., including *Q. robur.*	Low	UK unlikely to be climatically suitable. Uncertain taxonomy: PSHB appears to be distinct from *E. fornicatus* (tea shot-hole borer).	PSHB from SE Asia, introduced to California, USA & Israel. (*E. fornicatus* globally widespread).

Scientific name **Common name**	**Taxonomic group**	**Ecology**	**Damage**	**Risk rating**	**Risk Qualifier**	**Distribution**
Prionoxystus robiniae Carpenterworm	Lepidoptera: Cossidae	Damages live broadleaves when larvae bore into wood. Preference for damaged hosts.	Can cause girdling and structural failure of branches, and timber damage. Increases risk of drought/disease impact.	Low	Polyphagous on many broadleaves, Including oak.	Southern Canada, USA.
Acorn pests						
Curculio elephas Chestnut weevil	Coleoptera: Curculionidae	Adult chews hole into fruit for feeding and oviposition, larvae develop within.	Primarily a pest of European chestnut, but can reduce yield of acorns in *Quercus ilex* & *Q. robur.*	Low	Limited damage to oaks.	Continental Europe & Mediterranean region.
Sucking insects						
Phylloxera quercus Oak phylloxera	Hemiptera: Phylloxeridae	Feeds on wide range of deciduous & evergreen oaks. Life strategies include parthenogenesis & sexual reproduction, winged & non-winged forms, assisting population increase.	Feeding damage to leaves, accumulating particularly on evergreen oaks; can allow entry of secondary fungus contributing to leaf necrosis.	Low	Appears to prefer warmer climate, but unclear taxonomy does not rule out more northern records (e.g. Belgium, Netherlands).	S. Europe (Italy, France, Spain), North Africa and the Middle East.

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4. Pathogen threats to native oaks in the UK

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Introduction and scope

In general, native oak species (*Quercus robur* and *Q. petraea*) are well adapted to their UK environment and have a wide array of defences against native and established pathogens making them relatively resilient. However, as long-lived trees, oaks may progressively cumulate impacts of a wide range of pathogens while the costly defenses become less efficient with ageing; this can hasten their death, especially if environmental conditions are not favourable. Moreover, oaks, like all other trees, are increasingly under threat due to new, exotic, pathogens and pests (see chapter 3) introduced to the country, and also due to changed behaviours and impacts of organisms already present, as a consequence of disturbance and/or climate change [1]. The emergence of Acute Oak Decline (AOD) [2] is current evidence of a danger that threatens the health and survival of Britain's oak.

Diseases are the result of a host - pathogen encounter, shaped or influenced by the environment, which can have an effect on modulating host susceptibility or tolerance to infection as well as pathogen abundance, virulence and transmission (c.f. pest—host-environment triangle in the conceptual framework Figure 1.1) [Source 1]. The environment includes abiotic factors such as climate, soil properties and air pollutant effects; but, the effect of other biotic components affecting the host - pathogen interaction has been increasingly recognised. When considering all these effects and interactions it is evident that diseases should be considered as "pathosytems" with a holistic view.

In some diseases, however, where pathogen encounter is a major determinant of disease in a wide range of environmental conditions, the one pathogen – one disease model is fitting. Such "simple" or 'primary' diseases can occur, for example, when introduced non-native pathogens find highly susceptible host species that lack co-evolved resistance against them. In other cases, the disease or defective health is hardly attributable to a single organism but rather the result of the action from an assorted assembly of microbes that make up part of the pathobiome [3]. In addition, the environment may have an important role in affecting susceptibility of the host, for example through predisposing hosts to the action of "weak", or "opportunistic" pathogens, which are not able to cause disease on their own or on healthy, vigorous hosts [4,5,6]. At the extreme end of this disease continuum, are the "complex diseases" or syndromes, often called "declines". Oak decline is an example of a complex syndrome usually involving both abiotic predisposing factors and several biotic elements, acting in temporal sequence, having a cumulative effect [4,7]. Decline diseases of oak have been documented for more than 100 years [8,7], in the UK and elsewhere [7], and although hard evidence of causes and effects are challenging to prove, headway has been made in recent times [3,9,10].

Recently, emphasis has been placed on the importance of the involvement and interactions of microbial communities in oak health and disease, particularly declines, either as protecting agents at the plant-environment interface (for example the phyllosphere or rhizosphere microbiota, including mycorrhizae) or acting directly in causing disease, for example in AOD, with the pathobiome concept. In long lived woody hosts, the holobiont is considered important for health [10].

Oaks support an enormous microbial biodiversity including macro- and microfungi, bacteria, viruses and possibly other non-culturable organisms, such as Mollicutes (phytoplasmas), but little is known about the complete composition of microbial communities on oak and their function, which is important as many microbes play a crucial role in tree health, vitality and resilience. While some microbes may be able to colonise all parts of oak trees indiscriminately, the majority will be adapted to survive on specific environments related to tree part; for example, leaves, flowers, acorns, twigs, branches, stems, and buttress or feeder roots.

This chapter focusses on priority diseases of native oaks in the UK which are considered as the major threats. Databases on the incidence and abundance of stakeholder and citizen scientist reports to the Forest Research Tree Health Diagnostic and Advisory Service (THDAS) were consulted and used to guide importance based on the number of reports made, selecting where 10 reports had been made over that period (Table 4.1). A number of lead scientists in the UK, USA and Europe were also consulted about their evaluation of the most important threats in those countries. There was a limited response to this enquiry within the available time frame, but the views received were considered, together with using the available information and literature as an indicator of importance. The UK Plant Health Risk Register [Source 2] was also consulted for selection of priority diseases.

This review used only readily available, relatively recent (~1900 – 2017) literature identified by Scopus, Google Scholar and PubMed search engines for on oak diseases in the UK, and also France and Germany. France and Germany were selected as comparators to the UK because of similar climatic ranges, both oak species of interest are native and abundant there, and similar disease problems on oak have been reported.

State of knowledge

For simplicity and ease of reference, this review is organized by type of pathogens affecting different organs, covering the major threats affecting acorns, foliage, stem and roots, and finally oak declines.

Acorn pathogens
Mature acorns that fall to the forest floor are susceptible to infection by the soilborne fungus *Ciboria batschiana,* causing black rot [Source 4]. The impact of these infections in natural oak regeneration has not been assessed but this is a major concern for acorn storage. Thermotherapy applied to collected acorns before storage has proved an efficient way to control black rot. However, storage conditions can predispose the acorns to subsequent infection with another fungal pathogen, *Cylindrocarpon didymum* [Source 5] which does not appear to be affected by thermotherapy.

Drippy blight disease, a future threat. Initially recorded in California affecting acorns [11] has extended its geographical and host range becoming an emerging primary disease of a number of oak species. Disease expression in Colorado takes the form of extensive twig dieback, branch canker and tree decline, which is caused by the kermes scale insect (*Allokermes galliformis*) feeding on developing acorns, twigs or buds, and subsequent bacterial infection of the wound sites with *Lonsdalea quercina* [12,2]). The host range of this disease is expanding and now includes a number of white oak species; many trees die or are removed before death. The pathogen has also been reported in Spain [13] where it causes bleeding cankers and gummosis of acorns. It is unknown if the disease occurs in the UK; it is unlikely as *L. quercina* has not yet been reported in the UK but is of concern as it is an emerging disease in the USA and a wide range of oak species are susceptible.

Foliar diseases

Powdery mildew: is considered the most important primary foliar disease of oak in the UK and Europe. Mildew is widespread in the UK [Source 21 and 22], affecting native oaks in nurseries, gardens, parklands and woodlands. Characteristic symptoms are a white felt-like coating on the upper and lower leaf surfaces, leading to leaves turning brown, and in severe attacks, to defoliation and withering of shoots, and even in mortality of seedlings. Since infection leads to reduced photosynthetic activity [9], powdery mildew is typically a debilitating agent. Reduced radial stem growth has been observed after severe infection [15], and successive infections have been implicated in predisposing trees to oak decline [16,18,21]. A long term research project should aim at monitoring powdery mildew outbreaks annually with follow up assessments to obtain evidence of the involvement of mildew in oak declines and address the proposed hypothesis [16].

Oak powdery mildew emerged in Europe in the early 1900s. It has been recently shown to be caused by a number of fungal species including *Erysiphe alphitoides, E. hypophylla, E. quercicola,* which are very likely of Asian origin, and *Phyllactinia guttata,* which might be indigenous [17]. In the UK there are only a few reports that document mildew on oak and only *E. alphitoides* is reported [Source 6, 26,17], including the recent small citizen science project aimed at investigating species of mildew on oak in the UK carried out in 2017 (Dr. Ana Perez-Sierra personal communication). However, the real status of mildew species present in the UK is unknown, because this survey was not structured or representative spatially or temporally.

Previously in the UK the sexual stage of *E. alphitoides* (chasmothecia) had seldom been reported, although it is considered an important aspect of the epidemiology of mildews[19, 20]. However, the incidence of chasmothecia has increased in the UK since the 1990s, which could be a result of climate change or a genetic shift in populations [22]. Whilst studies showed that the dry season of 1947 in Britain resulted in abundant chasmothecia formation on *Q. robur* and *Q. petraea* [23], no research has been undertaken to assess the effects of various climatic extremes on inoculum production or subsequent disease intensity. Furthermore, no research has been carried out on the impacts of increased sexual recombination events. If several species co-occur, multiple attack is expected to be more damaging than single species infections, but research is yet to demonstrate this; a recent study in France did not show amplified or cumulative damage as a consequence of combined occurrence of *E. alphitoides* and *E. quercicola* at plot level [26].

Natural regulation of oak powdery mildew has received little attention. Several hyperparasites reducing powdery mildew infections have been described, and some of them have been reported in oak. The co-occurrence and possible relationships of *E. alphitoides* with other microbes in the phyllosphere has recently been published [129] and showed changes in microbial communities in response to *E. alphitoides* infection. Two fungal species *Mycosphaerella punctiformis* and *Monochaetia kansensis,* appeared to act as possible antagonists of *E. alphitoides* infection, and may be of interest with respect to control strategies. Variation in resistance/susceptibility to powdery mildew has been reported, with *Q. robur* generally assumed to be more susceptible than *Q. petraea* [22]. Interaction with phenology, and thus climate, is probably important. However, genetic and environmental factors modulating susceptibility/tolerance to infection are still important issues to be addressed. Some fungicides, including sulphur and ergosterol biosynthesis inhibitors have shown efficacy against oak powdery mildew but practical use is restricted to nurseries.

Due to the long-distance airborne spread of *Erysiphe* conidia [22], it is highly probable that all three species occur in the UK and therefore continual surveying and monitoring are required to determine distribution and species present. Future research should focus on assessing genetic diversity of both host and mildew, which is a measure of an organism's ability to adapt to changing conditions (e.g. climate, control, hosts etc.). Assessment of the long-term effects of powdery mildew on oak health and predisposition to declines is also required.

Anthracnose: is a leaf and twig disease characterised by necrotic patches or spots on leaves or dieback of shoots. The leaf spots can develop into an angular leaf blotch on young leaves, and infection may spread into petioles, along shoots and lead to wilt. The disease is widespread in the UK [Source 21 and 22] and can be serious in plantations. It is commonly reported on younger oak (seedlings and plantation oak 15-40 years-old) [29]. This disease is troublesome in other countries, including Germany and the Netherlands [31]; USA [32]; and many southern European countries, especially Italy where it is spreading northwards. The causal organism has been identified under many names (*Gleosporium* (or *Discula*) *quercinum*) but the currently accepted name for this fungus is *Apiognomonia errabunda*. Taxonomy issues may make some of the reports from various countries unreliable.

The fungus has an endophyte-pathogen life strategy linked to life cycle phases (asexual / sexual) life form [33]. The pathogenic life style is triggered by major stress, for example drought, which also induces sporulation. Gall forming insect attack can also trigger disease [34]. Anthracnose occurs on multiple site types and is not influenced by soils. The pathogen is adaptable to many environmental conditions and has an extensive host range. It is a prolific sporulator with a large infection potential, and has a triple-propagule survival mechanism, giving it ecological plasticity and heightened survival ability. Spore dispersal takes place through air currents, wind and rain. Optimal temperatures for growth are between 16°C - 20°C, and infection takes under moist conditions. In the UK inoculum is produced from May onwards (Murray in [35, 34]), but rainfall early in the growing season increases infection levels in March-April.

Numerous oak species are affected, but also *Acer*, *Aesculus* (buckeye), *Betula*, *Castanea sativa*, *Celtis*, *Cornus*, *Corylus*, *Fagus sylvatica*, *Fraxineus*, and *Tilia* [(see Source 23)]. Oak species include: *Q. cerris*; *Q. pubescens*, *Q. rubra*, but *Q. robur*, *Q. petraea* and *Q. palustris* are affected in Britain. There are no known natural enemies / biocontrols, but it is less common on sites with high levels of *Acremonium*, *Paecillomyces*, *Aureobasidium*, *Ramnichloridium* and *Trichoderma*. Microbiome-wide studies would be useful in this regard. Although first recorded in Britain by Grove[30], at present it is not considered a very significant problem on oak in the UK, but vigilance is required.

Root diseases

Armillaria species

Armillaria species, often referred to by the common name 'honey fungus', can act either as saprophytes or primary pathogens. Some species have specialised structures - rhizomorphs (or bootlaces) passing over and attaching in places to the exterior surfaces of buttress roots, penetrating superficially. In their pathogenic form they invade roots of trees causing damage through a progressive white rot, which often advances into the stem collar and may lead to tree death. Weeping stem patches, deteriorating crown condition and dieback are common symptoms [36]. Once the host can no longer survive on the remaining functional vascular tissue, it will die [36]. However, death is not always the outcome of infection and some trees are able to resist further ingress and heal (callus) damaged parts; reduced yield and possibly compromised tree stability may occur.

Until the late 1980s, most *Armillaria* species were classified as *A. mellea* and were widely reported on oak in the UK, France and Germany [37,8,18,38]. However, the recognition of inter-sterility groups and then the application of phylogenetic markers differentiated this genus into multiple species. *Armillaria mellea, A. gallica, A. tabescens* (now *Desarmillaria tabescens*, [39]), and *A. ostoyae* have been isolated from *Q. robur* in the UK [40,41,42,43, source 22]. The predominant species in UK woodland oak is *A. gallica* but recent studies suggest that *A. gallica* is polyphyletic, being made of a number of species (S. Denman, pers.comm.).

A. mellea is a highly virulent pathogen of oak [40] and is thus considered a primary pathogen. By contrast *A. gallica* has long been considered mainly as a saprotroph playing a role as a stump decomposer, cycling carbon and nitrogen in natural deciduous and mixed forests [44]. However, it may become pathogenic under certain conditions that are yet to be elucidated [44]. Evidence to support or understand their proclaimed roles in woodlands is lacking. *D. tabescens* is considered mostly saprophytic but can be an opportunistic weak pathogen when trees are predisposed under unfavourable conditions [44]. However, in a number of cases in the UK, *D. tabescens* appears to be a highly aggressive pathogen on a number of oak trees, causing severe stem bleeding and tree death [43]. *A. ostoyae*, a primary pathogen on softwoods, was found together with *A. gallica* in the same tree, raising questions about the ecological and pathogenic roles of this species on oak [43]. Amplified damage effects with multiple species inoculations (e.g. *A. gallica* and powdery mildew; or *Armillaria, Gymnopus* and *Phytophthora*) have been demonstrated [45,46].

It has been hypothesised that stress lowers tree resistance and increases susceptibility to root infection [47]. In this respect, *Armillaria* species have been associated with oak declines in Europe [48] and the UK [37,49,50,51,52]. Little information is available about the metabolic characterisation of oak trees predisposed to *Armillaria* attack, or indeed the predisposing effects to other diseases of *Armillaria* infection on the host. Interruption of carbon and nitrogen nutrition within the tree has been suggested but without evidence [53].

Spread of *Armillaria* species occurs via airborne basidiospores released from fruiting bodies (mushrooms), but most commonly through root to root contact in the soil by the rhizomorphs [36,54]. Wounded or cut surface of tree roots and stumps are minor infection avenues for germinating basidospores [40]. Spore infection is important for generating genetic diversity and facilitating long range spread of the fungus [55]. *A. gallica* produces prolific numbers of rhizomorphs, but fewer rhizomorphs have been observed for other *Armillaria* species [40]. Infected stumps and roots produce rhizomorphs long after felling, supporting saprophytic survival of *Armillaria* [56] and posing management challenges. Once the rhizomorphs are disconnected from their substrate, they are short lived [36]. Infection can also spread when a susceptible root comes into contact with an *Armillaria* infected root.

Following infection, mycelia colonise the cambial and cortex layers of oak root systems, and through enzymatic degradation, obtain their nutrition and advance through these layers as characteristic mycelial fans. Little information about this process and the enzymes produced is available.

Climate change could impact the spread and distribution of *Armillaria* species. Maximum production of *Armillaria* spp rhizomorphs was found to occur at 20°C with very little growth below 10°C and above 26°C [57]. Warmer winter temperatures could increase rhizomorph production and clonal spread of *Armillaria* sp. *D. tabescens* is more thermophilic than other *Armillaria* species, and although prevalent in Mediterranean regions [44], it is present in the UK in south-east and east England [47]. *A. ostoyae* is better adapted to cooler environments [58]. Warmer temperatures could cause higher incidences of *D. tabescens* infection and narrow the distribution range of *A. ostoyae* in warmer areas. Interestingly, *A. gallica* was shown to be as pathogenic as *A. mellea* under drought stress conditions [59]; this could have important consequences if predictions of hotter summers with less rain hold true.

Control measures for *A. mellea* focus mainly on limiting build-up of inoculum or reducing its impact. Cultural practices include reforesting with disease free trees/plants more resistant to *A. mellea*, minimising tree stress (which might also be achieved with less dense planting and more frequent thinnings) and preventing tree damage, reducing carbon availability by uprooting and/or burning stumps and roots [36, 60]. However, prescriptive details of these treatments are missing. Individual infected trees can be treated with chemical applications, although these have environmental implications and are not always effective at reducing rhizomorph spread [61]. There is scope for research on biocontrol options. Studies on hyperparasitism and niche competition are possibly economically attractive approaches. For example, in British Columbia research showed that inoculation of an *A. ostoyae* infected Douglas fir stand with *Hypholoma fasciculare* resulted in a statistically significant reduction of *A. ostoyae* infection [62]. However, *H. fasiculare* is itself a deadwood decay fungus that is widely found in Europe and Britain, and without knowledge of the conditions and mechanisms of infection and interaction its application in biocontrol cannot be considered.

Extensive studies on *Armillaria* incidence were performed in the UK by Risbeth between 1970 and 2000 ([e.g. 130]). However, very little research on *Armillaria* in the UK has since been published. Future research should address the distribution and genetic diversity of *Armillaria* species throughout the UK, noting associations of specific *Armillaria* species with oak declines (chronic and acute). There is a need for extensive *Armillaria* spp. collection and identification, and development of molecular markers to consider genetic diversity and potential of the species to recombine and adapt to changing conditions. Studies on the basic biology, infection, epidemiology and growth conditions will help towards understanding the distribution of the various *Armillaria* species across the UK and modelling the risk and spread under different climate conditions. Research on environmental factors such as drought stress, as a trigger for change of activity mode in these fungi requires investigation. Further information on infection pathways and mechanisms of infection, particularly in woodland environments, is needed. The interactive effects of *Armillaria* species with a range of microbial species including bacteria, is a research gap, and experimental evidence about the pathogenic-saprophytic behaviour, and causes of switches in life mode are also required. Scoring for presence of different *Armillaria* species in an ongoing oak genome wide association study (GWAS) will enable identification of genomic regions in oak that confer tolerance to *Armillaria* spp., which could help understand the genetic architecture of this complex trait and possibly have application in future resistance breeding work.

Gymnopus fusipes:
This species is commonly known as the spindleshank mushroom, causing rootrot of oaks. Infected trees do not show deterioration in crown health or sapwood increment until advanced stages, and the diseased condition of trees may not be realised for decades. This probably explains why the pathogenic role of this fungus was overlooked and for a long time was considered a harmless saprophyte. Lesions on roots of pedunculate oak (which is considered more susceptible than sessile oak) can be extensive before the cambium is penetrated [63]. *G. fusipes* destroys the deeply penetrating roots central to the root system, working its way back to the horizontal supporting roots so windthrow can be a consequence [63, 64]. The slow rate of rot is a key feature of this pathogen that is often interpreted as having less impact [65], but this is erroneous [66, 67].

Most reported scientific studies have been carried out in France where it is now recognised as a major pathogen in oak decline syndromes, especially *Q. robur*. The general importance of *G. fusipes* in oak declines in Germany has been contested [18], as correlations between root damage and symptoms were weak [63, 64]. However, it was conceded that *G. fusipes* could play a significant role locally [18], but in Northern Germany only a single case (out of 60 observed stands) detected fruiting bodies of *G. fusipes* in a stand of sessile oak on loess over calcareous parent rock [68]. In the UK, citizen scientist reports indicate that there is wide occurrence of this pathogen although many records originated from - England (www.naturespot.org.uk), and it has been recorded in Northern Ireland [Source 22]. There are very few reports of its incidence and pathogenicity in the scientific literature [52].

The taxonomic status of this pathogen has changed from *Collybia fusipes* to *Gymnopus fusipes* [69]. There may be other species of *Gymnopus* associated with oak in the UK but *G.*

fusipes appears to be the most important oak root pathogen amongst them. A rapid diagnostic to verify species identification would be useful.

Very little is known about the infection biology of this fungal pathogen; infection is thought to occur via basidiospores infecting the root collar, whereafter colonisation is slow and visualised as small white mycelial fans within the necrotic inner bark (lesions) on large roots. There have been a few reports of *G. fusipes* cords on the root surface [63] although it is not clear whether these are infectious like *Armillaria* sp. rhizomorphs. Examination of self-incompatibility groups of isolates from a French forest found that vegetative spread of the fungus is not common [70] and so the cord structures are unlikely to be significant in spread of the fungus. The fungus does not spread via root to root contact [70]. Data on mechanisms and pathways of dispersal and spread are missing.

Soil moisture holding capacity is inversely correlated with disease severity [71]. *G. fusipes* growth and infectivity is sensitive to waterlogging and hypoxic conditions. Thus, sporadic occurrence of floods predicted to occur as a result of climate change could affect distribution and spread of *G. fusipes.* Information on distribution in the UK would be useful in testing correlations between occurrence and environmental factors. Sessile oak are not as susceptible as pedunculate oak, both being less susceptible than the American red oak [72,73].

Future research direction should focus on: developing a rapid diagnostic assay for field identification especially in the absence of fruiting structures, and infection levels on trees if possible; the infection biology and epidemiology and mechanisms of degradative action of this pathogen, as well as its interactions with both beneficial and other pathogenic organisms; climatic factors influencing spread of the disease (temperature and moisture); role of cord like structures in disease spread; and mechanisms to eradicate and control the fungus.

Phytophthora

Phytophthora spp are soilborne oomycetes which have been increasingly recognized as important pathogens of tree species [76, 78]. Their impact has been dramatically increased in the recent period in relation to nursery trade of plants-for-planting. Indeed, *Phytophthora spp* often find ideal conditions for their development in well watered plants in nurseries and their presence may be masked by the use of chemical treatments with fungistatic (but not eradicant) effects. Contaminated plants and/or potting media circulating across continents are then an effective way to spread these pathogens.

In the UK and continental Europe *Phytophthora* species cause two main types of symptoms/ diseases on oak: (1) bleeding cankers which progress up the stem from infected roots, possibly but rarely resulting in tree mortality and (2) feeder root necrosis, which is thought to be strongly associated with oak declines. Each type disease is dealt with separately below.

Bleeding stem cankers result from necrosis of the underlying inner bark caused by the pathogen and response from the tree. Infected trees may present some level of crown deterioration and dieback and eventually die [82]. There are not a great number of records on this disease in the UK, but *Phytophthora* is difficult to isolate and identify, so current records probably under-represent the situation. More attention should be given to this disease particularly in the south and south east where *Phytophthora* on sweet chestnut is a problem (often referred to as "ink disease"), because the species that affect chestnut also attack oak.

The major species identified as causal in stem bleeding are *Phytophthora cambivora, P. cinnamomi* and *P. plurivora*. Other *Phytophthora* species may be involved in this disease in the UK. In France *P. cinnamomi* is of serious concern on red oak but can infect *Q. robur*; in the UK it is prevalent in the south and south east.

Attack by *P. cambivora* and *P. plurivora* is linked to soil conditions, being severe on heavy soils with fluctuating water-tables and periods of waterlogging [74,75]. Stem bleeding caused by *P. cambivora, P. cinnamomi* and *P. plurivora* is likely to continue to occur sporadically and increasingly, as these species have a wide host range and plant trade is a major pathway for dissemination of inoculum [75]. These *Phytophthora* species thrive in warm temperatures [74,77,78,79]. As global warming and climate change progress, more severe and frequent storms are predicted [80], so there is likely to be an intensification of disease in south and south-east England where high levels of inoculum are present in connection with disease of sweet chestnut [74,75], and further northerly spread can be expected as climates become less limiting for these pathogens.

Very little is known about feeder root rot on oak in the UK, especially in relation to *Phytophthora* infection. No records of this occur in the FR Advisory database, which is a reflection of a lack of awareness of the condition amongst the sector and the general public. Many *Phytophthora* species have been associated with feeder root rot on oak following sampling campaigns in different European countries: In Germany the species *P. cactorum* (not on oak although present on other tree hosts in the UK), *P. cambivora, P. europaea* [89], *P. gonapodyides*, *P. quercina* [90], *P. plurivora* [91], *P. psychrophila* [89], *P. undulata* [89] and a *Pythium* species P [78,79,82] are listed. *P. quercina* is widespread and appears to be host specific to the genus *Quercus*. Four species were isolated in association with oak in France [88]: *P. gonapodyides,* especially abundant in water, *P. megasperma, P. plurivora* and *P. quercina.* In the UK *P. cambivora, P. gonapodyides*, *P. quercina*, *P. plurivora* were isolated from oak soil [75,92]. In root inoculation studies the order of severity of root damage varied among species, as follows: *P. cinnamomi* (highly aggressive) > *P. cambivora* > *P. quercina* and *P. gonapodyides* > *P. plurivora* > *P. europaea,* but there were also significant differences in aggressiveness of isolates [93].

In 1998 a research project (PathOak) involving France, Germany, Italy and the UK was undertaken, with the main objective to assess the role of *Phytophthora* spp in oak (Q. robur and Q. petraea) declines. In contrast to Mediterranean oak decline (*Q ilex* and *Q suber*) where the role of *P. cinnamomi* has been clearly established, the role of other *Phytophthora* spp, especially *P. quercina* in pedunculate oak decline is more controversial.

The hypothesis developed in Germany, was that fine root necrosis caused by *P. quercina* leads to impairment of water relations [82,83], which weakens trees and paves the way for other factors to exert more visible effects. It was suggested that extensive fine root decay occurred before above ground symptoms became evident [84]. Above ground symptoms include general symptoms associated with oak declines, for example smaller leaves, foliage discolouration, crown thinning and dieback, and tree death [82]. Fine root rot was described as the first phase of oak decline [85]. Fine root necrosis is considered a multicyclic disease. The balance between root rot and disease expression in the crown depends on rootlet destruction and replacement [86], when rootlet death exceeds replacement the trees are forced into decline. Young trees are able to replace feeder roots more readily than old trees [83,87], and so older trees are more vulnerable to feeder root loss and the process of chronic oak decline. Two scenarios of oak decline were proposed by German pathologists [78,79]: (1) with *P. quercina* playing a major part; this was likely to occur on silty loam – clay soils of pH3.5-7, and favoured by heavy rainfall, fluctuating water tables, summer droughts or heavy defoliation; although some Phytophthoras e.g. *P. quercina* are present on both ‘healthy’ and declining trees, infection and root rot caused by these organisms was far worse in the declining trees. (2) drought-induced rapid mortality and decline on acidic, sandy sites. By contrast, no association between tree health status and *P. quercina* was found in the situations investigated in France.

Conclusions from PathOak stated that more focussed work (other than surveys) was required to determine whether or not *Phytophthora* played a role in oak decline [88].

A study [75] concluded that it is difficult to isolate *P. quercina* and so it may go undetected, more effective diagnostic tools are needed, and this is a research gap. Due to detection difficulties, the effects of *P. quercina* might be quite underestimated in oak forests and oak decline in the UK. *Phytophthoras* are seasonally active, delicate, ephemeral pathogens that are quickly replaced by other fungi and bacteria. This makes assessing their true impact difficult [75]. Different species may have different ecological strategies. Laboratory tests have demonstrated how plant part affects aggressiveness, and this may be linked to genetic or epigenetic effects. Sampling over a number of years and seasons is required to obtain better insights [93]. More discerning isolation and detection methods are required to get an understanding of abundance and activity; soil baiting only reveals presence and limited inferences about function, more focussed work (other than surveys) will be required to determine whether or not *Phytophthora* plays a role in oak decline [88].

Although not of high significance on oak in the UK presently, it is prudent to be aware of possible risks of “aerial” *Phytophthora* spp. For example, *P. ramorum*, the causal agent of ‘sudden oak death’ is a major pathogen of oak (*Notholithocarpus densiflorus, Q. agrifolia* and others) in North America [94]. Native oak species in the UK in the white oak family are probably ‘less susceptible’ to *P. ramorum* [95], but there are occasional records of bleeding cankers caused by *P. ramorum* on *Q. robur* in England [Source 21] and Northern Ireland [Source 22]. under high inoculum pressure produced by infected larch trees.

In conclusion, it is apparent that there is hardly any published information specifically on *Phytophthora* on oak in the UK, and only one systematic survey [92] has been carried out. Systematic surveys and monitoring, as well as focussed research are required to address the role of *Phytophthora* in oak decline in the UK. Determining, mapping and monitoring the extent of occurrence, and relationship with a range of environmental factors, would allow risk assessment and mapping. There should also be an attempt to develop an improved understanding of how and under what conditions infection occurs. Decontamination of infected environments is also a research gap. Nothing is known about the closely related *Pythium* spp. on oak in the UK, their role and that of other root pathogens in oak health in the UK is unknown. There is considerable scope to improve the understanding of the presence and effects of micro-organisms in oak roots, soils and rhizospheres, and the effects of the interactions amongst these on oak root health. The compositional and functional soil and rhizosphere microbiome of oak in relation to tree health status and environmental conditions also needs to be addressed.

Decay fungi and diseases

Many different types of fungi cause internal wood decay, or heart rot, in oak trees, and some of these are also implicated in root rots associated with oak dieback and decline, but there is little reliable supporting evidence, and this is a research gap. It is important to note that decay diseases are not considered by everyone as a disease problem, but rather a natural part of an ecosystem; as such they are not classified either as primary or secondary diseases, but simply as decays. Here five key fungal species are mentioned because they are commonly reported in the UK: *Ganoderma adspersum* (southern bracket), *Laetiporus sulphureous* (chicken of the woods), *Meripilus giganteus* (giant polypore), *Inonotus dryadeus* (oak bracket, warted oak polypore, weeping polypore or weeping conk), *Fistulina hepatica* (beefsteak fungus, beefsteak polypore or ox tongue).

White rot decay is characterised by pale to straw-coloured, wet, stringy wood (for example that caused by *G. adspersum,* or *I. dryadeus*). Brown rot is characterised by brown, dry, crumbly wood often with horizontal and vertical fissures (for example the rot caused by *L. sulphureus).* Death usually occurs when the entire tree is rotted and collapses upon itself leaving little evidence of fungal attack, aside from the fruiting bodies which may not appear for years after.

The above decay fungi are widespread on oak in the UK and usually only detected when fruiting but decay is usually well advanced by this time. The fruiting structures appear on tree trunks, base (collar region), or branches, typically in autumn. Two types of fruiting structures occur: Conks, shelf or bracket fungi, which are more or less woody in texture, with tiny pores on the underside; and mushrooms, with stems and caps that have gills. Large numbers of spores are produced and effectively dispersed by wind.

Prevention is difficult due to the longevity of the oaks and the management history; the interdependency with decay-dependent woodland biodiversity is not resolved. Early diagnosis of the disease is paramount, particularly where public safety is a concern; development of tools for early and rapid diagnostics is highly desirable. Decay fungi gain entry to trees through wounds, so avoidance of injury is recommended; spread may be restricted by pruing affected branches as close to the branch collar as possible. There is no cure if the fungus has spread to the trunk; removal of affected trees to avoid damage to surrounding trees is also practised.

Almost nothing is known about these decay fungi in terms of their biology, distribution and function in the UK, their economic importance and ecological significance on oak, and associated biological functional interactions. These are significant research gaps.

Declines

Oak declines have been documented for more than 100 years in the UK and elsewhere in Europe, in particular France [38] and Germany [8,7]. *Q. robur* was generally found to be much more affected than *Q. petraea* [38]. Declines are complex health disorders, which may vary in their etiology. According to the Manion[4] concept of tree decline, predisposing, inciting and contributory factors are involved, in combination and in a specific temporal sequence [96,97]. Most commonly cited factors are drought, insect defoliations, powdery mildew, site factors (soil, stand management), root rot fungi, bark beetle attacks, with various relative importance of each of the factors in different decline episodes and situations. Hard evidence of causes and effects are challenging to prove for such health disorders since mature trees are affected and there are potentially strong effects of environmental factors, thus limiting the possibility of experimental evidence. Moreover, "decline" refers to aspecific symptoms (more or less progressive crown deterioration) that may have different etiologic causes. Both biotic and abiotic factors and their relative importance may vary in different situations qualified under the same "oak decline" diagnostic. Acute Oak Decline (AOD), recently described in the UK, can be considered a new type of "oak decline" characterized by the rapidity of the process and the biotic agents (insects and newly described bacteria) that are involved [3,9,10]. However, knowledge on interactive effects of the different factors and the mechanisms leading to decline remain a research gap.

Acute Oak Decline (AOD): The recently described AOD is a complex decline disease that affects both species of native British oak (*Q. robur* and *Q. petraea*); it can lead to rapid tree death compared to some other oak decline syndromes, for example Chronic Oak Decline (COD). AOD has four diagnostic symptoms; (i) stem bleeds emanating from (ii) cracks in the outer bark plates, (iii) necrotic lesion tissue in the inner bark, and (iv) larval feeding galleries of the European bark-boring beetle *Agrilus biguttatus.* A combination of stem lesions resulting from microbial activity and activity of *Agrilus* larvae disrupt nutrient and water transport in the vascular tissue, resulting in rapid decline in tree health over 3-5 years and significant morbidity or mortality [96,2].

AOD is widespread across southern and central England, with recent incidences in south and east Wales. Approximately one third of woodland in England and Wales is now affected with AOD [96]. Similar declines, involving *Agrilus* and cortical necroses, have been described in continental Europe, although a lack of detailed descriptions and comparative analysis of potential biotic causal agents (insect pests and microbial pathogens) has made direct comparison difficult. A decline with similarities to AOD has been described on California black oak in the, United States, where *A. auroguttatus* is associated with stem lesions from which two bacterial species that are closely related to those found in AOD lesions in Britain, were isolated [99].

In the UK, *Brenneria goodwinii* [100] and *Gibbsiella quercinecans* [101], are significantly associated with AOD lesion tissue [102]. Molecular analysis of healthy and AOD trees demonstrated that AOD lesion tissue is dominated by a bacterial community in which *B. goodwinii* dominates, with *Rahnella victoriana*, *G. quercinecans* [43] and two currently uncharacterised Gram positive bacteria [103] also present. In contrast *Pseudomonadaceae* dominate healthy tree tissue [102,43]. Inoculation studies in oak logs demonstrated the ability of *B. goodwinii* and *G. quercinecans* to cause lesions. Combination of *B. goodwinii* and *G. quercinecans* caused larger lesions, and when *Agrilus* larvae were added to the inoculations, the diagnostic symptoms of AOD were produced.

It is hypothesised that AOD will only occur in predisposed tissue. A detailed risk map of AOD in Britain has been produced through a logistic regression model that incorporated soil type, climate, pollutant and nutrient concentrations, demonstrating that AOD is more prevalent in warmer and drier sites (lower elevations with low rainfall) with high dry nitrogen deposition and low dry sulphur deposition [104]. Spatial and temporal analysis of AOD epidemiology revealed that affected trees occur in clusters rather than at random, suggesting a biotic contagion as the source of disease. More information about environmental factors such as drought, and how it may weaken the tree to a point where pathogens are able to overwhelm tree defences, is necessary. Currently, the origin and environmental reservoirs of *B. goodwinii* and *G. quercinecans* and other bacteria associated with AOD are unknown. The mechanisms of necrogenic action and qualification of host condition necessary for disease to take place also remains unclear.

Chronic Oak Decline (COD): Is aligned with the traditional concept of oak decline [16]. Like AOD, COD is considered a secondary disease occurring in weakened or predisposed trees, rendering them susceptible to damaging effects of biotic agents. Environmental factors implicated in COD include severe drought, prolonged flooding, rapid fluctuation of soil water levels and cold winters [7]. In the UK a notable episode of COD occurred in 1989–1994, when drought damage weakened trees were then attacked by *A. biguttatus*, leading to death of many trees. *Phytophthora* spp., *Gymnopus* and *Armillaria* spp. are also biotic factors that have been implicated in COD of oaks [7,8,18,38,43]. Typical symptoms of COD include early foliage deterioration, progressive death of branches over several years and dieback in the crown. COD requires long term research and monitoring to understand how environmental factors predispose oak trees to pest and pathogen attack, what type of pests and pathogens contribute to this type of decline, and why the biotic agents involved are able to attack / colonise / change their relationship with oak to become damaging to the trees.

Threats on the horizon

Vascular mycoses

Xylella fastidiosa: is a high priority primary threat to native oak. It is considered one of the most dangerous plant bacterial species worldwide, causing a variety of diseases, with substantial economic impact for agriculture, public gardens and the environment. It is an insect vectored vascular wilt disease that forms a biofilm-like layer within xylem cells and tracheary elements blocking water transport in susceptible hosts [105]. This leads to symptoms similar to water deficiency including leaf scorch, stunting of leaves, fruit, and eventually death.

Xylella fastidiosa has four subspecies that show some host specialization. These are subsp. *fastidiosa,* subsp. *multiplex,* subsp. *pauca,* and subsp*. sandyi* (www.cabi.org). Four phylogenetic clades within subsp. *multiplex* are identified; 'almond', 'peach', 'oak' and 'other types' [109]. The oak group included isolates from periwinkle, pin (*Q. palustris*), red (*Q. rubra*) and turkey oaks (*Q. cerris*), as well as scarlet (*Q. coccinea*), English (*Q, robur*) and shumard (*Q. shumardii*) oaks. *Platanus*, *Ulmus*, *Alnus* and *Acer* were also represented in this group.

Xyllela fastidiosa is largely restricted to the Americas and it is regulated in the EU as quarantine organism under Council Directive 2000/29/EC. However, a European case was recently reported in the Apulia region of southern Italy where it was associated with 'rapid decline of olives' [106]. Sequence information identified the bacterium detected as *X. fastidiosa* subsp. *pauca*. Other suspected hosts associated with the Apulia outbreak include species of *Malva*, *Portulaca* (purslane), *Quercus*, *Sorghum* and periwinkle. The diagnosis of *X. fastidiosa* in *Quercus* has not been confirmed.

Most diseases caused by *X. fastidosa* have been limited to hot climates, except for scorch of hardwood trees caused by *X. fastidiosa* subsp. *multiplex* which was found as far North as Southern Ontario [107]. It is also associated with oak declines in North America. An ELISA test (AgDia®PathoScreen® Xf, cat# PSP34501, http://www.agdia.com/) and real time diagnostic PCR assays [108] are available for *X. fastidiosa*, and symptomatic plants should be screened with these tests. However, it is unlikely that these assays will distinguish subspecies, so follow up bacterial isolations and sequencing should be performed on positive samples.

X. fastidiosa is obligately transmitted by xylem-feeding insects, but the bacteria can be transmitted via vegetative propagation such as grafting. Xylem feeding insects, especially sharp shooters/leafhoppers (Cicadellidae), and spittle bugs (Cercopidae) are the most important known vectors of *X. fastidiosa* and these taxa are common in the UK (Pest Risk Analysis). The bacterium is not egg transmitted and is maintained in the adult foregut through the production of a bacterial biofilm [110]. In order to determine whether insects are possibly *X. fastidiosa* vectors in the UK, traps should be routinely set up, and the catch assessed for *X. fastidiosa*. The UK is towards the northern limit of where *X. fastidiosa* is expected to establish. As this is a quarantine pathogen laboratory research is difficult, but the UK needs to be equipped to carry out molecular assays for the different subspecies. Research priorities are pathways of introduction, methods of eradication and control. The pathogen poses considerable threat to a wide range of plant species, and land uses and is beginning to be the focus of considerable research (e.g. BRIGIT project) which will further inform research gaps and priorities in coming months.

Ceratocystis fagacearum: [recently reclassified as ***Bretziella fagacearum*** [111]] is currently confined to the eastern and mid-western states of the US and causes oak wilt disease. It is a high priority primary threat to native oak species in the UK (and more generally in Europe) as it is an insect vectored vascular wilt disease that would result in catastrophic mortality levels if it was introduced. It is a regulated species under the Council Directive 2000/29/EC and has been recently categorized as quarantine species in view of the EU Regulation 2016/2031 (EFSA PHL Panel).

Spread of this fungus over long distances is vectored by sap beetles (Nitidulidae: *Colopterus truncatus* and *Carpophilus sayi)* and oak bark beetles (*Pseudopityophthorus)*. Insects deposit conidia in bark cracks, which develop hyphae that grow in the xylem and sapwood, stimulate the formation of tyloses and block water conduction. If bark is removed, a grey mat of fungal mycelia is often seen, which grows between the inner bark and the opposing wood, eventually creating enough pressure for the bark to crack [112]. As the nitidulids feed on the sporulating mats, the sticky conidia and ascospores adhere to the insects and are then carried to healthy trees and deposited in wounds [113]. In order for the pathogen to be successfully transferred to healthy trees, there must be fresh wounds with exposed xylem, which are receptive to infection. Such wounds are usually produced by human activity or weather-related injuries, but wounds older than three days are not susceptible to infection [114]. Leaf discoloration and wilting begin in the upper crown within one or two months of infection, which usually occurs in late spring or early summer, and red oaks may be dead by the end of the season.

Species in the white oak group are less susceptible and may decline over many years before dying. European oaks *Q. robur, Q. pubescens* and *Q. petraea* were tested for susceptibility to *C. fagacearum* in US arboreta and developed extensive wilt symptoms very similar to those of susceptible red oaks (*Q. rubra*), with most inoculated trees dead or dying within a year of inoculation (70-100% wilt and dieback) [115]. Logs and sawn timber potentially comprise a high-risk pathway for entry of the pathogen into the UK as there is significant trade in oak timber between North America and Europe [116]. However, regulations are in place for oak wood imports from the US, and modelling has shown that these regulations reduce exposure to *C. fagacearum* by a factor of greater than 30,000 compared to a scenario where no regulations are in place [116]. Red oak logs are considered a much more likely pathway for entry of oak wilt than white oak logs [117] as the bark of infected red oaks can harbour sporulating mats of *C. fagacearum* as well as the sap beetles (Coleoptera: Nitidulidae), which vector the pathogen [118]. Future assessments of imported logs should include application of a recently developed *C. fagacearum* specific diagnostic PCR assay to assess any possible incidences of pathogen entry [119]. Neither nitidulid beetles of the genus *Colopterus,* nor scolytid beetles of the genus *Pseudopityophthorus* are represented in the UK. However, beetles of the genus *Carpophilus* (known as pollen beetles) are represented by 11 species in the UK [120] so potential vectors of the pathogen are present. An important research gap is the climate suitability of the UK for *C. fagacearum* and the distribution of *Carpophilus* sp. and whether there is overlap. In addition, research is required to ascertain whether *C. fagacearum* infected European oak species are able to produce sticky mycelial conidiating mats, which are necessary for spread of the pathogen by insect vectors.

Raffaelea quercivora: This is a recently described ambrosia fungus that has a symbiotic relationship with an insect vector, *Platypus quercivorus* and is implicated in Japanese oak wilt disease. Extensive mortality in oak in Japan has been attributed to this insect-fungus association, but it is uncertain whether the fungus can cause vascular blockages in mature oak and it is unknown if native British oak species are susceptible to the disease. The fungus was listed in the EPPO alert list from 2008.

The life cycle of *R. quercivora* is intimately related to the life cycle of the insect. Spores of *R. quercivora* are carried into host tissue when the insect bores into the wood of the tree to lay its eggs [121]. Spores germinate directly or produce sprout cells and hyphae grow in the tunnels and galleries excavated by the beetle, lining their surface [121]. While providing nourishment for the developing *Platypus* larvae, the fungus continues to grow, extending into the vessels of the sapwood, and the tree responds by forming tyloses, which are defence barriers that block the vessels in an attempt to prevent further spread by the fungus [122]. As a result, water transportation is disrupted; leaves curl and wither, and eventually become discoloured and die. Trees with significant blockage usually die within a year. Young adult insects consume and acquire the fungus in their mycangia and spread the fungus after emergence when they colonise new trees.

At this time, the only known hosts of *R. quercivora* are two species of *Quercus* that occur in Japan viz. *Q. serrata* and *Q. mongolica* var. *grosseserrata* [123]. Artificial inoculation of *Q. acutissima*, *Q. acuta*, and *Q. phyilliyraeoides* did not yield any symptoms [123]. However, oak species native to the UK and Europe have not been tested for their susceptibility to the fungus, and this needs to be assessed to ascertain whether the fungus and its vector could take hold under UK climatic conditions.

The distribution of *R. quercivora* in Japan suggests the fungus and insect are closely associated with temperate-broadleaf-and-mixed-forest, generally warm and humid during the growing season but with seasonal temperature and moisture fluctuations [124]. Although *P. quercivorus* is not present in the UK, a related ambrosia beetle, *Platypus cylindrus*, does occur. *P. cylindrus* was documented to associate with *Raffaelea ambrosiae* in the UK in 1965

[125], but there are no recent studies on this association in the literature. Research is required to assess whether *R. quercivora* could associate with *P. cylindrus*, and if so, would climatic conditions support the lifecycle of *R. quercivora* on native oaks. There are currently no diagnostic molecular assays for *Raffaelea* sp., which is probably because the genus is considered to be polyphyletic [126]. Resolution of the taxonomy of the species within *Raffaelea*, and development of molecular markers for rapid diagnostics are research priorities.

The assessment of knowledge

The assessment of knowledge is summarised in Table 4.2

Acorn pathology: In general acorn pathology is a much neglected area of oak research, with much of the information now outdated as pathogen taxonomy has evolved. In this review we pointed briefly to only a few known acorn diseases, but this emphasises the lack of knowledge in this area of oak biology. Seedborne diseases are very important in the context of tree breeding and provenance selection for adaptation. More research should be carried out on these topics in the future.

Powdery mildew: There is a vast amount of literature on this topic so only a small fraction of the literature was reviewed. However, in this review the most important current trends about taxonomy were reliably sourced. Thus, determining the *Erysiphe* and *Phyllactinia* species of mildew present in the UK remains an important research gap because the various species demonstrate different epidemiologies, and might require different management and control recommendations. If *E. quercicola* and *E. hypophylla* are not yet present in the UK, it would be important to avoid their entry. It is clear that in the UK we have the expertise to identify the various mildew species (Dr. Ana Perez-Sierra pers. comm.), but there is currently no prospect of a representative survey being carried out to accurately reflect the position in the UK, and this should be a research priority. A second key priority would be for the UK to determine the long-term effects of mildew infections on oak photosynthesis and secondary metabolism. This was not explicitly covered in the literature review. A focussed research initiative that addresses the powdery mildew species and distribution in the UK, as well as short- and long-term impacts on oak health is required. Some of this type of work is already underway in France, and collaboration and comparison should be encouraged.

Anthracnose: There was a limited amount of information on this disease. The taxonomy of the causal agents was also confused and requires clarification. As this disease is not a main concern on oak in the UK at present, it is not a research priority.

***Armillaria* root and butt rot.** There is a vast amount of literature on this topic, so reports by the most recognised scientific authorities were consulted. The evidence base is therefore strong and reliable, representative and highly applicable, but rather incomplete. Taxonomic clarity in *Armillaria* is an evolving field and the UK needs to be a part of this research frontier as *Armillaria* is a key pathogen of trees and woody shrubs in Britain. A small current research project funded by Woodland Heritage (WH) will carry out a minor taxonomic assessment of *A. gallica* on a very small sample of oak, but a much larger taxonomically focussed project on *Armillaria* species in the UK is required. Furthermore, focussed studies on the functional life strategies and triggers of changed behaviour are fundamental to managing the problem these fungi pose. This is because oak trees, specifically, are able to overcome some *Armillaria* attacks, purportedly those that are stressed induced, so predisposition metabolism is another key research frontier; this will be obliquely addressed in another WH research project on oak metabolomics but requires in depth studies per host and per *Armillaria* species.

***Gymnopus fusipes*.** There was not very much literature available on this topic, although reasonably thorough and comprehensive studies have been carried out in France, where it is considered important. However, the view from Germany contests the overall importance of this pathogen in oak decline. Almost nothing is known about this pathogen in the UK and it is a priority pathogen on oak, considering the frequency of THDAS reports and the views of scientists consulted (S. Denman pers. comm.). A PhD project to be supervised jointly by FR and Bangor University, and supported by Defra, is planned. This will be a start into this important area of research.

***Phytophthora*:** Published information on oak *Phytophthora* is strong and relevant, but controversial. In Germany it is considered a key element of oak decline, whereas in France it was only considered locally important. The position in the UK is unknown although the rising profile of *Phytophthora* on oak in the UK, especially *P. cinnamomi,* has previously been flagged [75, 76]. There is almost no work on this topic planned in the UK, although the FPPH project on Oak Resilience will carry out some testing for the presence of this pathogen. More research is required to clarify the position in the UK, but it should not be done in isolation; consideration of the role of *Pythium* spp., as well as other feeder root microbes is required.

AOD and other oak Declines

Up to now, AOD has only been described as such from the UK and all research therefore comes from British groups. However, the three bacteria associated with AOD have just been reported from bleeding sessile oaks in Switzerland (Bakterien-Schleimfluss an Traubeneichen) and from pedunculate oak in Latvia (S. Denman pers. comm.). Previous studies in France mentioned the occurrence of bacteria associated with cortical lesions and *Agrilus* galleries in diseased oaks but failed to demonstrate any pathogenicity [127, 128].

Future research in the UK needs to focus on the causes of emergence of decline diseases, particularly the interactions between environmental factors and emergence of biotic factors that lead to tree death. Specific research issues pertinent to AOD are, for example, whether the bacteria associated with AOD were introduced into the UK or whether there has there been a plant host shift. Is the evidence to show an increase in *Agrilus* numbers increased over the years and can AOD be attributed to this? Alternatively, have climatic factors changed predisposing trees to infection by existing pests and pathogens? Epidemiological field studies using approaches such as dendrochronology and ecophysiology will allow a better understanding of the contributing roles of predisposing factors as well as insects and pathogens.

Summary and priorities for new knowledge from review

Adopt holistic multidisciplinary research as diseases of oak are complex and affected by multiple factors and their interactions. Collaboration is required between different disciplines e.g. pathologists, entomologists, plant breeders, geneticists, biogeochemists and ecophysiologists, as well as spatial epidemiologists and modellers.

Develop and revise rapid diagnostics for all oak diseases. Many oak pathogens have been shown to be complexes or cryptic species with different spatial distributions, ecology and pathogenicity.

There is a dearth of information on diseases of oak in the UK. Establish a baseline of the current situation in the UK through a comprehensive evaluation of distribution, abundance and impact of priority pathogens/diseases of oak. Use survey and monitoring to provide early warning of changes.

Assess main pathways of potential introduction of new pathogens to prevent introduction.

Monitor pathogen populations to assess diversity. Essential information about origins of diseases (with consequent implications for policy) and adaptation potential will underpin risk assessment, management planning and policy formation.

There are large gaps in the information on the biology of many pathogens. Systematic studies elucidating infection biology, conditions affecting reproduction, survival, dispersal mechanisms and pathways, climatic requirements and tolerances, host range, factors affecting virulence and interactions with other pathogens and beneficial organisms, are essential.

Understanding of oak resistance to disease is still poor. Investigating natural variation in resistance between oak species and provenances, its genetic basis, the role of secondary metabolism towards a range of pathogens could give useful indications to advise management.

Develop epidemiological studies to correlate landscape and environmental predisposition factors with disease occurrence. This will inform management recommendations and risk modelling and mapping.

Engage with stakeholders to explore and distil feasible control options. Establish long term trials to evaluate and assess efficacy of controls and managemepnt of oak diseases.

Table 4.1 Diagnosis of oak damage: Biotic causes – Disease: number of reports from 1972-2017 to Forest Research Tree Health Advisory Service

Common name of disease	Species	Common name of pathogen	Plant part affected	No of cases
AOD	Acute Oak Decline* Complex syndrome	Complex of bacterial species	Stem	564
Stem bleeding, smelly stem bleeding	*Armillaria* spp.	Honey fungus, bootlace fungus	Roots and stems	111
White rot and decay	*Ganoderma adspersum*	*Ganoderma* (*G. resinosum* is also important on oak)	Stem	84
Oak Dieback	Oak dieback; Complex	Complex causes	Roots and stem	81
Powdery mildew	*Erysiphe alphitoides*	Mildew or powdery mildew	Foliage and young shoots	79
Oak bracket rot	*Pseudoinonotus dryadeus* (*Inonotus*)	Weeping polypore	Stem	59
Decay	Decay spp.	ND	Stem	52
Anthracnose	*Apiognomonia umbrinella* (including the old name *Gloeosporium*)	ND	Foliage	32
Cubical brown rot	*Laetiporus sulphureus*	Chicken of the woods or sulphur polypore	Stem	23
Root rot	*Collybia fusipes* (new name = *Gymnopus fusipes*)	Tough shank / Spindleshank fungus	Roots	22
Stem bleeding, buttress root and collar rot (Ink disease)	*Phytophthora cinnamomi*; *P. cambivora*; *Phytophthora* spp.	*Phytophthora*	Roots and stem collar and stem	16
Oak heart rot	*Fistulina hepatica*	Beefsteak fungus	Stem, root collar	15
White rot	*Grifola frondosa*	Hen of the woods	Stem	10
Stem decay	*Meripilus giganteus*	Giant polypore	Stem	10

* Reports from 2006 -2017

ND= No data

Table 4.2 Priority diseases currently causing significant or regular damage to oak and potential future threats to oak trees in the UK.

Foliar diseases						
Common name *Scientific name*	**Taxonomic group**	**Ecology (including symptoms and epidemiology)**	**Damage and Control**	**Risk rating[a]**	**Risk qualifier of spread and increased occurrence**	**Distribution and Assessment of knowledge**
Powdery mildew Caused by four species 1.*Erysiphe alphitoides*	Phylum: Ascomycota Order: Erysiphales Family: Erysiphaceae	Leaves are mostly affected. Signs of disease are white felt-like coating on upper leaf surface, symptoms are leaf browning and death. Young shoots also affected. Infectious sexual spores (ascospores) are released in late spring under wet conditions. The asexual spores (conidia) are produced in chains on the leaf surface giving it a white appearance. Conidia are wind dispersed under warm, dry conditions. Free moisture inhibits conidial germination. Many alternate hosts.	Young leaves become infected and wither or die. Infected shoots may delfoliate or flag at tips. Disease effects are killing leaves and shoots, reduced photosynthetic capacity and loss of radial increment (tree girth) Control is mostly in nursery situations: Application of colloidal suspensions of sulphur. Ammonium phosphite injections. There is some interest in exploring potential with biological hyperparasitic agents.	Medium	Damage may become more severe in wet springs and warmer summers. More damage will be sustained if repetive, severe (annual) infections occur	Widespread globally Not restricted to oak Significant amounts and reliable (peer reviewed) literature available
Powdery mildew *Erysiphe quercicola*	As for *E. alphitoides*.	Similar to *E. alphitoides*. Dominant early in the growing season. Overwinters as mycelium on buds. Infected buds give rise to infected flag shoots in spring.	As for *E. alphitoides* No specific control data	Low- medium, but medium in nurseries and potentially medium impact if it occurs in combination with other mildew species	Not know if in the UK. Conditions in the UK suitable for establishment and spread.	Known in Europe Some literature available but incomplete knowledge, more information required
2. *Erysiphe hypophylla*	As for *E. alphitoides*.	Similar to *E. alphitoides*. Can simultaneously infect oak *with E. alphitoides.* Predominantly infects the lower leaf surface.	Infection occurs on lower leaf surface. No specific control data	Medium -high	Not known if this pathogen is in the UK. If it enters the UK higest damage will be where it co-occurs with *E. alphitoides* as both leaf surfaces will be affected	Known in Europe Little international literature, very scant to no information on oak in the UK, more information required

3.Phyllactinia guttata	As for *E. alphitoides.*	Asexual and sexual spores predominantly produced on the lower leaf surfaces. Asexual spores wind dispersed. Sexual spores overwinter on plant litter. Widespread on oak species and other plant species.	Infection occurs on lower leaf surface. No specific control datadata	Low	Low Thought to be native)	Known from Europe, thought to be native Some literature available but incomplete knowledge
Oak anthracnose (*Apiognomonia errabunda*)	Phylum: Ascomycota Order: Diaporthiales Family: Gnomoniaceae	Symptoms on young leaves are spots that develop into angular leaf blotch, on older leaves infections are clear leaf spots. Disease can spread to petioles and into shoots. This fungus is present as and endophyte. It changes to a pathogenic lifestyle in response to stress. Spores colonise leaves in spring. Mycelium can spread to xylem. Asexual spores form in response to light. Sexual spores are produced in late summer. Overwinter on leaves.	Nitrogen fertiliser increases disease incidence.	Low- medium	This endophyte/ pathogen seems to have potential to be damaging if inoculum levels increase and high nitrogen levels stress hosts	Widespread in Europe and known in UK, distribution on a range of plant species. little to no information on oak in the UK

Root diseases

Common name *Scientific name*	Taxonomic group	Ecology (including symptoms and epidemiology)	Damage and Control	Risk rating[a]	Risk qualifier of spread and increased occurrence	Distribution and Assessment of knowledge
Spindleshank mushroom (*Gymnopus fusipes*)	Phylum: Basidiomycota Order: Agaricales Family:Omphalotaceae or Marasmiaceae	Affects woody roots just under the collar. Very damaging, rots buttress roots, leads to trees falling over, especially in stormy conditions. Reduces number of living roots. Slowly disease progression. Visible reduction in tree health in advanced stages of infection. No information available on the effect of temperature, moisture and light on fruiting. It can produce cord-like structures on the root surface. Main host is oak, but other alternate hosts also.	No information available.	High	Unknown but expected to be low-medium as it is soilborne and restriced to roots. Unknow if airborne inoculum is important, which could contribute to disease spread	Widespread in southern England, common and widespread in parts of Europe, especially France. A good amount of information but some conflicting views
Armillaria root rot on oak is caused by four species in the UK. 1.*Armillaria mellea*	Phylum: Basidiomycota Order: Agaricales Family:Physalacriaceae	Symptoms include: discoloured foliage, thinning crowns, weeping stem patches, dieback of branches and tree death. Infectionoccurs by root to root mycelial transfer and rhizomorph spread.	Virulent pathogen, tree death occurs. The most virulent and aggressive *Armillaria* species. Control shold include limit inoculum build-up.	High	Unknown but expected to be low-medium risk in woodlands but	Widespread throughout the UK and elsewhere in the world.

(honey fungus)		Wind dispersed basidiospores - long range spread. Produces less rhizomorphs than other *Armillaria* species. Infects many deciduous and hardwood tree species.	Reforest with disease free resistant species. Minimise stress. Avoid wounding. Reduce carbon sources: uproot and burn stumps.		higher in heritage parklands and gardens. Horticultural plant trade and composts could play a role but evidence is lacking.	significant and reliable literature
2.*Armillaria gallica* (bulbous honey fungus)	As for *A. mellea*	Predominantly saprophytic. Opportunistic parasite of weakened tree hosts. Infection as for *A. mellea*. In pathogenic mode it causes thinning crowns, dieback, stem bleeding, cankers and stem death, buttress root rot, which lead to tree death. Large number of rhizomorphs.	Damage can range from nothing (where this fungus behaves as a benign epiphyte), to virulent pathogen to saprophyte on dead material. Minimise stress. Avoid wounding.	Medium	Mostly it is unknown what triggers pathogenic mode. Stress considered important in this regard.	Widespread distribution globally, particlulary present on woodland oak in the UK, but also found on weakened conifer and broadleaved trees. There is a good amount of information but conflicting views or lacking knowledge on some aspects.
3. *Armillaria ostoyae* (dark honey fungus)	As for *A. mellea*	Primary pathogen of softwood trees and a secondary pathogen of hardwood trees. On oak it causes buttress root and collar rot, which may lead to tree death. Thinning tree crowns, and dieback amy also occur. It co-colonises with other *Armillaria* spp. Infection as for *A. mellea.* Able to produce long rhizomorphs (up 220 m). Colonises suppressed oak species.	Damage on oak can be severe resulting in root rot that may lead to tree death. Control: Avoid planting on sites previously planted to pine and other conifer, especially if there is a history of *Armillaria* on the softwood.	Medium	Low unless planted on infected conifer sites.	Widespread distribution globally, particlulary found on conifers. Little information on oak in the UK.
4.*Desarmillaria tabescens* (ringless honey mushroom)	As for *A. mellea*	Opportunistic weak pathogen. Causes root and collar rot, stem cankers. Thermophilic. Known to kill trees in warmer climates. Infection as per *A. mellea.* Rhizomorphs thin and not easily observed.	Infection can lead to substantial damage and even death of trees. No known control measures.	Medium-high	Low but could increase with warming temperatures.	Little to no information on oak in the UK.
Common name *Scientific name*	**Taxonomic group**	**Ecology (including symptoms and epidemiology)**	**Damage and Control**	**Risk rating[a]**	**Risk qualifier of spread and increased**	**Distribution and Assessment of**

					occurrence	knowledge
Phytophthora buttress, root, collar and stem rot *P. cambivora,* *P. cinnamomi,* *P. citricola* (*P. plurivora)*	Phylum: Oomycota Order: Peronosporales Family: Peronosporaceae	Symptoms include: Stem bleeding, necrosis of inner bark, root lesions and rot, and tree death. The chief infection propagules are zoospores, which are propagated in wet and acidic soils. Thrive in warm temperatures.	High levels of tree mortality can occur if the pathogen becaoes widespread, alternatively single tree or small clusters of trees are affected. There may be lasting damage to timber potential. Prevention of contamination through ensuring clean nursery stock.	High	Under conditions of high inoculum, favourable temperature and high levels of free moisture, the risk of spread and disease severity increases. Heavy soils also increase risk of damage.	Widespread globally and recorded in the UK. High levels of inoculum present in south and south-east England. Little to no information on oak in the UK.
Phytophthora feeder root rot *P. cactorum* (not yet reported on oak in the UK), *P. cambivora* *P. europaea* *P. gonapodyides* *P. quercina* *P. plurivora* *P. psychrophila* *P. undulata* *Pythium* spp.	Phylum: Oomycota Order: Peronosporales Family: Peronosporaceae	Symptoms included feeder root necros, loss of root tips, lesions on small roots. Fine root necrosis leads to impairment of water relations. Older trees more vulnerable to feeder root loss. *P. cambivora, P. gonapodyides*, *P. quercina*, *P. plurivora* isolated from oak soil in the UK. *Q. robur* more affected than *Q. petraea.*	Feeder root loss is the key form of damage but same species are known to progress into main and buttress roots (see above). Extensive fine root rot leads to decline and in very severs cases, even tree death. Little remedial control. As above.	Medium or Medium-High	As above. Fluctuating water tables often lead to severe disease and seasonally high levels of inoculum.	Widespread in Europe, less is known about distribution in the UK, some species occur on multiple hosts. There is a good amount of information but conflicting views.
Sudden oak death *P. ramorum*	Phylum: Oomycota Order: Peronosporales Family: Peronosporaceae	Symptoms of oak infected with *P. ramorum* are variblae dependent upon the oak species affected. Aerial infection court. Red oak species mostly affected in USA. Major pathogen of oak in North America. Native oak species in the UK are 'less susceptible'.	This is a quarantine-listed pathogen. *P. ramorum* is a devastating pathogen of some Californian native oaks but is less concerning on UK oak species. Control includes: Prevention of introduction and contamination through ensuring clean nursery stock and through phytosanitary regulation. Some remedial control using phosphites.	Low-medium	Native oak species in the UK are 'less susceptible'. High levels of inoculum required and often compromised tree health is a factor on whether infection will occur or not.	Widespread in parts of the UK and EU and western USA seaboard areas. There is a lot of information on this pathogen in general but only little information available on native oak in the UK.

Decline disease complexes						
Acute Oak Decline *Brenneria goodwinii* *Gibbsiella quercinecans*	Multiple bacterial speces from the families: Enterobacteriaceae Yersiniaceae Pectobacteriaceae	Diagnostic symptoms of the disease are: weeping fissures that seep black fluid. Lesions formed in tissue beneath bleeds. *Agrilus biguttatus* galleries closely associated with bacterial lesions. Near 100% co-occurrence. Exit holes present in 33% affected trees Widespread across southern and central England. Prevalent in warmer and drier sites with high dry nitrogen and low wet nitrogen and sulphur deposition.	High mortality 4 – 6 years from onset of stem weeping. Control recommendation include: removal of affected trees if appropriate. Good sanitation and biosecurity practices.	High or Medium – High	Data on disease spread, the role of vectoring, and host susceptibility restrict predictions about the risk of spread.	Present in the UK across southern and central England. Also in Europe. Prevalent in warmer and drier sites with high dry nitrogen and low wet nitrogen and sulphur deposition. There is a good amount of information but conflicting views.

Common name ***Scientific name***	**Taxonomic group**	**Ecology (including symptoms and epidemiology)**	**Damage and Control**	**Risk rating[a]**	**Risk qualifier of spread and increased occurrence**	**Distribution and Assessment of knowledge**
Vascular mycoses						
Multiple common names including: Oak leaf scorch, Peach phony disease, Pearce's disease of grapevines *Xylella fastidiosa* ssp. *multiplex*	Phylum: Proteobacteria Order: Xanthomonadales Family: Xanthomonadaceae	Symptoms are similar to those associated with water deficiencies. They include leaf scorching, stunting, dieback and defoliation and overall reduction in plant height. The disease is obligately insect vectored from saproxylic insects, especially sharp shooters/leafhoppers (Cicadellidae, subfamily Cicadellinae) and spittle bugs (family Cercopidae). The pathogen forms a biofilm-like layer within vascular system and itcompletely blocks water transport in affected vessels. There are numerous alternate horticultural hosts. The UK climate and insects could support the pathogen.	Control measures include: Legislation and monitoring to prevent pathogen entry into the UK. Training and research. Eradication of symptomatic plants. Non-symptomatic endophytic colonisation could lead to delayed symptoms development and lack of detection in plant imports.	**High – catastrophic But uncertainty about likelihood of establishing and impact**	Damage is on introduction to the UK, and spread may be limited by temperatures suitable to the pathogen and vector. The bacteria have a wide plant host range and large spectrum of insect species capable of vectors which should increase the bacterium's invasiveness	Not yet present in the UK, but present in France and Italy and the USA. Some literature available but incomplete knowledge.

Common name ***Scientific name***	**Taxonomic group**	**Ecology (including symptoms and epidemiology)**	**Damage and Control**	**Risk rating[a]**	**Risk qualifier of spread and increased occurrence**	**Distribution and Assessment of knowledge**
Japanese oak wilt *Raffaelea quercivora*	Phylum: Ascomycota Order: Ophiostomatales Family: Ophiostomataceae	Symptoms show leaf curl and withering leading to discolouration and death. Wilt. Significant xylem blockage causes death within a year. The fungus is associated with ambrosia pinhole borer beetle *Platypus quercivorus*. The fungus is introduced into trees during egg laying, and it colonises insect galleries and ingresses into the xylem. Emerging adults carry conidia to new trees. Not yet present in UK. UK climate and insects could support the fungus.	Constant monitoring to prevent entry of *P. quercivorus* and *R. quercivora* into the UK.	Unknown but could be medium - high	Medium - high because potential alternative vector, pinhole borer present in UK) but risk could be reduced with insect vector management	Some literature available but incomplete knowledge
Oak wilt disease *Bretziella fagacearum* (previously known as *Ceratocystis fagacearum*)	Leaf discoloration and wilting Infection occurs in late spring or early summer. Decline. Death.	Vectored by sap beetles (Nitidulidae: *Colopterus truncatus* and *Carpophilus sayi)* and oak bark beetles (*Pseudopityophthorus)*. Insects deposit spores in bark cracks. Fungus colonises xylem and sapwood, blocks water conduction. Insects feed on fungal mats and transmit spores. Root-root spread. Not yet present in the UK.	Prevention of pathogen and insect vector entry into the UK.	**Catastrophic dependent on entry and establishing, and transfer to local insect vectors**	High	Significant and reliable literature

[a] Risk Ratings:
These are based on professional experience and an estimation of damage potential indicated by reported outbreaks in the literature.
Low = likely to have very little impact on tree health in the UK.
Low-medium = typically having a small impact on tree health. Insects may be secondary pests and contribute to some reduction of host vigour, but other causal agents will be more important.
Medium = moderate damage to tree health may be expected, impairing growth and function of the tree. Affected hosts may recover, or suffer worsening health over the long term. Includes risks from invasive species which could become more aggressive pests on ‘naïve’ UK oak species.
Medium-high = significant, noticeable damage that often, but not always, leads to death of trees.
High = significant damage that usually leads to death of trees, often in a short time.
High-catastrophic = high levels of mortality across a large number of individuals are expected, impacting landscape levels of trees loss and having serious ecological and ecosystem service consequences
Catastrophic = loss of the species as it is known, over the affected range. Two known analogue cases are Dutch Elm Disease, and Chestnut blight in the USA.

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5. Oak health and biodiversity

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Introduction and scope of chapter

Trees are *foundation* species [1, 2] which define much of the structure of an ecological community by creating locally stable conditions for other non-tree species, and by modulating and stabilizing fundamental ecosystem processes [2]. Trees provide habitat for other species (termed *associated* species) in three main ways.

- Trees modify their surrounding environment, influencing light, moisture and temperature via the shade cast, and influencing the chemical composition of soil via the chemistry of their leaves/bark/wood/roots and root exudates. This creates suitable habitat for other species e.g. the plants comprising the forest ground flora, that do not directly utilise the tree but which do require the environmental conditions created by the trees.

- Secondly there are a range of habitats within the trees themselves, niches in the roots, bark, trunk, branches and leaves, which are utilized by a range of species for living space (e.g. lichens and bryophytes), or breeding/roosting spaces (e.g. birds and bats). Availability of these habitats depends on the age of the tree with some niches e.g. dead wood and sap runs generally being only available in older trees. Maintaining a continuity of older trees both temporally and spatially is important in providing habitat for certain oak dependent species. Oak has long had a reputation for supporting a large number of invertebrate species [4].

- Finally, trees support other species by providing food such as fruit, seeds, leaves, dead wood and bark.

Trees also influence ecosystem processes such as decomposition and water cycling and provide a range of ecosystem services [1, 3]. If a foundation species declines, this will have cascading impacts on associated species, processes and services because other tree species may not provide the same habitat/resources.

We review knowledge of the biodiversity associated with oak, both the taxonomic and the functional diversity and the impact of oak on ecosystem processes and functioning. Our aims were to assess how a decline in oak health would impact on a) the associated species supported and the ecosystem functions provided by oak and b) the functional role of oak associated species within the ecosystem. This includes the beneficial roles of some species in promoting oak health but excludes pests and pathogens which are covered in preceding chapters. We focus on above-ground biodiversity; previous chapters consider below-ground biodiversity, although there is some overlap with this chapter when discussing fungi. We assess how a decline in oak health will impact different taxa but do not assess how within-species diversity (local adaptation and genetics) may be affected by differing impacts.

We concentrated on gathering information concerning the two native oak species *Quercus robur* and *Q. petraea*, in all situations from woodlands through to isolated trees in parkland, hedgerows and gardens and all stages of the life cycle of trees including dead wood. Some dead wood will be present within a well-balanced oak ecosystem, but we do not review the potential biodiversity benefits of an increase in dead wood because of a decline in oak health. This might be only a short-term increase in dead wood in the event of acute decline in oak health, whereas a chronic decline will have longer term impacts including the potential replacement of oak with other tree species (this difference is being examined within the PuRpOsE project[5]).

The review covers knowledge from both the UK and internationally and we categorise our data sources as review papers (peer-reviewed) that provide an overview across the topic, peer-reviewed papers on one area/topic, grey literature and anecdotal/expert judgement, ordered with our view of greatest to least confidence.

State of knowledge – UK

The impact of a decline in oak health on biodiversity which uses oak trees
Oak has a reputation of supporting a large number of associated species[4, 6-8] although lists of such species tend to focus on specific groups e.g. lichens or invertebrates. A more comprehensive list is currently being collated by the PuRpOsE project[5] including a database of over 2000 species of bird, mammal, fungi, invertebrate, bryophyte and lichens known to use oak trees. Even this will be incomplete because information on some taxa e.g. the microbial communities supported by oak [9, 10] is limited.

Biodiversity varies between oak trees. The importance of an oak tree for biodiversity will depend on the context in which it is growing, e.g. pollution levels[161], surrounding land use and the woodland type in which the tree is growing[5]. In particular, the UK's Atlantic oakwoods (sometimes called Celtic oak rainforests) are of international importance for their assemblages of bryophytes and lichens[164]. Woodlands with mature or veteran trees are more likely to support a wider range of biodiversity than woodlands with just young or pole age trees[5]. In addition, oak woodlands with a mixed age structure and with a mixture of other tree species in addition to oak are likely to support more biodiversity than even-aged woodland or monocultures of oak (see section on international knowledge). There are studies comparing taxonomic diversity within oak plantation woods with coniferous plantations; these studies found greater diversity in the oak plantations for some but not all taxa [38-42]. Studies of plantations comparing oak mono-cultures versus two species poly-cultures (oak with 1 other species) show either no difference or greater species richness, abundance and diversity with the results being dependent on the taxa studied and the other tree species in the poly-culture[38, 40, 42-47]. Some species will only be found in certain types of oak woodland habitat, for example PuRpOsE lists 116 oak-associated species which are found in non-woodland/wood pasture situations but not in woodlands and 331 oak-associated species which are found in woodland situations but not non-woodland/wood pasture situations[5].

The species supported by oak trees change with the age of the oak, in particular veteran or ancient trees are known to support a greater diversity of associated species than younger trees [5]. Efforts to survey ancient oaks have so far been undertaken systematically only for England[11]; many examples are known from the other territories/countries but they have not been so comprehensively documented. Many English ancient and veteran oaks are lapsed pollards and on-going management of these is important. The dead wood associated with oak, in particular the older oak trees, is a valuable habitat for biodiversity, with 40% of the species listed by the PuRpOsE project being associated with dead wood.

Q. petraea and *Q. robur* probably support similar suites of species, and differences between them in the species recorded are more likely due to local environmental differences, although data are lacking to prove this. Non-native *Quercus* spp. may not support the same species as native oaks and data on this are being collated by the PuRpOsE project[5].

The impact of a decline in oak health on associated species is unknown, but it is assumed that species that are more specialised are at greater risk than generalists. Over 300 obligate species (only recorded on oak) and another 200 highly associated species (rarely occur on tree species other than oak) have been listed by the PuRpOsE project[5]. In addition those species with smaller populations, or whose population is already declining due to other factors, are more likely to be at risk, than those with large populations. Thus, in addition to its association with oak, the current conservation status of the species needs to be taken into account as was done in the assessment of the impact of a decline in ash trees on biodiversity[165]. There is little knowledge of the timescale over which any impacts will occur: the ecological impact of a decline in oak health may not be seen initially (i.e. there will be an extinction debt). If the impacts take a long while to show there may be an opportunity to apply mitigation actions such as through replanting and/or veteranisation of mature trees before species extinctions occur.

The impacts of a decline in oak health on biodiversity will also interact with other drivers of change on biodiversity such as climate change, landuse, habitat management and pollution. For example, nitrogen pollution[161] and non-native invasive species[162, 163] are known to impact biodiversity in Atlantic oak woodlands. In general, these interactions will increase the impact of oak decline although conceivably there could be circumstances where the impacts are counteracted. However, there has been little work on the interactions between drivers, decline in oak health and impacts on biodiversity, other than on species considered as pests/pathogens (see other chapters).

The impact of a decline in oak health on biodiversity associated with oak woodland ecosystems

Oak is found in a wide range of woodland communities[12] but is most abundant in four: W10 (*Quercus robus-Pteridium aquilinum-Rubus fruticosus* woodland), W11 (*Quercus petraea-Betula pubescens-Oxalis acetosella* woodland), W16 (*Quercus spp.-Betula spp.-Deschampsia flexuosa* woodland), W17 (*Quercus petraea-Betula pubescens-Dicranum majus* woodland). There is a general tendency for *Q. petraea* to dominate further north and west in Britain, and *Q. robur* in the south and east, but the species of oak does not seem to be associated with any exclusive floristic features[12]. Instead the ground flora of oak woodland communities seems to relate more closely to the nutrient status, continuity of woodland cover and management of the woodland.

There are no known higher plant species which are restricted to communities where oak is classed as a constant species[12]. However, western oak woods are renowned for their rich bryophyte flora especially in euoceanic areas, where they tend to be concentrated on boulders and rocky outcrops, by waterfalls and along streamsides (NVC Communities W11, W17)[12]. The link between the diversity of the bryophyte communities and the composition of the tree canopy appears to be indirect, via the shade regime, litter composition and continuity of cover of trees of all ages over many decades.

The impact of a decline in oak health on non-woodland oak and biodiversity

Trees outside woods form an important feature of the UK landscape (albeit the data coverage is inconsistent between countries), and oak is an important element of this. Non-woodland tree canopy is estimated to cover 11% of the urban land area and 3% of the rural land area in Britain[13]. Across GB oak is the second most common non-woodland tree after ash (9.6 v 7.2%) but there are country variations[166]. England mirrors the UK pattern with oak as the second most common non-woodland tree after ash (10.3% vs 7.7%)[14]and in Wales[168] oak and ash occur in equal abundance as non-woodland trees (10%). However, in Scotland oak forms a lower percentage of the trees outside woodlands (2%) and is only the seventh most common non-woodland tree[167]. Half of the known ancient oak trees (according to the UK Ancient Tree Inventory) are in non-woodland ecosystems.

Non-woodland trees, particularly ancient trees, can be important for biodiversity[23, 24]. Data tends to be taxon/site dependent with, for example, good information on their importance for saproxylic species, lichens and various invertebrates at some well known sites [16-22]. However, a recent IUCN report[25] suggested many saproxylic beetles are on the brink of extinction due to a lack of ancient trees (an example of extinction debt mentioned above). Much of the information on the biodiversity of non-woodland trees is not specific to oak, but the PuRpOsE project lists nearly one thousand species associated with non-woodland oak trees, although data was not available for many species[5].

Land use change has led to a reduction in the number of scattered trees in the landscape, although data specifically on oak trees are lacking, as are studies of the implications for habitat provision, connectivity and ecological networks[26]. New generations of potential veteran oak trees need to be established but pressures on land use mean that there is competition for land for natural oak regeneration to occur, outside woodlands[29]. In addition we do not fully understand the role played by young trees in bridging the ecological continuity gap between 200+ year old trees and those planted more recently[27, 28].

The impact of biodiversity on oak health
There is indirect evidence that bacteria species influence the metabolism of plant growth hormones, promoting plant growth, modifying leaf surface conditions, enhancing host plants nutrient acquisition and uptake, suppressing pathogens and removing contaminants via phytoremediation, all of which will influence oak health. However, these data are from other plant species but not oak[30-33]. Several woodland bat specialist species (e.g. Bechstein's bat) favour oak for roosting over other tree species[34] which may be partly related to the high numbers of associated insects on oak[4]. Bats may play an important role in population control (e.g. by predating pine processionary moth) since insects, and particularly moths, are an important component of their diet[35, 36]. However, there is no known research on bat numbers and effectiveness of their control of oak insect pests e.g. oak processionary moth.

There is evidence that tree species richness and particularly the specific tree species composition of stands impacts on tree health via pathogen infection rates, levels of insect herbivory, levels of biological control by insectivorous species (bats, birds) and vulnerability to drought[37], although specific evidence for oak trees is lacking. Thus, the taxonomic diversity within oak woodland has the potential to influence oak health.

The above generalizations on how the biodiversity supported will influence oak health will be heavily influenced by woodland management, grazing and woodland age[48, 49]. These impacts are taxon, site and context specific. Thus, making site specific predictions about impacts of biodiversity on oak health requires a greater understanding of the changing influences of management, grazing, woodland age and other factors over time.

It is clearer that, in some circumstances, species can have a negative impact on oak health (see previous chapters for details). This may be where they have either not co-evolved with oak, for example the introduction of non-native species to a naïve host, or when the ecological balance between species is disrupted, for example through a changing climate leading the tree to become more stressed and susceptible to pests/pathogens.

The impact of decline in oak health on the ecological processes provided by oak
Oak trees create specific environmental conditions e.g. via leaf litter fall and the shade they cast. Many studies compare decomposition rates and leaf litter chemistry between tree species. The PuRpOsE project is reviewing these studies and initial results show that *Q. petraea/robur* is similar in its litter quality and decomposition rates to species such as *Fagus sylvatica, Carpinus betulus,* and *Q. rubra*[5]. How other environmental conditions created by oak (e.g. shade), and the other processes/ functions (e.g. water cycling) provided by oak compares with other tree species has received little recent attention. There is limited evidence from one site that *Q. petrea* casts a slightly darker shade than *Q. rubra* and similar shade to *Acer platanoides*[169].

The impact of oak health on the functional role of biodiversity in oak ecosystems
The functional role of many of the species within oak woodlands in the UK is unknown. More is known internationally (see following section).

State of knowledge – internationally

The impact of a decline in oak health on biodiversity which uses oak trees

In common with the UK, oak has a reputation across Europe for supporting a large number of associated species but there is no known compiled list of them[5]. However, some aspects have been studied in more detail than in the UK. For example it is known that the phyllosphere microbial community is influenced by the quantitative traits of *Q. robur*[50] and that changes in climate influenced the species richness of bacteria in the leaves of *Q. ilex*[51, 52].

Acorns form an important food resource for many species, including rodents (mice, voles and squirrels), birds (jays, woodpeckers and pigeons) and ungulates (deer, wild boar and horses). The wide inter-annual variation in masting, varying by several orders of magnitude[53, 54] (but generally lower in the UK than continental Europe[55, 56]) has been shown to drive cyclical changes in rodent populations[57, 58] with a corresponding change in the population of avian predators of rodents[59-61]. The variation in acorn yield influences the breeding performance of female grey squirrels as well as squirrel population density[62], the fecundity and density of wild boar populations[63] and growth of deer fawns[64]. A reduction in seed production, sometimes due to disease, leads to lower and more variable density of mice[65] with cascading effects of avian predators switching to prey on fledgling song birds as rodents decline[59, 61] and increased predation on roosting bats by wood mice due to shortage of acorns[66]. Inter-annual variation in masting in oaks appears to be increasing globally in association with climate change[67]. If a decline in oak health results in a change in masting patterns this will drive changes in the abundance of associated species which are dependent on acorns, with cascading impacts on predators and other prey species.

The impact of a decline in oak health on biodiversity associated with oak woodland ecosystems

Species richness for a range of taxa (i.e. vascular plants, bryophytes, birds, ground-dwelling and canopy-dwelling arthropods) has been found to be generally greater in oak dominated woods (including oak monoculture plantations, semi-natural oak woods) compared with woodland dominated by other tree species, especially where these exert contrasting influences on environmental conditions (such as shading) compared with oak[68-77]. This suggests that if oak health declines and oak is no longer dominant then species richness may decline.

There are more studies in Europe than the UK where the biodiversity of oak ecosystems is compared with other ecosystems (other woodland types or open ground habitats). The majority of ten comparative studies showed that oak ecosystems contain higher biodiversity than the comparator ecosystem but there are differences depending on the species groups, and comparator ecosystems, considered[77-85]. Mixed forest stands with oak can have greater species diversity and/or abundance than comparable 'pure' stands due to greater structural heterogeneity (data available for birds, arthropods, ground-dwelling spiders, carabid beetles, night-flying macrolepidoptera)[73, 86-90]. However, there are instances where tree host preference by certain species overrules the effect of tree species diversity[88, 89].

There are many studies showing that declines in tree species due to disease can have large scale impacts on associated species e.g. the change in bird communities due to the loss of fir and hemlock trees from the woolly adelgid in N. America, [91, 92], and the decline in lichens in Europe due to ash dieback[93]. The above studies reinforce the idea that any decline in oak health will impact negatively on many associated species, and species found more generally in the oak ecosystem. However, globally there is a lack of data on how, and over what time period, a decline in oak health will impact on associated species.

The impact of a decline in oak health on non-woodland oak and biodiversity

The importance of wood pastures, where oaks are a typical feature, as biodiversity hotspots is widely acknowledged and described, as well as the likely impacts of the Common Agricultural Policy CAP on their long-term future[94]. Scattered trees are globally known to be keystone structures in the landscape [15]. Hollow oaks, their ecology and the species they support have been well studied in

Sweden[95]. In particular, old oaks are known to be important for beetles[18, 96] due to the availability of dead wood and the high levels of sunlight and warm temperatures of non-woodland trees[95, 97]. Knowledge of the importance of non-woodland oak trees for other taxa is generally lacking, although there is some information on birds[98]. Non-woodland trees are also important for connectivity as shown for Osmoderma[18, 95] but there is little published evidence of this role for other species. There is some information in both the published and grey literature on the biodiversity associated with non-woodland trees, but less specifically on oaks; what is lacking is any understanding on how a decline in oak health will impact on this biodiversity.

The impact of biodiversity on oak health

Increased tree species diversity and hence greater richness of associated species can lead to a greater biological control e.g. greater number of parasitoid wasps and increased rates of bird predation on insects[87, 99-105]. However, forest diversity cannot be said to generally and uniformly reduce insect herbivory.

Tree health (e.g. powdery mildew infection of *Q. robur*) can influence the leaf bacterial community composition. A study of damage to *Q. petraea* leaves by Lepidoptera from a site in Germany also found that the bacterial community changed[50, 106, 107]. Further studies, both of additional sites in Europe and in the UK, are required.

The impact of a decline in oak health on the ecological processes/functions provided by oak

In Europe, as in the UK, there is a lack of specific information on the ecological processes provided specifically by oak, although the PuRpOsE review on oak functioning includes international work.

The impact of a decline in oak health on the functional role of biodiversity in oak ecosystems

More is known internationally than in the UK about the functional role of many of the species associated with oak. Some oak-associated species are known to contribute to nutrient cycling. Epiphytic lichens on oaks play an important role in nutrient cycling in oak woodland[108, 109]. There is potentially a link between oak rhizosphere bacteria, litter decomposition and nutrient cycling[110], this is known for *Q. petrea* from a site in the Czech Republic but is not known for other sites or UK native species[111]. Bacteria that fix nitrogen, have been found to have a greater presence in the soil and the root zone of oak compared to that of pine in a site in Poland[112]. Mycorrhiza are also important in nutrient cycling and shifts in mycorrhizas with different functional traits have been detected across environmental gradients (e.g. levels of N deposition) in oak woods[113]. Thus, changes in oak abundance could indirectly drive changes in nutrient cycling.

Species that ‘cache’ acorns for later consumption contribute to acorn dispersal[114, 115]. Such species indirectly influence a) germination success with a greater proportion of acorns surviving if buried rather than left on the surface[53, 116-119]; b) the location of new regeneration as seed dispersers are selective about the habitats to which they take seeds; c) the relative abundance of tree seedlings[120] as dispersers are selective amongst the species and sizes of acorns dispersed[121, 122]. Rodent dispersal of acorns is influenced by grazing (acorn removal is faster, or carried further in grazed than un-grazed habitats)[123, 124] and landscape fragmentation has been found to result in reduced dispersal distances and lower caching rates[125, 126]. Regeneration of oaks has been found to fail as a result of local extinction of the disperser[127, 128]. While there is no knowledge of direct oak health impacts on acorn dispersal, increased nitrogen deposition was found to increase mast production in oak but result in reduced recruitment because of increases in the rate of weevil infestation and reductions in rodent dispersal[129].

Assessment of knowledge

The state of knowledge sections (UK and International) in this chapter were compiled from a series of topic related statements produced by the authors while reviewing the literature. For each statement a *weight of evidence* score was provided following the terminology described in Table 1.2.

We have formed a consensus on the overall weight of evidence for each knowledge section using these scores, and highlight where this differs between the UK and internationally.

The impact of a decline oak health on biodiversity which uses oak trees

- The biodiversity associated with oak trees ESTABLISHED BUT INCOMPLETE - both UK and Internationally
- How a decline in oak health will impact on oak associated biodiversity SPECULATIVE - both UK and Internationally

The impact of a decline in oak health on biodiversity associated with oak woodland ecosystems

- The biodiversity associated with oak woodlands ESTABLISHED BUT INCOMPLETE - both UK and Internationally
- How a decline in oak health will impact on oak woodland-associated biodiversity SPECULATIVE - both UK and Internationally

The impact of a decline in oak health on non-woodland oak and biodiversity

- The biodiversity associated with non-woodland oak trees: UK - ESTABLISHED BUT INCOMPLETE for non-woodland trees but less information specifically for oak trees. Internationally - ESTABLISHED BUT INCOMPLETE but with more information on the importance of non-woodland trees and oak trees.
- How a decline in oak health will impact on biodiversity associated with non-woodland oak trees SPECULATIVE - both UK and Internationally

The impact of biodiversity on oak health

- How tree species diversity impacts on oak health UK - ESTABLISHED BUT INCOMPLETE for non-oak tree species, SPECULATIVE for oak. Internationally ESTABLISHED BUT INCOMPLETE with more oak specific information than the UK.
- How specific oak-associated species impact on oak health UK – SPECULATIVE, Internationally ESTABLISHED BUT INCOMPLETE/ CONTEXT SPECIFIC with more information on the role of bacteria in influencing oak health

The impact of a decline in oak health on the ecological processes/functions provided by oak

- *Knowledge of the ecological processes/functions provided by oak* ESTABLISHED BUT INCOMPLETE for trees, data lacking on oak specific information for many processes/functions – both UK and internationally
- *Impact of decline in oak health on the ecological processes/functions provided by oak* SPECULATIVE – both UK and internationally

The impact of a decline in oak health on the functional role of biodiversity in oak ecosystems

- Knowledge of the functional role of biodiversity associated with oak UK – SPECULATIVE, Internationally ESTABLISHED BUT INCOMPLETE/ CONTEXT SPECIFIC
- How a decline in oak health will impact on the functioning of oak associated biodiversity SPECULATIVE – both UK and internationally

Key to determining the adequacy of knowledge on oak and biodiversity is a consideration of our ability to predict the consequences of changes in the oak resource in the UK. For this we consider five alternative futures for oak in (i) high forest oak ecosystems and (ii) trees in the open and wood pasture ecosystems. Alternative futures for oak ecosystems were developed from a review of the drivers of change (e.g. land use change, biotic threats, woodland management) and their influence on important aspects of oak ecosystems. Land use change could result in woodland loss[130, 131], reduction in woodland canopy[132, 133], and loss of individual trees in the open ecosystems. Biotic threats, climate change and woodland management could result in change in tree species composition away from native oak[68, 130, 134-137]. Woodland management (or lack of it) also could cause loss/ lack of ecological continuity[130, 137, 138], lead to structure change such as the development of old growth features[139] or canopy reduction[136, 140, 141]. Knowledge relating to the effect on biodiversity of a change to an alternative future is synthesized by taxon (for a summary see Figure 5.1 and 5.2, full dataset is captured in Tables 5.1 and 5.2). From the relevant studies, the overall effects (positive, negative or neutral) for the taxon under each future scenario is summarised and a *weight of evidence* score is also allocated; in the Figures 5.1 and 5.2 these are indicated by directional arrows and by cell colour, respectively.

At the simplest level, the greater numbers of rows in the review of high forest oak ecosystem futures (Figure 5.1) compared to the open oak ecosystem futures (Figure 5.2) indicates there is far less knowledge available for the latter woodland type. Within each figure, empty cells indicate knowledge gaps. By reading across rows it is possible to see how well a particular taxon is covered in respect of their response to oak eco
system future, and by reading down columns the consistency of impacts across taxa can be seen. In high forest oak ecosystem (Figure 5.1), vascular plants appear to be more thoroughly studied compared to other taxa.

- It appears that detrimental effects on biodiversity would occur as a result of loss of ecological continuity (i.e. continuity of cover of trees of all ages over many decades) and this is reasonably WELL ESTABLISHED for mammals, birds and vascular plants and reduction in the extent of woodlands (ESTABLISHED BUT INCOMPLETE knowledge for vascular plants and saprotrophic beetles; CONFLICTING EVIDENCE for lower plants and SPECULATIVE for song birds).
- Change in tree species composition in high forest oak ecosystem to include species other than oak, appears to have a positive effect for most taxa studied. This result is WELL ESTABLISHED for mycorrhizal fungi, ground beetles and ground dwelling spiders, and SPECULATIVE for seed feeding birds and canopy-feeding invertebrates.
- Ageing of oak trees may have a positive effect on biodiversity but evidence is available for only a few taxa and the weight of evidence is mostly SPECULATIVE.
- The effects of change in high forest oak ecosystem structure appear to be taxon specific, and for vascular plants and ground beetles, evidence is CONFLICTING. For open oak ecosystems (Fig. 5.2), detrimental effects on biodiversity are suggested with a reduction in the extent of the ecosystem and a positive effect for ageing of oak trees. Evidence is ESTABLISHED BUT INCOMPLETE for most of the taxa studied.
- Whilst the negative effect on saproxylic beetles of a change in tree species away from oak is WELL ESTABLISHED, this was the only taxon with evidence of this oak future.

Overall, there appears to be significant gaps in our knowledge for many taxa: mammals, lower plants, saprotrophic fungi, saproxylic beetles and changes in tree species composition and structure of oak ecosystems; lower plants, fungi, invertebrates and bacteria for loss of ecological continuity.

Summary and priorities for new knowledge from review

Management of Risk

- **Measuring the impact and rate of a decline in oak health on biodiversity**: The assumption is made that as oak is a foundation species any decline in its health will impact its associated biodiversity; this has not been tested and the impacts may differ between different groups of species altering inter-specific interactions. A long-term monitoring programme on oak associated biodiversity within woods impacted by a decline in oak health across a geographic spread of sites would address this issue.
- **Identification of species most at risk from a decline in oak health, in relation to where oak decline might be greatest:** The overlap between the distribution of the oak associated species most at risk (obligate and highly associated species) and the areas in the UK where oak health is predicted to decline the most is unknown. An initial attempt at this could be carried out using data from the PuRpOsE project on oak health risk maps and existing species distribution maps.
- **Interactions between changes in management and oak biodiversity:** as oak health declines a better understanding of how changes in management and different scenarios of change will impact on oak biodiversity is required. This could include assessment of the suitability of non-native oak trees for biodiversity.

Managing the oak resource

- **Regeneration of British Oaks:** Two aspects merit attention – i.) the biology of regeneration focusing on factors influencing masting, dispersal and successful oak establishment; ii.) identification of the societal and/or management changes needed to ensure the continued care of the current veteran oak resource and to establish the next generation of oak trees, in particular of non-woodland oak trees, including the role of grants or other incentives.
- **The importance of non-woodland oak trees for biodiversity and providing connectivity**: Without knowledge of the specific role of non-woodland oaks for species that depend on their open grown nature we cannot understand the relationship between dependent biodiversity and open grown trees. The role of non-woodland oak trees in providing landscape connectivity is poorly understood. The impact of tree loss on connectivity can be assessed by a combination of new approaches to modelling together with newly acquired data on species dispersal. Any increase in connectivity may have to be considered against the potential negative impacts of increase pest and disease spread.
- **Establishing new veteran oak trees:** To date, the UK has documented more ancient oaks than the rest of Europe has done. How can we secure the next generation of ancient oak? Does creating dead wood within young oak trees provide similar characteristics to veteran trees in terms of the biodiversity supported?

Working with nature

- **The role of different taxonomic groups in promoting oak health**: how do biological control agents (e.g. parasitoids, bats, birds, spiders, bacteria and other micro-organisms) and other functional significant species (e.g. species facilitating nutrient and water uptake) promote oak health? How are these species/taxonomic groups affected by oak forest composition (which tree species combinations?) and structure, especially elements that can be managed to support these functionally important species? Also, how are these taxa influenced by changing climate e.g. periods of drought? This kind of work could be linked with reciprocal work on the incidence of pests and diseases considering different stand/woodland composition and structure.

- **The functional role of species within oak woodlands:** The functional role of the circa 2000 species associated with oak is largely unknown. A better understanding of their functioning (especially functionally important species such as pollinators, parasitoids, insectivores) would allow us to assess the potential impacts if oak health and hence oak associated biodiversity declined. This should include an understanding the redundancy of oak associated biodiversity and how patterns of biodiversity will change as the climate changes.

Sources

The sources used are all referenced in the text and reference list.

Figure 5.1 Impacts on biodiversity under five alternative oak futures produced under current drivers of change for high forest oak ecosystems where impacts are indicated as increase (↑), decrease (↓) or no change (→), and a weight of evidence score is indicated by cell colour (WELL ESTABLISHED- amber; ESTABLISHED BUT INCOMPLETE- blue; COMPETING EXPLANATIONS- green; SPECULATIVE-yellow).

		Oak ecosystem futures:				
Taxon		**Loss in woodland extent**	**Loss of ecological continuity**	**Change in tree species from oak**	**Change in structure**	**Aging of oak trees**
Mammals	Rodents		↓			
	Ungulates		↓			
Birds	Song	↓	→↓			
	Seed feeders		→	↑	↑	
	Invertebrate feeders		↓			
Vascular plants	All woodland	↓→	↓	↓→↑	↑↓	↑↓
Lower plants	Lichens Bryphytes	↓				↑
Fungi	Saprotrophic					↑
	Mycorrhizal			→↑		
Invertebrates	Canopy herbivores			→↑	↓	
	Soil herbivores			↓	↓	
	Saproxylic beetles	↓				
	Ground beetles			→↑	↑↓	
	Ground spiders			→↑		
Bacteria	Slime moulds			↓→	↓→	↓

Figure 5.2 Impacts on biodiversity under five alternative oak futures produced under current drivers of change for open oak ecosystems where impacts are indicated as increase (🡅), decrease (🡇) or no change (➔), and a weight of evidence score is indicated by cell colour (WELL ESTABLISHED- amber; ESTABLISHED BUT INCOMPLETE- blue; COMPETING EXPLANATIONS- green; SPECULATIVE-yellow).

		Oak ecosystem futures:				
Taxon		**Loss in woodland extent**	**Loss of ecological continuity**	**Change in tree species from oak**	**Change in structure**	**Aging of oak trees**
Birds	Woodpecker	🡇				🡅
Lower plants	Lichens					🡅
Invertebrates	Lepidoptera	🡇				
	Saproxylic Beetles	🡇		🡇		🡅
	Weevils	🡅🡇				

Table 5.1 Impacts on biodiversity under five alternative oak futures produced under current drivers of change for high forest oak ecosystems (data collected in UK (UK) or outside UK (Int) and classed as 1: review journal article, 2: peer-reviewed paper, 3: reports/grey literature, 4: personal comm., anecdotal evidence). Superscript numbers refer to numbers in reference list.

		Alternative oak futures				
		Woodland loss: patch size reduction/ fragmentation	Loss /lack of ecological continuity	Change in tree species composition away from native oak	Change in structure – canopy reduction, associated disturbance	Change in structure - development of old growth features
Birds	Woodland breeding birds (mainly passerines)	Neg -Int.2[142] SPECULATIVE	Neut-Int.2 [130] Neg -Int.2 [59, 60] COMPET. EXPLANATIONS	Pos - Int.2. [86] SPECULATIVE	Pos- Int.2[140] SPECULATIVE	
	Graminivores		Neut-Int.2 [130, 143] ESTAB. BUT INCOMPLETE			
	Invertebrate feeders, herbivores and omnivores		Neg-Int.2 [61, 116, 130] ESTAB. BUT INCOMPLETE			
Mammals	Rodents		Neg –UK 2[61] Neg -Int.2 [57-59, 144, 145] WELL ESTABLISHED			
	Ungulates		Neg -Int. 2 [63, 146, 147] ESTAB. BUT INCOMPLETE			
Vascular plants	Forest specialists, woody plants & forest generalists	Neg/Neut- Int.2[148] ESTAB. BUT INCOMPLETE	Neg -UK/Int.1[149] ESTAB. BUT INCOMPLETE	Neg-Int.2 [137] Neut/Pos- UK.2 [38, 40, 41, 44] CONTEXT SPECIFIC	Variable -Int.2 [132] CONTEXT SPECIFIC	Pos-Int.2 [139] Neg -UK 2 [48] CONTEXT SPECIFIC
Lower plants	Lichens, bryophytes	Neg,-Int. 2[150] CONTEXT SPECIFIC				Pos- Int.2 [139] SPECULATIVE
Fungi	Wood-inhabiting					Pos- Int.2 [139] SPECULATIVE
	Ectomychorrizal			Neut/Pos-UK.2 [42, 43] ESTAB. BUT INCOMPLETE		
Invertebrates	Saproxylic oak beetles	Neg- Int.2 [151] ESTAB. BUT INCOMPLETE				

	Beetles (Coleoptera: Carabidae, Staphylinidae, Cerambycidae)			Neut/Pos- UK.2 [46, 88] Int.2. [87] WELL ESTABLISHED	Pos (but Neg for forest specialists)-Int.2 [140, 152] ESTAB. BUT INCOMPLETE	
	Collembola (soil invertebrates)				Neg- Int.2 [141] ESTAB. BUT INCOMPLETE	
	Earthworms			Neg-Int.2[85] SPECULATIVE		
	Litter fauna				Neg-Int.2 [153] ESTAB. BUT INCOMPLETE	
	Parasoid wasps			Pos – Int.2 [99] ESTAB. BUT INCOMPLETE		
	Lepidoptera			Neut/Pos- Int 2 [90] SPECULATIVE	Neg-Int.2 [140, 154] ESTAB. BUT INCOMPLETE	
	Ground dwelling spiders			Neut /Pos– UK.2 [46] Int.2 [87, 89] WELL ESTABLISHED		
	Sub canopy herbivores			Neut/Pos- UK.2 [45] SPECULATIVE		
	Canopy herbivores			Neut/Pos- UK.2 [45] SPECULATIVE		
Bacteria	Myxobacterial iodiversity			Neg/Neut-Int,2 [155] SPECULATIVE	Neg/Neut –Int.2 [156] SPECULATIVE	Neg- UK;2 [9] SPECULATIVE

Table 5.2 Impacts on biodiversity under five alternative oak futures produced under current drivers of change for oak trees in the open and wood pasture ecosystems (data collected in UK (UK) or outside UK (Int) and classed as 1: review journal article, 2: peer-reviewed paper, 3: reports/grey literature, 4: personal comm., anecdotal evidence). Superscript numbers refer to numbers in reference list

Taxon /entity for which response/ fate studied		Alternative oak futures				
		Woodland loss: patch size reduction/ fragmentation	Loss /lack of ecological continuity	Change in tree species composition away from native oak	Change in structure – canopy reduction, associated disturbance	Change in structure - development of old growth features
Invertebrates	Beetles (Curculio elephas)	Pos-Int.2 [157] Neg-UK.2 [17] COMPET. EXPLANATIONS				
	Beetles (Osmoderma eremita)	Neg-(Int) 2 [18, 95] ESTAB. BUT INCOMPLETE				
	Saproxylics	Neg-UK. 3 [27, 158] ESTAB. BUT INCOMPLETE		Neg - UK.3 [19, 20] Int.2 [95] WELL ESTABLISHED		Pos - UK. 3 [19, 20] ESTAB. BUT INCOMPLETE
	Lepidoptera	Neg-UK 2 [21, 22] ESTAB. BUT INCOMPLETE				
Lichens						Pos - UK.3 [159] SPECULATIVE
Birds	Woodpeckers	Neg –Int. 2 [16] ESTAB. BUT INCOMPLETE				Pos - Int.2 [16, 98] ESTAB. BUT INCOMPLETE
Biodiversity	Multiple species	Neg -UK 3 [159] SPECULATIVE	Neg UK 3[11, 159] UK 2 [160] Int. 2 [15, 94] ESTAB. BUT INCOMPLETE	Neg - UK 3 [159] SPECULATIVE		

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6. Fundamental knowledge of genetics and implications for health of oak trees

Joan Cottrell

Introduction and scope of chapter

This chapter deals with the broad topic of genetics of oak set mostly in the British context. Intra-specific genetic diversity provides a species with the building blocks for adaptation. The amount of diversity present in oak woodlands depends on the initial colonising material, subsequent geneflow and actions of natural selection. Geneflow amongst woodlands tends to homogenise diversity within a landscape, whereas natural selection acts to counteract this by promoting survival of those individuals that are best suited to local conditions, so that populations become differentiated.

There are two kinds of genetic diversity, neutral diversity provides individuals with no selective advantage and it is therefore immune to the forces of natural selection. This type of diversity is useful for identifying postglacial routes of colonisation and assessing contemporary geneflow. It is studied using molecular markers such as those found in the maternally inherited chloroplast DNA and in bi-parentally inherited highly variable markers such as microsatellites. In contrast, adaptive diversity influences how well individuals are adapted to the environment in which they grow, and this type of variation is subject to the forces of natural selection (including influences of pests and diseases).

Traditionally, multisite, common garden trials have been used to study adaptive diversity. These are experiments in which seed collected from many different locations are grown in a common environment, or environments. As the environment is common in these experiments, differences among provenances can be inferred to be due to their genotype. Such trials are needed to understand the relative importance of site and seed provenance (or origin) on the behaviour of material. Such information underpins seed sourcing advice and informs the potential for material to adapt to threats such as climate change and pathogens. In addition to provenance trials, the advent of sophisticated molecular approaches is beginning to allow investigation of genes involved in the expression of adaptive traits, although it should be noted that accurate assessment of phenotypes (the full complement of an individual's observable characteristics) in material of known genetic background is still required in applications of these molecular approaches. This review begins by describing what is known about neutral and adaptive diversity in British and European oak and goes on to outline our understanding of the processes of colonisation, geneflow and natural selection in British oak. It highlights the need to conserve natural British oak resources and outlines current activities that aim to achieve this and contribute to oak health.

Another important role of maintaining natural genetic diversity among oak populations is to provide the raw material on which to carry out selection and breeding programmes that aim to improve commercially important traits in a given species. Oak is an important timber tree and breeding and selection programmes are established in Britain and mainland Europe to improve heritable traits of economic importance such as growth rate, tree form and timber quality [1,2]. The review identifies the modest breeding resources that are available in Britain and outlines the particular difficulties that oak presents to the tree breeder.

Finally, the review provides an account of current molecular work on identifying desirable traits as well as weaknesses and vulnerabilities, outlining the different approaches that have been used and opportunities for the future. These advances may contribute to our understanding of species adaptation and susceptibility to pests and diseases including Acute Oak Decline (AOD). Potential approaches are outlined which experimental molecular scientists may adopt to improve our understanding of oak health and to determine whether or not there is a genetic basis to these health problems and a genetic solution to them.

State of knowledge UK and Internationally

Colonisation, geneflow and adaptation in *Quercus robur* and *Quercus petraea*
Postglacial origins of oak in Britain

This chapter pertains to *Quercus robur* and *Q. petraea*, collectively referred to as oak. Oak was entirely absent from Britain during the last glacial period. Pollen records indicate that colonisation of Britain started in the south of England about 9500 years ago before the formation of the English Channel about 8500 years ago [3]. Colonisation, probably initiated at multiple points along the (now) south coast, progressed northwards at a rapid rate of between 350 and 500 m yr^{-1} through England, Wales and southern Scotland and then slowed to 50 m yr^{-1} through central and northern Scotland [4,5]). Colonisation of Britain by oak was complete by 6000 years ago, which is relatively recent in terms of the generational time of oak.

Variation in the maternally inherited chloroplast genome can be used to identify glacial refugia (areas where populations survived unfavourable conditions), and to track the postglacial routes of spread by seed of a species [6]. Mutations accumulate in material present in the refugia, and the refugial lineages (a lineage is a temporal series of organisms, populations, cells, or genes connected by a continuous line of descent from ancestor to descendant) become molecularly differentiated. It is these differences that are used to track the postglacial colonisation routes of species.

Studies have revealed three major oak glacial refugia in Southern Europe: these are located in Southern Spain, Southern Italy and further east in the Balkans [7]. After the last ice age, Britain was entirely recolonised by material from the Southern Spanish refugium. However, much of the chloroplast DNA variation failed to migrate northwards from Spain, so oak in Britain contain less maternally inherited chloroplast DNA diversity than the Spanish refugial lineages.

By contrast, during the course of recolonisation, with the three maternal lineages exchanging pollen at suture zones in mainland Europe, a relatively high neutral nuclear genetic diversity resulted, and is reflected in British oak woodlands [8]. Chloroplast DNA markers can be used to identify whether planted oak material is sourced from western Europe (and likely to be native) or if it originates from a location further east and is definitely not native.

The majority of new oak woodland in Britain is established via planting but shortage of locally produced seed during some years is an enduring problem in Britain; it is thought that over the past decades or even centuries a considerable amount of seed has been imported from south-eastern Europe and planted in Britain. Small studies using chloroplast DNA markers to estimate the extent of this importation [9,10] have shown that some oak woodlands, particularly in the Forest of Dean, consist of material from non-Iberian lineages, presumably as a result of human mediated activity. By extending this work it might be possible to identify introduced material that could explain reasons for poor performance of some planting stock, resulting from maladaptation to local conditions.

Oak belongs to the genus *Quercus*, which comprises several hundred diploid and highly heterozygous species distributed throughout the northern hemisphere, from tropical to boreal regions [11]. Only two species of oak are native in Britain, the pedunculate oak (*Q. robur*) and the sessile oak (*Q. petraea*), both of which originate from maternal lineages that migrated postglacially from Spain. *Q. robur* is most abundant in east Devon, as well as in certain areas of Scotland [12]. In contrast, *Q. petraea* is more common in Wales, Devon and Cornwall, the west of Scotland, the Lake District and Yorkshire. Significant areas of mixed oak species woodlands and a high incidence of intermediate individuals with characteristics of both species, making them difficult to allocate to species, occur in southern Scotland, south central England [7] and Northern Ireland [13]. A method has been developed based on multiple leaf morphological characters to distinguish between the two oak species [14] which works well across the European distribution but does not recognize interspecific hybrids. Young hybrids resemble the morphology of their maternal parent [15], and if this is also the case in adult trees, it may be the reason for the difficulty in identifying hybrid adults based on morphological attributes only. With the availability of many thousands of SNP (Single Nucleotide Polymorphism) markers molecular methods can now be applied to discriminate the two species [16, 17]; INRA have developed a panel of markers based on SNP polymorphisms, which is being offered as a service to discriminate between the two species on the basis of 262 SNPs (E. Guichoux, pers comm). This method is based on the existence of polymorphisms in this particular panel of SNPs which are present in very different frequencies in the the two species, so that when used in combination they provide a highly effective method of discriminating between the two species and also identify hybrids; panels based on different sets of SNPs could be constructed to identify individuals with high disease or pest resistance provided susceptibility has a heritable component. It is somewhat remarkable that this species discrimination is possible given that the two species are sympatric (occur in the same / overlapping areas) over much of their distribution and are, to some extent, inter-fertile. The maintenance of the integrity of the two species and the evolutionary significance of this has been reviewed [18] and is considered to be due to a range of factors that include: low inter-specific pollen flow, backcross events, genetically controlled pollen discrimination, selection against hybrids at the juvenile stage and post-mating reproductive barriers ([19] and references therein).

The two species have contrasting environmental optima, a feature that has been used by molecular biologists to study drought and flooding tolerance and the genetic and molecular basis of these traits, by comparing the genomes of the two species (see later section). *Quercus robur* tolerates water logging and light exposure more effectively than *Q. petraea* whereas *Q. petraea* has a higher water use efficiency and is more shade tolerant, consistent with its role as a post pioneer species ([20] and references therein).

Within woodland genetic structure and gene flow

Microsatellite marker studies have demonstrated high neutral genetic diversity and the presence of weak but significant spatial genetic structure across short distances in oak woodlands, which is stronger in *Q. petraea* than in *Q. robur* ([21, 22]). This means that close neighbouring trees growing up to 150 meters apart are more related to one another than would be expected by chance. This absence of strong genetic structure likely reflects the pattern of geneflow in oak which occurs via wind dispersal of pollen, and bird and small mammal dispersal of seed. There have been several studies to explore pollination distances and seed flow in oak. This is an important consideration as trees are stationary organisms whereas their genes can be transported over long distances. Long distance geneflow acts to maintain genetic diversity and introduce genetic material from beyond the boundaries of woodlands which may be adapted to different environmental and biotic conditions. This may be important in supporting adaptation to environmental changes such as the current climate warming and challenges from novel pests and diseases.

The development of highly variable microsatellite markers has made it possible to identify the parentage of acorns or seedlings by matching the multilocus fingerprint of the acorn to a range of candidate parents fingerprinted in a stand. Estimates of pollen flow are easier to obtain than those of seed dispersal because the maternal parent is known in the case of an acorn picked from a tree, whereas neither parent is known in the case of a dispersed seedling. One study [23] found that a high percentage (averaging 65% for *Q. robur* and 69% for *Q. petraea*) of acorns were pollinated by male parents from outside the study site. Subsequent work [24] performed in a range of woodlands across Europe confirmed these average estimates but found large differences (ranging from 21–88%) between woodlands with pollination from sources outside the stand. In addition, this study also showed that there were also high levels of seed immigration into the stands, the magnitude of which varied considerably between stands, with estimates ranging from 20–66%. Such high levels of immigrant gene flow suggest that geographically remote oak stands are unlikely to be genetically isolated. Gene flow was found to be mostly intraspecific, but with large variation, as some trees and stands showed particularly high rates of hybridization.

The frequency of mating events declines with distance between pairs of candidate parents. The design of the above studies did not permit the maximum dispersal distance to be determined. However, a study of a geographically isolated small stand of *Q. robur* located at the species distribution limit in the eastern foothills of the Ural Mountains in Russia [25] was able to demonstrate very long-distance pollen flow, where 35% of all successful pollinations were attributable to trees growing at least 85 km away from the stand. While this may not be typical of trees growing in stands in more central parts of the distribution range, it does demonstrate that pollen flow can occur over extremely long distances. Evidence from other species also indicates that open grown solitary trees in the landscape may experience a higher proportion of long distance geneflow than woodland trees. This may be important in counteracting the effects of landscape fragmentation [26, 27].

A study [28] adopting a different experimental design by genotyping oak seedlings in birch woods located between 0.5-1.5 km away from the nearest adult oaks, found only 10% of the seedlings could be attributed to local woodland parentage; the remaining 90% were thought to be attributable to jays carrying acorns from more distant woodland oaks. The authors comment on poor regeneration of oak seedlings in oak stands in the UK and suggest that we should capitalize on natural regeneration in the wider landscape as a valuable resource. These studies provide sound evidence of the long-distance transfer of acorns and pollen and suggest that genetic isolation is unlikely to be a problem to oaks in Britain.

Distribution of adaptive variation within and between woodlands

Although differentiation between genotypes in UK oak woodlands in terms of neutral nuclear markers is low due to effective gene flow across the landscape, this does not mean that there are no differences in adaptive variation between woodlands. Provenance trials which test performance of seed from a broad range of origins under a common set of conditions are required to detect differences in adaptive diversity, but these are difficult to establish in oak owing to its long generation time and infrequent masting (seed producing) years. Such trials do nevertheless exist in Britain and contain a mixture of British and continental European provenances, so that the focus is on the pattern of differentiation at a broad geographic scale. A summary of the existing trials and their major findings are provided in Table 6.1. The within-trial differences between provenances reveal whether there is a genetic (G) basis to the differences in the traits observed. Differences between trial sites reveal whether the material exhibits phenotypic plasticity when grown on contrasting sites with a different environment (E). Provenance trials structured in this way can also be used to assess the amount of GxE i.e. genetic x environment interaction that occurs. This is often used by tree breeders to determine whether their ranking of superior genotypes is consistent across sites and whether the top performing provenance or genotype is consistently the best across a range of growing conditions. Most phenotypic traits in forest tree species show clinal (i.e. gradual change in an inherited characteristic across a geographic range, usually associated with an environmental factor) variation with increasing altitude or latitude both when plants are grown *in situ* and in common garden trials [29].

Provenance trial material in Britain

The oldest provenance trial in Britain, located at Penyard in the Forest of Dean, was planted in 1954 and contained six British provenances from Wales and the south of England, and three Scandinavian provenances. The trial ended in 1973 and subsequently was extensively thinned in 1983 to leave the best two trees per replicate i.e. twelve trees per seed origin. At this time an assessment of the timber structure of the best two felled trees per replicate was carried out [30]. An assessment of the unthinned trial in 1981 at the age of 27 years found that height and diameter growth was poorest in the Scandinavian provenances, and 'locally collected seed was as good as any other origin' [31]. Although well replicated, the trial included only a narrow geographic range of British provenances and apart from the three Scandinavian provenances no material from other European locations was tested.

Since the establishment of the Penyard trial in 1954 no provenance trials were planted until two series containing both species of oak were established by Forest Research in Great Britain in 1990 and 1992 [32]. The 1990 series consists of 6 trial sites mostly located in the south, but with one site in northern Scotland. The 1990 series contains 27 provenances (9 GB, 8 France, 5 Germany, 3 Ireland, 1 Netherlands and 1 Belgium). With the exception of one provenance from Perthshire and 1 from Morayshire, all the British provenances were from sites located in the south.

The 1992 series was organised by IUFRO and was planted in trials in Britain and elsewhere in Europe. In Britain the series consists of two sites in the south and one in northern England. The 1992 series consists of 28 provenances (13 GB, 4 France, 4 Germany, 2 Belgium, 1 Denmark, 1 Poland, 1 Turkey and 1 Hungary). Once again, with the exception of one provenance from Perthshire and one from Galloway, all the British provenances originated from the south of Britain.

Height assessments [32] from both trials at 10-13 years of age showed the difference between the tallest and shortest provenances was of the order of 1.5-2.0m. Provenances from *selected** (**Selected* category FRM (Forest Reproductive Material) is collected from stands showing superior characteristics, e.g. better form, growth rate, health.) British seed stands generally showed the best performance in terms of height, across all sites. This is in contrast to British provenances from non-selected British stands, which showed a wide range of height performance.

In general, the poorest performing provenances were those that had been moved from northern locations to southern trial sites, possibly due to their adaptation to a shorter growing season. The adaptation to shorter growing seasons in provenances from northern latitudes has been confirmed by phenological studies (bud burst) of material growing in the Alice Holt trial site [33], and in a four year old trial of oak in Scotland consisting of 16 British and European provenances [34]. These northern British provenances do, however, show high survival on challenging (colder and more exposed) sites. The majority of the European provenances came from *selected* stands and showed average height in the trials. The exception was a single Dutch provenance, which had exceptionally good growth in all sites in the 1990 series. However, care should be taken when using Dutch material since it is more likely to suffer from 'shake' and should not be used on sites that are prone to drought [35]. The provenances from Eastern Europe and Turkey were only planted at a single site but showed below average height growth, and it could be risky to grow these in Britain. In terms of survival, on the challenging sites there was superior survival of GB provenances. The study [31] concludes that for faster growth it is possible to move material from south to north, but this involves increasing risk. Although oak shows high survival on good sites, on more testing sites there is evidence that the adaptation of northern provenances to late frosts is an advantage for survival. In addition, material from central and Eastern Europe is not recommended [32]. These trials have not been examined in terms of susceptibility to pests or pathogens.

A further series of provenance trials was established by the Earth Trust in 2006. These were planted at three sites in Kent, Devon and Oxfordshire and consisted of 11 provenances (4 GB, 4 France, 2 Netherlands and 1 Spain). These were assessed for height in 2012 when they showed significant site and provenance effects with the Dutch provenances showing greatest height growth (Jo Clark pers. comm.).

Potential impacts of climate change

Data from all the sites at which the IUFRO provenance series of trials were planted across Europe were used to explore the differential population responses to climate. Tree height growth and survival were modelled for contemporary climate and then projected for years 2071-2100 using two greenhouse gas concentration scenarios. The models indicated oak populations at the northern limits in Europe were unlikely to show large changes in growth and survival in response to climate change [36], a result that suggests the policy of using locally sourced planting stock should be retained. Provenance work has also been carried out in young plants subjected to specific imposed conditions. For example, work has been carried out to examine the frost hardiness of three year old plants from provenances from a range of European countries: England (1), Denmark (1), France (1), Germany (6), Austria (1) and Poland (1), and grown in Scotland [37]. Shoots were removed at time intervals, placed in freezing chambers and subjected to various test low temperatures for a period of three hours, after which the cabinet was gradually returned to 2°C for several hours before performing conductivity measurements to assess cold damage. There were significant differences between provenances in cold damage. Two of the French provenances and the Austrian provenance were least frost hardy, whereas the Danish, Polish and German provenances were generally more tolerant of low temperatures. Phenology was shown to be of major importance for frost hardiness in spring and autumn. This highlights the risk of planting both early flushing provenances that are prone to damage in sites that experience late spring frosts, and also provenances that do not lose their leaves until late in the autumn in areas that are prone to early autumn frosts. The authors comment that since the French provenances used in the study were generally less hardy, were prone to flush early, and grew late in the autumn, they would seem a poor choice for very cold districts or where either late spring or early autumn frosts are frequent.

There is currently considerable debate regarding the choice of planting material [38]. With the threat of climate change, there is uncertainty over whether it is still advisable to adhere to previous advice which advocated sourcing material locally on the assumption that such material is likely to be best adapted to current environmental and biotic conditions [39]. Elsewhere in the world others advocate sourcing a proportion of material from areas currently experiencing the predicted future climate, on the assumption that this component of the planting scheme will be better adapted to future conditions, particularly those relating to increased drought pressures [40]. This uncertainty is leading to divergence in policy for sourcing native species planting material in the GB countries. We currently have little understanding of the main drivers of adaptation in oak and appropriately designed long term trials would greatly help to inform these questions. Current trials in Britain have the disadvantages that they: contain material collected at a very broad geographic scale, have not retained the seed in maternal progenies when planting the trials, frequently do not have exact details of the sites of origin so that the environment to which the seeds are adapted is poorly understood, and the provenance trials are located in less challenging sites in the south of England. There may also be a benefit in establishing material from a range of British provenances at trial sites in France to see how well British material copes with the warmer conditions that are predicted to occur in parts of Britain particularly southeast Britain, which is forecast to experience the warmest and driest future conditions.

It is important to consider which traits should be measured in provenance trials. Many of the existing trials have been set up by tree breeders who were mainly concerned with yield. Consequently, the majority of trials have been assessed only for survival, height and diameter. These traits are not always the best indicators of fitness and adaptation. Other traits of interest include phenology such as leaf flushing and leaf senescence, water related traits such as stomatal size, stomatal density, leaf size and carbon discrimination during photosynthesis as an indicator of stress. With the exception of a single study [33], there are no data on these traits in British oak trials although evidence does exist for other British broadleaved species such as ash, rowan and birch for which provenance trials containing large numbers of British provenances exist [41]. Data acquisition on a large number of informative traits are expensive and time consuming to collect but are vital in understanding the main drivers of adaptation in our tree species in Britain.

Virtually no work has been carried out on provenance differences in susceptibility to disease in oak in Britain, although work in other species has confirmed a genetic basis to susceptibility to diseases. For example, there have been studies in field based trials of *Pinus sylvestris* of provenance susceptibility to Dothistroma needle blight [42,43] and in provenance trials of ash to ash dieback [44]. In another example, studies carried out on Scots pine in controlled environments with high levels of inoculum and ideal conditions for infection were informative in identifying particularly resistant genotypes [45]. However, when interpreting results of disease susceptibility in provenance trials it is important to consider the factors that affect the amount of pathogen damage suffered by individual trees. Various abiotic factors, as well as biotic factors, including the genotypes of the tree and the pathogen, need to be considered, as well as the interaction between the abiotic and biotic components [46].

One of the consequences of rapid anthropogenic induced climate change will be loss of local environmental adaptation in tree populations, and a corresponding increase in environmental stress, which in itself could make trees more vulnerable to a range of pests and pathogens. Also, climate change could result in phenological asynchrony between host and pest/pathogen, a feature that is particularly important in herbivorous pest attacks and foliar diseases, such as powdery mildew, both of which depend on the availability of young leaves for foraging and for infection when inoculum is produced [47]. Interestingly and contrary to expectations, a common garden experiment examining the genetic diversity of powdery mildew populations on oak from a broad altitudinal range in the Pyrenees, did not find evidence of differentiation in the phenology of the powdery mildew pathogen [48]. The lack of phenotypically adapted mildew populations may be attributed to the high within-population genetic diversity of the host in terms of leaf phenology, so that strong selection for fungal phenology at the population level is unlikely to operate.

The role of genetic diversity of the host in determining the amount of damage due to ectophagous insects has been studied in France [49] and found, rather unexpectedly, that damage by such insects increased with genetic diversity of oak sapling populations. The authors suggested that this is because assemblages of different oak genotypes would benefit polyphagous herbivores via improved host patch location, spillover among neighbouring saplings and diet mixing.

Provenance trials can also be used to test whether local adaptation is important in determining the association between trees and their herbivore communities; for example, one study [50] was able to show that provenance explained significant variation in gallwasp abundance in an oak provenance trial in France.

Speed of adaptation to pest and disease attack
Evidence that evolution of higher quantitative resistance can occur in the presence of long-term increases in pathogen pressure comes from studies of live oak populations in Texas into which oak wilt, *Bretziella* (Syn. *Ceratocystis*) *fagacearum*, had recently spread and caused significant death of mature trees [51]. When inoculated with oak wilt, seedlings from adult trees that had survived oak wilt showed significantly higher survival (82 %) than seedlings from populations that had not yet been affected by oak wilt (62.5 %) [52]. These results demonstrate that effective natural selection for higher quantitative resistance had occurred and was associated with better containment of the disease by the seedlings.

Conservation of oak genetic resources in Britain

The diversity present in native tree resources in Britain may be particularly important given the location on the edge of the distribution range of many of these species; populations may therefore, through forces of natural selection, have become genetically adapted to a unique set of environmental conditions. Britain is a member of the EUFORGEN network which is a collaborative network of forest geneticists interested in the conservation of forest genetic resources. EUFORGEN/EUFGIS have developed an integrated initiative to establish a pan-European network of gene conservation units (GCUs) for each native tree species in Europe. Each GCU must conform to a set of criteria in order to be listed on the EUFGIS data base of GCUs [53]. Although there were over 3200 genetic conservation units in Europe covering about 100 species listed on the EUFGIS database in 2015 [54], Britain has lagged behind in this initiative and has yet to establish a single GCU for any of its native tree species. This may hinder involvement in any pan-European genetic monitoring of GCUs that may be planned to detect early signs of climate change and pest and disease impacts on European oakwoods.

Another recent conservation initiative in Britain has been the UK National Tree Seed Project [55], which aims to establish an *ex situ* gene conservation collection by conducting multi-provenance seed collections representative of the majority of the adaptive genetic diversity present in each native tree species in Britain and storing them in Kew's Millennium Seed Bank at Wakehurst. In this context, oak seeds present a particular challenge due to their well-documented recalcitrance in storage, which means that they cannot tolerate usual conditions suitable for storing seed and can therefore only be stored for a short period of time [56].

There is growing recognition that the UK requires a Strategy for Forest Genetic Resources (FGR) to integrate the various FGR conservation activities, develop joint understanding across the sectors, and provide simple, consistent messaging to policy makers and public. Recently, a workshop to highlight and agree the need for the strategy was held at Kew where it was agreed that establishment of GCUs in the UK was a priority, not only to protect UK FGR but to ensure that we do not fall further behind our European neighbours in terms of monitoring and other pan European activities (www.gentree-h2020.eu>documents>results). Oak would be an important focus for such action.

Genetic improvement

Although oak provides a range of ecosystem services, the economic value of the timber remains one of the main reasons it is grown. Oak is greatly valued and in high demand in the European timber market [57]. The market for high quality oak in Europe has increased steadily in recent years, consolidating its dominant position in the flooring and joinery chapters of the timber trade [58]. Quality of oak logs is determined by characteristics which include: diameter, clear bole length, straightness, annual ring width and absence of rot, shake, cracks and epicormic branches [59].

Despite the demand for oak and the desire to plant it in Britain there has been a chronic lack of British sourced nursery stock. This reflects the irregular masting years, the inability to retain viability in stored seed, poor seed supply chain and lack of confidence in the stability of the UK nursery market, leading to a reluctance to invest in home grown planting stock production. Figures provided by the Animal and Plant Health Agency highlight this and show that 1117696 oak plants were imported from other EU Members States between January 2013-July 2015, the majority of which came from the Netherlands and Belgium [60].

The chapters below outline the measures being taken to improve the quantity of seed and the genetic quality of planting material for timber objectives sourced within Britain.

Registered seed stands

The first level of genetic improvement compared with wild stock is to secure seed from stands that contain a large number of superior individuals. Such stands can be registered as *selected* seed stands if they meet EU wide Forest Reproductive Material (FRM) criteria based on quality and tree health. However, in 2010 there were only six *selected* oak seed stands registered in Scotland and 55 in England [61]. The quality and volume gains from seed collected from these stands is known to be modest but significant [62, 63] and this, combined with the fact that the seed is often difficult to access, means the stands are rarely visited by seed collectors and their seed does not make up a large proportion of the seed used to establish new plantations [61]. This is despite a study [32] which noted that *selected* British stands of oak performed better in provenance trials than provenances that are not in the *selected* category and identified only as *source identified* (not judged to be phenotypically superior stands) British material. A further 46 *Q. petraea* and 17 *Q. robur* stands have recently been added in the *source identified* category. Although not phenotypically superior these are listed in order to improve the supply of locally sourced seed material which in many years fails to meet demand. These newly registered stands are mostly in Scotland and reflect a push to address the shortage of locally sourced oak seed in this region. According to a recent audit *Q. robur* crops more reliably than *Q. petraea* and many of the stands would benefit from investment to clear undergrowth and manage for seed production [64]. Longer lead in times between award of woodland grant and planting deadline would allow more time to work with nurseries to source and grow up appropriate seedling material [65].

Plus tree selection

Tree breeding is the next step in improving the genetic quality of a species and large gains can be achieved by breeding from the best individuals in the first generation of selection. A summary of trials of oak in Europe [1] has shown that most traits of economic importance in oak (wood properties, stem straightness, branch angle, epicormics) show medium to high heritability. Focussing on improvement of economically important traits, considerable effort was put into selection of phenotypically superior 'plus' trees in the 1950s and 1960s [66], and 167 plus trees of oak were identified by the Forestry Commission in locations across Britain [2]. However, there was no further activity until 1991 when BIHIP (the British and Irish Hardwoods Improvement Programme, now Future Trees Trust) extended this search for superior oak trees. The situation for oak plus tree selection in 2010 is shown in Table 6.2, with a total of 159 plus trees identified across England, Wales and Scotland [67]. Since 2010, this number has increased to 193 with most of the additional plus trees being sourced from locations in England (Jo Clark pers. comm.). As stem quality is the key factor in timber value of hardwoods, BIHIP focused strongly on quality traits such as tree form (straightness) and placed less emphasis on growth rates and health/tolerance to pests and diseases.

Breeding trials

Having identified plus trees, efforts were made by BIHIP to collect seed from these trees to establish breeding seedling orchards in 2003 containing both *Q. robur* and *Q. petraea* at one location in Scotland and six in England. Sixty two half sib families are being tested across eight orchards with 21 families common to all sites [61]. Breeders are searching for plus trees that produce progeny that show consistently superior performance, and this is why the progenies are being tested across many sites in Britain. Considering that some of these sixty two families will not prove to be genetically superior, the number of trees that will qualify to progress to the next stage is very small. The chances of bringing about significant improvement would be enhanced if the number of individuals included in the breeding population was increased to at least several hundred. To put this in context, there were 2594 and 1174 families of plus trees tested for Britain's main conifer species, Sitka spruce and Scots pine respectively. Even the more minor conifer species included several hundred families in the progeny testing that was carried out on them (935 Corsican pine, 578 Lodgepole pine, 575 Douglas-fir, 330 Larch) [66].

In oak, trial site effects were already visible when the seedlings were seven years old, and average height ranged from 98-184 cm, with the sites in Scotland, Wales and Ireland showing the poorest form [61]. When considering the 21 families that were present across all sites, there was reasonable consistency in the ranking of the top and bottom four families in terms of height. When height per family is averaged across all trial sites the tallest families came from sites in mainland Europe, either in the Netherlands or Northern France, a result that may be due to the long history of selection of oak in these countries. These trials were assessed for phenology in 2012 and for height, dbh and form in 2014, but the data are not yet publicly available. These are the only trials in Britain which provide the opportunity to explore the genetic basis and heritability of a range of other traits, but currently only growth traits have been assessed. Information on the genetic component of other traits such as pest and disease susceptibilities and wood properties could also be obtained from these trials. The easiest traits to tackle from a breeding perspective are those that have high heritability, are expressed early in the life of the tree and are simple to assess accurately.

Recent work [68] has explored the feasibility of calculating heritability of a range of traits in *in situ* wild populations. Such populations have the advantage of providing the opportunity to assess the phenotype of two generations (mature adult and juvenile sapling cohorts) present in the same woodland. However, in contrast to previous assesements of heritability based on *ex situ* trial material with known half-sib family structure, the pedigree of trees growing *in situ* is unknown. Recent increased availability of thousands of SNP markers now provide the facility to determine the genomic relatedness of these *in situ* trees by making calculations of the kinship between wild individuals. This can be used to derive estimates of heritability of traits of interest providing steps are taking to account for possible non-independence of genetic and environmental effects resulting from spatial family structures and non-uniformity of environmental conditions in-situ. Comparison of *in situ* and *ex situ* estimates of heritability showed that *in situ* estimates were more precise than those based on *ex situ* material. This is due to the larger number of individuals available i*n situ* compared to *ex situ* trials and the availability of two generations in the *in situ* populations which provides a deeper understanding of the relatedness and pedigree of individuals in the stand. Although this work shows promise, it should be noted that it was carried out in the Petit Charnie stand in France which has been extensively studied and characterized in terms of individual tree traits, genetic structure and environmental variation.

It is anticipated that the existing oak breeding seedling orchards will begin to produce seed by 2040, but because mast years only tend to occur about once every seven years, the eight orchards are only expected to produce enough seed to plant 15-20 ha of new woodland per year [69], which may decrease if inferior lines are discontinued. Bulking up of plus trees by grafting is therefore being currently carried out by Future Trees Trust who plan to use the grafted material to establish a further four seed orchards of 50-80 accessions (one for *Q. robur* in the National Forest in Leicestershire and three for *Q. petraea* in Herefordshire, Shropshire and N. Ireland). Grafting results have been disappointing, so this will be an ongoing process over the coming three years (Jo Clark, pers. comm.). A recent review commissioned by Future Trees Trust [70] goes into considerable detail regarding the desirability and current feasibility of vegetative propagation of oak. There are several reasons why there has been interest in trying to improve the success of clonal reproduction in oak. These include the need to multiply small numbers of superior genotypes of oak for use commercially, because production by seed orchards is low and oak seeds do not store well. It is also desirable to be able to produce clonally replicated genotypes for physiological research to minimize the genetic effect when imposing physiological treatments. Such material is also needed in order to establish replicated full sib and half sib trials for genomic studies. Several propagation methods have been tried ranging from rooted cuttings of mature, young or hedged material. However, achieving rooted cuttings from mature phenotypically superior broadleaved trees, particularly oaks, is challenging and has achieved variable success. Even when rooted cuttings have been produced, they often develop a strange habit more akin to the branch they were taken from than the tree itself. Trees that are less than three years old tend to produce material that roots more successfully but these trees are too young to assess for mature economic traits.

In 1992, with a view to practising clonal forestry, work started on identifying superior juvenile oaks, and cuttings of these were found to root readily with an 80-100% success rate. Work was carried out to determine juvenile/mature correlations for important traits to facilitate early selection of superior individuals when they can be vegetatively propagated [71]. More sophisticated approaches are also available based on *in vitro* micropropagation of shoots from axilliary buds and on somatic embryogenesis [70]. If success could be achieved in this difficult research area it would increase the availability of oak planting stock with superior timber qualities or tolerance to pests and diseases.

Oak in the era of genomics

Genomic resources

As with many Angiosperm tree species, oak has a relatively small genome and the last twenty years have seen enormous progress in our understanding of its genome [72]. The oak nuclear genome consists of 12 chromosomes and the haploid genome size is ~740 megabases [73]. Sequencing and assembly of the whole genome of a *Q. robur* individual was started in 2012 by a consortium. A draft assembly based on Sanger, 454 and Illumina sequence data was published in 2015 [74]. A high density linkage map was published [19] using an 8000 gene-based SNP array to genotype 1000 full-sibs from two intraspecific and two interspecific full-sib families of *Q. robur* and *Q. petraea* produced via controlled crosses. The draft assembly and linkage map have now been combined, along with additional sequence data, into a more complex assembly that became publicly available on the website http://www.oakgenome.fr/ in November 2017. This latest assembly has 871 scaffolds that have been placed onto 12 pseudomolecules that should correspond to the 12 chromosomes of the oak haploid genome. These scaffolds represent 717 megabases of DNA. There are a further 538 scaffolds that are shorter and have not been assigned to chromosomes. In this assembly, 25,808 genes have been annotated, representing 75 megabases of gene-space. The consortium has sequenced pools of individuals from *Q. robur*, *Q. petraea*, *Q. pyrenaica* and *Q. pubescens* and have found 31.9 million SNPs. They have also sequenced 18 populations of *Q. petraea* and detected 30 million SNPs.

The genome of the Californian endemic oak species *Q. lobata* has been sequenced and assembled by UCLA and John Hopkins University. A first draft was published in 2016 [75] and the most recent assembly is now available at a chromosomal level, with 96% of the sequence in 12 scaffolds and 2016 unplaced scaffolds. This is available for download at http://valleyoak.ucla.edu/genomic_resources/. Methylation (see section on epigenetics) and transcription profiles of *Q. lobata* have also been analysed[76, 77]. The availability of these genomic resources allows researchers to study the genetic architecture of oak and to identify quantitative trait loci (qtl) which are responsible for key adaptive traits such as tolerance to drought. This should eventually facilitate the production of trees for desired end uses such as improved biomass yield, wood properties, and biotic and abiotic stress tolerance, although this may be made difficult by the fact that several of these traits are likely to be under the control of many genes with small effect. Another problem is that forest tree populations tend to have large effective population sizes (Ne) making molecular breeding approaches more difficult to implement in relatively undomesticated forest tree species than in domesticated annual crop species. This has led some to conclude that genomic selection approaches are only likely to be successful in populations in which Ne is much reduced such as highly selected breeding sub-groups or seed orchards. [78]. This underlines the need for trials of material of known pedigree.

The availability of these molecular resources in oak also provides the opportunity to study the genetics of adaptive radiations and speciation as oaks belong to the order Fagales which consists of over 1055 species distributed across both hemispheres. Genome sequences for many of these species may facilitate the discovery of ecologically relevant genes harbouring alleles that are adaptive in some environments but not in others, and regulatory mechanisms underlying adaptive variation.

If Britain is to participate and benefit from these scientific developments in oak, particular genetic resources are required to advance these studies and to begin to harness the power of genomics. Thus, the following three kinds of material are required: i. pedigreed populations, particularly those based on open pollinated half-sib progenies and full-sib controlled crosses replicated across several contrasting sites; ii. replicated common garden trials containing a large number of British provenances as well as some from mainland Europe for which detailed environmental data are available; and iii. intensive study sites based on semi-natural populations of oak. Such material is available in other European countries, but Britain has not yet made the necessary investment to establish such well-designed long-term trials and other genetic resources such as controlled cross material. Much practical progress can be made by traditional breeding in undomesticated species and research funders have to make informed decisions that strike a balance between advancing academic understanding and providing practical solutions to current forestry problems.

Examples of studies which harness this novel genomic knowledge are provided below. These range from studies which examine differences in DNA sequence in genes of adaptive significance across clinal environmental gradients (genomics), to investigations into differences in gene expression either between oak species with different ecological requirements or between sample sets subjected to different stress treatments (transcriptomics). Advances in metabolomics i.e. the systematic study of the unique chemical fingerprints, in the form of small-molecule metabolite profiles that are left by specific cellular reactions may help to back up results from transcriptomics. These kinds of studies have started to appear in the last ten years and doubtless there will be many more in the future as our knowledge of the oak genome expands, costs of obtaining RNA and DNA sequence reduce and our ability to handle enormous data sets improves diversity in candidate genes.

Genomic studies are being used to understand the genetic basis of adaptive differences between populations. For example, a study [79] examined diversity in nine candidate genes for timing of bud burst in nine *Q. petraea* populations in central and northern Europe. The nine genes were selected on the basis of their expression profiles during the process of leaf flushing and their functional role in model plants. However, there was no population differentiation and none of the 125 single nucleotide polymorphisms (SNPs) departed from neutral expectation. This suggests that none of the polymorphisms in the studied genes conferred any selective advantage in any of the sites of origin.

SNP variation in phenology related genes has also been examined across an altitudinal gradient in populations of *Q. petraea* which showed a clinal pattern of bud burst when grown in common garden trials [80]. Clinal variations were found for six SNPs.

A recent paper [81] harnessed variation in 31 million SNPs to explore genome wide differences between four species of oaks with contrasting ecological preferences. They identified in the genomes widely distributed islands of high differentiation between the species which are considered to represent the loci that act as barriers to interspecific mating. The SNPs in the candidate genes in these islands that showed the highest degree of interspecific differentiation included several that differentiated the southern (*Q. pyrenaica* and *Q. pubescens*) from the northern species (*Q. petraea* and *Q. robur*). Four of the seven genes involved in the differentiation of these two pairs of species are known to be involved in drought tolerance or in lateral root growth, which is consistent with the higher drought tolerance of the *Q. pyrenaica*/*Q. pubescens* pair compared to the *Q. petraea*/*Q. robur* pair.

Gene expression studies

Molecular approaches based on transcriptome analysis now make it possible to study the short-term responses of organisms to their biotic [82] and abiotic environments [83] and to infer the role of genes involved in adaptation [84].

A study [85] explored the effect of waterlogging on *Q. robur* and *Q. petraea*, the former can withstand higher moisture content in the soil. Significant differences in gene expression between the two species were detected, suggesting species specific molecular strategies in their response to hypoxia. The ability of *Q. robur* to maintain glycolysis and fermentation under hypoxic conditions may contribute to its superior ability to tolerate waterlogging.

Another study [77] used a whole transcriptome approach to investigate the response to water stress in *Q. lobata*. They subjected trees from contrasting origins to drought and identified which genes are involved in the response to drought stress. They showed that of the 68,434 gene contigs that were studied, 52% were differentially expressed before compared to after drought. The study identified several novel genes that are candidates for involvement in local adaptation to drought.

Metabolomics

Combined transcriptomic and metabolomic/metaproteomic approaches have been used to study host microbiota interactions in AOD [86] and resistance of pedunculate oak to the herbivore, *Tortrix viridana* [87]. Trees showing symptoms of AOD differed in their transcripts to those which were asymptomatic (216 transcripts present in trees with symptoms that were absent in asymptomatic trees). Most of these transcripts (94%) were bacterial in origin some of which were involved in virulence. The remaining 6% were produced by the host and were involved in cell wall synthesis and plant defence. The metaproteomic analysis found several proteins that were present in tissues of symptomatic trees that were absent in asymptomatic ones. The analysis revealed an increased abundance of bacterial proteins and a host response, in AOD lesions.

It has been suggested that it might be possible to develop biomarkers (associated with a systemic alteration of stem phloem/sapwood metabolome) than could underpin a robust diagnostic test to identify accurately oak trees potentially susceptible to, or in the early stages of, different types of decline. This would enable breeding stock or, if the test was cheap enough, also planting stock, to be screened for resistance/susceptibility so that only those individuals with higher putative susceptibility could be discarded at an early stage of development.

A study [87] used a similar combined transcriptomic and metabolomic approach to look at differences between susceptible and resistant oak trees to the major oak pest, *T. viridiana*. During a severe attack of the pest in Germany heavily defoliated trees were classified as susceptible and those that were only slightly defoliated were classified as resistant. Both cohorts contained early and late flushing trees to reduce any confounding effect of host phenology. Hundreds of genes showed differential expression in resistant and susceptible oaks. Distinct differences were found in the transcript levels and metabolic content in terms of tannins, flavonoids and terpenoids which are all compounds involved in defence against insect pests. The results may facilitate the development of biomarkers for early identification of resistance to this pest in natural oak populations in Europe.

Epigenetics

The term epigenetics covers chemical modifications to the DNA that influence gene activity and gene expression but do not alter the genotype of the organism i.e. heritable alterations that are not due to changes in DNA sequence. These changes, which are often induced by environmental stress, can be passed on to the next generation in a process known as epigenetic evolution. DNA methylation is recognised as one of the prime epigenetic mechanisms and involves the addition of a methyl group to one of the four bases of the DNA molecule (usually cytosine). Cytosine methylation leads to gene silencing as methylated genes are not transcribed. The majority of epigenetic studies have been carried out on annual model species such as *Arabidopisis* and these have shown that levels of methylation at sites throughout the genome vary among individuals and populations [88, 89]. However, the role of DNA methylation in climate variation is of particular interest in non-model long lived tree species such as oaks because their long generation time may limit the ability of their populations to respond to rapid environmental changes through genetic mechanisms [90]. A recent study has examined the methylation levels of *Q. lobata* individuals collected from across the species range which includes sites with highly contrasting environmental conditions. The recent availability of the draft genome sequence for this species permitted the genetic context of the climate associated methylation variants to be identified to determine the potential genes that are involved in mediating the phenotype [90].

Development of genome wide association studies and genomic selection approaches

The advent of fast, inexpensive sequencing has opened the door to two new molecular breeding approaches which have revolutionised selection in animal breeding programmes such as cattle. Genome Wide Association Studies (GWAS) use dense marker data to examine variation across the entire genome in contrast to previous methods, that did not fulfil their initial promise, and which concentrated on a small number of pre-specified candidate genes. In GWAS, individuals are divided into two classes e.g. a diseased and a healthy group and large numbers of individuals from each class are used to provide enormous numbers of sequence reads distributed across the entire genome. These are then searched for SNP variants which consistently show different frequencies across the two sample classes. The results of such studies are used to indicate which areas of the genome are involved in the control of the trait of interest. Poor definition of the two classes of samples and insufficient sample size can be a problem in this approach.

The sequence data obtained in GWAS studies can also be used in another selection approach known as genomic selection (GS). This involves populating the genome with dense marker coverage and exploiting the associations between markers and phenotype to identify genetically superior individuals [91]. This approach is particularly valuable for selection of quantitative traits such as growth which are likely to be under the control of many genes. GS has revolutionised animal breeding and there has been increasing interest in its application amongst tree breeders [92, 93].

Genetics and Genomics in Acute Oak Decline

The above sections outline our current knowledge and the efforts being made to understand the underlying genetic control of various adaptive traits in oaks which may play a role in tree health. These are based on quantifiable traits tested in appropriate pedigrees of material. For example, drought or flooding susceptibility can be tested in half sib progenies of susceptible and resistant mother trees to assess the heritability of these traits. The situation is rather more complex for AOD for several reasons. Firstly, AOD as a trait does not usually express itself on younger trees but rather is more prevalent on trees that are mature and can also occur on trees of considerable age. Secondly, the full suite of factors that lead to the susceptibility of trees to AOD is not yet fully known, which makes it difficult to set up trials that test the susceptibility of individuals to the threat. It also hampers the ability to diagnose trees that are suffering from the decline with a high level of accuracy, and it is not known if the observed symptoms are due to a genetic predisposition to AOD or to one or several features of the environment that induce the symptoms. In other words, the heritability of AOD susceptibility is not yet known.

Richard Buggs and Richard Nichols have proposed to estimate the heritability of susceptibility to AOD using GWAS. This is a novel application of GWAS as this approach has normally been used to identify candidate genes for a trait that is already known to be heritable. However, simulations by Lewis Spurgin (presented at Population Genetic Group 2018) show that GWAS can predict heritability more accurately than it can predict candidate genes. A GWAS study typically needs over 2000 samples in order to be effective. Buggs and Nichols are therefore proposing to gather genome sequence information for many hundred oak trees, and each tree will be accurately phenotyped for its AOD status. If they find that AOD is heritable, they should also be able to make genomic predictions of trees with low susceptibility using their data at a young age.

Another approach might be to use physiological experiments to test whether the offspring of symptomatic and asymptomatic trees differ in their response to certain environmental variables, which might induce stress e.g. drought and/or cycles of drought. It would be informative to know if the progeny of symptomatic versus asymptomatic trees differ in their ability to tolerate such stresses. The testing of the response to stress in half-sib progeny of symptomatic versus asymptomatic mother trees would determine whether there is a genetic component to the response. Looking further into the future, if the GWAS approach could accurately identify young trees that will eventually go on to develop symptoms of AOD, these could form the basis of physiological trials to elucidate whether their response to stress has a role in determining the likelihood of developing AOD.

A comprehensive list of sites and individuals where AOD occurs along with assessment of a comprehensive set of environmental variables in the immediate location of the tree assessed according to a uniform protocol is required to underpin these genetic and physiological studies. A uniform protocol to provide an assessment of the severity of the symptoms of AOD in each tree is also required.

Assessment of knowledge and resources leading to recommendations

Conservation of forest genetic resources of oak

British populations of oak contain high levels of genetic diversity. Gene flow between woodlands is very effective and can occur across long distances. Despite effective geneflow, provenances of British oak show clinal latitudinal differences in valued traits such as height growth. Although Britain has established some provenance trials, there should be the establishment of well designed, multisite provenance trials composed of a wider range of British provenances. This would inform our understanding of the distribution of adaptive diversity in oaks across Britain and would also act as a research resource to harness developments in molecular approaches. Those that do exist have mostly only been assessed for height and there is the potential to assess traits such as timber quality, phenology and disease/pest resistance.

Britain represents the north-western extreme of oak distribution and as such, may contain valuable and unique adaptive variants that are worthy of conservation.

Recommendations

a. Identify and place more source identified oak stands in England and Wales on to the National Register to complement those added from Scotland and thereby address the shortage of locally sourced oak seed.

b. Consider whether there should be investment in additional field and controlled environment provenance trials which:

   i. Include a broader geographic range of UK provenances from benign and challenging locations as well a range of continental provenances for which there are good environmental data.

   ii. Are planted at a range of sites which include several northern sites as well as some in France at locations which most closely match the future predicted conditions for the southeast of England.

   iii. Retain traceability of seed from each provenance to the maternal family to which it belongs. This would permit much clearer understanding of the distribution of adaptive diversity within progenies and provenances to be achieved.

   iv. Assess traits that have greater adaptive significance such as phenology, disease resistance and drought tolerance in existing and new trials. Also consider establishing short term trials in controlled environments to test resistance to disease under ideal inoculation conditions. Retain traceability to mother trees so that seed can be collected from these if they show particular promise in terms of resistance of their progeny.

   v. Take into consideration the needs of molecular breeders and the pedigrees and range of material and trait assessments required to make best use of advances in new approaches such as GWAS and GS.

c. Establish Genetic Conservation Units so that changes in composition of oakwoods due to climate change and pest and disease outbreaks can be monitored using a universal set of criteria and compared to changes occurring in GCUs elsewhere in Europe. The development of an initiative to develop a UK Forest Geneitc Resources Strategy may help to coordinate conservation efforts in the UK and identify knowledge gaps and improve understanding of the importance of genetics in conservation.

d. Set up a programme of research to improve retention of vitality of acorns in store. Explore other approaches to conservation such as cryopreservation.

Tree Improvement

Britain does not have the long tradition of oak selection and improvement that has occurred in countries like France, Germany and the Netherlands and therefore this, combined with poor silviculture and general neglect, means that Britain does not have oakwoods of high timber quality similar to those found in continental Europe.

Development of vegetative propagation methods has met with rather variable success despite the desirability of being able to mass propagate superior material and to establish clonal seed orchards based on phenotypically superior material. There have been major advances in the understanding of molecular aspects of oak which include the development of a full genome sequence, several detailed molecular maps, gene expression studies in several species with and without the imposition of stress and differences in sequences of adaptively relevant genes in different oak species. These all aim to understand the molecular basis of the physiology and adaptation of oaks in different environments. These have yet to yield practical benefits to oak production, pest/disease resistance or conservation but progress is rapid and benefits should begin to emerge in the coming years. Oak is one of the model deciduous tree species for this type of work.

Recommendations

Funders need to be aware of the relative benefits, timescales and costs of traditional versus genomic breeding and selection approaches and reflect these in decisions on how scarce research funding is spent. Much could be gained by doing simple things such as establishing more *selected* and *source identified* seed stands, planting additional seed orchards and developing ways to bulk up the products of seed orchards to ensure that oak that is planted is well adapted and likely to produce higher quality timber. The following points are worth noting -:

a. If Britain is serious about improving the timber quality of its oaks it needs to invest more in the assessment of existing trials using new assessment techniques and consider the need to establish new sets of breeding trials. Commitment is required to guarantee the long-term maintenance and assessment of existing and planned trials. Short term funding is a major problem and puts existing resources at risk.

b. Predicted seed output of current seed orchards is unlikely to meet demand. Possible funding sources need to be explored. Consideration should be given to the wisdom of weeding out inferior families from the existing progeny trials that are intended to act as seed orchards. These trials, which are owned by the Future Trees Trust, could be useful in molecular studies where half sib families can be a valuable research resource, particularly if a novel pest or disease arrives. Half sib progeny trials of ash in Denmark were informative when ash dieback arrived. This potential function may be as valuable as that of a seed orchard which provides genetically superior seed. It may be useful to establish some full sib crosses as well to aid genomic studies.

c. Renewed efforts to improve propagation success might be worth investment so that products from seed orchards and other genetically superior material can be multiplied up for planting stock as well as to establish a research resource. Testing chemical and silvicultural approaches to increase flowering of superior material might also be worthwhile.

d. Molecular approaches offer huge potential in tree improvement and it is important for British scientists to keep abreast of development and to have the capacity to utilise these advances. However, molecular studies require appropriate material of known genetic pedigree which has been phenotyped for a range of traits. Traits with known significant heritability (such as a disease with a known causative organism that expresses itself in young oak trees and is amenable to experimentation) or a quantitative trait (such as timber quality that can be accurately assessed at a young age) would provide appropriate model systems in which to test these new molecular technologies and selection approaches. Pedigreed populations grown under multi-site trial conditions would be the most appropriate material for such studies.

e. Recent developments in molecular resources and in analytical approaches such as GWAS may offer a novel way to determine whether susceptibility to various pests and diseases such as AOD is heritable using existing trees which have been accurately phenotyped for symptoms. If susceptibility has a significant heritable component, there is then potential to breed less susceptible planting stock.

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Table 6.1 The main oak provenance trial series located in Britain and elsewhere along with details of the total number of provenances, number of British provenances, number of sites, site locations, traits assessed and main findings (Modified from original material prepared by Richard Whittet). Much more information is available for *Q. petraea* than for *Q. robur*. (Abbreviations SCO=Scotland, ENG=England, FRA=France)

STUDY	TOTAL NUMBER OF PROVENANCES	NUMBER PROVENANCES (GB)	NUMBER OF SITES	TRIAL COUNTRY	TRAITS	MAIN FINDINGS
Worrell (1992) ([94])	?	?	?	?	SURVIVAL HEIGHT (>10 yr) STEM FORM	• Few details of experiments provided • British provenances generally showed better growth • French provenances had better form
Deans and Harvey (1995) ([34])	16	1	1	SCO	HEIGHT (< 10 YR) SPRING PHEN AUTUMN PHENOLOGY	• Earlier flushing in southerly and low altitude provenances • Higher levels of frost damage of French provenances.
Deans and Harvey (1996) ([37])	16	1	1	SCO	ECOPHYSIOLOGY	• French, English and Austrian provenances more sensitive to artificially imposed low temperatures than German, Danish and Polish
Hubert (2005) (i) ([32])	13	4	5	SCO ENG	SURVIVAL HEIGHT (<10 yr) HEIGHT (>10 yr)	• Large absolute differences among provenances • Survival was so poor at a trial site in N Scotland that it had to be abandoned.Survival of continental provenances at that site was particularly poor (c. 5%). • Lower than average growth of northern material transferred south but survival was higher • In general, greatest height from *selected* British seed sources
Hubert (2005) (ii) ([32])	23	7	3	SCO ENG		
Earth Trust 2006	11	4	3	ENG	HEIGHT (<10 yr)	No published results but Dutch material was tallest (Jo Clark, pers. comm.)

Wilkinson *et al* (2016) (33)	19	4	1	ENG	SPRING PHENOLOGY	• Latitude linearly related to timing of bud burst. Southern provenances flush first. • Bud burst earlier in warmer years.
Sáenz-Romero *et al.* (2017) (95)	116	7	23	MAN Y	SURVIVAL HEIGHT (>10 yr)	• Generated transfer functions from very large dataset • Annual dryness index best predictor of survival • Survival expected to be highest in sites environmentally similar to seed source • Growing season dryness index best predictor of height growth • For height, site effect much larger (60%) than provenance effect (1.4%)
Ducousso *et al.* (1996) (96)	50	?	4	FRA	SPRING PHENOLOGY	• Earlier flushing in southern and low elevation provenances • Higher frost damage in earlier flushing provenances

Table 6.2 List of oak plus trees and their origin according to country and seed zone (from Hubert *et al.* 2010 (97))

Country	**Seed zone**	**Number of oak plus trees**
Scotland	105	0
Scotland	106	1
Scotland	107	1
Scotland	108	1
Scotland/ N England/	109	3
Scotland	201	3
Scotland	202	1
Scotland	203	10
Scotland/ N England	204	5
N England	301	2
N England	302	1
Wales and SW England	Rest of region 30	9
England	Region 40	122
Total		159

Table 6.3 List of trial sites along with the number of half-sib families, number of plants per family, total number of plants planted and number of plants remaining in 2007.

Trial site	No of half sib families	No of plants per family	No of plants planted	No of plants remaining in 2007
Belmont, Kent	34	70	2380	1445
Dalkeith, East Lothian	31	85	2635	2198
Northmoor Trust, Oxon	56	39	2184	1948
Newton Rigg, Cumbria	40	63	2520	1446
Sotterley, Suffolk	61	50	3050	2358
Shakenhurst, Worcestershire	21	100	2100	1979
County Cork, Ireland	46	48	2208	2106
Carmarthenshire, Wales	44	52	2288	1975

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7. Monitoring Oak Health

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Introduction and scope of chapter

Oak is the third most common broadleaf tree in Great Britain's woodland (after birch and hazel respectively) and one of the most common tree species amongst open grown trees[1–3]. Moreover, oaks are foundation species in many ecosystems, are associated with a rich biodiversity (see chapter 5) and provide a variety of ecosystem services. However, oak condition in the future is uncertain due to a variety of biotic and abiotic threats (see chapters 2, 3 & 4.).

We need to understand the current age structure of the oak population and how it is likely to change in future. Oak has been noted to have difficulty regenerating naturally in Britain [15,16], perhaps reflecting the historic influence of planting on its distribution [17,18]. Despite recent efforts to increase native woodland cover, the long-term viability of oak populations should not be taken for granted and monitoring is needed to document future changes.

Modelling studies suggest that future climate change impacts on oak growth will vary across the country [4–6], with areas of improved yield in the uplands, but worsening suitability in southern England. Empirical data are needed to assess the validity of these predictions and ensure that current trends are understood [7].

Trees are also facing ever increasing threats from individual pest and disease species [8,9], often due to introduced species [10], although a changing climate is also enabling endemic species to have increased impact [11,12] (see chapters 3 & 4). In this moving context, monitoring is an important first step in detecting problems and mitigating their impacts. For example, understanding how distributions of pests and diseases, dieback and tree recruitment change over time [13,14] can reveal possible causal mechanisms and enable mitigation measures to be planned.

In this chapter, oak health monitoring is considered under the broad categories of individual tree condition, age structure of the population, and surveillance efforts for specific pests and diseases. In addition, there needs to be consideration of how we monitor the broader oak ecosystem (including the microbiome within and on individual trees, through to composition of oak woodland at a landscape scale).

- The condition of individual trees reflects their ability assimilate carbon and grow, these measures represent the cumulative impact of abiotic environment (including climate, soils and between tree competition) and biotic agents [19]. Traditionally, the health of individual trees has been assessed during Forest Condition Monitoring programmes, using crown condition and changes in stem diameter [20,21].
- Oak health is a wider concern than the condition of individual trees, demography and wider population dynamics are also important. Assessments of age structure reveal the ability of oak to regenerate naturally. The effects of stand structure and species mix are likely to impact oak health and resilience in woodland. Long-term studies of oak populations at individual sites such as Lady Park Wood [22] and dendrochronological analysis can aid our understanding of the impact of extreme events on recruitment and growth. Wider scale monitoring is also needed to understand whether these sites are representative of the wider landscape.

- The final aspect of monitoring that will be considered in this review is the surveillance of specific pest and diseases [23]. Individual threats to oak are covered independently in preceding chapters so here we will focus on the mechanisms of monitoring and detecting their presence.

The review considers the types of data needed to investigate tree health; how future efforts can be linked to current and historic monitoring schemes; and the potential to incorporate recent technological advances, such as web-based reporting and remote sensing. The primary goal of the discussion is to identify "what is not known" and prioritise areas for future research efforts in monitoring methods and schemes.

This review focuses on national scale assessments, along with the role of unstructured survey information in disease detection and considers how such data contributes to our understanding of oak health. Twenty percent of tree cover across Great Britain is located outside woodland [24], as such, this review will not only include woodland monitoring schemes. However, silvicultural trials or detailed environmental monitoring (ICP level 2 plots or the Environmental Change Network) at a limited number of sites will not be considered as these are discussed elsewhere (see chapter 9 and 2 respectively). Current and future survey programmes documenting oak in Great Britain are outlined in Table 7.1 and discussed in detail below.

State of knowledge – UK

Individual trees

Until 2007 Forest Condition Monitoring occurred under the 'International Cooperative Programme on the Assessment and Monitoring of Air Pollution Effects on Forests' (ICP Forests) as part of a series of monitoring plots across Europe. The ICP selected sites on a 16 x 16 km grid, originally comprising 113,000 trees at 4,900 plots[25]. The ICP forest protocol formalised assessments of crown condition, growth (DBH) and many pest and disease symptoms [20]. Great Britain had 89 oak plots which were monitored annually by Forest Research from 1987 until 2007, and although no longer recorded 84 of these plots remain intact. No plots were located in Northern Ireland, where forest condition monitoring has not been conducted in the past.

Correlations between inter-annual fluctuations in the condition of oak and specific types of biotic damage were described in annual reports [26] with major fluctuations in oak crown density between years often caused by biotic factors such as defoliating insects. However, the longer term trend showed that oak has declined in condition, and that this was correlated with an increase in abiotic factors [25] such as annual potential evapotranspiration (PET), ozone levels and soil moisture deficit in March and July. Further analysis of longer term trends in these data are ongoing, with current Forest Research modelling projects investigating forest health in relation to climate, deposition and local land use[27] and change points between decline and recovery (Michal Petr, personal communication). The accuracy of predictions from this work cannot however be tested, as monitoring no longer takes place. This has led to a major gap in our understanding of Britain's trees.

The ICP forest protocol is still widely used across Europe (see below) and represents current best practice for visual assessment of crown condition. Consideration should be given to whether the programme should be revived and, if so, extended to cover non-woodland trees.

Non- woodland trees require special focus for many reasons, including:

1) those which occur in urban environments are especially likely to be exposed to new pests and disease due to human mediated plant and packing movements and higher levels of pollutants e.g. associated with traffic;
2) in agricultural settings, trees are more likely to suffer root damage and be exposed to high levels of chemical fertilizer;

3) in grazed environments, soil compaction will affect tree health.

Open grown oak occur in many diverse environments and as such, are likely to show more variability in their responses to a changing environment. However, understanding tree health in a variety of open-grown environments would greatly improve recommendations for management practice.

Whilst detailed investigations of crown health are no longer conducted, more general assessments documenting occurrences of severe dieback are included as part of the National Forest Inventory (NFI – discussed below), which also records diameters of individual trees across multiple time points. These data could be analysed to reveal environmental and site-specific differences that influence oak health.

Population composition

The Forestry Commission has monitored the composition of woodland across Great Britain throughout the last century, broadly charting change over time. The various census and inventory schemes have employed differing methodologies that make some precise comparisons difficult, but they can be used to reveal broad trends. These national surveys were conducted as single exercises every two decades by the Forestry Commission [28–30], with the last single survey being the National Inventory of Woodland and Trees (NIWT), which was completed in 1999 [31,32].

This has been replaced by the NFI, a rolling programme composed of 5-year survey and reporting cycles (phase 1 2009-2015; phase 2 2015-2020) comprising 15,000 randomly selected one-hectare plots across Great Britain. The NFI is a stratified random sample of all woodland larger than 0.5 ha, based on aerial photography and remote sensing techniques [33]. Selection of NFI sites was independent of NIWT and earlier censuses and used a revised protocol so only broad comparisons are possible. However, the NFI is now revisiting the same sites at 5 year intervals, so current and future change can be directly assessed (https://www.forestry.gov.uk/inventory).

Site surveyors collect a wide variety of information whilst on site including species composition, samples of individual tree sizes and ecological indicators. This data set should answer many questions about oak at the population level, and have already revealed that oak timber volume (though not necessarily quality) will increase greatly in the near future due to the large areas of planting and replanting after WWII [1]. A recent summary of NFI data has been produced for Action Oak [3], this shows that there are an estimated 170 million oaks in woodlands across Great Britain, 129 million of which are found in England. Across Great Britain woodland oaks account for 31 million tonnes of stored carbon, with approximately 0.5 million tonnes sequestered annually. The largest proportion of oak stocked area was occupied by trees in the 81 to 100 years age class, although the biggest contribution to the standing volume of oak is from much smaller trees (15 to 20 cm). Further analysis of the NFI datasets to address oak health issues is needed.

In addition to the NFI, there are a limited number of studies which describe oak populations at particular sites over time. The best documented individual site is Lady Park Wood in the Wye Valley [22], but comparable transect surveys have been carried out in other woods for example: in Langley Wood, Wiltshire [34], and on Clairinsh in Loch Lomond [35]. Further study plots have been assessed at four time points in Wytham woods since 1973 [15]. Changes in woodland composition, including the oak component, have been directly recorded across 103 semi-natural woodlands with surveys in 1971 and 2001 [15]. These studies show that while oak is common as an established tree, its abundance is declining in existing woods (in the smaller/younger size categories) and natural regeneration is rare (oak seedlings contribute less than 3.5% of total regeneration at Wytham).

In the future citizen science may also contribute to these assessments. For example, the MyForest tool, launched by Sylva in 2009, already allows stakeholders to document their woods, allowing them to produce maps and reports suitable for management plans and felling licences (https://sylva.org.uk/myforest). This service is already used by 4,601 woodland owners and 1,046 agents to manage 77,175 ha across Britain. If consistently implemented over time, such schemes may have the potential to contribute to wider population monitoring.

All monitoring discussed so far, excludes the 20% of Britain's tree cover which is open grown, or found in smaller groupings of trees and in hedgerows [24]. Assessments of non-woodland trees have, however, been undertaken as part of the Countryside Survey, an audit of the UK's natural resources. The Countryside Survey has been carried out at regular intervals since 1978. Information is recorded for 1km squares across GB using a stratified random sampling system (based on land classes which are comprised of the major national ecological gradients e.g. soils, geology and climate) [36]. This enables scaling up from samples to produce national estimates using the land classes. The last survey took place in 2007 when 591 1 km^2 grid squares were sampled.

The wide range of data collected gives a complete assessment of the environment, but the costs of this thorough assessment keep the sample sizes small and as a consequence estimates of sub-classes, such as trees outside woodlands, carry large standard errors. The survey reports include details of individual tree species and their size classes, so can be used to assess population level dynamics [2]. A recent summary of the CS2007 survey produced for Action Oak shows that the estimated area of Oak in small woodlands (smaller than 0.5ha, and therefore not included in the NFI) across Great Britain was 15,653 ha[2]. In addition, it was estimated that 2.3 million individual Oak trees (outside of woodland) were present, which makes oak the most common species recorded in the survey. Most of these trees were in England (1.9 million), with Scotland and Wales having relatively fewer numbers (114,000 and 238,000 respectively). Most individual Oak trees were between 75 cm and 1 m diameter at breast height (DBH), the second most common grouping was 21 to 50 cm, indicating more recent cohorts are also present in the population. In hedgerows oak was the second most common tree species (after ash). The proportion of linear feature plots (including hedgerows) occupied by oak increased between 1978 and 2007, but there was no significant trend for open area plots over the same period.

Citizen science programmes have set out to fill the gap in monitoring of trees outside woodlands by cataloguing tree locations, along with details such as species and size that allow the impact on ecosystem services and biodiversity to be quantified, for example: iTree [37],Treezilla [38] and the Woodland Trust's UK wide Ancient Tree Inventory. These programmes are especially suited to urban situations and high value parkland sites, but collaborations with established interest groups such the Tree Council's "Tree Wardens" (https://www.treecouncil.org.uk/Take-Part/Tree-Wardens) could enable assessments to take place more widely. iTree assessments have been conducted to assess tree cover in several UK cities, including Edinburgh and London [39,40]. In Northern Ireland, local council initiatives have also been undertaken programmes to map trees and document their condition. For example, the city of Belfast has mapped and recorded data on over 15,500 trees. In addition, the remote sensing project Bluesky, has developed a National Tree Map. This commercial mapping product uses a combination of aerial photography and lidar to identify all trees above 3m, but this does not have species specific information and trees within groups are not always distinguished.

At present funding bids are being prepared for a future round of Countryside Survey, but this is likely to exclude the tree component. Insufficient monitoring of health, condition and age structure of open grown trees and their associated ecosystems thus represents a major research gap.

Surveillance of pests and diseases

Statutory monitoring occurs for Oak Processionary Moth (OPM), which was discovered in the UK for the first time in 2006. It has since established in West London and Surrey (known as the core zone) and a management plan is in place for this pest. There are a number of monitoring and detection methods such as visual surveys or light or pheromone traps [41,42]. Monitoring and control by plant health professionals occurs at infested sites outside the core zone, but official field surveys do not take place outside these locations (OPM operational programme 2017/2018). New detections therefore require stakeholders and the public to be informed and vigilant. In 2017, there were 495 statutory plant health notices issued for OPM outside the core zone.

Detailed surveillance does not occur for other pests and diseases of oak, with the exception of specific research projects such as Acute Oak Decline (AOD) and location specific studies (e.g. pheromone trapping in vicinity of ports for bark beetles). The NFI is used to assess basic oak tree health (as part of the wider woodland population) and acts as a fallback by flagging up any unexpected changes in woodland composition.

Training materials have been designed to help with the identification of key pests and diseases. These are available to land owners and volunteers, who act informally as citizen scientists reporting unhealthy trees to Forest Research Tree Health Diagnostic and Advisory Service (THDAS), often through the Tree-alert website (www.forestry.gov.uk/treealert). The number of disease reports varies between years and focus of tree health concerns, although this likely reflects levels of publicity as much as the prevalence and extent of the affected area. For example, there were approximately 600 reports of oak decline issues between 1972 and 2017, but in contrast there have been 564 reports of AOD since 2006; and when ash dieback was first reported in the mainstream media, hundreds of reports were provided in a few months [89].

Forest Research and partners have also developed a programme of tree health training days and a network of regular volunteers through Observatree (www.observatree.org.uk) to encourage citizen science reporting. As well as collecting ad-hoc reports Observatree volunteers have been engaged in specific initiatives, including collecting samples of oak mildew when it first appeared on flag leaf shoots, during spring 2016-2017, so that species level identifications could take place. During this exercise, only *Erysiphe alphitoides* was detected.

The citizen science programmes have been very successful; for example, they resulted in the first detections of new outbreaks of chestnut gall wasp *Dryocosmus kuriphilus*. However, it is unclear what impact this unstructured sampling has on detection rates across the country, which makes estimating risk and analysing data difficult.

Monitoring of AOD has shown that surveys can be designed to incorporate citizen science discoveries and allow potential reporting biases to be estimated [43]. Further analyses of these data have shown that engaging stakeholders and landowners can ensure hard to reach locations on private land are assessed for disease [44], but analytical methods are required to optimise the use of such data, detect reporter bias and get the most information from this resource.

Monitoring biodiversity changes consequent on oak decline
There are no biodiversity monitoring systems focussed specifically on oak, or oak woodland, but more general monitoring at a variety of levels could be used to detect and follow changes associated with any significant decline in oak.

At the broadest level, the National Biodiversity Network records species distributions across Britain. Oak-associated species most at risk might be identified and changes in their occurrence flagged. The same might be done with other national surveys such as the annual Breeding Bird Surveys.

Results from repeat surveys of woodland such as the ‘Bunce’ set of 103 sites could be mined to see if any changes in ground flora can be related to change in the oak component of the sites.

Detailed surveys of individual sites with a high oak content such as Alice Holt (ECN network) and some National Nature Reserves where change is being monitored could also be used.

Technological Advances

Recent technological advances allow tree condition to be measured consistently using reflection spectra. The condition of plants is reflected in the concentration of chlorophyll within their leaves. Non-invasive light meters can be clipped on to leaves to quickly measure "Chlorophyll fluorescence" [45]. These methods have been used successfully to assess photosynthetic activity in young oak (*Q. pubescens*) subjected to experimental drought; however, this required measurements of mature fully sun exposed leaves[46] and for most forest situations this would be impractical, requiring readings to be taken from the top of the crown.

Similar assessments could be made using remote sensing images, which can be used to identify vegetation stress caused by pest or disease [47]; offer economical means to study vegetation health [48]; and detect host species to aid ground inspections [49,50]. At present, remotely sensed health assessments can be implemented by examining changes between time points [14,51], but ground survey is needed to investigate and confirm species affected and causes of change [52]. However, new methods and improved resolution imagery are becoming available and may contribute to greatly improved assessments.

A first challenge to monitoring oak health remotely is developing methods to identify individual tree species. This has been difficult due to low spatial resolution of freely available satellite imagery [53], although the acquisition of high resolution images has now made this possible [54]. Single date high-resolution (8-band WorldView-2) imagery has been used to identify 10 tree species, including *Quercus robur*, with an accuracy of 85.4% [55]. A similar study used a drone to collect time series imagery to identify tree species including English oak (*Q. robur*) [54]. The study found that data collected at various times of year led to considerably improved accuracies. The accuracies achieved in these studies show promise, but there remains much room for improvement before they can reliably inform condition monitoring. Distinctions between *Q. robur* and *Q. petraea* are likely to be especially challenging if required. Fera Science Ltd are actively researching this area in the UK, assessing the potential for drone collected images to identify tree species [56]. All the studies discussed above have used limited test locations and it is likely that differences in phenotype and growth across national scales may complicate the process of extrapolating findings. To best achieve species identification at the landscape and national scales will require large quantities of field data to train algorithms and verify findings.

Remote sensing technology has been used to identify the impact and extent of different plant health diseases affecting oak:

- High resolution (1m) four band aerial imagery has been used to calculate Normalised Difference Vegetation Indexes (NDVI) to identify, count and map the number of dead and dying oak trees at Californian *Phytophthora ramorum* outbreak areas [57].

- AOD affected trees have been assessed on the ground for water content, fluorescence and with hyperspectral drone imagery as part of the PuRPOSE project, preliminary results suggesting affected trees have lower water content and subtle differences in reflectance spectra[58].

- A drone with a very high-resolution CIR sensor (2 cm) was able to identify oak trees (*Quercus sp.*) heavily infested with *Agrilus biguttatus* (exit holes visible) in Germany [59]. Here, resolution is important as individual trees can have healthy, infested and dead branches at the same time. Satellite imagery would not be able to achieve this level of detail. However, a large-scale study with drones would be impractical due to short operation times and flight ranges [59].

Where trees (and crops) are planted in monocultures remote sensing for disease is already a powerful tool. Recent studies of olive groves infected with *Xylella fastidiosa* have shown that not only can poor health be detected, but specific disease signatures are present and these can even identify non-symptomatic infections [60]. Technological advances also allow relationships between disease occurrence and spatial variables to be better understood. Machine learning can investigate patterns at known sites and predict occurrence across the wider landscape [61]. These methods allow the integration of large numbers of environmental parameters which are used to learn the relevant factors that explain the presence of disease.

The potential for field data from existing monitoring networks (such as the NFI) to act as validation samples for remote-sensing and machine learning projects should be explored, albeit there may be sensitivities due to the confidentiality of the plot locations.

A further technological advance that is worthy of inclusion involves the use of smart sensors. These devices could be placed on trees and left to automatically collect data and transmit it back to managers and researchers, without the need for repeated trips to sites of interest. Existing examples include Smart Forests in the USA (https://smartforests.org/), which allows weather stations to upload environmental data, and cameras placed in UK oak forests to document phenology [62]. Soon the scale of infrastructure required will be reduced with sensors able to upload data through mobile phone signals. These products are already being trialed with projects including automated dendrometers (https://business.esa.int/projects/iotrees) and environmental sensors that can detect forest fires (http://internetoftrees.io). Finally, a study in France used Google street view to identify areas that may be infested with the pine processionary moth [63]. Given the similarities with OPM and the noticeable symptoms of AOD, this method may be useful for directing surveyors to areas of interest.

State of knowledge – internationally

Forest condition monitoring continues across Europe, as part of ICP forests programme. To date there are over 240 peer reviewed publications listed as outputs on their web page (http://icp-forests.net). The continuity and consistency of monitoring is ideal for analysis of correlations with environmental variables and prediction of future trends (for example [64]). In 2014, the crown condition was assessed for 104,994 trees in 5,611 transnational Level I plots (across 24 participating countries). Of the main tree species and tree species groups, deciduous temperate oaks (*Q. petraea* and *Q. robur*) had the highest mean defoliation (25.2%) as well as the highest proportion of severely damaged trees and dead trees [21]. Data from ICP forests monitoring plots have been used to assess the interaction between Xylophage insects and declining oak in Spain [65], revealing the influence of climate change on this carefully balanced system.

In the USA, forest composition surveys began in 1928 and since then the USDA has conducted periodic inventories of forested land. Until 1998, each state had independent surveys, with cycles ranging from 7 to 15 years [66]. Since 1996 the Enhanced Forest Inventory and Analysis (FIA) established new plots based on 6000 ha hexagon grid (each hexagon contains a randomly located four-location cluster plot), with approximately 1 in 24 also having Forest Health Monitoring (FHM) designed to detect and evaluate environmental change [67]. Since 1980, crown condition assessments similar to those of ICP forests have been conducted and these are now integrated with the main FIA survey [68,69]. Since 1999 the FIA ensured that all states sampled some plots every year and reported a full dataset every 5 years [70].

The long term nature of FIA monitoring and its consistent data collection make possible many complex analyses such as investigating relationships between mortality and crown condition [71]. When new pest and disease issues arise FIA data can be used to quickly assess the large scale impacts [72,73]. Perhaps most promisingly these data have been used to suggest optimal management approaches to improve forest health under climate change[74]. The extended time period of consistent data collection has enabled many recent analyses, highlighting the importance of long-term monitoring and how an established resource can be applied to current and novel questions. The NFI is now producing a similar dataset so with time should prove equally valuable, provided the commitment to the future rolling survey programme is maintained.

In France, a specific agency dedicated to Forest Health, the "Département de la Santé des Forêts" (DSF), was created in 1989 (http://agriculture.gouv.fr/le-departement-de-la-sante-des-forets-role-et-missions). The DSF has three main activities: forest health monitoring (including 557 ICP forests sites), diagnosis of forestry problems, and assistance and advice to managers and owners. The DSF employs professional surveyors and in addition coordinates a network of "correspondent observers" who belong to various public and private forest organizations. These individuals collect specific field data following training by the DSF. Forest health monitoring collects details of specific damaging organisms through a general forest health watch and the surveillance of the regulated and emerging organisms. The DSF is a successful example of a public-private partnership that enables 16 million hectares of forest to be monitored, with the help of 230 correspondent-observers. Of the 10,000 observations received per year 1,700 identified problems on oak. Across almost 30 years more than 100 000 records have been collected, these have been used in many epidemiological studies, in particular for modelling potential impacts of climate change on disease distributions [75–78].

Surveillance for forest pests and diseases is often targeted to particular outbreaks, with detection linked to an eradication programme; for example, *P. ramorum* and huanglongbing (or yellow dragon disease) in the USA [23,79–81]. Detection in these cases may involve ground surveys, aerial assessments[52], insect trapping [82], or often a combination of all three. Sampling strategies can be designed to detect spread to new locations[83,84] and sampling effort can be optimised to ensure the probability of detection is within levels of risk chosen by policy makers [61,85,86].

Citizen science is used to increase the probability of ground-based detection. For example, in the USA *P. ramorum* is regularly monitored through a SODblitz program [87] in which organisers select locations for volunteers to assess, helping to control for reporter biases and capturing reporting of locations where disease is not detected. By adding structure to the volunteer efforts sampling effort is quantified, which aids analysis. This process does, however, ask more of the volunteers and may reduce the pool of individuals willing to participate.

In Australia, the issue of reporter bias has been addressed without limiting how and where volunteers can contribute to bird surveys [88]. Here, volunteer data from previous years are used to estimate the probability of locations being visited by the public and paid surveyors are directed to the areas that are most likely to go unreported. This adaptive method could work well for tree health issues. The ability to estimate bias would be greatly improved in situations where records from professional surveyors can be directly compared with those from volunteers.

Assessment of knowledge

The most complete dataset describing oak in Great Britain is collected by the NFI. Although, the main goals of the survey are centred on describing woodland composition, as well as future timber and carbon storage, the field data contains many attributes relevant to oak health such as growth and signs of crown dieback. Specific pests and diseases are recorded when noticed but currently oak decline agents are not explicitly documented.

The process of exploring NFI data has begun with assessments prepared for Action Oak. This has highlighted many further analyses could be conducted, especially once the second cycle is complete and changes can be described. In particular, data could be analysed to reveal important trends about oak health; general symptoms such as presence of extensive crown dieback could enable powerful analyses given the number of sites assessed in the survey.

Examples from France and the USA illustrate that having accurate baseline data available enables the impact of new threats to be quickly described. In addition, consistent long-term datasets allow tree responses to environmental change to be documented under a range of management regimes. NFI work is funded only though the current 5-year cycle, but it is well established that its value will only improve with continued monitoring.

Historical data from the FCS are still being analysed; statistical and computational methods have improved since monitoring ended, so data can be explored in new ways. FCS sites could be revisited, but it would be important to understand their representativeness and whether sites selected for past environmental conditions remain important for assessment of future threats.

There is currently no ongoing programme of tree health monitoring. A decision needs to be made regarding whether to revive the long running FCS monitoring project or whether a revised sampling design would offer even greater insights in the future. Sampling designs should be optimised to make best use of resources so that the correct balance is found between number of trees per site, number of sites visited and the frequency of monitoring.

Oak trees grown in more open conditions are poorly documented even though useful summaries have been extracted from the last round of Countryside Survey. Non-woodland trees require special focus as they occur in a wide range of situations and these factors complicate health studies. Oak is very common in the wider landscape and it is likely that understanding connectivity will have large impacts on both biodiversity assessments and predicting the spread of pests and diseases. Principles of organism movement through landscapes are well established, but analysis at national scale can only be described as speculative as species specific data are simply not available. Importantly, an improved understanding of how tree health is impacted in open grown locations would greatly improve recommendations for management practice.

A baseline assessment would be impractical for a single tree species. It makes more sense logistically and because of the range of other species also subject to disease threats, notably ash, to take a census approach and document all species. Although there are possibilities for citizen science to play a role in collecting oak specific information, extra care would be needed to ensure both native species are distinguished. At present, there are plans to monitor open grown trees, but no funded projects (Table 7.1).

Remote sensing has an important role in the future for health and disturbance monitoring. There are well established methods to compare images between time points and make use of field survey to investigate site specific causes. There is promise in new methods to identify tree species and assess condition, but there are competing explanations for how best to proceed. There is a trade-off between high resolution images, best collected locally, and the ability to extrapolate accurately at the national scale as local phenotypic and growth differences may confuse assessments of species or health. Large-scale assessments from satellite images are possible if enough field data are available. Both approaches require high image resolution and the availability of accurate field data. Further research is required before species-specific condition monitoring can be achieved from the air. For both local scale (drone) and broad scale (satellite) approaches, the use of existing field data could greatly reduce the costs involved in developing novel remote sensing methods.

Detailed knowledge of pest and disease distributions can inform our understanding of the epidemiology of outbreaks and enable targeted intervention and control. In the UK, such data have been collected but only in relation to statutory issues (OPM) or specific research projects (AOD). Similar information for a wider range of oak decline agents would be desirable, especially as combined survey efforts are likely to aid interpretation of citizen science data.

Citizen science could play an important role in collecting oak distribution data, if targeted training materials covering a wider range of pests and diseases were available. Forest Research has well established mechanisms for collecting pest and disease reports. Although analysis of unstructured survey data requires further development there are several context specific methodologies that could form the basis of future research projects. Improved data regarding citizen scientist activity would enable better assessment of biases in coverage; in addition, a positive sighting for one issue becomes a negative report for all others. This latter point would vastly increase the data available for all analyses and improve the analysis options.

Summary and priorities for new knowledge from review

Future work can be split into two broad topics: getting the most information from currently available data and collecting new survey data from the field.

Information on the distribution and demographics of open grown trees is lacking. Population dynamics are likely to differ regionally and may not be reflected in adjacent woodland [17]. This population level demography would be needed to select a representative sample for tree condition monitoring, although local comparisons could be conducted without this step. Having more information on the distribution of open grown trees would enable much novel research, including landscape scale assessments of connectivity and disease spread.

The NFI dataset offers further information that will be of great benefit to analyses of woodland ecology and tree health: future outputs could be improved with increased analysis and interpretation of the results and release of the findings into the public domain. Through continuation of the established composition monitoring in forests, the value of the NFI will increase with each cycle of new data.

The health of oak trees should be monitored, ideally aligned with international programmes. The assessment of crown condition is widely undertaken globally and is often used to understand environmental change. If the ICP monitoring scheme was resumed the analysis of long-term trends could begin immediately using historic data. Questions surrounding oak health can also be addressed using NFI information such as variations in growth, observations of tree death and signs of crown dieback. These general assessments could be improved in future by expanding the information and training available to surveyors regarding specific oak pests and diseases. There is also the potential to include crown condition assessments; the ICP protocol was designed to take 8 minutes per tree[20]. Consideration should be given to decide sample sizes (what would be necessary for later analyses in terms of both number of trees and number of sites to collect this additional information) and the impact of only having assessments intermittently as part of a rolling programme.

Citizen science programmes have proved very effective for first detection of pests and diseases in new areas, but more consideration needs to be given to how can we best use these data quantitively? Specifically, more research is needed on how these data can be used to improve assessments of risk, predict affected areas and develop management advice.

Increased monitoring for oak decline agents in both open grown and forest situations should be undertaken and reports from citizen scientists and landowners encouraged through the production of identification guides. Epidemiological approaches have helped develop our understanding of many pest and diseases, but these can only be applied to a wider suite of oak decline agents when sufficient information is available. Many of the biotic agents involved in oak decline are not introduced species and therefore not highlighted in existing monitoring programs.

Remote sensing shows promise for monitoring, but further research is required before this can comprise a core element of health monitoring. Field monitoring sites should be made available to enable ground truthing of techniques and remote sensed imagery.

Monitoring of oak and oak woodland should be fully integrated with that of trees and woodland more generally so that the information collected can be applied to the next tree species that comes under threat.

Sources

All sources are cited in the main text.

Figure 7.1 Distribution of historic (1987-2007) Forest Condition Survey (FCS) oak plots and their status in 2018. 84 sites have been revisited and monitoring could continue at these sites.

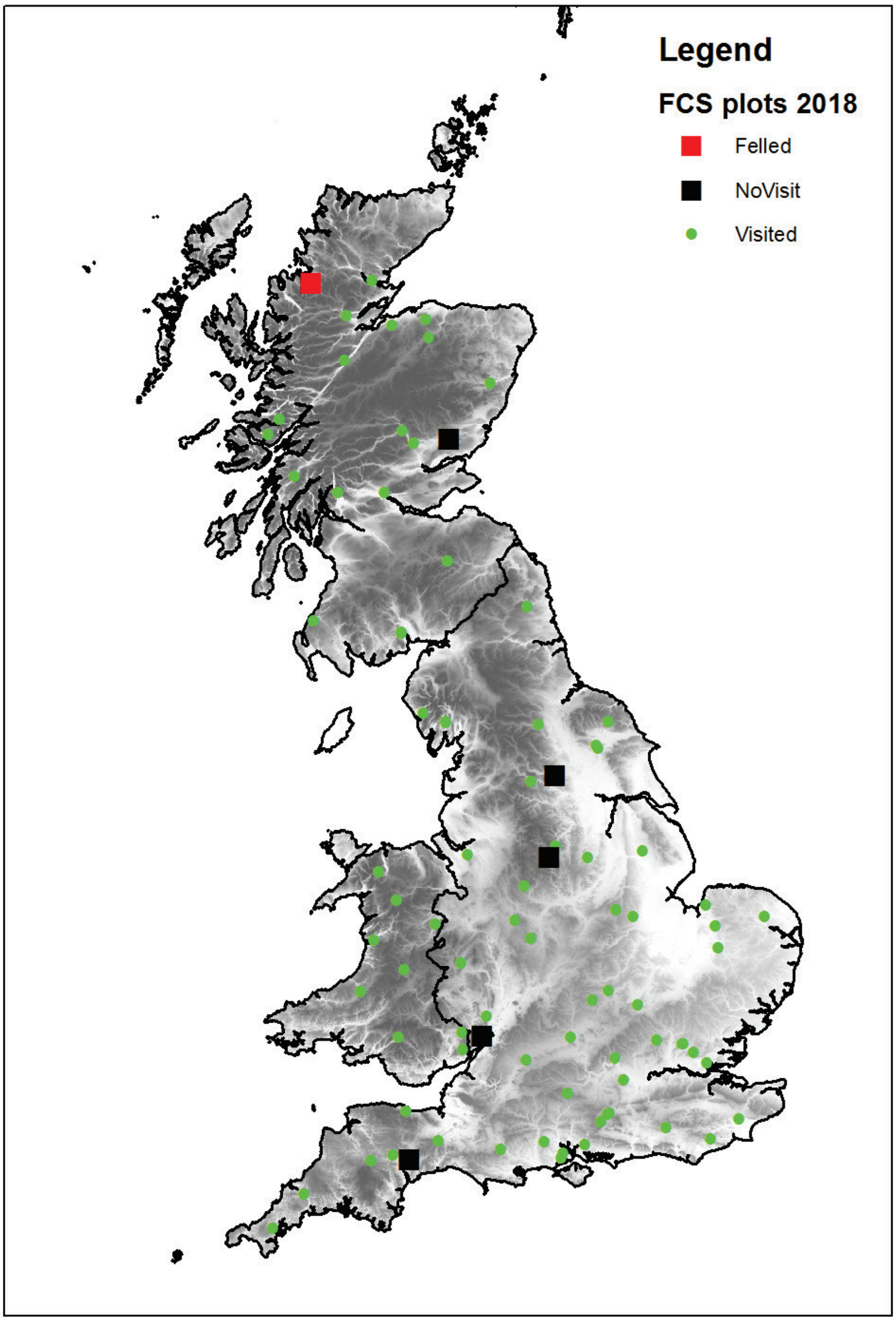

Table 7.1 Summary of available survey information. Green boxes show available data/ funded future surveys; Orange boxes show potential availability with further analysis or survey; Red boxes show not available with current data / survey protocols.

Survey	**Scale**	**Historic information**	**Current information**	**Future surveys**	**Comments**
NFI woodland area	National				Woodland maps produced annually in the same format since 2010.
	Regional				
	Local				
NFI woodland composition	National				The NFI is funded until the end of the current 5-year cycle.
	Regional				
	Local				
Countryside Survey	National			?	The country side survey was conducted in 1978, 1990, 2000, 2007 and could be repeated.
	Regional			?	
	Local				
NFI non-woodland tree cover	National				A tree cover map was produced in 2017 and is currently being refined.
	Regional				
	Local				
NFI non-woodland composition	National				A survey comparable NFI has been designed but no field work is yet funded.
	Regional				
	Local				
FCS canopy condition	National				84 oak survey sites could be re-established.
	Regional				
	Local				
AOD	National				Landowner data available since 2006. Surveys in 2013-2014
	Regional				
	Local				
OPM	National				Arrived in 2006. Distribution monitored.
	Regional				
	Local				
Other P & D	National				Only occasional ad-hoc reports and monitored as part of FCS.
	Regional				
	Local				

Table 7.2 Summary of priority research areas currently being investigated for Action Oak.

Topic	Description	Findings
Woodland oak	Summarise available information on oak composition, decline and growth using NFI data.	Oak is the 3rd most common broadleaf tree (after birch and hazel), and the standing volume is predicted to increase due to planting efforts since WWII. Reports of decline are regionally clustered across Great Britain.
Non-woodland oak	Summarise available information on oak abundance from Countryside Survey 2007	Oak is the most abundant individual tree and second most abundant hedgerow tree. The proportion of oak in hedgerows is increasing over time.
Forest condition plots	Assess the viability of using historic FCS plots, collect field data on woodland composition and assess landscape representativeness using GIS	Plots are not distributed randomly across the country, but clusters of plots are located in areas with high broadleaf tree cover. Plots are dominated by mature oak with little regeneration. Plots are representative of many environmental variables, but have high SOX and low NHX inputs. Plots are located in large woodlands and forests.
Sampling strategy for FCS	Statistical analysis to optimise survey effort. Power analysis using historical data - How many Trees/Plots/Time points to sample?	There are many combinations of survey design that could detect similar national scale trends. Sample frequency is most important, with annual or bi-annual visits required.
Remote Sensing	Review of current and future capabilities.	Species identifications can be achieved with moderate accuracy at present, but many projects are working on improving accuracies at present. Analysis is dependent on high resolution imagery and (ideally large amounts of) accurate field data.

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8. Land managers and publics: knowledge, attitudes and actions associated with threats to oak trees

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Introduction and scope of chapter

The Action Oak initiative, to which this Knowledge Review contributes, is focused on building oak resilience via targeted interdisciplinary research and a structured programme of research-based knowledge exchange and engagement with a broad range of stakeholders to ensure that scientific outputs are applied 'on the ground'. This chapter directly addresses the need for this structured approach to knowledge exchange and engagement and presents the state of the art in relation to five review topics and associated review questions – see Text box 1; in doing so it directly addresses the society and management/policy elements of the Knowledge Review conceptual framework (see Figure 1.1)

Text box 1: Review topics and associated questions

Topic 1: Values, attitudes and perceptions of risk – how do people value oak trees and what do they think about threats to Oak?
Topic 2: Knowledge – what do people know about threats to Oak trees?
Topic 3: Behaviours – what actions do people carry out to address these threats?
Topic 4: Enablers and barriers – what motivates or enables people's actions, and what are the barriers to taking action?
Topic 5: The role of science - What evidence is there of management for oak resilience being informed by scientific knowledge about threats to oak health?

The order in which these topics and questions are presented is based on the (social) science of human behaviour: People's actions and behaviours are underpinned by their values, beliefs and attitudes (Topic 1). In turn, knowledge (Topic 2) can inform and direct behaviours and actions (Topic 3), and can also be facilitated or constrained by institutional, social, economic or technical barriers or enablers (Topic 4). Scientific knowledge provides one representation of a barrier or enabler to action that is of particular interest to initiatives such as Action Oak (Topic 5).

This chapter combines multiple sources, including a literature review, discussions with relevant contacts and informants, and draws on expert knowledge from lead and contributing authors. Key search terms for the literature review based on the topics and questions set out above were agreed by the review team. Search strings were developed and used in Scopus and Science Direct. Google Scholar was also searched. An example of a search string (for Topic 2) is provided in Text box 2, below.

Text box 2: Search string for Topic 2 - Knowledge of threats to Oak health

(Public OR People OR Resident OR Household* OR Citizen OR Stakeholder OR Landowner OR “Land Manager” OR Soci* OR Volunteer OR Scientist OR Communit*) AND (“Oak Tree” OR “Oak Woodland” OR “Oak Forest”) AND (Disease OR Pest OR “Tree health” OR Invasive OR Threat OR Alien or “Non-native”) AND (Knowledge OR Understand* OR Awareness)

Four principal stakeholder types and groups are covered under each topic, including: 1) The general public (*i.e.* people with low levels of knowledge and engagement with oak / tree health issues); 2) Informed publics (*i.e.* those who are more knowledgeable and / or who take action, for example as citizen scientists, or volunteers involved in management and conservation activities); 3) Land owners and managers (including private and public land, and land owned by third sector organisations); and 4) Forestry, policy and research professionals with a stake in oak and tree health. Search terms were derived to cover each stakeholder type (see examples in text box 2).

We adopted a phased approach to the completion of the knowledge review for this chapter. Phase 1 targeted knowledge and evidence specifically focused on oak and oak health from the United Kingdom (UK) and internationally using the search strings described above. This resulted in 1463 hits; to make the review process manageable we sorted by relevance and extracted only the first 50 hits where individual searches yielded more than this. This extracted 360 titles and abstracts and, after screening for relevance, 36 papers and reports were used in the review.

Working on the assumption that useful insights could be drawn from evidence not specifically related to oak, Phase 2 broadened the scope to include other (non-oak) tree species and tree health more generally, as well as broader values related to trees. We drew on expert knowledge from the lead and contributing authors and also compiled a list of key references known to the team. A further 32 papers and reports were identified through this process.

State of knowledge – UK

Oak specific

Here we present a summary of UK-based oak specific and non-oak specific evidence related to the five review topics. The oak specific evidence comes largely from recent studies concerning Oak Processionary Moth.

Topic 1 - Values, attitudes and perceptions of risk

Recent work by Defra has estimated the social and environmental value of oak at £280m per year, though this excludes many important aspects of value, including physical and mental wellbeing, and cultural, symbolic and education benefits[1]. The social and environmental value of oak forest/woodland in Great Britain is estimated by apportioning oaks as 7% forest/ woodland proportion of an overall £4bn estimated annual value of forestry/woodland (based on Willis *et al.* 2003 with a number of updates since), reflecting recreation, landscape, carbon sequestration, air pollution absorption and elements of biodiversity value. This estimate of value will exclude many important aspects that cannot easily be monetised (including water quality/availability, noise, flood and heat reduction, physical and mental wellbeing, and cultural, symbolic education benefits).

Qualitative research in England has shown that oak is valued as a symbol of British life, with specific reference made to oak as an historic ship building material[2]. In this study, reference was also made to oak trees in folklore, art and literature through, for example, discussion of Sherwood Forest, the Major Oak, and associated stories of Robin Hood. The recent rise in popularity of tree books with high quality photographs also indicates the iconic value of British oaks and their role in shaping perceptions of the British and English landscape. Within this literature there is a particular focus on individual ancient and veteran oak trees, highlighting that Britain has recorded more of these trees than all other European countries combined due to a variety of historical reasons[3,4,5]. In the UK over 49,000 ancient, veteran and notable oak trees have been recorded in the Ancient Tree Inventory[5,6]. This helps demonstrate the high value associated with trees outside of woodland and single trees.

Despite the relative paucity of evidence related to the values which people attach to oak *per se*, it is our strong opinion that the more extensive evidence base related to the value of UK trees, woods and forests in general (see ‘non oak specific’ sub-chapter below) should be considered relevant. This position is strengthened by the knowledge that oak is one of the most commonly occurring broadleaved species in Great Britain (accounting for 16 per cent of stocked broadleaf woodland) and the most common broadleaved species in woodlands in England (19 per cent)[7].

Recent research with landowners in London is showing that oak trees are highly valued, and this high value attachment shapes attitudes to the control of one notable pest, oak processionary moth (OPM) *Thaumetopoea processionea* [8]. Public attitudes to the control of oak pests have been found to be dependent upon the perceptions of the risks associated with the pest in question (this relates specifically to OPM)[9]. Similarly, expert risk perception (in this case also related to OPM) is influenced and mediated by professional role and organisational affiliation[10]. A recent study investigated resident and stakeholder attitudes and identified different narratives about OPM and tree pests and diseases. The stakeholders included professional and private land managers, householders, managers of other public sites, third sector employees, and tree management professionals. Some participants were of the view that better biosecurity was needed, others believed the presence of OPM should be accepted, others still had a somewhat laissez-faire attitude towards the tree pest, and an additional view showed a strong level of concern about the human health impacts of OPM[11].

Topic 2 - Knowledge

There is a relatively strong evidence base demonstrating that public knowledge of threats to oak health is low[12,9,13]. Levels of knowledge and awareness of OPM varies across land owners and managers and this variation is related to land ownership type[8]. For example, knowledge amongst private residential owners is much lower than amongst public land owners who have a duty of care to visitors.

Topic 3 - Behaviours

The management of OPM by land owners and managers will be influenced by the broader management objectives of a given site; for example, owners are more likely to manage OPM if public access is a priority management objective[8].

Topic 4 - Barriers and enablers

Research on OPM with landowners in London is showing that lack of knowledge, low levels of awareness, and uncertainty about the pest and the risks posed can all be barriers to action[8]. The costs associated with controlling pests and diseases can also be a barrier for land managers[8,14], and landowners indicate that the availability of public funding for control has a strong influence on whether action is taken[14]. Action can also be discouraged by lack of clarity over who has statutory responsibility for urban trees[15]. The lack of coordination between landowners within specific locations can also be a significant barrier because it raises concerns that control effort by one landowner will be wasted if inaction by neighbours results in the re-infestation of treated sites and trees[15].

Topic 5 - The role of science

No evidence found.

UK – Not oak specific

Topic 1 - Values, attitudes and perceptions of risk

A large body of literature provides evidence of the high value of trees, woods and forests to society. This evidence does not attribute values to individual tree species, rather it provides broader statements about the values that people attach to variety and complexity in wooded landscapes[16,17,18], and the wide range of values and wellbeing benefits associated with trees and woodlands in general[19]. Studies suggest people value particular attributes or services provided by woodlands, for example:

- Woodlands can provide diverse groups of people with physical and mental wellbeing benefits, social connections, a feeling of escape and freedom, connections to nature, learning and skills development opportunities, and are places that can provide fun and enjoyment[20,21 ,22 ,23 ,24 ,25 ,26 ,27 ,28,29];
- Woodlands engender feelings of security, shelter and screening from others or the built environment;
- Old trees and woods can provide people with a sense of history and continuity as well as create a sense of place and natural grandeur, and can be symbolic as markers of time with their longevity seen as a mark of strength and resilience[30];
- Individual veteran trees can be seen as charismatic and provide visible connections for people to natural and seasonal cycles, further highlighting how important trees outside of woodland are to people;
- Qualitative research in England also suggests that people often find woodlands atmospheric and immersive due to their impact on a number of the senses[31].

The proposed ‘sell off’ of the public forest estate in England in 2011 and the resulting protests in forests and across social media also highlight that many feel a strong connection to woodlands, that may only be articulated with concerns that access to woodlands may be under threat[32].

A review of ecosystem service benefits delivered by urban forests[33] has helped to highlight the importance of trees outside of woodland. By linking ecosystem service delivery to the different scale components of the urban forest the review was able to demonstrate that single trees and lines of trees along streets and waterways, as well as small clusters of trees, are all important. Benefits included the provision of food (fruit, nuts, berries) and woodfuel, as well as carbon storage, temperature regulation, aesthetics, nature and landscape connections, noise mitigation, health and wellbeing, and social development and connections.

Research has shown that the public generally express high levels of concern about the threats posed to trees from introduced pests, even for those respondents whose knowledge is low[34]. Levels of concern about different pests and diseases can vary across demographic categories (e.g. older rural residents are more concerned than younger urban residents)[35]. Knowledge of health threats to trees affects people’s attitudes. For example, providing additional information about pests and diseases has been shown to affect public attitudes to tree health and, in particular, to the way in which they express the values associated with different threatened tree species[36]. A UK study of the general public used a choice experiment to assess preferences and willingness to pay for forest disease control methods. The study found that disease control programmes in publicly funded forests or those run by charities were more likely to gain support than those in privately owned or commercial forests. Respondents with higher income, greater knowledge of tree diseases who were more frequent visitors to forests had a greater willingness to support publicly funded tree disease control programmes[37]. Research with woodland managers has revealed the high level of concern about threats to tree health, with many agreeing that the impacts of pests and diseases will be large; the associated negative impacts on their organisations and businesses, included financial impacts, increased workload, loss of timber supplies and a reduction in amenity value of woodlands[38].

Public attitudes to control methods are linked to perceptions of risk of the pest/disease in question and can vary between control methods[39]. This reflects a tension within attitudes to disease control between perception of benefits through avoided losses (i.e. trees are not lost) and risks associated with control (e.g. due to use of chemicals), and perception of the risks and losses associated with doing nothing. This becomes particularly important when the public are aware of the risks of loss associated with control measures, such as through negative impacts on wildlife or aesthetics[40]. A recent survey has revealed that a high proportion of forestry professionals and woodland owners think the control of pathogens and pests is the most important issue for the future resilience of British woodlands[41].

Topic 2 - Knowledge
Research has shown that public knowledge and awareness of threats to tree health varies between pests/diseases. Some 'high profile' examples, such as ash dieback and Dutch elm disease are associated with high levels of public awareness, but more generally public awareness is low[34,36,42,35]. Research suggests that people are aware of Dutch elm disease in part due to the scale of the disease with 30 million trees lost and profound changes to the lowland landscape of the UK[43,44]. The intense media response to ash dieback in 2012 led to the social amplification of risk; it became part of a public debate, in part linked to heightened awareness of the value of trees and woodlands following the controversy surrounding the proposed 'sell off' of the public forest estate in England[45]. Public knowledge and awareness of threats to tree health can also be high at a local level when there is a specific localised outbreak[40].

Research with owners / managers has shown that knowledge of certain tree health issues (in this case, Dothistroma needle blight (DNB)) *Dothistroma septosporum* is varied and is dependent upon several factors[34]. Forestry professionals, agents and land owners do report high levels of observation of pathogen or invertebrate damage[41]. However, self-reported knowledge of pests and diseases is low amongst land owners and managers, but again there are some examples of high profile pests / diseases which are associated with higher levels of awareness[38].

Topic 3 - Behaviours
There are a number of studies which investigate tree health related behaviours and activities of the stakeholder category 'informed public'. Survey-based research with members of garden-related organisations, for example, shows that only a minority would think to report a diseased tree on their property, or to search for more information, or to discuss it with friends or family. Only 1% would attempt to treat the problem[34]. However, this stakeholder group express a high level of willingness to carry out positive biosecurity behaviours such as avoiding bringing plants and plant materials into the country from overseas, cleaning footwear, vehicles and bikes, buying accredited plants, avoiding plants grown outside of the UK, avoiding areas known to be affected by a pest or pathogen, and contributing to surveillance survey work[34].

A number of studies have investigated the tree health related behaviours and activities of woodland/forest owners and managers. One study revealed that application of biosecurity measures amongst woodland owners is low[41]. Another study showed that there is greater experience of surveillance than management amongst woodland owners and managers[38].

Topic 4 - Barriers and enablers
Interviews with volunteers in the Observatree project (a UK citizen science tree health early warning system) have revealed that participation in the project is motivated by wanting to do something of value, wanting to engage with other people, and by an interest in conservation, trees and protection of the environment[46]. Thus, individual motivations are important for certain behaviours related to tree health including monitoring activities. However, experience from the Observatree project shows that it can be challenging to achieve adequate geographical coverage in citizen science-based surveillance programmes as remote and less accessible areas receive lower levels of survey effort than areas near to where volunteers live.

Barriers to disease management reported by professional stakeholders include lack of resources, incompatibility with management objectives, and acceptability of control measures by others, perceived efficacy of control measures, and difficulty of applying control measures[35]. There is evidence to show that biosecurity behaviours of woodland owners and managers can be correlated with levels of self-reported knowledge of tree pests and diseases; higher levels of knowledge are associated with higher incidence of good biosecurity. However, knowledge is only one of a number of factors that influence biosecurity behaviours[38]. Woodland managers with experience of surveillance or management of tree pests or diseases are also more likely to apply good biosecurity measures; hence experience is important as a motivator of action[38]. Other studies have shown that the majority of woodland managers consider risks when acquiring planting stock[47], and that control measures are implemented by land owners when served with statutory notices by the Forestry Commission[40]. Hence, issues as diverse as risk perceptions and regulation are important for influencing actions.

Topic 5 - The role of science

There are a number of studies that provide methodologies, frameworks or tools aimed at engaging stakeholders and providing support for forest and tree health management. For example, participatory GIS (geographic information systems) has been used with land managers to agree a map which could be linked with ecological models and work out where deer were likely to move. This technique tended to reduce conflict and helped to improve the quality of ecological models by using local expertise[48]. A decision support system (DSS) provides assistance to foresters to predict and reduce damage and costs due to the large pine weevil (*Hylobius abietis)*[49]. A study of the concept of resilience and tree health identified four key components that forest managers need to take into account in their decision making: resistance, recovery, adaptation and transformation. These components can be used with a series of decision steps by stakeholders to develop a resilience implementation framework for their system of interest[50].

A review of the uptake of DSS in UK forestry (including ForestGALES, Ecological Site Classification (ESC), *Hylobius* Management Support System) highlighted many influential factors including the level and quality of stakeholder engagement during development and implementation. The study recommends a need to focus on the process of DSS development and not just the product, to identify and understand the needs of end users and work collaboratively with them to build trust and credibility[51].

State of knowledge – internationally

International – Oak specific

Here we present a summary of international oak specific and non-oak specific evidence related to the five review topics.

Topic 1 - Values, attitudes and perceptions of risk

Community appreciation of the risks to oak health from Sudden Oak Death (*Phythophthora ramorum*) develops more quickly where the impacts of the disease are more visible in accessible forests than in remote inaccessible areas[52]. Private land managers ranked pests and diseases as the highest threat to holm oak (*Quercus ilex*) health from 12 threats representing a range of categories and types, including land management choices and other socio-economic factors, and a lack of natural regeneration[53].

Topic 2 - Knowledge

Knowledge of an oak pest in the USA (Red Oak Borer *Enaphalodes rufulus*) has been found to vary between rural and urban landowners[54]. Levels of knowledge of oak pests also varied between landowners, depending on how active they are at managing their forests[54]. Highest levels of knowledge were reported amongst those who were both rural landowners and active managers. Lowest levels of knowledge were reported by passive urban landowners.

Topic 3 - Behaviours

A range of actions have been taken in different locations to tackle Sudden Oak Death in the USA. These include practical management such as felling and burning of cut material[55]. The management of threats to oak from gypsy moth *Lymantria dispar* has led to the development of novel collaborative partnership working amongst land owners[56]. Research has also shown that private woodland managers can be encouraged to take an active part in citizen science pest detection programmes, and have engaged with training, sampling and reporting activities[57].

Topic 4 - Barriers and enablers

Studies in the USA highlight the significance of collaboration and cooperation between landowners in relation to the effective management of threats to oak health. Local management actions to address holm oak threats are more successful when there is strong interaction between stakeholders[52]. Similarly, where private and public land managers are unified in their concern for oak health, this can lead to prompter and more effective action[55]. The development of partnerships of land owners with a shared recognition of the risks and synchronising the timing of disease management with wider forest management plans, can be important for achieving adequate levels of proactive management[56]. On a more cautionary note, however, the engagement of multiple land managers and owners in an affected area requires investment of resource to achieve coordination, and this can delay action[55]. Similarly, inconsistencies between broader woodland management policies, such as conservation, and the management objectives for oak health, can cause confusion and hinder action[56].

Location can be an important factor in determining levels of engagement with the management of threats. For example, participatory oak disease monitoring programmes are most likely to be successful in areas where forests are accessible and / or in areas of higher property density. Management (including monitoring) is more challenging in remote locations with poor access[52]. Engagement in management can also depend on the geographical context of affected areas, with higher levels of engagement likely in areas of high conservation value and / or cultural significance[55]. An evaluation of local management initiatives for oak pests shows that engagement varies between rural and urban land owners, and that levels of engagement are highest amongst active land owners[54].

Availability of resources also emerges as an important factor. The success of Oak Wilt management programmes in Minnesota against Oak wilt (*Bretziella fagacearum*, formerly *Ceratocystis fagacearum*) was limited due to a lack of personnel and funding needed to enforce tree removal orders[58]; in the study, detection programmes were constrained by the availability of funding[58].

Topic 5 - The role of science

No evidence found.

International – non oak specific

Topic 1 - Values, attitudes and perceptions of risk

A review looking at preferences for different silvicultural attributes at a European level revealed a preference for large trees in moderately stocked, open stands, giving a sense of 'managed naturalness'. Tree species type was found to have a relatively small impact on preference compared to the structural qualities of stands[59]. In relation to management interventions to protect tree health, the study showed that residents are supportive of control methods, with a preference for biological control. Residents also show greater support for protecting certain areas from outbreaks, in particular, ecologically sensitive areas and high value wildlife habitat[40].

Topic 2 - Knowledge
Resident's knowledge of pests and diseases can vary by location[61]. This can be linked to previous experiences of particular diseases or pests, but also the degree of urbanity or rurality of the residential location. A recent pan-European survey looking at between-country variation in levels of public awareness of invasive forest pathogens has shown that awareness of forest pathogens generally are similar across the countries sampled (Austria, Bulgaria, France, Norway, Portugal, Spain, Sweden, Turkey, and the UK). However, awareness of specific diseases (e.g., ash dieback) varied between countries, with variation attributable to levels of media exposure[62].

Self-reported levels of knowledge about topics such as the pest susceptibility varied between professionals and practitioners in urban areas of Canada (landscape architects, non-profit organisations, retail nurseries and garden centres, and municipal forestry staff). On average the professionals rated their knowledge as good, with a minority saying it was either excellent or moderate[63]. Other evidence suggests tree professionals across Europe have relatively low levels of self-reported awareness of pests and pathogens, but this varies across different threats, with some high profile threats associated with higher levels of knowledge[64].

Tree farmers in Ohio demonstrated strong interest in learning more about forest disease and insect problems and associated controls[60].

Topic 3 - Behaviours
Some high profile tree pests have provoked a significant level of management response. One example is emerald ash borer *Agrilus planipennis* in the USA, where management activities have been extensive, widespread and with broad stakeholder participation [40]. In this case, the management response has included surveying and inspection, monitoring, research, regulation, control through insecticide use, felling, outreach and extension services, and co-ordinated administration. This example demonstrates that it is possible to achieve high levels of activity and high participation rates in response to threats[40].

Topic 4 - Barriers and enablers
One of the primary obstacles to implementing actions in response to new diseases in forest ecosystems relates to problems in achieving adequate levels of understanding of the science of tree health (including biology, pathology and entomology) amongst policy stakeholders[65].

Barriers to action against tree health threats can also be economic and political. For example, the politics of free trade and a reluctance to accept supra-national governance in coordinating activity between nations can become significant barriers to international level action [65].

Topic 5 - The role of science
There are a number of international studies which examine the relationship between science and forest management and, in some cases, management for tree health and resilience.

One study identified the issue of incompatible timescales as one of the fundamental obstacles to the integration of science and management responses to tree health threats; scientific knowledge may take some time to be acquired, while practictioners and policy makers need more rapid evidence to inform immediate response actions. The study highlighted the mismatch between the requirements of managers and agencies who need to act swiftly when threats arise, and the timescales of scientists who are often reluctant to offer opinions and advice without a high level of supporting evidence which takes time to accumulate. This mismatch can act as a barrier to effective action[65]. One proffered solution is for the forest biosecurity sector to further develop and apply the science of decision making in uncertain environments[67].

Other studies focus either on i. mechanisms and tools for decision making, or ii. explore the themes of knowledge sharing, knowledge co-production and mobilisation which yield useful insights for those working to support the integration of science and forest management and management for tree health:

Tools and mechanisms - A USDA Forest Service publication provides an example of a 'decision matrix' to utilise available scientific knowledge (for example about invasive species) to (1) prioritise habitats/ areas for targeted management intervention, and (2) determine appropriate management strategies and treatments[67]. Another publication proposes Structured Decision Making (SDM) allowing participation by decision-makers, analysts, scientists, and stakeholders in the design of adaptive forest management initiatives. The SDM process entails four stages: (1) problem structuring (framing the problem and defining objectives and evaluation criteria); (2) problem analysis (defining alternatives, evaluating likely consequences, identifying key uncertainties, and analysing trade-offs); (3) decision point (identifying the preferred alternative), and (4) implementation and monitoring the preferred alternative with adaptive management feedbacks [68].

Knowledge sharing, co-production and knowledge mobilisation - A constant theme emerging from the studies is the need for revisions to conventional models of knowledge production and transfer. In particular, in favour of more inclusive, participatory and collaborative approaches to mobilising multiple sources of knowledge (including scientific knowledge) and achieve improvements in adaptive forest management strategies and actions. A study addressing contemporary challenges of forest health and wildfire concluded that integration and application of traditional knowledge alongside western science for improved stewardship of natural resources will require enduring commitments to knowledge sharing that extend beyond the usual boundaries of professional training and cultural orientation[69]. An analysis of forest research networks indicated the emergence of a model of knowledge co-production involving knowledge producers and users, with the goal of fostering innovation and addressing challenges facing the forest sector. It suggested the need to prioritise diverse and tailored knowledge mobilisation strategies, rather than emphasising knowledge production. Knowledge mobilisation strategies involve engagement with partners and an emphasis on creativity and transformation, rather than the transfer or dissemination of information[70]. One case study of emerald ash borer highlights the pivotal role played by a research team as a 'boundary organisation' that helped facilitate connections between stakeholders, paying particular attention to how the group interacted in a context where power and knowledge were unevenly shared[71].

Assessment of knowledge

This evidence review highlights that much of the UK oak specific evidence relates to OPM which is a very specific case with some unique properties – namely the potential human and animal health impacts. The non-oak specific evidence provides a significant body of research that outlines the values of trees and woodlands to publics and a broad range of stakeholders. Much of the evidence on public values is not focused on specific trees species.

The majority of the international literature is focused on the USA, although there is some evidence from Canada and a limited number of European studies. Much of the evidence is context, location and time specific, with studies focussing on specific places, diseases and types of stakeholder. Therefore, high levels of agreement across the different studies are rare.

The evidence base shows that a variety of research methods are being used to explore values, attitudes and behaviours, including surveys, interviews, workshops, data gathering at public events, as well as mixed method approaches.

Evidence concerning the role of science only comes into the chapters on non-oak specific literature. There is also a significant amount of further evidence which is not related to forestry but to broader natural resources, ecosystem and agricultural management that might be of use – however, this is not reported here.

There are four pieces of research currently underway or recently completed that will be highly relevant to the evidence base on oak specific tree health issues, including:

- Forest Research's Programme 7, 'Integrating research for policy and practice', aims to understand and demonstrate how the impact of research into trees, woods and forests can be enhanced through dialogue and collaboration between scientists, policy-makers, land managers and other stakeholders across the public and private sectors. Case studies are being compiled which demonstrate the impacts of a range of research projects and two will focus on tree health: '*Hylobius* Management Support System' and 'Advice for *Phytophthora ramorum'*.
- Protecting Oak Ecosystems (PuRposE) - this project is providing an understanding of the current and future health threats to native oaks in the UK and involves scientists from a range of disciplines. The research has examined land manager and other stakeholder values, attitudes, behaviours, motivations and barriers to action. Workshops have examined how decisions are made about managing threats to oak. An online survey with experts including researchers across Europe has also been undertaken to uncover additional evidence about knowledge of threats to oaks, and in-depth interviews held with land managers and others regarding values and attitudes.
- Understanding public risk in relation to tree health (UNPICK) was a three year research project designed to investigate how UK publics understand and perceive the growing threats to tree health from invasive pests and diseases. One of the case studies identified local community and local stakeholder narratives about the risk perceptions associated with OPM. Some results are still being prepared for publication.
- Forest Research is also currently involved in research examining landowner's (and public) knowledge and perceptions of risks associated with OPM in London. This work also looks at opportunities and barriers to landowner action to manage OPM risks.

Summary and priorities for new knowledge from review

Values and attitudes: Oak trees are highly valued by the public, with this high value partly attributable to their status as icons of British history, identity and landscape. There is some evidence to suggest that these understandings and values apply to landowners and managers and are influencing attitudes and management actions in response to threats to oak health. **Further research is required to understand how these values, attitudes and understandings can be used to encourage engagement in a collective societal effort to protect oak trees and to develop and implement management strategies to build oak resilience.**

Knowledge: Knowledge of threats to oak trees is low amongst the general public and private landowners. Landowners, and particularly those responsible for public land, have higher levels of knowledge and awareness of threats to tree health, but knowledge is concentrated on pests and diseases that have received higher levels of media and public attention. There is some evidence (restricted to OPM) concerning landowners and the public that shows lack of knowledge, low levels of awareness, and uncertainty about risks can all be barriers to action. **More research is required to understand how knowledge mobilisation about the various threats to oak, and opportunities to engage and contribute to oak resilience, can be tailored to different stakeholders. More evidence is needed of local and land manager knowledge including tacit knowledge based on local experiences and insights. Research on social learning and social networks could provide a particularly fruitful area for research. Further evidence is also needed of the range of people, organisations and institutions that have a stake in oak health through a detailed stakeholder analysis, with a particular focus on knowledge needs.**

Behaviours: The evidence shows that levels of action and engagement in relation to oak health specifically, and tree health more generally, are far from uniform across the stakeholder landscape. There are ‘pockets’ of action and positive behaviours, for example amongst engaged gardeners, sub-chapters of the woodland owner / manager category, and citizen scientists. We draw the general conclusion that engaged, informed and ‘active’ (as opposed to passive) landowners and stakeholders are more likely to be taking positive action in relation to oak (and tree) health – actions such as looking for and reporting pests and diseases, adopting good biosecurity behaviours, and supporting efforts to control pests and diseases and manage the risks associated with them. It is likely, however, that these actors represent the ‘tip of the (stakeholder) iceberg’. **Research is urgently required to better understand how to engage and encourage action from the vast majority of stakeholders who are inactive. We suggest that passive woodland owners and managers should be considered a priority group for the focus of this work.**

Barriers and enablers: In addition to the lack of awareness, knowledge and understanding as a significant barrier to action (see above), the evidence also highlights how a lack of coordination can restrict the willingness of individual landowners and managers to take action to manage the risks and threats posed by (oak) pests and diseases. This conclusion is strengthened by research from the USA which highlights the significance of collaboration and cooperation between landowners. Management actions, particularly at the local level to address oak threats, are more successful when there is strong interaction between stakeholders. Furthermore, lack of coordination may prevent action because of fears of free-riding and wasted effort due to the (re-)infection risk posed by trees on neighbouring land. **There is a significant research gap in relation to barriers to, and intervention measures required to encourage, the development of partnerships that bring together land owners and other stakeholders in the collective effort to reduce the threats and manage the risks posed by pests and diseases.** Recognising the highly fragmented nature of woodland and forest ownership in the UK, and especially in England, we conclude that this represents a high research priority.

Science into practice: Lack of knowledge and understanding of threats to oak health emerges as a significant barrier to action (see above). There is also a low level of knowledge about what, precisely, is required in terms of effective and practical management responses to protect against the various threats and to manage their associated risks. There are significant challenges to the application of the science of oak health and resilience for practical management interventions – in particular, the issue of incompatible timescales. There is evidence to suggest that successful attempts to integrate science into practice for tree health have occurred when the established conventions and rules governing the transfer of scientific knowledge have been relaxed in favour of more open, exploratory, inclusive and participatory initiatives where science represents one of many sources of potentially useful information that can inform practical actions and solutions. We conclude that **further research is urgently required to explore how models of knowledge sharing, co-production and knowledge mobilisation might be applied in the context of management for oak health and resilience**. This research should help to shape the science of oak tree health and resilience so that it addresses the need for decision-making and action in the context of uncertainty. Fundamental to this is the need for social scientific research that supports the development of a transformational model of science involving scientists and stakeholders working together within the investigative process and, through practical experimentation, developing co-designed solutions to oak tree health threats and associated risks. Action Oak partners are currently working to develop a network of demonstration sites. A primary function of these demonstration sites will be to enable close and collaborative working between scientists and site owners to explore ways in which practical management interventions, informed by science, can be developed, tested and disseminated to other owners and practitioners. **We recommend that there is a strong social science dimension to the selection, design and delivery of this demonstration site network to ensure that these collaborations are successful**.

General conclusion: The review of knowledge presented in this chapter reveals that what people know, what attitudes people have, how people perceive risks/benefits, and the values people hold, all have an influence on the extent to which they take on board new knowledge and modify existing or adopt new behaviours. If we do not adequately understand people's knowledge, attitudes, values and perceptions we are unlikely to communicate effectively, and to motivate, facilitate, and influence positive behavioural change. As such, we conclude that **research to understand stakeholders needs to be conceived and understood as an integral and complimentary part of Action Oak activities to ensure action 'on the ground'. As such, we argue that an understanding of knowledge, values, attitudes and behaviours is essential to ensure that those who are tasked with taking action for oak resilience are actively engaged in identifying potential solutions and adaptive approaches**.

Sources

The following outlines some of the resources and knowledge sources we utilised in the completion of this evidence review. It lists the databases and search engine used, along with a selection of the web sites and web pages visited, as well as key external and internal contacts and experts whose knowledge was drawn upon.

Databases
ScienceDirect https://www.sciencedirect.com/
Scopus https://www.scopus.com/search/form.uri?display=basic
Search engine
Scholar Google https://scholar.google.com/

Web sites and web pages
USDA Forest Research web pages https://www.fs.fed.us/research/
UNPICK project web pages http://www.imperial.ac.uk/unpick/
Purpose project web pages https://protectouroaks.wordpress.com/
FR web pages e.g. https://www.forestry.gov.uk/fr/infd-9pyf6w
IUFRO – Working Party Social Dimensions of Tree Health
https://www.iufro.org/science/divisions/division-7/70000/70300/70315/
Cost Action PERMIT web pages http://www.cost.eu/COST_Actions/fps/FP1002
FR PERMIT web pages https://www.forestry.gov.uk/fr/permit
European Innovation Partnership website https://ec.europa.eu/eip/agriculture/en/european-innovation-partnership-agricultural
Rothamsted Research https://www.rothamsted.ac.uk/news/data-amateur-naturalists-can-improve-quality-predicted-disease-distributions
Some specific US universities- e.g. Minnesota https://trees.umn.edu/
Defra Future Proofing Plant Health e.g.
http://randd.defra.gov.uk/Default.aspx?Menu=Menu&Module=More&Location=None&ProjectID=17957
Purpose video – of event at Epping workshop https://protectouroaks.wordpress.com/work-packages/wp4/in-conversation-with-oak-trees/
Collaboration for Environmental Evidence
http://www.environmentalevidence.org/information-for-authors

External Contacts
Hilary Geoghegan (University of Reading), Alison Dyke (Stockholm Environment Institute, York centre at University of York), Julie Urquhart (University of Gloucester)

Contacts within Forest Research
Michal Petr, Bianca Ambrose-Oji, Mariella Marzano, Chris Quine, David Edwards

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9. Management of oak tree health

Gary Kerr and Rob Coventry

Introduction and scope of chapter

This chapter summarises what is known/not known/needs to be known about management of oak tree health in the field – including forest management, silviculture, risk assessment and some consideration of control methods for pests, both in the UK and globally. The work consisted of two parts, firstly a literature review of scientific studies where the influence of silviculture and forest management on the health of oak trees had been quantified and analysed, and secondly a broader knowledge review.

The literature review was carried out using the following outline method. The formal method can be found in Appendix 1.

- A repeatable method was used to carry out a search on the Scopus academic database. Studies were located involving the genus *Quercus* where aspects of silviculture, forest management and tree health had been discussed. Search terms were selected based on 'A Dictionary of Forestry[1].

- This search resulted in 462 articles. A subset of these which met the criterion of demonstrating 'good quality quantification of the silviculture and/or forest management factor studied and its effect on tree health' was selected to be included in the review. This resulted in a total of 62 papers being worthy of more detailed examination (these papers are shown marked with an * in the reference list).

In addition to the material collected in this process, the review was broadened by: (1) considering published management guidance in the UK and elsewhere on oak tree health; (2) liaising with other chapter authors to challenge our findings from the literature review, and (3) interacting with stakeholders at a meeting in Birmingham on 5th March 2018.

State of knowledge – UK

The authoritative guide to management of oak woodland in the UK is *Managing Native Broadleaved Woodland* [2]. This advocates a pragmatic approach to the management of native broadleaved woodlands that should acknowledge each is different and represents a unique combination of history of intervention by people, site factors and vegetation. The guidance makes the assumption that trees are healthy; the only mention of 'diseased trees' is in reference to using dead, dying and diseased as a selection criterion when deciding which trees to remove when thinning.

When considering the subject of oak health in the UK it is important to be aware of the recent history of broadleaved woodland. Until the revival of interest in broadleaved woodland in the late 1970s and early 1980s, which culminated in the 1985 policy, it was common to approach the management of this woodland type in a similar way to that for conifers. The management of conifer woodland had a strong economic basis and this entailed thinning at marginal thinning intensity (the rate of removal that does not reduce cumulative volume production) and then felling when mean annual volume increment of stands was at its maximum. This approach, combined with poor economics of timber extraction at that time, meant that many broadleaved woods underwent a long period with little thinning and so between-tree competition was very high [26]. This may be a predisposing factor in terms of the current concerns about tree health.

Present concerns about oak tree health in the UK are focussed on Acute Oak Decline (AOD) and links with the two-spotted oak buprestid (*Agrilus biguttatus*), oak processionary moth (OPM) (*Thaumetopoea processionea*) in addition to mammal damage and the general effects of climate change; chapters 3 and 4 also identify many future threats. Guidance on management of AOD and OPM has been developed and is available via the Forest Research website. For AOD this involves forest managers surveying, recording and monitoring infected trees and taking recommended action, which may include felling diseased oaks and not removing bark and sapwood from affected sites[3]. OPM poses a significant risk to human health and because of this any treatment (e.g. nest removal or pesticide treatment) requires carefully timing and execution by professionals with specific training and equipment.

Management actions for oak tree health in the UK are typically reactive to problems, i.e. a problem is identified, effort goes into understanding it, based on this an effort is made to mitigate the effects of the problem. Whilst this is an inevitable approach when new threats occur, and which is also typical internationally, it means that the main management interventions aimed at maintaining or improving the health of oak trees are based on the application of general principles. These principles centre on reducing risk and in terms of silviculture and management this can be achieved through manipulating the species composition or diversifying the structure of the stand. To diversify the species composition of a stand of oak trees the key considerations are to select species that: (1) will help achieve the objectives of management and (2) that will survive and grow on the site[2]. Diversifying stand structure refers to the change from an even-aged structure (all trees are of the same age and generally uniform) to one which is more irregular (trees vary in terms of age and size). There are well established silvicultural systems that can help guide management [4] as well as guidance on how to make the transition[5].

In summary, our knowledge of the effects of silviculture and management on oak tree health is extremely limited and what management is undertaken is based on the application of general principles. A key finding of this review is that only one of the 62 scientific papers which met the criterion for review originated from the UK, indicating a substantial knowledge gap. At a time when there are significant concerns about the health of our oak trees, as well as other important native broadleaved species such as ash, it is suggested that a changed emphasis in the management of native broadleaved woodland is required from being focussed primarily on economic and social objectives to paying greater attention to maintaining and enhancing forest health.

State of knowledge – internationally

Five of the 62 considered papers were concerned with the effects of nitrogen on oak tree health and these were brought to the attention of authors of the environmental factors chapter. A further 23 papers were judged to be of only passing interest because they either dealt with very different environments or management intensities (e.g. *Q. suber*), were found not to pass the criterion of quantification or used a surrogate measure of tree health.

The remaining papers were read and grouped into areas of common interest as a basis for the main outcomes of the review. The seven conclusions are presented below in the format of: (A) the general finding and (B) the supporting evidence.

1. The effects of forest management on tree health are complex and the literature describing rigorous research in this area is sparse.

For example, one paper [6] notes that 'few studies have experimentally evaluated the effectiveness of improvement harvests for mitigating oak decline' whilst another [7] states that 'forest management may have an important role in attenuating oak decline….and there is scarce literature available on the effects of silvicultural treatments'. This lack of evidence is due to the complex nature of forests and 'oak health' both of which are highly variable, difficult to measure experimentally, and need to be studied for long periods of time to cover temporal variation. These factors combined with the difficulty of finding the required uniform forests and large areas make effective research into this area especially challenging.

2. Studies on survival analysis and mortality risk have been used successfully to understand some of the complex and interacting factors involved in oak decline.

Examples of this approach include studies of oak decline in Missouri, USA [8, 9] and of oak decline in the whole of the south-eastern USA [10, 11]. However, these approaches require high quality data over long periods of time where appropriate measures have been made and repeated. This type of data is collected and rapidly placed in the public domain by the USDA Forest Service Forest Inventory and Analysis National Program (https://www.fia.fs.fed.us/), thus facilitating timely research outcomes (see also Monitoring chapter 7).

3. There are many advocates of thinning (reducing stocking density) to increase resilience to oak decline; there is some evidence to support this from experiments but stronger support from the results of survival analysis.

One paper [6] reported an experiment to examine 'improvement harvests' (thinning) as a method to mitigate the effects of decline in Missouri Ozark forests. The study covered two sites, used a replicated experiment design and lasted for 14 years. However, the main conclusion was 'although improvement harvests did not mitigate oak decline, they did not make it worse and had benefits of increasing the diameter growth of trees in the residual stand'. In contrast, another study [12] confirmed earlier findings [13] that thinning can be used to render a stand less susceptible to defoliation by gypsy moth (*Lymantria dispar*). A small study[7] (16 trees of 50 cm DBH) also confirmed that thinning of declining trees could improve fine root dynamics (and it is assumed help mitigate decline). The studies referred to earlier [8,9,10] all produced results which quantified the risk of mortality of declining trees that could be incorporated into stand level silvicultural prescriptions without elaborating on processes and mechanisms.

4. Soil compaction and drought are widely cited as predisposing/inciting factors in oak decline; there is evidence for this in the literature and the extent to which forest management (including comparison with techniques developed in urban settings) can alleviate compaction/drought and improve oak health generally is worthy of further study.

Work in Germany [15,16] tested the hypothesis that deficiencies in soil gas permeability reduce fine root formation of oak trees and thereby reduce stress tolerance. They did not directly measure oak tree health but the paper was examined as being one of a limited number to consider below ground effects of oak decline. Others [17] undertook a study on Q. *palustris* (DBH=30 cm) but failed to show the underlying causes of tree decline and death commonly associated with soil compaction. However, despite the mixed evidence from these studies many of the papers cite soil compaction/drought as a factor in oak decline [18,19,20]. Various options in the professional management of trees (including in urban settings) can be used to reduce compaction and drought but knowledge of the effect on oak tree health appears to be lacking.

5. There is good evidence that pesticides can be used to improve/protect oak health in response to specific causal factors.

Seventeen of the 62 selected papers provided evidence for this conclusion and these are listed in Table 9.1.

6. Response strategies to oak decline are often based on general principles and good science combined with clear communication.

This was a theme with a number of studies in the final 62 papers. Examples include a study [21] which reviewed treatment options and their efficacy to slow down the spread of oak wilt (*Ceratocystis fagacearum*) and another [22] which describes a 10 year programme of measures to increase stand resilience to gypsy moth defoliation in upland oak forests in Kentucky, USA; and others [23 24]. This approach is common with that taken in the UK and reinforces the principle that it is more effective to do something based on general principles and good, albeit limited, science, than to delay until knowledge is complete.

7. Most studies reviewed are responsive to a problem of oak health and aim at recovery. Few studies have been reported where healthy oak trees or stands are treated to increase resilience as a pre-emptive treatment.

While none of the core 62 papers examined pre-emptive treatments, one study provided evidence for the use of thinning to reduce the effects of gypsy moth (*L. dispar*) in advance of infestation of oak in the eastern states of the USA [13]. Figure 9.1 illustrates the different stages which many forests pass through after a disturbance; it is clear that between tree competition is intense in the stand initiation and stem exclusion stages. These periods of competition can also be exacerbated at any time by a lack of management, a situation applicable to approximately 42% of forests in England [27]. Forest management primarily focussed on economic objectives favours such phases of competition because it helps in the selection of the best growing or better formed trees. However, the presence of such long phases of competition and the absence of management may not be conducive to maintaining and enhancing forest health. A recent study [25] suggested that reducing competition between trees in the forests of the southwest USA may be a good strategy to reduce tree mortality and combat increasing aridity; this is an example of adaptive forest management based on good evidence. A knowledge gap is that similar pre-emptive treatments could form the basis of forest management to maintain or enhance the health of oak forests but remain largely untested.

Assessment of knowledge

The research literature on the effects of forest management on tree health is sparse both in the UK and internationally. However, a number of themes have emerged as outlined in the conclusions above. The evidence and associated knowledge base supporting these conclusions has been rated in Table 9.2 using the ratings introduced in Table 1.2. In most cases the evidence has been rated as 'speculative', due to its limited extent or / and the lack of agreement between studies. The main exception was for the use of pesticides and for which there is a comparatively large volume of evidence confirming effectiveness, albeit in specific circumstances.

Summary and priorities for new knowledge from review

Despite the lack of evidence, the process of considering the literature and wider sources of knowledge and exchanging information with stakeholders has suggested five clear priorities for future action:

1. The potential of existing long-term processes of data collection to add knowledge to factors influencing oak tree health should be investigated.

At a time when resources for carrying out research are limited it would seem sensible to examine how existing data collection could be adjusted to achieve greater focus on oak tree health, provide perspectives on how health varies across the UK, and examine contributory factors such as climate, soil and management intensity. There are good examples of how this has been achieved in the literature in North America; the National Forest Inventory is an obvious starting point for this work in Britain (see also Monitoring chapter 7).

2. Greater knowledge of the extent to which soil compaction and drought can affect oak tree health is needed but this must be integrated with work to examine forest management options to offset these effects, and in the case of non-woodland trees, of surrounding land use also.

This is a clear priority from the review, but a mixture of approaches would be required for such a research programme to be successful. A key element would be to establish long-term research trials established at an appropriate scale that take full account of the variability in forest history, climate and soils of the sites on which they are established.

3. There is a requirement to provide an evidence base for pre-emptive forest management actions that focus on maintaining or enhancing health.

Despite the high social and environmental values of oak woodland much of it has been “unmanaged” or “neglected” for long periods of time due to the high costs and low returns of management. There has been little study of the consequences or risks posed by such lack of management and further examination is merited; for example, is the main phase of stem exclusion now over for existing cohorts and so health might be expected to improve? Following extended periods of non-intervention many oak woodlands in the UK have experienced intense between-tree competition and this could be a predisposing factor in oak tree health. Research is required to examine the consequences of lack of management for health, and specifically the extent to which reducing between tree competition, i.e. through thinning, can be used as a pre-emptive treatment to maintain and enhance oak tree health.

4. The evidence base for management of non-woodland trees has not been systematically examined but is thought to be limited. Further scoping of the research needs is necessary.

Trees in non-woodland situations may experience a similar degree of neglect and be stressed by climatic and soil changes. Some exacerbating factors (e.g. agricultural ploughing, past pollarding, spray drift, road and pavement works, pollutant loading) may differ substantially from those experienced in woodland environments and deserve greater attention – including monitoring to observe changes, experiments to elucidate processes, and trials of potential mitigation methods.

5. Established silvicultural practice in the UK should be assessed in an interdisciplinary manner to identify whether there are options for revising guidance to focus more on the maintenance and enhancement of oak health.

Much existing silvicultural practice for oak, as codified in FC publications, has focussed on economic productivity and was developed at a time when there was less concern over threats due to pests and diseases. Whilst fundamental research will, in time, provide a sounder scientific basis for new guidance, there appears to be merit in reconsidering existing practice by bringing fresh, multi-disciplinary perspectives to bear (e.g. as a form of risk assessment of current practice).

Figure 9.1 Schematic stages of stand development following major disturbances (Oliver and Larson, 1996)

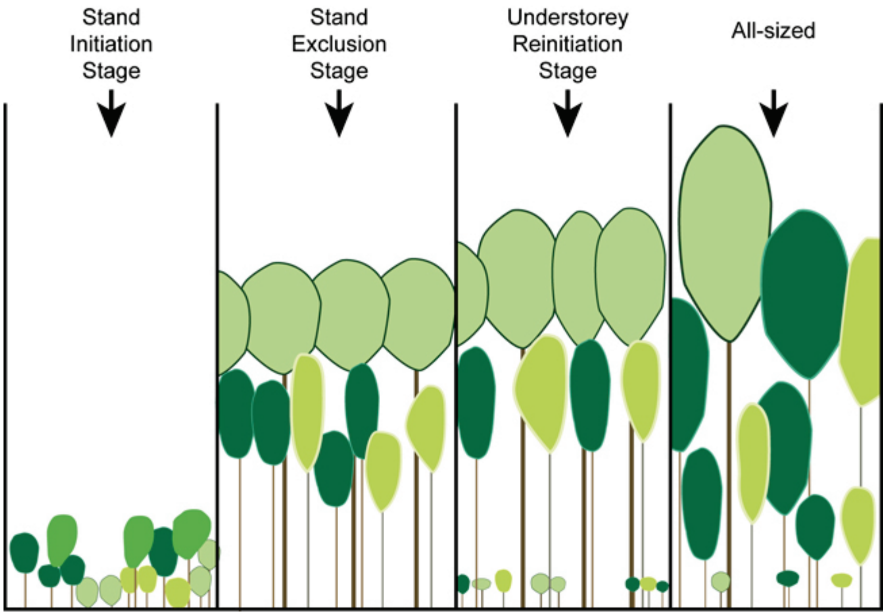

Table 9.1 Summary of selected studies on subject of pesticides

Reference	I or F*	Context
Olochowik *et al*. 2017	F	Nursery production of *Q. robur* and powdery mildew
Dabrowski *et al.* 2017	F	*Q. robur* and powdery mildew
Chen *et al*. 2014	I	Control of Agrilus auroguttatus and oaks in California
Serrano *et al*. 2015	F	Botryosphaeria and *Q. suber*
Kanaskie *et al.* 2011	F	*Phytophthora* and *Notholithocarpus densiflorus*
Rajkovic *et al.* 2010	F	Biofungicide on *Q. robur*
Blaedow *et al.* 2010	F	Fungicide on oak wilt disease
Garbelotto *et al.* 2007/9	F	Control of *Phytophthora* on oaks in California
Solla *et al.* 2009	F	*Phytophthora cinnamomi* and *Q. ilex*
Percival *et al.* 2008	F	*Quercus* spp. and powdery mildew
McPherson *et al.* 2008	I	Permethrin/beetles/*Phytophthora ramorum*
Roversi 2008	I	Aerial spraying to control OPM in *Q. cerris* forests
Percival et al. 2006	film	Film forming polymers on broadleaved trees in UK
Turner *et al.* 2005	I	Red-oak kermes scale on *Quercus* in eastern USA
Eliason *et al.* 2002	I	Control of parasitoids on oaks in eastern USA
Fernandez et al. 1999	F	Antifungal materials to treat oak decline

Insecticide (I) or fungicide (F)

Table 9.2 Assessment of weight of evidence for main conclusions of the review using the terminology introduced in Table 1.2.

Main conclusions of review	Weight of evidence	
	In the UK	**International**
1. Effects of management on oak tree health	**SPECULATIVE**	**SPECULATIVE**
2. Survival analysis using inventory data to examine factors affecting oak tree health	**SPECULATIVE**	**COMPETING EXPLANATIONS**
3. Use of stand level silviculture to improve oak tree health	**SPECULATIVE**	**SPECULATIVE**
4. Methods to reduce effects of soil compaction and drought on oak tree health	**SPECULATIVE**	**SPECULATIVE**
5. Use of pesticides to improve oak tree health	**SPECULATIVE**	**WELL ESTABLISHED** **(in specific contexts)**
6. Effectiveness of response strategies on oak tree health	**SPECULATIVE**	**SPECULATIVE**
7. Use of pre-emptive management on oak tree health	**SPECULATIVE**	**SPECULATIVE**

Appendix 1. Method used for literature review

The initial stage of the literature review was carried out on the Scopus database using the search term:

(TITLE (quercus OR oak)) AND (TITLE-ABS-KEY (health OR vigour OR decline OR death OR pathology OR disease AND silvicultur* OR management OR treatment))

This search returned 463 results (18th December 2017, including 1 duplicate) which were subsequently exported to Mendeley for ease of managing the information. The list was sorted into categories of “Not Forestry Related” (84), “Not Relevant” (252) “Important Context and Reviews” (11), “Other Interesting” (52) and “Selected” (63). Studies were selected if they examined the effect of silviculture or management operations on oak tree health either as a pre-emptive or a recovery treatment. A further criteria for selection was that both the treatment and the effect were measured and quantified. Selection was based on the title and where necessary the abstract with clarity being provided on borderline cases by discussions between authors.

It was necessary to include some caveats during the selection process to: (1) exclude references that were not relevant material and (2) to limit the volume of material to a manageable amount for the time available. These are listed below.

Excluded as management variable	Excluded as health variable
• Cork harvesting • Campaign management • Work on seed preservation • Monitoring and mapping • Dust	• Regeneration success • Surrounding vegetation • Height and diameter growth • Avian, mammal and reptile populations

Even with clear criteria and caveats, there were still grey areas about what constituted a management or health variable. For instance:

- When does understanding pheromone release become a potential silvicultural treatment?
- Is fire history a management factor that’s relevant for the review?
- Is the ability of trees to recover from pollarding relevant to the review?

A pragmatic approach was taken to these grey areas with the authors using personal judgement as to which topics fit within the scope of the review.

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10. Semiochemical-based strategies

Jozsef Vuts and Mike Birkett

Semiochemical-based strategies

Semiochemicals are naturally occurring behaviour- and development-modifying chemical signals that govern intra- and interspecific interactions and which act *via* non-toxic modes of action. Intra-specific semiochemicals are termed pheromones, whereas chemical signals used in inter-specific chemical communication are termed allelochemicals [1]. For insects, semiochemical-based interactions are mediated mainly *via* perception of small lipophilic molecules by olfactory receptor neurons located on the antennae, and, consequently, olfaction is a key sensory modality target of Integrated Pest Management (IPM) approaches to insect pest management. Chemical ecology research has identified semiochemicals for hundreds of species, which are now implemented in IPM programmes [2]. The main goal is to incorporate semiochemical-based strategies in IPM such that the use of broad-spectrum toxicant pesticides is reduced, thereby slowing the rate at which pesticide resistance develops. For forestry, there are several ways in which pheromones and allelochemicals can be utilised for pest control, all requiring fundamental studies into pest behavioural and chemical ecology. Implementation of any semiochemical tools must be preceded by bioassay-guided fractionation, where biological and chemical approaches are applied in an iterative and complementary manner to ensure elucidation of full biological activity in the laboratory and the field. Here, we provide a brief overview on semiochemical tools against two insect species identified as oak pests in the UK: *Agrilus biguttatus* and *Platypus cylindrus*, as well as two species that have the potential to become serious pests i.e. *Lymantria dispar* and *Thaumetopoea processionea*.

Semiochemical-based tools for monitoring forestry pests

Early detection of insect pests can facilitate timely intervention, enabling management tools to be applied at low population levels, i.e., before rapid population growth or gradation. Sex pheromone-baited traps have proved to be ideal tools for non-invasive, cost-effective detection of pest insects, due to their species-specificity and high efficacy. They are routinely used at entry points of goods, such as ports, to survey the presence of quarantine pests, which can then be eradicated if appropriate control measures are initiated promptly. Surveillance of spatial and temporal fluctuations in insect numbers with monitoring traps can help pinpoint potential population eruption zones in any given plantation or, considered together with climatic data, indicate swarming periods.

Females of *Th. processionea* produce a sex pheromone comprising a blend of (*Z,Z*)-11,13-hexadecadienyl acetate and (*Z,E*)-11,13,15-hexadecatrienyl acetate, that attracts males in large numbers [3]. Studies with traps baited with the synthetic pheromone revealed that whereas sticky traps are excellent in detecting the very first individuals during the season, high capture-capacity funnel traps are required for long-term monitoring. A survey carried out in 2011 helped establish an up-to-date distribution map in the UK of this moth of high human health and silviculture risk [4]. Similarly, traps baited with the pheromone of *L. dispar* [(7S,8R)-*cis*-7,8-epoxy-2-methyloctadecane] [5,6], a serious oak defoliator in Eurasia and an invasive pest in North America, have been used to study population trends across South East England. It is suspected that *L dispar*, as for *Th. processionea*, was introduced into the UK from mainland Europe on imported timber, which highlights the importance of monitoring for quarantine pests at ports of entry.

Larval galleries of *A. biguttatus* are associated with Acute Oak Decline (AOD) in the UK [7], and, therefore, management options should consider control of *A. biguttatus*, whereby early detection and monitoring of beetles could help map woodlands at risk of AOD and trigger preventative measures. In the closely related *A. planipennis*, which is a serious pest of ash in North America, the female-produced sex pheromone has been identified as a mixture of (3*Z*)- and (3*E*)-dodecen-12-olide. These were attractive, as well as a synthetic pheromone analogue, dodecane-12-olide, for both sexes, and attraction was synergised by the host plant volatile (*Z*)-3-hexenol [8]. If detection can occur before infested ash trees exhibit signs then the development of trapping devices, harbouring bioactive semiochemicals and colour cues, has the potential to reduce mortality to *A. planipennis* within stands [9]. Host-derived volatile blends that are attractive for both female and male *A. biguttatus* have been identified from *Quercus robur*, comprising (*Z*)-3-hexenal, (*Z*)-3-hexen-1-ol and (*Z*)-3-hexenyl acetate (`leaf blend`) and *p*-cymene, 1,8-cineole, (*E*)-ocimene, *γ*-terpinene and (*R*/*S*)-camphor (`bark blend`) [10], and synthetic blends of the identified leaf and bark compounds will be evaluated in the field for their ability to trap *A. biguttatus*. Also, the pheromone biology of *A. biguttatus* is under study, and we already have behavioural evidence for volatiles from feeding females being more attractive than from males, which indicates the presence of a female-emitted pheromone (Vuts, unpublished data).

Semiochemical tools for mass trapping and push-pull strategies

Whereas sex pheromone traps, except for a few species, catch male individuals, aggregation pheromones or combined pheromone/plant volatile lures can also capture females. This is important from a pest management perspective, because removing females of a given pest species from a local population has more profound effects on the size of future generations than the removal of males. Mass aggregation of bark beetles is coordinated by male-produced pheromones that attract both sexes, as well as host tree volatiles, and mass-trapping is suggested as a viable strategy against several species [11]. Push-pull approaches combine the use of attractants, e.g., aggregation pheromones and tree volatiles, and repellents, e.g., anti-aggregation pheromones or non-host volatiles, to protect a certain forest stand. A pull element can be a baited tree that beetles are attracted to, which is either pre-treated with a pesticide or is removed from the stand after mass attack. This approach was used successfully against several bark beetle species, as well as *A. planipennis*, where insecticide-treated and girdled ash trees attracted egg-laying females effectively, most probably by means of tree stress volatiles [12]. The above-mentioned synthetic blends for *A. biguttatus* [10] may offer an opportunity beyond surveillance to be combined with the female pheromone to develop a mass-trapping device, once the identity of the pheromone is revealed. In the UK, *P. cylindrus* is considered a pest of oak and can cause sensitive damage if timber is left untreated. Chemical ecology studies identified components of a putative aggregation pheromone from males as 1-hexanol, 6-methyl-5-hepten-2-one and 6-methyl-5-hepten-2-ol [13]. Similar investigations in congeneric species led to the identification of 6-methyl-5-hepten-2-one and (*S*)-6-methyl-5-hepten-2-ol as part of the male pheromone in *P. mutatus* Chapuis [14], and citronellol, nerol, neral, geraniol and geranial in *P. koryoensis* [15]. Further studies with the *P. cylindrus* male volatile blend have the promise to assign pheromone activity to the identified compounds, thereby creating a platform for the development of practical control solutions.

Wood-boring beetles are associated with pest pathogens, including both bacteria and fungi, and are responsible for their transmission into the wood tissue they develop in, eg *Platypus* spp., which introduce ambrosia fungi into oak timber, or *Scolytus scolytus*, which vectors *Ophiostoma* spp., the causative agents of Dutch elm disease [16]. Semiochemicals associated with insect-pathogen interactions can also be potential targets of control measures [17], which is currently being investigated between oak, *A. biguttatus*, AOD bacteria and *Armillaria* spp. fungi. Such microbial compounds can synergise the effects of insect-emitted volatiles, e.g., aggregation or anti-aggregation pheromones, thus can be used to develop more effective push-pull systems or utilised as biomarkers.

Semiochemical tools for recruitment of beneficial natural enemies of forest pests
Host-derived semiochemicals provide the basis for multi-trophic interactions between hosts, pest insects and their carnivorous natural enemies. As has been widely established for crop and non-crop plants, trees respond to attack by defoliators, wood-boring or root-feeding insects, by stress volatile signalling that either provides direct defence by repelling further individuals of a given pest or provides indirect defence by recruiting beneficial natural enemies at higher trophic levels. The discovery of such intricate mechanisms fuelled research into semiochemical-based manipulation of natural enemies and management of pest insects via conservation biological control. Whereas this concept has been established for agro-ecosystems [18], the approach is less well-established for forest species. Biological control of *A. biguttatus* at low population levels by parasitoids [19] may become a reality via semiochemical manipulation of parasitic wasp behaviour, and the discovery of a male-produced aggregation pheromone for the *A. planipennis* parasitoid *Spathius agrili* supports this approach [20].

Rhizophagus grandis is a bark beetle predator in the UK, and previous work developed a synthetic lure of monoterpenes, identified from bark beetle larval frass, to increase *Rh. grandis* densities in heavily infested pine stands [21]. Leaf volatile emissions from poplar leaves damaged by *L. dispar* caterpillars are a key cue to locate host larvae by *Glyptapanteles liparidis* parasitic wasps [22]. Such volatiles are also expected to govern prey-finding in parasitoids and predators of *A. biguttatus* and *P. cylindrus*.

Recommendations
A holistic approach on the direct and indirect chemical resistance system of oak trees is needed to provide better understanding of the semiochemicals acting in different interactions with pest and disease organisms, similar to those for elm trees (*Ulmus*) [23]. This would provide the underpinning science for development of semiochemical-based interventions for oak tree pest management.

Furthermore, the use of smart sensors tuned to characteristic stress oak volatiles or herbivore pheromone compounds as biomarkers would potentially provide field diagnostics of symptomatic trees under stress by microorganisms (bacteria, fungi) or herbivore insects, and provide the basis for management of declines in forests.

A strategic plan for implementing the holistic approaches for forest pest management is urgently required.

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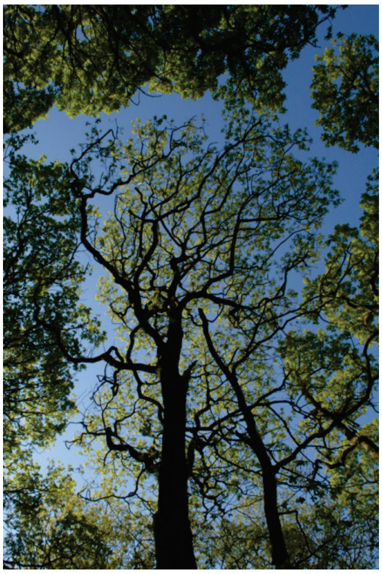
The Action Oak public/private partnership is a new initiative to protect and improve the UK's oak trees – acknowledging their iconic and important role and responding to concerns over multiple threats to their health. This knowledge review was commissioned by Defra on behalf of the partnership to establish a baseline against which new knowledge is gained and proposals for new research are assessed.



The review aims to provide a clear, succinct assessment of the current evidence on oak health in all its dimensions and identify evidence gaps and priority research needs. The review addresses oak throughout the UK, in woodlands and other settings (e.g. hedgerows and as individual trees), both the existing cohort of oak trees (reflecting the historical legacies) and those of the future. It takes a broad perspective on oak health (encompassing current and foreseeable threats) and the drivers/factors shaping the UK's oak demography. This report provides a summary of the evidence and identifies the major gaps – so that further research and action can be initiated. It is not an exhaustive scientific literature review, more a 'state of the art' account of relevant information.

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