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Powdery mildew infection of neem in the Dominican Republic; another tropical host of *Erysiphe necator*

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Summary. This study identified the causative agent of powdery mildew on *Azadirachta indica* (*Sapindales, Meliaceae*) in the Dominican Republic, using molecular phylogenetic analysis of internal transcribed spacer (ITS) and large subunit (LSU) sequences of rDNA, and morphological examinations. The infection was caused by *Erysiphe necator*, a pathogen primarily associated with *Vitis* spp. Together with other recent reports of *E. necator* on different host plants in Brazil, the host range of this pathogen has been expanded in tropical regions of Central America and the Caribbean region.

Keywords. Erysiphales, *Azadirachta indica*, host range expansion, phylogenetic analysis.

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INTRODUCTION

Azadirachta indica A. Juss., (*Meliaceae*), commonly known as neem, margosa, nimtree, or Indian lilac, is an evergreen tree, whose native range is Assam to Indo-China, but is naturalized and grown in tropical and subtropical regions, including the Dominican Republic (POWO, 2025). Neem is valued for its ecological resilience, and for its medicinal and pesticidal properties, including antibacterial, antiviral, antifungal, anti-inflammatory, and antioxidant effects. In medicine, neem is used to treat illnesses including eye disorders, nose bleeding, loss of appetite, and liver problems. Because of its various pharmacological and therapeutic effects, neem is included in the Ayurvedic pharmacopoeia and cosmetic industry (Gupta *et al.*, 2017; Gautam and Mittal, 2021). Active substances in neem, including azadirachtin,

nimbin, nimbidin, and gedunin, have strong biological effects on range of pathogens and insect pests, making extracts from this plant important natural pesticides in sustainable agriculture (Koul *et al*., 1990; Bailey *et al*., 2010). In recent decades, interest in neem has increased in Asia, Europe, and North America, where its potential as an ecological alternative to synthetic chemicals in medicine and plant protection is being explored (Singh *et al*., 2010; Tufail *et al*., 2025).

Powdery mildews (Erysiphaceae) are an internationally widespread group of biotrophic plant pathogens with approx. 10,000 known Angiosperm host species (Braun and Cook, 2012). Powdery mildews are typically associated with their hosts, with which they are co-evolutionarily related, and they differ in the level of specificity. Species can be distinguished by their narrow host ranges – one host genus or species (monophagous), or species with host ranges covering entire plant families (oligophagous), as well as species with host ranges including numerous plant families (polyphagous) (Lebeda *et al*., 2017).

Braun and Cook (2012) showed that *Erysiphe necator* (previously *Uncinula necator*) has a narrow host range, including only some Vitaceae. These authors distinguished two varieties: var. *necator* with a host range including various species Vitaceae, mainly *Vitis* and *Cissus*, but also *Ampelopsis glandulosa* var. *heterophylla* with circumglobal distribution; and var. *ampelopsidis* with a host range confined to *Parthenocissus* (*cuspidifera, quinquefolia, tricuspidata, vitacea*, Vitaceae) occurring in North America (Canada, United States of America). The second variety differs from var. *necator* in having shorter, stiff chasmothecial appendages, that have appendages that are approx. 2 times (0.75 to 2.5) their chasmothecial diameters. Based on obvious morphological and genetic differences, distinguished using sequence analyses, Bradshaw *et al.* (2023) introduced the new combination *Erysiphe ampelopsidis*, as a species separate from *E. necator.*

Later studies confirmed occurrence of *E. necator* also on *Cissus rhombifolia* (Cho *et al*., 2012), *Caryocar brasiliense* (Caryocaraceae), and *Carica papaya* (Caricaceae) (Braun *et al*., 2017; Seress *et al.,* 2021); cashew (*Anacardium occidentale*) (Fonseca *et al*., 2019); and rubber tree (*Hevea brasiliensis*) (Pieroni *et al*., 2020). These infections have been seen mainly in Brazil, but also in Hawaii, and indicate adaptation of *E. necator* to new hosts. This supports the assumption of Braun *et al.* (2017), that the important and widespread grapevine powdery mildew can cause infections on unrelated hosts, and raises epidemiological questions.

Powdery mildew infecting *Azadirachta indica* was mentioned by Braun and Cook (2012) as *Pseudoidium azadirachtae*. This species was recorded in Africa (Niger) and Asia (India, Pakistan). Recently, Jayalakshmi *et al.* (2024) confirmed the occurrence of *Ps. azadirachtae* on *A. indica* in Pune, Maharashtra (India). In their study, however, only microscopical observation of the anamorph stage was reported. These authors also mentioned previous records of powdery mildew on neem in Bangladesh (Mridha *et al*., 2005), and in Tamil Nadu (India) (Narayanaswamy and Ramakrishnan, 1969). However, the specific identities of the powdery mildews involved cannot be verified in these cases, due to lack of sequence data.

Problems with identifying powdery mildew anamorphs on *Azadirachta* are further exacerbated by apparent occurrences of several species. Wagh *et al.* (2024) confirmed the identity of an Indian specimen as *Erysiphe aquilegiae* (*s. lat.*), using sequencing. However, the conidium length of 35 to 48 µm in the Indian collection (Wagh *et al*., 2024), did not agree with the description given for *Ps. azadirachtae* by Braun and Cook (2012), that is, conidia (22–)25–34.5 µm long. As with other groups of organisms, molecular biology methods have influenced methodological approaches in fungus identification, and in phylogenetic analyses of relationships between taxa. Standardized genomic DNA regions are available for molecular identifications of fungi. Sequence determination of the internal transcribed spacer (ITS) region of nuclear ribosomal DNA (nrDNA) has proven to be the most useful for identification of powdery mildews at the species level (e.g. Braun *et al*., 2002; 2019; Kelly *et al*., 2025; Yeh *et al*., 2025), while sequences of the 18S and 28S nrDNA regions have supported identifications and classification of genera (Marmolejo *et al*., 2018; Křivánková *et al*., 2025). Although other DNA regions have also been tested as molecular barcodes (Inuma *et al*., 2007; Pirondi *et al*., 2016; Ellingham *et al*., 2019; Qiu *et al*., 2020), the use of ITS sequences is still considered to be the standard for species-level DNA barcoding available for this fungal group (e.g., Kiss *et al*., 2020; Kelly *et al*., 2025), although ITS does not provide sufficient resolution at species level for some complexes of closely related powdery mildew species. For these, sequencing of additional loci is necessary, as in the case of the *Erysiphe alphitoides* complex (Bradshaw *et al*., 2025a), and for North America oak powdery mildews (Bradshaw *et al*., 2025b).

The aim of the present study was to carry out a precise morphological and molecular study of neem powdery mildew found in the Dominican Republic, and to increase knowledge of the host range of *E. necator* in tropical regions.

MATERIAL AND METHODS

Plant material and sampling

Leaves of *Azadirachta indica* (*Meliaceae*) exhibiting typical powdery mildew symptoms were collected on March 20, 2024, at the Dr. Rafael Ma. Moscoso National Botanical Garden, Santo Domingo, Dominican Republic (18°29.8512′ N, 69°57.3432′ W; 86 m a.s.l.; collector, Kitner, sample ID M17). A voucher specimen was deposited in the OL herbarium (Department of Botany, Palacký University, Olomouc, Czech Republic).

Microscopy and morphology

Leaf fragments (approx. 20 × 20 mm) were processed following the modified method of Shin (2000). Infected tissues were stained with lacto-fuchsin solution to visualize fungal structures, and presence of fibrosin bodies was checked using 3% KOH (Lebeda, 1983). Microscope examinations were carried out using an Olympus BX60 light microscope at 400× magnification. Only asexual morphs were developed on the leaf fragments.

Morphological traits included conidium length, width, and shape index, conidiophore length, foot cell length, number of distal cells, presence or absence of fibrosin bodies, and conidium germination pattern. Thirty conidia and 20 conidiophores were measured per sample (due to limited availability). Digital micrographs were captured using an Olympus BX60 light microscope equipped with an Olympus DP72 CCD digital camera, and measurements were carried out manually using an ocular micrometer.

Statistical analysis

Descriptive statistics (mean, standard deviation, range) were calculated for each trait using MS Excel 2010. To assess morphological similarity, the obtained values were compared with previously published data (Braun and Cook, 2012) for *Erysiphe necator* on other hosts.

Molecular identification

For molecular identification of the pathogen, the complete ITS and partial 28S regions (D1 and D2 domains) of rDNA were sequenced. For amplification of the ITS region, the powdery mildew-specific PMITS1/PMITS2 primers were used (first PCR; Cunnington *et al*., 2003), and ITS1-F/ITS4 primers (second PCR; Gardes and Bruns, 1993; White *et al*., 1990). Amplification of D1/D2 domains of the 28S rDNA was carried out according to Takamatsu *et al*. (2013), using primer sets PM3/TW14 and NL1/TW14 for the two nested PCR runs. The description of the preparation of PCR mixes and PCR conditions for both loci is described in detail elsewhere (Lebeda *et al*., 2019).

The PCR products were visualized on agarose gel, purified using an enzymatic purification protocol (Kim and Blackshaw, 2001), and were bidirectionally sequenced by Macrogen Europe (Amsterdam), and assembled in Geneious 7.1.7 (Kearse *et al*., 2012). The resulting sequences were deposited in the NCBI nucleotide database (https://www.ncbi.nlm.nih.gov/) under accession numbers PX397430 and PX397429, and their taxonomic identity was verified by BLASTn against GenBank.

For phylogenetic reconstruction, sequences from both sequenced regions of the M17 sample were concatenated. Furthermore, *Erysiphe* sequences containing both ITS and 28S regions, with *Golovinomyces bolayi* as outgroup, were downloaded from GenBank (Supplementary Table 1).

Multiple sequence alignment was generated using MAFFT v.7 (Katoh *et al*., 2019), and is provided as Supplementary data 1. Maximum Likelihood (ML) phylogenetic trees were reconstructed with RAxML (Stamatakis, 2014). The optimum substitution model was automatically selected by ModelFinder (Kalyaanamoorthy *et al*., 2017), implemented in IQ-TREE (Nguyen *et al*., 2015; Trifinopoulos *et al*., 2016) under the Bayesian Information Criterion (BIC). Branch support values were estimated using the ultrafast bootstrap approximation (Hoang *et al*., 2018), with 1000 replicates. For graphical presentation of the phylogenetic analyses, Bayesian Analysis (BA) was carried out in MrBayes 3.2.6 (Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003), implemented in Geneious 7.1.7. BA, and was performed under the General Time Reversible model, run for 3 M generations, sampled every 1000th generation, and 3000 trees were discarded as burn-in. All other settings were set as the default. The resulting phylogenetic tree was graphically adjusted in MS Word, where posterior probabilities (≥ 0.7) and bootstrap support values (≥ 70 %) were displayed on the main nodes.

RESULTS

Morphological characteristics

Microscope examination of the powdery mildew on the *Azadirachta indica* specimen (isolate M17) revealed hyaline, superficial mycelium with typical *Erysiphe*-like asexual structures. Conidiophores of the *Pseudoidium* type had mean length 68.5 ± 10.0 µm (range 46.4 to 80.5

Table 1. Comparative morphological characteristics of *Erysiphe necator* and *Pseudoidium azadirachtae* reported from *Azadirachta indica*, including comparison of parameters obtained in the present study (*E. necator* M17) with data from Braun and Cook (2012).

Parameter	*E. necator* M17	*E. necator*	*P. azadirachtae*
Conidiophore length (µm)	68.5 ± 10.0 (46.4–80.5)	40.0–400.0	50.0–75.0
Foot-cell length (µm)	32.2 ± 2.9 (29.3–36.6)	25.0–160.0	35.0–55.0 × 7.5–11.0
Distal cells per conidiophore	1.9 ± 0.7 (1–3)	–	1(–2)
Conidial length (µm)	28.5 ± 2.8 (24.4–34.2)	22.5–48.0	(22.0–)25.0–34.5
Conidial width (µm)	12.5 ± 1.2 (9.8–17.1)	12.2	11.0–19.0
Conidial shape index (L/W)	2.29 ± 0.31	2.29	–
Host range and distribution		cosmopolitan, mainly *Vitis* spp. (also *Carica*, *Caryocar*)	*A. indica* only; Africa (Niger), Asia (India, Pakistan)

µm), and had foot cells averaging 32.2 ± 2.9 µm (range 29.3–36.6 µm). The number of distal cells per conidiophore averaged 1.9 ± 0.7 (range 1 to 3). Conidia were cylindrical-ovoid, 28.5 ± 2.8 µm long (range 24.4 to 34.2 µm) and 12.5 ± 1.2 µm wide (range 9.8 to 17.1 µm), yielding a mean length-to-width ratio (shape index) of 2.29 ± 0.31 (Table 1).

Conidium germination occurred via single germ tubes emerging from conidium ends. Presence of fibrosin bodies was not observed, and no chasmothecia were formed even on heavily infected *A. indica* leaves (Figure 1).

Molecular identification

Sequencing of both genomic regions resulted in identical, high-quality electrophoretograms, allowing reliable molecular identification of the powdery mildew infections on *Azadirachta indica*. The ITS region sequencing results of sample M17 were subjected to BLASTn search against the GenBank nucleotide database, and this showed 100% identity with twenty published ITS powdery mildew records from various hosts and countries (Supplementary Table 2). These are: *Vitis vinifera* (Azerbaijan, Canada, France, Hungary, Israel, Mexico, New Zealand, Pakistan, Taiwan, Thailand, United States of America: Abasova *et al*., 2018; Bradshaw *et al*., 2023; Brewer and Milgroom, 2010; Cooper *et al*., 2015; Gregorio-Cipriano *et al*., 2026; Gul *et al*., 2025; Gur *et al*., 2021; Hsiao *et al*., 2022; Jaswa *et al*., 2026; LaGreca *et al*., 2025; Meeboon and Takamatsu, 2017; Péros *et al*., 2005; Pintye *et al*., 2023; Sholberg *et al*., 2005); *V. coignetiae* (Japan; Takamatsu *et al*., 2015); *V. flexuosa* (South Korea, Park *et al*., 2026); *Caryocar brasiliense* (Brazil; Braun *et al*., 2017); and *Carica papaya* (Hungary; Seress *et al*., 2021). The record from the United States of America by Brewer and Milgroom (2010) on *Vitis vinifera* (acc. no. GQ255473) represents the *E. necator* haplotype, which those authors also identified on *V. aestivalis*, *V. labrusca*, *V. riparia* and *V. rotundifolia*, From the 28S region comparison, greatest similarity (99.88%) was found in three published records of *E. necator* infections on *V. vinifera* in Mexico (Marmolejo *et al*., 2018) and *V. flexuosa* in South Korea (Park *et al*., 2026).

To verify the taxonomic status of the sample analyzed in the present study, its position relative to other representative Erysiphales, a phylogenetic tree was constructed using Genbank records containing ITS and 28S regions. From the list of identical ITS sequences listed above, only the complete acc. nos. LC777882, LC028995 and LC028996 could be used, which were derived from *Vitis vinifera* and *V. coignetiae*. As a result, samples of *E. necator* from *Carica papaya* are not present on the phylogenetic tree, contrary to records of *Carica papaya* infections caused by *E. fallax*. The phylogenetic reconstruction using Bayesian analysis showed a well-resolved tree topology representing main evolutionary lineages of Erysiphaceae (Helotiales, suborder Erysiphineae) (Figure 2).

Sequences of members of *Erysiphe* are divided into six clades. The nucleotide sequence derived from the powdery mildew infection of *Azadirachta indica* from the Dominican Republic is placed in a separate clade, together with *E. necator* sequences from *Vitis vinifera* and *V. coignetiae*. *Erysiphe necator* along with the sister clade *E. ampelopsidis* samples, are the basal clade of *Erysiphe* (Bradshaw *et al*., 2023).

DISCUSSION

Results from the present study provide the first evidence of *E. necator* occurring on *Azadirachta indica* in the Dominican Republic. The morphological characteristics of the powdery mildew isolate (M17) closely matched the diagnostic features of *E. necator* described by Braun and Cook (2012). The conidiophore and foot-cell dimensions of the examined material were near the lower limits of the wide range reported for *E. neca-*

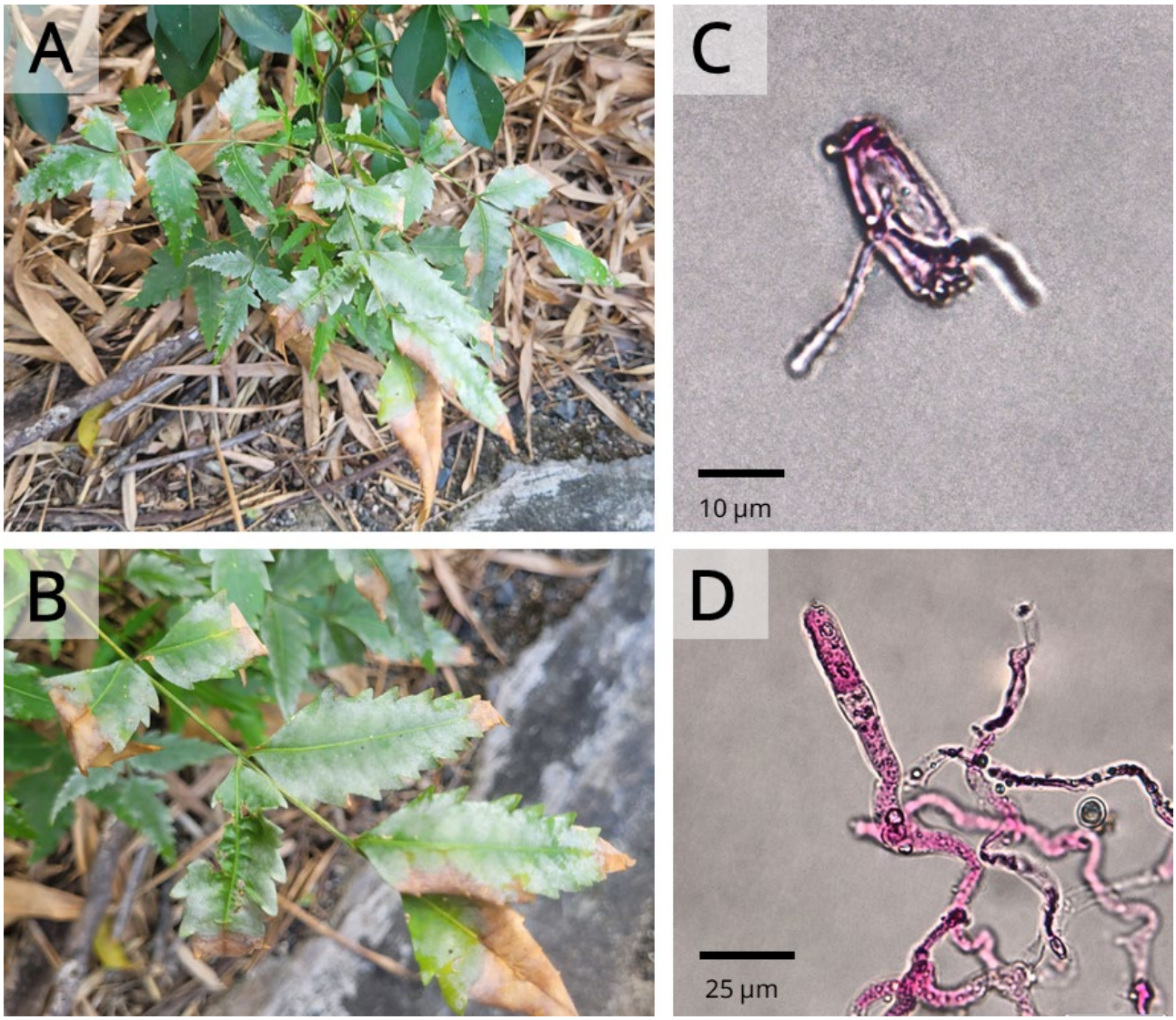

Figure 1. A and B, Symptoms of powdery mildew observed on *Azadirachta indica* in the field. C, Conidium of *Erysiphe necator*. D, Conidiophore of *Erysiphe necator* with twisted foot-cell.

tor, while conidium size and shape index fell within the mean reference values for this fungus. The molecular analyses confirmed that the powdery mildew found on *Azadirachta indica* in the Dominican Republic is *E. necator*. The collection M17 from *A. indica* nested within a strongly supported *E. necator* lineage (1.00 PP / 100 BS) containing sequences from grapevine (*Vitis* spp.).

Previous reports of powdery mildew on *A. indica* have been consistently assigned to *Pseudoidium azadirachtae* as the causative agent of infections (Braun and Cook, 2012; Jayalakshmi *et al*., 2024). A comparative analysis (Table 1) distinguished *E. necator* from *P. azadirachtae*. According to Braun and Cook (2012), *P. azadirachtae* has shorter and narrower conidia, and fewer distal cells per conidiophore, than *A. indica*. Fibrosin bodies do not occur in both species.

It is almost impossible to reliably distinguish individual powdery mildew species within *Erysiphe* anamorphs (*Pseudoidium*) only based on morphological analyses (Cook *et al*.,1997, 2009). Therefore, it is currently not possible to clarify the taxonomic affinity of *P. azadirachtae*. As type material of *Oidium azadirachtae* is not preserved, according to Art. 9.12 (Madrid Code) it would be absolutely necessary to designate the original illustration (Narayanaswamy and Ramakrishnan, 1969: Figure 25) as lectotype, and an Indian specimen morphologically

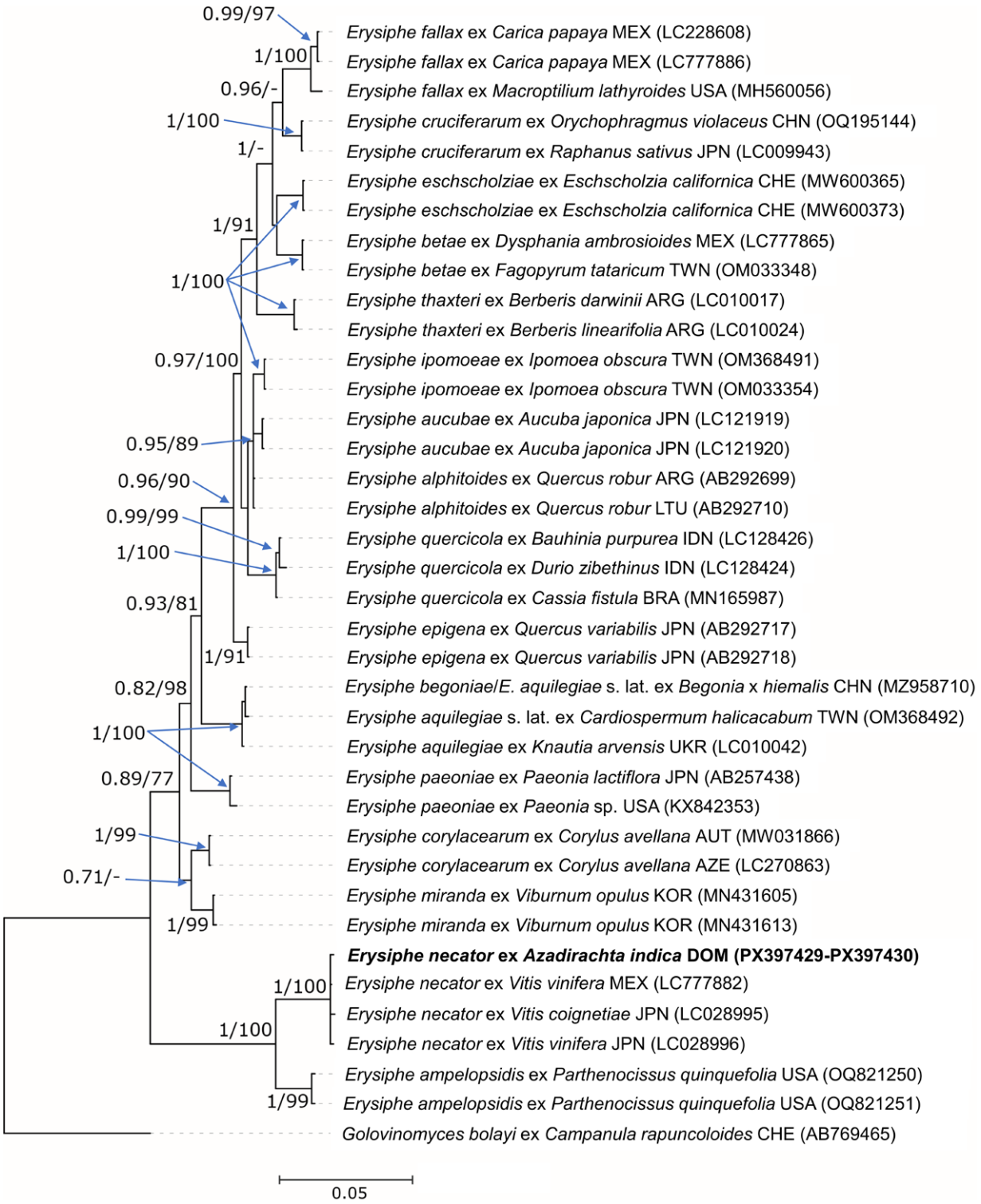

Figure 2. Phylogenetic tree based on Bayesian analysis (BA) of the ITS and 28S rDNA alignment, demonstrating the identity of *Erysiphe necator* infections from *Azadirachta indica* (in bold font) or *Vitis* spp. NCBI accession numbers and in parentheses. Bayesian posterior probabilities (≥ 0.7), and bootstrap support values for maximum likelihood (≥ 70%) are shown on main tree nodes.

in concordance with the original description should be designated as epitype with ex-epitype sequences. This would elucidate the phylogenetic-taxonomic status of this species. A morphological comparison between *P. azadirachtae* and the anamorph of the grapevine powdery mildew is difficult or impossible, mainly due to the great variability of the asexual morph of *E. necator* (Braun and Cook, 2012). In contrast to the very long conidia of *E. aquilegiae* s. lat. on neem in India (Wagh *et al*., 2024), the conidium size of the powdery mildew on this host in the Dominican Republic aligns with the original description of *O. azadirachtae* (Narayanaswamy and Ramakrishnan, 1969; Braun and Cook, 2012).

Tropical/subtropical regions host many species, with recent studies finding new species of *Erysiphe*, *Podosphaera*, and other genera, on various hosts in regions including Taiwan, Indonesia, Thailand, and Australia (Kiss *et al*., 2020; Kelly *et al*., 2025; Yeh *et al*., 2025). In Southeast Asia alone, 14 genera and 96 species have been documented. Among these, *Erysiphe* is the most species-rich genus (25 species), and several of its members are of major economic importance in tropical agriculture. Among the important pathogen species, *E. necator*, which causes grapevine powdery mildew, has been recorded throughout Southeast Asia, including from Thailand, Cambodia, Indonesia, Malaysia, Myanmar, and Vietnam, and additionally on cultivated strawberry (*Fragaria* × *ananassa*) in the Philippines (Aumentado *et al*., 2023). This is, however, a highly dubious host record (Aumentado *et al*., 2023), based solely on an entry in a checklist without morphological data or molecular confirmation.

Beyond Southeast Asia, significant powdery mildew diversity has also been documented in other tropical regions. A comprehensive survey in Puerto Rico identified 14 species on 38 host plants, with *Erysiphe* being the most frequent genus (University of Puerto Rico at Mayaguez, 2009). In Taiwan, a subtropical/tropical region with a high diversity of powdery mildews, recent surveys have documented multiple species across several genera, including *Erysiphe*, *Golovinomyces*, and *Podosphaera* (Yeh *et al*., 2025). Thirteen species (or species complexes) were confirmed on 28 host plants, many representing new island or international records. Particularly noteworthy is the detection of *E. necator* on *Ampelopsis brevipedunculata* (a new host for Taiwan), and on *Causonis japonica*, which is the first host record for this fungus.

In warm, humid environments, the asexual (anamorph) stage is often prevalent, making morphological identification difficult. DNA sequencing (mainly ITS region) is therefore crucial for species confirmations. As a consequence, many historical records from tropical plant disease surveys have identified powdery mildew pathogens only at genus levels, most frequently as *Oidium* sp. Kelly *et al.* (2025) reported that the Australian climate, and in some pathogen species, broad host ranges, allow continual survival of asexual stages of powdery mildew species on multiple hosts throughout each year. Only a few powdery mildew species have been reported to develop chasmothecia in tropical and subtropical regions (Vaghefi *et al*., 2022; Aumentado *et al*., 2023).

Powdery mildews are biotrophic parasites with highly specific linkages to their hosts, which are due to relatively long-term and complex co-evolutionary relationships (Bradshaw *et al*., 2024, 2026). Among representatives of Erysiphaceae, there are species with very narrow host ranges, and species with very wide host ranges encompassing several families (Lebeda *et al*., 2017; Mieslerová *et al.,* 2020). Beenken (2017) reported that host jumps occur regularly in powdery mildews. This process involves isolation of certain pathogen subpopulations, eventually leading to genetic differentiations and, in the long term, speciation, resulting in successful colonization of previously non-susceptible host species (Schulze-Lefert and Panstruga, 2011; Thines, 2019). Currently, sufficient information is lacking to fully elucidate the processes associated with successful transition (host jump) of a given powdery mildew species to other plants, that enable expansion of the pathogen's host spectrum. This is particularly true for host jumps to species belonging to other (and phylogenetically distant) plant families (Kusch *et al*., 2024).

In this context, limits to the present study are relevant. The herbarium material available did not allow verification of infection of the host species by the pathogen. Thus, the current study did not fulfil Koch's postulates for the pathogen, so direct causality was not confirmed, but an association is indicted between *E. necator* and the symptoms observed in *Azadirachta indica*. The *E. necator* infection on *A. indica* detected was found outside the natural range of this host (Braun and Cook, 2012; Gadoury *et al*., 2012). The present results on occurrence of *E. necator* on *A. indica* expand knowledge about the host spectrum of *E. necator.* The ability of *E. necator* to colonize unrelated hosts (*Azadirachta*, *Caryocar, Carica, Anacardium, Hevea*; Braun *et al*., 2017; Fonseca *et al*., 2019; Pieroni *et al*., 2020) indicates a broad ability for adaptation of this species than was previously recognized. Also, it supports previous hypotheses that cross-host infections may reflect incidental infections under suitable environmental conditions, or ecological overlaps between host species. This wide range across geographically and taxonomically distinct host species

indicates broad ecological plasticity of *E. necator*, and supports its role as a cosmopolitan pathogen capable of occasional host jumps.

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