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A review on oak decline: The global situation, causative factors, and new research approaches

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Abstract

Oak decline as a complex syndrome is one of the most relevant forest diseases worldwide. This disease has a complex and multifactorial nature, and this has caused conventional methods in plant pathology not to provide researchers with a correct and comprehensive analysis of oak decline. This issue entails the need for a multidisciplinary approach in examining and evaluating the disease, which will provide researchers with a more exhaustive understanding of the disease. The present review examines the concept of decline, the factors that contribute to the occurrence and development of the disease, its global distribution, and indexes used in the assessment of the disease. Furthermore, it draws attention to various research approaches that have been utilized to investigate oak decline.

Additional key words: *Quercus*; disease; remote sensing; metagenomics.

Abbreviations used: AI (artificial intelligence) ANNs (artificial neural networks), AOD (acute oak decline); COD (chronic oak decline); DAI (decline acuteness index); LiDAR (light detection and ranging); PDI (phenotypic decline index).

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Supplementary material (Table S1) accompanies the paper on Forest System's website

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Introduction

Oak trees (*Quercus* spp.) have a high level of genetic variability and about 450 different species have been identified in the world (Sun et al., 2021). This genus is native to the Northern Hemisphere and has a wide habitat in Europe (England, Ireland, France, Spain, Germany, Italy, Poland, Romania, etc.), Asia (Iran, Turkey, part of Afghanistan, Pakistan, Indochina, etc.), America (USA, Mexico, Guatemala, Colombia, etc.), and North Africa (Morocco, Tunisia, and Algeria). The largest number of oak species is in North America, with approximately 160

species in Mexico of which 109 are endemic and about 90 in the United States. China has approximately 100 species of oak, making it the second region with a vast variety of this taxon of tree (Hogan, 2011).

Oak decline is a significant issue in oak forests worldwide. In recent years, millions of oaks around the world have died as a result of this phenomenon (Laakili et al., 2016; Attarod et al., 2017). It would have a significant negative impact on wildlife, as many species depend on oak trees for both habitat and food (McShea et al., 2007). Oak decline has been recorded since the mid-1700s with high frequency around the world from the 1980s

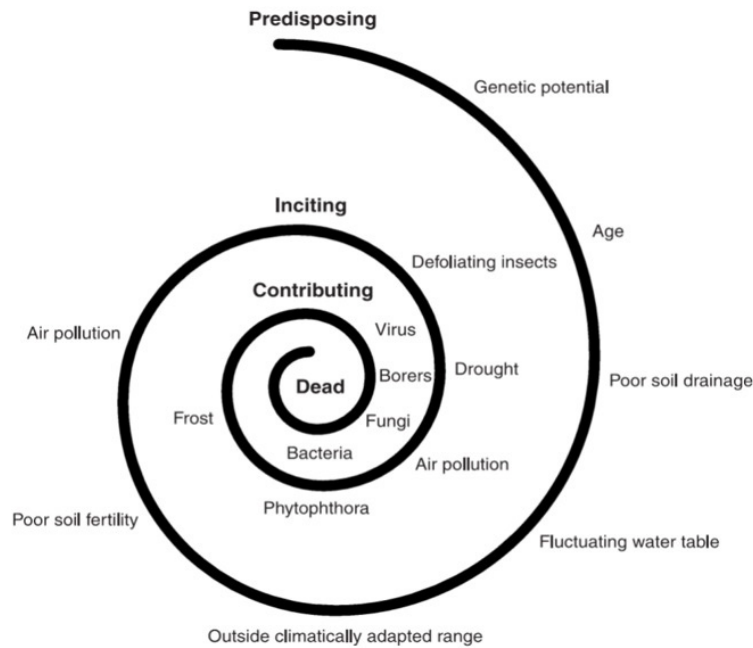


Figure 1. Interaction of possible biotic and abiotic factors involved in oak decline (Manion, 1981).

onwards (Thomas, 2008), being recognized as a major challenge to environmental management in wide areas such as Mediterranean climate zones of the Northern Hemisphere.

The concept of decline disease has been revised by multiple authors (Ostry et al., 2011). These revisions generally maintain many of Sinclair's (1967) original ideas. Sinclair's concept of decline is perhaps the most versatile and adaptable to various situations, as it encompasses multiple concepts (Sinclair, 1967; Sinclair & Hudler, 1988). By recognizing that decline diseases differ in the types and sequences of causal factors, he avoids trying to fit all declines into a single pattern. Sinclair defines decline as the premature, progressive loss of vitality caused by stressing factors over a period of years. He presents several interesting propositions, which could be viewed as principles that are helpful in understanding decline diseases (Sinclair, 1965, 1967; Sinclair & Hudler, 1988; Sinclair & Lyon, 2005). Shigo (1986) defines decline as a general loss in vitality over the entire tree caused by a systemic disease or by a series of events that disrupt essential life processes. Manion (1981) and Manion & Lachance (1992) defined decline as an interaction of interchangeable abiotic and biotic factors that produce a gradual general deterioration of trees, often leading to their death. Recently, Rodriguez-Calcerrada et al. (2017) summarized tree decline as a visible lack of vigor in mature individuals that, by age, should be exhibiting near-optimal performance. According to Denman et al. (2022), decline diseases involve individual predisposing factors that may occur in phases or waves, but there is continuous overall predisposition pressure that disrupts the normal

functioning of the tree. Based on the definition of disease as a deviation from the normal functioning of an organism caused by a continuously applied factor or irritation, it is clear that declines fit within this definition and can be classified as a disease.

There are several important points to consider when discussing the decline phenomenon, such as the need to distinguish between "forest decline" and "tree decline". Forest decline refers to the large-scale deterioration and mortality of one or more tree species, whereas tree decline typically occurs on a smaller scale, affecting individual trees or groups of trees, and is usually specific to certain species. Although distinguishing between the two is typically straightforward, it may become challenging if the situation is monospecific and of significant scale. Hence, it is vital to provide a comprehensive report of the condition including its nature, extent, and species affected. There are various types of forest declines caused by a wide range of single or interacting factors, but the causes of some forest declines may not be apparent at first. The knowledge of the scale and spatial distribution of affected trees and their species is crucial in understanding the causal factors that explain forest decline occurrences. For instance, large-scale forest decline in some areas was attributed to poor air quality due to high pollutant levels and acid rain. In other cases, the decline was due to non-synchronous fluctuations of forest conditions and recurrent episodes of defined and unresolved declines. It should be noted that cohort senescence, characterized by the synchronized death of senescent trees in an even-aged stands as part of primary succession, is distinct from decline diseases (Denman et al., 2022).

Factors involved in the oak decline

There are various theories about the occurrence of oak decline, but what most researchers agree on is that one factor can't be the only cause of this phenomenon, instead it is influenced by several factors that occur simultaneously or frequently (Crampton et al., 2020; Pourhashemi & Sadeghi, 2020; Finch et al., 2021). The multidimensionality of the disease has made it difficult to manage. Studies have shown that biotic factors such as oomycetes (Grunwald et al., 2012; Hyun & Choi, 2014; Forrestel et al., 2015), fungi (Costa et al., 2020, 2022; Denman et al., 2022), bacteria (Crampton et al., 2020; Gathercole et al., 2021; Denman et al., 2022), nematodes (Maleita et al., 2015; Pedram et al., 2018; Ahmadi et al., 2019), insects (Thomas, 2008; Brown et al., 2015; Haavik et al., 2015; Denman et al., 2022), viruses (Bandte et al., 2020), and hemiparasitic plants (e.g., mistletoe) (Dolezal et al., 2010, 2016), as well as abiotic factors such as drought, frost damage, soil waterlogging, cultural practices, air pollution, excess of nitrogen, and fires (Thomas et al., 2002; Thomas, 2008; Gentilesca et al., 2017; Denman et al., 2022; Machacova et al., 2022), are involved in this disease. As the oak phenology shifts due to global warming, abiotic factors are becoming increasingly important (Machacova et al., 2022). Climate change is causing the initiation of cambial activity and leaf

development earlier than several decades ago. This results in a higher risk of spring defoliation caused by late spring frost in the case of early oaks (Dantec et al., 2015; Puchalka et al., 2017). In the conceptual model for the interaction of abiotic and biotic factors crucial in the emergence of oak decline, we can consider three key factors: insect defoliation, summer drought with heat waves, and winter and/or spring frost (Thomas et al., 2002; Machacova et al., 2022).

The disease decline spiral (Fig. 1) addresses both the phenomenon of multidimensionality and the role of each factor in the disease cycle (Manion, 1981). By moving to the center of the spiral, apart from abiotic factors, an increase in the number of biotic factors involved in the disease becomes apparent. While abiotic factors can initiate the disease cycle and contribute to its continuation, biotic factors tend to play a more significant role in the later stages of the disease. The spiral emphasizes the interdependence of various factors in the disease cycle and underscores the need for a comprehensive approach to disease diagnosis and management. By understanding the role of each factor in the spiral, researchers and managers can develop strategies to break the cycle and prevent further tree decline. This may involve implementing measures such as proper tree care, monitoring for pests and diseases, and promoting healthy ecosystems (Thomas et al., 2002;

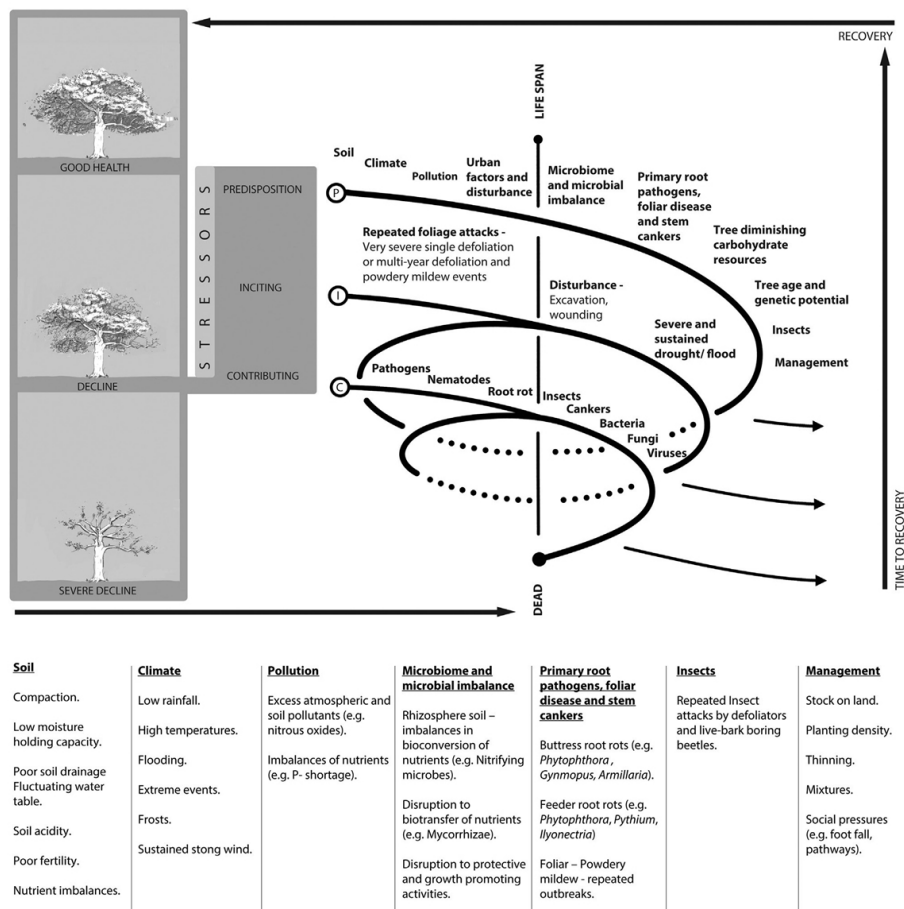


Figure 2. Decline disease spiral model revised by Denman et al. (2022).

Table 1. Phenotypic decline index (PDI) and decline acuteness index (DAI) indexes in the field of oak decline in assessing the disease status.

PDI		DAI		
Status	Domain	Syndrome	Status	Domain
Healthy	0.000	-	Neutral	0.000249
Moderate decline	0.524	AOD	Moderate	0.504000
		AOD	Severe	1.000000
Severe decline	1.000	COD	Moderate	-0.508000
		COD	Severe	-1.000000

AOD: acute oak decline. COD: chronic oak decline

Denman et al., 2014; Bendixsen et al., 2015; Haavik et al., 2015). Denman et al. (2022) suggest an update to the decline disease spiral model (Fig. 2), emphasizing the passage of time, which was implied in the original model but requires an annotation for clarity. They note that the original model did not include a microbial component in the predisposing phase, despite the crucial and under-researched role microorganisms can play in predisposition, considering both primary and secondary pathogens, as well as saprophytic and beneficial organisms. Non-lethal pathogens and insects can also play a significant role in predisposing trees through direct and indirect effects, such as feeder root necrosis and loss of ectomycorrhizal relationships, predisposing trees in an initial phase.

Symptoms and types of oak decline

The oak decline can be related with various symptoms depending on the environmental conditions and the tree species affected. Decline symptoms may include leaf yellowing, wilting, thinning of the crown, bark and cambium tissue necrosis, trunk cankers, and infestation by wood-boring beetles. The disease can lead to dieback of branches and twigs, reduced tree growth and vigor, and acorn production. Infected trees may also become more susceptible to other pests and diseases, and in severe cases, the disease can result in the tree's death. In fact, oak decline is a general term that refers to several health issues affecting oak trees. Due to the complexity of each type of decline and the need for effective management strategies, scientists have worked to identify the key components involved in these distinct diseases and establish proof of cause and effect. The rate of disease development and symptomatology are among the metrics used to differentiate types of decline (Denman et al., 2022).

According to scientific literature, oak decline can be classified into various types:

a) Chronic oak decline (COD): It is characterized by a slow development of symptoms and disease, which can take several decades with emphasis on failing root health as a primary causal factor of the decline. The disease is primarily

identified by thinning crowns, fine twig shedding, and stubby small branch ends. In advanced stages, the dieback of scaffold branches can occur. The mortality rate is low and some trees can recover partially or completely (Denman & Webber, 2009; Lonsdale, 2015; Gagen et al., 2019).

b) Sudden oak death: In most cases, due to biotic factors (usually pathogens), affected trees can die in a very short time. An example is a sudden oak death that occurred on the coast of California in the mid-1990s due to the phytopathogenic oomycete *Phytophthora ramorum* (Rizzo et al., 2002; Grunwald et al., 2012; Forrestel et al., 2015).

c) Acute oak decline (AOD): It is a recently identified decline disease affecting native oak species in the United Kingdom (*Quercus robur* and *Q. petraea*). It has also been reported in other European countries as well as the Middle East (Iran) on other species such as *Q. ilex*, *Q. castaneifolia*, *Q. pyrenaica*, *Q. fabri*, *Q. brantii*, *Q. suber*, *Q. cerris*, *Q. pubescens*, *Q. rubra* (Moradi-Amirabad et al., 2019; Ruffner et al., 2020; Fernandes et al., 2022; Pernek et al., 2022). Acute oak decline is characterized by episodes of rapid decline over 5-10 years, associated with high levels of tree mortality although sometimes trees may stabilise and even recover. There are four primary characteristics that define the disease: weeping patches that are vertically aligned on the trunk of oak trees, cracks between bark plates that seep dark fluid, necrosis of the inner bark, and the presence of larval galleries of the oak buprestid, *Agilus biguttatus*, on the phloem-sapwood interface in over 90 percent of cases. Given the clear and distinctive symptoms associated with acute oak decline, it is hypothesized that it is a distinctive, identifiable condition within the broader oak decline syndrome (Denman et al., 2014, 2022; Brown et al., 2015; Crampton et al., 2020).

Distribution of oak decline in the world

The first verified reports of oak decline date back to the 18th and 19th centuries in Central Europe and Northeastern United States of America (USA), as recorded in the literature. From the 1900s to the 1970s, more cases of oak decline were reported in these regions and in adjacent areas

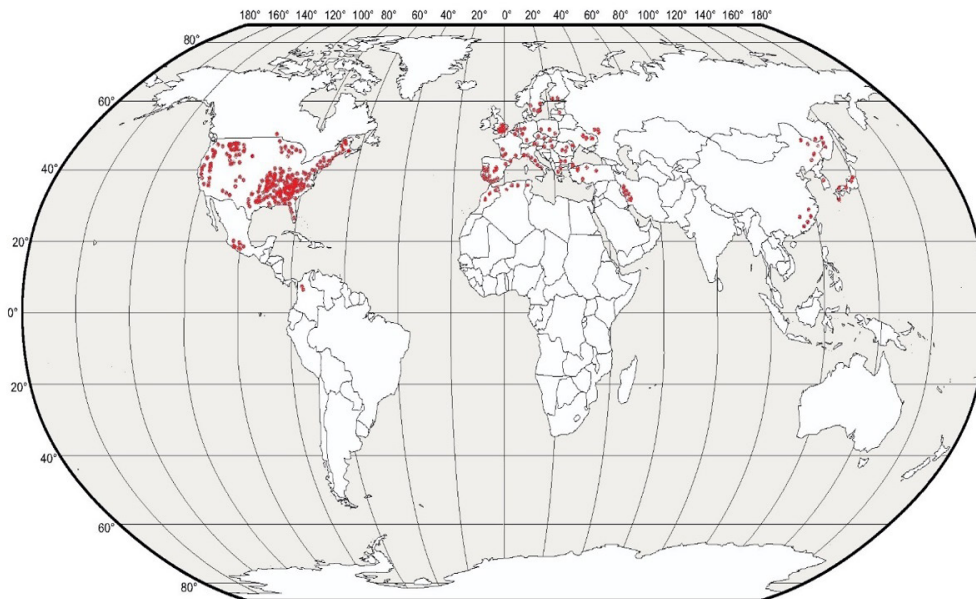


Figure 3. Map of the distribution of oak decline worldwide.

such as Western and Northeastern Europe and Central USA. During this time, deciduous oaks, particularly those from the *Quercus* and *Lobatae* groups, were the most affected by the decline. Starting from the 1980s, oak decline episodes were frequently reported across a wide range of northern hemisphere forests, affecting both deciduous species from the *Cerris* group and evergreen species such as *Q. ilex* from the *Ilex* group. Oak decline records emerged in Southern Europe, North Africa, Western USA, Mexico, Colombia, China, and Japan (Thomas, 2008; Gil-Pelegrin et al., 2008; Rodriguez-Calcerrada et al., 2017).

According to scientific sources, oak decline is currently affecting 39 countries worldwide. These countries are listed in Table S1 [suppl] and include Ukraine, Croatia, Colombia, Italy, the Netherlands, France, Germany, Bulgaria, Portugal, Austria, Switzerland, the Baltic States, Moldavia, Poland, Sweden, Spain, Mexico, Turkey, Japan, Belgium, Canada, Romania, Greece, the Czech Republic, UK, Algeria, China, Hungary, Iran, Latvia, Slovakia, Finland, South Korea, Russia, Slovenia, Serbia, USA, Tunisia, and Morocco (Fig. 3). As shown in Table S1, the framework used to present the distribution, factors, and host species is the same as that employed by Gottschalk & Wargo (1997). However, this paper provides new official records from around the world on previously unrecorded countries, biotic and abiotic agents, and hosts for oak decline. Some of these records were not mentioned in detail or were not included in Gottschalk & Wargo's study from 1997.

Disease assessment in oak decline via new indexes

Researchers use some indexes to evaluate plant diseases. This helps the management and epidemiology

of the diseases, including topics such as determining the number of losses, assessing the disease threshold for control, understanding the effectiveness or ineffectiveness of some treatments for the disease, and studying the resistance and tolerance levels of cultivars. Therefore, methods of assessing the incidence and severity of the disease are important issues. If they are not properly assessed, subsequent measures in its management may also fail. Assessments can vary depending on the host plant, the type of disease, and even the region of occurrence of the disease, and the same version of the assessment cannot be used for all diseases (Campbell & Neher, 1994; Chiang et al., 2017; Finch et al., 2021).

Numerous visual phenotypic descriptors aid in classifying declining oak trees. When severe decline occurs, symptoms such as low foliage density and multiple dead branches are noticeable. However, some symptoms develop slowly, particularly in cases of chronic decline, which can make it difficult to obtain a complete classification of healthy versus declining trees. Because the symptoms are evaluated visually, the results of the disease assessment will also be variable because of the several factors contributing to the oak decline and surveyor bias. Furthermore, differences in tree age and size at different geographical locations can make it difficult to objectively compare health status between sites. These factors must be standardized to reduce potentially distorting comparisons of tree health status (Pontius & Hallett, 2014; Denman et al., 2014, 2017; Ahmadi et al., 2019).

Recently, due to the importance of disease assessment, some researchers have made good efforts to achieve a valid disease assessment in oak decline (Finch et al., 2021). They analyzed the issues surrounding oak decline and then presented the phenotypic decline index (PDI) and

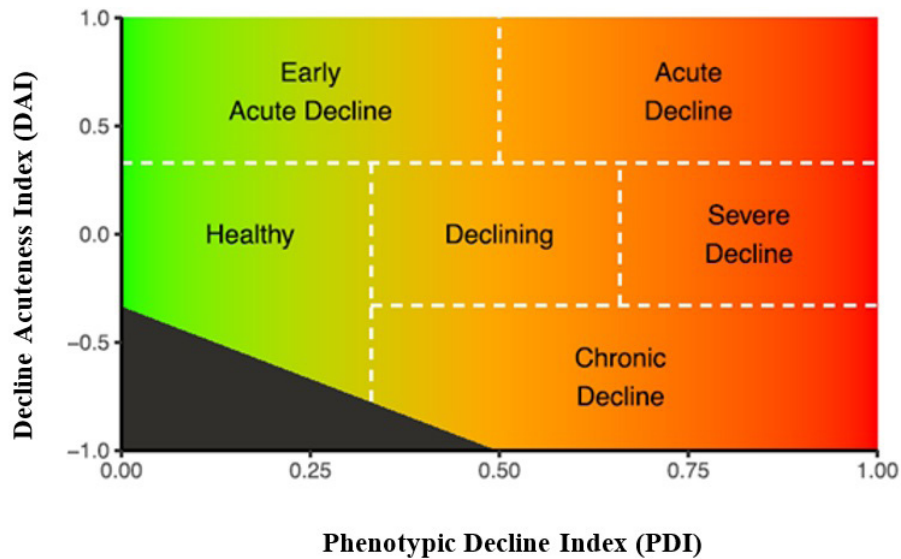


Figure 4. Two-dimensional continuum of the phenotypic decline indexes for oak decline severity (Finch et al., 2021).

the decline acuteness index (DAI). An important feature of the above study is that phenotypic descriptors are easily measurable in the field and based on well-established tree condition assessment protocols. In addition, the machine learning approach used to extract these indexes could be applied to long-established oak health monitoring programs to help sensitivity in diagnosing overall trends in tree health. The collected phenotypic measurements (36 descriptors) from 174 trees were checked from nine locations across England and included healthy, AOD, COD, and AOD trees in remission. PDI and DAI indexes derived from unsupervised random forest machine learning models, trained using the collected phenotypic information. PDI is an index to measure decline severity and DAI is an index to measure differentiating between chronically and acutely declining oak trees (Table 1). The results showed that two descriptors, crown condition, and trees size, contributed positively to the PDI. Trees with smaller crowns (less foliage and smaller canopy) in poor condition had greater PDI values. Descriptors including tree stature and the presence of stem bleeding, contributed a lot to the DAI, allowing differentiation between trees with AOD and COD syndromes. AOD trees had relatively larger stature and the presence of stem bleeding while COD trees had a small stature and stem bleeding was absent. PDI and DAI indexes can be shown as a 2-dimensional continuum under which the spectrum of decline severity and type can be assessed (Fig. 4) (Finch et al., 2021). It is crucial to note in this section that the research by Finch et al. (2021) primarily focuses on AOD, and PDI and DAI are only validated for *Q. petraea* and *Q. robur*, which are significantly different from other *Quercus* species. Consequently, these phenotypic indexes must be adapted and validated for various *Quercus* species.

Research approaches in oak decline disease

Remote sensing data

Remote sensing data can provide valuable information for the assessment of oak decline, as it can capture detailed information on vegetation properties and structure at a large scale. Different remote sensing technologies, such as hyperspectral imaging, LiDAR, and satellite imagery, can be used to detect changes in vegetation properties related to oak decline. Remote sensing data can be analyzed using various techniques, such as machine learning algorithms, to identify complex patterns and relationships related to oak health and decline. These techniques can effectively process large volumes of data and provide valuable information for informed management decision-making. There are challenges and limitations to the use of remote sensing technologies for assessing oak decline. For example, the accuracy of the classification may be affected by factors such as atmospheric conditions, sensor calibration, and variations in vegetation properties. Nevertheless, remote sensing offers a valuable tool for assessing oak decline at a detailed level and detecting early signs of decline. By providing more precise information on vegetation properties, it can help to inform targeted management interventions aimed at mitigating the impact of the decline (Pontius et al., 2020; Liu et al., 2020).

Artificial neural networks (ANNs) in oak decline

Since oak decline is influenced by a range of environmental factors, and numerous parameters are

involved in this disease, identifying these factors and selecting an appropriate modeling approach are key challenges in this field. Accurately determining the factors that contribute to oak decline can be challenging due to the complexity of the disease and the numerous variables that can be involved. Therefore, selecting an appropriate modeling method is essential for accurately representing the complex relationships between environmental factors and oak decline (Ahmadi et al., 2014). Since the 1990s, artificial intelligence (AI) has been utilized to model processes with high complexity. Artificial neural networks (ANNs) is a notable example which have proven to be effective in modeling complex systems due to their ability to identify patterns and relationships in large datasets. ANNs consist of interconnected nodes, called “neurons”, organized into layers. The input layer receives data, which is then passed through one or more hidden layers that perform computations, before reaching the output layer. During the training process, ANNs learn to adjust the weights of the connections between neurons in order to optimize their performance on a specific task. Once the ANN has been trained, it can be used to make predictions or classifications on new input data (Rosa, 2013; Aggarwal, 2018).

In the context of oak decline, ANNs can be used to analyze large and complex datasets that include environmental and biological variables. These variables can include factors such as climate data, soil conditions, tree age and species, as well as biotic factors such as pest and disease presence. By training ANNs on these datasets, researchers can identify patterns and relationships that are not easily discernible through traditional statistical methods as in Gutierrez-Giron et al. (2019) in Mediterranean forests predicting the severity and distribution of oak decline under future climate scenario, Guo et al. (2019) in the Loess Plateau of China and Martin-Benito et al. (2017) to improve the accuracy of oak decline risk assessment in Mediterranean woodlands and to identify the most important factors contributing to oak decline. Zhao & Zhang (2018) were able to accurately predict the risk of oak decline using ANNs and logistic regression. Li et al. (2020) developed multi-scale ANN models to predict oak decline through the use of environmental and biological variables at different spatial scales, including landscape, patch, and tree levels. This study highlights the potential of ANNs to incorporate information at multiple spatial scales in the study of oak decline.

There are potential troubleshooting challenges in the use of AI methods for oak decline assessment. One of the main challenges is the need for large amounts of high-quality data to train the ANN models effectively. In addition, the results of ANN models can be difficult to interpret and explain, which can limit their usefulness for informing management decisions. Furthermore, different studies may use different datasets or modeling approaches, which can lead to inconsistencies or contradictions in the results

(Zhang et al., 2018). This highlights the importance of considering multiple modeling approaches and comparing their results to identify the most accurate and reliable predictions. With continued research and development, AI methods have the potential to contribute significantly to our understanding of oak decline and inform management decisions to mitigate its impact.

Metagenomics in oak decline

Metagenomics, the study of genetic material recovered directly from environmental samples, has emerged as a powerful tool in understanding the complex microbial communities in forest ecosystems. Over the last decade, there has been a growing interest in the use of metagenomics in studying forest decline and identifying the role of microbial communities in maintaining healthy forest ecosystems (Cardenas et al., 2015; Eaton et al., 2017; Denman et al., 2018b; Venice et al., 2021). Metagenomics has been used to develop new approaches for forest restoration. A study by Bahram et al. (2013) used metagenomics to assess the impact of different forest restoration strategies on the microbial communities in degraded forests, suggesting that microbial diversity is an important factor in the success of forest restoration efforts. This technique has also been used to identify potential bioindicators of soil health and forest decline (Deveau et al., 2018; Duque-Zapata et al., 2023).

Recently, there has been a growing interest in studying the microbiome of oak ecosystems and its potential role in oak decline. The use of metagenomics in oak decline research has often involved comparing the microbial communities associated with healthy trees and diseased trees to identify potential differences and determine which microbial taxa or pathways may be involved in oak decline (Lamichhane & Venturi, 2015; Broberg et al., 2018; Denman et al., 2018b; Pinho et al., 2020). However, it's worth noting that not all studies have focused solely on comparing the microbiome of healthy and diseased trees. Some studies have also investigated the impact of environmental factors, such as soil type and tree age (Meaden et al., 2016; Denman et al., 2018a), physicochemical properties (Poudel et al., 2020) and land use (Barrios-Masias et al., 2019), on the microbial communities of oak ecosystems, or have examined the potential role of specific microbial taxa or functional genes in oak health and decline (Barcenas-Moreno et al., 2019). In addition to metagenomics, some studies on oak decline are using multi-omic methods such as metatranscriptomics (Barcenas-Moreno et al., 2019; Poudel et al., 2020) and metaproteomics (Poudel et al., 2020) to investigate the functional potential and activity of microbial communities associated with oak ecosystems.

The rhizosphere is indeed the front line of plant defense against pathogens, and it can help plants overcome biotic and abiotic stresses (Mendes et al., 2013; Berg et al., 2014;

Munir et al., 2022). Deepening studies on the rhizosphere microbiome of oak trees can be effective in managing oak decline by identifying dominant microbial plant growth promoters and understanding the complex interactions between microbes and oak trees. Studying the rhizosphere microbiome of oak trees can also help identify potential biocontrol agents that can be used to manage oak decline (Fernandez-Gonzalez et al., 2017; Poudel et al., 2020). Overall, these studies highlight the importance of studying the rhizosphere microbiome of oak trees for managing oak decline and promoting oak health. By identifying dominant microbial plant growth promoters and potential biocontrol agents, researchers can develop effective strategies for managing oak decline and mitigating the impact of disease-causing pathogens.

Conclusion

Oak decline refers to a complex and multifactorial disease that affects oak trees. It is characterized by a range of symptoms, including leaf discoloration, premature leaf drop, canopy thinning, and dieback of branches and twigs. The disease can be caused by a variety of factors, including insect infestations, diseases, climate change, and environmental stressors. Oak decline can have significant ecological and economic impacts, as oak trees are important components of many forest ecosystems with a key role in their economic sustainability. Effective diagnosis and management of oak decline is therefore critical for preserving oak populations and maintaining healthy and sustainable forest ecosystems. Due to the multifactorial and complex nature of oak decline, it requires a comprehensive approach for effective diagnosis and management. Traditional methods of disease diagnosis and management may not be sufficient to address the multifaceted nature of oak decline. However, advances in fields such as artificial intelligence, remote sensing, and metagenomics show great promise in providing a more comprehensive understanding of the disease and its underlying causes. Several studies have demonstrated the usefulness of these tools in identifying key biotic and abiotic factors involved in oak decline, allowing for more accurate disease diagnosis and targeted management strategies. By using these tools, we can better understand the complex interactions between the oak tree and its environment, ultimately leading to more effective disease control and preservation of oak populations for future generations.

Authors' contributions

Conceptualization: M. Kowsari, E. Karimi

Data curation: M. Kowsari, E. Karimi

Formal analysis: Not applicable

Funding acquisition: M. Kowsari

Investigation: M. Kowsari, E. Karimi

Methodology: Not applicable

Project administration: M. Kowsari

Resources: M. Kowsari

Software: Not applicable

Supervision: M. Kowsari

Validation: M. Kowsari, E. Karimi

Visualization: M. Kowsari, E. Karimi

Writing – original draft: M. Kowsari, E. Karimi

Writing – review & editing: M. Kowsari, E. Karimi

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Table 1. Distribution of oak decline in the world including the oak species and biotic/abiotic factors involved in the disease

Continent	Oak species	Abiotic factors	Biotic factors	References
<i>Asia</i>				
China	<i>Q. dentate</i> <i>Q. mongolica</i> <i>Q. variabilis</i>	Drought	<i>Armillaria</i> spp. (fungus) <i>Cytospora quercinum</i> (fungus) <i>C. vinacea</i> (fungus) <i>Coryneum sinense</i> (fungus) <i>Co. songshanense</i> (fungus) <i>Cryphonectria quercus</i> (fungus) <i>Cr. quercicola</i> (fungus) <i>Cr. japonica</i> (fungus) <i>Dendrostoma quercus</i> (fungus) <i>D. donglinensis</i> (fungus) <i>D. parasiticum</i> (fungus) <i>D. qinlingense</i> (fungus) <i>D. quercinum</i> (fungus) <i>D. dispersum</i> (fungus) <i>Diatrype quercicola</i> (fungus) <i>Diplodia quercicola</i> (fungus) <i>Cyrtopistomus castaneus</i> (insect)	Zhu et al., 2012 Gottschalk & Wargo, 1997
Far East Russia	<i>Q. dentate</i> <i>Q. mongolica</i> <i>Q. robur</i>	Drought	<i>Armillaria</i> spp. (fungus) <i>Ophiostoma grandicarpum</i> (fungus) <i>O. fusiforme</i> -like (fungus) <i>O. quercus</i> (fungus) <i>Lymantria dispar</i> (insect) <i>Operophtera brunata</i> (insect)	Selochnik et al., 2015 Gottschalk & Wargo, 1997
Japan	<i>Q. serrata</i> <i>Q. mongolica</i> <i>Q. crispula</i> <i>Q. dentate</i> <i>Q. myrsinifolia</i>	Drought	<i>Armillaria</i> spp. (fungus) <i>Ophiostorna</i> spp. (fungus) <i>Raffaelea quercivora</i> (fungus) <i>Platypus quercivorus</i> (insect) <i>Bursaphelenchus parvispicularis</i> (nematode) <i>Xanthomonas arboricola</i> (bacterium)	Kamata et al., 2002 Kanzaki & Futai, 2005 Gottschalk & Wargo, 1997
Iran	<i>Q. brantii</i> <i>Q. infectoria</i> <i>Q. libani</i> <i>Q. castaneifolia</i> <i>Q. macranthera</i>	Drought Dust Cultural practices	<i>Loranthus europaeus</i> (plant/mistletoe) <i>Biscogniauxia mediterranea</i> (fungus) <i>Obolarina persica</i> (fungus) <i>Inonotus krawtzevii</i> (fungus) <i>Epicoccum nigrum</i> (fungus) <i>Chaetomium globosum</i> (fungus) <i>Immersidiscosia eucalypti</i> (fungus) <i>Kalmusia variispora</i> (fungus) <i>Petriella sordida</i> (fungus) <i>Neocamarosporium obiones</i> (fungus) <i>Sordaria fimicola</i> (fungus) <i>Paecilomyces formosus</i> (fungus) <i>Phaeoacremonium tuscanicum</i> (fungus) <i>Discula quercina</i> (fungus) <i>Armillaria mellea</i> (fungus) <i>Dematophora</i> sp. (fungus) <i>Fusarium</i> sp. (fungus) <i>Alternaria</i> spp. (fungus) <i>Phytophthora cryptogea</i> (oomycetes) <i>Pythium aphenidermatum</i> (oomycetes) <i>Megopsis scabricornis</i> (insect) <i>Osphranteria coerulescens</i> (insect) <i>Acmaeodera wethloi</i> (insect) <i>Lugubris longicollis</i> (insect) <i>Laimaphelenchus belgradiensis</i> (nematode) <i>L. hyrcanus</i> (nematode) <i>Bacillus pumilus</i> (bacterium) <i>Brenneria goodwinii</i> (bacterium) <i>Rahnella victoriana</i> (bacterium) <i>B. roseae subsp. roseae</i> (bacterium) <i>Stenotrophomonas maltophilia</i> (bacterium)	Mirabolfathy, 2013 Ghobad-Nejhad et al., 2018 Moradi-Amirabad et al., 2019 Ahmadi et al., 2019 Alidadi et al., 2019 Alidadi et al., 2020 Pourhashemi & Sadeghi, 2020 Bakhshi ganje et al., 2020
South Korea	<i>Q. mongolica</i> <i>Q. serrata</i> <i>Q. variabilis</i> <i>Q. acutissima</i> <i>Q. aliena</i> <i>Q. dentata</i>	Drought	<i>Raffaelea quercus-mongolicae</i> (fungus) <i>Phytophthora</i> spp. (as a threat)	Hyun & Choi, 2014 Nguyen et al., 2020

Turkey	<i>Q. petraea</i> <i>Q. cerris</i> <i>Q. robur</i> <i>Q. hartwissiana</i> <i>Q. frainetto</i> <i>Q. vulcanica</i>	Drought	<i>Phytophthora quercina</i> (oomycetes) <i>P. citricola</i> (oomycetes) <i>P. plurivora</i> (oomycetes) <i>Pythium anandrum</i> (oomycetes)	Balci & Halmschlager, 2002 Balci & Halmschlager, 2003
Europe				
Austria	<i>Q. petraea</i> <i>Q. robur</i>	Soil/Site conditions	<i>Loranthus europaeus</i> (plant/mistletoe) <i>Ceratocystis</i> spp. (fungus) <i>Phytophthora quercina</i> (oomycetes) <i>P. citricola</i> (oomycetes)	Berger & Glatzel, 1994 Gottschalk & Wargo, 1997
Belgium Netherlands	<i>Q. petraea</i> <i>Q. robur</i>	Drought Excess moisture Frost damage	<i>Armillaria</i> spp. (fungus) <i>Verticillium</i> sp. (fungus) <i>Agrilus biguttatus</i> (insect) <i>Operopthera brumata</i> (insect)	Vansteenkiste et al., 2004 Losseau et al., 2020 Oosterbaan & Nabuurs, 1991 Gottschalk & Wargo, 1997
Bulgaria	<i>Q. cerris</i>	Drought	<i>Armillaria</i> spp. (fungus) <i>Ganoderma</i> (fungus) <i>Diplodia mutila</i> (fungus) <i>Hypoxyylon mediterraneum</i> (fungus)	Alexandrov & Rosnev, 1992 Gottschalk & Wargo, 1997
Czech Republic Slovakia	<i>Q. cerris</i> <i>Q. petraea</i> <i>Q. robur</i>	Drought Air pollution	<i>Loranthus europaeus</i> (plant/mistletoe) <i>Ophiostoma</i> spp. (fungus) <i>Diaporthe fasciculata</i> (fungus) <i>Ceratocystis fagacearum</i> (fungus) <i>Agrilus</i> spp. (insect)	Dolezal et al., 2010 Saniga et al., 2014 Gottschalk & Wargo, 1997
Finland	<i>Q. robur</i>	Drought	-	Sohar et al., 2014
France	<i>Q. ilex</i> <i>Q. petraea</i> <i>Q. pubescens</i> <i>Q. robur</i> <i>Q. suber</i>	Drought Frost damage Soil/Site factors Off-Site planting	<i>Collybia fusipes</i> (fungus) <i>Armillaria</i> spp. (fungus) <i>Ceratocystis</i> spp. (fungus) <i>Ophiostoma</i> spp. (fungus) <i>Collybia fusipes</i> (fungus) <i>Erysiphe alphitoides</i> (fungus) <i>Erysiphe quercicola</i> (fungus) <i>Phytophthora cinnamomi</i> (oomycetes) <i>Agrilus</i> spp. (insect) <i>Platypus cylindrus</i> (insect)	Delatour & Morelet, 1991 Gottschalk & Wargo, 1997
Germany	<i>Q. petraea</i> <i>Q. robur</i> <i>Q. rubra</i>	Drought Frost damage Excess nitrogen	<i>Armillaria</i> spp. (fungus) <i>Ophiostoma (Ceratocystis)</i> spp. (fungus) <i>Collybia fusipes</i> (fungus) <i>Microsphaera alphitoides</i> (fungus) <i>Phytophthora</i> spp. (oomycetes) <i>Agrilus biguttatus</i> (insect) <i>Operopthera brumata</i> (insect) <i>Tortrix viridana</i> (insect) <i>Emaravirus</i> (virus)	Falck, 1918 Hartmann et al., 1991 Thomas et al., 2002 Bandte et al., 2020 Gottschalk & Wargo, 1997
Switzerland	<i>Q. robur</i> <i>Q. petraea</i> <i>Q. cerris</i> <i>Q. pubescens</i> <i>Q. rubra</i>	Drought followed by a high frost	<i>Amphiporthe leiphaemia</i> (fungus) <i>Pezicula cinnamomea</i> (fungus) <i>Phomopsis quercella</i> (fungus) <i>Fusarium</i> sp. (fungus) <i>Dichomera saubinetii</i> (fungus) <i>Colpoma quercinum</i> (fungus) <i>Brenneria goodwinii</i> (bacterium) <i>Gibbsiella quercinecans</i> (bacterium) <i>Rahnella victoriana</i> (bacterium)	Sieber et al., 1995 Ruffner et al., 2020
Serbia	<i>Q. robur</i> <i>Q. cerris</i>	Drought Inappropriate forest management	-	Cater et al., 2008 Stojanovic et al., 2015a Stojanovic et al., 2015b
Croatia	<i>Q. ilex</i> <i>Q. cerris</i> <i>Q. pubescens</i>	Drought	<i>Biscogniauxia mediterranea</i> (fungus) <i>Brenneria goodwinii</i> (bacteria) <i>Gibbsiella quercinecans</i> (bacteria) <i>Lonsdalea britannica</i> (bacteria) <i>Agrilus sulcicolis</i> (insect) <i>A. olivicolor</i> (insect)	Prpic & Raus, 1987 Diminic et al., 2019 Pernek et al., 2022
Greece	<i>Q. coccifera</i>	-	<i>Diplodia corticola</i> (fungus)	Tsopelas et al., 2010
Slovenia	<i>Q. robur</i>	Drought	-	Cater et al., 2008 Cater, 2015
Hungary	<i>Q. petraea</i> <i>Q. robur</i> <i>Q. cerris</i>	Drought Excess moisture Frost damage Soil/Site conditions	<i>Armillaria</i> spp. (fungus) <i>Ceratocystis fagacearum</i> (fungus) <i>Ophiostoma</i> spp. (fungus) <i>Collybia fusipes</i> (fungus) <i>Verticillium dahliae</i> (fungus) <i>Agrilus</i> spp. (insect)	Misik et al., 2013 Gottschalk & Wargo, 1997
Latvia	<i>Quercus robur</i>	Drought	<i>Brenneria goodwinii</i> (bacteria) <i>Gibbsiella quercinecans</i> (bacteria)	Matisons et al., 2013 Zalkalns & Celma, 2021

Moldavia Ukraine Western Russia	<i>Q. ineretina</i> <i>Q. longipes</i> <i>Q. petraea</i> <i>Q. robur</i>	Drought Silvicultural manipulations	<i>Armillaria</i> spp. (fungus) <i>Ophiostoma</i> spp. (fungus) <i>Agrilus</i> spp. (insect)	Lobanov & Rozkov, 1972 Gottschalk & Wargo, 1997
Poland	<i>Q. robur</i>	Drought Frost damage	<i>Armillaria</i> spp. (fungus) <i>Ceratocystis</i> spp. (fungus) <i>Fusicoccum quercus</i> (fungus) <i>Ophiostoma</i> spp. (fungus) <i>Tortrix viridana</i> (insect) Defoliation (insect)	Siwecki & Ufnalski, 1998 Gottschalk & Wargo, 1997
Sweden	<i>Q. robur</i>	Drought	<i>Phytophthora quercina</i> (oomycetes) <i>P. cactorum</i> (oomycetes) <i>P. cambivora</i> (oomycetes) Defoliation - insect	Sonesson, 1999
Italy	<i>Q. cerris</i> <i>Q. fainetto</i> <i>Q. ilex</i> <i>Q. pubescens</i> <i>Q. robur</i> <i>Q. suber</i>	Drought	<i>Armillaria</i> spp. (fungus) <i>Apiognomonium quercina</i> (fungus) <i>Colpoma quercinum</i> (fungus) <i>Collybia fusipes</i> (fungus) <i>Ganoderma</i> (fungus) <i>Diplodia mutila</i> (fungus) <i>Diplodia corticola</i> (fungus) <i>Hypoxylon mediterraneum</i> (fungus) <i>Phomopsis quercina</i> (fungus) <i>Stuartella formosa</i> (fungus) <i>Phytophthora cinnamomi</i> (oomycetes) <i>P. quercina</i> (oomycetes) <i>P. pseudocryptogea</i> (oomycetes) <i>P. tyrrhenica</i> (oomycetes) <i>P. gonapodyides</i> (oomycetes) <i>P. psychrophila</i> (oomycetes) <i>P. syringae</i> (oomycetes) <i>Bursaphelenchus eremus</i> (nematode) Defoliation - insects	Ragazzi et al., 1989 Seddaiu et al., 2020 Gottschalk & Wargo, 1997
Portugal	<i>Q. suber</i> <i>Q. cerris</i> <i>Q. ilex</i>	Drought Cultural practices	<i>Armillaria</i> spp. (fungus) <i>Hypoxylon mediterraneum</i> (fungus) <i>Diplodia corticola</i> (fungus) <i>Brenneria goodwinii</i> (bacterium) <i>Phytophthora cinnamomi</i> (oomycetes) <i>Platytypus cylindrus</i> (insect) <i>Laimaphelenchus heidelbergi</i> (nematode)	Brasier et al., 1993 Maleita et al., 2015 Fernandes et al., 2022 Gottschalk & Wargo, 1997
Spain	<i>Q. canariensis</i> <i>Q. faginea</i> <i>Q. ilex</i> <i>Q. pyrenaica</i> <i>Q. suber</i> <i>Q. lusitanica</i>	Drought	<i>Diplodia mutila</i> (fungus) <i>Diplodia corticola</i> (fungus) <i>Hypoxylon mediterraneum</i> (fungus) <i>Armillaria</i> spp. (fungus) <i>Biscogniauxia mediterranea</i> (fungus) <i>Phomopsis</i> sp. (fungus) <i>Apiognomonium errabunda</i> (fungus) <i>Cryptospora quercis</i> (fungus) <i>Coryneum</i> spp. (fungus) <i>Phytophthora cinnamomi</i> (oomycetes) <i>P. quercina</i> (oomycetes) <i>P. psychrophila</i> (oomycetes) <i>P. plurivora</i> (oomycetes) <i>Platytypus cylindrus</i> (insect) <i>Tortrix viridana</i> (insect) <i>Lymantria dispar</i> (insect) <i>Malacosoma neustria</i> (insect) <i>Periclista Andrei</i> (insect) <i>Lonsdalea iberica</i> (bacterium) <i>Gibbsiella quercinecans</i> (bacterium)	Gallego et al., 1999 Perez-Sierra et al., 2013 Gottschalk & Wargo, 1997 Gallego et al., 1999 Perez-Sierra et al., 2013 Gottschalk & Wargo, 1997
United Kingdom	<i>Q. petraea</i> <i>Q. robur</i> <i>Q. cerris</i> <i>Q. fabri</i>	Drought Frost damage	<i>Armillaria</i> spp. (fungus) <i>Pezicula</i> sp. (fungus) <i>Botryosphaeria stevensii</i> (fungus) <i>Fusarium solani</i> (fungus) <i>Neonectria</i> spp. (fungus) <i>Agrilus biguttatus</i> / <i>Agrilus</i> spp. (insect) <i>Brenneria goodwinii</i> (bacterium) <i>Gibbsiella quercinecans</i> (bacterium) <i>Erwinia billingiae</i> (bacterium) <i>Rahnella victoriana</i> (bacterium) <i>Lonsdalea britannica</i> (bacterium) <i>Pseudomonas taxon fulva-like</i> (bacterium)	Gibbs & Greig, 1997 Denman et al., 2010 Denman et al., 2014 Denman et al., 2017 Denman et al., 2022 Brown et al., 2017 Gottschalk & Wargo, 1997

Romania	<i>Q. cerris</i> <i>Q. frainetto</i> <i>Q. pedunculiflora</i> <i>Q. petraea</i> <i>Q. pubescens</i> <i>Q. robur</i>	Drought Soil/Site conditions	<i>Armillaria</i> spp. (fungus) <i>Ophlostoma</i> spp. (fungus) Defoliation (insect)	Simonca & Taut, 2010 Gottschalk & Wargo, 1997
America				
North America				
Western United States	<i>Q. douglasii</i> <i>Q. agrifolia</i> <i>Q. lobato</i> <i>Q. engelmannii</i> <i>Q. kelloggii</i> <i>Q. palustris</i> <i>Q. rubra</i>	Drought Excess moisture Air pollution	<i>Phoradendron villosum</i> (plant/mistletoe) <i>Armillaria</i> spp. (fungus) <i>Diplodia quercina</i> (fungus) <i>Cryptocline cinerescens</i> (fungus) <i>Discula quercina</i> (fungus) <i>Ceratocystis fagacearum</i> (fungus) <i>Phytophthora cinnamomi</i> (oomycetes) <i>Phytophthora ramorum</i> (oomycetes) <i>Agrilus</i> spp. (insect) <i>Lymantria dispar</i> (insect) <i>Gibbsiella greigii</i> (bacterium) <i>Lonsdalea quercina</i> (bacterium)	Bendixsen et al., 2015 Gottschalk & Wargo, 1997
Eastern United States	<i>Q. alba</i> <i>Q. coccinea</i> <i>Q. ellipsoidalis</i> <i>Q. palustris</i> <i>Q. prinus</i> <i>Q. rubra</i> <i>Q. velutina</i> <i>Q. falcata</i> , <i>Q. laurifolia</i> <i>Q. marilandica</i> <i>Q. nigra</i> , <i>Q. phellos</i> <i>Q. stellate</i> <i>Q. uehlenbergii</i>	Drought Excess moisture Air pollution	<i>Armillaria</i> spp. (fungus) <i>Hypoxylon atropunctatum</i> (fungus) <i>Biscogniauxia mediterranea</i> (fungus) <i>Botryosphaeria obtuse</i> (fungus) <i>Discula quercina</i> (fungus) <i>Phytophthora cinnamomi</i> (oomycetes) <i>Agrilus bilineatus</i> (insect) <i>Enaphalodes rufulus</i> (insect)	Bendixsen et al., 2015 Gottschalk & Wargo, 1997
Canada	<i>Q. alba</i> <i>Q. coccinea</i> <i>Q. rubra</i> <i>Q. macrocarpa</i>	Drought	<i>Armillaria</i> spp. (fungus) <i>Agrilus</i> spp. (insect)	Catton et al., 2007 Gottschalk & Wargo, 1997
Mexico	<i>Q. glaucooides</i> <i>Q. peduncularis</i> <i>Q. salicifolia</i> <i>Q. affinis</i>	Drought Air pollution	<i>Phoradendron villosum</i> (plant/mistletoe) <i>Hypoxylon</i> spp (fungus) <i>Ganoderma</i> spp. (fungus) <i>Armillaria</i> sp. (fungus) <i>Apiognomonia quercina</i> (fungus) <i>Phytophthora cinnamomi</i> (oomycetes) <i>Pythium</i> sp. (oomycetes) <i>Andricus quercuslaurinus</i> (insect) Overgrazing	Tainter et al., 2000
South America				
Colombia	<i>Q. humboldtii</i>	Drought	Hemiparasitic plants <i>Phialophora</i> sp. (fungus) <i>Pestalotia</i> sp. (fungus) <i>Dothiorella</i> sp. (fungus) Defoliation (insect) Nematode	Ramirez Corea, 1988
Africa				
Morocco Tunisia Algeria	<i>Q. suber</i> <i>Q. ilex</i>	Drought	<i>Hypoxylon mediterraneum</i> (fungus) <i>Biscogniauxia mediterranea</i> (fungus) <i>Botryosphaeria corticola</i> (fungus) <i>Ophiostoma quercus</i> (fungus) <i>O. stenoceras</i> (fungus) <i>Phytophthora</i> spp. (oomycetes) <i>Ceramhyx</i> beetles (insect) <i>Platypus cylindrus</i> (insect) Human impact Overgrazing	Kim et al., 2017 Kim et al., 2017 Belhoucine et al., 201 Gottschalk & Wargo, 1997

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