Regional Epidemiological Divergence and Climate-Driven Range Dynamics of Oak Wilt (Bretziella fagacearum) in North American Oak Forests

by

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Keywords: Bretziella fagacearum; oak wilt; Quercus; oak; climate change; species distribution modeling; climate niche modeling; climatic suitability.

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Abstract

Oak wilt, caused by *Bretziella fagacearum*, is expanding beyond its historical U.S. range, and its confirmation in Canada has increased concern about future disease risk and management costs. The disease threatens oak-dominated forests and is difficult to eradicate once established, making early detection, sustained surveillance, and preventive management essential. Oak wilt epidemiology is influenced by climate-sensitive interactions among the host, pathogen, and insect vectors, but the implications of these relationships for future geographic suitability remain poorly resolved. This study first examined regional variation in oak wilt epidemiology and its underlying biotic and abiotic drivers and then evaluated where changing climatic conditions may permit future establishment and expansion.

A PRISMA-guided review of 121 studies revealed two mechanistically distinct epidemics. In the Lake States, seasonal insect transmission and spread through intertree root grafts produce disease-center expansion of 3.6-7.7 m yr^{-1}. In Texas, continuous clonal live-oak root systems and year-round transmission permit expansion approaching 40 m yr^{-1}. Four geographically structured pathogen populations further support regional divergence and help explain the limited transferability of management practices. The synthesis further showed that temperature regulates vector phenology, precipitation and moisture influence fungal mat development, and drought increases host susceptibility, linking regional epidemiology to climate.

Climatic suitability was modeled using 880 confirmed occurrences, 853 spatially stratified background locations, 25 predictors, and seven species distribution algorithms.

The four highest-performing models were combined in an AUC-weighted ensemble. Under repeated random 70/30 validation, the ensemble achieved high predictive performance (AUC = 0.940; TSS = 0.802). Independent spatial-block 90/10 validation produced an ensemble AUC of 0.955 and TSS of 0.754, indicating strong geographic discrimination with moderately lower threshold-dependent classification skill. Precipitation, climatic moisture, and relative humidity were the dominant predictors. Historical suitability covered 23.35% of North America and 17.91% of the Asia-Pacific region, including extensive areas beyond the pathogen's known distribution. Projections under SSP1-2.6, SSP2-4.5, and SSP3-7.0 consistently indicated future expansion. Under SSP3-7.0, by 2071-2100, the suitable area increased to 27.97% in North America and 26.16% in the Asia-Pacific region, with pronounced northward expansion in North America.

By linking climate-sensitive disease mechanisms with regional epidemiology and continental-scale projections, this thesis provides a novel integrated decision framework for surveillance, biosecurity, region-specific intervention, and climate-adaptive oak wilt management.

Artificial Intelligence (AI) Use Disclosure Statement

In the preparation of this thesis, the following Artificial Intelligence (AI) tools were used: Microsoft 365 Copilot. This tool was used primarily to support the presentation and readability of the text. The author acknowledges full responsibility for the intellectual content of this work and has ensured that all AI-assisted sections have been reviewed and revised for accuracy and appropriate academic style. All AI-generated content was reviewed and validated for relevance, appropriateness, and accuracy before incorporation into the final document to maintain scholarly integrity of this research.

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In the preparation of this thesis, the following digital accessibility tools were used to ensure this document complies with federal requirements: Microsoft Word Accessibility Checker. The author acknowledges full responsibility for the intellectual content of this work and has made a good faith effort to comply with digital accessibility requirements in publishing, wherein the nature of the content does not significantly change in order to do so. Furthermore, all content has been reviewed and revised to meet these requirements prior to final publication.

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List of Abbreviations

AFLP	Amplified Fragment Length Polymorphism
AFPE	Alien Forest Pest Explorer
ANUCLIM	Australian National University Climate
AUC	Area under the receiver operating characteristic curve
CAD	Canadian dollar
CCI	Chlorophyll/carotenoid index
CMIP6	Coupled Model Intercomparison Project Phase 6
CNMs	Climate niche models
CODIT	Compartmentalization of Disease in Trees
CRISPR	Clustered Regularly Interspaced Short Palindromic Repeats
DEM	Digital elevation model
DNA	Deoxyribonucleic acid
EASE-Grid	Equal-Area Scalable Earth Grid
EDC	Expanding disease center

EDDMapS	Early Detection and Distribution Mapping System
ENMs	Ecological niche models
EPA	Environmental Protection Agency
GATS	Global Agricultural Trade System
GBM	Gradient boosting machine
GCM	General circulation model
GDP	Gross domestic product
GNB	Gaussian naïve Bayes
IUCN	International Union for Conservation of Nature
LAMP	Loop-mediated isothermal amplification
LR	Logistic regression
MAT	Mean annual temperature
MaxEnt	Maximum entropy
MAXTHM	Mean daily maximum temperature of hottest month
MINTCM	Mean daily minimum temperature of the coldest month
NDVI	Normalized difference vegetation index

PCA	Principal component analysis
PREC	Precipitation
PRECCP	Precipitation of coldest three-month period
PRECHP	Precipitation of hottest three-month period
PRISMA	Preferred reporting items for systematic reviews and meta-analyses
qPCR	Quantitative polymerase chain reaction
RF	Random forest
RFLP	Restriction fragment length polymorphism
SDM	Species distribution model
SEDI	Symmetric extremal dependence index
SSP	Shared Socioeconomic Pathway
SVM	Support vector machine
TSS	True skill statistic
UAV	Unmanned aerial vehicle
US	United States
USDA	United States Department of Agriculture

VOC	Volatile organic compound
WGS	Whole-genome sequencing
WGS84	World Geodetic System 1984
XGBoost	Extreme gradient boosting

CHAPTER 1

One Pathogen, Two Epidemics: A Biological and Epidemiological Synthesis of Oak Wilt in North America

Abstract

Oak wilt, caused by the vascular wilt fungus *Bretziella fagacearum* (T.W. Bretz) Z.W. de Beer, Marinc., M.J. Wingf. & T.A. Duong, has been managed as a single epidemic process for more than eight decades in the U.S. Yet the disease comprises two regionally distinct epidemiological expressions, i.e., Texas and Lake States regimes; consequently, management tactics and climate projections calibrated for one transfer poorly to the other. Using a PRISMA 2020-compliant corpus of 121 studies selected from 17,014 records and recent findings from whole-genome resequencing of 93 isolates from 15 states, we synthesized two mechanistically distinct epidemic patterns. In the live-oak (*Quercus fusiformis* and *Quercus virginiana*) mottes and savannas of central Texas, the dominant pathway is belowground spread via continuous clonal root systems, resulting in radial disease-center expansion of approximately 40 m yr^{-1} under year-round vector activity. In the oak-dominated hardwood forests of the Lake States, an insect-mediated inoculation pathway couples with spread through natural inter-tree root grafts to yield substantially slower expansion (3.6-7.7 m yr^{-1}) constrained to spring and fall inoculation periods. Recent population genomic analysis (Chahal et al., 2025a) identified four geographically structured genetic clusters - Upper Midwest, Mid-Atlantic/Southeast, Michigan, and Texas, with Texas forming a genetically distinct population consistent with historical reproductive isolation.

Therefore, the epidemics are not only ecologically distinct but also driven by genetically distinct pathogen lineages. This coupling provides a mechanistic explanation for the limited transferability of management practices across regions and supports regime-specific parameterization of intervention programs and disease-distribution models. We traced the divergence through transmission biology, host xylem anatomy, and environmental controls; evaluated the diagnostic and remote-sensing toolkit; and identified the gap between detection and intervention capacity. Five falsifiable propositions convert the two-epidemics framework from a descriptive synthesis into a tractable experimental and modeling agenda, now feasible given the available reference genome (27.07 Mb, 9 chromosomes) and multi-state isolate panel.

1.1 Introduction

Oaks (*Quercus* L.) are the keystone trees of eastern North American hardwood forests; the genus comprises an estimated 400–500 species globally (Denk et al., 2017; Tischenko et al., 2024), with 91 species native to the U.S. and Canada (Cavender-Bares, 2019; Quesada et al., 2025). In the continental U.S., oaks sequester more carbon than any other woody lineage (Bocsi et al., 2021; Bronson et al., 2023; Subedi et al., 2024) and contribute an estimated $22.3 billion annually in ecosystem services - including timber production, carbon sequestration, watershed regulation, and biodiversity support (Cavender-Bares et al., 2022; Pinto-Ledezma et al., 2023). The economic significance of hardwoods is shown in Figure 1.1, and detailed information about these data is provided in Appendix Table 1.7. Despite this ecological and economic prominence, the genus is disproportionately threatened: 31% of assessed oak species globally and 17 species in the U.S. carry IUCN Red List designations

(Carrero et al., 2020; Spence et al., 2021; Tischenko et al., 2024). Moreover, non-native pests and pathogens that accumulate in North American forests at approximately 0.5 high-impact organisms per year (Lovett et al., 2016) disproportionately affect this genus at unusually high rates (Cavender-Bares et al., 2022). More information on *B. fagacearum* impacts and threat indicators in the U.S. and Canada is summarized in Table *1.1*, while other major biotic and abiotic threats affecting *Quercus* spp. are presented in Appendix Table 1.1.

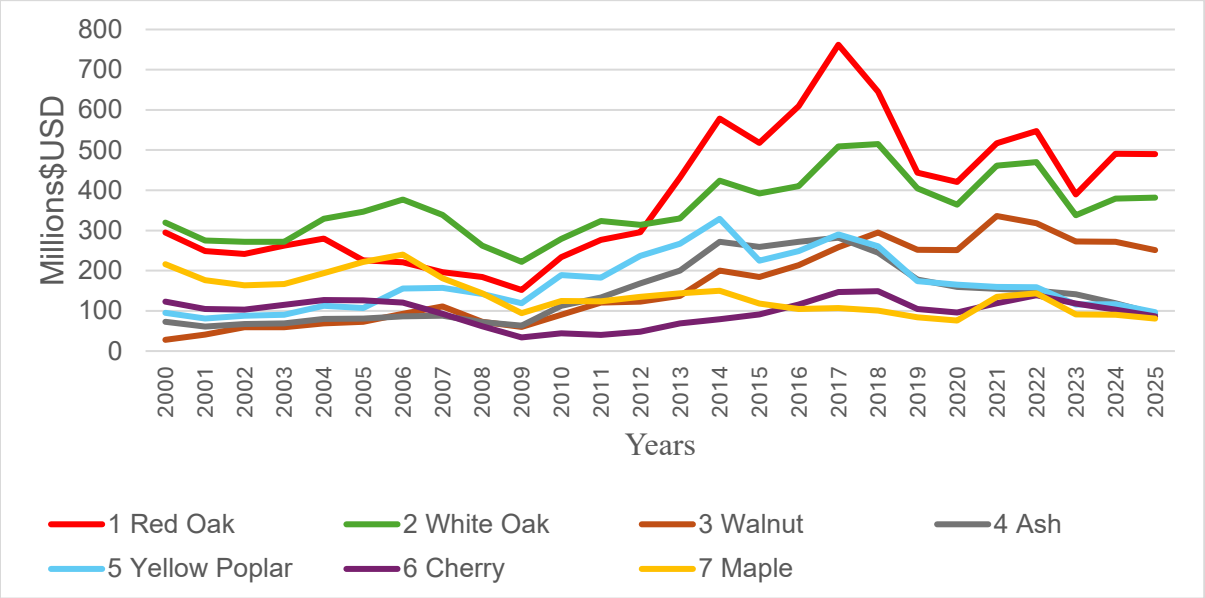

Figure 1.1 U.S. hardwood lumber exports by species from 2000 to 2025. Note. Data sourced from the USDA Foreign Agricultural Service's Global Agricultural Trade System (GATS) online database (https://apps.fas.usda.gov/gats/default.aspx), accessed on March 2, 2026. The data source and the table related to this figure are in Appendix Table 1.7.

Table 1.1 Oak wilt (*Bretziella fagacearum*) impacts and threat indicators in the U.S. and Canada.

Threat / Impact	Study Region	EPA Ecoregion (Level III)	Evidence Type	Key Sources
A. Disease Spread and Range Expansion				
Disease-center expansion rate: up to 12 m yr^{-1} (Lake States); up to 40 m yr^{-1} in Texas live oak (root systems)	Minnesota, Michigan, Texas	Northern Lakes & Forests (MN, MI); Edwards Plateau (TX)	Field monitoring + aerial survey	Gearman and Blinnikov (2019); Chahal et al. (2025a)
≥800 active disease centers across ~87,900 ha (~1 center per 150 ha)	Fort Hood, Central Texas	Edwards Plateau	Aerial and ground survey, GIS mapping	Downing et al. (2009)
Pathogen range expanded northeast by ≥300 km; first confirmed record in New York (Schenectady County, 2008)	New York	Northeastern Highlands	First confirmed record; molecular identification	Jensen-Tracy et al. (2009)
First Canadian confirmed interception (June 2023; Ontario)	Ontario, Canada	Mixed Wood Plains	First confirmed record; molecular identification (eDNA + culture)	Gauthier et al. (2024)
Tens of thousands of oaks die annually in the Lake States (anecdotal expert estimate)	Minnesota, Wisconsin, Michigan	Northern Lakes & Forests; Northern Glaciated Plains	Expert estimate	Appel (1995); Juzwik et al. (2011)
Millions of oaks have died in Texas since discovery (~1940)	Texas (statewide)	Edwards Plateau; Blackland Prairies; others	Expert estimate	Appel (1995); Juzwik et al. (2011)
Sap beetles (*C. truncatus, Ca. sayi*) can transmit inoculum up to ~600 m in a single season via overland flight	Minnesota	Northern Glaciated Plains	Controlled vector trapping study	Shelstad et al. (1991); Bourgault et al. (2022)
>90% of local spread (within established disease centers) occurs through inter-tree root grafts	Minnesota	Northern Lakes & Forests; Northern Glaciated Plains	Field epidemiology	Cook (2001); Morrissey (2019)

B. Ecological Consequences				
≥2,500 ha affected by oak wilt; loss threatens Endangered golden-cheeked warbler (*Setophaga chrysoparia*) nesting habitat	Central Texas	Edwards Plateau	Aerial survey; habitat assessment	Harrington (2013)
Large-scale oak mortality may increase surface-fire risk and alter stand successional trajectory	U.S. forests (general)	Multiple	Expert opinion / ecological inference	Wilson (2001)
Oak wilt-killed trees resprout poorly; may accelerate long-term oak loss relative to fire-driven regeneration dynamics	U.S. forests (general)	Multiple	Ecological observation / comparative study	Menges and Loucks (1984); Davies (1992)
C. Economic Impacts				
Red oak timber stumpage value (Michigan): ~$1.6 billion (2011 FIA data); projected removal costs in one MN county: $18–60 million (Anoka Co., 2007–2016 outlook)	Michigan; Anoka County, Minnesota	Northern Lakes & Forests; Northern Glaciated Plains	Economic assessment (stumpage values + removal-cost projection)	Corrigan (2023); Haight et al. (2011)
1988–2010: 2,654 disease centers treated; ~1.14 million m of trenching installed; total federal program cost ~$2.7 million (Central Texas)	Central Texas	Edwards Plateau	Administrative records (Texas A&M Forest Service)	Juzwik et al. (2011)
Additional MN program costs: ~$11.6 million; ~187 km of root cutting; 9,107 red oaks removed	Minnesota	Northern Glaciated Plains	Administrative records (USFS NRS)	Juzwik et al. (2011)
By 2004: >$1 billion estimated cumulative economic damage statewide; 250–400 new infection centers established per year	Texas (statewide)	Edwards Plateau; others	Economic estimate (extension report)	Wilson (2005)
Projected tree-removal and replacement costs for 485 urban areas: CAD $266–420 million (eastern Canada scenario modeling)	Eastern Canada	Mixed Wood Plains; Boreal Shield	Scenario-based cost modeling	Pedlar et al. (2020)

Cost per tree saved under a $1 million management budget: ~$5,400 (at 8% infection rate) vs. ~$3,610 (at 12% infection rate)	Anoka County, Minnesota	Northern Glaciated Plains	Cost-effectiveness analysis	Horie et al. (2013)

Note. Entries are organized by three thematic categories: (A) disease spread and range expansion; (B) ecological consequences; (C) economic impacts. EPA Ecoregions follow the Level III classification (U.S. EPA, 2013). Spread rate figures in section A represent measured field values, not model projections. Economic values in section 'C' are in USD unless noted. Abbreviations: FIA = Forest Inventory and Analysis; GIS = Geographic Information System; MN = Minnesota; MI = Michigan.

Among these threats, oak wilt holds a distinctive position by virtue of its geographic breadth, host lethality, and persistent failure to manage it effectively at the landscape scale (Jagemann et al., 2018; Juzwik, 2007; Juzwik et al., 2011). The causative agent, *Bretziella fagacearum* (T.W. Bretz) Z.W. de Beer, Marinc., M.J. Wingf. & T.A. Duong (De Beer et al., 2017), formerly *Ceratocystis fagacearum* (T.W. Bretz) J. Hunt, is an ascomycete vascular wilt pathogen that colonizes and occludes the xylem vessels of susceptible hosts, disrupting water transport and triggering foliar wilt, cambial death, and tree mortality. In addition to *Quercus*, the pathogen can infect several other members of the Fagaceae, including chestnuts (*Castanea* spp.), chinkapins (*Chrysolepis* spp.), and tanoak [*Notholithocarpus densiflorus* (Hook. & Arn.) Manos, Cannon & S.H.Oh] (Bretz, 1955, 1956; Bretz & Long, 1950). Most records for non-*Quercus* originate from artificial inoculation studies, with natural infections documented only for Chinese chestnut (*Castanea mollissima*) and chestnut hybrids (*Castanea sativa* × *Castanea crenata*) (Chahal, 2024). Apple (*Malus domestica* Borkh.) has been reported as a host exclusively following artificial inoculation (Bart, 1956, 1960). Henry (1944) described the disease for the first time from wilting oaks in Wisconsin; it is now documented in 25 U.S. states and more than 900 counties (EDDMapS, 2025), and was confirmed in Canada for the first time in June 2023 (Gauthier et al., 2024), and has

recently been reported from orchard-grown chestnut, a potential intergeneric host bridge whose epidemiological consequences remain unresolved (Chahal et al., 2026). A map of oak wilt-affected counties in the U.S. is shown in Figure *1.2*; data sources for the map are summarized in Appendix Table 1.6. In three independent expert-elicitation surveys, oak wilt ranked among the foremost current threats to eastern North American oaks (Conrad et al., 2020; Lovett et al., 2016; Pedlar et al., 2020). Red oaks (*Quercus* section Lobatae) are especially susceptible, with mortality occurring within three to six weeks of infection in many cases (Gibbs & French, 1980; Morris et al., 2024; O'Brien et al., 2011). Oak wilt has caused well over $1 billion in economic damage to oak resources in Texas alone, with 250–400 new expanding disease centers (EDCs) established annually (Wilson, 2005).

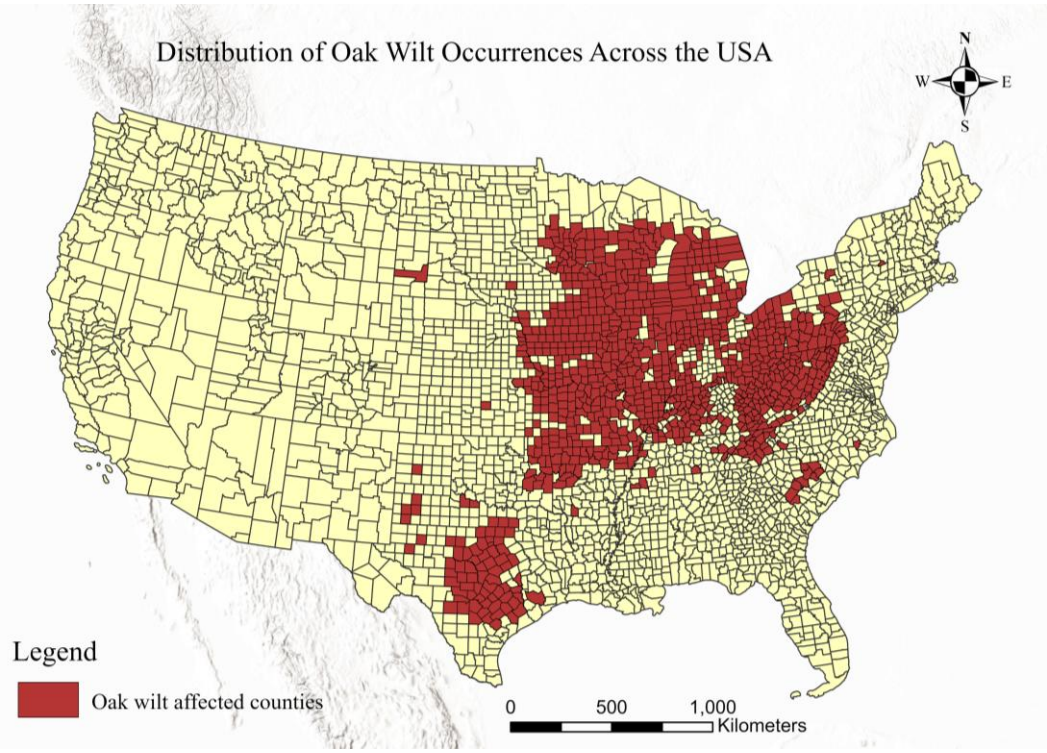

Figure 1.2 Map of oak wilt-affected counties in different states of the U.S. (from 1987 to 2025). Note. Data source is EDDMapS 2025. Early Detection & Distribution Mapping

System. The University of Georgia - Center for Invasive Species and Ecosystem Health. Available online at http://www.eddmaps.org/; last accessed December 13, 2025. and Fei, S., Morin, R., Li, S., Kong, N., Crocker, S., Krist, F., Liebhold, A.M., & Grong, K. A. (2024). Alien Forest Pest Detection by Counties in the U.S. Purdue University, Research Repository. https://doi.org/10.4231/HWQF-V087.

In this review, we aim to: 1) develop the two-epidemics framework from the existing literature; 2) synthesize the population genomic evidence for pathogen geographic structure; 3) trace how the epidemiological divergence propagates through transmission biology, human-mediated dispersal, host xylem anatomy, and abiotic environmental controls; 4) evaluate the current detection and surveillance toolkit; 5) characterize the gap between detection and intervention capacity; and 6) assess the methodological frontier and advance falsifiable propositions that convert the framework into a concrete experimental and modeling program. Throughout, we clearly distinguish among established findings, supported inferences, and unresolved hypotheses.

1.2 Materials and methods

1.2.1 Systematic literature search

This review followed the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) 2020 guidelines (Page et al., 2021). We adopted a systematic rather than narrative approach to minimize confirmation bias in a field where the regional literatures of the Lake States and Texas have developed with limited cross-citation.

1.2.2 Primary search

We searched the Web of Science Core Collection on 14 January 2026 using the query: ("oak wilt" OR "*Bretziella fagacearum*" OR "*Ceratocystis fagacearum*") AND ("*Quercus*" OR "oak") applied to title, abstract, and keyword fields. Pre-screening filters restricted results to English-language records from the U.S. and Canada within the subject categories of plant sciences, forestry, ecology, environmental sciences, biodiversity conservation, entomology, and remote sensing, and limited document types to articles, reviews, book chapters, conference proceedings, and early access publications. These filters reduced 17,014 initial records to 2,791 forwarded for three-stage screening.

1.2.3 Screening

Stage 1 (title screening): we excluded 2,343 records that were not relevant to oak wilt biology, epidemiology, or management; 448 records advanced. Stage 2 (abstract screening): we evaluated records against three prespecified inclusion criteria: (i) spatial or temporal distribution of the disease; (ii) abiotic or biotic drivers of disease dynamics; (iii) detection, diagnostic, or management strategies, and excluded an additional 340 records; 108 advanced. Stage 3 (full-text review): we excluded 25 records (9 full texts inaccessible; 16 insufficient, either insufficiently relevant or lacking methodological detail), retaining 83 studies from the primary search.

1.2.4 Citation-based supplementation

To reduce publication bias inherent in database-only searches, we applied backward and forward citation tracking in Google Scholar using three thematically

representative, highly cited anchor publications, each selected from three different periods (2000-2010, 2011-2020, and 2021-2025). Detailed information about this is presented in Appendix Table 1.4**.** This procedure yielded 628 candidate records. We excluded 550 at title and abstract screening; 78 advanced to full-text review. Of these, 7 full texts were unavailable, and 33 records were already represented in the final primary-search dataset, yielding a net addition of 38 studies.

Our final corpus comprised 121 peer-reviewed studies spanning 1944–2025 (83 from the primary search; 38 from citation tracking). The PRISMA diagram showing the literature search strategy is in Figure *1.3*.

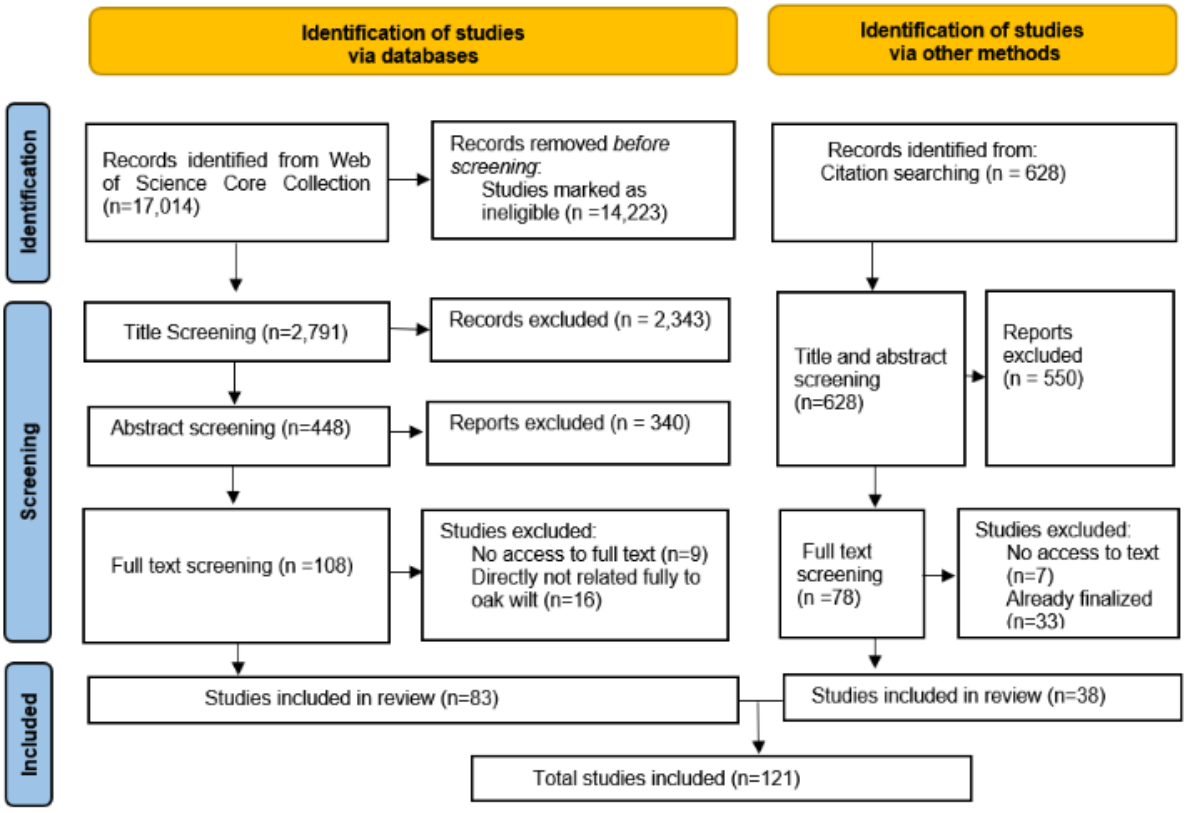

Figure 1.3 PRISMA 2020 flow diagram of the literature search and selection process for oak wilt research.

1.2.5 Bibliometric analysis

The 83 Web of Science records were analyzed to characterize the temporal, disciplinary, and thematic development of oak wilt research. Publication and citation counts were summarized by decade, Web of Science research categories were consolidated into ten major disciplinary groups, and keyword co-occurrence was analyzed using VOSviewer (Van Eck & Waltman, 2010).

Publication output remained limited before 1980 but increased substantially after 2000, rising from 13 publications in 2000–2009 to 30 during the incomplete 2020–2026 period (Figure *1.4*). Citations peaked for publications from 2010–2019, whereas the lower citation count for 2020–2026 likely reflects the shorter time available for recent studies to accumulate citations.

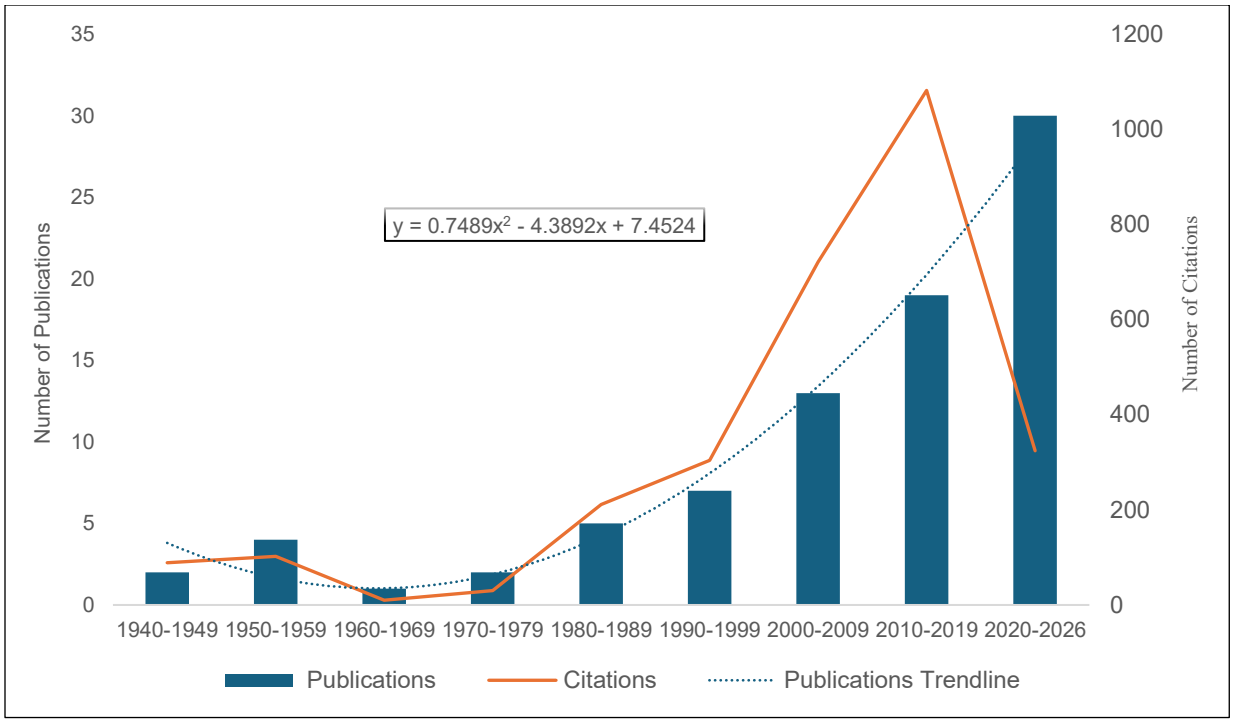

Figure 1.4 Temporal trends in oak wilt research output and citations by decade (Web of Science, n = 83).

The disciplinary distribution also broadened over time (*Figure 1.5*). Plant and Agricultural Sciences accounted for 37 assignments, followed by Forestry with 30 and Environmental Sciences, Ecology and Biodiversity Conservation with 15. Together, these fields represented 82 of the 99 major-area assignments, confirming that oak wilt research remains centered on plant pathology, forestry, and forest ecology. The recent appearance of climate science, genetics, molecular biology, remote sensing, and computer science indicates increasing interdisciplinarity, but these areas remain comparatively underrepresented.

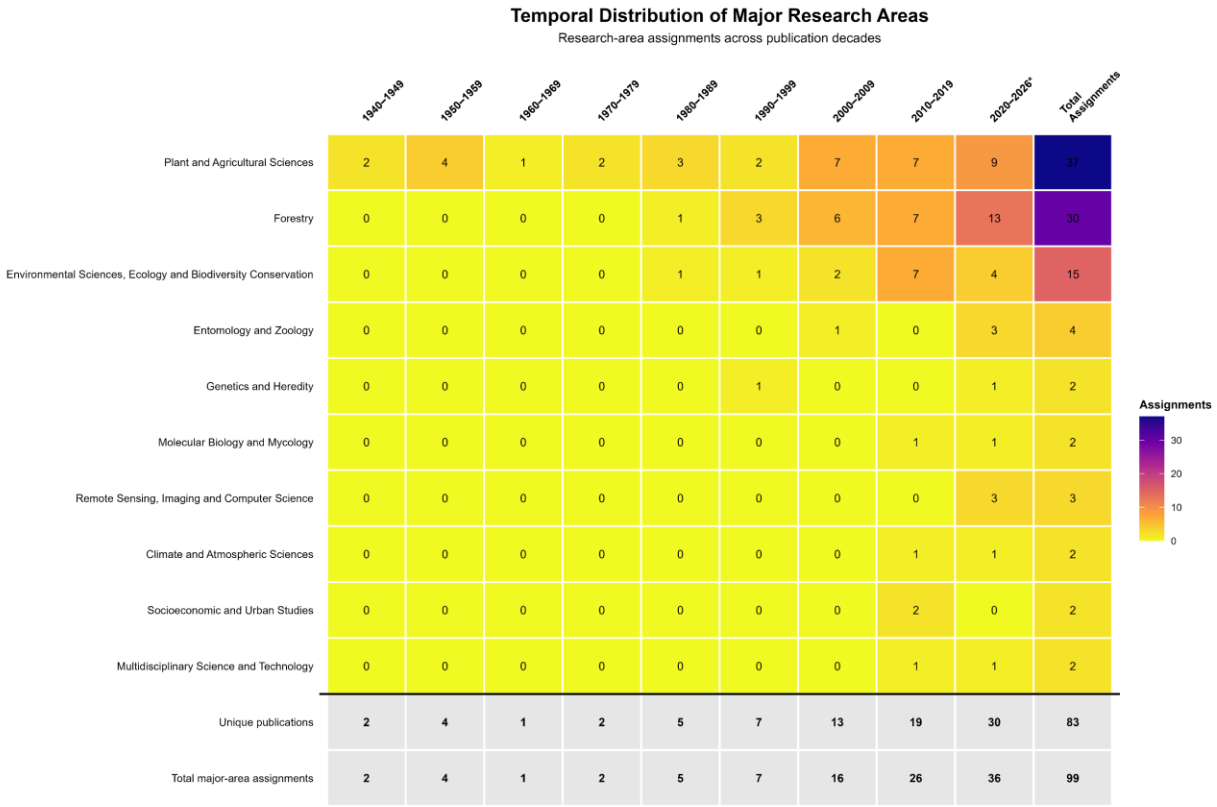

Figure 1.5 Temporal distribution of major research-area assignments in oak wilt publications by decade. Note. Cell values show research-area assignments; bottom rows show unique publications and total assignments. Publications may belong to multiple areas, and 2020–2026 is incomplete.

Keyword co-occurrence analysis identified five major thematic clusters: A, pathogen biology, virulence, and infection mechanisms; B, disease management and control; C, climate and environmental drivers; D, host susceptibility and physiological stress; and E, transmission pathways and vector ecology (Figure *1.6*). These clusters support the objective of this review by showing that regional oak wilt epidemiology is shaped by interacting pathogen, host, vector, environmental, and management processes.

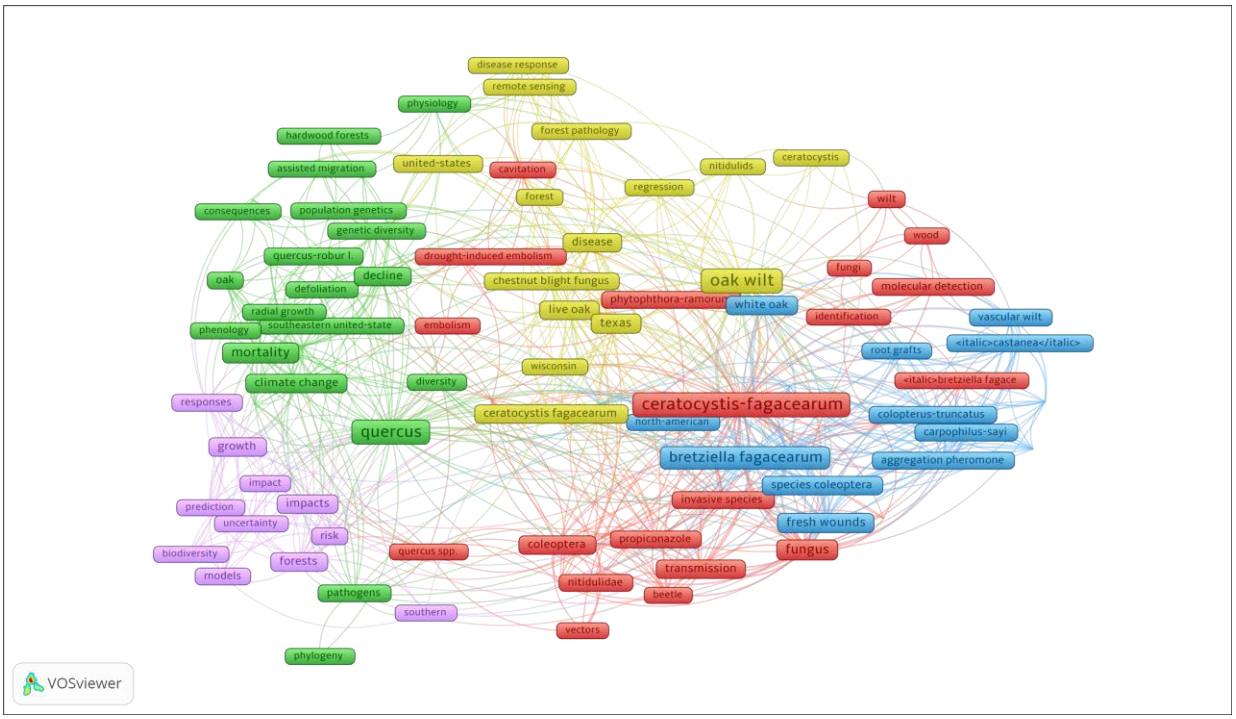

Figure 1.6 Keyword co-occurrence network revealing thematic clusters in oak wilt research. Note. The five clusters represent: A, pathogen biology, virulence, and infection mechanisms; B, disease management and control; C, climate and environmental drivers; D, host susceptibility and physiological stress; and E, transmission pathways and vector ecology. The clusters are shown in blue, yellow, violet, green, and red, respectively.

The complete corpus of 121 studies, comprising 83 Web of Science records and 38 additional studies identified through citation tracking, provided the evidence base for the subsequent synthesis.

1.3 Review of oak wilt disease in North America

1.3.1 Two epidemics, one pathogen

The Lake States and Texas regimes do not differ in the identity of the pathogen, *B. fagacearum* causes both, but in nearly every parameter that governs how the pathogen moves, how fast disease centers expand, and which interventions work (Chahal et al., 2025a). Table 1.2 consolidates the contrast; here we draw out its three major consequences.

Table 1.2 The two-epidemics framework of oak wilt in the U.S.: contrasting Lake States and Texas live oak systems.

Parameter	Lake States (Upper Midwest)	Texas Live Oak
Dominant host section	Sect. *Lobatae* (red oaks); primarily *Q. rubra* and *Q. ellipsoidalis (Juzwik et al., 2011)*	Sect. *Virentes* (live oaks); primarily *Q. fusiformis* and *Q. virginiana* (Appel, 1995; Chahal, 2024; Juzwik et al., 2011)
Dominant belowground pathway	Inter-tree root grafts in sandy outwash soils; grafts form readily between neighboring red oaks (Cook, 2001; Morrissey, 2019)	Extensive clonal root systems; vegetative root connections among ramets of *Q. fusiformis* can span large areas (Appel, 1995; Chahal et al., 2025a; Chahal et al., 2026)
Spread rate	Root-graft spread: mean 3.47 m yr^{-1} (MN); up to 12 m yr^{-1} (MI). Overland (insect) spread: 150–600 m yr^{-1} (Juzwik, 2007; Shelstad et al., 1991)	Root-connection spread: up to 40 m yr^{-1}. Overland (insect) spread: up to 1.6 km yr^{-1} (Appel, 2007; Chahal et al., 2025a)
Vector-active period	Spring to early summer (April–July); coincides with peak fresh-wound susceptibility and fungal mat availability (Chahal et al., 2025a; Morris et al., 2024)	Year-round; peak activity February–May. Summer heat can reduce mat production, but epidemics still occur (Appel, 1995; Chahal et al., 2025a)
Fungal mat formation	April–July (peak May); occasional autumn mats (September–October); very low or absent mid-November to mid-April (Bershing, 2025; Juzwik, 2007; Juzwik et al., 2011)	Primarily late winter and spring; mat formation is reduced or absent in autumn compared to the Lake States (Appel, 1995; Appel et al., 2008; Juzwik et al., 2011)

Key abiotic limiters	Coldest-month minimum temperature; climate moisture regime; spring temperature controls both vector emergence and mat formation (Morris et al., 2024; Pedlar et al., 2020)	Summer heat can suppress pathogen at extremes (optimum ~25°C); however, severe epidemics still occur during hot, dry summers (Appel, 1995; Wilson, 2005)
Pathogen genetic cluster	Upper Midwest and Michigan clusters; relatively low mitochondrial diversity with evidence of regional gene flow (Chahal et al., 2025a; Harrington, 2009; Kurdyla et al., 1995; Peacock, 2008)	Texas forms a genetically distinct population (Texas cluster); potentially limited gene flow from Midwest populations; may reflect local adaptation (Chahal, 2024)
Primary management approach and documented success	Vibratory plow/root barrier: 84% of disease centers successfully contained for 4–6 years (Juzwik et al., 2010). Stump excavation (root rupture): 63–93% success in preventing symptoms in previously infected trees (Yang et al., 2024)	Trenching with impermeable liner: reported 100% success over 6 years; 81% over 30 years in a single installation study (Gomez et al., 2025). Girdling: ~50% success (Greene et al., 2008). Note: propiconazole is fungistatic, not fungicidal-it suppresses symptom development rather than eliminating the pathogen (Koch et al., 2010)
Key gap/risk of over-generalization	Protocols developed primarily for the Lake States have limited applicability south of ~38°N due to different host biology, root architecture, and year-round vector activity (Appel et al., 1990; Appel, 1995; Juzwik et al., 2011)	Should not be prematurely extrapolated as the future warming-driven analog for the entire U.S.; southeastern frontier populations may not match either epidemic type (Appel, 1995; Chahal, 2024)

Note. This framework captures the two most thoroughly documented and spatially distinct oak wilt epidemic types. Southeastern U.S. populations and the newly documented Canadian occurrence (Ontario, 2023) may not conform fully to either type. Spread rates are measured field values. Containment success rates represent results from single or multiple trials as cited and should not be extrapolated without accounting for site-specific soil, terrain, and host conditions.

Belowground transmission dominates both regimes, exceeding 90% of new infections in Minnesota studies (Cook, 2001; Koch et al., 2010; Morrissey, 2019) and is established as the proven primary pathway in central Texas (Appel et al., 2008), but the substrate of belowground transmission is fundamentally different. In the Lake States, inter-tree root grafts are more frequent in sandy outwash soils than in silt loam (Bruhn et al., 1991; Juzwik et al., 2011). Spread rate in the Upper Midwest is therefore soil-dependent. In central Texas, it is the clonal root system of live oak (*Quercus fusiformis*,

the dominant Escarpment live oak of the Hill Country, and *Q. virginiana* in coastal zones), in which many stems share one continuous root mass; here, transmission is less dependent on soil texture and yields the highest expansion rates documented for the disease (Appel, 1995; Appel, 2007). The same epidemiological label "belowground spread" therefore denotes two mechanistically different processes.

Three consequences follow: First, management does not transfer. Texas trenching-efficacy figures derive from systems in which the belowground pathway is a clonal root architecture rather than inter-tree grafts. A 30-year assessment of the Texas Oak Wilt Suppression Project found an overall trenching success of ~81% (19% breakout across 2,124 trenches), but with breakout rising sharply where root zones are deep and soils are clayey (Gomez et al., 2025). This soil-dependent breakout underscores that the efficacy of trenching in Texas cannot be assumed to apply to Lake States deciduous stands, where the severed object is an inter-tree graft rather than a shared clonal root system. Generalizing Texas parameters northward is therefore unsupported.

Second, region-free forecasting misallocates risk. Predictors that dominate the leading correlative niche models are fall precipitation and spring temperature in the Pedlar et al. (2020) Canadian models and are appropriate to the Lake States regime but partly orthogonal to Texas dynamics, where summer maximum temperature and host clonality drive spread (Appel, 1995; Chahal, 2024). Recent climate niche projections indicate that eastern Canada will become increasingly suitable for *B. fagacearum* under future climate scenarios, further emphasizing the need for regime-specific forecasting (Pedlar et al., 2025).

Third, the regimes meet at an untested frontier. The southeastern states, Georgia, South Carolina, Tennessee, and North Carolina, are where the deciduous root-graft and live-oak clonal regime converge, and neither region's parameters can be assumed valid. This is precisely where the two-epidemics framework is most consequential and least tested.

Environmental controls are considered here only where they explain regional epidemiological divergence; their broader mechanistic role in defining the climatic niche of oak wilt is reviewed in Chapter 2.

1.3.2 The geography of the pathogen and the disease

The two-epidemics framework would be a useful ecological abstraction even if the pathogen were genetically uniform across its range. The stronger claim and the conceptual core of this review is that the pathogen is not uniform and that its population structure tracks the epidemiological divide.

B. fagacearum was long considered genetically monolithic. Early molecular marker studies reported extremely low diversity consistent with a severe founder bottleneck: AFLP analysis of isolates from the Great Lakes, Texas, and West Virginia showed low diversity consistent with bottlenecked population structure, with only a single polymorphic locus across sampled populations, indicating greater than 99% similarity (Peacock, 2008), and RFLP analysis of mitochondrial and nuclear DNA found Texas, Wisconsin, and West Virginia populations nearly identical (Kurdyla et al., 1995). The pathogen's status as a recently introduced exotic-most plausibly from Mexico, Central America, or northern South America, where diverse oaks occur was inferred

from this near-clonal uniformity and from the absence of close North American relatives (Harrington, 2009; Irgens-Moller, 1955; Juzwik et al., 2008).

Whole-genome resolution refines the picture of uniformity without contradicting the founder-bottleneck inference. The chromosome-level reference genome of isolate C519, obtained from an infected *Q. rubra* in Sherburne County, Minnesota, comprises 27,072,536 bp across nine chromosomes, has a GC content of 47.29%, and contains 7,554 predicted proteins (Chahal et al., 2025a) provided the scaffold for population-scale resequencing. Resequencing of 93 isolates from 15 states resolved four geographically structured genetic clusters: Upper Midwest, Mid-Atlantic/Southeast, Michigan, and Texas, with the Texas population genomically distinct under low to moderate genetic differentiation, suggesting restricted gene flow, as revealed by principal component and ancestry analyses (PCA) (Chahal, 2024). What earlier low-resolution markers read as a single clone is, at the whole-genome scale, a structured set of regional lineages.

The Texas epidemic, the clonal-root, year-round, fastest-spreading regime, is associated with a pathogen population that is also the genomic outlier. In contrast, a different genetic cluster drives the epidemic in the Upper Midwest. Thus, the two epidemics are not only ecologically distinct; they are also, to a first approximation, driven by genetically distinct pathogen populations. This coupling matters for three reasons. It provides a mechanism for why the regimes behave differently that does not rest on the environment alone. Second, it raises the unresolved question of whether regional clusters differ in epidemiologically important traits, such as virulence, mat production, thermal tolerance, and vector association, which have not yet been

compared in common gardens across clusters. Third, it reframes biosecurity: low to moderate genetic differentiation between clusters implies that long-distance human movement of infected wood (firewood, logs) may not merely spread the pathogen but could also bring previously isolated lineages into contact, with unknown consequences for virulence, adaptation, and future disease dynamics.

Though the four-cluster structure was established (Chahal, 2024); the functional differentiation among clusters is, at present, a hypothesis. Testing is the single highest-value experiment the field can now perform, and it is feasible precisely because the reference genome and a multi-state isolate panel already exist.

1.3.3 Transmission biology and its human amplification

B. fagacearum spreads by two natural pathways whose relative weight defines each regime, plus a third, human-mediated pathway that overrides the natural geography of spread. These transmission mechanisms are presented in Figure 1.7.

Belowground: Root-mediated transmission is the dominant local pathway in both regimes, driving the radial expansion of disease centers (Chahal et al., 2026). Following infection, the fungus produces asexual conidia that are transmitted to neighboring trees through connected roots (Blaedow & Juzwik, 2010; Bourgault et al., 2022; Jones & Partridge, 1961), generating the concentric mortality fronts characteristic of red-oak stands but rarely observed in white oaks (Engelhard, 1954). The pathogen can live in diseased roots for more than three years, sustaining local inoculum (Yount, 1955). Expansion proceeds at approximately 3.6-7.7 m yr^{-1} in Lake States red-oak stands, with the lower end of the range documented by Shelstad et al. (1991) and the

upper end on sandy soils in Michigan by Bruhn et al. (1991) and up to ~40 m yr^{-1} in Texas live-oak mottes (Appel, 1995).

Aboveground: Overland spread initiates new disease centers and is driven primarily by sap-feeding nitidulid beetles (Coleoptera: Nitidulidae; ~173 North American species; Reed et al., 2023). *Carpophilus* and *Colopterus* species are the principal insect vectors (Ambourn et al., 2005; Kyhl, 2006; Stevens et al., 2024), but Morris et al. (2024) recovered the pathogen's spores from additional nitidulid beetles- *Glischrochilus sanguinolentus*, *G. fasciatus*, *Carpophilus brachypterus*, and *Ca. dimidiatus*, implying that vector-risk assessments built on the classic two-genus picture may understate transmission potential. Oak bark beetles (*Pseudopityophthorus* spp.) contribute marginally (Juzwik et al., 2011). Beetles can carry spores up to 600 m in a single year, establishing 0.011–0.025 new disease centers ha^{-1} yr^{-1} (Gauthier et al., 2024; Shelstad et al., 1991).

The aboveground pathway is through the fungal mat, the pathogen's sole sporulating structure and the feature that most strongly distinguishes *Bretziella* from its Ceratocystidaceae relatives (Chahal, 2024; De Beer et al., 2017). Mats form beneath the bark of recently killed red oaks (>7.6 cm in diameter), rupturing the bark via specialized pressure pads, and their size ranges from 4 to 208 cm^2 with gray to tan in color (Chahal, 2024; Juzwik et al., 2011; True et al., 1960). They emit volatile organic compounds (VOCs) that attract nitidulid beetles (Juzwik, 1984; Juzwik & French, 1983; Morris et al., 2024); visiting beetles acquire spores and carry them to fresh wounds. Because *B. fagacearum* is heterothallic, mats can support sexual reproduction where opposite mating types meet (Appel, 1995; Hepting et al., 1952), producing sticky

ascospores in a gelatinous matrix well suited to insect dispersal (Bretz, 1951); the roughly equal representation of both mating types in natural populations supports an epidemiologically meaningful role for the sexual stage (Appel, 1995; Yount, 1955). Mat phenology itself is regionally split: spring and fall in Minnesota, winter and spring (but not fall) in Texas (Appel, 1995; Juzwik & French, 1983), another axis along which the two epidemics diverge.

Importantly, the overland spread accounts for more than 90% of new infections in Minnesota studies (Cook, 2001; Koch et al., 2010; Morrissey, 2019); no equivalent quantification is available for Michigan, Wisconsin, or other Lake States, and this figure should not be generalized beyond the Minnesota literature.

Human amplification: Transport of infected firewood and logs moves inoculum beyond the dispersal limit of any beetle (Haight et al., 2011; Haugen et al., 2022), and is implicated in long-distance jumps to West Texas (Appel, 1995) and New York (Jensen-Tracy et al., 2009; Juzwik et al., 2011). At local scales, wounding from pruning, construction, or harvesting during periods of high vector activity opens infection courts that remain susceptible for only a few days (Harrington, 2013; Haugen et al., 2008; Wilson, 2001). No transmission via nursery stock or seed has been documented (Juzwik et al., 2011).

Human movement of infected wood is doubly significant: it is the one pathway capable of breaching the low-to-moderate genetic differentiation that currently separates the four pathogen clusters. Long-distance admixture could introduce Upper Midwest or Mid-Atlantic/Southeast lineages into the Texas gene pool, or vice versa, with consequences for virulence and vector association that are entirely uncharacterized.

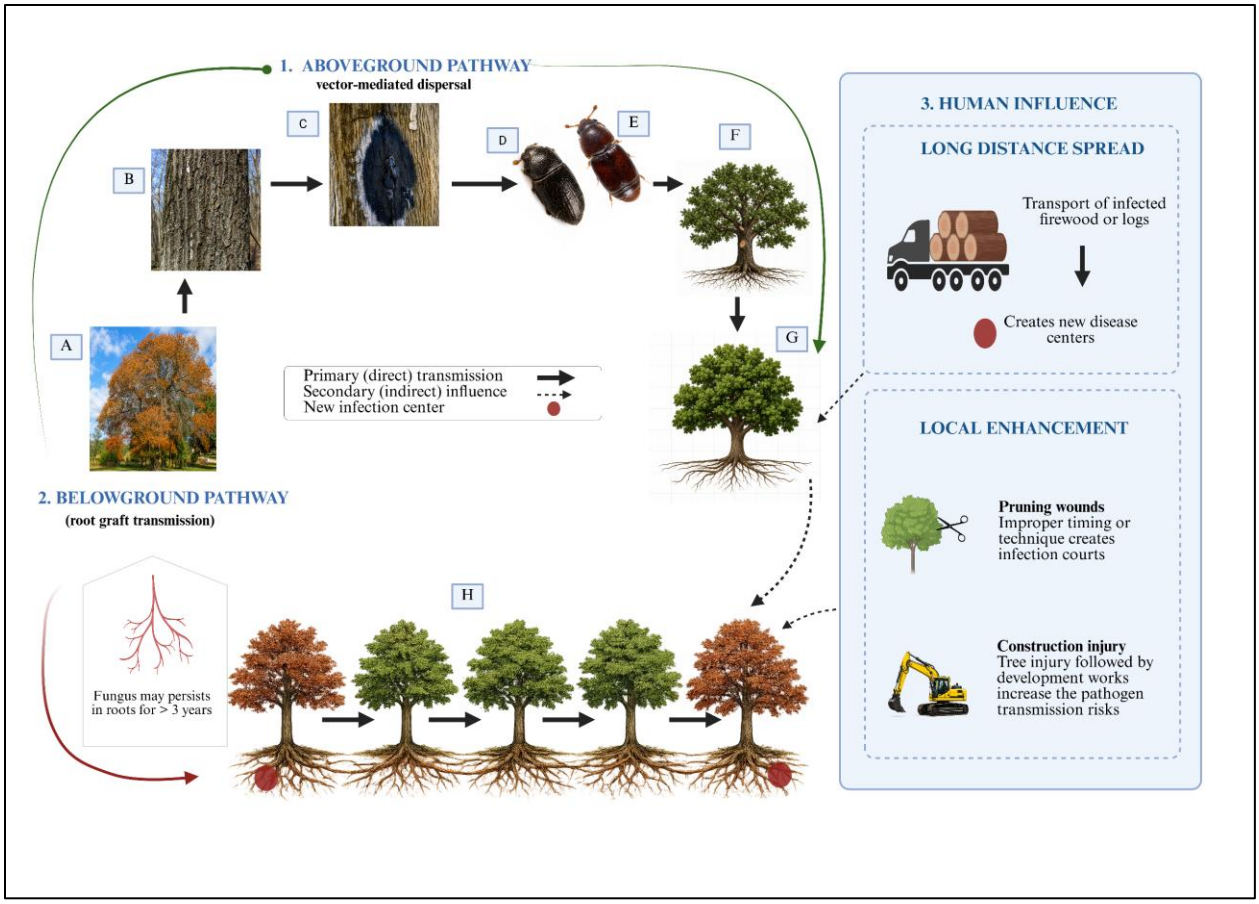

Figure 1.7 Major transmission pathways of oak wilt, including aboveground vector-mediated transmission (1), belowground root-graft transmission (2), and human-mediated transmission (3). Note. A, Oak wilt-affected tree; B, Bark crack associated with fungal mat formation; C, Exposed fungal mats; D, *Carpophilus sayi*; E, *Colopterus truncatus*; F, Fresh wound on a healthy oak tree; G, Newly affected oak tree; H, Pathogen transmission from oak-wilt-affected to healthy oak via root graft.

Photo credit: Joseph O'Brien, USDA Forest Service, Bugwood.org (Forestry Images). Available at: ForestryImages.org (accessed 15 July 2026).

1.3.4 Signs, symptoms, and the diagnostic ambiguity that delays response

The definitive sign of *B. fagacearum* infection is the sporulating mycelial mat beneath the bark of recently killed host material-diagnostic but transient; viable spore production is sustained for approximately two to three weeks following bark rupture (Appel, 2001; Koch et al., 2010), after which mat tissues desiccate and ascospore viability declines sharply. Mat occurrence is constrained by host section and season: mats form reliably on red oaks (*Quercus* sect. *Lobatae*) in the Upper Midwest during spring and fall, and have been documented on a small number of white oak species, including *Q. macrocarpa* Michx. and *Q. alba* L., under specific wounding and moisture conditions (Cones, 1967; Nair & Kuntz, 1963), and are essentially absent on live oaks (O'Brien et al., 2011). The most reliable diagnostic sign is simultaneously the most ephemeral and the most restricted by host-section: symptom-based surveillance is structurally biased toward red-oak stands in the Upper Midwest regime and structurally unreliable in live-oak stands in Texas, where detection must depend on molecular methods rather than visual indicators.

Foliar symptom expression is host-section specific in ways that compound this ambiguity. Red oaks wilt rapidly from crown symptom onset to death within three to six weeks (Gibbs & French, 1980; Morris et al., 2024), with discoloration progressing from crown apex downward and leaf bronzing advancing from margins inward; premature leaf drop occurs at the height of the growing season (Juzwik et al., 2011; Koch et al., 2010; O'Brien et al., 2011; Sinclair & Lyon, 2005). White oaks develop diffuse, multi-year crown dieback that unfolds over seasons to years, reflecting a sustained capacity to compartmentalize infection within individual annual rings; partial or complete recovery

without intervention is common (Haugen et al., 2022; Peacock, 2008; Shigo & Marx, 1977). Live oaks exhibit veinal chlorosis, tip burn, and leaf curl, with internal vascular discoloration often preceding visible foliar symptoms that may persist for three to eight months (O'Brien et al., 2011; Tainter & Baker, 1996).

All three symptom profiles overlap substantially with symptoms caused by co-occurring agents across the same landscapes: two-lined chestnut borer (*Agrilus bilineatus* Weber), cynipid gall wasp damage, drought scorch, bacterial leaf scorch (*Xylella fastidiosa* Wells et al.), bur oak blight (*Tubakia* spp.), *Armillaria* root rot, and general oak decline (Chahal et al., 2025b; Novi et al., 2024). Visual diagnosis alone cannot reliably support management-triggering decisions. Molecular confirmation using qPCR or LAMP is generally required for definitive diagnosis in management contexts (Bourgault et al., 2022; Gauthier et al., 2024; Novi et al., 2024).

The diagnostic lag that confirmation imposes is an epidemiological variable, not merely a logistical inconvenience. Delays ranging from days to weeks, depending on access to laboratory services or field-deployable assays, allow mat-producing trees to remain in place, sustaining the inoculum supply used by the aboveground transmission pathway. In the Upper Midwest red-oak regime, where mats persist for two to three weeks and pruning wounds remain susceptible for only two to four days during spring and fall flight peaks, each week of diagnostic lag represents a compounding expansion of infection courts. Deployment of validated field-portable assays including LAMP and CRISPR-DETECTR (Chahal et al., 2025b; Novi et al., 2024) directly into survey workflows-eliminating laboratory transit time is the single intervention most likely to close the gap between detection and response.

1.3.5 Host xylem anatomy as the proximate control on susceptibility

Oak wilt severity is a continuum, rather than a discrete binary state. The red oak-white oak dichotomy is an epidemiologically useful shorthand but an anatomically imprecise predictor of outcomes at species margins. Xylem anatomy is the proximate variable that governs the rate of fungal colonization and the capacity to arrest it.

White oaks (sect. *Quercus*). Narrow, isolated earlywood vessels restrict longitudinal fungal advance by limiting the axial hydraulic continuity available for colonization (Jacobi & MacDonald, 1980; Marchetti, 1962; Robert et al., 2017). Infected vessels are occluded by tylosis formation and enclosed by phenolic and suberin rich barrier zones, producing a response consistent with the Compartmentalization of Disease in Trees (CODIT) model: reaction-zone walls (walls 1-3) confine colonization to the infected xylem increment, and the cambium-derived barrier zone (wall 4) isolates the pathogen from vascular tissue formed after the infection event (Rioux & Blais, 2023; Shigo & Marx, 1977). White oaks thereby persist for years with localized chronic infection and may recover without mortality in many cases (Bretz, 1951; Jacobi & MacDonald, 1980; Schoeneweiss, 1959). A mechanistic revision has emerged: Rioux and Blais (2023) present evidence that tylosis formation is primarily a response to vessel cavitation rather than a direct, anticipatory defense against fungal advance. Under this interpretation, tylosis-mediated occlusion in white oaks may represent wound closure following cavitation failure rather than active wall-by-wall containment. Whether occlusion is better characterized as an active defense or as hydraulic collapse-driven sealing with incidental pathogen containment remains contested and has direct

implications for predicting outcome variability across white oak species-a live debate with practical diagnostic consequences.

Red oaks (sect. *Lobatae*). Wide, long-element earlywood vessels are hydraulically efficient but embolism-prone: large-diameter ring-porous vessels air-seed at low water potentials and rank among the most cavitation-vulnerable conduits in temperate angiosperm xylem (Lens et al., 2011; Rauschendorfer et al., 2022). These conduits provide rapid axial pathways for fungal advance before tyloses can form quickly enough to contain colonization (Fallon et al., 2020; Jacobi & MacDonald, 1980). Barrier zones in red oaks are diffuse or discontinuous (Jacobi & MacDonald, 1980), allowing extensive stem colonization, cambial failure, and the subcortical mat formation that sustains the overland transmission pathway (Struckmeyer et al., 1958). Symptomatic red oaks in both regimes die within three to six weeks of infection (Gibbs & French, 1980; Morris et al., 2024).

Live oaks (*Quercus* sect. *Virentes*). Anatomically intermediate as semi-diffuse-porous (Gray, 2009). Live oaks' epidemiological behavior in the Texas regime is governed primarily by clonal root connectivity rather than vessel anatomy: pathogen movement through continuous shared root systems proceeds independently of the per-vessel anatomy that controls within-stem colonization rate in the other sections. Infected live oaks die over three to eight months (Appel et al., 2008; O'Brien et al., 2011).

Anatomical exceptions that clarify the mechanism. Three species break the section-level prediction and, in doing so, strengthen the anatomical hypothesis. Chestnut oak (*Q. montana* Willd., sect. *Quercus*) has earlywood vessel dimensions in the red-oak size range; its susceptibility exceeds what taxonomic placement predicts

(Rioux & Blais, 2023). Bur oak (*Q. macrocarpa*) has unusually wide vessels for a white-oak-section species and exhibits correspondingly elevated susceptibility (Chahal, 2024). Turkey oak (*Q. laevis* Walter, sect. *Lobatae*) is reported to show slower disease progression than co-occurring red oaks despite anatomically similar earlywood vessels. We propose this as an explicit, testable hypothesis: *Q. laevis* has a pit-membrane ultrastructure, a reaction-zone phenolic composition, or constitutive antimicrobial deposition that delays colonization independently of vessel diameter, distinguishable from co-occurring red oaks by comparative transmission electron microscopy of bordered-pit membranes and histochemical staining of reaction zones. A targeted anatomical comparison across these three anomalous species would simultaneously test the vessel-size hypothesis and identify the additional determinants of within-section susceptibility variation. Oak wilt susceptibility to each species and by oak group is presented in Figure *1.8*; detailed information, along with the species authority name, is presented in Appendix Table 1.2 and Appendix Table 1.5, respectively.

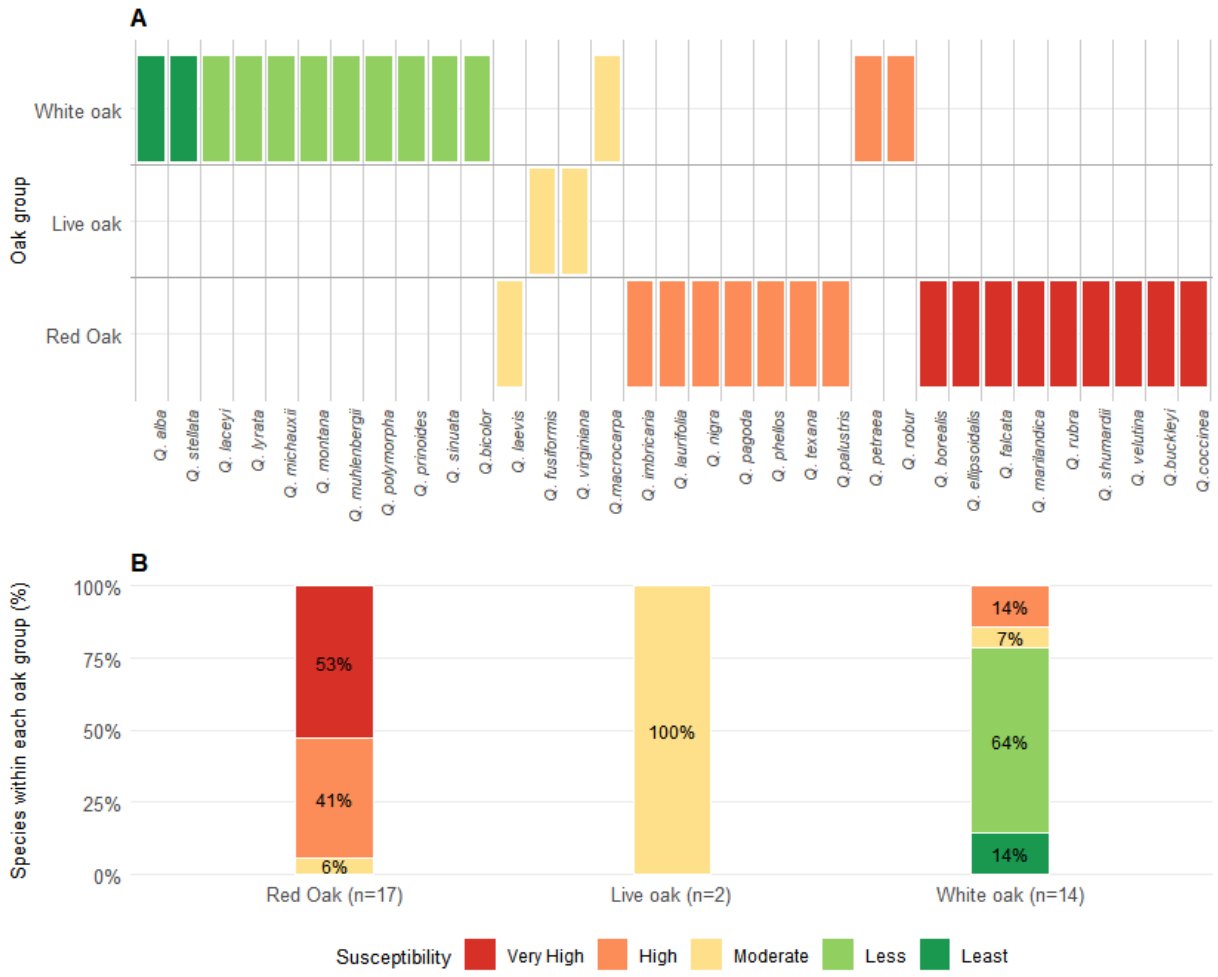

Figure 1.8 Heat map showing the susceptibility of oak species to oak wilt. Note. Colors indicate very high (red), high (orange), moderate (yellow), less (light green), and least (dark green) risk based on published literature. Species-level susceptibility ratings, grouped by oak type and resistance mechanisms, are detailed in Appendix Table 1.2.

1.3.6 Diagnostic tools and surveillance: from symptom to signal

Oak wilt detection has advanced from field symptom recognition to rapid molecular confirmation and, most recently, to landscape-scale remote sensing. Figure *1.9* summarizes the evolution of detection methods from 1940 to 2025. The three fronts-molecular diagnostics, vector-based surveillance, and remote sensing have developed

largely in parallel, and the gap between their individual capabilities and an integrated operational early-warning system remains open.

Molecular diagnostics. Symptom-based field diagnosis is structurally unreliable across the three major host groups, so molecular confirmation can be the emerging standard for definitive diagnosis. Early visual symptoms overlap with those of drought, bacterial leaf scorch (*Xylella fastidiosa*), and other foliar fungal diseases (Chahal et al., 2025a; Novi et al., 2024), requiring laboratory or molecular support. Historically, nested PCR has demonstrated high diagnostic sensitivity for *B. fagacearum* in symptomatic tissue and stained wood, enabling confirmation when visible fungal mats are absent (Wu et al., 2011; Yang & Juzwik, 2017). Field-deployable assays have since reduced the confirmation times from days to hours: loop-mediated isothermal amplification (LAMP) with a colorimetric, naked-eye readout achieved analytical sensitivity and 100% specificity against a panel of 15 other forest pathogens in independent benchmarking (Novi et al., 2024).

A TaqMan real-time PCR assay applied to fallen leaf petioles-a non-destructive, high-throughput sample type achieved 100% detection of *B. fagacearum* in northern red oak and chestnut samples regardless of visible symptom severity and substantially outperformed culture-based recovery from dry samples (Chahal et al., 2025b). Because fallen petioles can be collected without destructive stem sampling, this approach could expand surveillance in asymptomatic or minimally symptomatic stands. Quantitative PCR applied to environmental DNA (eDNA) enables sensitive detection in infection-associated substrates such as mycelial mats and insect vectors. Comparative evaluation of TaqMan qPCR and CRISPR-Cas12a DETECTR assays demonstrated

high specificity across pure cultures, insect vectors, and environmental samples, with multi-user field testing confirming effective operational performance (Bourgault et al., 2022; Gauthier et al., 2024).

Fungal volatile organic compound profiling represents an additional frontier in detection. Proton transfer-reaction mass spectrometry detected the characteristic *B. fagacearum* volatile signature from one-day-old cultures in less than 30 seconds, providing a substantially faster analytical approach than conventional gas chromatography–mass spectrometry (Meher & Abbas, 2025). Because fungal mats emit VOCs that attract nitidulid vectors, this approach is directly connected to the pathogen's transmission biology and merits evaluation using infected tissues, fungal mats, and field-deployable sensor formats. The companion diagnostic and management guide for oak and chestnut consolidates available molecular protocols into a format suitable for regional programs and state extension services (Chahal et al., 2025b).

The regime-differentiated epidemiological value of rapid confirmation differs in one specific way. In the Lake States, the spring inoculation window is approximately 6-12 weeks, and the mat-viability period after bark rupture is 2-3 weeks (Koch et al., 2010); confirmations that trigger sanitation within this window directly reduce the pool of active sporulating mats and open infection courts. In Texas, where expanding disease center (EDC) spread is substrate-continuous and year-round, the priority use of rapid confirmation is early EDC detection-identifying expanding centers before they have grown beyond the depth-reachable root zone that determines trenching feasibility (Gomez et al., 2025).

Vector-based surveillance. Nitidulid beetle trapping converts vector activity into an early-detection signal that can precede the identification of symptomatic trees. Double-nested PCR applied to trap-collected nitidulid beetles detected *B. fagacearum* in 10-13% of samples across years, including detections from sites where infected trees had not previously been recorded by conventional surveys, demonstrating the utility of vector-based surveillance for early pathogen detection (McLaughlin et al., 2022). This signal pre-dates mat formation, which requires tree death following infection, and therefore provides a detection advantage of weeks to months at low-prevalence sites. Amplicon sequencing of ITS-based PCR products from trap-collected nitidulid beetles resolved inconclusive gel-based detections by distinguishing true *B. fagacearum* amplification from off-target fungal taxa, and further revealed diverse co-occurring forest and beetle-associated fungi not identifiable by standard qPCR interpretation (Gordon et al., 2025). Vector-based surveillance is best suited to range margins and early-detection priority areas-regions such as New York, Ontario, and the southeastern frontier, where the low background prevalence of infection makes symptom-based survey inefficient and early-detection value is highest.

Remote sensing. Spectroscopic and satellite approaches detect at scales between individual trees and entire landscapes, bridging the gap between molecular confirmation and distributional mapping. Leaf-level hyperspectral analysis demonstrated that oak wilt can be spectrally distinguished from drought stress and foliar fungal disease through near-infrared and shortwave-infrared signals linked to reduced photosynthetic performance and altered water status-and that this spectral signal is detectable before visible wilting in greenhouse inoculations (Fallon et al., 2020). Scaling

from leaf to canopy, airborne and multiscale spectroscopic imagery combined phylogenetic discrimination against red oak signals with disease-specific spectral indices to achieve landscape-level oak wilt detection with high accuracy (Cavender-Bares et al., 2021; Sapes et al., 2022). Land-surface phenology extracted from satellite time series detected oak wilt distribution at county and regional scales using anomalous early-season greenup and summer canopy decline signatures, producing maps validated against ground-survey records (Pinto-Ledezma et al., 2023). The physiological mechanism underlying spectral detection-reduced photosynthesis and increased non-structural carbohydrates in infected tissue-has now been linked to canopy-scale spectral signatures in a framework that provides the biological basis for previsual remote sensing (Sapes et al., 2022). These advances shift surveillance from reactive diagnosis of individual trees toward anticipatory detection across landscapes. However, remote sensing, vector trapping, molecular diagnostics, and spatial risk models have not yet been integrated into a standardized, multi-site operational early-warning system.

Model-informed surveillance. Spatial models can combine climatic suitability, host distribution, and introduction pathways to identify and priority surveillance areas, while remote sensing and vector trapping support early detection, and molecular assays confirm pathogen presence (Gauthier et al., 2024; McLaughlin et al., 2022; Pedlar et al., 2020; Pinto-Ledezma et al., 2023). Chapter 2 explains the climatic and ecological basis for this prioritization, while Chapter 3 identifies areas of current and future climatic suitability. Together, these tools provide a tiered framework for prioritization, detection, and confirmation. The key remaining challenge is to integrate them into a standardized yet regionally adaptable early-warning system that supports timely management.

Figure 1.9 Evolution of Oak Wilt Detection Methods Across Field, Laboratory, Molecular, and Remote-Sensing Approaches (1940–2025). Note. Detailed information on this figure is summarized in Appendix Table 1.3.

1.3.7 Oak wilt control and disease management: the intervention gap

No single management method addresses both belowground and aboveground transmission pathways simultaneously, and no available method is biologically capable

of eradicating *B. fagacearum* from an established landscape. Every primary method is effective at small scales, degrades with EDC size and landscape heterogeneity, and requires regime-specific calibration that current management protocols inconsistently provide.

Belowground pathway disruption. Mechanical root-graft disruption by vibratory plow remains the primary method for EDC containment in both regimes. In the Lake States, a synthesis of Minnesota field studies found that vibratory plow trenching controlled belowground spread in approximately 84% of infection centers over four to six years (Juzwik et al., 2011). In Texas, the 30-year audit of the Texas Oak Wilt Suppression Project recorded 81% containment success across 2,124 installed trenches, with breakout rising markedly in clay-rich soils due to deeper root zone development that can exceed the standard ~1.2 m trenching depth, limiting effective root severance (Gomez et al., 2025).

Lake States failures reflect incomplete graft-zone mapping or graft re-initiation via lateral roots above the trench depth or laterally outside the trench line; Texas failures reflect root-zone lateral depth exceeding the trench installation depth, typically a consequence of shallow-installed liners on high-clay soils where root compression forces bypass points. Trenching with root barrier inserts (Biobarrier, Typar, or geomembrane liners) achieved 100% control over six years in one Texas study with engineered liner materials (Wilson & Lester, 2002). This finding indicates that containment failure rates are not inherent to the method but depend on installation completeness and site conditions, including liner depth relative to mapped root

architecture and the presence of sub-surface obstructions (rock outcrops, hardpan layers) that force roots to horizontal bypass points above the liner.

Root rupture by excavator-removing stumps and associated root mass to break graft connections demonstrated 63–93% cumulative prevention of symptoms over five years in northeast Wisconsin, with efficacy decreasing in larger infection centers and in stands with higher host composition heterogeneity (Yang et al., 2024). This method is appropriate when subsurface obstructions limit the vibratory plow's penetration or when the extent of the graft zone is uncertain. Its per-unit cost is higher than that of vibratory plow trenching, but it does not require pre-treatment graft-zone mapping with the same precision.

Aboveground pathway disruption. Removal of potential spore-producing trees (PSPTs), often combined with sanitation of adjacent hosts within ~15.2 m, has reduced new infection centers in Missouri and Iowa (Jones & Bretz, 1958; Young, 1949). Effectiveness depends strongly on timing, as delayed felling (>6 weeks post-defoliation) can result in fungal mat formation in ~31% of trees, increasing inoculum availability in Pennsylvania (Morris, 1954). Removal of large red oaks (>7.6 cm diameter), which are more likely to produce mats, is recommended for effective sanitation (Bruhn, 1995). Basal girdling has also been evaluated as a mat-suppression treatment and reduced fungal-mat production in Texas red oaks by as much as 50% (Greene et al., 2008).

However, sanitation and mat suppression alone do not ensure landscape-scale control, particularly in Texas, where belowground transmission through interconnected live-oak root systems dominates disease dynamics (Greene et al., 2008; Koch et al., 2010). Therefore, the same management methods should not be assumed to be equally

effective in both epidemiological regimes. Aboveground sanitation is particularly important where insect-mediated transmission contributes substantially to the formation of new disease centers, whereas root-graft disruption remains central where belowground spread dominates.

Systemic fungicide. Preventive trunk injection with propiconazole (Alamo formulation) delays symptom development and reduces mortality across all oak groups when applied to high-risk trees adjacent to active disease centers (Koch et al., 2010). Propiconazole does not kill *B. fagacearum* within colonized xylem; it suppresses colonization rate and slows the progression of cavitation-associated vessel occlusion. Its practical application is as ring-injection protection for high-value individual trees, not as a landscape-scale management strategy; treatment intervals of two to three years and per-tree injection costs make area-wide application economically infeasible in most management contexts.

Breeding and resistance. Near-term management priorities rest on prevention, surveillance, rapid diagnosis, and timely disruption of belowground pathways. Resistance breeding represents a long-horizon complement. Genetic diversity in white oak (*Q. alba*) has been characterized with microsatellite markers, providing the marker infrastructure needed to screen populations for resistance-associated alleles (Thunder et al., 2022). However, whether any loci documented in that diversity study are functionally associated with resistance to *B. fagacearum* infection has not been tested; the population structure and diversity estimates from Thunder et al. (2022) therefore provide a foundation for resistance-gene mapping, rather than evidence that heritable resistance to oak wilt has already been demonstrated. A haplotype-resolved white oak

genome now provides an improved framework for identifying candidate resistance genes and conducting finer-scale genomic analyses (Larson et al., 2025).

In analogous forest pathosystems, resistance breeding programs for eastern white pine (*Pinus strobus*) blister rust transferred resistance through hybridization with Himalayan blue pine (*P. wallichiana*), with backcross progenies retaining functional resistance while recovering species-specific physiological traits including drought and frost tolerance (Sniezko & Nelson, 2022). Genomic tools in *Castanea dentata* restoration -where hybrids with approximately 70–85% *C. dentata* ancestry combine blight resistance with species characteristics demonstrate that selective breeding and modern genomics can accelerate disease-resistant tree deployment for forest restoration (Westbrook et al., 2026).

In oaks, resistance breeding programs that aim to identify resistant individuals, conduct controlled crosses, and ultimately deploy improved genotypes will require integrating genomic insights with resistance screening, multi-year field trials, and long-term progeny evaluation (Sniezko & Nelson, 2022). Progress is constrained by the long juvenile period (typically 20–50 years to reproductive maturity in most *Quercus* spp., compared to 5–10 years for *Pinus* spp. used in operational resistance programs), the absence of confirmed heritable resistance to *B. fagacearum* at the species level, the need for multiple breeding cycles, and the genetic complexity of the pathogen population-*B. fagacearum* comprises at least four genetically differentiated clusters (Chahal, 2024) that may exert distinct and potentially variable selection pressures on host resistance traits. Until resistance is confirmed across pathogen populations and

breeding cycles, it should remain a long-term complement to prevention and ecologically informed disease management.

The pattern across methods and Species Distribution Modeling projections. Management efficacy is highest at small EDC size and early detection and degrades consistently as area increases and establishment age advances. Prevention is substantially more cost-effective than post-establishment control regardless of method (Koch et al., 2010). The logic of the disease therefore points toward early surveillance and predictive targeting-precisely the domain where advances in vector-based and remote-sensing detection provide the greatest untapped value.

The intervention gap is not primarily a gap in available methods; it is a deployment gap-specifically, a gap in 1) surveillance systems capable of triggering intervention before EDC expansion exceeds cost-effective management range; 2) contractor and equipment capacity to respond in remote or low-road-access stands; and 3) the integration of regime-specific epidemiology into management protocols. Management approaches calibrated to one epidemiological regime may transfer poorly to another because the relative contributions of aboveground and belowground transmission differ geographically. Effective oak-wilt management therefore requires early detection, rapid deployment, and rapid response as the most cost-effective management strategies because eradication is rarely feasible once oak wilt becomes established (Juzwik et al., 2011).

At the landscape level, early surveillance and rapid diagnosis are key for disease prevention. In parallel, modeling approaches such as Species Distribution Modeling (SDM) can identify areas climatically suitable for the pathogen, hosts, and vectors under

current and future environmental conditions, thereby informing proactive monitoring and management in the context of climate change.

1.3.8 Methodological frontier and future falsifiable research questions

Four advances now make the two-epidemics framework testable rather than merely descriptive. (1) The reference genome and a multi-state isolate panel (Chahal, 2024; Chahal et al., 2025a) permit common-garden comparison of regional clusters for epidemiologically relevant traits. (2) Field-deployable molecular assays and nitidulid metabarcoding (Gordon et al., 2025; Novi et al., 2024) allow standardized, regime-matched surveillance. (3) Remote sensing validated against the mechanism (Fallon et al., 2020; Sapes et al., 2022) bridges leaf-level pathology to canopy-scale detection. (4) Process-based and niche-modeling platforms (Pedlar et al., 2020; Pedlar et al., 2025; Stevens et al., 2024) can, in principle, be parameterized separately per regime. The bottleneck is no longer measurement; it is the conceptual commitment to treating the two epidemics as distinct in study design.

We propose the following five falsifiable predictions based on the two-epidemics framework:

Cluster–regime coupling is functional, not incidental. If the four genetic clusters (Chahal, 2024) are compared in common gardens, the Texas cluster will differ from the Upper Midwest cluster in at least one epidemiologically consequential trait (mat production rate, thermal optimum, or vector-association profile). Falsifier: no between-cluster trait differences exceed within-cluster variation, implying environment alone drives regime divergence.

Management parameters are regime-specific. Texas-derived trenching/sanitation efficacy will fail to predict outcomes in the Lake States once soil and root architecture are controlled. Falsifier: a single soil-and-spacing model predicts breakout equally well in both regimes.

Region-blind climate models can be limited. A model with shared predictors (e.g., fall precipitation, spring temperature) will systematically over- or under-predict suitability in Texas relative to a regime-specific model. Falsifier: a single predictor set is equally skillful in both theaters.

The southeastern frontier is where the framework breaks or holds. In Georgia–South Carolina–Tennessee–North Carolina, where the regimes converge, neither region's parameters will transfer cleanly; disease behavior will be intermediate and predictable only by a model that represents both pathways. Falsifier: Southeastern dynamics are fully captured by extrapolating one regime.

Human wood movement admixes clusters with measurable consequences. Long-distance firewood and log transport will, over time, erode the currently low-to-moderate genetic differentiation between clusters, detectable as admixture signatures at documented introduction (e.g., West Texas and New York). Falsifier: clusters remain genetically discrete despite documented human-mediated long-distance introductions, implying that introduced propagules either fail to establish or are eliminated by local competition.

1.4 Conclusion

Oak wilt has been studied as one disease for eighty years. The weight of the evidence in transmission biology, host anatomy, environmental control, and now

pathogen population genomics supports a different interpretation: two epidemics, one pathogen, separated by a geographic divide that is reflected in the host system, the environment, and the genome of *B. fagacearum*. The clonal-root Texas regime and the root-graft Lake States regime are not regional flavors of a uniform process; they are mechanistically distinct epidemics driven by genetically distinct pathogen populations, and they converge at a southeastern frontier that current models cannot describe. This reframing explains why management and forecasting have transferred poorly between regions, and it specifies what to do about it: parameterize the two epidemics separately, test whether the pathogen's genetic clusters differ in epidemiological function, and replace region-blind correlative models with process-based, vector-coupled, genomics-informed forecasting. The functional tests proposed in section ‘Methodological frontier and future falsifiable research questions’ are now feasible and will either confirm or refute the core hypothesis of this review; such experiments should be prioritized. The diagnostic and surveillance tools to act anticipatorily already exist. What the field lacks is a clear conceptual framework that recognizes oak wilt as two mechanistically distinct regional epidemics.

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Appendix A. Supplementary materials for Chapter 1

Appendix Table 1.1 Major biotic and abiotic threats affecting *Quercus* spp. in the U.S.

Biotic threats	Host species	Impacts	Sources
Sudden Oak Death (*Phytophthora ramorum*)	Coast live oak (*Q. agrifolia*)	9.02 million stems were affected in California by 2012.	Cobb et al. (2020); Frankel et al. (2022)
Spongy moth (*Lymantria dispar*)	Chestnut oak (*Q. prinus* Willd), *Q. alba*	Severe defoliation (>75%) over consecutive years leads to rapid mortality, increasing after the second year in the northeastern U.S.; In the northeastern U.S., mortality is highest in oak-dominated forests on poor sites with limited predators (>50%), especially among suppressed/intermediate trees.	Coleman (2023); Davidson et al. (2001); Gottschalk (1993)
Oak shothole leaf miner (*Japanagromyza viridula* Coquillett)	*Q. rubra* and scarlet oak (*Q. coccinea*) -highly susceptible *Q. alba*- least susceptible	2019-2020 outbreak in the Mid-Atlantic & Northeast U.S. caused extensive foliar damage (>90% leaves affected in some stands), but doesn't kill trees unless combined with drought or repeated stress; Defoliated oaks show reduced growth, root biomass, and mast production, with broader impacts on timber and carbon sequestration.	Quesada et al. (2025); Ferretti et al. (2021); Jacobs et al. (2022); Jacquet et al. (2012)
Goldspotted oak borer (*Agrilus auroguttatus*)	*Q. agrifolia*, California black oak (*Q. kelloggii*), Canyon live oak (*Q. chrysolepis*, low levels)	First detected in 2004 in San Diego County, causing significant oak mortality in 2008; It prefers large diameter oaks (>18-20 inches in diameter at breast height); Killed approximately 27,000 mature oaks in Southern California.	Corella et al. (2020) Venette et al. (2015)
Canker and dieback pathogen (*Diplodia corticola*)	*Q. rubra,* *Q. velutina,* *Q. virginiana,* *Q. alba*, and *Q. macrocarpa* (newly recognized U.S. host)	Greenhouse inoculation caused 100% shoot tip death in red and white oak seedlings within a month; On average, lesion lengths of 75-88 mm in red oaks (~75-78% of shoot length); 63-75 mm lesions in white oaks (~40-42% of shoot length).	Aćimović et al. (2016); Martin et al. (2017); Onufrak et al. (2022); Pathak et al. (2018)

Red oak borer (*Enaphalodes rufulus*)	*Q. rubra,* *Q. velutina,* *Q. coccinea,* *Q. marilandica*	Outbreak in Arkansas, Missouri, and Oklahoma (1995–2005): High-density infestations (>100 beetles/tree) disrupted vascular tissues, leading to stress, dieback, and large-scale mortality of dominant oaks; In Arkansas oak-hickory forests, 13% of all trees >12.7 cm dbh were dead/dying; in red oak–dominated stands, mortality reached 30–100% of basal area.	Haavik et al. (2012); Stump et al. (2024)
Foamy bark canker (*Geosmithia pallida*) Vector: Western oak bark beetle (*Pseudopityophthorus pubipennis*)	*Q. agrifolia*	Represents a new disease complex (native bark beetle + introduced fungal symbiont). It has killed many coast live oaks in Southern California and is spreading northward.	Swain et al. (2017)
		Climate-induced stress	
Drought	*Q. velutina*, and *Q. coccinea*	3 to 6 times the mortality of the red oak species compared to Q. alba and Q. stellata due to drought.	Fan et al. (2006)
Summer Droughts	*Q. agrifolia*, and *Q. lobata*	Summer droughts accounted for 47.49% of the oak seedlings' deaths.	López-Sánchez et al. (2019)
Extreme drought	*Q. alba*, and *Q. velutina*	In 2012, an extreme drought in Missouri raised the annual mortality rates of 1.7%-2.1% to 10% in white oak and 26.5 % in black oak	Wood et al. (2018)
Drought, extreme weather, and pathogens	*Q. rubra,* *Q. alba,* *Q. prinus,* *Q. stellata,* *Q. velutina,* *Q. marilandica,* *Q. montana,* *Q. garryana,* *Q. lobata*	Increase oak stress and mortality on shallow, acidic soils and in drier topographic positions, such as upper slopes and south- or west-facing aspects. Shifts in temperature and rainfall alter soil moisture, favor pathogens, and reduce oak resilience in mature stands. In the U.S., southern drought-tolerant oaks may expand, while northern red and black oaks are vulnerable to drought and pathogens; future persistence depends on management and disturbance regimes.	Bratu et al. (2025); Radcliffe et al. (2021)
Drought and frost	*Q. stellata*, and *Q. marilandica*	Severe drought (2006), combined with a false spring/late frost (2007), caused nearly complete canopy mortality across 3.5% of the forest area	Bendixsen et al. (2015)
Temperature	*Q. lobata*	Highest growth in cooler temperatures, maladaptation at current temperatures, and growth rate expected to be reduced by ~5.6% by 2100.	Browne et al. (2019)

Heat and drought	*Q. alba,* *Q. rubra,* *Q. coccinea,* *Q. montana,* *Q. marilandica,* *Q. velutina*	Heat and drought stress suppress growth, particularly at low-elevation, south-facing xeric sites.	White et al. (2011)

Appendix Table 1.2 Oak species susceptibility to oak wilt.

Species	Susceptibility	Sources
Red oak group		
Q. rubra	Very High	Chahal (2024); Harrington (2013); Jacobi and MacDonald (1980)
Q. ellipsoidalis	Very High	Bruhn et al. (1991); Harrington (2013); Bretz (1951)
Q. velutina	Very High	Appel (1995)
Q. coccinea	Very High	Appel (1995)
Q. buckleyi	Very High	Wilson (2005)
Q. marilandica	Very High	Wilson (2005)
Q. shumardii	Very High	Wilson (2005)
Q. laurifolia	High	Wilson (2005)
Q. laevis	Moderate	Wilson (2005); Tainter and Ham (1983)
Q. falcata	Very High	Juzwik et al. (2011)
Q. phellos	High	Juzwik et al. (2011); O'Brien et al. (2000); Wilson (2001)
Q. nigra	High	Chahal (2024); Juzwik et al. (2011); O'Brien et al. (2000); Davidson et al. (2001)
Q. imbricaria	High	Juzwik et al. (2011); Wilson (2001)
Q. pagoda	High	Juzwik et al. (2011); O'Brien et al. (2000); Wilson (2001)
Q. palustris	High	Juzwik et al. (2011); O'Brien et al. (2000); Wilson (2001)
Q. texana	High	Juzwik et al. (2011); O'Brien et al. (2000); Wilson (2001)
White oak group		
Q. robur	High	Juzwik et al. (2011)
Q. petraea	High	Juzwik et al. (2011)
Q. alba	Least	Appel (1995); Chahal (2024); Juzwik et al. (2011)
Q. macrocarpa	Moderate	Appel (1995); Chahal (2024); Harrington (2013); Yang (2015)
Q. stellata	Least	Juzwik et al. (2004); Wilson (2005)
Q. muehlenbergii	Less	Wilson (2005)
Q. prinoides	Less	Juzwik et al. (2011); O'Brien et al. (2000); Wilson (2001)
Q. polymorpha	Less	Juzwik et al. (2004); O'Brien et al. (2000)
Q. laceyi	Less	Juzwik et al. (2004); O'Brien et al. (2000)
Q. sinuata var. breviloba	Less	Juzwik et al. (2004); O'Brien et al. (2000)
Q. bicolor	Less	Juzwik et al. (2004); O'Brien et al. (2000)
Q. lyrata	Less	Juzwik et al. (2004); O'Brien et al. (2000)
Q. montana	Less	Juzwik et al. (2004); O'Brien et al. (2000)
Q. michauxii	Less	Juzwik et al. (2004); O'Brien et al. (2000)
Live oaks		
Q. virginiana	Moderate	Wilson (2005)
Q. fusiformis	Moderate	Chahal (2024); Wilson (2005)

Appendix Table 1.3 Table of Oak wilt detection approaches.

Detection/Diagnostic Milestone	Category	Year	Sources
Symptoms -based field surveys that include foliar discoloration/bronzing, marginal necrosis, rapid upper crown wilt, sudden defoliation, sapwood discoloration, basal sprouting (first recognition in Wisconsin)	Detection	1944	Henry et al. (1944)
Root graft transmission recognition (concentric spread, infection centers)	Epidemiological detection (spread-based)	1950	Kuntz and Riker (1949)
Anatomical diagnostic confirmation (xylem vessel plugging by tyloses/gums, confirming hydraulic failure as the cause of wilting)	Diagnostic	1951	Beckman et al. (1951)
Pathognomonic field diagnostic sign: fungal mats/pressure pads (under bark of recently oak-wilt killed trees)	Diagnostic	1952	Morris and Fergus (1952)
Rapid liquid-culture laboratory diagnosis of oak wilt (accelerated sporulation from infected wood chips in liquid media; confirmation in ~5 days)	Diagnostic	1952	Barnett (1952)
Selective culture-based diagnostic isolation (glucose–phenylalanine agar for *C. fagacearum*)	Diagnostic	1953	Barnett (1953)
Overland transmission of the oak wilt pathogen by Nitidulid beetles	Epidemiological detection (vector-based)	1953	Dorsey et al. (1953)
GIS and Color-infrared imagery based spatial temporal surveillance to quantify oak wilt spread rate, and infected center expansion	Surveillance/spatial spread assessment	1984	Appel and Maggio (1984); Everitt et al. (1999)
Species-specific molecular DNA-based diagnostic detection of *B. fagacearum* using ITS-targeted nested and real-time PCR directly from sapwood drill shavings, demonstrating superior sensitivity over culture isolation, reliable detection in white oaks, and the first successful detection of *B. fagacearum* from dead sapwood tissues (up to one year after branch or whole-tree death)	Diagnostic	2011	Wu et al. (2011); Yang and Juzwik (2017); Yang (2015)
Physiology-based hyperspectral detection of oak wilt at leaf and canopy scales, enabling differentiation from drought and other foliar diseases using supervised spectral classification	Diagnostic (remote sensing / spectral)	2020	Fallon et al. (2020)
Multi-scale (leaf, UAV, airborne, satellite) spectral detection of oak wilt, integrating physiological spectroscopy with a phylogenetically informed, stepwise classification framework; demonstrates superior performance of VIS–SWIR (410–2400 nm) hyperspectral data and enables landscape-scale detection of infected trees	Detection (remote sensing, multi-scale spectral+ modeling)	2021	Cavender-Bares et al. (2021)
Fast on-site molecular diagnosis of oak wilt using qPCR and CRISPR-based DETECTR assays, enabling pathogen confirmation within one hour	Diagnostic (on-site molecular/ CRISPR-based)	2022	Bourgault et al. (2022)

Spaceborne phenology-based detection of oak wilt using chlorophyll/carotenoid index (CCI) time-series and machine-learning classification to map symptomatic oak trees at regional scales	Detection (remote sensing/ phenology-based)	2023	(Pinto-Ledezma et al., 2023)
Insect-trap bio surveillance using qPCR to detect *B. fagacearum* DNA for early warning in Canada	Detection (Surveillance - molecular detection)	2024	Gauthier et al. (2024)
Rapid on-site oak wilt diagnosis using LAMP, with results visible using a gold-nanoparticle (AuNP) pellet readout.	Diagnostic (on-site molecular)	2024	Novi et al. (2024)
Nondestructive detection of *B. fagacearum* using leaf petiole sampling coupled with optimized real-time PCR	Tree-level diagnostic detection (nondestructive)	2025	(Chahal et al., 2025)
UAV-based early detection using RGB imagery and deep learning. Transformer models (e.g., SwinV2-Tiny) reached ~98.6% F1 on a labeled canopy dataset. Includes a real-time web tool with geospatial mapping and Reinforcement Learning from Human Feedback refinement.	Detection (UAV RGB+ AI/transformers)	2025	Bismoy (2025)
Metabarcoding Amplicon Sequencing: It uses sequencing to resolve PCR inconclusive results, identifies co-occurring taxa from beetle and forest microbiomes, improve pathogen detection accuracy	Diagnostic (metabarcoding sequencing)	2025	Gordon et al. (2025)

Appendix Table 1.4 Representative high-impact studies selected for citation tracking across decades in oak wilt research.

Name of the paper	Publication	Citation	Total papers from backward citation	Total papers from forward citation
The origin of *Ceratocystis fagacearum*, the oak wilt fungus.	2008	73	4	1
Challenges and Successes in Managing Oak Wilt in the United States.	2011	75	21	8
Review and new insights into wood anatomy that help understand and control oak wilt.	2023	4	4	0

Appendix Table 1.5 Common names, scientific names, and botanical authorities of oak species included in this study.

Common name	Scientific name	Scientific name (with authority)
White oak	*Q. alba*	*Q. alba* L.
Post oak	*Q. stellata*	*Q. stellata* Wangenh.

Chinkapin Oak	*Q. muehlenbergii*	*Q. muehlenbergii* Engelm.
Dwarf Chinkapin oak	*Q. prinoides*	*Q. prinoides* Willd.
Monterrey/ Mexican oak	*Q. polymorpha*	*Q. polymorpha* Schltdl. & Cham.
Lacey oak	*Q. laceyi*	*Q. laceyi* Small
White shin oak	*Q. sinuata var. breviloba*	*Q. sinuata var. breviloba* (Torr.) C.H.Mull.
Swamp white oak	*Q. bicolor*	*Q. bicolor* Willd.
Overcup oak	*Q. lyrata*	*Q. lyrata* Walter
Chestnut oak	*Q. montana*	*Q. montana* Willd.
Swamp chestnut oak	*Q. michauxii*	*Q. michauxii* Nutt.
Turkey oak	*Q. laevis*	*Q. laevis* Walter
Bur oak	*Q. macrocarpa*	*Q. macrocarpa* Michx.
Coastal live oak	*Q. virginiana*	*Q. virginiana* Mill.
Texas live oak	*Q. fusiformis*	*Q. fusiformis* Small
Laurel oak	*Q. laurifolia*	*Q. laurifolia* Michx.
Willow oak	*Q. phellos*	*Q. phellos* L.
Water oak	*Q. nigra*	*Q. nigra* L.
Shingle oak	*Q. imbricaria*	*Q. imbricaria* Michx.
Cherrybark oak	*Q. pagoda*	*Q. pagoda* Raf.
Pin oak	*Q. palustris*	*Q. palustris* Münchh.
Nuttall oak	*Q. texana*	*Q. texana* Buckley
English oak	*Q. robur*	*Q. robur* L.
Sessile oak	*Q. petraea*	*Q. petraea* (Matt.) Liebl.
Northern red oak	*Q. rubra*	*Q. rubra* L.
Northern pin oak	*Q. ellipsoidalis*	*Q. ellipsoidalis* E.J.Hill
Black oak	*Q. velutina*	*Q. velutina* Lam.
Scarlet oak	*Q. coccinea*	*Q. coccinea* Münchh.
Texas red oak or Spanish oak	*Q. buckleyi*	*Q. buckleyi* Nixon & Dorr
Blackjack oak	*Q. marilandica*	*Q. marilandica* Münchh.
Shumard oak	*Q. shumardii*	*Q. shumardii* Buckley
Southern red oak	*Q. falcata*	*Q. falcata* Michx.
Havard oak	*Q. havardii*	*Q. havardii* Rydb.
Oregon white oak	*Q. garryana*	*Q. garryana* Douglas ex Hook.

Appendix Table 1.6 Sources of the data collection and data point numbers.

Source	Observation years	Points
EDDMapS. (2025). Early Detection & Distribution Mapping System. The University of Georgia - Center for Invasive Species and Ecosystem Health. Available online at http://www.eddmaps.org/. Accessed December 13, 2025.	1987-2024	17,456
New York State Department of Environmental Conservation (NYSDEC) (NY)	2008-2019	29
Indiana Department of Natural Resources	2001-2024	64
Department of Entomology, Michigan State University	2014-2024	152
Kentucky Division of Forestry	1989-2024	8
Minnesota Department of Natural Resources	2016-2021	168
Alien Forest Pest Explorer (Available online at: https://doi.org/10.4231/HWQF-V087)	Till April 2023	968

Appendix Table 1.7 U.S. hardwood lumber exports by species from 2000 to 2025.

SN	Product	Yearly Exports in Millions of Dollars																									
		2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020	2021	2022	2023	2024	2025
1	Red Oak	295	249	242	262	280	226	221	196	184	152	234	277	296	432	578	518	609	762	645	444	421	517	547	390	491	490
2	White Oak	320	275	272	272	329	347	377	339	262	222	279	324	314	330	424	392	410	509	515	405	364	461	470	338	379	382
3	Walnut	28	41	59	59	69	73	93	111	73	60	90	121	123	137	200	184	214	258	295	252	251	336	318	273	272	251
4	Ash	73	61	67	69	80	81	86	88	72	63	113	133	168	200	272	259	272	282	245	178	160	155	150	141	119	93
5	Yellow poplar	95	81	88	90	113	107	156	157	142	119	189	183	237	267	329	225	249	290	261	174	165	160	159	116	117	97
6	Cherry	123	105	103	115	127	126	121	93	62	34	44	40	48	69	79	91	116	147	149	105	96	119	139	118	103	86
7	Maple	216	176	164	167	194	222	240	181	144	94	125	124	135	144	150	118	105	107	101	84	76	135	144	91	90	81

Note. Data sourced from the USDA Foreign Agricultural Service's Global Agricultural Trade System (GATS) online database (https://apps.fas.usda.gov/GATS/default.aspx), accessed on March 2, 2026.

CHAPTER 2

Climate, Ecology, and Distribution Drivers of Oak Wilt: A Literature Review Supporting Climate Niche Modeling and Future Invasion Risk

2.1 Introduction

Non-native forest pests introduced through international trade have substantially affected North American forests (Gauthier et al., 2024). Approximately two major invasive forest pests are introduced into the U.S. each year, and biological invasions cause estimated annual economic losses of US$26.8 billion (Aukema et al., 2010; Diagne et al., 2021; Frankel & Palmieri, 2014). Climate change may further increase these impacts by weakening environmental barriers that previously limited the establishment and spread of invasive species (King et al., 2021) and increasing host susceptibility (Beckman, 2019). Oak wilt, caused by the vascular fungus *Bretziella fagacearum*, is among the most destructive diseases of North American oaks. Susceptible red oaks may die within weeks, while white oaks can persist longer (Juzwik et al., 2011). Oak species are also increasingly affected by habitat loss, climate change, and other human-induced pressures (Subedi et al., 2024).

Chapter 1 established that oak wilt occurs through two epidemiologically distinct systems: a predominantly root-graft-mediated epidemic in the Lake States and a clonal-root-mediated epidemic in central Texas. These regional systems differ in host composition, transmission pathways, vector activity, environmental controls, and

management requirements. Consequently, management practices developed in one region may not be transferred directly to another.

Oak wilt is climate-sensitive because temperature, precipitation, humidity, drought, storms, and seasonal variation influence host susceptibility, fungal mat formation, pathogen survival, wound availability, and insect-vector phenology (Haight et al., 2011; Morris et al., 2024; Stevens et al., 2024). Climate change may also alter the geographic overlap among the pathogen, susceptible hosts, vectors, and suitable environmental conditions, potentially creating new areas where oak wilt could establish or intensify. However, climatic suitability should not be interpreted as equivalent to disease occurrence or invasion risk (Araújo et al., 2019).

Predicting future climatic suitability is important because oak wilt is difficult to manage after establishment, and existing control methods are primarily designed to contain localized disease centers. Early detection, biosurveillance, and prevention of long-distance introduction are more effective than attempting to suppress widespread outbreaks (Bronson et al., 2023; Juzwik et al., 2011; Koch et al., 2010). This chapter synthesizes the biological and ecological processes that shape the climatic niche and potential future distribution of oak wilt. It reviews the major climatic, host, vector, landscape, and human-mediated drivers, identifies key biological, modeling, and management gaps, and presents a conceptual framework linking these factors to climatic suitability, surveillance, and management decisions.

2.2 Climate drivers of oak wilt

Climate influences oak wilt by acting directly on *B. fagacearum* and indirectly through host physiology, fungal mat formation, vector activity, and transmission

opportunities (Appel, 1994; Haight et al., 2011; Morris et al., 2024; Stevens et al., 2024). Together, these processes determine where environmental conditions support pathogen survival and disease development.

2.2.1 Temperature

Temperature regulates fungal growth, symptom development, fungal-mat production, host stress, and insect-vector activity. Experimental studies have identified approximately 25-26°C as favorable for *B. fagacearum* growth and disease development, whereas higher temperatures may suppress fungal activity while increasing host stress (Appel et al., 1990; Fenn et al., 1975; Tainter & Ham, 1983). Colder winters restrict fungal mat production in the Lake States, and warmer conditions support longer periods of biological activity in Texas (Appel, 1995; Juzwik & French, 1983).

Vector phenology is also temperature dependent. In Wisconsin, *Colopterus truncatus* emerged before 50 accumulated degree-days and peaked at approximately 200-350 degree-days, whereas *Carpophilus sayi* peaked later at 450-500 degree-days (Jagemann et al., 2018; Morris et al., 2024). Although warming may extend beetle flight activity, infection risk also depends on the short period during which fresh wounds remain susceptible to inoculation (Harrington, 2013; Haugen et al., 2008; Wilson, 2001). However, potential differences in thermal tolerance among regional pathogen populations remain unresolved. The net effect on inoculation-period duration and new-center initiation rate under projected warming remains unquantified and represents a specific modeling gap.

2.2.2 Moisture

Fungal mats require suitable moisture and temperature conditions to remain biologically active (Boyce, 1957; Tainter & Baker, 1996). Spring precipitation and high humidity can prolong fungal-mat activity and ascospore release, whereas drought and extreme heat may accelerate desiccation and reduce inoculum availability (Juzwik & French, 1983; Stevens et al., 2024). Seasonal precipitation affects root zone moisture and host water relations. Longer-term moisture deficits can impose chronic drought stress on host trees. Climatic moisture indices that integrate precipitation with atmospheric evaporative demand may therefore provide more biologically informative indicators than precipitation totals alone (Pedlar et al., 2020).

Previous modeling studies also indicate the importance of moisture in determining oak wilt distribution. Fall precipitation was the strongest predictor in a Canadian MaxEnt model, while summer soil moisture contributed to disease occurrence in northern Wisconsin (Pedlar et al., 2020; Stevens et al., 2024). However, moisture may have contrasting effects: wetter conditions can support fungal-mat viability and spore release, whereas drought may increase host hydraulic stress while reducing inoculum persistence. These relationships support using seasonal precipitation, relative humidity, soil moisture, and CMI in oak wilt models. Seasonal CMI may better capture water availability and its effects on host stress, pathogen activity, and transmission than annual precipitation alone.

2.2.3 Seasonality

Oak wilt transmission depends on synchronization among fungal-mat availability, vector movement, host phenology, and the presence of fresh wounds. Seasonality is therefore a central epidemiological process.

In the Lake States, fungal mats and nitidulid activity occur mainly in spring, with a smaller secondary period in autumn (Appel, 1995; Jagemann et al., 2018; Juzwik & French, 1983). Infection risk is highest when active vectors, viable mats, and recently wounded oaks coincide (Harrington, 2013; Haugen et al., 2008; Jagemann et al., 2018; Wilson, 2001). Seasonal patterns differ in Texas, where warmer conditions allow longer periods of vector activity and belowground transmission through clonal live-oak roots is less restricted by short infection windows. Climate warming may shift vector emergence and extend seasonal activity, although fungal-mat production and wound susceptibility may remain limited to specific temperature and moisture conditions. Accordingly, seasonal climate variables may capture oak wilt transmission dynamics more effectively than annual climate averages.

2.3 Host distribution and climatic constraints

Susceptible red oaks are widely distributed across eastern and central North America and are particularly important because of their high susceptibility and ability to produce fungal mats (Cavender-Bares, 2019; Juzwik et al., 2011; O'Brien et al., 2011; Rauschendorfer et al., 2022). Live oaks form a distinct epidemic in Texas and the southern coastal region, where clonal root systems enable rapid belowground transmission, whereas white oaks are generally less susceptible but not uniformly

resistant (Appel, 1995; Appel et al., 2008; Gibbs & French, 1980; Jacobi & MacDonald, 1980).

Climate change may shift suitable red-oak habitat northward, but limited regeneration, slow migration, herbivory, and competition may prevent host populations from occupying all suitable areas (Peters et al., 2019a, 2019b; Prasad et al., 2008; Rauschendorfer et al., 2022). Species-specific responses are also important; for example, suitable habitat for *Quercus arkansana* is projected to shift northward while declining within much of its current range (Subedi et al., 2024). Integrating host distribution, oak abundance, forest composition, and stand connectivity with pathogen and insect vector distribution models would provide a more complete estimate of future oak wilt establishment.

2.4 Vector ecology under changing climate

Temperature controls the emergence and seasonal activity of oak wilt vectors. *Colopterus truncatus* becomes active earlier in spring, whereas *Carpophilus sayi* peaks later, creating successive periods of vector activity during the infection season (Jagemann et al., 2018; Morris et al., 2024).

Climate warming may advance emergence, extend flight periods, and allow competent vectors to persist farther north. However, transmission risk increases only when vector activity overlaps with fungal-mat production and fresh host wounds. Future models should incorporate degree-day thresholds and seasonal overlap rather than relying only on mean climatic conditions.

2.5 Environmental drivers of disease development

Studies in the Upper Midwest show that sandy soils, short inter-tree distances, high red-oak basal area, and homogeneous stand composition increase root contact, graft formation, and local disease-center expansion (Bruhn et al., 1991; Haight et al., 2011; Juzwik, 2007; Juzwik et al., 2011). Wind exposure and severe spring storms may further increase infection opportunities by creating fresh wounds (Juzwik & Schmidt, 2000). In Texas, continuous clonal live-oak root systems permit rapid belowground transmission without requiring newly formed inter-tree grafts (Appel, 1995; Appel et al., 2008).

Landscape context also changes the dominant transmission pathway. Forest structure and host connectivity primarily regulate local epidemic expansion, whereas pruning, construction injury, and movement of infected firewood or logs can initiate new infections and facilitate long-distance spread in urban and fragmented landscapes (Haight et al., 2011; Juzwik et al., 2011). Thus, climate defines broad environmental suitability, while soil, stand structure, disturbance, and human movement determine whether the pathogen is introduced, establishes, and spreads locally.

Collectively, these studies demonstrate that oak wilt development is governed by interacting climatic, edaphic, biotic, stand-level, and human drivers whose importance differs among epidemiological regions. The regional evidence is summarized in Table 2.1, while Figure 2.1 integrates these drivers within the host–pathogen–environment framework.

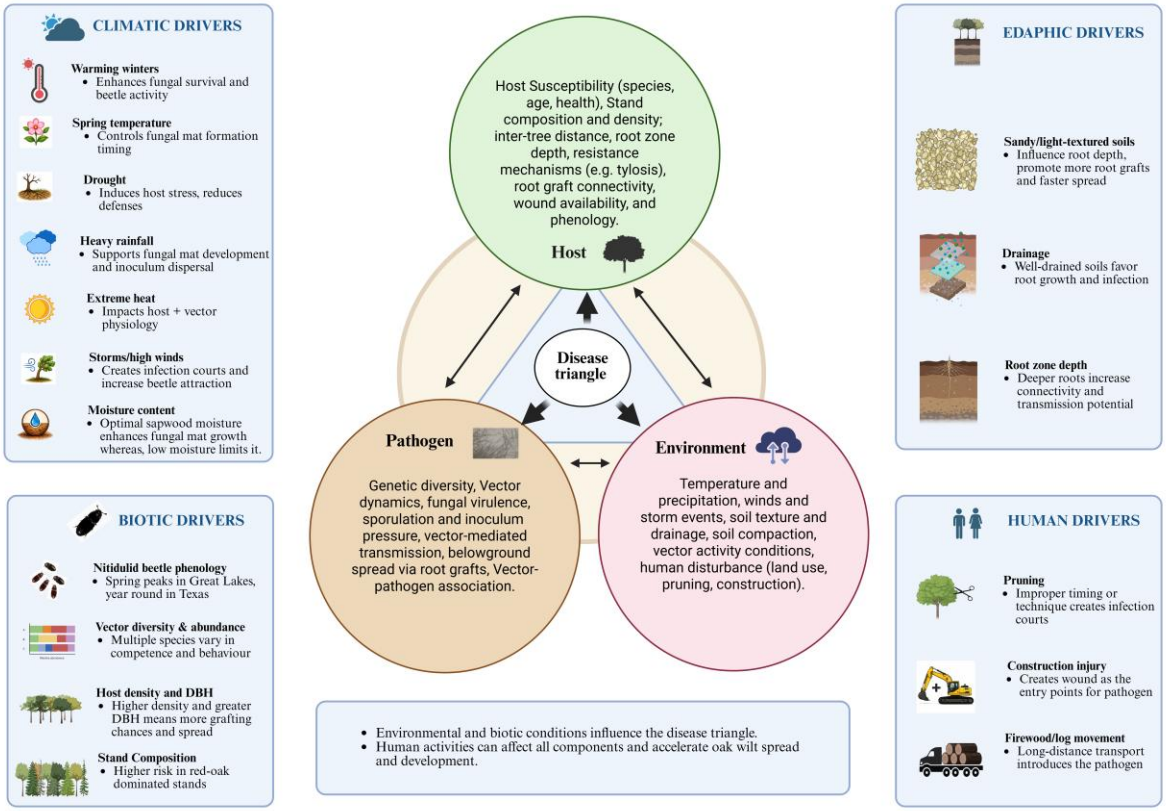

Figure 2.1 Disease Triangle Framework Illustrating the Biotic and Abiotic Drivers of Oak Wilt Epidemiology.

Table 2.1 Summary of the literature review: biotic and abiotic stress factors driving oak wilt (Bretziella fagacearum) outbreaks by study region.

Study Region	Oak Species	Biotic Stress Factors	Abiotic Stress Factors	Source
Northern Wisconsin, U.S.	*Q. rubra, Q. ellipsoidalis*	High oak density and clustering; root-graft transmission; sap beetle vectors (*Carpophilus* spp., *Colopterus* spp.); human-transported infected firewood initiated earliest infection clusters	Higher elevation (~2× incidence); wind-exposed ridges and slopes; shallow valleys; sandy outwash soils (enhance root grafting). Optimal fungal growth at ~24°C with 40–45% wood moisture;	Stevens et al. (2024)

			extreme heat or low moisture suppresses inoculum production	
Michigan, U.S.	*Q. rubra*	Sap beetle vectors: *Carpophilus sayi*, *Ca. dimidiatus*, *Ca. fasciatus*, *Colopterus truncatus*, *Glischrochilus sanguinolentus*. Peak spore transmission in May–June (96% of cases)	Degree-day (DD) thresholds control vector phenology: beetle emergence at <50 DD (base 10°C); peak activity at ~112 DD (2018) and ~212 DD (2019). Warm springs advance peak; cool, wet springs delay but extend beetle activity, prolonging transmission window	Morris et al. (2024)
Great Lakes region (Minnesota, Wisconsin, Michigan) and Texas, U.S.	*Q. rubra, Q. velutina, Q. nigra, Q. fusiformis, Q. alba, Q. macrocarpa, Q. palustris, Q. ellipsoidalis, Q. buckleyi, Q. havardii, Q. laceyi*	Nitidulid sap beetles and *Pityophthorus* oak bark beetles as vectors; host stand homogeneity and density; root-graft transmission (dominant local pathway)	Cold winters suppress mat formation (no mats mid-November to mid-April in Great Lakes). Warm climates (Texas) permit year-round vector activity and mat production. Sandy soils, spring temperature and moisture, and drought/heat stress all increase disease risk	Chahal (2024)
Minnesota and Wisconsin, U.S.	*Q. rubra, Q. ellipsoidalis*	Nitidulid beetles as primary overland vectors	Climatic seasonality drives vector phenology and mat availability windows; abiotic factors are not the primary analytical focus of this study	Pinto-Ledezma et al. (2023)
Ontario, Manitoba, and New Brunswick, Canada	*Q. macrocarpa, Q. rubra, Q. alba, Q. velutina, Q. bicolor, Q. muehlenbergii, Q. ellipsoidalis, Q. shumardii*	Potential vectors newly recorded in Canada: *Ca. corticinus*, *C. nepos*, and *Glischrochilus obtusus* (all Nitidulidae); presence confirms vector risk ahead of confirmed oak wilt establishment	Abiotic suitability for vectors not formally assessed in this study	Reed et al. (2023)
Eastern Canada (emphasis: southern Ontario, southern Quebec, Maritime Provinces)	*Q. rubra, Q. alba, Q. macrocarpa, Q. bicolor, Q. garryana*	Primary insect vectors: *C. truncatus*, *Ca. sayi*; occasional oak bark beetles (*Pseudopityophthorus* spp.); root grafts; host density and proximity. Human-mediated movement of infected logs and firewood	Fall precipitation (41.2% relative variable importance) and spring temperature (35.6%) were the top climatic predictors in the MaxEnt model. Moisture balance and coldest-month temperature contributed <20% combined	Pedlar et al. (2020)
East-central and	*Q. ellipsoidalis, Q. rubra*	Pathogen genetic diversity; Nitidulid and oak	Psamments and Hemists soils: ~88% and ~82%	Gearman and

southeastern Minnesota, U.S.		bark beetles (*Pityophthorus* spp.) as vectors; red oak-dominated stand composition; root-graft transmission; low-intensity urban land cover (~79% predicted risk)	predicted occurrence probability, respectively. Higher elevation, moderate July temperatures, and higher precipitation increase predicted suitability; exposed terrain adds slight additional risk	Blinnikov (2019)
Minnesota, U.S.	*Q. rubra, Q. ellipsoidalis, Q. macrocarpa, Q. alba*	*C. truncatus* and *Ca. sayi* as major overland vectors	Deep sandy soils favor root grafting; root-graft spread rate 7.6–12 m yr^{-1}. Temperature and precipitation regulate mat formation and longevity (37–55% wood moisture required for mat production)	Yang (2015); Tainter and Baker (1996)
U.S. (national review)	Red oak group (*Q. rubra, Q. velutina, Q. falcata, Q. shumardii, Q. ellipsoidalis*); White oak group (*Q. alba, Q. macrocarpa*); Live oak group (*Q. fusiformis, Q. virginiana*)	Root grafts (dominant local spread); Nitidulid sap beetles and oak bark beetles (overland transmission); red oak stand homogeneity and high host density; human activity (firewood transport; pruning during beetle activity window)	Warmer temperatures, drought, and altered precipitation patterns accelerate disease. Sandy soils enhance root grafting relative to clay or rocky substrates. Temperature, precipitation, and sapwood moisture regulate seasonal peaks in aboveground transmission	Juzwik et al. (2011)
Anoka County, Minnesota, U.S.	Red and white oak (mixed stands)	Short inter-tree distances and high red-to-white oak ratio accelerate root-graft transmission. Large DBH of diseased trees increases root overlap and grafting probability. ~93% of observed root-graft transmission occurred at <9 m (≈30 ft); maximum observed transmission distance ~12–13 m (≈40–41 ft)	Grayling soil series (loamy sand) promotes extensive lateral root spread, increasing root-graft frequency. Inter-tree distance is a critical predictor of graft-mediated transmission risk	Haight et al. (2011); Menges and Loucks (1984); Juzwik (2007); Bruhn et al. (1991)
Carlos Avery Wildlife Refuge, Chisago County, Minnesota, U.S.	*Q. rubra*	No biotic stress factors were separately reported in this study	Sandy soils (Zimmerman loamy sand, Sartell fine sand) promote root grafting and lateral spread. In this study, 13 inter-tree grafts and 162 self-grafts were found within 1 m of the soil surface (within 2.5 m of the root collar), although the number may	Blaedow and Juzwik (2010)

			be higher because roots extend beyond that depth.	
U.S. (multiple places, review paper)	No species mentioned	Host dependence: the common root live oak system drives faster spread (~40 m yr^{-1} disease expansion per year in Texas live oaks vs < 15.2 m yr^{-1} in Midwestern deciduous oaks lacking common roots).	-	Koch et al. (2010); Wilson (2001)
Missouri and Texas, U.S.	Red oaks	In Missouri, *C. truncatus, C. semitectus, and C. niger* are dominant in disease transmission, with an April peak, whereas in Texas, *C. truncatus* predominates with peak contamination from February to April, highest near mats and fresh wounds, and during warm midday flight periods.	-	Hayslett et al. (2008)
Central Texas	*Q. fusiformis, Q. virginiana, Q. buckleyi, Q. marilandica*	Root graft spread in clonal live oak, nitidulid vectors. Human activities like *pruning* during peak beetle activity (spring), and the movement of infected firewood.	High temperatures, drought stress, ridge/upper-slope exposure affect disease development and mat formation.	Appel (2007)
Midwestern, Middle, and South Atlantic States of the U.S.	*Q. falcata* *Q. rubra* *Q. ellipsoidalis,* *Q. velutina* *Q. shumardii*	Nitidulid beetles (*C. truncatus, Carpophilus* spp.), Oak bark beetles (*P. minutissimus, P. pruinosus*), Occasional secondary vectors: ambrosia beetles, buprestids, cerambycids, High red-oak composition and basal area=more fungal mats and higher vector pressure, Self, intra, and interspecific root grafting increases more from heavy soils to light-textured soils (silt loam<sandy soil)	Average minimum February temperature and total spring precipitation were directly correlated with the number of fungal mats per tree, Root graft frequency increases from heavy to light textured soils (silt loam<sandy soils), Shallow or restricted soils favor graft transmission, Dry and dry-mesic sites, low site index (<50), upper slopes and ridgetops, flat, low-relief areas with oak dominance associated with the highest disease severity	Juzwik (2007)

Minnesota, U.S.	*Quercus* stands with and without oak wilt	*C. truncatus* peaked in April-May, with pathogen abundance from July to September, *Ca. sayi* peaked in October, but with pathogen abundance during May and June	-	Ambourn et al. (2005)
Minnesota, U.S.	-	*C. truncatus* and *Ca. sayi* are the principal sap beetles, mainly active in May		Juzwik et al. (2004)
Minnesota, U.S.	Red oak group	Multiple insect vectors- *Ca. sayi, C. truncatus, Epuraea corticina, Glischrochilus fasciatus, G. quadrisignatus, G. sanguinolentus, G. siepmanni*	-	Cervenka et al. (2001); Juzwik and French (1983); Ambourn et al. (2005)
Upper Midwest, U.S. (IL, IN, IA, MI, MN, MO, WI)	*Q. rubra, Q. ellipsoidalis, Q. velutina, Q. marilandica, Q. alba, Q. macrocarpa, Q. muehlenbergii, Q. stellata*	-	Violent spring storms and high winds create infection courts and increase host susceptibility due to large-diameter springwood vessels	Juzwik and Schmidt (2000)
Central Texas, U.S. (Specific locations: Burnet, Austin, Kerrville, Round Rock)	Live oak (*Q. fusiformis* and *Q. virginiana),* Spanish oak (*Quercus texana*), Blackjack oak (*Q. marilandica*)	Nitidulid beetles, *C. maculatus, Cryptarcha concinna, Lobiopa undulata* with contamination highest in April.	Elevated temperatures increase host stress (especially live oaks and red oaks)	Appel et al. (1990)
South Carolina, U.S.	*Q. laevis (Turkey oak)*	-	Summer temperatures that rise above the fungus's ~25 °C growth optimum suppress or weaken fungal activity	Tainter and Ham (1983)
Wisconsin, U.S.	*Q. rubra*	-	In a controlled-environment study using red oak seedlings, disease developed most rapidly and consistently at 26 °C.	Fenn et al. (1975)

Note. Studies are ordered geographically from the Great Lakes south to Canada. All oak species names follow the current ITIS taxonomy. Biotic factors include biological agents that interact with the host or pathogen; abiotic factors include physical environment variables. Beetle degree-day (DD) thresholds in Morris et al. (2024) use a base temperature of 10°C. Wood moisture percentages refer to sapwood moisture content relevant to fungal mat production and longevity. Abbreviations: DD = degree-days; DBH = diameter at breast height; DNR = Department of Natural Resources; SDM = species distribution model.

2.6 Climate change and forest diseases

Climate change does not affect all forest diseases in the same direction. Warmer, wetter conditions may favor moisture-dependent pathogens, whereas drought and heat may increase disease indirectly by weakening host trees (Sturrock et al., 2011).

North American examples illustrate this contrast. Warmer minimum temperatures and greater rainfall increased Dothistroma needle blight in British Columbia, while warmer winters and spring moisture favored Swiss needle cast in the Pacific Northwest (Manter et al., 2005; Stone et al., 2008; Woods et al., 2005). In contrast, severe drought and heat contributed to sudden aspen decline near the warmer edge of the host's climatic range (Rehfeldt et al., 2009; Worrall et al., 2010). Milder winters are also facilitating the northward expansion of invasive forest pests such as hemlock woolly adelgid and southern pine beetle in the eastern U.S. (Swanston et al., 2018).

For oak wilt, the primary concern is a geographic redistribution of climatic suitability rather than a uniform increase in disease. Northern areas may become more suitable, while extreme heat or moisture deficits may reduce suitability elsewhere. This uncertainty supports the use of species distribution models to estimate the present and future climatic niche of *B. fagacearum*.

2.7 Species distribution modeling in forest pathology

Species distribution models link occurrence records with environmental variables to estimate geographic suitability and project shifts across space or time. In forest pathology, they support surveillance, climate-change assessment, and invasion-risk screening.

2.7.1 Ecological niche theory

Hutchinson defined the ecological niche as the multidimensional conditions under which a species can persist. The fundamental niche includes suitable abiotic conditions, whereas the realized niche is constrained by dispersal, biotic interactions, and historical accessibility (Hutchinson, 1957; Soberón & Nakamura, 2009).

Oak wilt records reflect more than pathogen tolerance; they also depend on host, introduction, transmission, and detection. Correlative models therefore estimate conditions associated with observed disease rather than the full fundamental niche of *B. fagacearum*.

Outside the known range, predicted suitability indicates climatic similarity to occupied areas. It does not confirm pathogen presence, establishment, or disease severity. Thus, such projections should be interpreted as climatic suitability rather than invasion probability.

2.7.2 Modeling approaches and algorithms

Correlative Species Distribution Models (SDMs) relate occurrence records to environmental variables and are widely used when physiological data are insufficient for mechanistic modeling. MaxEnt is suitable for presence-background data, whereas

Random Forest, gradient boosting machines, and XGBoost can capture nonlinear responses and interactions (Breiman, 2001; Friedman, 2001; Phillips et al., 2006). Because predictions vary among algorithms, ensemble models combine their outputs and can give greater weight to models with stronger validation performance (Araújo & New, 2007).

Model reliability depends on occurrence quality, background selection, predictor choice, spatial resolution, and transfer to novel climates. Random train-test partitions may overestimate performance when nearby records share similar environments, whereas spatial-block validation provides a stronger test of geographic transferability (Roberts et al., 2017; Valavi et al., 2018).

Validation metrics such as Area Under the Receiver Operating Characteristic Curve (AUC) measure discrimination across thresholds, while True Skill Statistic (TSS) summarizes sensitivity and specificity at a selected threshold (Allouche et al., 2006; Lobo et al., 2008). However, high metric values do not remove uncertainty caused by sampling bias or climatic extrapolation. Future and intercontinental projections should therefore be evaluated using spatial validation, agreement among algorithms and climate models, and identification of environmental conditions outside the calibration range.

2.7.3 Previous oak wilt and forest-pathogen models

Previous models differ in purpose, scale, predictors, and modeled entity, as summarized in Table 2.2. Pedlar et al. (2020) used MaxEnt to identify climatically suitable areas for oak wilt in Canada, whereas Stevens et al. (2024) combined climate, soil, host, and stand variables to explain disease occurrence at a finer scale in northern

Wisconsin. These studies show that continental models are useful for broad surveillance, while landscape models better represent local disease processes.

Models of sudden oak death, *Armillaria* root disease, and pine wilt provide additional guidance. They demonstrate the value of incorporating host distributions, comparing multiple algorithms, and evaluating uncertainty under future climates (Aierken et al., 2024; Kim et al., 2021; Kluza et al., 2007). Overall, climatic suitability is most informative when interpreted alongside host availability, introduction pathways, and model transferability.

Table 2.2 Oak wilt and related forest pathogen species distribution modeling (SDM) and niche modeling studies.

Study Region and Spatial Resolution	Model Type	Key Predictors / Inputs	Validation Metrics	Key Output	Source
Oak Wilt (*Bretziella fagacearum*) Distribution and Spread Models					
Europe (10°W–45°E; 33°N–72°N); 2.5 arc-minute resolution; baseline climate 1970–2000; future projections for 2061–2080 under SSP1-2.6, SSP2-4.5, SSP3-7.0, and SSP5-8.5	MaxEnt (presence-only machine-learning SDM)	42 confirmed *B. fagacearum* occurrence records; 10,000 background points; 19 WorldClim 2.1 bioclimatic variables; UKESM1-0-LL climate projections. Most important predictors: precipitation of the driest month (Bio14), precipitation of the driest quarter (Bio17), and temperature seasonality (Bio4)	Fivefold cross-validation with five replicate runs. Mean test AUC = 0.991 ± 0.009; binary suitability classified using the maximum test sensitivity-plus-specificity threshold	Identified current climatic suitability primarily in southern and central Europe. Projected northward and eastward expansion under climate change, with suitable area increasing from 96,432 km² under current conditions to 436,310 km² under SSP3-7.0. Responses were non-monotonic across scenarios, with a smaller suitable area projected under SSP5-8.5 than under SSP3-7.0	(Tkaczyk & Lisiewicz, 2026)

Global occurrences projected onto Canada and the U.S.; baseline climate 1971–2000; CMIP6 projections (12 GCMs) under SSP1-2.6, SSP2-4.5, SSP5-8.5; periods 2011-2040, 2041-2070, 2071-2100; occurrences spatially thinned at 10 km	MaxEnt (machine-learning SDM) and ANUCLIM / Bioclim (climate envelope)	MAT; MINTCM; MAXTHM; PREC; PRECCP (coldest 3-month precipitation); PRECHP (hottest 3-month precipitation)	Species-level AUC and TSS reported via web application; not comprehensively reported in the main text	Identified temperature and precipitation constraints shaping insect–disease niche. National-scale current and future suitability maps for >4,000 insects and fungi including B. fagacearum; projected northward shift under warming scenarios	Pedlar et al. (2025)
Chequamegon-Nicolet National Forest, northern Wisconsin; ~76 km²; model evaluated on 10 m and 30 m grids; USGS DEM 10 m; POLARIS soils ~30 m; WiscLand2 land cover 30 m	Generalized Additive Models (GAMs; discrete/lattice approach) and Neyman-Scott Cluster Process Models (CPMs; continuous point-process approach)	586 confirmed oak wilt sites (2004–2021); soil physical and chemical properties; terrain/topography (USGS DEM); forest composition and host distribution	Trained on 449 sites (2004–2018, 81%); tested on 106 sites (2019–2021, 19%). Model comparison via AIC, likelihood ratio tests, and out-of-sample prediction accuracy	Most important predictors: spatial dependence (contagion) and oak host distribution; terrain and soil had minor independent influence. Best models combined host distribution + spatial dependence + quantitative terrain/soil. GAMs with host distribution + spatial dependence alone were a close approximation	Stevens et al. (2024)
North America (emphasis eastern Canada); national scale; ~10 km resolution for pathogen occurrences; future climate 2011-2040 and 2041-2070	MaxEnt (machine-learning SDM)	Fall precipitation; spring temperature; annual climate moisture index; average minimum temperature of coldest month (1981–2010 normals and future projections). Occurrence data for *B. fagacearum*, *C. truncatus*, and *Ca.*	AUC and SEDI (Symmetric Extremal Dependence Index) using 25% withheld occurrence data;	Projects northward expansion of *B. fagacearum* and its insect vectors (*C. truncatus*, *Ca. sayi*) under climate change. Eastern Canadian oak range becomes climatically suitable within ~two decades under moderate warming. Fall precipitation and spring	Pedlar et al. (2020)

		sayi. 10,000 random background points within treed North American ecosystems	~10 km resolution for pathogen occurrences	temperature are the dominant suitability drivers	
33 counties in east-central and southeastern Minnesota; PRISM climate 800 m; DEM 30 m; land cover 30 m	MaxEnt (machine-learning SDM)	460 oak wilt occurrence records (2007–2016; Minnesota DNR and Three Rivers Park District). 30-year climate normals (1981–2010): avg. annual precipitation, avg. coldest-month temperature, avg. temperatures of the three hottest months (June, July, August). Topography (slope, aspect; ArcMap). Minnesota land cover 1991–92 (40 of 49 classes present). Soil suborder. Population density	AUC (ROC) on random 25% test split; TSS as independent validity measure; omission/commission analysis	Highest predicted oak wilt probability within and surrounding the Minneapolis–St. Paul metro area. Identified high-suitability zones with few current detections (southern Dakota and northern Rice counties; Cannon River corridor) as priority monitoring and management areas	Gearman and Blinnikov (2019)
Comparative Disease Distribution / Spread Forecasting Models (Other Forest Pathogens)					
Global; emphasis on southern/northeastern China, South Korea, Southeast Asia, Europe, and Canada; regional downscaling for projections (not explicitly stated)	Ensemble SDM (ESDM): MaxEnt, Random Forest, Boosted Regression Trees (BRT)	Summer temperature (most significant); soil clay content; summer precipitation; annual total precipitation; winter precipitation	Cross-validation + multiple SDM comparison. AUC, TSS, sensitivity/specificity	Current and future (2041–2090) risk maps for Pine Wilt Disease (*Bursaphelenchus xylophilus*). Projected northward expansion into Canada and Europe by 2070 under SSP5-8.5	Aierken et al. (2024)
Western North America (U.S., Canada–BC, northern Mexico); 2.5 arcminute (~5 km) bioclimatic grids	MaxEnt	382 DNA-confirmed *Arceuthobium solidipes* occurrence points; 11,826 *Pseudotsuga menziesii* (Douglas-fir) occurrence points; 19 bioclimatic variables; 292,639 absence/background points for	AUC	Douglas-fir climate suitability shifts strongly northward under SSP5-8.5, with large losses within its current range. *A. solidipes* remains climatically suitable in many areas where Douglas-fir becomes maladapted, indicating increased future	Kim et al. (2021)

		pathogen; 10,000 random background points for host; CMIP6 and CanESM5 future climate (SSP2-4.5 and SSP5-8.5)		disease pressure due to host stress	
North America and global projections; ~8 km resolution	GARP (Genetic Algorithm for Rule-set Prediction; ecological niche model)	68 spatially unique Phytophthora ramorum occurrence records; temperature, precipitation, frost frequency, solar radiation, vapor pressure, wet-day frequency, topographic variables, NDVI, host distribution	ROC-AUC	Predicted high suitability for Sudden Oak Death (*Phytophthora ramorum*) in southeastern U.S. Identified eastern Asia as the most likely geographic source region of the pathogen	(Kluza et al., 2007)

Note. The upper section presents SDM studies directly modeling *B. fagacearum* or its insect vectors. The lower section presents SDM studies of other forest pathogens included for methodological comparison. AUC = area under the receiver operating characteristic curve (values >0.7 indicate acceptable discrimination; >0.9 excellent). TSS = True Skill Statistic (range −1 to +1; >0.5 considered good). SEDI = Symmetric Extremal Dependence Index. MAT = mean annual temperature; MINTCM = mean daily minimum temperature of coldest month; MAXTHM = mean daily maximum temperature of hottest month; PREC = annual precipitation; PRECCP = precipitation of coldest quarter; PRECHP = precipitation of hottest quarter; GCM = general circulation model; SSP = shared socioeconomic pathway; DEM = digital elevation model; NDVI = normalized difference vegetation index; CMIP6 = coupled model intercomparison project phase 6.

2.8 Global biosecurity and future invasion risk

International trade has introduced forest pathogens through several commodity pathways. Chestnut blight, caused by *Cryphonectria parasitica*, was probably introduced on Japanese chestnut nursery stock and subsequently dispersed through commercial plant movement (Anagnostakis, 2000). White pine blister rust, caused by *Cronartium ribicola*, entered North America on infected five-needle pine seedlings imported from Europe during the early twentieth century (Kinloch Jr, 2003). The nursery

trade has also moved *Phytophthora ramorum*, the cause of sudden oak death and ramorum blight, among regions through infected ornamental plants (Frankel, 2008).

Wood pathways have produced similar invasions. The laurel wilt fungus, *Raffaelea lauricola*, was likely transported from Asia within the mycangia of the redbay ambrosia beetle vector, *Xyleborus glabratus*, introduced in solid-wood packaging material (Harrington et al., 2011). Emerald ash borer, an invasive insect rather than a pathogen, was probably introduced in infested solid-wood packaging from Asia (Poland & McCullough, 2006). Dutch elm disease was associated with imported elm logs carrying *Scolytus multistriatus*, an important vector of *Ophiostoma* species (May, 1934). These examples show that establishment can begin when trade introduces viable pathogens or vectors into regions containing suitable climate and hosts.

For oak wilt, movement of infected logs and firewood is the documented long-distance pathway (Juzwik et al., 2011). Transported wood may contain viable *B. fagacearum* or produce fungal mats that attract vectors after arrival. Consequently, regions outside the current range may become suitable when human introduction coincides with susceptible oaks and favorable climatic conditions.

2.9 Knowledge gaps and research priorities

Despite advances in oak wilt biology and distribution modeling, important uncertainties remain about climatic responses, regional variation, model transferability, and translating suitability maps into surveillance and management.

2.9.1 Biological gaps

The thermal and moisture tolerances of *B. fagacearum* remain insufficiently quantified across pathogen populations. Although variation among geographically separated pathogen populations has been identified, their differences in growth, virulence, fungal-mat production, environmental tolerance, and vector association have not been tested under standardized conditions (Appel et al., 1990; Chahal et al., 2025; Fenn et al., 1975; Tainter & Ham, 1983).

Vector phenology has been studied mainly in northern locations. Regional degree-day requirements, winter survival, vector competence, and responses to warming remain uncertain across the southern U.S., transition zones, and potential invasion regions (Jagemann et al., 2018; Morris et al., 2024).

The effect of drought also remains unresolved. Drought may increase host hydraulic stress while reducing the moisture needed for fungal-mat development. Future experiments should distinguish effects on disease progression within trees from effects on aboveground transmission (Boyce, 1957; Juzwik & French, 1983; Stevens et al., 2024).

Finally, susceptibility varies among oak species and cannot be represented fully by broad oak-group classifications. Future risk assessments should incorporate species-level host susceptibility, distribution, abundance, and responses to climatic stress (Jacobi & MacDonald, 1980; Juzwik et al., 2011; Rauschendorfer et al., 2022).

2.9.2 Modeling gaps

Oak wilt occurrence records are spatially uneven and may reflect survey effort, road access, reporting systems, and research concentration. Areas with few records should not be assumed to be disease-free. Because verified absences are limited, background selection also strongly influences estimated environmental relationships in presence-background models (Araújo et al., 2019; Phillips et al., 2006).

Climate-only models predict the climatic suitability associated with observed disease occurrences. Future models should integrate host and vector distributions, identify extrapolation zones, and quantify uncertainty across algorithms, global climate models, scenarios, and time periods (Araújo et al., 2019; Araújo & New, 2007).

Regional differentiation creates an additional challenge. Regime-specific models may better support management within the Lake States and Texas, whereas pooled full-range models are useful for broad global climatic screening. However, pooled models still estimate the realized climatic association of observed disease and should not be described as representing the pathogen's full fundamental niche.

2.9.3 Management and biosecurity gaps

Surveillance remains uneven across the current range and potential invasion fronts. Molecular diagnostics, vector trapping, remote sensing, and spatial models have not yet been integrated into a standardized, multi-state early-warning network (Gauthier et al., 2024; McLaughlin et al., 2022; Pinto-Ledezma et al., 2023).

Risk maps are also often developed separately from operational management. Their practical value depends on connections with surveillance capacity, inspection

pathways, host inventories, intervention thresholds, and available management resources.

Better information is needed on the movement of firewood, logs, and other wood products. Combining pathway data with climatic suitability and host distribution would identify locations where entry and establishment risks overlap (Juzwik et al., 2011; Lovett et al., 2016).

Outside North America, host susceptibility, vector competence, and pathogen survival remain poorly understood. Climatically suitable regions should therefore be treated as priorities for host, pathway, and surveillance assessment rather than as locations of inevitable invasion. Future decision-support systems could integrate these data but would require independent validation and transparent uncertainty.

2.10 Conclusions

Oak wilt distribution is shaped by interactions among climate, pathogen biology, susceptible hosts, vectors, landscape conditions, and human movement. Temperature, moisture, and seasonality regulate fungal activity, host stress, vector phenology, and opportunities for transmission, while host composition, root connectivity, soils, and stand structure influence local spread.

Species distribution models provide a practical method for estimating climatic suitability when complete physiological and epidemiological data are unavailable. However, their reliability depends on occurrence quality, background selection, validation design, algorithm choice, climate projections, and transfer into novel environments.

Regime-specific models may provide greater ecological precision for management within the Lake States and Texas, whereas pooled full-range models support broad global climatic screening. Neither approach directly predicts pathogen entry, establishment, spread, or impact. Climatic suitability must therefore be interpreted with host, vector, pathway, and surveillance information.

These findings provide the foundation for Chapter 3, which applies an ensemble species distribution framework to estimate historical and future climatic suitability across North America and the Asia-Pacific region.

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CHAPTER 3

Ensemble niche modeling reveals expanding climatic suitability for oak wilt in the context of global biosecurity

Abstract

Oak wilt, caused by the vascular wilt fungus *Bretziella fagacearum*, is an emerging forest disease that threatens oak-dominated ecosystems, yet its potential climatic distribution under future climate change remains poorly resolved. We developed an ensemble climate niche model using 880 confirmed occurrence records, 853 spatially stratified background locations, 25 highest-ranked climatic predictors, and seven species distribution modeling algorithms, which were evaluated using repeated random 70/30 validation and an independent spatial-block 90/10 holdout. The four highest-performing algorithms were integrated into an AUC-weighted ensemble to reconstruct historical climatic suitability and project future suitability across North America and the Asia-Pacific region under three climate scenarios through 2100. The ensemble achieved high predictive performance (AUC = 0.940 ± 0.003; TSS = 0.802 ± 0.011), with precipitation, climatic moisture, and relative humidity-related variables contributing most strongly to climatic suitability. Under an independent spatial-block 90/10 holdout, the ensemble retained high geographic discrimination (AUC = 0.955) and good classification skill (TSS = 0.754). Historical projections identified extensive climatically suitable areas beyond the pathogen's currently known distribution, identifying areas where climatic conditions may permit establishment following introduction. Future projections consistently indicated an expansion of climatic

suitability, with suitable terrestrial area increasing from 23.35% to 27.97% in North America and from 17.91% to 26.16% in the Asia-Pacific region – the evolutionarily naïve ecosystem - under SSP3-7.0 by 2071-2100. Together, these projections identify regions where climate may increasingly favor oak wilt establishment and support targeted forest health surveillance, biosecurity planning, and climate-adaptive management.

3.1 Introduction

Oak wilt, caused by the vascular wilt fungus *Bretziella fagacearum*, is an economically and ecologically significant vascular disease of oaks (*Quercus* spp.) that affects both natural and urban forest ecosystems when the disease epicenters remain undetected and unmanaged (Chahal et al., 2025b; Gauthier et al., 2024; Gordon et al., 2025; Juzwik et al., 2011). Since its initial detection in the mid-twentieth century, oak wilt has been reported in 25 U.S. states and was first confirmed in Ontario, Canada, in June 2023, raising concerns about continued range expansion, with invasion of previously unaffected regions and long-term impacts on forest health (Gauthier et al., 2024; Tischenko et al., 2024). Oaks are among the most ecologically important tree lineages in North America, functioning as foundation species that shape forest structure, biodiversity, carbon storage, nutrient cycling, and wildlife habitat while providing substantial economic, cultural, and urban forestry benefits (Bocsi et al., 2021; Bronson et al., 2023; Hanberry & Nowacki, 2016; Subedi et al., 2024). Therefore, the expansion of oak wilt threatens not only oak populations but also the ecosystem services, resilience, and long-term functioning of oak-dominated forests across broad geographic regions (Cavender-Bares et al., 2022; Juzwik et al., 2011; Pedlar et al., 2020).

The epidemiology of oak wilt is driven by a complex interaction among hosts, vectors, pathogens, and environmental conditions (Appel, 1994; Bershing, 2025). Disease transmission occurs through both belowground root grafts, which are particularly important in live oak systems of Texas (Gomez et al., 2025), and aboveground insect-mediated pathways, which are more prominent in regions such as the Great Lakes, where red oaks predominate (Morris et al., 2024). However, the successful establishment and spread of the pathogen are not determined solely by the presence of susceptible hosts or transmission pathways. Environmental variables, including temperature, precipitation, soil conditions, drought stress, and seasonal climatic variability, influence oak wilt epidemiology by affecting pathogen development, fungal mat formation, vector activity, phenology, and host physiological stress responses (Haight et al., 2011; Morris et al., 2024; Stevens et al., 2024; Stump et al., 2024). These interacting biotic and abiotic factors collectively shape pathogen transmission dynamics, host susceptibility, and the establishment and expansion of disease centers, making them key determinants of current and future disease risk. Collectively, these interactions indicate that oak wilt is a climate-sensitive disease system whose distribution and severity are influenced by environmental conditions operating across multiple spatial and temporal scales. Figure *3.1* summarizes the major epidemiological components of the oak wilt disease system, including its current distribution, regional transmission pathways, host susceptibility, representative symptoms, and the principal climatic drivers influencing pathogen development and disease spread.

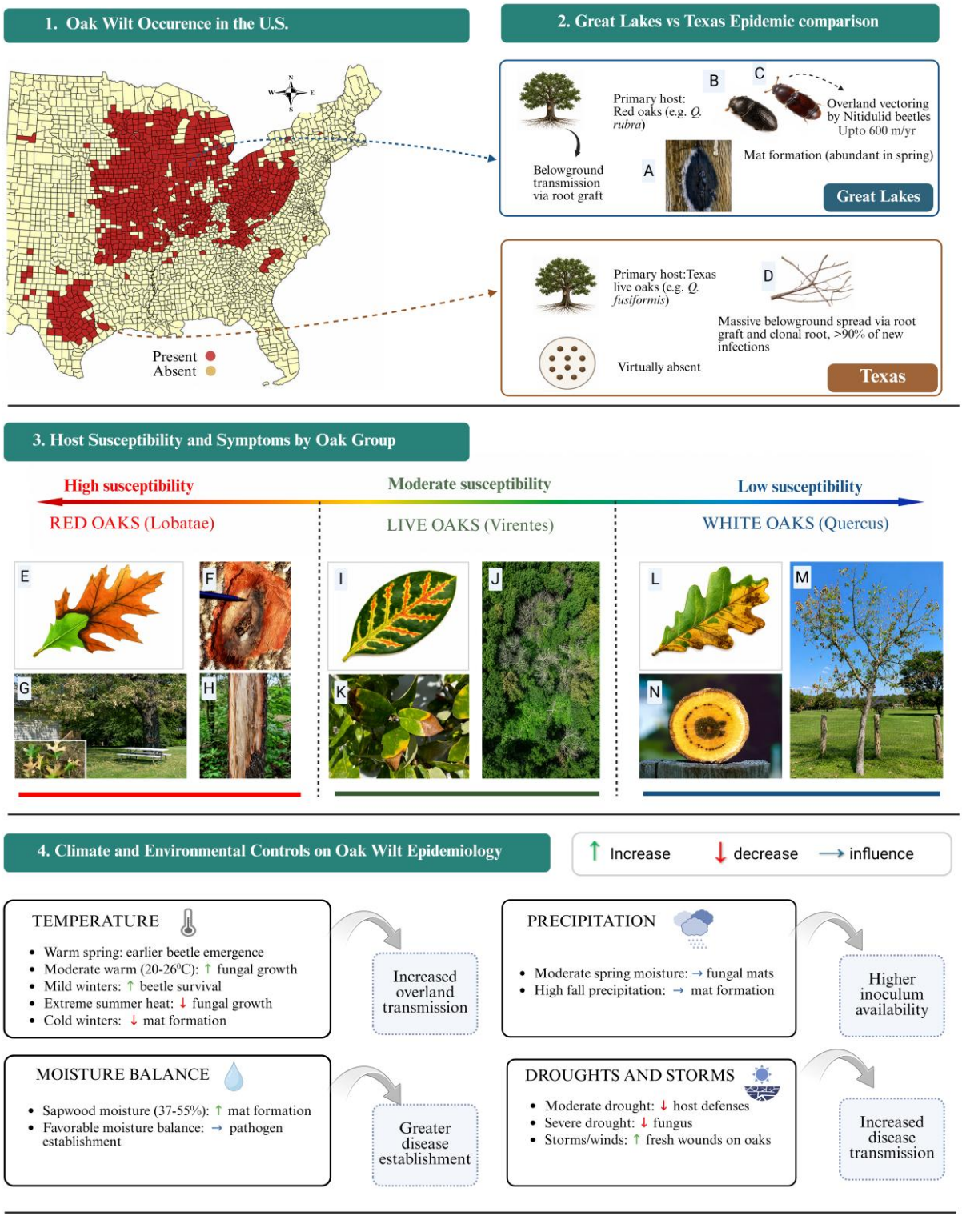
1. Oak Wilt Occurence in the U.S.
Present
Absent
2. Great Lakes vs Texas Epidemic comparison
Primary host: Red oaks (e.g. Q. rubra)
Belowground transmission via root graft
B
C
Overland vectoring by Nitidulid beetles Upto 600 m/yr
A
Mat formation (abundant in spring)
Great Lakes
Primary host:Texas live oaks (e.g. Q. fusiformis)
D
Massive belowground spread via root graft and clonal root, >90% of new infections
Virtually absent
Texas
3. Host Susceptibility and Symptoms by Oak Group
High susceptibility
Moderate susceptibility
Low susceptibility
RED OAKS (Lobatae)
LIVE OAKS (Virentes)
WHITE OAKS (Quercus)
E
F
G
H
I
J
K
L
M
N
4. Climate and Environmental Controls on Oak Wilt Epidemiology
↑ Increase
↓ decrease
→ influence
TEMPERATURE
Warm spring: earlier beetle emergence
Moderate warm (20-26°C): ↑ fungal growth
Mild winters: ↑ beetle survival
Extreme summer heat: ↓ fungal growth
Cold winters: ↓ mat formation
Increased overland transmission
PRECIPITATION
Moderate spring moisture: → fungal mats
High fall precipitation: → mat formation
Higher inoculum availability
MOISTURE BALANCE
Sapwood moisture (37-55%): ↑ mat formation
Favorable moisture balance: → pathogen establishment
Greater disease establishment
DROUGHTS AND STORMS
Moderate drought: ↓ host defenses
Severe drought: ↓ fungus
Storms/winds: ↑ fresh wounds on oaks
Increased disease transmission

Figure 3.1 Conceptual overview of oak wilt epidemiology, illustrating disease occurrence, regional transmission dynamics, host susceptibility, symptom development, and climatic drivers influencing pathogen spread and development. Note. A, Exposed fungal mats; B, *Carpophilus sayi*; C, *Colopterus truncatus;* D, root grafts; E, Leaf bronzing; F, Fungal mats; G, Carpet of leaves in summer; H, Xylem streaking; I, Veinal necrosis; J, Aerial view of oak-wilt pocket; K, Leaf tip burn; L, Leaf necrosis and marginal chlorosis; M, Thinning and flagging oak tree; N, Compartmentalized vascular discoloration.

Photo credit: Joseph O'Brien, USDA Forest Service, Bugwood.org (ForestryImages.org); T.W. Bretz, USDA Forest Service, Bugwood.org; https://utia.tennessee.edu/; https://www.missouribotanicalgarden.org/; https://texasoakwilt.org/; D. W. French, University of Minnesota, Bugwood.org; T.W. Bretz, USDA Forest Service, Bugwood.org; William Klingeman, University of Tennessee.

Global environmental change affects ecosystem processes and reshuffles species distributions worldwide (Adger et al., 2005; Pecl et al., 2017; Tumer et al., 2026), with global mean temperatures projected to increase by approximately 1.5^0 C during this century under continued warming scenarios (Masson-Delmotte et al., 2021; Tian et al., 2026). Forest pathogens are particularly sensitive to climatic conditions because disease development depends on interactions among hosts, pathogens, vectors, and the environment (Ghelardini et al., 2017; Roussin-Léveillée et al., 2024). As a result, pathogen survival, reproduction, dispersal, host susceptibility, and disease severity are further affected, thereby creating new opportunities for disease emergence, invasion, and expansion across forested landscapes (Singh et al., 2023). Epidemics of mobile or easily dispersed pests and pathogens are expected to increase in frequency under changing climatic conditions, while pathogen spread rates and host mortality may

be substantially altered (Ayres & Lombardero, 2000; Sturrock et al., 2011). Many disease systems are experiencing poleward and elevational range shifts as previously unsuitable regions become climatically favorable (Parmesan, 2006; Pecl et al., 2017; Sturrock et al., 2011).

The impact of invasive species under the changing environment is often difficult to predict, particularly in novel environments where ecological interactions and baseline information remain limited (Hrinkevich et al., 2016). These uncertainties are of growing concern given the increasing economic burden associated with biological invasions. In the U.S., economic costs associated with invasive species have increased dramatically in recent decades, exceeding $21 billion annually during the 2010-2020 period, with the most reported costs from terrestrial habitats (53%) (Fantle-Lepczyk et al., 2022). Understanding how climate influences species distributions and future range shifts is therefore essential for anticipating emerging threats and guiding proactive management strategies (Benavides Martínez et al., 2026; Robinson et al., 2017; Tumer et al., 2026).

Ecological Niche Models (ENMs), including Climate Niche Models (CNMs), have become one of the most widely used approaches for predicting the effects of environmental change on biodiversity, species distributions, and habitat suitability assessments (Guisan et al., 2013; Xu et al., 2025; Zurell et al., 2020). Their increasing application has been facilitated by advances in computational methods and the growing availability of high-resolution regional and global climate datasets (Tumer et al., 2026). More than 6,000 niche- and distribution-modeling studies have been published over the last 25 years, and their use continues to expand rapidly across ecological disciplines (Araújo et al., 2019; Kindlmann et al., 2025). In a systematic review of the SDM

literature, North America accounted for 68 of 200 studies (~34%), reflecting its strong representation in climate–biodiversity modeling research (Tumer et al., 2026). ENMs characterize relationships between species occurrence records and environmental variables to estimate climatic suitability and project potential geographic distributions under alternative climate scenarios (Tian et al., 2026; Tumer et al., 2026; Xu et al., 2025). Climate niche models (CNMs), a subset of ENMs, focus specifically on climatic variables and are widely used to assess climate-driven changes in species and disease distributions (Xu et al., 2025). Because CNMs are typically calibrated using observed occurrence records, they represent the realized climatic niche of a species (Holt, 2009; Pearson & Dawson, 2003; Wang et al., 2016b) rather than its fundamental niche, which is defined solely by physiological and environmental requirements (Hutchinson, 1957). Consequently, CNMs predict climatically suitable habitat rather than actual species distributions, which are further influenced by dispersal limitations, host availability, biotic interactions, and other ecological processes (Aitken et al., 2008; Wang et al., 2016b). Despite these limitations, CNMs provide a well-supported framework for identifying regions that may become climatically suitable under future climate scenarios and are widely used to evaluate species vulnerability, invasion risk, and potential range shifts under climate change (Frans et al., 2021; Zhang et al., 2024). Model performance is typically assessed using split-sample validation approaches and metrics such as the Area Under the Receiver Operating Characteristic Curve (AUC) and the True Skill Statistic (TSS) (Newbold, 2018; Tumer et al., 2026).

Beyond their role in understanding species-environment relationships, ENMs and CNMs have become important decision-support tools for conservation planning,

invasive species risk assessment, forest health monitoring, and climate-adaptive management (Alfaro et al., 2014; Fettig et al., 2013; Huntley et al., 2010; Wang et al., 2016b). Model outputs have been used to identify biodiversity hotspots, prioritize protected areas, guide habitat restoration, evaluate species reintroduction programs, and assess species vulnerability to climate change (Guisan et al., 2013; Kujala et al., 2013). In forest health applications, ENMs and CNMs have been increasingly employed to predict the potential spread of invasive pests and pathogens, identify regions at elevated risk of establishment, and support surveillance and early detection programs (Guisan et al., 2013; Robinson et al., 2017). Because oak wilt is difficult to eradicate once established and disease spread can be costly and operationally challenging, proactive surveillance and preventive management are particularly important for reducing ecological and economic impacts (Bronson et al., 2023; Koch et al., 2010; Wilson, 2005). By projecting future habitat suitability under alternative climate scenarios, CNMs provide spatially explicit information that can guide monitoring efforts, resource allocation, and climate-adaptive management decisions (Robinson et al., 2017).

Despite growing concerns regarding the continued spread of oak wilt and its recent expansion into Canada, thorough assessments of its climatically suitable habitat at a global scale remain limited (Gauthier et al., 2024; Weed et al., 2013). Most previous studies have focused on regional evaluations of disease risk, leaving uncertainty about how climate change may alter future patterns of environmental suitability and disease establishment across broader geographic regions. Given the widespread distribution of susceptible oak species across multiple continents and climatic zones (Denk et al., 2017), a broad cross-regional assessment is needed to identify areas that may become

increasingly climatically suitable for disease establishment as climatic conditions change (Zhang et al., 2024). Recent advances in species occurrence databases, high-resolution environmental datasets, climate projection frameworks, and machine-learning approaches have greatly expanded the use of ecological niche models, particularly climate niche models, to assess climate-change impacts on forest ecosystems (Carrillo-García et al., 2023; Xu et al., 2025). These developments provide an unprecedented opportunity to characterize the climatic niche of oak wilt and project future patterns of climatic suitability under alternative future climate scenarios. To reduce uncertainty associated with individual algorithms, multiple statistical and machine-learning models can be integrated into weighted ensemble frameworks that generally provide more consistent and reliable predictions than single-model approaches.

Therefore, the objectives of this study were to (1) develop and evaluate an ensemble climate niche model representing the realized climatic niche of oak wilt using occurrence records from North America; (2) quantify the relative importance of climatic predictors associated with disease occurrence; and (3) project current and future climatic suitability across North America and the naïve habitat, e.g., Asia-Pacific region under multiple climate scenarios to identify areas at risk of future disease establishment. Our research provides a framework for identifying regions vulnerable to disease persistence, expansion, and potential invasion, thereby supporting proactive surveillance, biosecurity, and climate-informed forest disease management.

3.2 Materials and methods

3.2.1 Study design and modeling workflow

Species distribution models (SDMs) were developed to estimate climatic suitability (ecological niches) for oak wilt disease in North America and to project future suitability under different environmental scenarios in North America and Asia-Pacific. The analysis employed a presence-background design, contrasting confirmed oak-wilt occurrence records with background locations representing available environmental conditions within the modeling domain. Seven complementary modeling algorithms representing statistical, machine-learning, and maximum-entropy approaches were evaluated and integrated into a performance-weighted ensemble model.

The modeling workflow is divided into five main stages. First, cleaned occurrence, background, and climate-enriched datasets were prepared for model development. Second, selected climatic predictors were assembled into a common predictor matrix. Third, candidate SDM algorithms were evaluated using five iterations of stratified shuffle cross-validation with a 70% training set and a 30% testing split. Fourth, models with a mean TSS ≥ 0.6 were ranked by mean cross-validated AUC, and the four highest-performing algorithms were retrained on the complete dataset to construct an AUC-weighted ensemble; a new independent spatial-block 90/10 validation was then conducted to assess geographic transferability. Finally, the ensemble model was transferred to future climate datasets to generate spatial predictions of climatic suitability, followed by water masking and visualization of terrestrial suitability patterns.

3.2.2 Study area and prediction domain

Model calibration was performed using oak wilt occurrence and background locations from the U.S. Spatial projections were then generated for North America and the Asia-Pacific region. Because *B. fagacearum* is native to the Americas, likely originating in Central or South America or Mexico, Asian oak species (*Quercus* spp.) are evolutionarily naive to it. If the pathogen is introduced to Asia, it meets a naive ecosystem. Due to a lack of co-evolved resistance, Asian *Quercus* spp. can suffer catastrophic, rapid mortality, like what occurred when the Asian chestnut blight (*Cryphonectria parasitica*) decimated naive American chestnuts in the early 1900s.

Continental boundary shapefiles were obtained from Natural Earth (https://www.naturalearthdata.com) and projected to the WGS 1984 EASE-Grid 2.0 Global coordinate reference system (EPSG:6933). Land polygons were used to exclude water bodies, and regular 10 × 10 km grids were generated across the terrestrial domain. Centroid coordinates were extracted from each grid cell to represent prediction locations for subsequent climate data extraction and spatial projection.

3.2.3 Occurrence and background data

B. fagacearum records were compiled from multiple verified sources, including state forestry departments, the Alien Forest Pest Explorer (AFPE; accessed 29 May 2025), and the Early Detection and Distribution Mapping System (EDDMapS; accessed on December 13, 2025, Available online at: http://www.eddmaps.org). Duplicate records, observations lacking geographic coordinates, and records with obvious spatial errors were removed during data preprocessing.

The final modeling dataset consisted of 880 confirmed oak wilt occurrence records. To address sampling bias inherent in opportunistic occurrence data, we implemented a systematic spatial thinning approach, informed by research demonstrating the effectiveness of stratified sampling in reducing citizen science bias (Warton & Shepherd, 2010). Background locations (n=853) were generated using spatial stratification based on ecoregions and elevation zones, with sampling intensity proportional to sampling effort as estimated by occurrence density patterns. This approach helps account for sampling bias while providing representative background conditions across the study area (Barbet-Massin et al., 2012). The resulting presence: background ratio of approximately 1:1 (880:853) is lower than the 10,000 background points recommended by Barbet-Massin et al. (2012) for regression-type methods and MaxEnt. Our stratified design prioritized environmental representativeness over sample size; however, we acknowledge that a larger background sample may improve model calibration, particularly for MaxEnt and logistic-regression-type algorithms. Sensitivity analyses comparing model outputs trained with larger, randomly generated background sets are recommended to assess the influence of this design choice on predicted suitability. Occurrence records were assigned a response value of 1 and background locations a value of 0, resulting in a modeling dataset comprising 1,733 observations.

3.2.4 Climate data

Baseline climatic variables (1961-1990 climate normals) were extracted for all occurrence, background, and prediction-grid centroid locations using ClimateNA v7.7 for North America (1 km spatial resolution) (Wang et al., 2016a) and ClimateAP v3.10 for the Asia-Pacific region (4 km resolution) (Wang et al., 2017). For spatial projection,

baseline and future climatic variables were extracted for all 10 × 10 km grid-cell centroids within each prediction domain. Future climate projections were generated for three projection periods 2011-2040, 2041-2070, and 2071-2100 under the SSP1-2.6, SSP2-4.5, and SSP3-7.0 emission scenarios using the eight General Circulation Model (GCM) ensemble: ACCESS-ESM1-5, BCC-CSM2-MR, CNRM-ESM2-1, EC-Earth3, GFDL-ESM4, MIROC6, MPI-ESM1-2-HR, and MRI-ESM2-0.

For each projection period and emission scenario, climatic variables from the eight GCMs were averaged into a single multi-model ensemble mean at each grid-cell centroid prior to model input (pre-modeling aggregation). This approach reduces the influence of individual GCM biases but collapses inter-GCM variability; the reported suitability projections therefore reflect ensemble-mean climate trajectories and do not represent the full range of GCM uncertainty.

3.2.5 Predictor selection and multicollinearity assessment

To optimize model performance and reduce overfitting, we implemented a data-driven predictor selection approach using feature importance scores from preliminary Random Forest models. The initial set of 265 climatic variables generated by ClimateNA was ranked by importance, and the 25 highest-ranking predictors that were also available in ClimateAP were retained for subsequent modeling. These variables primarily represented precipitation, climatic moisture index, relative humidity, and reference evapotranspiration, thereby capturing key aspects of moisture availability and atmospheric water balance that are ecologically relevant to oak wilt occurrence. The selected predictors are summarized in Appendix Table 3.1.

To assess redundancy among the 25 retained climatic predictors, pairwise Pearson correlation coefficients and variance inflation factors (VIFs) were calculated using the complete modeling dataset. Predictor pairs with an absolute correlation coefficient greater than 0.80 were classified as strongly correlated, whereas VIF values greater than 10 were considered indicative of substantial multicollinearity. The analysis was used as a post-selection diagnostic to evaluate the robustness and interpretability of ensemble predictor-importance estimates rather than to remove predictors or retrain the models.

3.2.6 Species distribution modeling algorithms

Seven SDM algorithms were evaluated using the same binary response variable and identical climatic predictor set: Random Forest (RF), Gradient Boosting Machine (GBM), Logistic Regression (LR), Gaussian Naïve Bayes (GNB), Support Vector Machine (SVM), Extreme Gradient Boosting (XGBoost), and Maximum Entropy (MaxEnt). These algorithms were selected to represent a diverse range of statistical, machine-learning, and maximum-entropy approaches. The model configurations used in the Python pipeline are summarized in Appendix Table 3.2.

3.2.7 Model evaluation and cross-validation

Model performance and selection were initially assessed using five repeated stratified random 70/30 train-test splits while preserving the presence-to-background ratio. All seven candidate algorithms were evaluated, and models with mean true skill statistic (TSS) ≥ 0.6, a threshold generally considered indicative of good predictive performance in species distribution modeling, were ranked by mean area under the

receiver operating characteristic curve (AUC) (Suicmez & Avci, 2023; Zhao et al., 2025). The four highest-performing models, RF, XGBoost, Gradient Boosting, and MaxEnt, were retained for the final AUC-weighted ensemble and for all future projection maps.

When occurrence records are spatially clustered, random splits may place spatially proximate observations in both training and testing sets, potentially inflating AUC and TSS (Roberts et al., 2017; Valavi et al., 2018). To evaluate the robustness and spatial transferability of the selected models, we supplemented the original random 70/30 validation with an independent spatial-block 90/10 holdout to quantify changes in performance under geographic separation. All occurrence and background records were assigned to 48 occupied 4° × 4° latitude-longitude blocks, with all observations from the same block kept together. Of these, 43 complete blocks containing 1,562 records were assigned to the training set, and five complete blocks containing 171 records were withheld as an independent spatial test set (Appendix Figure 3.1). Thus, the 90/10 division refers to the proportion of occupied spatial blocks rather than the exact proportion of individual observations. The five test blocks were excluded from model fitting, ensemble weighting, probability-threshold selection, and all other model-development decisions. Only the four selected models and their ensemble were evaluated under this spatial validation design.

We evaluated model performance using both TSS and AUC, following the criticisms regarding the limitations of using AUC alone (Lobo et al., 2008; Peterson et al., 2008; Song et al., 2025). TSS, calculated as sensitivity + specificity − 1, ranges from −1 to +1, with higher values indicating better predictive performance and values ≤ 0 indicating performance no better than random (Allouche et al., 2006). Within the 43

training blocks, fivefold spatial cross-validation generated out-of-fold predictions for RF, XGBoost, Gradient Boosting, and MaxEnt. Training-only AUC values were used to calculate the four-model ensemble weights, and TSS-optimal thresholds for the individual models and ensemble were derived from training-only out-of-fold predictions by evaluating thresholds from 0.01 to 0.99 in increments of 0.01. The four models were then refitted using all training records and evaluated once on the five independent test blocks. Their test-set probabilities were combined using the fixed training-derived weights to evaluate the ensemble. AUC and TSS were the primary performance metrics; random 70/30 results were reported as mean ± standard deviation across the five splits, whereas the spatial-block 90/10 holdout was reported as a single estimate.

3.2.8 Ensemble model construction

Following the evaluation of the individual models, algorithms with a mean TSS ≥ 0.6 were considered eligible for ensemble construction. Eligible models were ranked by their mean cross-validated AUC, and the four highest-performing algorithms were selected for inclusion in the final ensemble. The selected models were subsequently retrained using the complete modeling dataset (n=1,733). Ensemble modeling, which combines predictions from multiple individual models, was used to reduce model-specific uncertainty and improve the robustness of climatic suitability predictions (Araújo & New, 2007; Grenouillet et al., 2011; Song et al., 2025). The final ensemble suitability was then calculated as an AUC-weighted average of the predicted probabilities from the constituent models:

$$P_{\text{ensemble}} = \sum_{i=1}^{n} w_i P_i \qquad (1)$$

where $P_i$represents the predicted probability from the model i, and $w_i$is the normalized weight assigned to model i, calculated as

$$w_i = \frac{AUC_i}{\sum_{i=1}^{n} AU\ C_i} \qquad (2)$$

where $AUC_i$is the mean cross-validated area under the receiver operating characteristic curve of model i. Consequently, models with greater discriminatory ability contributed proportionally more to the final ensemble prediction while preserving continuous suitability estimates for subsequent threshold optimization and spatial projection. Because the AUC values of the four constituent models were closely clustered (range: approximately 0.927 to 0.938), the normalized weights were approximately equal (~0.25 per model), making the AUC-weighted ensemble functionally close to an unweighted arithmetic mean of the four model predictions.

3.2.9 Predictor importance analysis

Predictor importance was assessed separately for each constituent model of the final ensemble. Random Forest, Gradient Boosting Machine, and XGBoost used their native feature-importance measures. For MaxEnt, native importance estimates were used where available; otherwise, permutation importance was applied. Importance values from each model were normalized to sum to one and subsequently combined using the normalized AUC-derived ensemble weights. The resulting weighted

importance scores were summed across all ensemble members and ranked to quantify each predictor's relative contribution to the final ensemble model.

3.2.10 Future climate projections and spatial visualization

The final ensemble model was transferred to climate datasets representing three projection periods (2011-2040, 2041-2070, and 2071-2100). Spatial predictions were generated by applying the trained ensemble model to climate-enriched 10 × 10 km terrestrial prediction grids covering North America and the Asia-Pacific region. Each prediction grid contained the same set of climatic predictor variables used during the model calibration, thereby ensuring consistency between the calibration and projection datasets.

For each grid-cell centroid, the ensemble model generated a continuous probability representing climatic suitability for oak wilt establishment. Prior to prediction, future climate datasets were preprocessed to ensure compatibility with the calibrated models by harmonizing predictor names, variable ordering, and data types. Continuous suitability probabilities were subsequently converted into binary suitability classes using the TSS-optimal threshold of 0.410, selected during model evaluation to maximize TSS.

Predicted suitability values were visualized as geographic maps for each future period. Major inland water bodies were excluded from the displayed outputs using land-based masking to avoid assigning terrestrial suitability to aquatic environments. Individual maps were produced for each projection period, together with composite summaries illustrating temporal changes in the spatial distribution of climatically suitable areas and overall suitability across the prediction domains.

3.2.11 Software environment and reproducibility

The modeling workflow was implemented in Python using the scikit-learn machine learning framework, with XGBoost and Elapid for Extreme Gradient Boosting and Maximum Entropy modeling, respectively. All randomized procedures used a fixed random seed (42) to ensure reproducibility. Model outputs, trained models, performance summaries, ensemble predictions, and predictor-importance estimates were archived throughout the modeling workflow to facilitate reproducibility and subsequent analyses.

3.3 Results

3.3.1 Model performance and ensemble construction

The predictive performance of the seven SDMs varied across the five iterations of stratified shuffle cross-validation (Table *3.1*, Figure *3.2*). Among the individual algorithms, Random Forest achieved the highest single-model discriminatory ability (AUC = 0.938 ± 0.005; accuracy = 0.896 ± 0.006; TSS = 0.801 ± 0.014). XGBoost and Gradient Boosting also performed well, achieving mean AUC values of 0.936 ± 0.005 and 0.929 ± 0.005, respectively. MaxEnt exhibited moderate-to-high performance, whereas Logistic Regression showed slightly lower performance but still exceeded the predefined TSS inclusion criterion. In contrast, Support Vector Machine and Gaussian Naïve Bayes produced the lowest TSS values and did not satisfy the ensemble inclusion criterion (mean TSS ≥ 0.6). Accordingly, Random Forest, XGBoost, Gradient Boosting, and MaxEnt were selected as the four constituent models of the final AUC-weighted ensemble. The final AUC-weighted ensemble achieved the highest overall classification performance as assessed by TSS (TSS = 0.802 ± 0.011), with an

ensemble AUC of 0.940 ± 0.003 and a mean optimal threshold of 0.410 ± 0.070, which was subsequently used to convert continuous suitability predictions into binary suitable and unsuitable classes for all current and future distribution maps (Table *3.1*). The ensemble therefore provided predictive performance comparable to the best individual model while integrating predictions across four complementary algorithms.

Supplementary validation showed that the four-model ensemble maintained high predictive performance under the independent spatial-block 90/10 holdout, retaining high discriminatory performance (AUC = 0.955) and good classification skill (TSS = 0.754) (Table 3.2). Random Forest was the strongest individual model under the spatial holdout, while XGBoost showed the largest reduction in TSS. These results indicate that the models retained strong geographic ranking ability, although threshold-dependent classification became more conservative for several algorithms.

Table 3.1 Predictive performance of individual species distribution models and the final AUC-weighted ensemble under repeated random validation.

Model	AUC (mean ± SD)	Accuracy (mean ± SD)	TSS (mean ± SD)	TSS-optimal threshold (mean ± SD)
Random Forest	0.938 ± 0.005	0.896 ± 0.006	0.801 ± 0.014	0.446 ± 0.058
XGBoost	0.936 ± 0.005	0.888 ± 0.005	0.789 ± 0.010	0.360 ± 0.139
Gradient Boosting	0.929 ± 0.005	0.877 ± 0.010	0.771 ± 0.021	0.350 ± 0.130
MaxEnt	0.927 ± 0.004	0.832 ± 0.012	0.742 ± 0.020	0.222 ± 0.055
Logistic Regression	0.917 ± 0.009	0.860 ± 0.008	0.733 ± 0.011	0.424 ± 0.039
SVM	0.863 ± 0.011	0.786 ± 0.013	0.593 ± 0.019	0.572 ± 0.059
Naïve Bayes	0.863 ± 0.011	0.784 ± 0.009	0.589 ± 0.020	0.800 ± 0.212
Ensemble (Top four)	0.940 ± 0.003	0.891 ± 0.010	0.802 ± 0.011	0.410 ± 0.070

Note. Predictive performance was evaluated using five iterations of stratified shuffle cross-validation (70% training, 30% testing). Values are presented as mean ± standard deviation across five cross-validation iterations. Models with mean TSS ≥ 0.6 were eligible for ensemble construction, and the four eligible models with the highest mean AUC were retained. The mean TSS-optimal threshold is the average probability threshold that maximizes the True Skill Statistic (TSS) across iterations.

Table 3.2 Comparison of repeated random 70/30 validation and independent spatial-block 90/10 holdout performance.

Model	Random 70/30 AUC	Random 70/30 TSS	Spatial-block 90/10 AUC	Spatial-block 90/10 TSS	Δ AUC	Δ TSS
Random Forest	0.938	0.801	0.970	0.801	0.032	-0.000
XGBoost	0.936	0.789	0.924	0.590	-0.012	-0.199
Gradient Boosting	0.929	0.771	0.944	0.719	0.015	-0.052
MaxEnt	0.927	0.742	0.946	0.674	0.019	-0.068
Ensemble (Top four)	0.940	0.802	0.955	0.754	0.015	-0.048

Note. Random 70/30 values represent mean performance across five repeated stratified shuffle-split iterations. For the independent spatial-block 90/10 holdout, 43 complete 4° × 4° blocks were used for training, and five complete blocks were reserved for testing. The test blocks were excluded from model fitting, ensemble weighting, and threshold selection. Δ values represent spatial-block 90/10 performance minus random 70/30 performance.

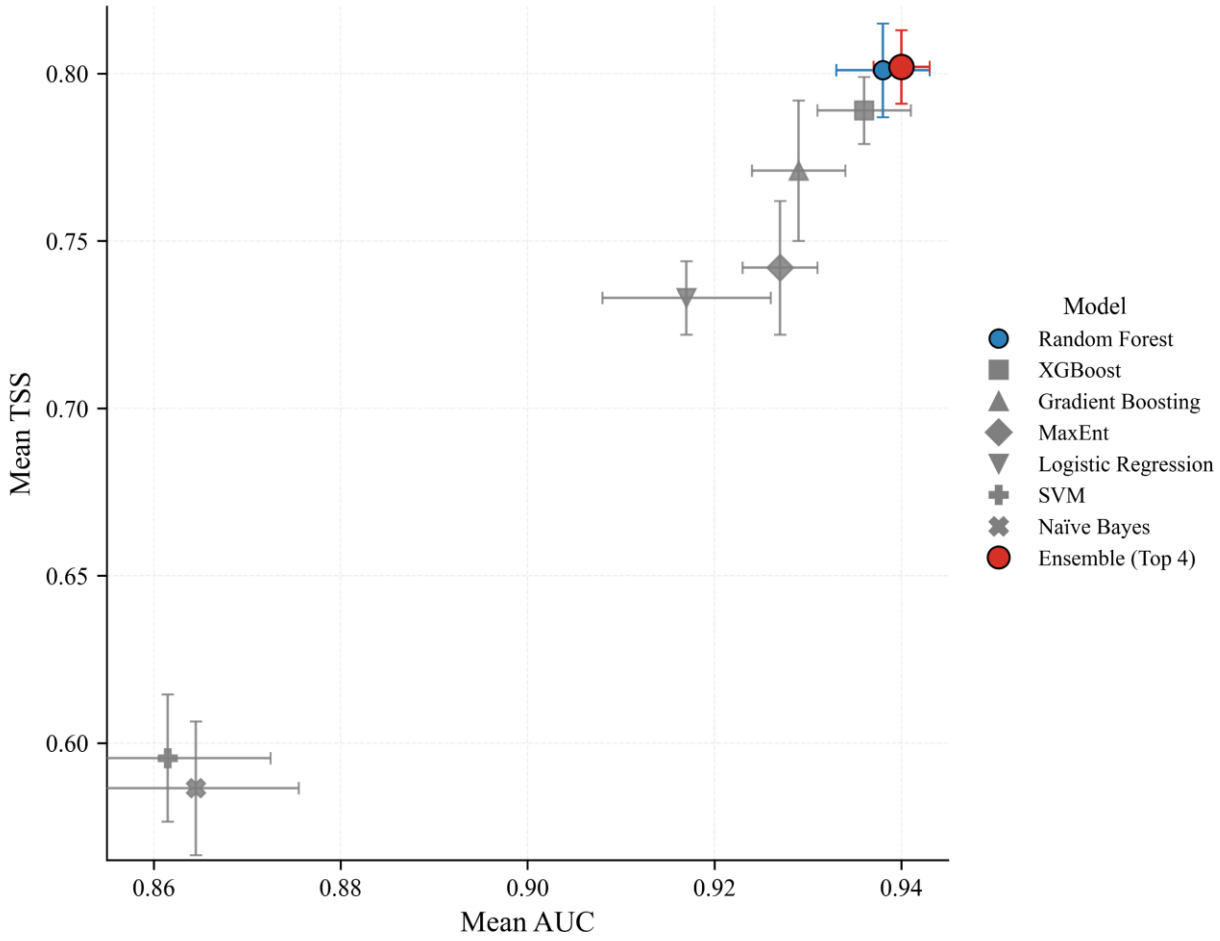

Figure 3.2 Predictive performance of individual species distribution models and the final AUC-weighted ensemble. Note. Each point represents the mean area under the receiver operating characteristic curve (AUC) and the mean True Skill Statistic (TSS) obtained from five stratified shuffle cross-validation iterations. Horizontal and vertical error bars indicate ±1 standard deviation of the mean AUC and mean TSS, respectively.

3.3.2 Ensemble predictor importance

The ensemble-weighted importance of the 25 climatic predictors varied considerably among the selected variables (Figure *3.3*). January precipitation (PPT01) was the most influential predictor, contributing 21.9% of the total ensemble importance, nearly four times greater than the second-ranked predictor. Relative humidity in

September (RH09) contributed 5.8%, followed by February precipitation (PPT02; 5.0%), October climatic moisture index (CMI10; 4.9%), winter precipitation (PPT_wt; 4.3%), mean annual precipitation (MAP; 3.7%), and July reference evapotranspiration (Eref07; 3.6%). Each of the remaining predictors contributed less than 3.6% of the total ensemble importance. Collectively, precipitation-, moisture-, and relative humidity-related predictors accounted for most of the total ensemble importance.

Post-selection diagnostics revealed substantial multicollinearity among the 25 retained climatic predictors. All predictors had variance inflation factor values greater than 10, and 55 predictor pairs had absolute Pearson correlation coefficients greater than 0.80 (Appendix Table 3.3; Appendix Figure 3.2). These findings indicate considerable redundancy among the climatic variables. Therefore, ensemble predictor-importance values were interpreted as relative associations with model predictions rather than as independent or causal effects.

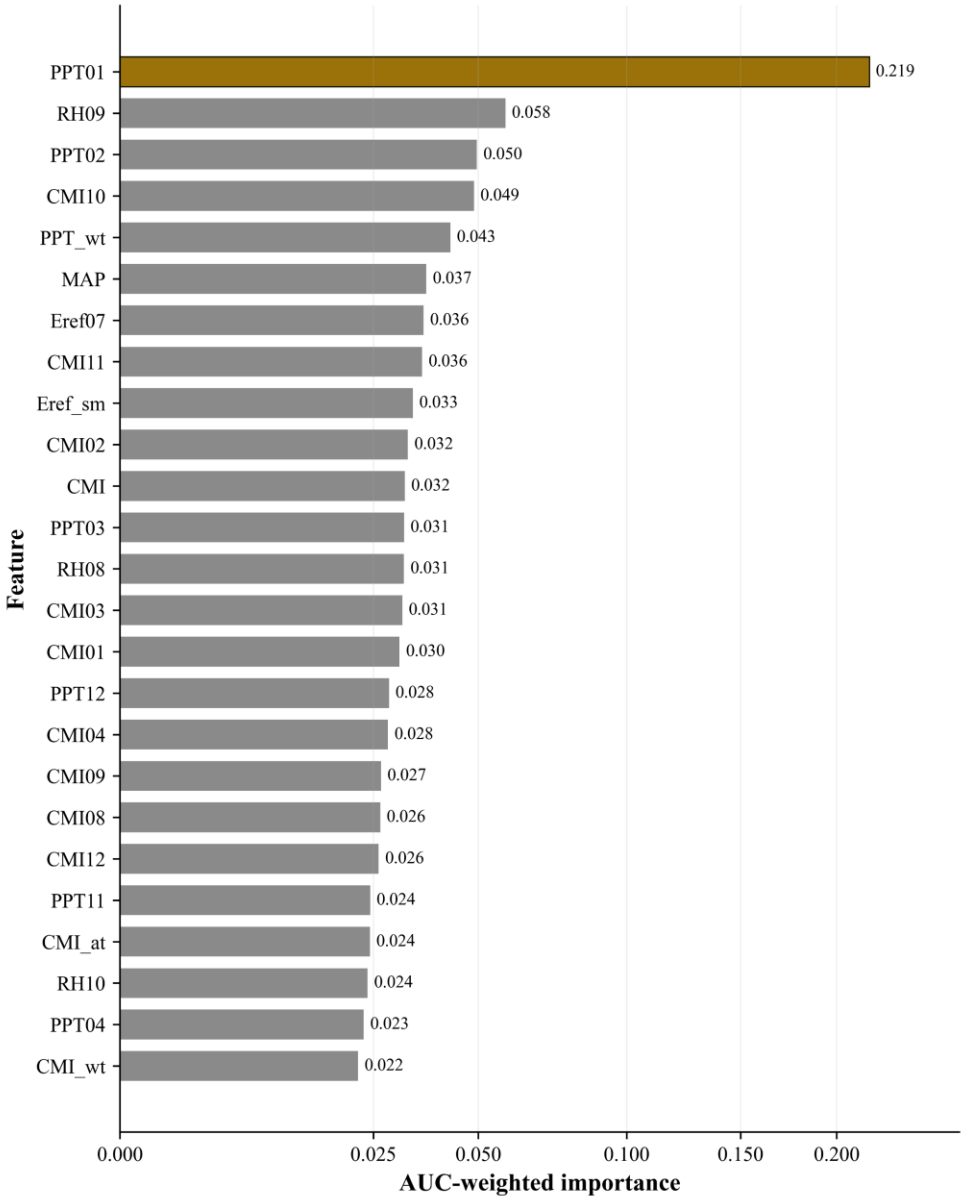

Figure 3.3 Ensemble-weighted importance of the 25 climatic predictors contributing to oak wilt climatic suitability. Note. Predictor importance was estimated separately for each constituent model of the final ensemble (RF, XGBoost, Gradient Boosting Machine, and MaxEnt), normalized within each model, and combined using normalized AUC-derived ensemble weights. Bar lengths indicate the relative contribution of each predictor to the final ensemble prediction, with values shown at the end of each bar.

3.3.3 Historical climatic suitability

The North America-trained AUC-weighted ensemble predicted marked spatial variation in historical climatic suitability across North America and the Asia-Pacific region under the 1961-1990 climate baseline (Figure *3.4*). Within North America, high climatic suitability was concentrated across much of Mexico and the south-central and eastern U.S., extending from southern Texas and the Gulf Coast through the lower Mississippi Valley into portions of the Midwest and eastern U.S. (Figure *3.4*A). In contrast, Alaska and most of northern and western Canada exhibited consistently low climatic suitability.

When transferred to the Asia-Pacific region, the calibrated model predicted predominantly low-to-moderate climatic suitability across much of the region (Figure *3.4*B). Moderate suitability was evident across parts of eastern China, the Korean Peninsula, southern Japan, portions of mainland Southeast Asia, and southeastern Australia, whereas much of the Indonesian archipelago, New Guinea, and surrounding tropical islands remained characterized by low predicted suitability. Overall, historical climatic suitability in the Asia-Pacific was characterized by broader areas of low-to-moderate suitability than in North America, where high climatic suitability was concentrated in more distinct geographic regions.

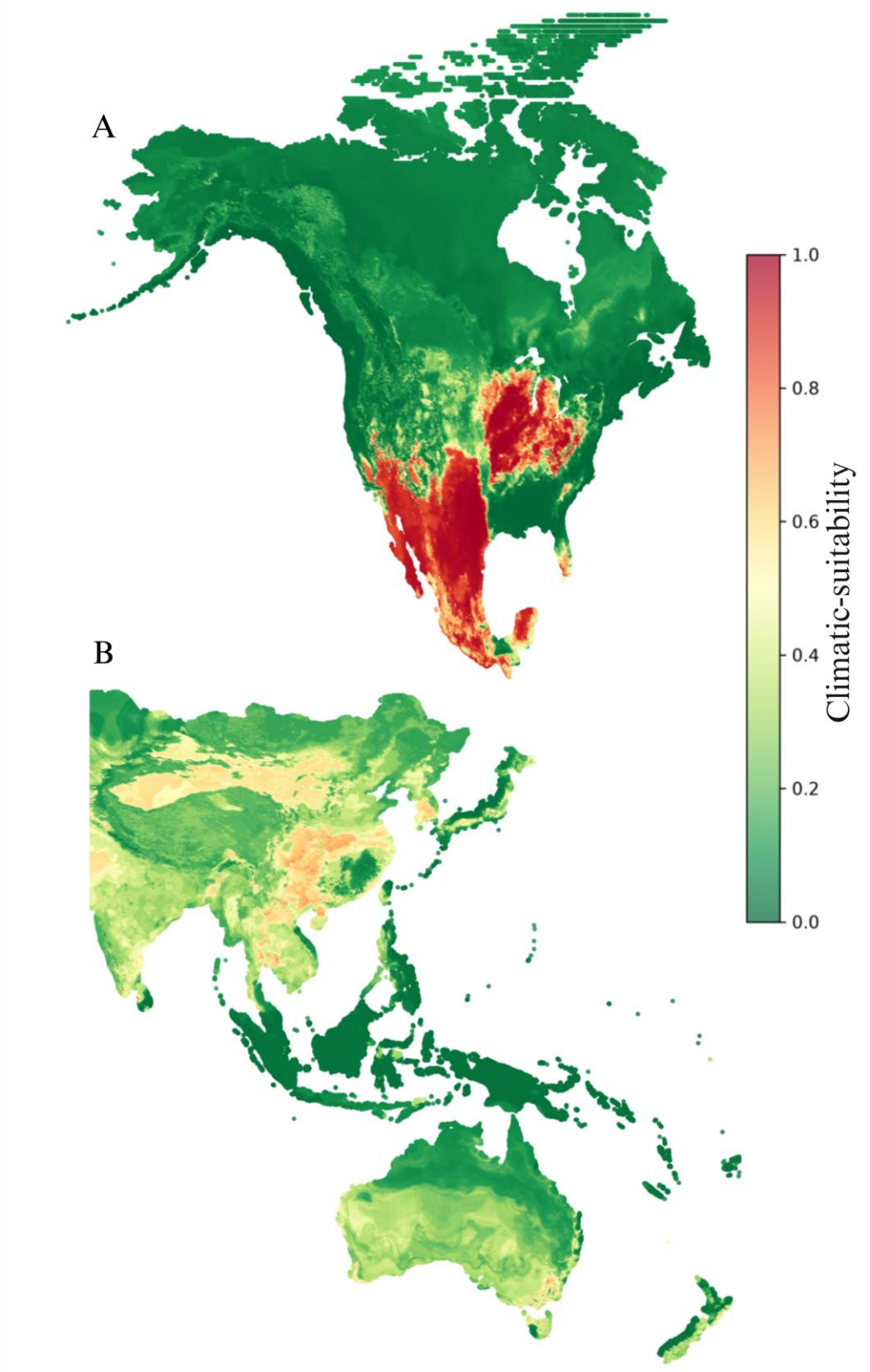
A
B
1.0
0.8
0.6
0.4
0.2
0.0
Climatic-suitability

Figure 3.4 Historical climatic suitability for oak wilt realized ecological niche in North America and potential naïve habitat in the Asia-Pacific region. Note. A, North American suitability under the 1961-1990 climate baseline; B, projected suitability in the Asia-Pacific using the North America-trained AUC-weighted ensemble. Values range from 0 (lowest) to 1 (highest) suitability.

3.3.4 Future climatic suitability in North America

Projected climatic suitability remained concentrated within the historical core regions but expanded progressively through time under all climate scenarios (Figure *3.5*). Expansion occurred primarily along the margins of existing climatically suitable areas and was accompanied by increased climatic suitability within established hotspots, rather than by the emergence of entirely new centers of suitability. As climatic suitability expanded, the two major historical regions of high suitability became increasingly connected as a more continuous belt of moderate-to-high climatic suitability developed across the central U.S. Among the three scenarios, SSP1-2.6 produced the most gradual increase, SSP2-4.5 showed greater spatial expansion and intensification, whereas SSP3-7.0 resulted in the largest expansion of climatically suitable areas by 2071-2100. The temporal trend panels similarly showed progressive increases in both the proportion of climatically suitable land and mean climatic suitability across successive projection periods, with the greatest increases occurring under SSP3-7.0.

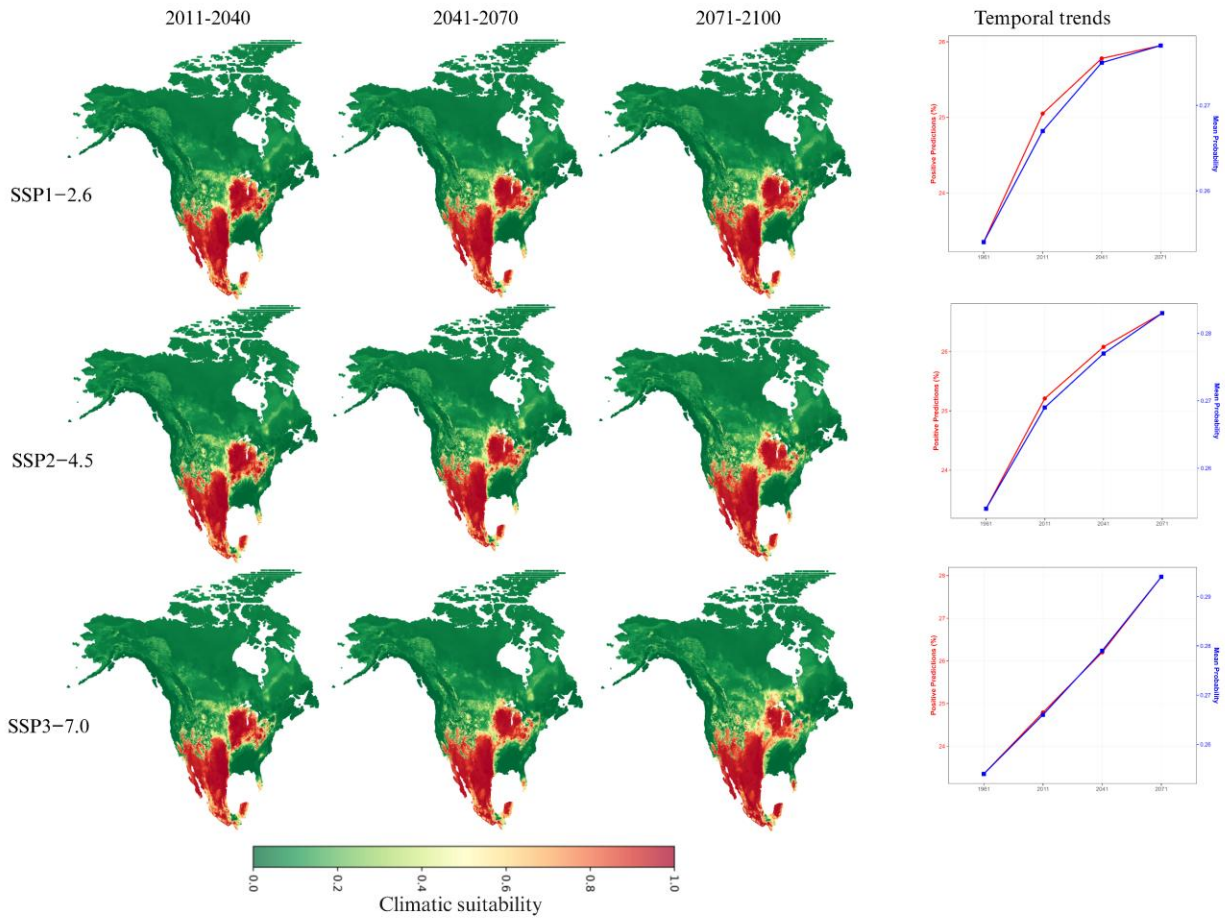

Figure 3.5 Projected climatic suitability for oak wilt realized niche in North America under future climate scenarios. Note. Maps show climatic suitability under SSP1-2.6, SSP2-4.5, and SSP3-7.0 for the projection periods 2011-2040, 2041-2070, and 2071-2100. Temporal trend panels illustrate changes in the proportion of climatically suitable land (positive prediction,%) and mean climatic suitability relative to the historical baseline (1961-1990). Colors represent ensemble-predicted climatic suitability after terrestrial land masking, ranging from 0 (lowest) to 1 (highest).

3.3.5 Future climatic suitability in Asia-Pacific

Projected climatic suitability in the Asia-Pacific increased progressively under all future climate scenarios while largely retaining the historical spatial pattern (Figure *3.6*).

Moderate climatic suitability remained concentrated across eastern China, the Korean Peninsula, Japan, parts of mainland Southeast Asia, and southeastern Australia, whereas much of the Indonesian archipelago, New Guinea, and surrounding tropical islands remained characterized by low climatic suitability. Across all scenarios, projected expansion occurred primarily through the gradual enlargement and intensification of existing moderately suitable regions rather than the emergence of new climatically suitable centers. The greatest increase in climatic suitability was observed under SSP3-7.0 by 2071-2100, whereas SSP1-2.6 exhibited the most gradual changes. Temporal trend panels likewise showed progressive increases in both the proportion of climatically suitable land and mean climatic suitability across successive projection periods, with the largest increases occurring under SSP3-7.0.

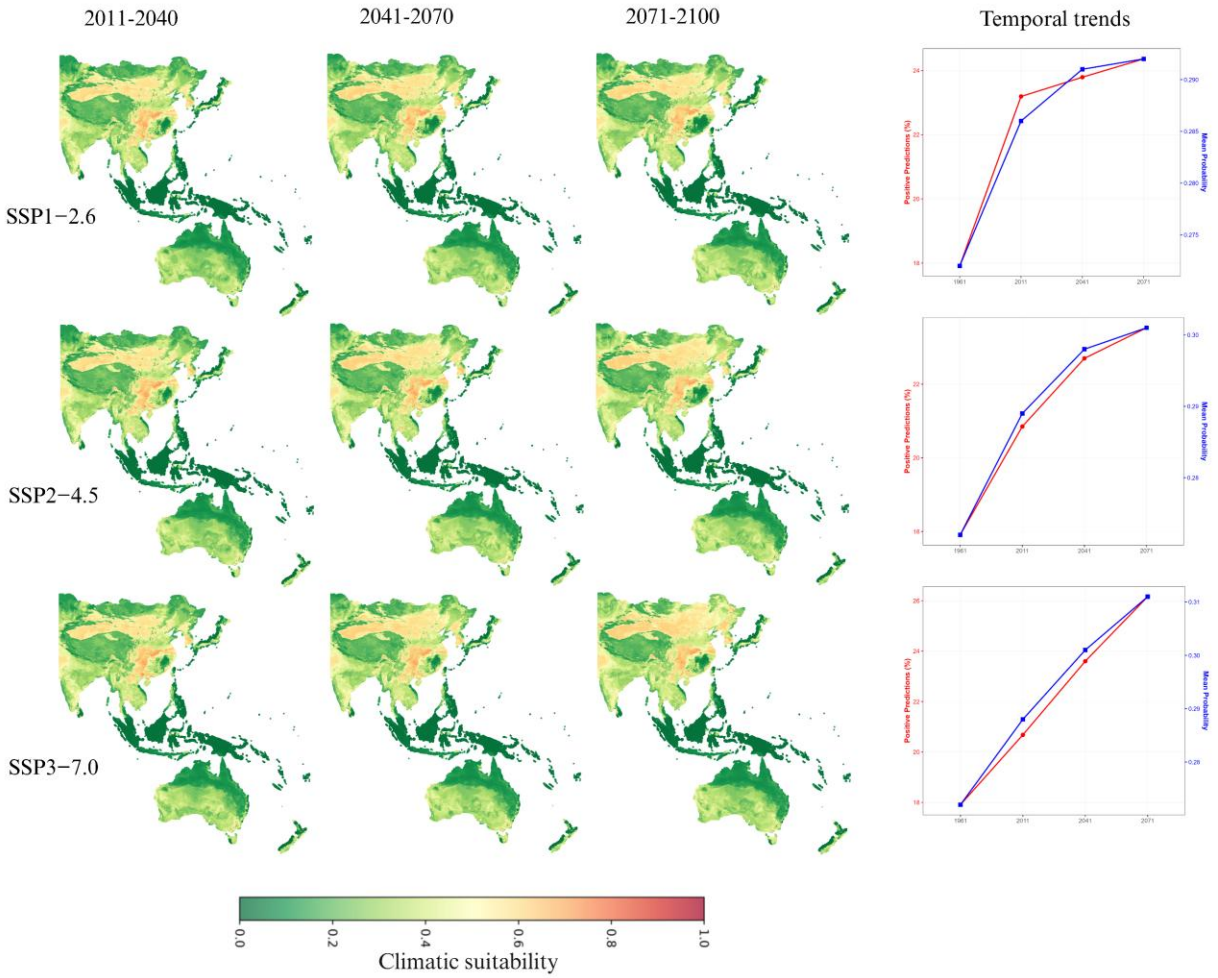

Figure 3.6 Projected climatic suitability for oak wilt in the Asia-Pacific region, the naïve habitats, under future climate scenarios. Note. Maps show projected climatic suitability under SSP1-2.6, SSP2-4.5, and SSP3-7.0 for the projection periods 2011-2040, 2041-2070, and 2071-2100. Temporal trend panels illustrate changes in the proportion of climatically suitable land (positive prediction, %) and mean climatic suitability relative to the historical baseline (1961-1990). Colors represent climatic suitability after terrestrial land masking, with values ranging from 0 (lowest) to 1 (highest).

3.3.6 Temporal changes in climatically suitable area

Across North America, the extent of climatically suitable land increased under all future climate scenarios relative to the historical baseline (Table *3.3*). The proportion of terrestrial grid cells classified as climatically suitable, reported as positive prediction (%), increased from 23.35% during 1961-1990 to 25.95%, 26.65%, and 27.97% by 2071-2100 under SSP1-2.6, SSP2-4.5, and SSP3-7.0, respectively. Mean climatic suitability increased from 0.254 under the historical baseline to 0.277, 0.283, and 0.294 under the respective scenarios.

A similar pattern was observed in the Asia-Pacific region. Positive prediction increased from 17.91% historically to 24.36%, 23.53%, and 26.16% by 2071-2100 under SSP1-2.6, SSP2-4.5, and SSP3-7.0, respectively, while mean climatic suitability increased from 0.272 to 0.292, 0.301, and 0.311. Although the suitable area under SSP2-4.5 was slightly smaller than under SSP1-2.6 at the end of the century, its higher mean suitability indicates intensification within a somewhat smaller area rather than broader areal expansion. Across both regions, SSP3-7.0 consistently produced the greatest increase in climatically suitable land and mean climatic suitability by the end of the twenty-first century.

Table 3.3 Climatically suitable area and mean climatic suitability under historical and future climate scenarios.

Region	Scenario	Projection period	Suitable area (km²)	Unsuitable area (km²)	Positive prediction (%)	Mean climatic suitability

	Normal	1961-1990	4,928,100	16,181,500	23.35	0.254
		2011-2040	5,286,900	15,817,500	25.05	0.267
	SSP1-2.6	2041-2070	5,441,000	15,663,400	25.78	0.275
		2071-2100	5,477,600	15,626,800	25.95	0.277
North		2011-2040	5,319,800	15,784,600	25.21	0.269
America	SSP2-4.5	2041-2070	5,503,600	15,600,800	26.08	0.277
		2071-2100	5,625,300	15,479,100	26.65	0.283
		2011-2040	5,231,700	15,872,700	24.79	0.266
	SSP3-7.0	2041-2070	5,529,100	15,575,300	26.20	0.279
		2071-2100	5,903,700	15,200,700	27.97	0.294
	Normal	1961-1990	5,242,300	24,033,700	17.91	0.272
		2011-2040	6,789,500	22,485,700	23.19	0.286
	SSP1-2.6	2041-2070	6,965,900	22,309,300	23.79	0.291
		2071-2100	7,131,700	22,143,500	24.36	0.292
Asia-		2011-2040	6,103,800	23,171,400	20.85	0.289
Pacific	SSP2-4.5	2041-2070	6,644,800	22,630,400	22.70	0.298
		2071-2100	6,889,700	22,385,500	23.53	0.301
		2011-2040	6,055,100	23,220,100	20.68	0.288
	SSP3-7.0	2041-2070	6,910,000	22,365,200	23.60	0.301
		2071-2100	7,659,800	21,615,400	26.16	0.311

Note. Projected climatically suitable and unsuitable terrestrial areas, proportion of climatically suitable land (positive prediction), and mean climatic suitability for oak wilt in North America (NA) and the Asia-Pacific (AP) region under the historical baseline (1961-1990) and future climate scenarios (SSP1-2.6, SSP2-4.5, and SSP3-7.0). Suitable and unsuitable areas were calculated using the TSS-optimal threshold of the final AUC-weighted ensemble model following terrestrial land masking. Positive prediction (%) represents the proportion of terrestrial grid cells classified as climatically suitable, whereas mean climatic suitability represents the average predicted suitability across all terrestrial grid cells.

3.3.7 Spatial changes in climatic suitability relative to the historical baseline

Relative to the historical baseline, projected changes in climatic suitability were characterized predominantly by gains rather than losses under all future climate scenarios (Table *3.4*). In North America, newly suitable areas occurred primarily along the northern margin of the historical distribution, indicating a progressive poleward shift of climatically suitable conditions into southern Canada, together with localized expansion along the western margin of the existing suitable range (Figure *3.7*A-C). Most historically suitable areas remained climatically suitable across all scenarios, whereas areas becoming unsuitable were comparatively limited and confined mainly to the periphery of the historical distribution. Net gains increased with climate forcing, reaching 975,700 km² under SSP3-7.0 by 2071-2100.

A similar spatial pattern was observed in the Asia-Pacific region, although the magnitude of change was substantially greater (Figure *3.7*D-F). Newly suitable areas expanded primarily across northern and northeastern China and adjacent parts of eastern Asia, while most historically suitable regions remained climatically suitable throughout the projection period. Areas becoming unsuitable remained localized and consistently smaller than areas of gain under all scenarios. However, the Asia-Pacific exhibited larger net increases in climatically suitable area than North America, with the greatest net gain (2,417,500 km²) projected under SSP3-7.0 by 2071-2100. Comparable gain-loss maps for the mid-century (2041-2070) and near-future (2011-2040) projection periods are provided in Appendix Figure 3.3 and Appendix Figure 3.4.

Table 3.4 Changes in climatically suitable area relative to the historical climate normal.

Region	Scenario	Projection period	Gain (km²)	Loss (km²)	Unchanged suitable (km²)	Unchanged unsuitable (km²)	Net change (km²)
North America	SSP 1-2.6	2011-2040	589,500	230,600	4,697,400	15,586,900	358,900
		2041-2070	787,000	274,000	4,654,000	15,389,400	513,000
		2071-2100	803,600	254,000	4,674,000	15,372,800	549,600
	SSP 2-4.5	2011-2040	591,200	199,400	4,728,600	15,585,200	391,800
		2041-2070	874,300	298,700	4,629,300	15,302,100	575,600
		2071-2100	1,064,000	366,700	4,561,300	15,112,400	697,300
	SSP 3-7.0	2011-2040	531,000	227,300	4,700,700	15,645,400	303,700
		2041-2070	911,300	310,200	4,617,800	15,265,100	601,100
		2071-2100	1,384,800	409,100	4,518,900	14,791,600	975,700
Asia-Pacific	SSP 1-2.6	2011-2040	1,982,200	435,000	4,807,300	22,050,700	1,547,200
		2041-2070	2,382,300	658,700	4,583,600	21,650,600	1,723,600
		2071-2100	2,480,400	591,000	4,651,300	21,552,500	1,889,400
	SSP 2-4.5	2011-2040	1,439,900	578,400	4,663,900	22,593,000	861,500
		2041-2070	2,086,100	683,600	4,558,700	21,946,800	1,402,500
		2071-2100	2,455,600	808,200	4,434,100	21,577,300	1,647,400
	SSP 3-7.0	2011-2040	1,426,700	613,900	4,628,400	22,606,200	812,800
		2041-2070	2,345,700	678,000	4,564,300	21,687,200	1,667,700
		2071-2100	3,303,300	885,800	4,356,500	20,729,600	2,417,500

Note. Binary climatic suitability predicted by the final AUC-weighted ensemble model was compared between the historical baseline (1961-1990) and each future projection. Gain represents areas changing

from unsuitable to suitable (0→1), loss represents areas changing from suitable to unsuitable (1→0), unchanged suitable represents areas remaining suitable (1→1), and unchanged unsuitable represents areas remaining unsuitable (0→0). Net change represents the difference between gain and loss. Areas are reported after terrestrial land masking.

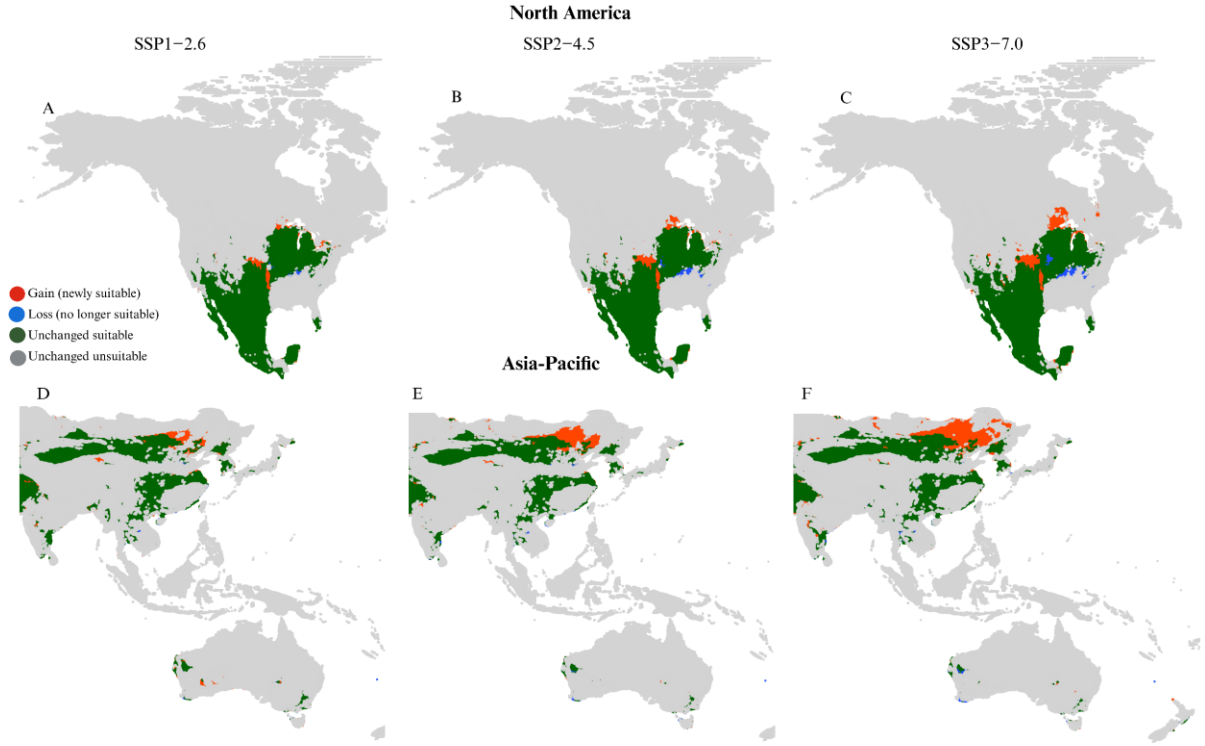

Figure 3.7 Projected changes in climatic suitability relative to the historical normal for the realized ecological niche, North America (A, B, C), and the naïve habitats, Asia-Pacific (D, E, F). Note. Projected changes by the end of the twenty-first century (2071-2100) relative to the historical baseline (1961-1990) under SSP1-2.6 (A, D), SSP2–4.5 (B, E), and SSP3-7.0 (C, F) for North America (top row) and the Asia-Pacific region (bottom row). Red indicates newly suitable areas (gain), blue indicates newly unsuitable areas (loss), dark green indicates areas that remain climatically suitable (stable suitable), and light gray indicates areas that remain climatically unsuitable (stable unsuitable).

3.4 Discussion

3.4.1 Climatic controls of oak wilt suitability and ensemble predictions

Our ensemble model identified extensive climatically suitable areas beyond the currently known distribution of *B. fagacearum*, suggesting that additional regions may be vulnerable to pathogen establishment. Since occurrence-based models estimate climatic suitability from observed occurrence records, projected suitable areas should be interpreted as regions at potential risk if the pathogen is introduced, rather than evidence of current pathogen occurrence (Holt, 2009; Pearson & Dawson, 2003). The presence of the pathogen may be constrained by historical dispersal, geographic isolation, the availability of suitable hosts and vectors, and human-mediated introduction pathways rather than by climatic limitations alone (Juzwik et al., 2011; Pedlar et al., 2020; Soberon & Peterson, 2005). By using an AUC-weighted ensemble of the highest-performing modeling algorithms, the ensemble reduces model-specific uncertainty while retaining the strengths of multiple statistical and machine-learning methods. The independent spatial-block 90/10 holdout further showed that the ensemble retained strong discrimination across geographically withheld blocks (AUC = 0.955; TSS = 0.754), supporting its use as a broad climatic-suitability screening model. However, because this result was based on a single holdout of five spatial blocks, it should not be interpreted as evidence of complete spatial transferability. This approach is consistent with recent studies that have used SDM and ensemble or multi-model frameworks to forecast climatic suitability for agricultural and forest pathogens, including *Wilsonomyces carpophilus* (Shi et al., 2025), *Ralstonia solanacearum* and *Clavibacter michiganensis* (Hubab et al., 2025), *Botryosphaeriaceae* species (Batista et al., 2022),

B. fagacearum (Pedlar et al., 2020; Pedlar et al., 2025; Tkaczyk & Lisiewicz, 2026). However, to our knowledge, no previous study had applied a multi-algorithm ensemble calibrated with an extensive North American occurrence dataset to compare future climatic suitability across both the pathogen's established continental range and the evolutionarily naïve Asia-Pacific region.

Among the climatic predictors, precipitation and moisture-related variables dominated the final ensemble, with January precipitation being the most influential predictor. Moisture can influence multiple components of oak wilt epidemiology. Previous studies have linked drought stress with increased host susceptibility (Appel, 2007), precipitation with greater fungal mat longevity (Tainter & Baker, 1996), wood moisture of 40-45% with favorable fungal growth (Stevens et al., 2024), and spring precipitation with increased fungal mat production (Juzwik, 2007). Pedlar et al. (2020) also included fall precipitation and annual climate moisture index as biologically relevant moisture variables for *B. fagacearum* climate-suitability modeling, supporting the importance of moisture availability in oak wilt risk assessment. Independent modeling of *B. fagacearum* in Europe provides additional support for the importance of hydroclimatic controls. Tkaczyk and Lisiewicz (2026) also identified precipitation of the driest month and precipitation of the driest quarter as the two most influential predictors of *B. fagacearum* suitability, together accounting for 49.9% of their MaxEnt variable contribution, followed by temperature seasonality. Moreover, annual precipitation and precipitation during the coldest and hottest three-month periods were among the six predictor variables used for climate niche modeling of more than 4,000 forest insect and fungus species in Canada (Pedlar et al., 2025). Although the climatic datasets, predictor

definitions, and modeling algorithms differed among these studies, their consistent identification of precipitation-related variables as influential predictors strengthens the conclusion that moisture availability is an important component of the realized climatic niche of *B. fagacearum*. January precipitation should therefore be interpreted as a broader seasonal moisture signal that integrates effects on pathogen survival, host physiology, and opportunities for transmission, rather than as a direct causal factor. The comparatively lower contributions of temperature variables do not indicate that temperature is unimportant; rather, they suggest that moisture-related predictors explain a greater proportion of the spatial variation in the modeled climatic suitability of *B. fagacearum*.

3.4.2 Climate change and invasion risk beyond the current geographic range

Spatially, our future projections showed a northward expansion of climatic suitability for *B. fagacearum*, with the greatest expansion projected under SSP3-7.0 by 2071-2100. Areas of current high suitability largely remained suitable across scenarios, while newly suitable areas gradually emerged along the northern and western margins of North America's present climatic range. This pattern is consistent with a previous climate-based assessment by Pedlar et al. (2020), which projected increasing suitability for oak wilt in southern Ontario and adjacent regions, together with climatically suitable conditions of the pathogen’s principal insect vectors, *Colopterus truncatus* and *Carpophilus sayi*. The relevance of these projections is reinforced by the first confirmation of oak wilt in Ontario in 2023, indicating that B. *fagacearum* has moved beyond its historically recognized U.S. distribution (Gauthier et al., 2024). Similarly, Tkaczyk and Lisiewicz (2026) projected substantial future gains in climatic suitability

(highest under SSP3-7.0) across central and eastern Europe, suggesting that climate-driven changes in oak wilt establishment risk may extend beyond North America. Collectively, these findings indicate a broader cross-continental tendency for climate change to redistribute and, under many scenarios, expand areas potentially suitable for oak wilt establishment.

The high and persistent climatic suitability projected for Mexico is also notable, given that the geographic origin of *B. fagacearum* remains unresolved. Juzwik et al. (2008) suggested that the pathogen may be non-native to the U.S. and could have originated in Mexico, Central America, or northern South America. Therefore, the high suitability projected for Mexico should not be interpreted as evidence of current pathogen presence, but rather as support for targeted surveillance in a climatically suitable and biogeographically relevant region. Together, these findings suggest that continued warming may further increase the risk of establishment in climatically favorable regions where susceptible oak hosts, competent vectors, and introduction pathways are present. Nevertheless, these projections should be interpreted as estimates of climatic suitability and potential risk, rather than predictions of realized disease occurrence.

3.4.3 Biosecurity implications beyond the current geographic range

Although *B. fagacearum* is not known to be established in the Asia-Pacific, our model projected climatically suitable areas across parts of this region. Eastern China is particularly noteworthy because the pathogen's climatic niche overlaps with regions containing diverse oak and chestnut resources. Although oak wilt is primarily associated with *Quercus*, historical isolation of the pathogen from Chinese chestnut (*Castanea*

mollissima) in Missouri (Bretz & Long, 1950), and recent (Chahal et al., 2024) confirmation in hybrid chestnut (*Castanea sativa* × *Castanea crenata*) in Michigan indicate that the potential host range may extend beyond oaks. Therefore, projected suitability in eastern China should be interpreted as a potential risk of establishment following accidental introduction, rather than as evidence of current occurrence or predicted disease impact. Future susceptibility testing of dominant Asian oak and chestnut species would improve global risk assessment for oak wilt.

3.4.4 Risk-based surveillance implications

These projections can support risk-based surveillance by identifying regions where climatic suitability may enable *B. fagacearum* to establish following introduction. However, climate-suitability maps should function as an initial screening layer rather than as stand-alone predictions of realized disease risk. Surveillance should be prioritized where suitable climate coincides with abundant susceptible hosts, suitable conditions for competent insect vectors, and likely introduction pathways. Accordingly, surveillance priorities should include the northern margin of the pathogen's current range, oak-rich areas in southern Canada, climatically suitable oak-growing regions in the Asia-Pacific and Europe, and locations associated with the movement or storage of nursery stock, firewood, logs, and other wood products. However, because the model estimates only climatic suitability, future risk assessments should integrate host distribution, vector occurrence, trade pathways, and field surveillance data to better distinguish potential establishment zones from realized disease risk.

3.4.5 Limitations and future research

This study estimates climatic suitability rather than realized disease risk because host and vector distributions, topographic and edaphic conditions, biotic interactions, and human-mediated introduction pathways were not included. Occurrence records used in this study were pooled across the known range of *B. fagacearum*, assuming that geographically structured populations share a broadly similar climatic niche despite evidence of regional genetic differentiation (Chahal et al., 2025a). Future studies should integrate these ecological factors and develop lineage-specific models to improve regional estimates of establishment risk.

Under the independent spatial-block 90/10 holdout, the ensemble retained high discriminatory performance (AUC = 0.955), while its TSS decreased to 0.754 relative to repeated random validation. Thus, geographic ranking ability remained strong, whereas threshold-dependent classification was moderately reduced. Because this estimate was obtained from one reproducible holdout of five complete blocks, it may be sensitive to the selected test blocks and the 4° block size. Predictor selection was also conducted using the full dataset before cross-validation, which can introduce a potential optimistic bias in the reported metrics, while the collinearity assessment revealed substantial redundancy among the 25 retained predictors. Predictor-importance values should therefore be interpreted as indicators of broad climatic associations, particularly moisture-related conditions, rather than as independent or causal effects. Future analyses should nest predictor selection within spatial-validation folds, test alternative block sizes, and evaluate reduced, biologically informed predictor sets.

Transferring the North America-trained model to the Asia-Pacific region may involve climatic conditions that are poorly represented in the calibration data and assumes that the pathogen's climatic niche is transferable to a different host and vector context. These projections should therefore be used as preliminary biosecurity and surveillance-screening layers rather than forecasts of disease occurrence. A multivariate environmental similarity surface analysis would help distinguish interpolation from extrapolation in future projections (Elith et al., 2010). Finally, the models relied on opportunistically collected occurrence records and background locations rather than confirmed absences; residual sampling bias and the approximately 1:1 presence-to-background ratio may therefore influence fitted climatic relationships.

3.5 Conclusions

Oak wilt (*B. fagacearum*) is likely to become an increasingly important climate-sensitive threat to global biosecurity as environmental conditions continue to change. Using an AUC-weighted ensemble climate niche model, we identified extensive climatically suitable areas beyond the pathogen's currently known distribution (realized niche) and projected a continued expansion of suitable environments under future climate scenarios (naïve habitats). These findings indicate that climate can support pathogen establishment across a substantially broader geographic range than is currently occupied, while highlighting that realized disease occurrence remains constrained by additional ecological and epidemiological factors.

The predominance of precipitation, moisture, and relative humidity-related variables indicates that hydroclimatic conditions were the dominant associations with modeled suitability. Future climatic changes are therefore likely to influence not only the

geographic extent of suitable environments but also the potential for naïve ecosystems where suitable climate overlaps with susceptible hosts, competent vectors, and introduction pathways.

These projections provide a quantitative framework for climate-informed ecology, biosecurity, and forest health management by identifying regions where early detection and preventive actions may be most effective. Integrating climatic suitability with host distributions, vector ecology, pathogen population structure, and human-mediated dispersal will further improve predictions of disease emergence and strengthen strategies for protecting forest ecosystems under ongoing environmental change.

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Appendix B. Supplementary materials for Chapter 3

Appendix Table 3.1 Description of climatic predictors retained for model development.

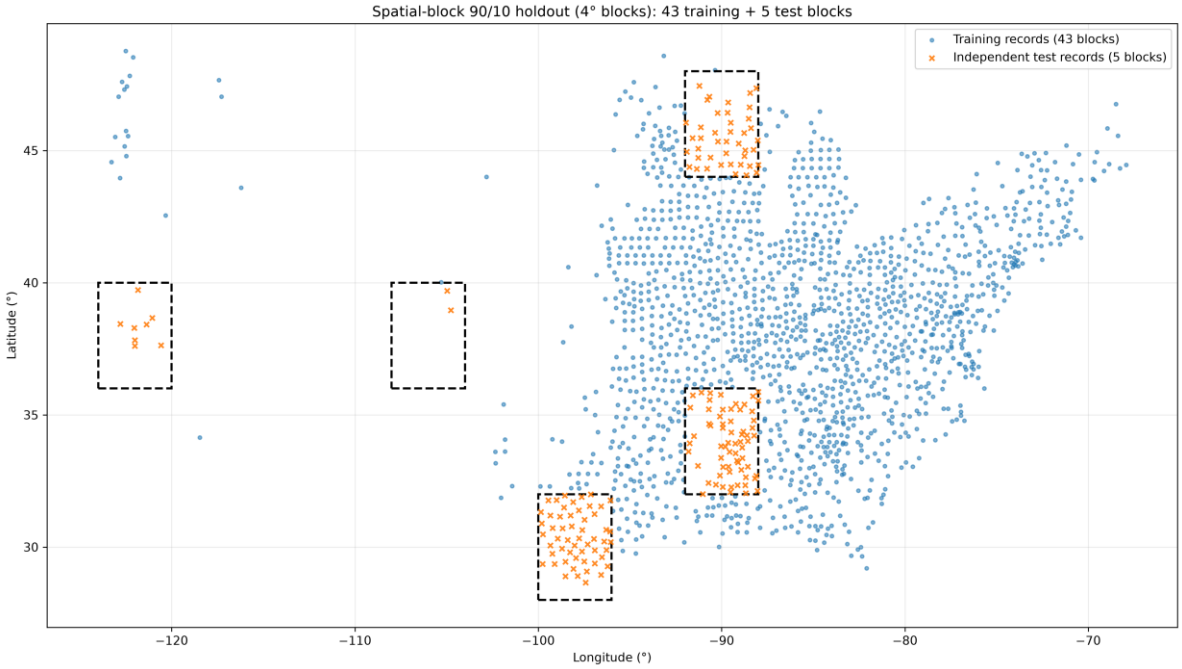
Climate category	Predictor	Description
Precipitation	MAP	Mean annual precipitation (mm)
	PPT_wt	Winter precipitation (mm)
	PPT01	January precipitation (mm)
	PPT02	February precipitation (mm)
	PPT03	March precipitation (mm)
	PPT04	April precipitation (mm)
	PPT11	November precipitation (mm)
	PPT12	December precipitation (mm)
Climatic moisture index (CMI)	CMI	Hogg's climate moisture index (mm)
	CMI_wt	Winter Hogg's climate moisture index (mm)
	CMI_at	Autumn Hogg's climate moisture index (mm)
	CMI01	January Hogg's climate moisture index (mm)
	CMI02	February Hogg's climate moisture index (mm)
	CMI03	March Hogg's climate moisture index (mm)
	CMI04	April Hogg's climate moisture index (mm)
	CMI08	August Hogg's climate moisture index (mm)
	CMI09	September Hogg's climate moisture index (mm)
	CMI10	October Hogg's climate moisture index (mm)
	CMI11	November Hogg's climate moisture index (mm)
	CMI12	December Hogg's climate moisture index (mm)
Relative humidity	RH08	August relative humidity (%)
	RH09	September relative humidity (%)
	RH10	October relative humidity (%)
Reference evaporation	Eref07	July Hargreaves reference evaporation (mm)
	Eref_sm	Summer Hargreaves reference evaporation (mm)

Appendix Table 3.2 Configuration of the species distribution modeling algorithms implemented in the Python pipeline.

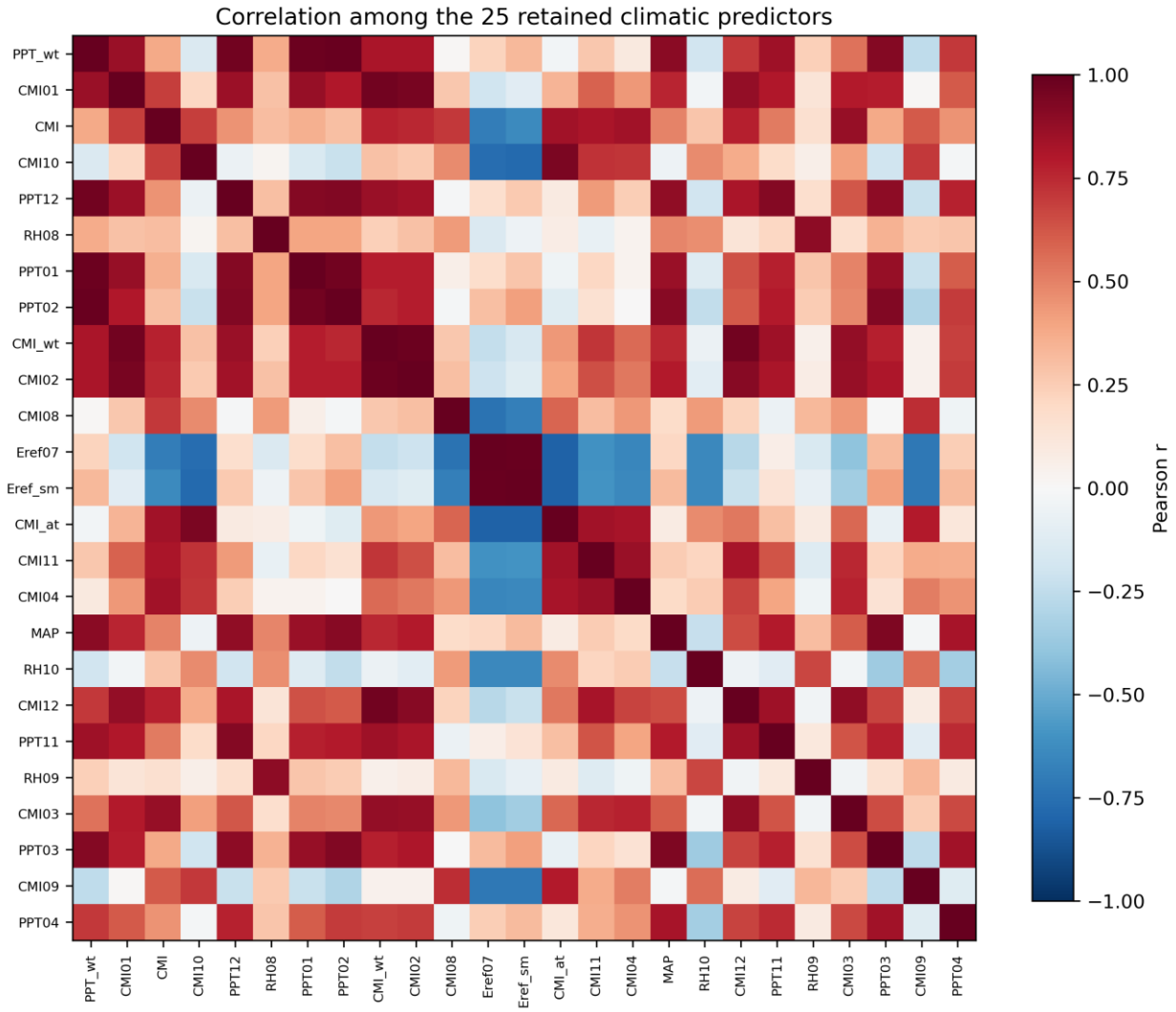
Algorithm	Configuration implemented in the Python pipeline
Random Forest	500 trees; random seed = 42; balanced class weights; parallel fitting where available.
Gradient Boosting Machine	500 boosting stages; random seed = 42.
Logistic Regression	Maximum of 1,000 iterations; random seed = 42; balanced class weights.
Gaussian Naive Bayes	Default classifier settings.
Support Vector Machine	Probability estimates enabled; random seed = 42; balanced class weights.
XGBoost	500 estimators; random seed = 42; log-loss evaluation metric.
MaxEnt	Implemented using the Elapid library and wrapped to provide a classification-style interface.

Appendix Table 3.3 Variance inflation factors for the 25 climatic predictors retained in the ensemble modeling analysis.

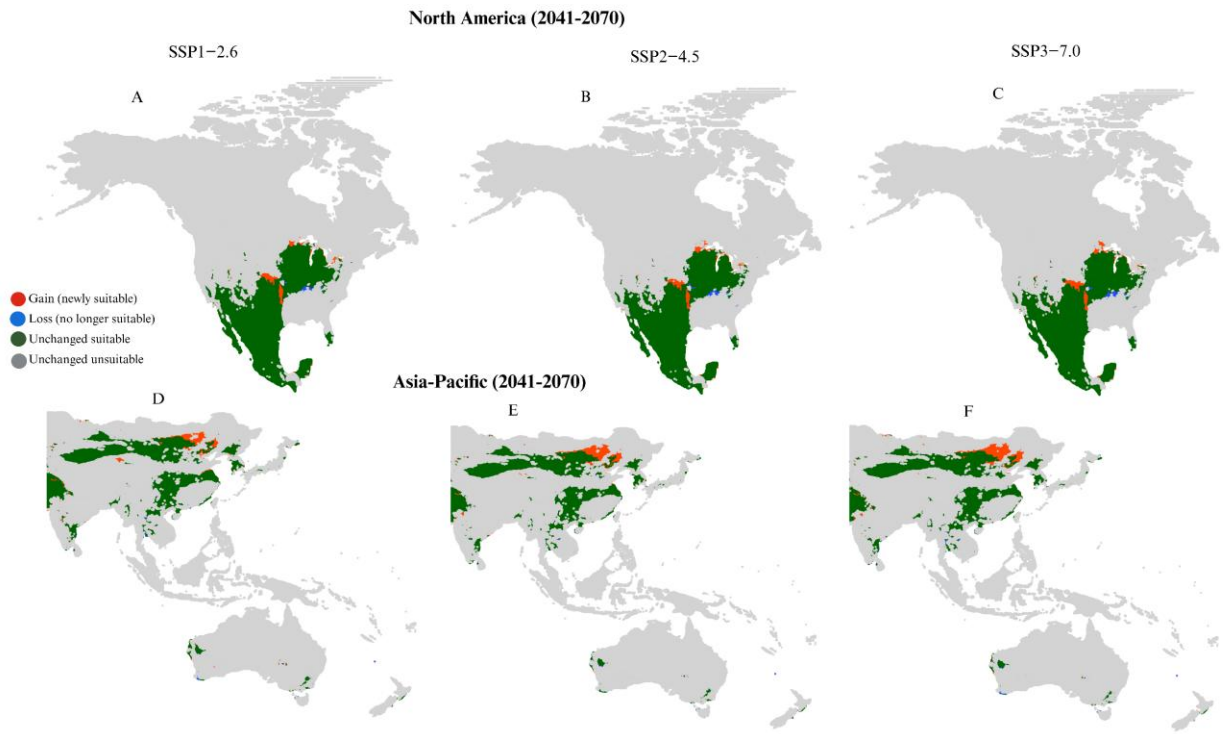
Predictor	VIF
CMI_wt	2346484.77
CMI_at	1289810.96
CMI12	323915.47
CMI01	281815.38
CMI11	257390.79
CMI02	232444.7
CMI09	186240.04
CMI10	155107.1
PPT_wt	43183.02
PPT12	6606.37
PPT01	6203.79
PPT02	5731.91
CMI	1652.42
MAP	1260.66
PPT03	522.11
Eref_sm	418.56
CMI03	352.77
PPT11	266.88
Eref07	230.63
CMI04	131.89
PPT04	98.39
RH09	26.52
RH08	22.2
CMI08	19.96
RH10	13.32



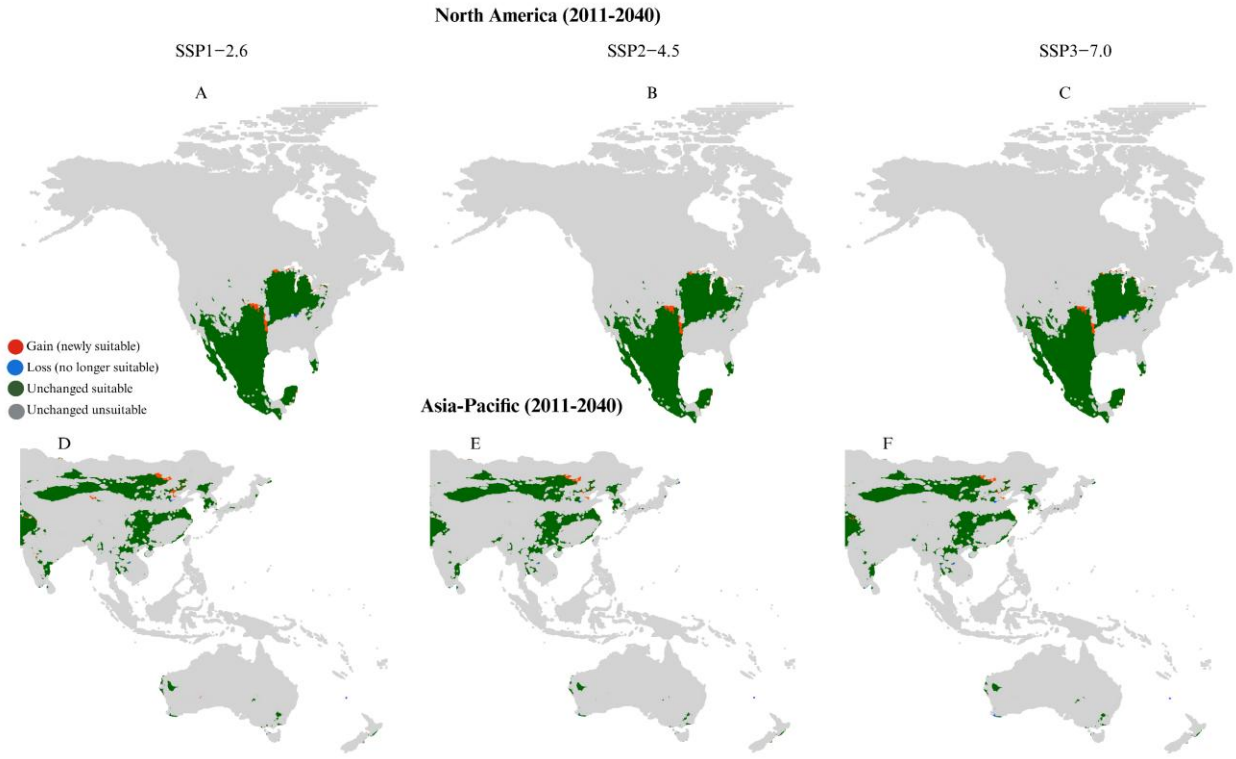
Appendix Figure 3.1 Independent spatial-block 90/10 holdout used to evaluate geographic transferability. Note. All occurrence and background records were assigned to 48 occupied 4° × 4° spatial blocks. Blue points represent records from the 43 training blocks, whereas orange crosses represent records from the five independent test blocks outlined by dashed boxes. All observations within each block were kept together, and the test blocks were excluded from model fitting, ensemble weighting, and probability-threshold selection.



Appendix Figure 3.2 Pairwise correlations among the 25 climatic predictors retained for ensemble modeling. Cell colors represent Pearson correlation coefficients ranging from −1 to +1. Strong correlations among numerous precipitations, climatic moisture index, relative humidity, and evapotranspiration variables demonstrate substantial redundancy within the retained predictor set.



Appendix Figure 3.3 Spatial changes in projected climatic suitability between the historical baseline (1961-1990) and the mid-century period (2041–2070) under three future climate scenarios for the realized niche (A, B, C) and the potential naïve habitat in Asia-Pacific (D, E, F). Note. Maps illustrate changes in binary climatic suitability relative to the historical baseline for North America (top row) and the Asia-Pacific region (bottom row) under SSP1-2.6, SSP2-4.5, and SSP3-7.0. Red indicates newly suitable areas (gain), blue indicates areas that became unsuitable (loss), dark green indicates areas that remained suitable, and light gray indicates areas that remained unsuitable.



Appendix Figure 3.4 Spatial changes in projected climatic suitability between the historical baseline (1961-1990) and the early-century period (2011–2040) under three future climate scenarios for the realized niche (A, B, C) and the potential naïve habitat in Asia-Pacific (D, E, F). Note. Maps illustrate changes in binary climatic suitability relative to the historical baseline for North America (top row) and the Asia-Pacific region (bottom row) under SSP1-2.6, SSP2-4.5, and SSP3-7.0. Red indicates newly suitable areas (gain), blue indicates areas that became unsuitable (loss), dark green indicates areas that remained suitable, and light gray indicates areas that remained unsuitable.

CHAPTER 4

Synthesis and Conclusions

4.1 Overview

This thesis set out to answer two linked questions about a single pathogen. First, does the eight-decade tradition of treating oak wilt as a single disease obscure epidemiologically and genetically distinct regional processes that require different management? Second, where might climatic conditions permit *B. fagacearum* to establish as the climate changes, both within North America and in regions where susceptible hosts have never encountered the pathogen? Chapter 1 addressed the first question through a PRISMA-guided synthesis of 121 studies and recent population-genomic evidence; whereas Chapter 2 examined the climatic factors influencing disease development and transmission, while Chapter 3 developed an ensemble climate niche model using 880 U.S. occurrence records to project historical and future climatic suitability across North America and the Asia-Pacific region. This concluding chapter explains how the epidemiological synthesis and climatic model address different but complementary scales.

The central finding is that oak wilt is best understood as one pathogen expressed through two mechanistically distinct epidemics, and that this regional divergence has direct consequences for how the disease should be forecast and managed. The two major chapters, 1 and 3, approach divergence from opposite ends of the spatial scale. Chapter 1 from the stand and landscape, Chapter 3 from the continent and beyond -

and the apparent difference in their modeling choices reflects that difference in scale and purpose rather than any contradiction in the underlying biology.

4.2 The two-epidemics framework and its genomic context

Chapter 1 demonstrated that the Texas and Lake States expressions of oak wilt differ in nearly every parameter that governs how the pathogen moves and how fast disease centers expand. In the live-oak (*Q. fusiformis* and *Q. virginiana*) mottes and savannas of central Texas, transmission is dominated by continuous clonal root systems in which many stems share a single root mass, resulting in radial disease-center expansion approaching 40 m yr^{-1} under year-round vector activity and year-round mat production. In the oak-dominated hardwood forests of the Lake States, an insect-mediated inoculation pathway, coupled with spread through natural inter-tree root grafts, yields substantially slower expansion of roughly 3.6–12 m yr^{-1}, constrained to spring and fall inoculation windows set by nitidulid flight phenology and mat availability. Belowground movement dominates local expansion in both regimes, although the estimate exceeding 90% comes primarily from Minnesota studies; yet the same label, "belowground spread," denotes two mechanistically distinct processes: soil-gated root grafting in the north versus clonal-root continuity in the south.

Crucially, this ecological divergence is mirrored in the pathogen's genome. Whole-genome sequencing resolved four geographically structured genetic clusters - Upper Midwest, Mid-Atlantic/Southeast, Michigan, and Texas- with the Texas population forming a genetically distinct lineage consistent with historical reproductive isolation (Chahal et al., 2025). The two epidemics are therefore not merely regional flavors of a uniform process; they are ecologically distinct and, at least in the Texas case,

associated with a genetically distinct population of pathogens. This coupling supplies a mechanistic explanation for a long-standing practical frustration: management tactics and climate projections calibrated in one region transfer poorly to the other. It also reframes the four genomic clusters and two epidemiological regimes as complementary rather than competing descriptions - four clusters describe ancestry, two regimes describe mechanism, and Texas is distinctive on both axes.

4.3 Reconciling the two chapters: why a pooled model serves a partitioned framework

The most important question this thesis must answer arises precisely because its two chapters are internally consistent. Chapter 1 concludes that regime-partitioned distribution models - trained and validated separately on Texas and Lake States occurrences are the correct forecasting architecture, because a model trained on pooled records averages across two mechanistically distinct predictor relationships. Chapter 3 then builds a single pooled model across the whole known range, considering the climatic controls on disease triangle components discussed in Chapter 2. Taken at face value, the third chapter appears to ignore the recommendation of the first. It does not, and the reconciliation rests on a difference in objective and two concrete data constraints rather than a change of mind.

The two chapters pursue different objectives. Chapter 1 is concerned with within-range management forecasting at local and regional scale, where the goal is to have an overview of the disease while asking where and how fast the disease will spread in stands that already harbor the pathogen; there, capturing the regime-specific predictor relationships is decisive, and partitioning is important. Chapter 3 focuses on continental-

to-global biosecurity screening to identify regions whose climate could support establishment following introduction, including evolutionarily naïve habitats in the Asia-Pacific, where the pathogen has never occurred. For that objective, the model must represent the full realized climatic niche of *B. fagacearum*, because extrapolation to novel climatic space requires the complete envelope of conditions under which the species persists, not a regional subset. A Texas-only model would carry only warm, semi-arid, live-oak climate space abroad and miss the northern temperature-and-precipitation niche that governs range expansion; a Lake States-only model would understate suitability in subtropical zones. Combining two partial models into one global projection would also compound model-combination uncertainty on top of the already substantial inter-GCM spread.

Two data constraints made regime partitioning inconvenient in practice, independent of its theoretical appeal. First, occurrence records for oak wilt are archived at the county level without validated regime-assignment labels; no public dataset assigns individual records to the Texas or Lake States regime. Regime membership can only be approximated geographically, roughly south of ~38°N for Texas, and that boundary fails in the southeastern convergence zone (Georgia, South Carolina, Tennessee, North Carolina), where the two regimes meet, and neither region's parameters apply cleanly (Appel, 1995; Chahal, 2024). Partitioning on an approximate boundary would inject classification error into the training data at exactly the location most consequential for future range-shift projection. Second, the occurrence density is insufficient to support a stable Texas-regime model. Of the 880 georeferenced presences, only an estimated 270–300 fall within counties reflecting the Texas regime,

and after spatial thinning to reduce autocorrelation, this subset would yield roughly 80–100 spatially independent records, near or below the lower bound of approximately 100–200 records that Barbet-Massin et al. (2012) identified for stable performance in Random Forest and MaxEnt. Fitting one regime model on ~80–100 points and another on ~600 would also make their global projections structurally non-comparable.

The two chapters are complementary rather than contradictory. Chapter 1 supports regime-specific forecasting for within-range management, whereas Chapter 3 uses a pooled model to represent the broader realized climatic niche for biosecurity screening. This trade-off improves species-level climatic coverage but may obscure regional responses. Regime-specific models based on validated regional occurrence data therefore remain an important future direction. The strong performance retained under independent spatial-block testing supports the pooled model's use for broad species-level climatic screening, while the reduction in TSS reinforces the need for regionally parameterized models when local management decisions are required.

4.4 A unified, regime-specific framework for surveillance and management

Integrating the two chapters yields a single practical principle: because the two epidemics are mechanistically distinct, effective intervention must be regime-specific, and forecasting must tell managers which regime they are operating in. In the Upper Midwest and Lake States, where risk is amplified by high red-oak density and structural homogeneity, mechanism-targeted measures include converting red-oak monocultures toward mixed-species assemblages, reducing stand density to lower inter-tree root-graft probability, disrupting established graft connections by vibratory plowing or root rupture, and replacing calendar-based pruning advisories with real-time degree-day models that

bracket the nitidulid inoculation window. In central Texas, where continuous clonal root systems drive the fastest documented spread, the structurally opposite approach is required: motte-boundary interruption and root-zone disconnection rather than species-composition adjustment, combined with strict avoidance of wounding during periods of vector activity. Treating the two regimes as interchangeable will underperform in at least one of them.

The forecasting products of Chapter 3 feed directly into this framework as a fast-screening layer. Climatic suitability is necessary but not sufficient for disease occurrence, so suitability maps should be used to prioritize where surveillance is deployed rather than to predict realized occurrence, especially in naïve habitats. The projected northward expansion of suitability into southern Canada, aligning with the previous studies, the persistent high suitability in Mexico, and the newly suitable margins along the western edge of the range identify where early-detection effort will be beneficial, particularly where suitable climate coincides with abundant susceptible hosts, competent vectors, and plausible introduction pathways such as firewood, logs, and nursery stock. Chapter 1 showed that the detection toolkit to act on these priorities already exists - TaqMan qPCR from fallen petioles, LAMP, metabarcoding, rapid VOC profiling, and validated remote sensing. So, it will be cost-effective to combine these tools for regime-matched surveillance and rapid response before disease centers exceed the projected.

4.5 Biosecurity beyond the current range

Chapter 3's projection onto the Asia-Pacific region suggests that oak wilt is a global biosecurity issue. Because *B. fagacearum* is native to the Americas and Asian *Quercus* and *Castanea* species are evolutionarily naïve to it, an introduction into climatically suitable Asian habitat could produce catastrophic, rapid mortality analogous to the destruction of native American chestnuts by the introduced Asian chestnut blight, *Cryphonectria parasitica*, in the early twentieth century, a historical inversion of the source and recipient continents as an instructive analogy. The model projected moderate climatic suitability across eastern China, the Korean Peninsula, southern Japan, parts of mainland Southeast Asia, and southeastern Australia, with suitability increasing under future climate scenarios. Eastern China is especially important because areas of suitable climate overlap with diverse oak and chestnut resources. These projections are estimates of climatic suitability and potential establishment risk, not predictions of disease, and are best treated as a rationale for targeted host-susceptibility testing of dominant Asian species and for surveillance at ports and along wood-movement pathways.

4.6 Limitations of the integrated work

Several limitations qualify the conclusions of this thesis. The PRISMA-guided review reflects geographic and thematic differences in the available literature, and the two-epidemics framework represents a synthesis of published epidemiological and genetic evidence rather than a direct experimental comparison. The species distribution model estimates climatic suitability only and does not incorporate host distribution, vector occurrence, soil and topographic controls, or human-mediated dispersal, all of which

further constrain realized establishment. Under the independent spatial-block 90/10 holdout, the ensemble retained high discriminatory performance (AUC = 0.955), while TSS declined from approximately 0.800 under repeated random validation to 0.754. This indicates strong geographic ranking ability but a moderate reduction in threshold-dependent classification across withheld regions. Because the spatial estimate was derived from a single holdout of five 4° blocks, its magnitude may be sensitive to block size and the blocks selected for testing. Predictor selection before cross-validation may have introduced information leakage, while multicollinearity limits the independent interpretation of predictor importance. In addition, pooling occurrences across the pathogen's range may obscure region-specific climatic responses, and transferring the model to the Asia-Pacific region may involve climatic and ecological conditions not represented in the U.S. calibration data. These limitations support interpreting the projections as broad surveillance and biosecurity-screening tools rather than predictions of realized disease occurrence.

4.7 Concluding statement

Oak wilt has been studied as one disease for eighty years. The combined weight of transmission biology, host anatomy, environmental control, and now pathogen population genomics supports the trend: two epidemics driven by one pathogen, divided along a geographic seam that runs through the host system, the environment, and the genome, and converging at a southeastern frontier that current models do not yet fully describe. This thesis makes reframing explicit and shows what follows: region-specific management and forecasting are necessary, and the remedy is to parameterize the two epidemics separately. Regarding global biosecurity, the research retains a full-niche

model of the pathogen’s climatic tolerance. By linking climate-sensitive disease mechanisms to regional epidemiology and to continental-scale projection, the work provides an integrated basis for surveillance, biosecurity, and region-specific, climate-adaptive management of a pathogen whose suitable range is projected to expand well beyond the current habitat.

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