



Citation: Vovlas, A., Ajobiewe, E.I., Fanelli, E., Troccoli, A., & De Luca, F. (2024). Bibliometric and sequence analyses of the pathogenic *Helicotylenchus* nematodes. *Phytopathologia Mediterranea* 63(3): 453-463. doi: 10.36253/phyto-15749

Accepted: December 7, 2024

Published: December 30, 2024

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Data Availability Statement: All relevant data are within the paper and its Supporting Information files.

Competing Interests: The Author(s) declare(s) no conflict of interest.

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Review

Bibliometric and sequence analyses of the pathogenic *Helicotylenchus* nematodes

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Summary. Publications between 2000 and 2024 on plant pathogenic species of *Helicotylenchus* nematodes were reviewed using bibliometric analyses with VOSviewer software. Sequences in GenBank for the same period were used to reconstruct phylogenetic relationships and correctly assign all the *Helicotylenchus* sequences in the database. The Scopus database was selected for its professional standards, international visibility, broad coverage, and controlled-vocabulary thesaurus available for indexing and retrieving documents. GenBank collects nucleotide sequences and relevant bibliographic and biological annotations for sequence analyses. This study highlighted research trends and specific complexities of working with *Helicotylenchus*, and the suitability of molecular markers used for identification of the main pathogenic species and confirmation of occurrence of species complexes or cryptic species.

Keywords. Nematodes, phylogeny, VOSviewer.

INTRODUCTION

Members of *Helicotylenchus* Steiner, 1945 are emerging concerns because of their broad host ranges and high numbers in soils (da Silva *et al.*, 2023). These nematodes are cosmopolitan with more than 230 species distributed around plant roots, occurring in most soil samples of cultivated and uncultivated soils. They are known as spiral nematodes, through their coiled *habitus mortis* (Firoza and Maqbool, 1994; Decraemer and Geraert, 2006; Uzma *et al.*, 2015). *Helicotylenchus* spp. are migratory ectoparasites that complete their life cycles in the soil, feeding on cortical parenchyma tissues of colonized roots. Several species are semi-endoparasites, penetrating plant tissues with their anterior body regions (Wouts and Yeates, 1994) attacking outer cortical tissues of host plant roots, reducing ability of roots to adsorb water and nutrients (Subbotin *et al.*, 2011; Crozzoli, 2014; Xia *et al.*, 2022). Infestations of *Helicotylenchus* spp. do not directly reduce crop yields, so their true impacts on agricultural production remain unclear.

Increasing numbers of papers report the wide distribution of *Helicotylenchus*, its wide host range, and association with other plant-parasitic nematodes. A few *Helicotylenchus* spp., including *H. digonicus* Perry, 1959, *H. dihystra* (Cobb, 1893) Sher, 1961; *H. indicus* Siddiqi, 1963, *H. multicinctus* (Cobb, 1893) Golden, 1956, *H. pseudorobustus* (Steiner, 1914) Golden, 1956, and *H. oleae* Inserra, Vovlas and Golden, 1979, are considered pathogenic, as they are abundant in soil and cause damage to agricultural crops and turfgrass (Subbotin *et al.*, 2015; Rybarczyk-Mydlowska *et al.*, 2019; Mwamula *et al.*, 2020; Mwamula and Lee, 2021; Mwamula *et al.*, 2024). Recently, *H. multicinctus*, *H. dihystra*, *H. varicaudatus* and *H. erythrinae* have been reported as important pathogens of banana (Riascos-Ortiz *et al.*, 2020), and *H. cavenessi*, *H. microcephalus* and *H. microlobus* are pathogens of agricultural crops and turfgrass (Subbotin *et al.*, 2011; Mwamula and Lee, 2021; Mwamula *et al.*, 2024).

Helicotylenchus consists in many species with conservative morphology but phenotypic plasticity, leading to potential species misidentification. Subbotin *et al.* (2011) demonstrated that *H. pseudorobustus* is a species complex exhibiting high intraspecific variability at the genetic level.

The present review aimed to explore trends and research activity in the scientific literature on *Helicotylenchus* spp., for the five well-characterized pathogenic species during the period 2000 to 2024. To achieve this, a bibliometric and sequence analyses in the Scopus database by using VOSviewer software (van Eck and Waltman, 2010) and in GenBank database, respectively, were carried out. The Scopus Database was selected for the large and multidisciplinary content, its professional standards, international visibility, broad coverage, and controlled-vocabulary thesaurus available for indexing and retrieving documents (Zong *et al.*, 2012; Alryalat *et al.*, 2019; Baas *et al.*, 2020). The GenBank database collects nucleotide sequences and relevant bibliographic and biological annotations for sequence analyses.

MATERIALS AND METHODS

The literature search was carried out from the Scopus database (<https://www.scopus.com/>), using the keyword “*Helicotylenchus*” in paper titles, abstracts, and keyword lists, and selecting studies published from 2000 to September 2024 in indexed journals (Figure 1). No language restriction was made. The titles of all identified

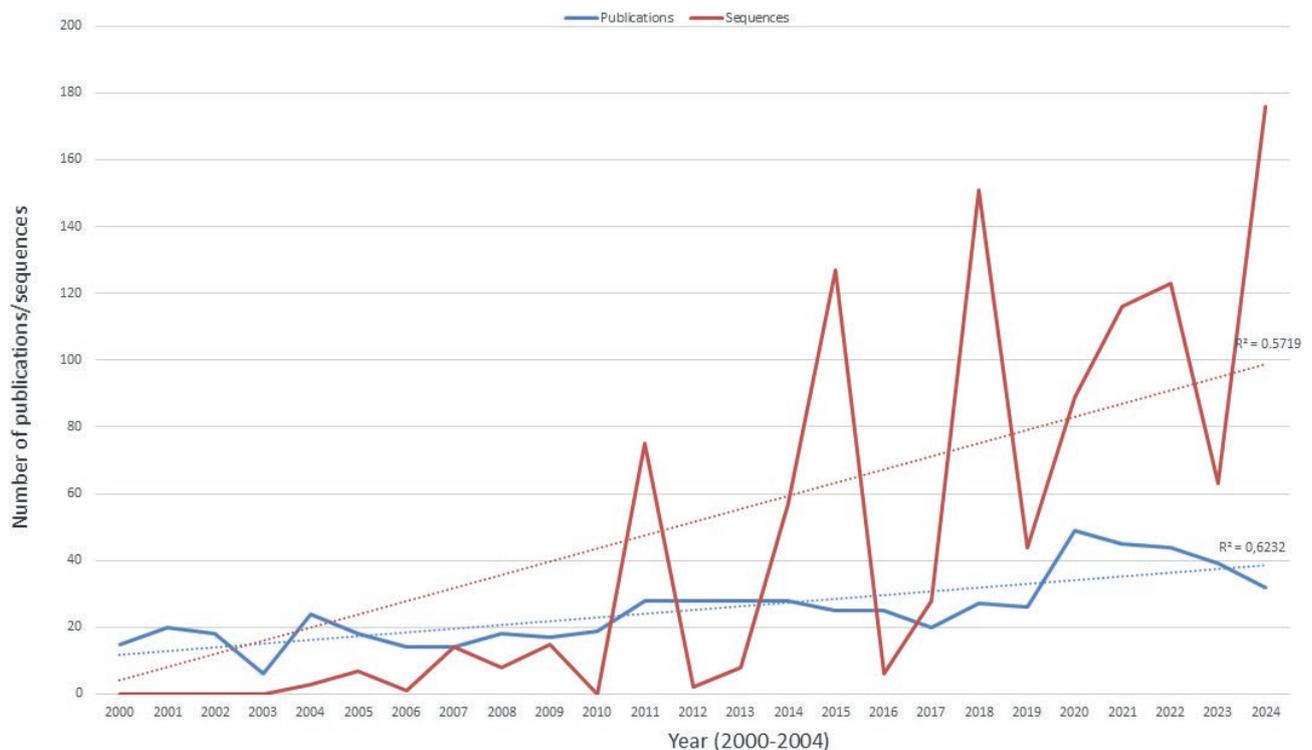


Figure 1. Publications and sequence trends relating to *Helicotylenchus* spp. between 2000 and 2024. The publications were retrieved from the SCOPUS database and sequences were from GenBank in the subject areas.

articles and their abstracts were also screened to ensure reliability of the search.

Bibliometric analysis

Bibliometric network analysis of *Helicotylenchus* literature was conducted using VOSviewer software (van Eck and Waltman, 2010), allowing creation of maps using bibliometric data. The output results consisted of maps showing several clusters, in different colours, and links based on keywords. Each cluster reflects groups of keywords that are strongly related. In the graphics, each node size is represented by a circle, the larger the circle at the node indicates greater the number of references on *Helicotylenchus* spp. The strongest relatedness between terms is also indicated by curved lines. Each network map can provide a temporal perspective on average publication per year, and a density visualization map was produced to indicate the most important areas of research. The time axis indicates research interest at the beginning of the study period (blue zone), while the yellow zone indicates the emerging direction in the research.

All selected papers were further analysed using the terms ‘co-authorship countries network’ and ‘co-occurrence’. Co-authorship countries network used the terms “researchers” and “research institution” for each country, providing a map with several clusters, in different colours, linked to each other according to the number of papers that authors have jointly published. Co-occurrence of author keywords analysis, using the Boolean operators “*Helicotylenchus dihystrera*” OR “*Helicotylenchus digonicus*” OR “*Helicotylenchus pseudorobustus*” OR “*Helicotylenchus indicus*” OR “*Helicotylenchus multicinctus*” AND “plants”, produced an overlay visualization map showing the number of papers in which the keywords were found, and distance between terms indicate relationships of the terms, while the lines connecting the nodes indicated how many times a specific *Helicotylenchus* sp. is present on a specific host plant. With

the requirement that a keyword occurs at least ten times, 4792 keywords met this threshold.

Sequence retrieval

Genbank at NCBI contains multiple types of nucleotide sequences from different sources and directly from authors, providing an interface for searching, visualization, and analysis of sequences.

Using “*Helicotylenchus*” as query in GenBank, 1113 sequences were found as submitted from 2000 to September 2024 (Figure 1). In addition to making use of search terms, a manual check was carried out on each resulting number of sequences per species and per molecular marker, to ensure accuracy. All sequences of *Helicotylenchus* were then re-analysed using the terms “ribosomal DNA”, “mitochondrial COI gene”, “mitochondrial COII gene” and “*hsp90*”. This analysis also delivered 1113 sequences, 513 corresponding to D2-D3 expansion domains of the 28S rRNA gene, 291 to partial 18S rRNA gene, 211 to the ITS region, 86 to the mitochondrial COI gene, one to COII, and 11 sequences corresponding to the *hsp90* gene.

The total number of *Helicotylenchus* sequences was then screened to obtain ribosomal and mitochondrial sequences belonging to the five major pathogenic species, *H. dihystrera*, *H. pseudorobustus*, *H. digonicus*, *H. multicinctus* and *H. indicus* retrieved from 2000 to 2024 (Table 1).

Phylogenetic analysis

The retrieved sequences for D2-D3, ITS and COI were aligned by MAFFT version X and edited by using BioEdit software. For D2-D3 alignment, 99 sequences between lengths 600 and 700 bp were used, with *Hoplolaimus galeatus* (EU626787) used as the outgroup. For ITS alignment, 100 sequences between lengths 800

Table 1. *Helicotylenchus* sequences belonging to the five pathogenic *Helicotylenchus* species that have been released between 2000 and 2024.

<i>Helicotylenchus</i> species	Molecular markers						Total number of sequences
	ITS	18S	28S	COI	COII	<i>hsp90</i>	
<i>H. dihystrera</i>	71	46	149	4	1	0	271
<i>H. pseudorobustus</i>	10	73	58	10	0	1	152
<i>H. digonicus</i>	9	11	25	3	0	1	49
<i>H. multicinctus</i>	9	5	25	0	0	0	39
<i>H. indicus</i>	2	7	2	0	0	0	11
Total	101	142	259	17	1	2	522

and 1000 bp long were used, with *Rotylenchus pumilus* (JX015436) used as the outgroup. COI, 47 sequences were used, with *Heterodera elachista* (MH144207) as the outgroup. Phylogenetic analyses of both sequence datasets were based on Bayesian inference (BI), using MrBayes 3.1.2 (Ronquist and Huelsenbeck, 2003). The best-fit model of DNA evolution was selected employing the Akaike Information Criterion (AIC), using JModel-Test V.2.1.10 (Darriba *et al.*, 2012) for all the datasets: a general time-reversible model with invariable sites and a gamma-shaped distribution (GTR + G + I) was used for COI, a general time-reversible model for ITS and a gamma-shaped distribution (GTR + G) distributed rates across sites for 28S. For this analysis, the best-fit models (including the base frequencies), the proportion of invariable sites, gamma distribution shape parameters, and the substitution rates derived from the AIC, were subsequently applied within Mr Bayes.

The Markov chain Monte Carlo search was carried out separately for each dataset, using four chains for 2×10^6 generations, sampled at intervals of 100 generations. Two runs were carried out for each analysis. Following the elimination of 25% of samples for the burn-in and evaluating convergence, the remaining samples were retained for in-depth analyses. The resulting topologies were used to generate a 50% majority-rule consensus tree, with posterior probabilities (PP) calculated for appropriate clades. The phylogenetic trees from all analyses were visualized, using iTOL (Letunic and Bork, 2021), and were edited with GIMP version 2.10.32 (available at <http://www.gimp.org>).

RESULTS

Bibliometric analysis

The literature search for *Helicotylenchus* spp. in Scopus identified 627 documents published between 2000 to September 2024 (Figure 1). These were of three types: 607 were scientific articles (96.8%), 12 reviews (1.9%), and eight edited book chapters (1.3%). This showed few papers at the beginning of the temporal period and increasing and then constant interest in *Helicotylenchus* during the period. The low number of publications is probably because most *Helicotylenchus* spp. do not directly lead to significant reductions in crop yields, and only a few species are considered as crop pathogens (Subbotin *et al.*, 2011; Brücher *et al.*, 2019). A total of 160 scientific journals published papers (at least 1 per year) on *Helicotylenchus*, but only five journals published large numbers of papers. These were *Nematropica* (55 papers), *Nematology* (47), *Journal of Nematology* (38), *Archives*

of Phytopathology and Plant Protection (22) and *Applied Soil Ecology* (21 papers). The main research topics of studies on *Helicotylenchus* spp. were soil nematode communities, molecular and morphological characterization, and control strategies.

Co-authorship countries network

Figure 2 shows the map of co-authorship analysis among countries. Reports on occurrence of *Helicotylenchus* spp. were from a total of 89 countries, but using a threshold of five publications per country, 42 countries were selected for the co-authorship network map. The most productive country was the United States of America (USA), with 114 papers, followed by India (64), Brazil (61), and China (53 papers). Figure 2 shows seven main clusters in different colours, highlighting high level of co-operation/collaboration. The USA had strong relationships with many of the countries with the greatest link strength. Belgium also had strong interactions with other countries. Of the 480 papers on *Helicotylenchus*, 221 reported the occurrence of *Helicotylenchus* spp. in association with nematode communities, and the remaining papers reported morphological, molecular and phylogenetic analyses, and nematode control strategies.

Co-occurrence author keywords

The overlay visualization map (Figure 3) provides the average publication year for keywords, summarizing the dynamics of old and emerging words. Each term is represented by a circle, and the size of each circle depends on the number of publications in which the term was found, and the distance between two terms indicates the relationships between them. The close relationships between terms are also highlighted by curved lines, and the same colour identifies terms strongly related with each other. Figure 3 shows increasing use of the keywords *H. dihystrera* and *H. multincinctus*, followed by banana, musa, maize, sugarcane, soybean, and cotton, during the period assessed. The density visualization map showed that grain and cereal crops (*Avena* spp., *Secale* spp., *Zea* spp., *Triticum* spp.) were the crops assessed early in the assessment period, and more recently assessed crops were peanut, coffee, cocoa, or tomato (brighter yellow colour). The density map also shows that *Helicotylenchus* spp. have been found on numerous woody plants, and that *H. multincinctus* and *H. digonicus* have been recently recorded as pests on date-palm (*Phoenix dactylifera*). Several papers have reported *H. digonicus* on pines, oaks, and in olive groves, and this

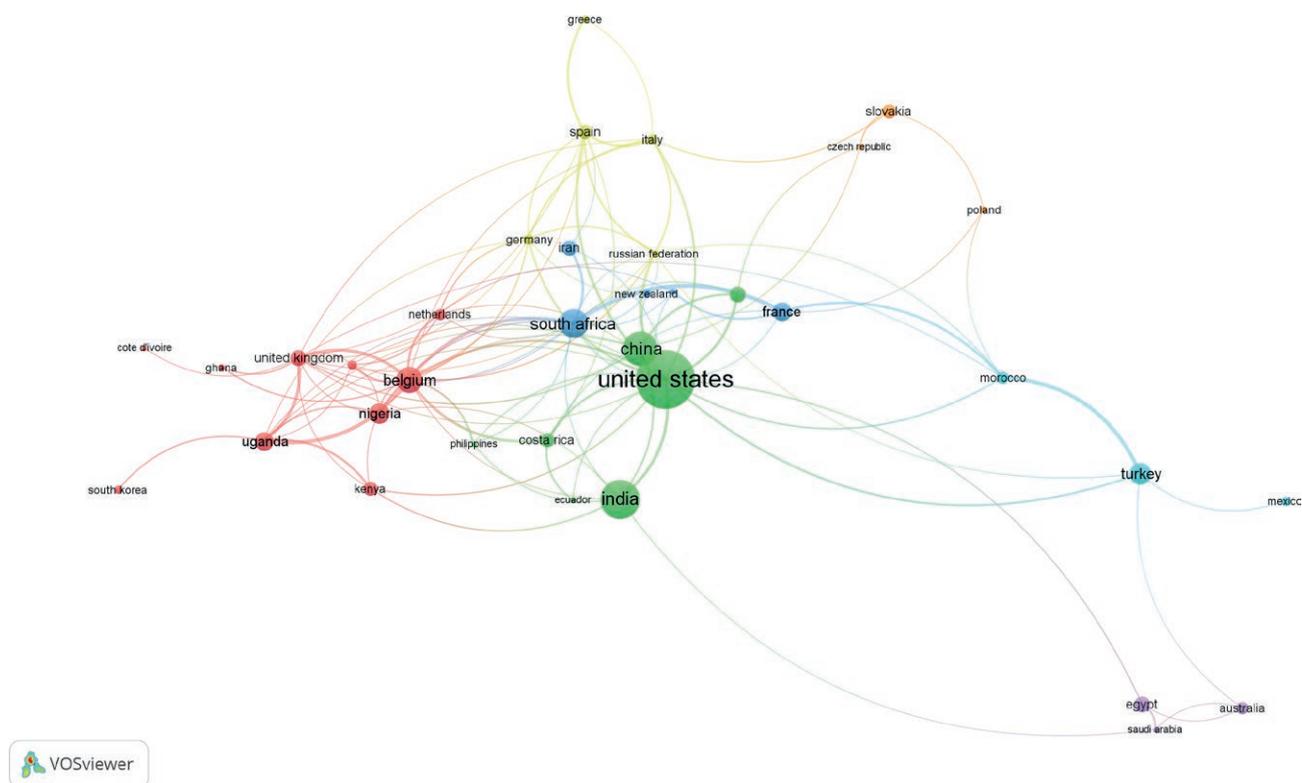


Figure 2. Co-authorship network map (developed with VOSviewer) showing countries where research on *Helicotylenchus* spp. has been carried out between 2000 and 2024. Each node number indicates the number of publications for each country, and the node size indicates occurrence of keywords.

nematode has been more recently detected on prunus, peach, and walnut. Research interest in *H. pseudorobustus* has increased, occurring in *Malus* sp. and *Prunus* sp. orchards.

Sequence analysis

A total of 1113 *Helicotylenchus* sequences were recorded in the GenBank database between 2000 and September 2024, corresponding to 513 sequences for D2-D3 expansion domains of the 28S rRNA gene, 291 for the 18S rRNA gene, 211 for ITS, 86 for COI, one for COII, and 11 for *hsp90*. Forty-seven percent (522) of the total sequences belonged to the five major known pathogenic *Helicotylenchus* species (Table 1), 259 corresponded with D2-D3 expansion domains of the 28S rRNA gene, 142 to the 18S rRNA gene, 101 to the ITS region, 85 to mitochondrial COI, one to COII, and two to the *hsp90* gene. Table 1 emphasizes the increase of sequence numbers during the 2000 to September 2024 period.

Phylogenetic analyses were reconstructed, based on D2-D3 expansion domains, ITS, and partial mitochon-

drial COI sequences of the major pathogenic *Helicotylenchus* spp. The topologies of the D2-D3 and ITS trees agree with those in research literature (Figures 4 and 5), confirming that several sequences in Genbank were misidentified and sometimes displayed sequencing mistakes, as has been elsewhere reported (Mwamula *et al.*, 2024).

Helicotylenchus pseudorobustus (type A), *H. microlobus* (type B), and *H. digonicus* (type A) were closely related to each other, and *H. dihystra* showed sister relationships with these three species types. *Helicotylenchus digonicus* (type B) grouped with *H. crassatus*. Presence along the tree of different sequence groups erroneously indicates presence and occurrence of species complexes.

DISCUSSION

The main objective of this study was to evaluate reported research on *Helicotylenchus*, with particular focus on the major pathogenic species, and spatio-temporal trends between 2000 and September 2024. The increasing trend in annual numbers of publications on *Helicotylenchus* spp. reflects increasing interest by the

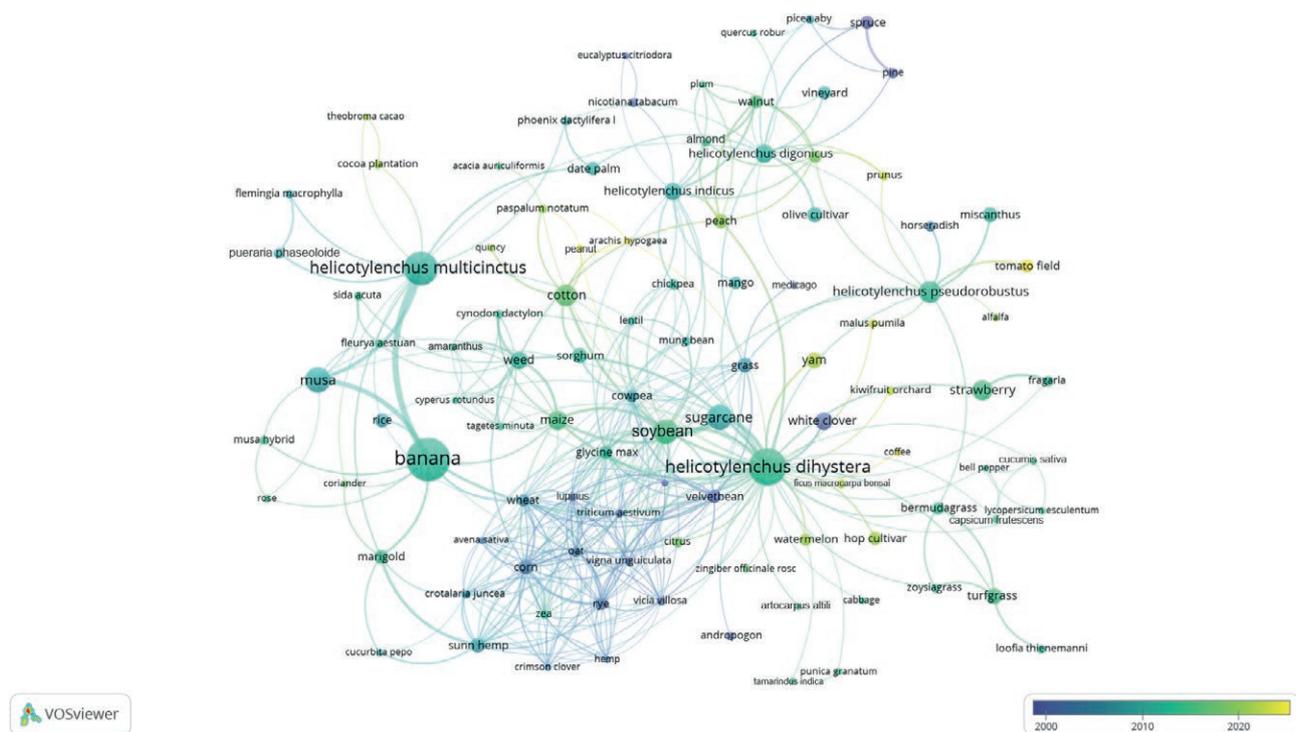


Figure 3. Cluster visualization of co-occurrence keywords for host plants and five plant pathogenic *Helicotylenchus* species. Each node number indicates the number of documents for the keywords, and the size of each node indicates the occurrence of the keywords. Different colours represent groups of terms that are strongly related to each other, and the curved lines indicate strong relationships between terms.

international nematologist community (Figure 1). The analysis of authorships and collaboration showed that researchers from the USA were the greatest contributors, followed by those from China, India, and Brazil (Figure 2), and that USA researchers have most collaborations with other countries. The keyword co-occurrence network map showed that the plant pathogenic *Helicotylenchus* species, particularly *H. dihystra* and *H. multicinctus* and their host plants are increasingly important research topics (Figure 3). The density visualization map showed that pathogenic *Helicotylenchus* species mainly attack banana, followed by musa, maize, sugarcane, soybean, and cotton, and this map also showed that grain and cereal crops (*Avena* spp., *Secale* spp., *Zea* spp, *Triticum* spp.) were the earliest studied in the review period, with other crops more recently attracting researcher attention. Pathogenic *Helicotylenchus* species have also been found on several woody plants in recent years. These observations indicate that climate changes may have increasingly act affected *Helicotylenchus* abundance, and new crops can be attacked and new pathogen species may evolve.

Helicotylenchus comprises more than 230 species, and most of these have conserved gross morphology, so molecular identification followed by sequencing

of molecular markers has been useful to discriminate among species. This has been confirmed by the increasing number of sequences in GenBank over the 2000 to 2014 period (Figure 1). Most sequences in GenBank belong to the most important plant pathogenic species of *Helicotylenchus* (Table 1). Several publications have reported incorrect sequences present in the public database, due to sequencing errors, misidentifications, and identification errors based on nematode morphology. In the present review, all D2-D3 and ITS sequences of the pathogenic *Helicotylenchus*, released in the database until September 2024, were used for phylogenetic analyses to correctly identify *Helicotylenchus* species by clusters. The phylogenetic trees illustrated in Figures 4 and 5 have identical topologies, showing that *H. pseudorobustus* sequences form three subgroupings (92% support), one containing the sequences of *H. pseudorobustus*, the second containing sequences identified as *H. digonicus* type B, and the third with sequences belonging to *H. microlobus*, as has been reported by Subbotin *et al.* (2015) and Mwamula *et al.* (2020). This confirms that *H. pseudorobustus* and *H. microlobus* are valid species, closely related but genetically distinct from each other. *Helicotylenchus digonicus* populations clustered in different groupings, types A and B, suggesting possible existence of spe-



Figure 4. Phylogenetic relationships among the five pathogenic *Helicotylenchus* species, as indicated using a Bayesian 50% majority rule consensus tree inferred from D2-D3 expansion domains of the 28S rRNA gene sequence alignment under a transversional with gamma-shaped distribution model (GTR + G). Posterior probabilities of greater than 0.50 are given for appropriate clades, and the scale bar indicates expected changes per site.

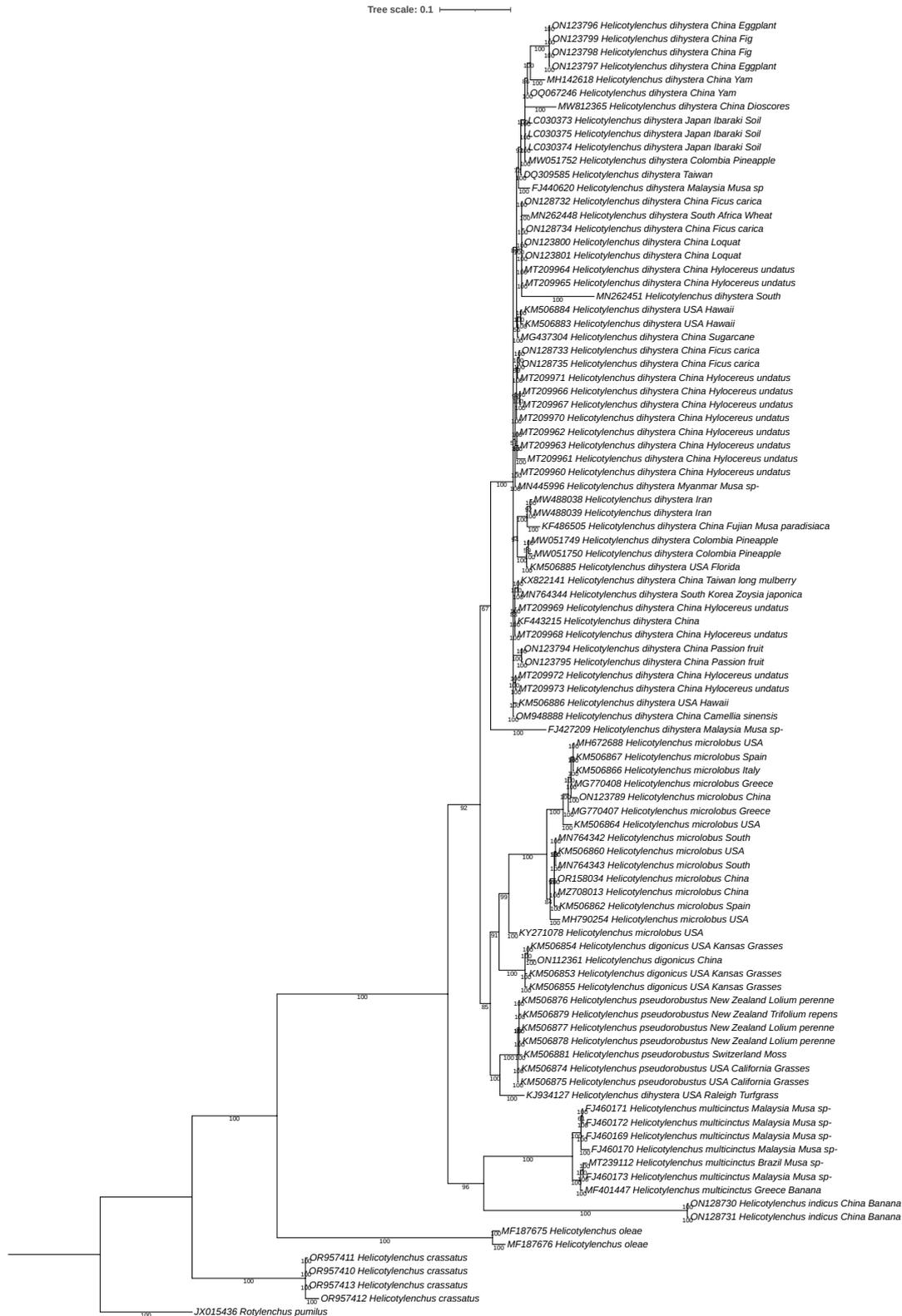


Figure 5. Phylogenetic relationships among the five pathogenic *Helicotylenchus* species, as indicated using a Bayesian 50% majority rule consensus tree inferred from ITS sequence alignment under a transversal with gamma-shaped distribution model (GTR+ G). Posterior probabilities of greater than 0.50 are given for appropriate clades, and the scale bar indicates expected changes per site.

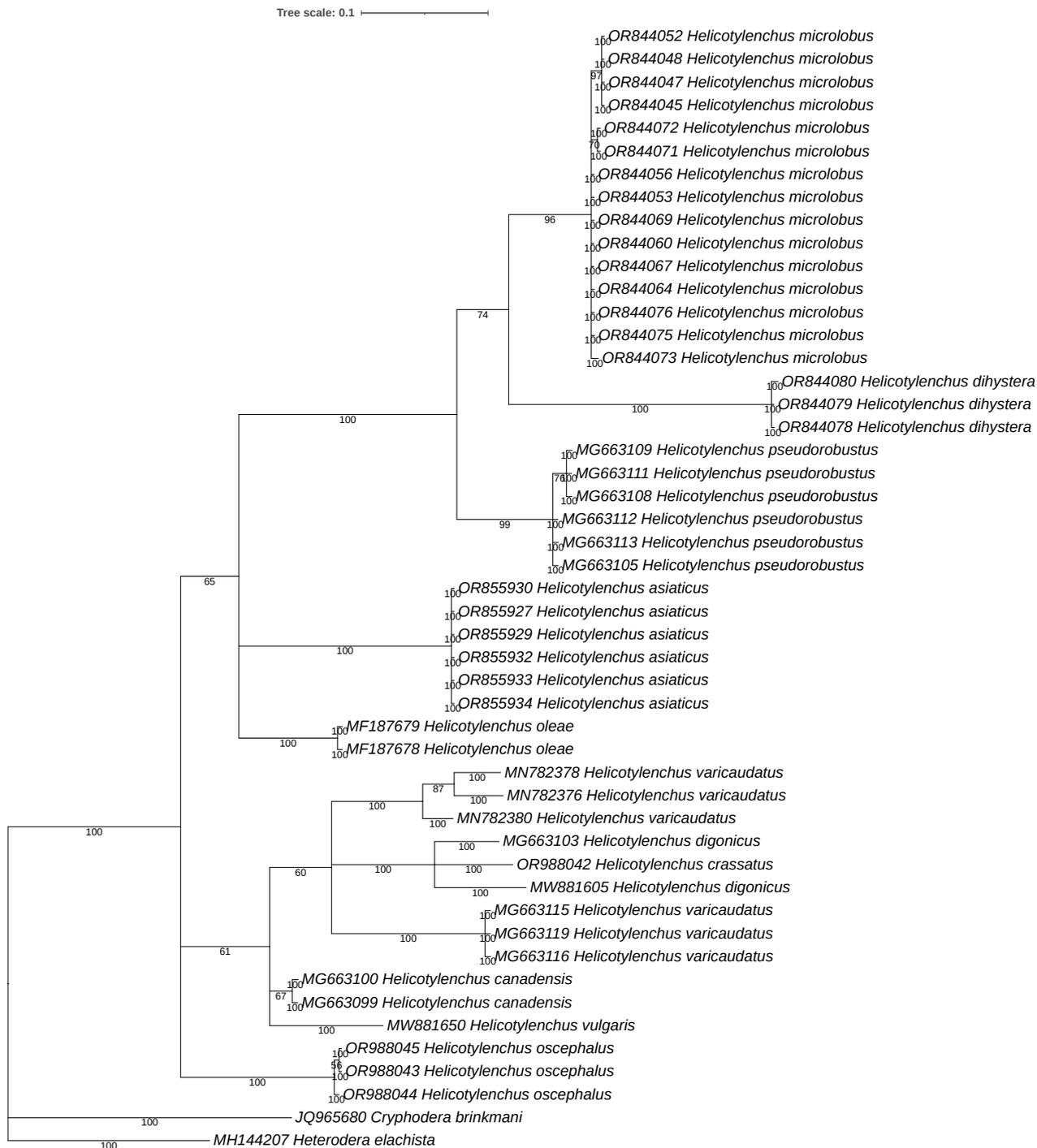


Figure 6. Phylogenetic relationships among the five pathogenic *Helicotylenchus* species using Bayesian a 50% majority rule consensus tree as inferred from COI sequence alignment, under a transversional with correction for invariable sites and a gamma-shaped distribution model (GTR + I + G). Posterior probabilities of more than 0.50 are given for appropriate clades. The scale bar indicates expected changes per site.

cies complexes or cryptic species, and further study is required to elucidate this suggestion. The mMitochondrial COI phylogenetic tree (Figure 6) confirms that each

species group are separated from the others. It is interesting to note that only *H. pseudorobustus* and *H. oleae* COI sequences contain stop codons, indicating genetic code

alterations or the occurrence of pseudogenes (Palomares-Rius *et al.*, 2018; Rybarczyk-Mydlowska *et al.*, 2019).

In conclusion, our observations reveal an increase of host plants infected by *Helicotylenchus* spp. and this could be explained by the species complexes of these nematodes. Identification of *Helicotylenchus* spp. therefore required polyphasic approaches, combining morphology, molecular and phylogenetic analyses, to correctly discriminate *Helicotylenchus* species, and through that knowledge, development of effective nematode management strategies. Bibliometric analysis is a method that can be useful for understanding past research, and development of new knowledge leading to worthwhile research advances.

ACKNOWLEDGEMENTS

This work was supported with funds provided by Lombardy Region (Bando 2018 per Progetti di ricerca in campo agricolo e forestale – d.d.s. n. 4403 del 28/03/2018) for the project NEMAGEST.

AUTHOR CONTRIBUTIONS

AV and EIA equally contributed to bibliometric and sequence analyses; AV used VOSviewer and phylogenetic programs; EIA contributed to NCBI/GenBank sequence retrieval; AV and EIA contributed to writing, review and editing; EF and AT contributed to review and editing; FDL contributed to the study conception and design, writing original draft, review and editing. FDL contributed to fund acquisition. The first draft of the manuscript was commented by all authors and then they approved the final manuscript.

DATA AVAILABILITY

All sequences in this paper are freely available through GenBank database.

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