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Herbarium Specimens Provide Evidence for the Early Introduction of *Erysiphe quercicola* Into the United States and Document New Hosts

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ABSTRACT

The powdery mildew fungus *Erysiphe quercicola* (*Erysiphaceae*) has a complex taxonomic history that has long complicated assessments of its geographic distribution and host associations. Although knowledge of the global host range of this species has expanded substantially over the past two decades, sequencing-confirmed records from North America remain scarce, and despite its recognition as an introduced pathogen, the timing of introduction and the geographic extent and host range of *E. quercicola* in the United States are poorly understood. In this study, herbarium specimens of *E. quercicola* from North America, spanning both historical and contemporary collections, were examined using molecular phylogenetic approaches. Specimens collected from multiple *Quercus* species across several regions of the United States, as well as from related hosts within the *Fagaceae*, were evaluated. Sequence data confirm the presence of *E. quercicola* in North America on *Quercus* species based on herbarium specimens collected as early as 1944, as well as on mango (*Mangifera indica*; *Anacardiaceae*) in Florida from material collected in 1935. These records raise the possibility of historical introduction pathways associated with cultivated hosts, potentially from the horticulturally important mango tree (*M. indica*); however, additional multilocus phylogenetic analyses and host range inoculation experiments will be required to determine whether powdery mildew populations infecting mango and *Quercus* in North America represent the same lineage. Additional sequencing-confirmed records document the species on multiple native oak species representing different sections of *Quercus* including *Q. bicolor*, *Q. gambelii*, *Q. garryana*, *Q. geminata*, *Q. kelloggii*, *Quercus* × *jolonensis* and *Q. macrocarpa* as well as on *Notholithocarpus densiflorus*. Together, these findings clarify the long-term presence of *E. quercicola* in the United States, expand knowledge of its North American host range, and demonstrate the value of herbaria for reconstructing the invasion history of forest pathogens.

1 | Introduction

Herbarium specimens provide an important historical record for understanding the invasion, establishment, and spread of plant pathogenic fungi. Molecular analyses of historical material from fungaria allow the timing of pathogen presence to be reassessed independently of first reports in the literature, which often reflect detection rather than initial establishment.

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This approach has proven especially valuable for powdery mildews (*Erysiphaceae*), where recent studies have demonstrated substantial delays between pathogen introduction and formal recognition. For example, Bradshaw et al. (2021) showed that a powdery mildew infecting *Acer* species had been present in North America for approximately 80 years prior to its description, and analysis of fungarium samples allowed documentation of the global spread of a North American native powdery mildew to blueberry hosts over 150 years (Bradshaw, Ivors, et al. 2025). Similarly, herbarium-based analyses revealed that *Erysiphe quercicola* was present in Europe by at least 1911 (Bradshaw et al. 2022), consistent with findings of Gross et al. (2021), who identified multiple European specimens collected between 1900 and 1920.

Erysiphe quercicola and E. alphitoides are phylogenetically and morphologically closely related powdery mildew species that primarily infect *Quercus* spp. The resolution of this species complex, including the formal taxonomic description of *E. quercicola*, can be traced to Takamatsu et al. (2007), who demonstrated that *E. quercicola* has a broad host range extending well beyond oaks (*Fagaceae*), particularly in tropical and subtropical regions. Since then, the number of confirmed host species across multiple plant families has increased substantially (Kirschner and Liu 2014; Meeboon and Takamatsu 2020; Azevedo Silva et al. 2021; Afshan et al. 2022; Fonseca et al. 2023; Banerjee and Pandey 2024; Yeh and Kirschner 2024; Zhang et al. 2024, 2026). Subsequent phylogenetic and nomenclatural work clarified the application of species names within the *E. alphitoides* complex, including *E. quercicola*, providing a stable taxonomic framework for interpreting host and distributional data (Bradshaw et al. 2022; Braun et al. 2022; Bradshaw, Braun, Németh, et al. 2025).

Erysiphe quercicola is particularly widespread in tropical and subtropical regions of eastern Asia (Bradshaw, Braun, Mitchell, et al. 2025), and its occurrence in Europe has been investigated and confirmed (Mougou et al. 2008). In contrast, until recently, little was known about the distribution and host range of this species in North America, especially on oak trees. Prior to recent studies, only a single sequencing-confirmed record from the United States was available, occurring on the non-native host *Quercus robur* in Washington State (Bradshaw et al. 2022). Subsequent work added confirmed records from Mexico on *Q. agrifolia* (Bradshaw, Braun, Mitchell, et al. 2025) and from Florida on *Q. shumardii* and *Mangifera indica* (Bradshaw, Braun, Mitchell, et al. 2025; Bradshaw, Quijada, et al. 2025), whereas additional Mexican records involve hosts from other plant families, including lemon (*Citrus* × *limon*; *Rutaceae*; Yáñez-Morales et al. 2009) and mango (*M. indica*; *Anacardiaceae*; Pérez-Rodríguez et al. 2018). More broadly, extensive phylogenetic–taxonomic studies of North American *Erysiphe* species on oaks have led to the description of multiple new species and the recognition of previously overlooked taxa (Bradshaw et al. 2022; Bradshaw, Ivors, et al. 2025; Bradshaw, Braun, Németh, et al. 2025).

In the present study, we extend these efforts by sequencing additional herbarium and fresh specimens of powdery mildews collected from oak trees across the United States. This data represents new native *Quercus* hosts for *E. quercicola* and demonstrates that this pathogen has been present in North America for at least 90 years, substantially predating its formal recognition in the region.

2 | Materials and Methods

2.1 | Sample Collection and Morphological Examinations

Fresh samples were collected in California and Illinois. From Illinois, the specimens were collected from the Morton Arboretum. From California, the specimens were collected from San Vicente Redwoods as well as from Central California by the western slope of the Sierra Nevada. All freshly collected specimens were deposited in the Larry F. Grand Mycological Herbarium (NCSLG). Herbarium specimens were evaluated from The US National Fungal Collections (BPI) and previously from the Florida Museum of Natural History (FLAS).

Morphological examinations were accomplished by using clear tape to adhere to an infected portion of leaf surface, carefully peeling off the tape and placing it onto a slide with a drop of 3% KOH solution. Photographs of the asexual morphs used for figures were taken with a Nikon Eclipse Ti2 compound microscope and a Nikon DS-Ri2 camera unit. Macroscopic photographs of the infected leaves were taken by phone or a Canon EOS 5D Mark II camera controlled by Capture One Pro software and with a Nikon SMZ1270 dissecting microscope with a Nikon DS-Ri2 camera unit.

2.2 | Sequencing

DNA extractions were performed using the Chelex method (Walsh et al. 1991; Hirata and Takamatsu 1996). Polymerase chain reaction (PCR) was used to amplify the ITS and LSU rDNA regions using the primer pairs PM10 (Bradshaw and Tobin 2020)/PM2 (Cunnington et al. 2003) for all specimens. If PCR was unsuccessful, a nested approach was applied using primers AITS/PM11 (Bradshaw and Tobin 2020) followed by PM10/PM2. PCR specifications were as follows for a 50 μL solution reaction: 35.7 μL molecular grade H_2O, 4 μL BSA (20 mg/mL), 1 μL of forward primer and 1 μL reverse primer at a 10 μM concentration, 2 μL of DNA, 5 μL of Buffer, 0.3 μL of TAQ DNA Polymerase (5 units per μl) and 1 μL dNTPs (10 mM). Cycling included initial denaturation at 95°C for 3 min followed by 40 cycles of denaturation at 95°C for 30 s, annealing at 53°C (AITS/PM11) or 58°C (PM10/PM2) for 1 min, and elongation at 72°C for 2 min and then a final elongation of 72°C for 10 min. DNA amplicons were sent to Genewiz (South Plainfield, New Jersey) to be purified and directly sequenced.

2.3 | Phylogenetic Analyses

Phylogenetic trees were generated from ITS+28S sequences. The taxa for the tree were chosen based on Bradshaw, Braun, Mitchell, et al. (2025). Sequences were aligned and edited using Geneious Prime 2025.0.3. A GTR+G+I evolutionary model was used for phylogenetic analyses as it is the most inclusive model of evolution and includes all other evolutionary models (Abadi

et al. 2019). The phylogeny was inferred using Bayesian analysis of the combined loci using a Yule tree prior (Gernhard 2008) and an uncorrelated lognormal relaxed clock, in the program BEAST version 1.10.4 (Suchard et al. 2018). A single MCMC chain of 10^7 steps was run with a burn-in of 25%. Posterior probabilities were calculated from the remaining 7500 sampled trees. A maximum likelihood analysis was accomplished using raxmlGUI (Silvestro and Michalak 2012) under the default settings with a GTR+G+I evolutionary model. The resulting ML tree was visualised using FigTree ver. 1.3.1 (Rambaut 2009). Bootstrap analyses were conducted using 1000 replications (Felsenstein 1985).

3 | Results

3.1 | Molecular, Phylogenetic and Morphological Analyses

All sequences aligned 100% with each other and with the ITS sequence from the type specimen of *E. quercicola* from GenBank (AB193591) as well as with multiple other *E. quercicola* sequences. All sequences were deposited in GenBank (Table 1). Only the anamorph of *E. quercicola* was observed on all the analysed specimens (Figures 1 and 2). A phylogenetic tree was constructed revealing all specimens sequenced fell into a highly supported clade in both the ML and Bayesian analyses with other *E. quercicola* sequences (Figure 3).

3.2 | Host Range and Distribution of *E. quercicola* in North America

The following host species of *E. quercicola* have been confirmed in the United States: *Notholithocarpus densiflorus* (Hook. & Arn.) (≡ *Quercus densiflorus*), California, 2023 (NCSLG24564), *Quercus agrifolia* Née, California, 2023 (NCSLG24548, NCSLG24549), *Quercus bicolor* Willd., Pennsylvania, 1944 (BPI859616) and 1949 (BPI859905), *Quercus gambelii* Nutt., Illinois, 2025 (NCSLG29705), *Quercus garryana* Douglas ex Hook., 2007 (NCSLG30623), *Quercus geminata* Small., Florida, 2018 (USF297880), *Quercus kelloggii* Newb., California, 2025 (NCSLG29954), *Quercus* × *jolonensis* Sarg., California, 2025 (NCSLG29929), *Quercus macrocarpa* Michx., Illinois, 2024 (NCSLG 29641, NCSLG 29642), *Q. robur* L., Washington State, 2018 (Bradshaw et al. 2022), *Quercus shumardii* Buckley, Florida, 1996 (FLAS-F-56236) and *M. indica* L., Florida, 1935 (FLAS-F-20906) (Bradshaw, Braun, Mitchell, et al. 2025; Bradshaw, Quijada, et al. 2025).

Unconfirmed exotic host records from the United States include *Bixa orellana* and *M. indica*, which were reported in the older literature under the anamorphic designation *Oidium* sp.

TABLE 1 | List of taxa, hosts, vouchers, collection localities, and GenBank accession numbers of the specimens examined in the current study.

Taxa	Host	Collection date	Collection locality	Voucher	ITS+28S GenBank no.
Erysiphe quercicola	*Mangifera indica*	1935	USA:Florida	FLAS-F-20906	PP680841
Erysiphe quercicola	*Notholithocarpus densiflorus*	2023	USA:California	NCSLG24564	PX722893
Erysiphe quercicola	*Quercus* × *jolonensis*	2025	USA:California	NCSLG29929	PX715354
Erysiphe quercicola	*Quercus agrifolia*	2023	USA:California	NCSLG24549	PX722894
Erysiphe quercicola	*Quercus agrifolia*	2023	USA:California	NCSLG24548	PX722895
Erysiphe quercicola	*Quercus agrifolia*	2022	Mexico	FH01131088	OR424960
Erysiphe quercicola	*Quercus bicolor*	1944	USA:Pennsylvania	BPI859616	PX722888
Erysiphe quercicola	*Quercus bicolor*	1949	USA:Pennsylvania	BPI859905	PX722889
Erysiphe quercicola	*Quercus gambelii*	2024	USA:Illinois	NCSLG29705	PZ048186
Erysiphe quercicola	*Quercus garryana*	2007	USA:Washington	NCSLG30623	PZ048187
Erysiphe quercicola	*Quercus geminata*	2018	USA:Florida	USF297880	PZ048188
Erysiphe quercicola	*Quercus kellogii*	2025	USA:California	NCSLG29954	PX722890
Erysiphe quercicola	*Quercus macrocarpa*	2024	USA:Illinois	NCSLG29641	PX722891
Erysiphe quercicola	*Quercus macrocarpa*	2024	USA:Illinois	NCSLG29642	PX722892
Erysiphe quercicola	*Quercus robur*	2018	USA:Washington	FH00941198	OM436188
Erysiphe quercicola	*Quercus shumardii*	1996	USA:Florida	FLAS-F-56236	OR424961
Erysiphe quercicola	*Quercus* sp.	2025	USA:California	NCSLG29925	PX993581
Erysiphe quercicola	*Quercus* sp.	2025	USA:California	NCSLG29921	PX993579
Erysiphe quercicola	*Quercus* sp.	2025	USA:California	NCSLG29927	PX993580

Abbreviations: BPI, U.S. National Fungus Collection; FH, Harvard University, Farlow Herbarium; FLAS, University of Florida Herbarium; NCSLG, North Carolina State University; USF, University of South Florida.

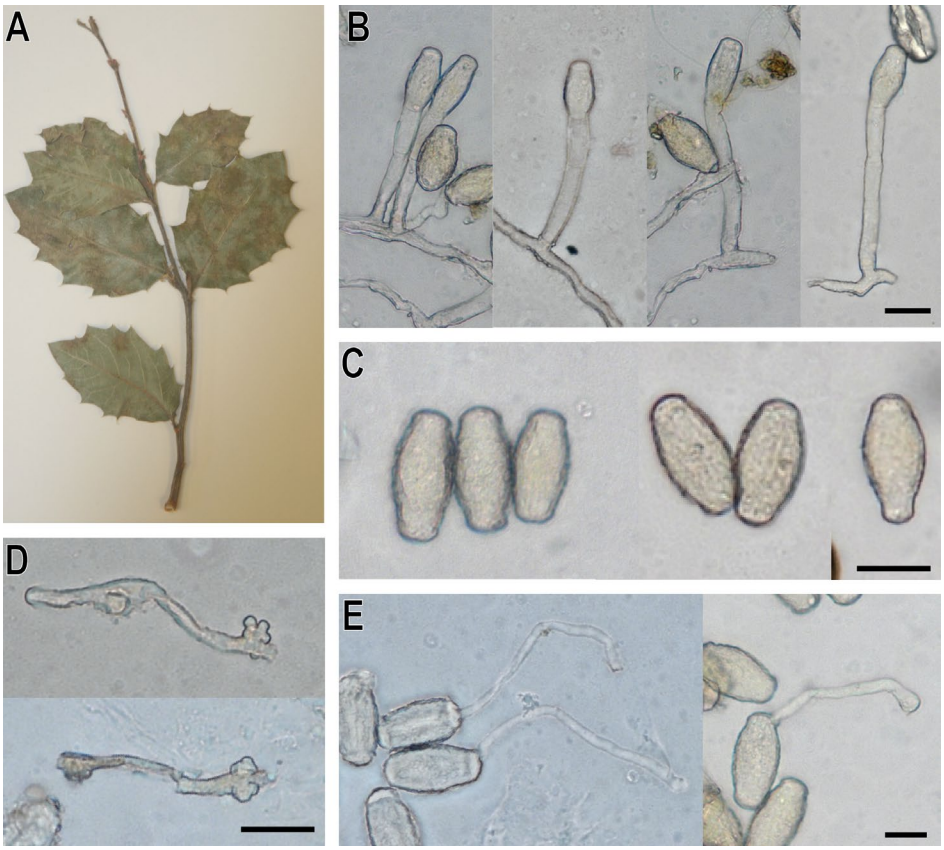


FIGURE 1 | Morphology of the asexual morph of *Erysiphe quercicola* from herbarium specimens: NCSLG24548, NCSLG24549 and NCSLG24564. (A) Infected leaves of *Quercus agrifolia*. (B) Conidiophores. (C) Conidia. (D) Lobed Hyphal Appressoria. (E) Conidia with Germ Tubes. Scale bars B–E = 20 μm.

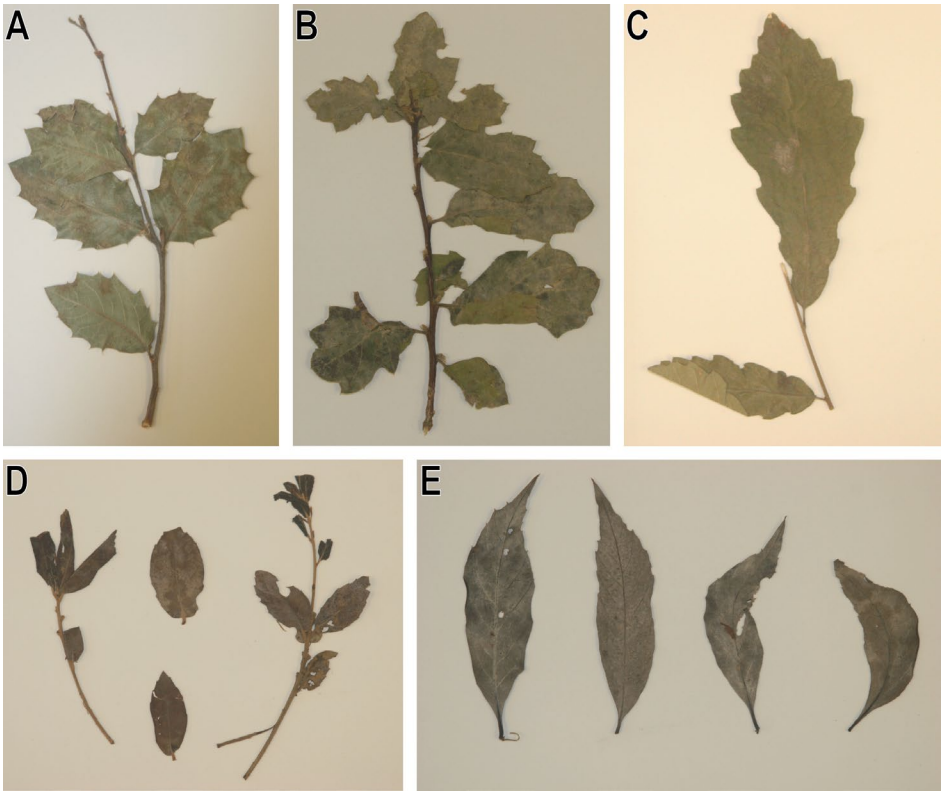


FIGURE 2 | Select *Quercus* species infected by *Erysiphe quercicola* at NCSLG. (A) *Quercus agrifolia*; NCSLG24548, (B) *Quercus* × *jolonensis*; NCSLG29929, (C) *Quercus crispula*; NCSLG26732, (D) *Quercus phillyreoides*; NCSLG26263 and (E) *Quercus glauca*; NCSLG26261.



FIGURE 3 | Maximum likelihood tree of the ITS+28S regions of *Erysiphe quercicola* specimens as well as other select, closely related, taxa. Fungal species are denoted and followed by the host, collection locality, and year collected in the case of the herbarium specimens. Type status (HT: holotype, NT: neotype and TS: type specimen) of the specimens concerned is denoted as well as reference sequences for phylogenetic purposes (RS). Posterior probabilities ≥90 are displayed followed by bootstrap values greater than 70 for the maximum likelihood (ML) analyses.

(Amano 1986; Campbell 1961). In subsequent taxonomic treatments, these records have been associated with the names *Oidium bixae* (on *B. orellana*) and *Oidium mangiferae* (on *M. indica*), both of which are now considered synonyms of *E. quercicola*. However, because these historical reports lack molecular data, their assignment to *E. quercicola* remains unconfirmed and requires sequencing-based verification.

Additional North American records derive from Mexico, including a sequencing-confirmed occurrence of *E. quercicola* on *Q. agrifolia* from Puebla (FH01131088). Furthermore, several reports document *E. quercicola* on cultivated hosts in Mexico, including *Citrus* × *limon* (Yáñez-Morales et al. 2009), *M. indica* (Arias et al. 2004; Félix-Gastélum et al. 2013; Pérez-Rodríguez et al. 2018), and *Tamarindus indicus* (Yáñez-Morales et al. 2008, 2009).

3.3 | *Erysiphe quercicola* Worldwide—An Overview of the Current State of Knowledge

Erysiphe quercicola S. Takam. & U. Braun, Mycol. Res. **111**: 819, 2007, nom. cons. [against *Oidium anacardii* Noack; Braun 2013].

= *Oidium anacardii* F. Noack, Bol. Inst. Estado São Paulo **9**(2): 77, 1898.

≡ *Pseudoidium anacardii* (F. Noack) U. Braun & R.T.A. Cook, Taxonomic Manual of the Erysiphales (Powdery Mildews): 497, 2012.

= *Oidium mangiferae* Berthet, Bol. Agric. (São Paulo) **15**: 818, 1914.

≡ *Acrosporium mangiferae* (Berthet) Subram., Hyphomycetes (New Delhi): 834, 1971.

≡ *Oidium erysiphoides* f. *mangiferae* (Berthet) J.M. Yen & Chin C. Wang, Rev. Mycol., Paris **37**(3): 138 "1972" 1973.

= *Erysiphe cinnamomi* Sawada, Rep. Dept Agric., Govern. Res. Inst. Formosa, Spec. Bull. Agric. Exp. Station Formosa **19**: 144, 1919.

≡ *Pseudoidium cinnamomi* (Sawada) U. Braun & R.T.A. Cook, Taxonomic Manual of the Erysiphales (Powdery Mildews): 601, 2012.

= *O. bixae* Viégas, Bragantia **4**(1–6): 19, 1944.

= *Oidium erysiphoides* f. *peltophori* J.M. Yen, Revue Mycol., Paris **31**(4): 289, 1966.

≡ *Oidium peltophori* (J.M. Yen) Boesew. Bot. Rev. **42**(2): 172, 1980.

≡ *Pseudoidium peltophori* (J.M. Yen) U. Braun & R.T.A. Cook, Taxonomic Manual of the Erysiphales (Powdery Mildews): 615, 2012.

= *Oidium erysiphoides* f. *tamarindi* J.M. Yen, Revue Mycol., Paris **31**(4): 294, 1966.

≡ *Oidium tamarindi* (J.M. Yen) U. Braun, Zentralbl. Mikrobiol. **137**: 323, 1982.

≡ *Pseudoidium tamarindi* (J.M. Yen) U. Braun & R.T.A. Cook, Taxonomic Manual of the Erysiphales (Powdery Mildews): 619, 2012.

= *Oidium erysiphoides* f. *bixae* J.M. Yen, Cah. Pacifique **11**: 88, 1967.

= *Oidium erysiphoides* f. *cinnamomi* J.M. Yen, Cahiers Pacif. **11**: 96, 1967.

≡ *Oidium cinnamomi* (J.M. Yen) U. Braun, Mycotaxon **25**(1): 266, 1986.

= *Oidium erysiphoides* f. *citri* J.M. Yen, Cah. Pacifique **11**: 99, 1967.

≡ *Oidium citri* (J.M. Yen) U. Braun, Zentralbl. Mikrobiol. **137**: 323, 1982.

= *Oidium nephelii* Hadiw. ex U. Braun, Mycotaxon **25**: 267, 1986.

≡ *Pseudoidium nephelii* (Hadiw. ex U. Braun) U. Braun & R.T.A. Cook, Taxonomic Manual of the Erysiphales (Powdery Mildews): 613, 2012.

Oidium nephelii Hadiw., Landbouw (Landbouwkundig maandblad voor Indonesié) **22**(5–6): 253 (1950), nom. inval. (Art. 39.1, Madrid).

Oidium erysiphoides f. *nephelii* J.M. Yen [as "(Hadiw.) J.M. Yen"], Rev. Mycol. **31**(4): 286, 1966, nom. inval. (Art. 39.1, Madrid).

Host range and distribution: Almost circumglobal (Africa, Asia, Australia, Europe, North and South America, West Indies, Oceania). **Anacardiaceae**—*Anacardium occidentale* [Africa, Malawi (Anonymous 1990), Mozambique (Caligari 1997), Tanzania (Amano 1986), South Africa (Swart 2004); Asia, India (Amano 1986); South America, Brazil (Amano 1986; Freire et al. 2002; Cardoso et al. 2017), Panama (Braun 2013); West Indies, Puerto Rico (Amano 1986)]; *M. indica* [Africa, Angola, Congo, Egypt, Ethiopia, Kenya, Madagascar, Malawi, Mauretania, South Africa, Tanzania, Zambia, Zimbabwe (Amano 1986; Iqbal et al. 2024); Asia, Bangladesh, India, Iran, Israel, Japan, Lebanon, Myanmar, Nepal, Pakistan, Sri Lanka, Taiwan, Turkey, Vietnam, Yemen (Amano 1986; Tam 2017; Adhikari 2022; Iqbal et al. 2024; Ajitomi et al. 2020), Laos (PDD 48035); Australia (Amano 1986; Kiss et al. 2020; Iqbal et al. 2024); Europe, Spain (Desprez-Loustau et al. 2018); North America, Mexico (Félix-Gastélum et al. 2013; Pérez-Rodríguez et al. 2018), USA, Florida, California (Amano 1986; Iqbal et al. 2024); West Indies, Barbados, Cuba, Jamaica (Amano 1986; Iqbal et al. 2024); South America, Brazil, Colombia, Costa Rica, Guatemala, Guyana, Honduras, Paraguay, Peru, Colombia, Venezuela (Ribeiro De Oliveira Pinto et al. 2016; Iqbal et al. 2024)]; Oceania, New Caledonia (Amano 1986), Hawaii (Nelson 2008); **Bixaceae**—*B. orellana* [Africa, Kenya, Malawi, Uganda (Amano 1986); Asia, India, Taiwan (Amano 1986; Yeh and Kirschner 2025); North America, USA? (Amano 1986, as *Oidium* sp.); South America, Brazil, Venezuela (Amano 1986; Fonseca, Cardoso, Viana, et al. 2019), El Salvador (BPI409331); West Indies (Jamaica, Puerto Rico; Amano 1986)]; **Cucurbitaceae**—*Hodgsonia macrocarpa* [Asia, Thailand (Meeboon and Takamatsu 2020)]; **Euphorbiaceae**—*Hevea brasiliensis* [Asia, China (He et al. 2025), Thailand (Meeboon and Takamatsu 2020), Vietnam (Tam, Cuong, et al. 2016)]; *Jatropha curcas* [Asia, China (Zhao et al. 2019), Thailand (Meeboon and Takamatsu 2020)]; *Mallotus philippensis* [Asia, Thailand (Meeboon and Takamatsu 2020)]; **Fabaceae**—*Acacia auriculiformis* [Asia, India (Thite et al. 2017)], *A. holosericea* [Australia (Kiss et al. 2020)], *A. mangium* [Australia (Kiss et al. 2020)]; *Cassia fistula* [Asia, India, Singapore (Braun and Cook 2012), Thailand (Meeboon and Takamatsu 2020)]; *Clitoria fairchildiana* [South America, Brazil (Fonseca, Cardoso, Ootani, et al. 2019)]; *Mimosa pudica* [Asia, Thailand (Meeboon and Takamatsu 2020)]; *Peltophorum pterocarpum* [Asia, India, Singapore (Braun and Cook 2012), Taiwan (Yeh and Kirschner 2024)]; *Tamarindus indica* [Asia, Taiwan (Yeh et al. 2025), Thailand (Meeboon and Takamatsu 2020); South America, Brazil (Azevedo Silva et al. 2021)]; **Fagaceae**—*Castanopsis argyrophylla* [Asia, Thailand (Meeboon and Takamatsu 2020)]; *Notholithocarpus densiflorus* (≡ *Q. densiflorus*) [North America, USA, California, present study]; *Q. agrifolia* [North America, Mexico (Bradshaw, Braun, Németh, et al. 2025), USA, California, present study], *Q. baloot* [Asia, Pakistan (Afshan et al. 2022)], *Q. bicolor* [North America, USA, Pennsylvania, present study]; *Q. cerris* [Asia, Turkey; Europe, Bulgaria (Desprez-Loustau et al. 2018)], *Q. coccinea* (= *Q. calliprinos*) [Asia, Israel (Desprez-Loustau et al. 2018)], *Q. crispula* [Asia, Japan (Takamatsu et al. 2007)], *Q. gambelii* [North America, USA, Illinois, present study]; *Q. garryana* [North America, USA, Washington State, present study]; *Q. geminata* [North America, USA, Florida, present study]; *Q. glauca* [Asia, Japan (Takamatsu et al. 2018)], *Q. guyavifolia* [Asia, China (Zhang et al. 2024)], *Q. infectoria* [Europe, Slovakia (Desprez-Loustau et al. 2018)], *Q. infectoria* subsp. *veneris* (= *Q. boissieri*) [Asia, Israel (Desprez-Loustau et al. 2018)], *Q. ithaburensis* [Asia, Israel, Turkey (Desprez-Loustau et al. 2018)], *Q. kelloggii* [North America, USA, California, present study], *Q. macranthera* [Caucasus, Armenia (Desprez-Loustau et al. 2018)], *Q. macrocarpa* [North America, USA, Illinois, present study], *Q. mongolica* [Asia, China (Qiu et al. 2017), South Korea (Lee and Nguyen 2017)], *Q. myrsinifolia* [Asia, Japan (Takamatsu et al. 2018)], *Q. petraea* [Europe, France (Desprez-Loustau et al. 2018)], *Q. phillyreoides* [Asia, Japan, South Korea (Takamatsu et al. 2007; Lee et al. 2011)], *Q. pubescens* (= *Q. virgiliana*) [Europe, France, Slovakia (Desprez-Loustau et al. 2018)], *Q. pyrenaica* [Europe, Portugal, Spain (Desprez-Loustau et al. 2018)], *Q. robur* [Australia (Kiss et al. 2020);

Europe, Bulgaria, France, Portugal, Spain (Desprez-Loustau et al. 2018); North America, Washington State (Bradshaw et al. 2022); South America, Brazil (Piveta et al. 2018)], *Q. serrata* [Asia, Japan (Takamatsu et al. 2007)], *Q. shumardii* [North America, USA, Florida (Bradshaw, Ivors, et al. 2025)], *Q. vulcanica* [Asia, Turkey (Desprez-Loustau et al. 2018)], *Quercus* sp. [Asia, Iran, Thailand (Takamatsu et al. 2007, Desprez-Loustau et al. 2018); Australia (Takamatsu et al. 2007; Kiss et al. 2020); Europe, Hungary, Sweden (Desprez-Loustau et al. 2018)]; **Lauraceae**—*Camphora officinarum* (≡ *Cinnamomum camphora*) [Asia, Taiwan (Yeh and Kirschner 2025); South America, Brazil (Dorneles et al. 2018)]; **Malvaceae**—*Cullenia ceylanica* (= *Durio zibethinus*) [Asia, Thailand (Meeboon and Takamatsu 2020)]; *Kydia calycina* [Asia, Thailand (Meeboon and Takamatsu 2020)]; **Myrtaceae**—*Eucalyptus camaldulensis* [Australia (Kiss et al. 2020)], **Rhamnaceae**—*Ziziphus jujuba* [Asia, Thailand (Meeboon and Takamatsu 2020)]; **Rutaceae**—*Citrus* × *limon* [North America, Mexico (Yáñez-Morales et al. 2008)], *C. reticulata* [Asia, Vietnam (Tam, Dung, and Liem 2016)], *Citrus* sp. [Asia, Taiwan (Yeh and Kirschner 2025)]; *Murraya paniculata* [Asia, India (Banerjee and Pandey 2024), Taiwan (Yeh and Kirschner 2025)]; **Sapindaceae**—*Lepisanthes rubiginosa* (≡ *Erioglossum rubiginosum*) [Asia, China (Zhang et al. 2026)] and *Nephelium lappaceum* [Asia, Brunei, India, Malaysia, Singapore (Amano 1986), Thailand (Amano 1986; Meeboon and Takamatsu 2020)].

Notes: *Erysiphe quercicola* is probably much more widespread on some of the proven host species, such as *T. indicus*, listed in Amano (1986) as host of *Oidium* sp. from Ghana, India, Indonesia (Java), Malaysia, South Africa, and Sri Lanka. There is also a report of *E. quercicola* on *Rumex crispus* (*Polygonaceae*) from Brazil by Dorneles et al. (2019). The authors conducted sequencing and Koch's postulates to confirm their finding. To date, no other confirmed records of *E. quercicola* are known from *Polygonaceae*. It should be noted that *E. quercicola* has not yet been conserved against all older heterotypic synonyms, especially since, over time, more and more anamorph-typified names have emerged as synonyms for *E. quercicola*, and further names are likely to be added. Several earlier names remain nomenclaturally available and therefore continue to compete with *E. quercicola*. Therefore, maintaining the teleomorph-typified name *E. quercicola* for this important powdery mildew requires formal nomenclatural action in terms of conservation (Art. 14) or better protection (Art. F.2.1, Madrid Code).

4 | Discussion

Despite the steadily increasing number of publications on *E. quercicola* since its description by Takamatsu et al. (2007), relatively little was known about the host range and distribution of this species in North America until recently. Prior to molecular confirmation, reports from the United States were limited to *O. anacardii* (a synonym of *E. quercicola*) on *Anacardium occidentale* (Amano 1986; Iqbal et al. 2024), and *Oidium* sp., likely *O. bixae* (Amano 1986). The first sequencing-confirmed reports of *E. quercicola* infecting oak trees in North America were published by Bradshaw et al. (2022); Bradshaw, Ivors, et al. (2025); Bradshaw, Braun, Németh, et al. (2025). The present study adds further native host species, substantially expanding current knowledge of the host range and distribution of *E. quercicola* in the United States. With the exception of *Q. robur*, all oak species confirmed here as hosts are native to North America. These hosts span a broad phylogenetic range within *Quercus*, including species of *Quercus* subgen. *Quercus*, sect. *Quercus* (*Q. bicolor*, *Q. gambelii*, *Q. garryana*, *Q. macrocarpa*, *Q. robur*), sect. *Virentes* (*Q. geminata*) and sect. *Lobatae* (*Q. agrifolia*, *Q. kelloggii*, *Q. shumardii*).

The expanded host range and distribution documented here reinforce the view of *E. quercicola* as a nearly circumglobal species, with confirmed records from Africa, Asia, Australia, Europe, North and South America, the West Indies and Oceania. At present, 49 host species representing 22 genera and 12 plant families are known. Although all hosts are dicotyledonous, they span a wide taxonomic breadth, including *Cucurbitales* (*Cucurbitaceae*), *Fabales* (*Fabaceae*), *Fagales* (*Fagaceae*), *Laurales* (*Lauraceae*), *Malpighiales* (*Euphorbiaceae*), *Malvales* (*Bixaceae*, *Malvaceae*), *Myrtales* (*Myrtaceae*), *Rosales* (*Rhamnaceae*) and *Sapindales* (*Anacardiaceae*, *Rutaceae*, *Sapindaceae*), highlighting the exceptional host breadth of *E. quercicola* as a plant pathogenic fungus.

The observation that *E. quercicola* in North America is currently known only from the anamorphic stage provides evidence that is consistent with an introduced pathogen. Similar patterns have been documented for other powdery mildew invasions, where early populations are dominated by asexual reproduction following introduction, with sexual reproduction emerging only after the arrival of compatible mating types (Cooper et al. 2015; Sawant et al. 2015). A comparable phenomenon was recently documented for powdery mildews infecting blueberry, in which a North American native species spread throughout the world and has only been detected in its anamorphic form (Bradshaw, Ivors, et al. 2025; Bradshaw, Braun, Németh, et al. 2025; Bradshaw, Braun, Mitchell, et al. 2025; Bradshaw, Quijada, et al. 2025). In the present case, the absence of chasmothecia in North American collections of *E. quercicola* is consistent with the introduction of a single mating type, although alternative explanations, such as host-specific constraints or regional climatic conditions limiting sexual reproduction, cannot be ruled out at this time and require further research.

Powdery mildew infecting mango was first noted in the nineteenth century as *Erysiphe* on mango leaves in a brief horticultural report by Berkeley (1874), published in the British journal *The Gardener's Chronicle*. Although this early account establishes mango as a host, it did not specify a locality, and there is no evidence that the observation originated from North America. To the best of our knowledge, the earliest vouchered North American record associated with mango derives from Florida in 1934 (BPI 409638), with additional early records from California dating to 1944 (BPI 409640). An earlier Florida record of *Oidium tingitaninum* on *Citrus nobilis* from 1912 (BPI 409785) could potentially correspond to *E. quercicola*; however, sequencing failed on this specimen. Outside North America, the earliest known vouchered specimen of mango powdery mildew is from Brazil in 1931 (MICH 326559). Phylogenetic analyses consistently place *E. quercicola* close to other oak-associated *Erysiphe* species (Takamatsu et al. 2007; Desprez-Loustau et al. 2018; Bradshaw, Braun, Németh, et al. 2025; Bradshaw,

Braun, Mitchell, et al. 2025). Taken together, these records are consistent with the hypothesis that *E. quercicola* was historically associated with oak hosts, subsequently shifted to mango and potentially citrus in cultivated systems, and then spread globally via human-mediated movement.

An important outcome of this study is the clarification of the temporal presence of *E. quercicola* in North America using molecular data. Sequencing of herbarium specimens demonstrates that the species has been present on *Quercus* in the United States since at least 1944, substantially predating its formal recognition on oaks by Bradshaw et al. (2022). Moreover, sequence-confirmed records from *M. indica* indicate that *E. quercicola* was present in Florida by at least 1935. Together, these findings indicate a prolonged period of undetected establishment in North America. We hypothesize that *E. quercicola* may have been introduced into North America via cultivated mangos or citrus, followed by subsequent host shifts to native *Quercus* species, where the pathogen is now widespread across multiple regions of the United States. Experimental evidence suggests that powdery mildews associated with *Quercus* and mango can be cross-inoculated under controlled conditions (Desprez-Loustau et al. 2017; Ajitomi et al. 2020). However, artificial inoculations may not accurately reflect natural host associations and can yield atypical outcomes. Consequently, future multilocus and whole-genome analyses, combined with natural host range assessments, will be necessary to determine whether *E. quercicola* represents a single species with an unusually broad host range or a complex of closely related, host-associated lineages.

A further unresolved question concerns the geographic origin of *E. quercicola*. As emphasised by Desprez-Loustau et al. (2018), this issue cannot yet be answered. Although early reports suggested possible origins in the Indian subcontinent or Brazil (Nelson 2008; Briton Jones 1923), such interpretations are inherently uncertain, as initial disease observations are often opportunistic and frequently associated with cultivated hosts. Phylogenetic studies consistently place *E. quercicola* and *E. alphitoides* phylogenetically close to each other (Takamatsu et al. 2007; Desprez-Loustau et al. 2018; Bradshaw, Braun, Németh, et al. 2025; Bradshaw, Braun, Mitchell, et al. 2025). *Erysiphe alphitoides* is generally considered an oak-associated species introduced to Europe from East Asia, and herbarium evidence indicates that *E. quercicola* was present in Europe prior to *E. alphitoides* (Bradshaw et al. 2022; Gross et al. 2021). The close phylogenetic relationship between these species, coupled with the strong association of *E. alphitoides* with oaks, suggests that East Asia, with *Quercus* spp. as principal hosts, may represent a plausible region of origin for *E. quercicola*. Similar to *E. alphitoides*, *E. quercicola* shows a pronounced tendency to infect hosts beyond oaks, including hosts outside the *Fagaceae* (Takamatsu et al. 2007; Braun and Cook 2012; Bradshaw, Braun, Németh, et al. 2025), underscoring the need for additional phylogenetic and molecular clock analyses to robustly address questions of origin and evolutionary history.

Future research should focus on multilocus and whole-genome analyses, mating-type characterisation, and population-level sampling across the global range of *E. quercicola* to better resolve patterns of spread, host association, and origin. Such efforts will be essential for distinguishing between a single species with an exceptionally broad host range and a complex of closely related, host-associated lineages. More broadly, this study underscores the importance of herbarium specimens as long-term archives for reconstructing invasion histories, revealing cryptic introductions, and refining our understanding of the temporal and geographic dynamics of emerging plant pathogens.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in GenBank at https://www.ncbi.nlm.nih.gov/genbank/, reference number (see Table 1).

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