Mycological Progress (2025) 24:20
https://doi.org/10.1007/s11557-024-02025-4

ORIGINAL ARTICLE

Genomic features and evolution of lifestyles support the recognition of distinct genera among fusarioid fungi

Bartosz Ulaszewski[1] · Marcelo Sandoval-Denis[2] · Johannes Z. Groenewald[2] · Marileide M. Costa[2] · Bagdevi Mishra[3] · Sebastian Ploch[3] · Pedro W. Crous[2,4] · Marco Thines[3,5]

Received: 3 June 2024 / Revised: 9 December 2024 / Accepted: 10 December 2024 / Published online: 24 February 2025

Abstract

The family *Nectriaceae* (*Hypocreales*, *Sordariomycetes*) includes saprobes, endophytes and numerous important pathogens, several of which are of high commercial interest. Presently there are numerous genera scattered throughout the *Nectriaceae* that have a fusarioid asexual morph (*i.e.*, genera with fusarium-like macroconidia). Fusarioid fungi encompass diverse lifestyles, including plant, human, and animal pathogens or associates, saprobes, lichenicolous species, endophytes, and mycophilic taxa. The fusarioid genera in *Nectriaceae* do not only differ in their sexual morphs, but also in their asexual morphology and biology, although their ecology has remained rather unclear. While genome data are available for numerous species, this has been mostly focused on *Fusarium* sensu stricto, as the genus encompasses most of the economically important species in this generic complex. To compliment this, we expanded the sampling, and generated whole genome sequences for 40 isolates representing the genera *Atractium*, *Bisifusarium*, *Cinnamomeonectria*, *Corinectria*, *Cosmospora*, *Cyanonectria*, *Cylindrodendrum*, *Dialonectria*, *Fusarium*, *Fusicolla*, *Geejayessia*, *Ilyonectria*, *Macroconia*, *Macronectria*, *Microcera*, *Neocosmospora*, *Neonectria*, *Pseudofusicolla*, *Rectifusarium*, *Rugonectria*, *Scolecofusarium*, *Thelonectria*, and *Tumenectria*. Phylogenomic ancestral reconstructions showed that plant pathogenicity is most likely ancestral to *Fusarium* and cylindrocarpioid genera, and revealed multiple and frequent lifestyle transitions. Although many species are prolific generalists, several genera appear to be more specialised, being primarily plant pathogens, mycophilic, or insect associated, while endophytism or plant pathogenicity evolved several times, and more recently in *Fusarium.* The broadly sampled *Nectriaceae* genomes supported morphological differences between most genera of *Nectriaceae*, mirrored by genome sizes, lactic enzymes, biosynthetic gene clusters, and small secreted proteins. Furthermore, it also supported a narrow circumscription of *Fusarium* in *Nectriaceae* that equals its morphology (*Gibberella* sexual morphs), and biology.

Keywords Biosynthetic gene clusters · CAZymes · Comparative genomics · Endophytes · *Fusarium* · Lifestyle evolution · Plant pathogens · Saprobes · Small-secreted proteins

---

Section Editor: Cobus CM Visagie

Bartosz Ulaszewski and Marcelo Sandoval-Denis contributed equally.

✉ Pedro W. Crous
p.crous@wi.knaw.nl

✉ Marco Thines
m.thines@thines-lab.eu

[1] Department of Genetics, Faculty of Biological Sciences, Kazimierz Wielki University, Chodkiewicza 30, 85-064 Bydgoszcz, Poland

[2] Westerdijk Fungal Biodiversity Institute, Uppsalalaan 8, 3584CT Utrecht, The Netherlands

[3] Senckenberg Biodiversity and Climate Research Centre, Senckenberganlage 25, 60325 Frankfurt Am Main, Germany

[4] Department of Biochemistry, Genetics and Microbiology, Forestry and Agricultural Biotechnology Institute (FABI), University of Pretoria, Pretoria, South Africa

[5] Department of Biological Sciences, Institute of Ecology, Evolution and Diversity, Goethe University, Max-Von-Laue-Straße 13, 60483 Frankfurt Am Main, Germany

Introduction

The abolishment of dual nomenclature in *The International Code of Nomenclature for algae, fungi and plants* (ICN; McNeill et al. 2012), determined that each morph competed equally for priority. Geiser et al. (2013, 2021), Rossman et al. (2013) and Crous et al. (2021) were in full agreement that *Fusarium* equals *Gibberella*. Rossman et al. (2013) therefore proposed that the sexual morph, *Gibberella* (1877), be discontinued in its use in favour for its asexual morph, *Fusarium* (1809). The fusarioid morphology (falcate, multiseptate, hyaline conidia with basal foot cells), however, has evolved in several genera throughout the *Sordariomycetes*, and prominently in *Nectriaceae*, where these asexual morphs are linked to a range of different nectrioid sexual morphs (Rossman et al. 1999; Samuels et al. 2009; Gräfenhan et al. 2011; Schroers et al. 2011; Lombard et al. 2015; Sandoval-Denis et al. 2019). This phenomenon of convergent evolution is similar to that observed in other families in *Sordariomycetes*, such as *Bionectriaceae* (Hou et al. 2023), *Ceratocystidaceae* (de Beer et al. 2014), *Cryphonectriaceae* (Jiang et al. 2020), *Microascaceae* (Sandoval-Denis et al. 2016), *Ophiostomataceae* (de Beer et al. 2022), *Plectosphaerellaceae* (Giraldo and Crous 2019), *Pyriculariaceae* (Klaubauf et al. 2014), and *Stachybotriaceae* (Lombard et al. 2016), to name but a few.

A revision of *Fusarium* by Crous et al. (2021) accepted 20 segregate fusarioid genera with clear-cut synapomorphic traits, with an additional genus, *Longinectria*, introduced by Savary et al. (2021) to accommodate taxa isolated from Swiss and Italian cheese. These morphologically distinct genera have been phylogenetically separated based on multi-gene studies that used three (Crous et al. 2021), 10 (Lombard et al. 2015), 19 (Geiser et al. 2021), or 1001 genes (Han et al. 2023). In general, studies on fusarioid fungi suffered from incomplete datasets with missing loci and/or (ex-)type cultures, or unbalanced sampling, primarily focusing on the genus *Fusarium s. str.*, which currently contains more than 341 validly described and accepted species (https://www.fusarium.org/; accessed 14 May 2024). *Fusarium s. str.* (type species *F. sambucinum*) is a genus of primarily soil-borne fungi, many of which have a biological association with grasses and herbs. The vast majority of *Fusarium s. str.* species produce fumonisins, gibberellins, or trichothecene mycotoxins as a chemical synapomorphy, and have *Gibberella* (type species *G. pulicaris*) sexual morphs, characterised by subhyaline, ellipsoidal to fusoid, 1–3-septate, smooth-walled ascospores, and purple to black perithecia (Crous et al. 2021). *Fusarium* is the fourth highest cited fungal genus (Bhunjun et al. 2024), and ranks among the top 10 fungal plant pathogens (Dean et al. 2012), causing devastating diseases such as Panama disease of banana (Maryani et al. 2019a, b). However, many fusarioid genera and species are not reported as pathogens (of plants, animals or humans), but exhibit other fungal lifestyles, being saprotrophic, endophytic, insect symbionts, or associated with other fungi (mycophilic) (Leslie & Summerell 2006; Crous et al. 2021).

In trying to categorise lifestyles of *Fusarium* and allied fusarioid taxa, Hill et al. (2022) performed whole genome sequencing, assembly, and annotation of five novel endophytic *Fusarium* strains. These data were added to genomes of other publicly available fusarioid strains, *Albonectria* (two isolates), *Geejayessia* (one), and *Neocosmospora* (eight), to determine how lifestyles evolved across the phylogeny. These results revealed multiple and frequent lifestyle transitions in *Fusarium*, with a major exception being *Neocosmospora* which exhibited an insect mutualist lifestyle. Although the ambrosia clade of *Neocosmospora* is strictly associated with beetles in the genus *Euwallacea*, other members of the genus are plant pathogenic, soilborne, or endophytic, but were not included in the analyses of Hill et al. (2022). In addition, several genera were missing that are needed to infer genomic signatures of adaptation to various lifestyles in *Nectriaceae*. For the present study, therefore, we expanded the sampling, and generated whole genome sequences for 40 isolates representing the genera *Atractium* (two isolates), *Bisifusarium* (two), *Cinnamomeonectria* (one), *Corinectria* (one), *Cosmospora* (three), *Cyanonectria* (two), *Cylindrodendrum* (three), *Dialonectria* (one), *Fusarium* (one), *Fusicolla* (one), *Geejayessia* (one), *Ilyonectria* (two), *Macroconia* (two), *Macronectria* (two), *Microcera* (two), *Neocosmospora* (one), *Neonectria* (one), *Pseudofusicolla* (one), *Rectifusarium* (two), *Rugonectria* (two), *Scolecofusarium* (two), *Thelonectria* (three), and *Tumenectria* (two). These taxa were supplemented with 236 publicly available genomes (Supplementary Table S2). We produced a genome-scale phylogeny of *Fusarium* and allied fusarioid genera to address the following questions: 1) What is the ancestral lifestyle of fusarioid fungi? 2) Do genomic properties of closely related genera reflect their lifestyles? 3) Is there a genomic differentiation between lineages of the *Nectriaceae* that underpin genus boundaries?

Materials and methods

Genome sequencing and assembly

Forty isolates representing 23 fusarioid genera (Supplementary Table S1) were selected for whole genome sequencing based on the taxonomic identifications determined in Crous et al. (2021) from the culture collection of the Westerdijk Fungal Biodiversity Institute (CBS), Utrecht, the Netherlands. Genomic DNA was isolated from actively growing cultures using a modified CTAB-based protocol (Damm et al. 2008).

Pair-end reads (PE-150) provided by BGI (Hongkong, PRC) were trimmed with *Trimmomatic* v. 0.39 (Bolger et al. 2014) with the following settings: remove leading and trailing low quality (<3) or N bases; cutting when the average quality per base drops below 15 in a 4-base sliding window; Illumina adaptor removal; removing reads shorter than 70 bp. Trimmed reads were used to assemble genomes with *velvet* v. 1.2.10 (Zerbino and Birney 2008) using three hash/k-mer values: 65, 85 and 93. Metrics of each assembly was checked with the *stats.sh* script from the BBTools package (Bushnell 2021) and the genome quality was measured with BUSCO v. 4.1.2 against the *fungi_odb10* dataset (Manni et al. 2021). In terms of sequence statistics *e.g*. assembly size, number of scaffolds, N50 and BUSCO results (97.6–99.3%) (for details, see Supplementary Table S1), $K=93$ performed the best for all genomes.

BUSCO assisted phylogeny

The phylogenetic analysis was conducted using the 40 new assemblies and 236 *Nectriaceae* genomes downloaded (in October 2021) from GenBank (235) and JGI (1) and *Sarocladium implicatum* was chosen as outgroup. The quality of the acquired 236 references was measured also by BUSCO and the *fungi_odb10* dataset. All (276) genomes met the established threshold of $\geq 95\%$ out of 758 genes assessed by BUSCO (for details, see Supplementary Table S2). A subset of 263 non-fragmented genes was present in all of the analysed references and used for the phylogenetic analysis. For each genome, the protein sequences were extracted by a custom bash script. Sequence alignments were done separately for each gene with *mafft* v. 7.490 (Katoh and Standley 2013) in *auto* mode, followed by trimming done with *trimAl* v. 1.4.rev15 (Capella-Gutiérrez et al. 2009) using the *automated1* option in the first round and by removing columns in an alignment with gaps $>5\%$, in the second round. The final alignment merging was done with the python script *superalignment.py* (Waterhouse et al. 2018).

The main phylogenetic tree was generated with RAxML v. 8.2.12 (Stamatakis 2014) using the PROTGAMMAJTT model and 1 000 alternative runs to infer the tree with the best likelihood score and 1000 bootstrap replicates. Single gene-based phylogenies were inferred from individual trimmed alignments using RAxML (PROTGAMMAJTT + 100 bootstrap), the generated *bestTrees* were examined and used as *pseudo*-bootstrap runs to show the number of genes supporting each node. Visualisation of the trees was done with *FigTree* v. 1.4.4 (https://github.com/rambaut/figtree) and *InkScape* v. 1.2 (https://inkscape.org/).

Genome annotations

All genomes were annotated by using *MAKER* v. 3.01.03 (Cantarel et al. 2008) by inferring predictions from protein homology of 81 453 *Fusarium oxysporum* (FUSOX) amino acid sequences downloaded (in October 2021) from the UniProt/SwissProt database (https://www.uniprot.org/). Metabolite biosynthetic gene clusters were investigated with the fungal *antiSMASH* online tool (https://fungismash.secondarymetabolites.org, in the version available on the server in December 2023) (Blin et al. 2021) using relaxed detection strictness and all available extra features. The carbohydrate-active enzyme (CAZymes) annotation was done with standalone tool *run_dbcan* v. 3.0.5 (Zhang et al. 2018) and default settings. Signal proteins (SP) including small secreted proteins (SSP; <300 aa) were searched with *SignalP6* v. 6.0 g (Teufel et al. 2022) with default settings. Outputs for all programs were processed with custom bash scripts; visualisation of the results was done with *InkScape*. Detailed results for all annotation features of the genomes can be found in Supplementary Table S2. All genomes were submitted to GenBank (see Supplementary Tables S1 and S2 for details).

Reconstruction of ancestral ecological character states

Known lifestyles of each species were codified in nine categories according to published data (Supplementary Fig. S1) and Farr et al. (2021). These categories included: animal associate (reported from an animal host without clear indication of pathogenicity), animal pathogen, endophyte, human pathogen, insect symbiont, mycophilic, plant associate (reported from a plant host without clear indication of pathogenicity), plant pathogen, and saprotroph. Ancestral state reconstructions were carried out using an unordered parsimony model for multistate ecological characters, and a maximum-likelihood reconstruction with Mk1 (Markov k-state 1 parameter) model using the Parsimony and Stochchar packages, respectively, as provided in *Mesquite* v. 3.81 (Maddison and Maddison 2023). Analyses were carried out separately for the main (primary) reported lifestyles and with up to eight combinations/analyses according to the variability of reported secondary lifestyles. Branch lengths for likelihood analyses were estimated from the 263-gene phylogeny as indicated above.

Results

Phylogeny

The phylogenomic tree (based on 263 non-fragmented genes) was similar in topology (i.e. no conflicting topology receiving strong support was found) with the multigene phylogeny obtained by Crous et al. (2021), and separated *Fusarium s. str.* from other genera of *Nectriaceae* (Fig. 1). The F3 node, representing *Fusarium* as defined in a narrower sense as applied by Crous et al. (2021), received 100% bootstrap support and

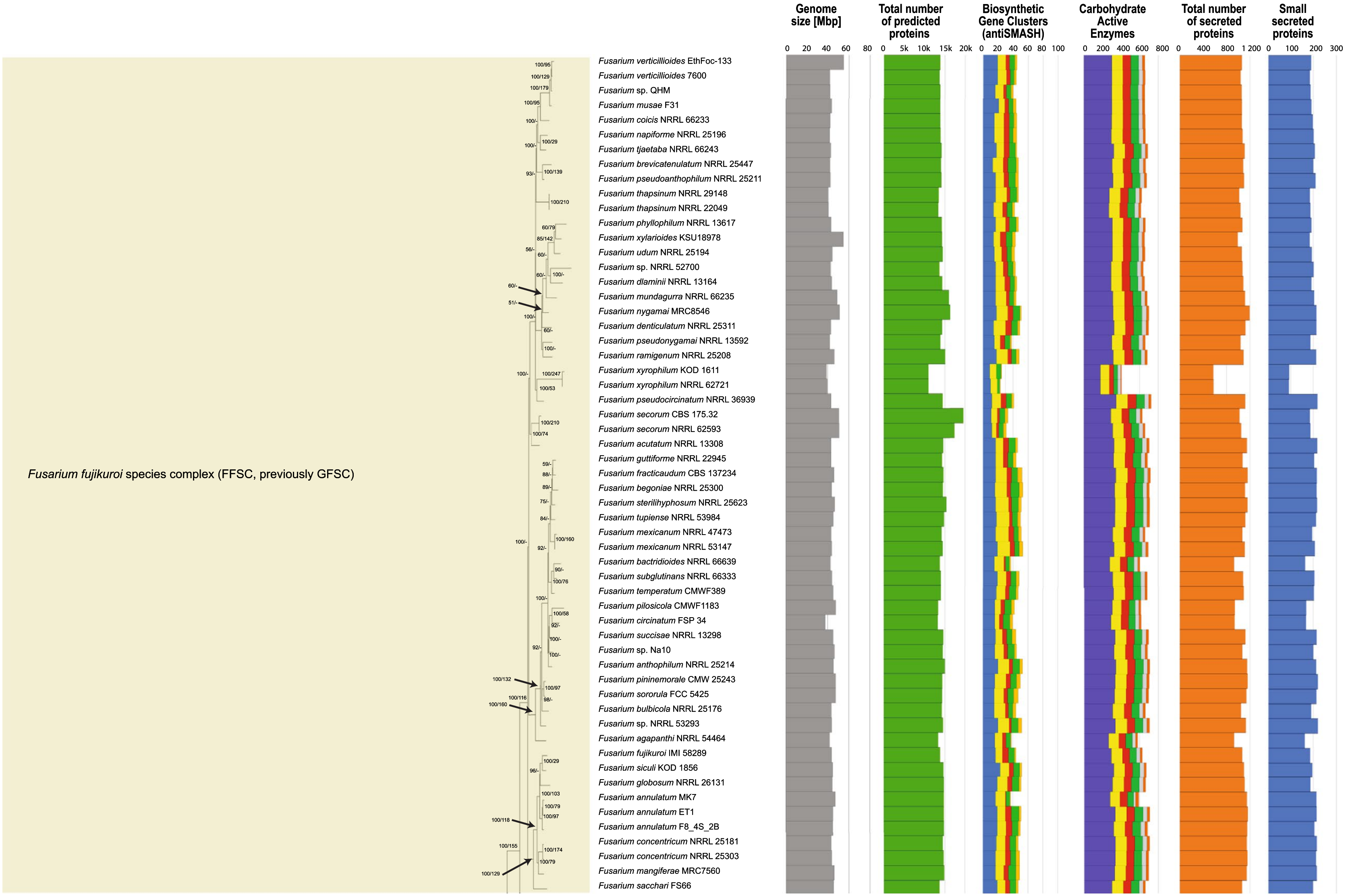


Fig. 1 Annotated phylogenomic tree. Maximum likelihood phylogenetic tree inferred from 263 complete BUSCO genes. The tree was rooted to *Sarocladium implicatum* strain TR. Species complexes and genera are shown to the left of the tree and genome size, total number of predicted proteins, biosynthetic gene clusters, carbohydrate active enzymes, total number of secreted proteins and small secreted proteins are provided to the right of the tree. A legend to the colours for the biosynthetic gene clusters and carbohydrate active enzymes columns are provided on the fifth part of the tree. Some of the basal branches were shortened to facilitate layout. The numbers at the nodes represent the bootstrap support value followed by the number of genes supporting each node, i.e. the number of genes that resolved the same node when used singly for inferring the phylogeny of *Nectriaceae*. The red ovals denote the three concepts of *Fusarium* sensu Geiser et al. (2013, 2021)

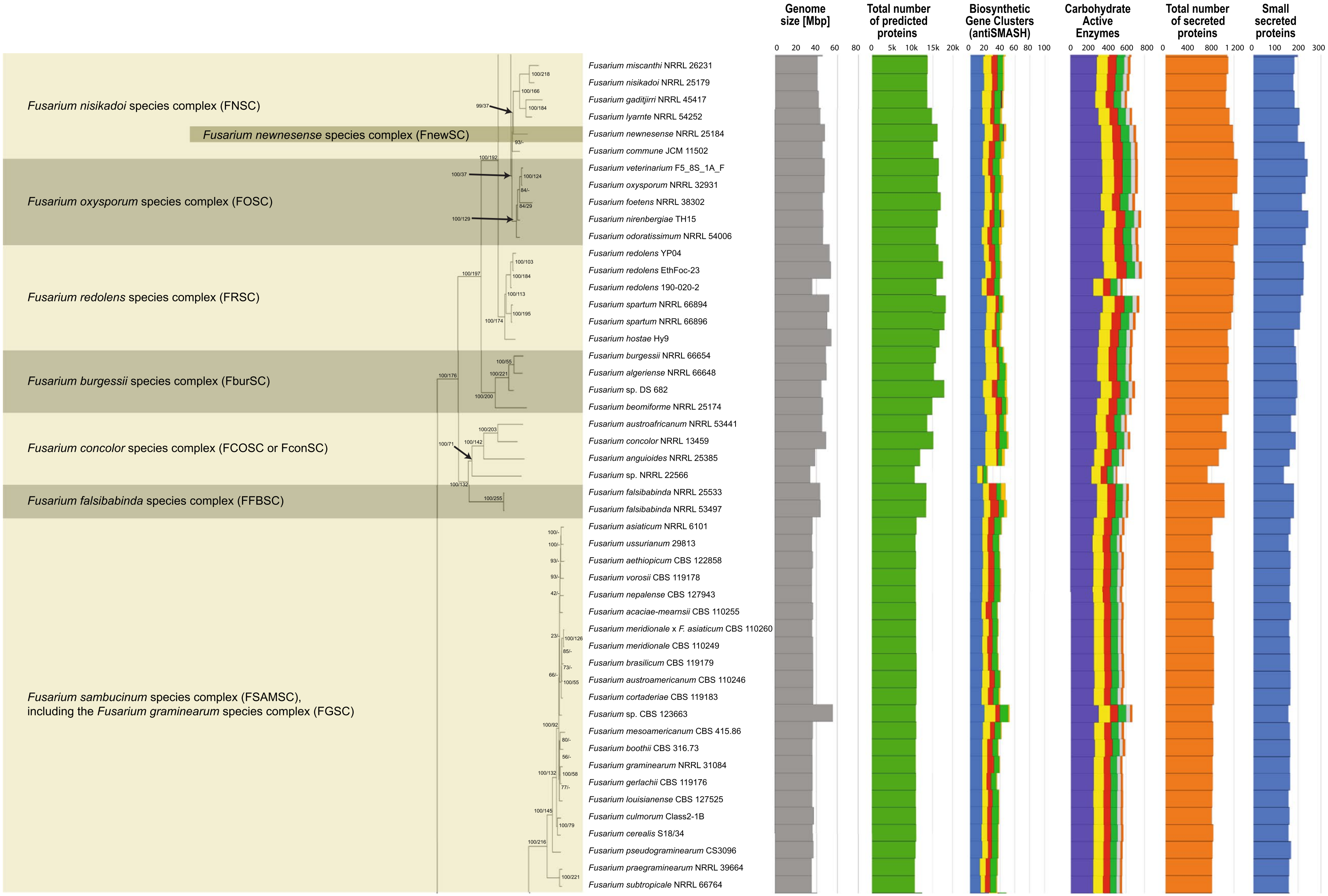


Fig. 1 (continued)

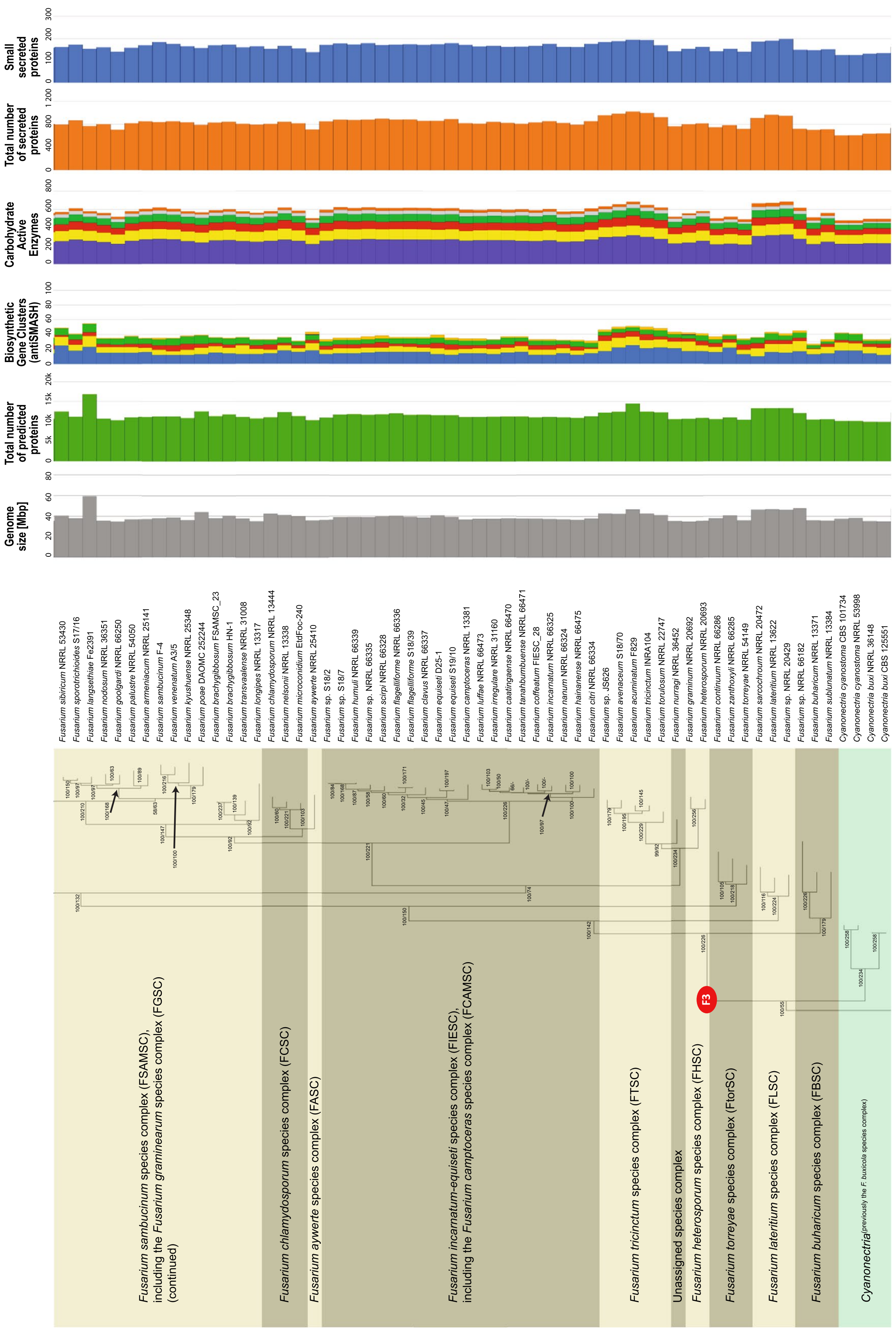


Fig. 1 (continued)

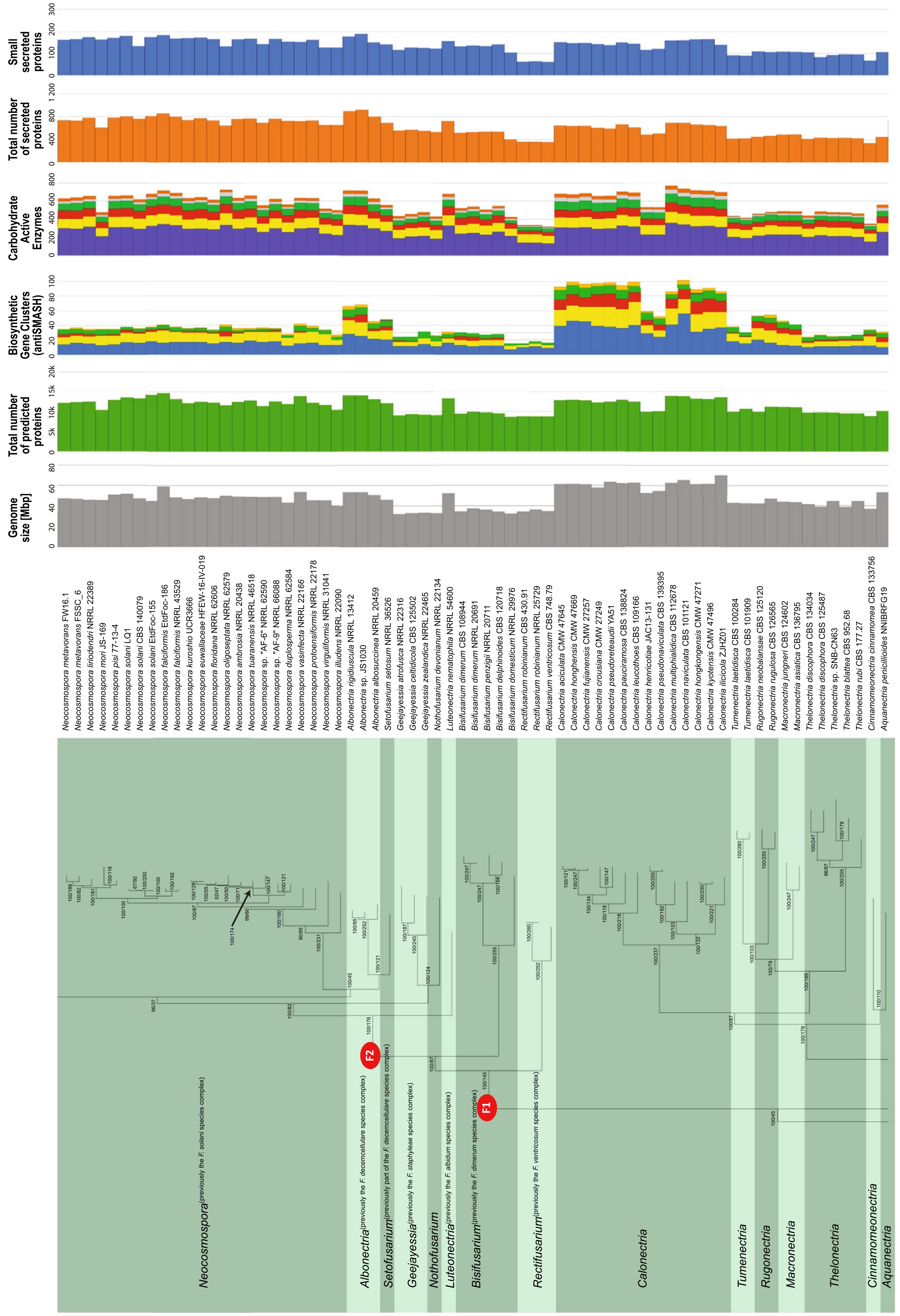


Fig. 1 (continued)

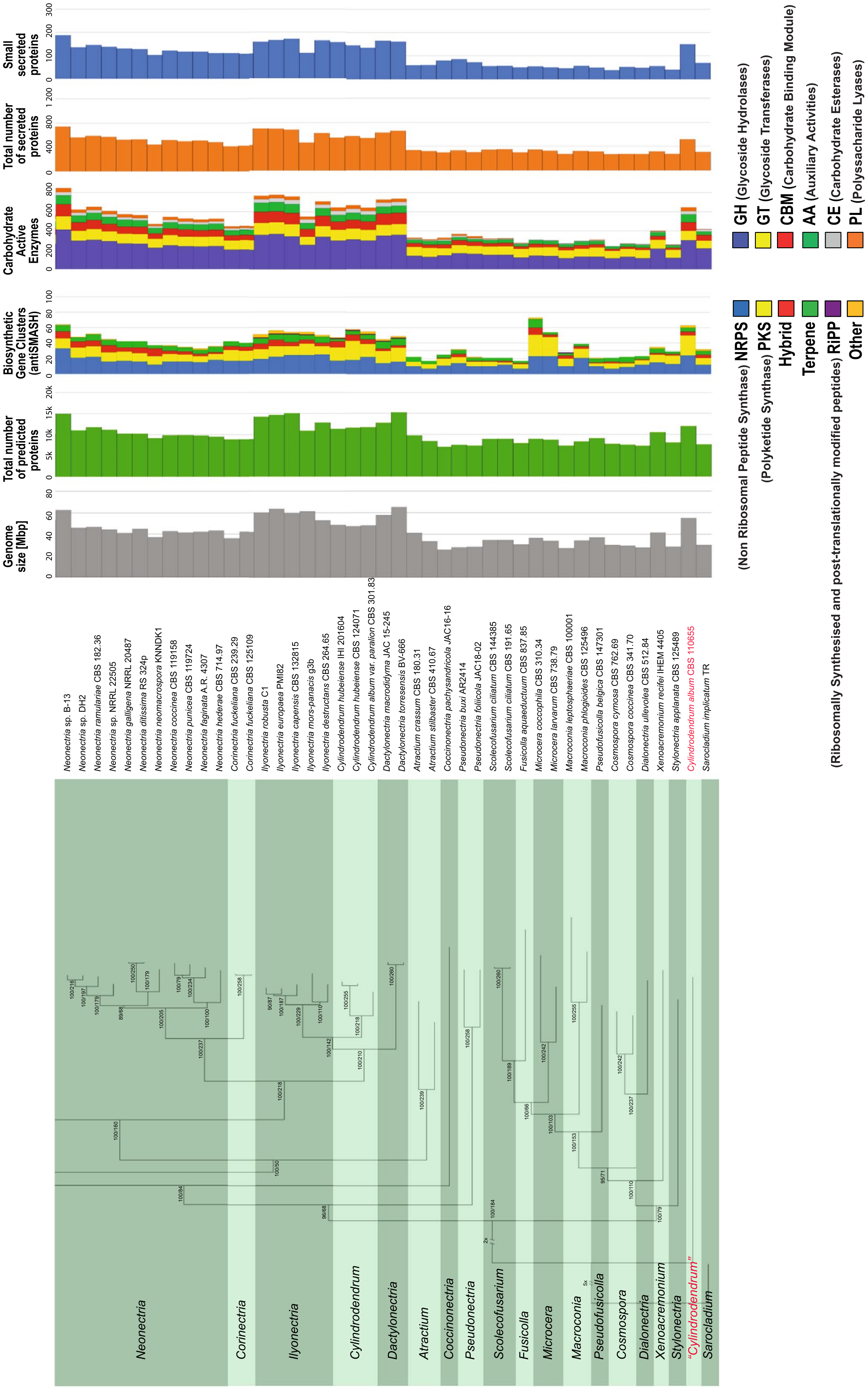


Fig. 1 (continued)

support from 226/263 of the single gene phylogenies while the two alternative nodes representing *Fusarium* in a broader sense, although also with 100% bootstrap support each, received less support on the total number of individual genes (F2: 176/263 and F1: 145/263). The overall topology agrees with previous studies – see discussion on the phylogenetic backbone below.

Seventeen of the 20 currently accepted species complexes in *Fusarium* s.str. are presented in the phylogenetic tree; only the more recently introduced *Fusarium citricola* species complex (FCCSC; Sandoval-Denis et al. 2018), *Fusarium steppicola* species complex (FSTEPSC; Akhmetova et al. 2023) and *Fusarium yunnanense* species complex (FYSC; Liu et al. 2023) are not represented. All species complexes were fully supported in terms of bootstrap support values, with the exception of the *Fusarium nisikadoi* / *Fusarium newnesense* species complexes where *Fusarium newnesense* was nested within the *Fusarium nisikadoi* species complex as currently defined. If *Fusarium commune* is considered as an additional lineage separate from the *Fusarium nisikadoi* / *Fusarium newnesense* species complexes, then the more restricted *Fusarium nisikadoi* species complex (FNSC) would be fully supported. *Fusarium commune* also forms a sister lineage to the other species in the FNSC in the phylogeny of Han et al. (2023; Figs. 10, 14), with *Fusarium newnesense* being the most early-diverging lineage to this treatment of the FNSC.

Genome properties throughout *Nectriaceae*

The assembled genome size of the strains sequenced ranged from about 26 Mb in *Coccinonectria pachysandricola* to about 70 Mb in *Calonectria ilicicola*, while monophyletic subgroups mostly had consistent genome sizes. For example, the clade consisting of *Dactylonectria*, *Cylindrodendrum*, and *Ilyonectria* had the larger genome sizes, ranging from 48 to 65 Mb, while its sister clade, *Neonectria*, had, with one exception, genome sizes below 47 Mb. Similarly, *Calonectria* has the biggest genomes among *Nectriaceae*, ranging from 58 to 70 Mb, while its sister clade, consisting of *Macronectria*, *Rugonectria*, and *Tumenectria* had maximum genome sizes of 47 Mb. *Fusarium* genomes ranged from 34 Mb in *Fusarium* sp. NRRL 22566 to 60 Mb in *Fusarium langsethiae*, while only 13 of 162 *Fusarium* genomes included were larger than 50 Mb. Overall, genome size variation was in line with delineation of several genera in *Nectriaceae*.

Biosynthetic gene clusters

In terms of biosynthetic gene clusters, significant variation was observed across *Nectriaceae*. The genus *Rectifusarium* had the lowest number of biosynthetic gene clusters, while both *Calonectria* and the cluster consisting of *Albonectria* and *Setofusarium* were comparatively rich in such clusters. However, it is noteworthy that also within *Fusarium*, which was mostly of intermediate richness in terms of biosynthetic gene clusters, some species had significantly less of these clusters, *e.g. Fusarium xyrophilum*, which causes pseudoflowers in *Xyris surinamensis*, a member of the *Poales* (Laraba et al. 2020). Interestingly, also the domesticated species *Bisifusarium domesticum* in the genus *Bisifusarium* that diverges next in the phylogenetic reconstructions had very low numbers of biosynthetic gene clusters.

CAZymes

The number of carbohydrate active enzymes is expectedly low in the saprotrophic genus *Rectifusarium*, which is basal to the chiefly saprotrophytic genus *Bisifusarium*, and remains similar in the plant-associated genera diverging next. However, in both the following *Fusarium/Cyanonectria* clade and the *Setofusarium/Albonectria/Neocosmospora* clade, which both mark transitions to a plant pathogenic/symbiotic lifestyle, the number of CAZymes markedly increases. Interestingly, the rise in CAZyme numbers can also be observed in the lineage containing *Calonectria*, *Neonectria*, and other plant-pathogenic genera, while in the earlier-diverging cylindrocarpioid plant-pathogenic genera *Coccinonectria* and *Pseudonectria*, the amount of CAZymes is rather low.

Secretome

The secretome of *Nectriaceae* varies greatly, mostly according to lifestyle. It is smallest in the early-diverging lineages and the saprotrophic genus *Rectifusarium*, with less than 400 total secreted proteins and only about 60 small secreted proteins (SSPs). In contrast, it is greatest in *Fusarium*, where less than 10% of the species code for fewer than 800 secreted proteins and all except for the pseudo-flower-inducing *F. xyprophilum* code for more than 700 SSPs. Also, SSP numbers are high in *Fusarium*, with about 95% of the coding for more than 150 SSPs (up to more than 240), while the genomes of the sister genus of *Fusarium*, *Cyanonectria* code for a maximum of 134 SSPs and also has a lower amount of secreted proteins as compared to *Fusarium*, rendering the genera distinct in terms of their secretomes. Similarly, the secretome of the plant-associated genus *Atractium*, which is the earliest-diverging lineage in the *Calonectria/Ilyonectria* clade, is smaller than 400 secreted proteins and 100 SSPs, while the plant-pathogenic species in the cluster all have a secretome with more than 400 proteins and mostly code for more than 100 SSPs.

Distinctive features of the genera of *Nectriaceae*

Most of the genera of *Nectriaceae* included in this study showed a distinctive combination of genomic features that distinguished them from sister genera. However, there were some monophyletic clades that shared genomic features, despite a somewhat deviating morphology.

The genus *Fusarium* is characterised by a relatively low number of biosynthetic gene clusters, which is contrasted by its rather large secretome, with an abundance of CAZymes and small secreted proteins. Its sister genus, *Cyanonectria*, also had a rather low number of biosynthetic gene clusters. It had both a smaller secretome and lower numbers of CAZymes and small secreted proteins, in line with those *Fusarium* species that evolved a hemibiotrophic to endophytic lifestyle, while *Cyanonectria* is a plant associate, invading moribund plant tissue and mostly living on dead plant material.

The *Cyanonectria* and *Fusarium* clade clustered sister to the clade consisting of *Albonectria*, *Neocosmospora*, and *Setofusarium*. Notable synapogenomic traits are that the genomes in this clade are larger than in its sister clade and that all species have a relatively high amount of polyketide synthases (PKS) while at the same time having a low amount of hybrid PKS / non-ribosomal protein synthases (NRPS). The genus *Albonectria* (characterised by its white ascomata) and its sister genus *Setofusarium* (characterised by setose sporodochia) both had a relatively high amount of biosynthetic gene clusters as compared to their sister clade, *Neocosmospora*. It is notable that *Albonectria* and *Setofusarium* had a similar number of CAZymes and small secreted proteins as their hemibiotrophic sister group, *Neocosmospora*, suggesting that the traditional characterisation as plant associates might need re-examination.

The genera *Geejayessia* and *Nothofusarium* were sister to all previously mentioned genera and were characterised by rather small genome sizes (all smaller than 35 Mb) and low numbers of biosynthetic gene clusters, CAZymes, and small secreted proteins, in line with being opportunistic plant pathogens. There were no genomic features to separate the genera *Geejayessia* and *Nothofusarium*.

The genus *Luteonectria*, which together with all beforementioned genera forms the clade subtending the node F2, is characterised by a rather large genome with more than 50 Mb and a high number of CAZymes, while at the same time coding for a low number of biosynthetic gene clusters. At the same time, it has a larger secretome, similar to *Neocosmospora*, suggesting that it might be an (opportunistic) plant pathogen, despite its characterisation as a plant associate.

Bisfusarium, characterised by small, (1–)2(–3)-septate macroconidia, is sister to all beforementioned groups. In its genetic makeup it is similar to *Geejayessia*, and has a substantial amount of small secreted proteins. This suggests that the genus might have a so far hidden pathogenic lifestyle.

In contrast, the genus *Rectifusarium*, branching below the previous groups, has only a very low number of small-secreted proteins, in line with its saprotrophic nature. In addition, the two members of the genus have a low number of genes coding for CAZymes and biosynthetic gene clusters, suggesting that they might be substrate specialists.

Collectively, the aforementioned genera form a clade representing the node F1, and are sister to a second larger basal clade containing genera that are equally diverse in their genetic repertoire. Also in the basal group, the different genera are mostly well-delimitated in terms of their genomic toolkit. For example, the genus *Calonectria* features the largest genomes of the *Nectriaceae* with very high numbers of biosynthetic gene clusters, in line with its plant pathogenic nature, while the plant associate *Atractium* contains only very low numbers of biosynthetic gene clusters, CAZymes, and small secreted proteins.

In the basal group, there are some generic boundaries that are not supported by genomic features. Examples of these are the separation of *Corinectria* and *Neonectria* (chiefly separated on perithecial wall anatomy; González and Chaverri 2017), as well as the separation of *Ilyonectria*, *Cylindrodendrum*, and *Dactylonectria* (separated on perithecial morphology, asexual morphs and culture characteristics; Lombard et al. 2014). In both cases, the genomic features are not differentiated within the clades, while there are pronounced differences in the sister clades.

Reconstruction of ancestral lifestyles

A lifestyle dataset was compiled including all ecological niches known for each species included in this study; the data sources for lifestyles and hosts for terminal taxa are listed in Table 1 and in the References section. Since most taxa were found to lack a unique lifestyle, conversely reported with multiple lifestyles related to host or substrate associations, ancestral lifestyles were reconstructed using Maximum Likelihood (ML) and Parsimony methods in different combinations, including all published lifestyles. Ancestral lifestyle reconstructions inferred by both methods from the most commonly reported lifestyle (main lifestyle) are shown in Fig. 2, while results based on less common reports (secondary lifestyles) are shown in Supplementary Fig. S1.

The last common ancestor for all taxa included in this study was ambiguous, mapped by ML as most probably a plant pathogen; however, with only a marginal difference (proportional likelihood (PL) 0.155) over plant associate (PL 0.128) and mycophilic (PL 0.124). Parsimony identified

Table 1 Known lifestyles of fungal species included in this study

Species name	Strain[a]	Main lifestyle	Additional recorded lifestyles	Known substrates (for the species)	Reference
Albonectria albosuccinea	NRRL 20459	plant associate	endophyte, saprotroph	*Nectandra lineatifolia*, wood	Rossman et al. (1999)
Albonectria rigidiuscula	NRRL 13412	plant pathogen	plant associate, endophyte, saprotroph	Various angiosperms	Rossman et al. (1999), Farr et al. (2023)
Albonectria sp.	JS1030	plant associate	plant associate	*Distylium racemosum*	Unpublished, as in GenBank
Aquanectria penicillioides	NNIBRFG19	saprotroph	endophyte	Submerged plant material, *Acer* sp.	Wardeh et al. (2015), Farr et al. (2023)
Atractium crassum	**CBS 180.31**	plant associate	-	Submerged plant material, metallic water pipe	Gräfenhan et al. (2011), Wollenweber (1931)
Atractium stilbaster	**CBS 410.67**	plant associate	-	Submerged plant material, decaying bark	Gräfenhan et al. (2011)
Bisifusarium delphinoides	**CBS 120718**	saprotroph	plant associate, human pathogen, plant pathogen, mycophilic	*Bryophyllum* sp., *Citrus* sp., *Hoodia gordonii, Plasmopara viticola, Cucumis melo, Homo sapiens*	Farr et al. (2023)
Bisifusarium dimerum	**CBS 108944** NRRL 20691	saprotroph	human pathogen, plant pathogen, endophyte	Various angiosperms, *Homo sapiens*	Farr et al. (2023)
Bisifusarium domesticum	NRRL 29976	saprotroph	-	Cheese	Schroers et al. (2011)
Bisifusarium penzigii	NRRL 20711	saprotroph	human pathogen,	*Fagus sylvatica, Homo sapiens*	Schroers et al. (2011)
Calonectria aciculata	CMW 47645	plant pathogen	-	*Eucalyptus urophylla* × *E. grandis* hybrid clone	Farr et al. (2023)
Calonectria crousiana	CMW 27249	plant pathogen	-	*Eucalyptus grandis*	Farr et al. (2023)
Calonectria fujianensis	CMW 27257	plant pathogen	-	*Eucalyptus* spp.	Farr et al. (2023)
Calonectria henricotiae	JAC13-131	plant pathogen	-	*Buxus* spp.	Farr et al. (2023)
Calonectria honghensis	CMW 47669	plant pathogen	saprotroph	Soil	Farr et al. (2023)
Calonectria hongkongensis	CMW 47271	plant pathogen	saprotroph	Soil, *Nephelium lappaceum*	Farr et al. (2023)
Calonectria ilicicola	ZJHZ01	plant pathogen	saprotroph	Various angiosperms and gymnosperms, *Homo sapiens*	Farr et al. (2023)
Calonectria kyotensis	CMW 47496	plant pathogen	-	Soil, various angiosperms and gymnosperms	Farr et al. (2023)
Calonectria leucothoes	CBS 109166	plant pathogen	-	*Leucothoe axillaris*	Farr et al. (2023)
Calonectria multiphialidica	CBS 112678	plant pathogen	-	Soil, *Musa* sp.	Farr et al. (2023)
Calonectria naviculata	CBS 101121	plant pathogen	-	Soil	Crous et al. (2002)
Calonectria pauciramosa	CBS 138824	plant pathogen	-	Various angiosperms, *Wollemia nobilis*	Farr et al. (2023)
Calonectria pseudonaviculata	CBS 139395	plant pathogen	-	*Buxus* spp., *Pachysandra* spp., *Sarcococca* spp.	Farr et al. (2023)
Calonectria pseudoreteaudii	YA51	plant pathogen	-	*Eucalyptus* spp.	Farr et al. (2023)
Cinnamomeonectria cinnamomea	**CBS 133756**	saprotroph	-	Recently dead and decaying woody plants	Salgado-Salazar et al. (2016)

Table 1 (continued)

Species name	Strain[a]	Main lifestyle	Additional recorded lifestyles	Known substrates (for the species)	Reference
Coccinonectria pachysandricola	JAC16-16	plant pathogen	-	*Pachysandra terminalis, Sarcococca hookeriana, Sarcococca hookeriana var. humilis*	Farr et al. (2023)
Corinectria fuckeliana	**CBS 239.29** CBS 125109	plant pathogen	saprotroph	*Abies* spp., *Picea* spp., *Pinus* spp., *Larix* sp.	Farr et al. (2023), González and Chaverri (2017)
Cosmospora coccinea	**CBS 341.70**	mycophilic	-	*Inonotus* sp., *Fagus* sp., *Alnus* sp.	Rossman et al. (1999)
Cosmospora cymosa	**CBS 762.69**	mycophilic	-	*Inonotus radiatus on alnus glutinosa*	Gräfenhan et al. (2011)
Cyanonectria buxi	**CBS 125551** NRRL 36148	plant associate	-	*Buxus sempervirens*	Schroers et al. (2011)
Cyanonectria cyanostoma	**CBS 101734** NRRL 53998	plant associate	-	*Buxus sempervirens. Buxus* sp.	Schroers et al. (2011), Farr et al. (2023)
Cylindrodendrum album var. paralion	**CBS 301.83**	plant pathogen	-	*Fucus distichus*	Summerbell et al. (2011)
Cylindrodendrum hubeiense	**CBS 124071** IHI 201604	plant pathogen	-	*Rhododendron* sp., *Viscum album, Castanea sativa*	Wardeh et al. (2015), Farr et al. (2023)
Dactylonectria macrodidyma	JAC 15–245	plant pathogen	-	Unknown	Farr et al. (2023)
Dactylonectria torresensis	BV-666	plant pathogen	-	*Vitis vinifera*	Farr et al. (2023)
Dialonectria ullevolea	**CBS 512.84**	mycophilic	-	Ascomycete stromata	Gräfenhan et al. (2011)
Fusarium acaciae-mearnsii	CBS 110255	plant pathogen	saprotroph	*Acacia mearnsii, Triticum aestivum, soil*	Farr et al. (2023)
Fusarium acuminatum	F829	saprotroph	plant associate, plant pathogen, endophyte, mycophilic	Various angiosperms, *Pinus* sp., *Homo sapiens*	Wardeh et al. (2015), Farr et al. (2023)
Fusarium acutatum	NRRL 13308	plant associate	animal associate, human pathogen, plant pathogen	*Homoptera* sp., *Homo sapiens, Cajanus* sp., *Triticum* sp., *Cyamopsis tetragonoloba*	Farr et al. (2023)
Fusarium aethiopicum	CBS 122858	plant pathogen	-	*Triticum* sp.	Farr et al. (2023)
Fusarium agapanthi	NRRL 54464	plant pathogen	-	*Agapanthus africanus, Agapanthus praecox*	Farr et al. (2023)
Fusarium algeriense	NRRL 66648	plant pathogen	-	*Triticum* sp. *Triticum durum, Triticum aestivum*	Farr et al. (2023)
Fusarium anguioides	NRRL 25385	plant associate	saprotroph	Soil, various angiosperms	Farr et al. (2023)
Fusarium annulatum	ET1 F8_4S_2B MK7	endophyte	plant associate, human pathogen, plant pathogen, mycophilic, saprotroph	Soil, various angiosperms and gymnosperms, *Homo sapiens*	Farr et al. (2023)
Fusarium anthophilum	NRRL 25214	plant associate	human pathogen, plant pathogen, endophyte	Various angiosperms, *Homo sapiens*	Wardeh et al. (2015), Farr et al. (2023)
Fusarium armeniacum	NRRL 25141	saprotroph	animal pathogen, plant pathogen, endophyte	Soil, various animals	Lu et al. (2012), Al-Hatmi (2016), Farr et al. (2023)

Table 1 (continued)

Species name	Strain[a]	Main lifestyle	Additional recorded lifestyles	Known substrates (for the species)	Reference
Fusarium asiaticum	NRRL 6101	plant pathogen	plant associate	Various angiosperms	Farr et al. (2023)
Fusarium austroafricanum	NRRL 53441	saprotroph	endophyte	*Pennisetum clandestinum*	Jacobs-Venter et al. (2018)
Fusarium austroamericanum	CBS 110246	plant pathogen	endophyte, mycophilic	*Hordeum vulgare, Polyporus* sp., *Zea mays*	O'Donnell et al. 2004, Farr et al. (2023)
Fusarium avenaceum	S18/70	plant pathogen	plant associate, animal pathogen, endophyte, saprotroph	Various angiosperms, various animals	Farr et al. (2023)
Fusarium aywerte	NRRL 25410	plant associate	saprotroph	*Triodia basedowii*	Sangalang et al. (1995)
Fusarium bactridioides	NRRL 66639	endophyte	animal associate, mycophilic	*Cronartium* spp. on *Pinus* spp., *Cucumis sativus, Narcissus poeticus,* various animals	Wardeh et al. (2015), Farr et al. (2023)
Fusarium begoniae	NRRL 25300	plant pathogen	endophyte	*Begonia elatior*	Farr et al. (2023)
Fusarium beomiforme	NRRL 25174	saprotroph	plant associate, plant pathogen	Soil, *Sorghum bicolor, Zea mays*	Farr et al. (2023)
Fusarium boothii	CBS 316.73	plant pathogen	animal pathogen	*Carya illinoinensis, Triticum* sp., *Vachellia erioloba, Zea mays,* various animals	Lu et al. (2012), Farr et al. (2023)
Fusarium brachygibbosum	HN-1 FSAMSC_23	plant pathogen	endophyte, mycophilic, saprotroph	Various angiosperms, *Plasmopara viticola*	Farr et al. (2023)
Fusarium brasilicum	CBS 119179	plant pathogen	-	*Avena sativa*	Farr et al. (2023)
Fusarium brevicatenulatum	NRRL 25447	plant pathogen	endophyte	*Eleusine* spp., *Oryza sativa, Panicum repens, Striga asiatica, Zea mays*	Farr et al. (2023)
Fusarium buharicum	NRRL 13371	plant pathogen	-	*Gossypium* spp., *Hibiscus cannabinus*	Farr et al. (2023)
Fusarium bulbicola	NRRL 25176	plant pathogen	endophyte, saprotroph	*Glycine max, Haemanthus* sp., *Nerine bowdenii*	Farr et al. (2023)
Fusarium burgessii	NRRL 66654	saprotroph	-	Soil	Laurence et al. (2011)
Fusarium caatingaense	NRRL 66470	animal pathogen	-	Various angiosperms, *Juniperus chinensis*	Santos et al. (2019), Farr et al. (2023)
Fusarium camptoceras	NRRL 13381	saprotroph	animal pathogen, endophyte	Various angiosperms and animal species	Lu et al. (2012), Farr et al. (2023)
Fusarium cerealis	S18/34	saprotroph	plant pathogen, endophyte	Various angiosperms	Farr et al. (2023)
Fusarium chlamydosporum	NRRL 13444	saprotroph	human pathogen, endophyte	Various angiosperms, *Pinus halepensis, Homo sapiens*	Taylor et al. (2001), Farr et al. (2023)
Fusarium circinatum	FSP 34	plant pathogen	animal associate, endophyte	*Pinus* spp., *Pseudotuga menziesii, Picea abies*	Farr et al. (2023)
Fusarium citri	NRRL 66334	endophyte	-	*Citrus reticulata, Capsicum* sp.	Farr et al. (2023)
Fusarium clavus	NRRL 66337	saprotroph	plant associate, human pathogen, endophyte	Various angiosperms, *Homo sapiens*	Xia et al 2019, Farr et al. (2023)

Table 1 (continued)

Species name	Strain^a	Main lifestyle	Additional recorded lifestyles	Known substrates (for the species)	Reference
Fusarium coffeatum	FIESC_28	saprotroph	plant associate, plant pathogen, endophyte	*Cynodon lemfuensis*	Lombard et al. (2019a, b)
Fusarium coicis	NRRL 66233	endophyte	-	*Coix gasteenii*	Farr et al. (2023)
Fusarium commune	JCM 11502	saprotroph	plant associate, plant pathogen, endophyte	Various angiosperms and gymnosperms, sediments, soil	Farr et al. (2023)
Fusarium concentricum	NRRL 25181 NRRL 25303	endophyte	plant pathogen, saprotroph	*Musa sapientum, Nilaparvata lugens, Oryza sativa*	Wardeh et al. (2015), O'Donnell (2018), Farr et al. (2023)
Fusarium concolor	NRRL 13459	saprotroph	endophyte	Soil, *Hordeum vulgare, Coffea* sp.	Farr et al. (2023)
Fusarium continuum	NRRL 66286	plant pathogen	-	*Zanthoxylum bungeanum*	Farr et al. (2023)
Fusarium cortaderiae	CBS 119183	plant pathogen	-	*Cortaderia jubata, Lolium multiflorum, Zea mays*	Farr et al. (2023)
Fusarium culmorum	Class2-1B	saprotroph	plant associate, animal associate, plant pathogen, endophyte, mycophilic	Various angiosperms and gymnosperms, soil, various animals including *Homo sapiens*	Lu et al. (2012), Wardeh et al. (2015), Farr et al. (2023)
Fusarium denticulatum	NRRL 25311	plant pathogen	endophyte	*Ipomoea batatas*	Wardeh et al. (2015), Farr et al. (2023)
Fusarium dlaminii	NRRL 13164	saprotroph	saprotroph	Soil, *Zea mays* plant debris	Farr et al. (2023)
Fusarium equiseti	D25-1	plant pathogen	human pathogen, endophyte	Various angiosperms and gymnosperms, *Homo sapiens*, diverse fungal species	Lu et al. (2012), Wardeh et al. (2015), Farr et al. (2023)
Fusarium equiseti	S19/10	endophyte	human pathogen, plant pathogen	*Homo sapiens, diverse fungal* spp.	Lu et al. (2012), Wardeh et al. (2015), Farr et al. (2023)
Fusarium falsibabinda	NRRL 25533 NRRL 53497	endophyte	animal associate, animal pathogen, saprotroph	*Lymantria dispar*, soil, *Pinus strobus, Adelges tsugae, Pseudotsuga menziesii, Gleditsia triacanthos*	Jacobs-Venter et al. (2018)
Fusarium flagelliforme	NRRL 66336 S18/39	endophyte	endophyte, plant associate	*Glycine max, Pinus negra, Triticum* sp., *Thuja* sp. *Hordeum vulgare*	Farr et al. (2023)
Fusarium foetens	NRRL 38302	plant pathogen	-	*Begonia* spp. *Nicotiana tabacum*	Farr et al. (2023)
Fusarium fracticaudum	CBS 137234	plant pathogen	plant associate, endophyte	*Pinus maximinoi*	Wardeh et al. (2015), Farr et al. (2023)
Fusarium fujikuroi	IMI 58289	plant pathogen	human pathogen, endophyte, saprotroph	Various angiosperms and gymnosperms, *Homo sapiens*	Wardeh et al. (2015), Al-Hatmi (2016), Farr et al. (2023)
Fusarium gaditjirri	NRRL 45417	endophyte	-	*Heteropogon triticeus, Themeda triandra*	Farr et al. (2023)
Fusarium gerlachii	CBS 119176	plant pathogen	endophyte	*Triticum aestivum, Arundo donax, Dactylis glomerata*	Farr et al. (2023)
Fusarium globosum	NRRL 26131	plant associate	plant pathogen, endophyte	*Austrostipa aristiglumis, Hordeum vulgare, Triticum aestivum, Triticum* sp., *Zea mays*	Farr et al. (2023)

Table 1 (continued)

Species name	Strain[a]	Main lifestyle	Additional recorded lifestyles	Known substrates (for the species)	Reference
Fusarium goolgardi	NRRL 66250	endophyte	-	*Xanthorrhoea glauca*	Wardeh et al. (2015), Farr et al. (2023)
Fusarium graminearum	NRRL 31084	plant pathogen	plant associate, endophyte, mycophilic, saprotroph	Various angiosperms and gymnosperms, *Sclerotinia sclerotiorum*	Farr et al. (2023), Torbati et al. (2021)
Fusarium graminum	NRRL 20692	endophyte	-	*Axonopus affinis, Malus sylvestris, Paspalum dilatatum, Secale cereale, Trifolium subterraneum, Vicia faba*	Farr et al. (2023)
Fusarium guttiforme	NRRL 22945	plant pathogen	endophyte	*Ananas comosus*	Wardeh et al. (2015), Farr et al. (2023)
Fusarium hainanense	NRRL 66475	endophyte	-	*Acacia* sp., *Musa* spp., *Oryza australiensis, Oryza* sp.	Farr et al. (2023)
Fusarium heterosporum	NRRL 20693	endophyte	plant pathogen, mycophilic, saprotroph	Various angiosperms and gymnosperms	Wardeh et al. (2015), Farr et al. (2023)
Fusarium hostae	Hy9	plant pathogen	plant associate, endophyte	*Hosta* sp., *Hyacinthus* sp., *Triticum* spp.	Wardeh et al. (2015), Farr et al. (2023)
Fusarium humuli	NRRL 66339	endophyte	-	Various angiosperms	Farr et al. (2023)
Fusarium incarnatum	NRRL 66325	plant pathogen	animal associate, human pathogen, endophyte	*Various angiosperms,* diverse animal species including *Homo sapiens*	Taylor et al. (2001), Lu et al. (2012), Wardeh et al. (2015), Al-Hatmi (2016), Farr et al. (2023)
Fusarium irregulare	NRRL 31160	endophyte	human pathogen	Bamboo, *Homo sapiens*	Xia et al. (2019), Wang et al. (2019)
Fusarium kyushuense	NRRL 25348	plant pathogen	animal pathogen, saprotroph	Animal spp., *Nicotiana tabacum, Oryza sativa, Triticum aestivum, Zea mays*	Lu et al. (2012), Wardeh et al. (2015), Farr et al. (2023)
Fusarium langsethiae	Fe2391	plant associate	human pathogen, plant pathogen, endophyte	*Avena sativa, Homo sapiens, Triticum* spp.	Al-Hatmi (2016), Farr et al. (2023)
Fusarium lateritium	NRRL 13622	endophyte	plant pathogen	Various angiosperms and gymnosperms	Lu et al. (2012), Wardeh et al. (2015), Farr et al. (2023)
Fusarium longipes	NRRL 13317	saprotroph	plant pathogen, endophyte, mycophilic	*Elettaria cardamomum, Musa* sp., *Oryza* sp., *Parkinsonia aculeata, Paspalum* sp., *Pennisetum typhoides, Sclerospora graminicola, Stylosanthes* sp.,	Lu et al. (2012), Wardeh et al. (2015), Torbati et al. (2021), Farr et al. (2023)
Fusarium louisianense	CBS 127525	endophyte	endophyte	*Triticum aestivum*	Wardeh et al. (2015), Farr et al. (2023)
Fusarium luffae	NRRL 66473	endophyte	-	*Humulus scandens, Luffa aegyptiaca, Setaria verticillata*	Farr et al. (2023)
Fusarium lyarnte	NRRL 54252	endophyte	saprotroph	Soil, *Sorghum interjectum*	Walsh et al. 2010, Farr et al. (2023)
Fusarium mangiferae	MRC7560	plant pathogen	endophyte	*Mangifera indica, Sansevieria trifasciata, Vanilla planifolia*	Farr et al. (2023)

Table 1 (continued)

Species name	Strain^a	Main lifestyle	Additional recorded lifestyles	Known substrates (for the species)	Reference
Fusarium meridionale	CBS 110249	plant pathogen	endophyte	*Amorphophallus konjac, Citrus* sp., *Glycine max, Hordeum vulgare, Oryza sativa, Solanum lycopersicum, Triticum aestivum, Zea mays*	Farr et al. (2023)
Fusarium meridionale x *Fusarium asiaticum*	CBS 110260	plant pathogen	endophyte	*Amorphophallus konjac, Citrus* sp., *Glycine max, Hordeum vulgare, Oryza sativa, Solanum lycopersicum, Triticum aestivum, Zea mays*	Farr et al. (2023)
Fusarium mesoamericanum	CBS 415.86	plant pathogen	endophyte	*Musa* sp.	Farr et al. (2023)
Fusarium mexicanum	NRRL 47473 NRRL 53147	plant pathogen	-	*Mangifera indica, Swietenia macrophylla*	Wardeh et al. (2015), Farr et al. (2023)
Fusarium microconidium	EtdFoc-240	saprotroph	plant associate, endophyte	*Cicer arietinum*	Unpublished, as in GenBank
Fusarium miscanthi	NRRL 26231	endophyte	-	*Miscanthus sinensis*	Wardeh et al. (2015), Farr et al. (2023)
Fusarium mundagurra	NRRL 66235	saprotroph	plant associate, human pathogen	*Homo sapiens,* soil	Laurence et al. (2015), Al Yazidi et al. (2019)
Fusarium musae	F31	plant pathogen	plant associate, animal associate, human pathogen	*Musa* sp., *Homo sapiens*	Al-Hatmi (2016), Bartoszewicz et al. (2022), Farr et al. (2023)
Fusarium nanum	NRRL 66324	endophyte	-	*Musa nana, Oryza* sp., *Solanum lycopersicum, Triticum* sp.	Farr et al. (2023)
Fusarium napiforme	NRRL 25196	endophyte	plant associate, human pathogen, plant pathogen, saprotroph	*Homo sapiens, Oryza sativa, Pennisetum typhoides,* soil, *Sorghum* spp., *Vanilla planifolia*	Taylor et al. (2001), Al-Hatmi (2016), Farr et al. (2021)
Fusarium nelsonii	NRRL 13338	plant pathogen	-	*Medicago* sp., *Cucumis sativus, Sorghum caffrorum, Sorghum* sp., *Triticum aestivum, Zea mays*	Wardeh et al. (2015), Farr et al. (2023)
Fusarium nepalense	CBS 127943	endophyte	plant associate	*Oryza sativa*	Wardeh et al. (2015), Farr et al. (2023)
Fusarium newnesense	NRRL 25184	saprotroph	-	Soil	Laurence et al. (2015)
Fusarium nirenbergiae	TH15	endophyte	plant associate	*Agathosma betulina, Asparagus officinalis, Bouvardia longiflora, Chrysanthemum* sp., *Dianthus caryophyllus, Passiflora edulis,* soil, *Solanum* spp., *Tetrastigma hemsleyanum, Tulipa* sp.	Farr et al. (2023), Xiang et al. (2021)
Fusarium nisikadoi	NRRL 25179	endophyte	-	*Bertholletia excelsa, Phyllostachys nigra, Phyllostachys nigra* var. *henonis, Triticum aestivum*	Farr et al. (2023)
Fusarium nodosum	NRRL 36351	endophyte	-	*Arachis hypogaea, Arundo donax, Triticum aestivum, Triticum* sp.	Farr et al. (2023)

Table 1 (continued)

Species name	Strain[a]	Main lifestyle	Additional recorded lifestyles	Known substrates (for the species)	Reference
Fusarium nurragi	NRRL 36452	saprotroph	endophyte	Soil, *Spinifex* sp.	Benyon et al. (2000), Leslie & Summerell (2006)
Fusarium nygamai	MRC8546	endophyte	human pathogen, plant pathogen, saprotroph	Various angiosperms, *Homo sapiens*	Al-Hatmi (2016), Farr et al. (2023)
Fusarium odoratissimum	NRRL 54006	plant pathogen	endophyte, saprotroph	*Albizzia julibrissin, Asparagus officinalis, Musa acuminata* spp., soil	Farr et al. (2023)
Fusarium oxysporum	NRRL 32931	plant pathogen	plant associate, human pathogen, endophyte, mycophilic, saprotroph	Various angiosperms, gymnosperms and fungal species soil, *Homo sapiens*	Taylor et al. (2001), Lu et al. (2012), Wardeh et al. (2015)
Fusarium palustre	NRRL 54050	endophyte	-	*Spartina alterniflora*	Wardeh et al. (2015), Farr et al. (2023)
Fusarium phyllophilum	NRRL 13617	plant pathogen	endophyte	*Dracaena deremensis, Gasteria excavata, Gasteria* sp., *Sansevieria dooneri*	Wardeh et al. (2015), Farr et al. (2023)
Fusarium pilosicola	CMWF1183	endophyte	-	*Bidens pilosa*	Yilmaz et al. (2021)
Fusarium pininemorale	CMW 25243	plant pathogen	plant associate, endophyte	*Pinus tecunumanii*	Wardeh et al. (2015), Farr et al. (2023)
Fusarium poae	DAOMC 252244	plant pathogen	endophyte	Various angiosperms	Farr et al. (2023)
Fusarium praegraminearum	NRRL 39664	plant pathogen	plant associate, endophyte, saprotroph	Litter in maize field	Gräfenhan et al. (2016)
Fusarium pseudoanthophilum	NRRL 25211	plant associate	plant pathogen, endophyte	*Zea mays*	Wardeh et al. (2015), Farr et al. (2023)
Fusarium pseudocircinatum	NRRL 36939	plant associate	animal associate, human pathogen, plant pathogen, endophyte, saprotroph	*Handroanthus chrysotrichus, Heteropsylla incisa, Homo sapiens, Homoptera, leaves, dead, Mangifera indica, Musa acuminata, Pinus kesiya, Sansevieria trifasciata, Solanum* sp., *Swietenia macrophylla, Vanilla planifolia*	Wardeh et al. (2015), Farr et al. (2023)
Fusarium pseudograminearum	CS3096	plant pathogen	plant associate, animal associate, endophyte, saprotroph	*Avena sativa, Hordeum vulgare, Medicago* sp., *Medicago truncatula, Phalaris paradoxa,* putative animal hosts, *Triticum* sp.	Bartoszewicz et al. (2022), Farr et al. (2023)
Fusarium pseudonygamai	NRRL 13592	endophyte	plant pathogen	*Oryza sativa, Pennisetum typhoides, Plasmopara viticola*	Wardeh et al. (2015), Farr et al. (2023)
Fusarium ramigenum	NRRL 25208	endophyte	human pathogen	*Ficus carica, Homo sapiens*	Wardeh et al. (2015), Al-Hatmi (2016), Farr et al. (2023)

Table 1 (continued)

Species name	Strain[a]	Main lifestyle	Additional recorded lifestyles	Known substrates (for the species)	Reference
Fusarium redolens	190–020-2	endophyte	plant associate, plant pathogen, animal pathogen	Soil, various angiosperms, *Pinus halepensis*	Farr et al. (2023), O'Donnell et al. (2012), Rashmi et al. (2019)
	EthFoc-23				
	YP04				
Fusarium sacchari	FS66	endophyte	human pathogen, plant pathogen	Various angiosperms and gymnosperms, *Homo sapiens*	Taylor et al. (2001), Rashmi et al. (2019), Farr et al. (2023)
Fusarium sambucinum	F-4	plant associate	plant pathogen, endophyte, saprotroph	Various angiosperms, *Pinus* spp.	Rashmi et al. (2019), Farr et al. (2023)
Fusarium sarcochroum	NRRL 20472	plant associate	plant pathogen, endophyte	*Citrus* spp., *Lycopersicon esculentum, Persica vulgaris, Sarothamnus scoparius, Trifolium pratense, Viscum album, Zea mays*	Wardeh et al. (2015), Farr et al. (2023)
Fusarium scirpi	NRRL 66328	plant pathogen	endophyte	Various angiosperms	Farr et al. (2023)
Fusarium secorum	**CBS 175.32**	plant pathogen	plant associate, saprotroph	*Beta vulgaris,* soil	Secor et al. (2014), Farr et al. (2023)
	NRRL 62593				
Fusarium sibiricum	NRRL 53430	endophyte	-	*Avena sativa*	Farr et al. (2023)
Fusarium siculi	KOD 1856	endophyte	saprotroph	*Citrus sinensis*	Farr et al. (2023)
Fusarium sororula	FCC 5425	plant pathogen	plant associate, endophyte	*Pinus patula*	Farr et al. (2023)
Fusarium sp.	CBS 123663	saprotroph	-	Soil	Unpublished, as in GenBank
	DS 682	saprotroph	-	*Bouteloua gracilis* rhizophere	Bhattacharjee et al. (2021)
	JS626	endophyte	-	*Rubus takesimensis*	Unpublished, as in GenBank
	Na10	endophyte	-	*Narcissus* sp.	Unpublished, as in GenBank
	NRRL 22566	endophyte	-	Bamboo culm	Farr et al. (2023)
	NRRL 52700	animal associate	-	*Mahanarva andigena*	O'Donnell et al. (2012)
	NRRL 53293	saprotroph	-	*Cinchina* sp.	Otero-Colina et al. (2010)
	NRRL 66182	plant pathogen	-	*Hibiscus moscheutos*	Kim et al. (2020)
	NRRL 66335	saprotroph	-	*Triticum* sp.	Villani et al. (2019)
	QHM	saprotroph	-	Water	Zhu et al. (2020)
	S18/2	endophyte	plant associate	*Glycine max*	Unpublished, as in GenBank
	S18/7	endophyte	plant associate	*Glycine max*	Unpublished, as in GenBank
Fusarium spartum	NRRL 66894	endophyte	saprotroph	*Macrochloa tenacissima,* soil	Gargouri et al. (2020)
	NRRL 66896				
Fusarium sporotrichioides	S17/16	saprotroph	animal pathogen, plant pathogen, endophyte	Various angiosperms and animal species, *Pinus* spp.	Lu et al. (2012), Rashmi et al. (2019), Farr et al. (2023)
Fusarium sterilihyphosum	NRRL 25623	plant pathogen	endophyte	*Butea monosperma, Mangifera indica*	Rashmi et al. (2019), Farr et al. (2023)

Table 1 (continued)

Species name	Strain[a]	Main lifestyle	Additional recorded lifestyles	Known substrates (for the species)	Reference
Fusarium stilboides	NRRL 20429	plant pathogen	endophyte	*Brachiaria brizantha, Citrus* spp., *Coffea arabica, Eriobotrya japonica, Linum usitatissimum, Lycopersicon esculentum, Pinus* spp.	Wardeh et al. (2015), Farr et al. (2023)
Fusarium subglutinans	KOD 1611 NRRL 66333	plant pathogen	plant associate, human pathogen, endophyte	Various angiosperms, *Pinus* spp., *Homo sapiens*	Taylor et al. (2001), Rashmi et al. (2019), Farr et al. (2023)
Fusarium sublunatum	NRRL 13384	saprotroph	-	Soil	Gerlach & Nirenberg (1982)
Fusarium subtropicale	NRRL 66764	plant pathogen	-	*Hordeum vulgare*	Farr et al. (2023)
Fusarium succisae	NRRL 13298	plant pathogen	endophyte	*Coreopsis verticillata, Musa* sp., *Succisa pratensis, Zea mays*	Rashmi et al. (2019), Wardeh et al. (2015), Farr et al. (2023)
Fusarium tanahbumbuense	NRRL 66471	endophyte	-	*Musa acuminata* var. *Pisang Talas*	Maryani et al. (2019a, b)
Fusarium temperatum	CMWF389	plant pathogen	human pathogen	*Homo sapiens, Zea mays*	Al-Hatmi (2016), Wardeh et al. (2015), Farr et al. (2023)
Fusarium thapsinum	NRRL 22049 NRRL 29148	endophyte	plant associate, animal associate, human pathogen	*Austrostipa aristiglumis, Brachiaria* sp., *Glycine max, Homo sapiens, Musa* sp., *Oryza sativa, Sorghum bicolor, Sorghum* sp., *Zea mays*	Wardeh et al. (2015), Al-Hatmi (2016), Farr et al. (2023)
Fusarium tjaetaba	NRRL 66243	endophyte	-	*Sorghum interjectum*	Farr et al. (2023)
Fusarium torreyae	NRRL 54149	plant pathogen	-	*Torreya taxifolia*	Wardeh et al. (2015), Farr et al. (2023)
Fusarium torulosum	NRRL 22747	plant pathogen	endophyte, animal pathogen	Various angiosperms, *Galleria mellonella*	Lu et al. (2012), Rashmi et al. (2019), Farr et al. (2023)
Fusarium transvaalense	NRRL 31008	saprotroph	-	*Kyphocarpa angustifolia, Melhania acuminata, Sida cordifolia*	Farr et al. (2023)
Fusarium tricinctum	INRA104	endophyte	plant pathogen	Various angiosperms, *Pinus banksiana*	Rashmi et al. (2019), Farr et al. (2023)
Fusarium tupiense	NRRL 53984	plant pathogen	-	*Mangifera indica*	Wardeh et al. (2015), Farr et al. (2023)
Fusarium udum	NRRL 25194	plant pathogen	animal pathogen, endophyte	*Aiolopus longicornis, Cajanus* spp., *Crotalaria* spp., *Digitaria eriantha, Glycine max, Gossypium herbaceum, Gypsophila* sp., *Lactarius pubescens*	O'Donnell et al. (2012), Farr et al. (2023)
Fusarium ussurianum	29813	plant pathogen	-	*Avena sativa*	Wardeh et al. (2015), Farr et al. (2023)
Fusarium venenatum	A3/5	saprotroph	plant associate, plant pathogen, endophyte	*Hordeum vulgare, Humulus lupulus, Humulus* sp., *Solanum tuberosum, Tanacetum cinerariifolium, Triticum aestivum, Zea mays*	Farr et al. (2023)

Table 1 (continued)

Species name	Strain[a]	Main lifestyle	Additional recorded lifestyles	Known substrates (for the species)	Reference
Fusarium verticillioides	EthFoc-133 7600	plant pathogen	animal associate, human pathogen, endophyte, saprotroph	Various angiosperms and gymnosperms, various animals	Taylor et al. (2001), Farr et al. (2023), O'Donnell et al. (2012), Al-Hatmi (2016)
Fusarium veterinarium	F5_8S_1A_F	animal pathogen	-	Several animal and animal related substrates	Lombard et al. (2018)
Fusarium vorosii	CBS 119178	plant pathogen	-	*Hordeum vulgare, Oryza sativa, Triticum aestivum, Triticum* sp., *Zea mays*	Farr et al. (2023)
Fusarium xylarioides	KSU18978	plant pathogen	-	*Coffea* spp., *Glycine max, Gossypium hirsutum*	Farr et al. (2023)
Fusarium xyrophilum	NRRL 62721	endophyte	plant associate, plant pathogen	*Xyris* spp.	Laraba et al. (2020)
Fusarium zanthoxyli	NRRL 66285	plant pathogen	-	*Zanthoxylum bungeanum*	Farr et al. (2023)
Fusicolla aquaeductuum	**CBS 837.85**	saprotroph	plant associate, plant pathogen	Tap water	Gräfenhan et al. (2011)
Geejayessia atrofusca	NRRL 22316	plant pathogen	-	*Staphylea trifolia*	Wardeh et al. (2015), Farr et al. (2023)
Geejayessia celtidicola	**CBS 125502**	saprotroph	plant associate	*Celtis occidentalis*	Farr et al. (2023)
Geejayessia zealandica	NRRL 22465	plant associate	-	*Hoheria populnea, Plagianthus* sp.	Farr et al. (2023)
Ilyonectria destructans	C1 **CBS 264.65**	plant pathogen	animal pathogen, human pathogen	*Cyclamen persicum*, animal species including *Homo sapiens*	de Hoog et al. (2020), Cabral et al. (2012)
Ilyonectria europaea	PMI82*	plant pathogen	-	*Actinidia chinensis, Aesculus hippocastanum, Phragmites australis, Vitis* spp.	Farr et al. (2023)
Ilyonectria mors-panacis	g3b	plant pathogen	-	*Panax* spp.	Farr et al. (2023)
Luteonectria nematophila	NRRL 54600	plant associate	-	*Hedera helix*	Crous et al. (2021)
Macroconia leptosphaeriae	**CBS 100001**	mycophilic	-	*Leptosphaeria* sp., on dead stem of *Urtica dioica*	Gräfenhan et al. (2011), Farr et al. (2023)
Macroconia phlogioides	**CBS 125496**	plant associate	saprotroph	*Quercus* sp.	Crous et al. (2021)
Macronectria asiatica	**CBS 136795**	plant associate	saprotroph	Bark	Salgado-Salazar et al. (2016)
Macronectria jungneri	**CBS 124602**	plant associate	saprotroph	Bark	Salgado-Salazar et al. (2016)
Microcera coccophila	**CBS 310.34**	insect symbiont	animal associate	Scale insects, *Citrus* spp., *Laurus nobilis, Salix* sp., *Fraxinus excelsior*	Gräfenhan et al. (2011), Farr et al. (2023)
Microcera larvarum	**CBS 738.79**	insect symbiont	animal associate	*Quadraspidiotus perniciosus, Prunus* sp., *Malus* sp., *Pyrus communis*	Gräfenhan et al. (2011), Schroers et al. (2011), Farr et al. (2023)
Neocosmospora ambrosia	NRRL 20438	insect symbiont	animal associate, plant pathogen	*Camellia sinensis*	Farr et al. (2023)
Neocosmospora cf. falciformis	EtdFoc-186	saprotroph	animal pathogen, human pathogen, plant pathogen, endophyte	Various angiosperms and gymnosperms, animal species including *Homo sapiens*	Taylor et al. (2001), Farr et al. (2023)

Table 1 (continued)

Species name	Strain[a]	Main lifestyle	Additional recorded lifestyles	Known substrates (for the species)	Reference
Neocosmospora cf. solani	EtdFoc-155	plant pathogen	plant associate, animal associate, animal pathogen, human pathogen, endophyte, saprotroph	Various angiosperms and gymnosperms, animal species including *Homo sapiens*	Taylor et al. (2001), Farr et al. (2023)
Neocosmospora duplosperma	NRRL 62584	insect symbiont	animal associate, plant pathogen	*Euwallacea perbrevis*	Aoki et al. (2021)
Neocosmospora euwallaceae	HFEW-16-IV-019	insect symbiont	plant associate, animal associate, plant pathogen	*Persea americana, Acer negundo, Camellia sinensis, Diospyros kaki, Euwallacea fornicatus, Ficus carica, Platanus* spp., *Prunus dulcis, Quercus ithaburensis, Ricinus communis*	Kasson et al. (2013), Farr et al. (2023)
Neocosmospora falciformis	NRRL 43529	saprotroph	animal pathogen, human pathogen, endophyte	Various angiosperms and gymnosperms, animal species including *Homo sapiens*	Taylor et al. (2001), Farr et al. (2023)
Neocosmospora floridana	NRRL 62606	insect symbiont	animal associate, plant pathogen	*Acer negundo, Euwallacea interjectus*	Aoki et al. (2019), Farr et al. (2023)
Neocosmospora haematococca	LQ1	plant pathogen	animal associate, human pathogen	*Acacia* sp., *Alysicarpus vaginalis, Arachis hypogaea, Homo sapiens, Passiflora edulis*	Samuels et al. (1990), Taylor et al. (2001), Farr et al. (2023)
Neocosmospora illudens	NRRL 22090	saprotroph	endophyte	*Beilschmiedia tawa, Melicytus* sp., *Phoenix dactylifera*	Booth (1971), Gräfenhan et al. (2011)
Neocosmospora kuroshio	UCR3666	insect symbiont	animal associate, plant pathogen	Various angiosperms and animal species	Na et al. (2018), Farr et al. (2023)
Neocosmospora liriodendri	NRRL 22389	saprotroph	-	*Liriodendron tulipifera*	O'Donnell et al. (2008)
Neocosmospora metavorans	FSSC_6 FW16.1	saprotroph	human pathogen, plant pathogen, endophyte, mycophilic	Dead wood, *Ganoderma* sp., *Malus sylvestris, Ceresa bubalus, Homo sapiens,* soil	Sandoval-Denis & Crous (2018), Farr et al. (2023)
Neocosmospora mori	JS-169	endophyte	-	*Morus alba*	Farr et al. (2023)
Neocosmospora oligoseptata	NRRL 62579	insect symbiont	animal associate, plant pathogen	Various angiosperms and gymnosperms, *Euwallacea validus*	Aoki et al. (2018), Farr et al. (2023)
Neocosmospora pisi	77–13-4	plant pathogen	human pathogen, endophyte	*Glycine max, Homo sapiens, Pisum sativum, Quercus garryana,* soil, *Solanum tuberosum, Trifolium subterraneum*	Lu et al. (2012), Farr et al. (2023)
Neocosmospora protoensiformis	NRRL 22178	saprotroph	saprotroph	Dicot tree	Sandoval-Denis et al. (2019)
Neocosmospora solani	**CBS 140079**	plant pathogen	plant associate, animal associate, animal pathogen, human pathogen, endophyte, saprotroph	Soil, various angiosperms and gymnosperms, various animals including *Homo sapiens*	Taylor et al. (2001), Farr et al. (2023)
Neocosmospora sp. "AF-6"	NRRL 62590	insect symbiont	animal associate, plant pathogen	*Euwallacea* sp., *Persea americana*	Aoki et al. (2018)
Neocosmospora sp. "AF-9"	NRRL 66088	insect symbiont	animal associate, plant pathogen	*Delonix regia, Xyleborus ferrigineus*	Aoki et al. (2018)
Neocosmospora tuaranensis	NRRL 46518	insect symbiont	animal associate, plant pathogen	*Hevea brasiliensis*	Farr et al. (2023)

Table 1 (continued)

Species name	Strain^a	Main lifestyle	Additional recorded lifestyles	Known substrates (for the species)	Reference
Neocosmospora vasinfecta	NRRL 22166	plant pathogen	endophyte	Various angiosperms and gymnosperms	Farr et al. (2023)
Neocosmospora virguliformis	NRRL 31041	plant pathogen	-	*Glycine max*	Farr et al. (2023)
Neonectria coccinea	CBS 119158	plant pathogen	saprotroph	Various angiosperms, *Vitis vinifera*	Farr et al. (2023)
Neonectria ditissima	RS 324p	plant pathogen	saprotroph	Various angiosperms	Farr et al. (2023)
Neonectria faginata	A.R. 4307	plant pathogen	saprotroph	*Fagus* spp.	Farr et al. (2023)
Neonectria galligena	NRRL 20487	plant pathogen	saprotroph	Various angiosperms	Farr et al. (2023)
Neonectria hederae	CBS 714.97	plant pathogen	saprotroph	*Hedera helix*	Farr et al. (2023)
Neonectria neomacrospora	KNNDK1 NRRL 22505	plant pathogen	saprotroph	Various angiosperms and gymnosperms	Farr et al. (2023)
Neonectria punicea	CBS 119724	plant pathogen	saprotroph	Various angiosperms	Farr et al. (2023)
Neonectria ramulariae	**CBS 182.36**	plant pathogen	saprotroph	Soil, *Malus sylvestris*	Farr et al. (2023)
Neonectria sp.	B-13	saprotroph	-	Soil	Unpublished, as in GenBank
	DH2	endophyte	-	*Meconopsis grandis*	Unpublished, as in GenBank
Nothofusarium devonianum	NRRL 22134	plant pathogen	-	*Ruscus aculeatus*	Crous et al. (2021)
Pseudofusicolla belgica	**CBS 147301**	saprotroph	-	Recycled water from spray humidifier and air-conditioners	Triest et al. (2016)
Pseudonectria buxi	AR2414	plant pathogen	-	*Buxus* sp.	Farr et al. (2023)
Pseudonectria foliicola	JAC18-02	plant pathogen	-	*Buxus* sp.	Farr et al. (2023)
Rectifusarium robinianum	**CBS 430.91** NRRL 25729	saprotroph	-	*Robinia pseudoacacia*, soil	Lombard et al. (2015)
Rectifusarium ventricosum	**CBS 748.79**	saprotroph	human pathogen	Soil, *Homo sapiens*	Taylor et al. (2001), Lombard et al. (2015)
Rugonectria neobalansae	**CBS 125120**	plant pathogen	-	Bark	Chaverri et al. (2011)
Rugonectria rugulosa	**CBS 126565**	plant pathogen	-	*Falcataria moluccana*, *Myrica rubra*	Chaverri et al. (2011), Farr et al. (2023)
Sarocladium implicatum	TR	saprotroph	plant associate	*Saccharum officinarum*, soil	Farr et al. (2023)
Scolecofusarium ciliatum	**CBS 191.65** **CBS 144385**	endophyte	plant associate, plant pathogen	*Fagus sylvatica*	Crous et al. (2021)
Setofusarium setosum	NRRL 36526	plant pathogen	-	Tree bark	Crous et al. (2021)
Stylonectria applanata	**CBS 125489**	mycophilic	-	Ascomycete on *Betula* sp.	Gräfenhan et al. (2011)
Thelonectria blattea	**CBS 952.68**	saprotroph	-	Soil	Wardeh et al. (2015), Farr et al. (2023)
Thelonectria discophora	**CBS 125487** **CBS 134034** SNB-CN63	plant pathogen	saprotroph	Soil, *Aesculus hippocastanum*, *Tepualia stipularis*, *Aesculus* sp., *Pinus radiata*	Wardeh et al. (2015), Farr et al. (2023)

Table 1 (continued)

Species name	Strain[a]	Main lifestyle	Additional recorded lifestyles	Known substrates (for the species)	Reference
Thelonectria rubi	CBS 177.27	plant pathogen	endophyte	*Rubus* spp.	Wardeh et al. (2015), Farr et al. (2023)
Tumenectria laetidisca	**CBS 100284** **CBS 101909**	saprotroph	-	Bamboo	Salgado-Salazar et al. (2016)
Xenoacremonium recifei	IHEM 4405	human pathogen	-	*Homo sapiens*	Lombard et al. (2015)

[a] *CBS* Culture collection of the Westerdijk Fungal Biodiversity Institute, Utrecht, The Netherlands. *CMW* Collection of the Forestry and Agricultural Biotechnology Institute (FABI), University of Pretoria, South Africa. DAOMC: Canadian Collection of Fungal Cultures, Ottawa, Ontario, Canada. IHEM: Belgian Co-ordinated Collections of Micro-organisms, Sciensano Section Mycology and Aerobiology, Brussels, Belgium. IMI: International Mycological Institute, CABI-Bioscience, Egham, Bakeham Lane, United Kingdom. INRA: National Research Institute for Agriculture, Food and the Environment, Paris, France. KOD: Personal collection of Kerry O'Donnell, Agricultural Research Service, USDA, Beltsville, Maryland, USA. KSU: Department of Plant Pathology, Throckmorton Plant Sciences Center, Kansas State University, Manhattan, Kansas, USA. MRC: PROMEC, Medical Research Council, Tygerberg, South Africa. NRRL: Agricultural Research Service Culture Collection, National Center for Agricultural Utilization Research, US Department of Agriculture, Peoria, IL, USA. UCR: University of California, Riverside, CA, USA. Other strain accessions as listed in GenBank. *: genome data obtained from JGI (Joint Genome Institute). Genomes newly generated in this study are shown in **bold**. For details of genome accession numbers see Supplementary Table S1

both plant pathogen and mycophilic as equally parsimonious states for the same node.

The earliest divergent clade (including *Cosmospora*, *Dialonectria*, *Fusicolla*, *Macroconia*, *Microcera*, *Pseudofusicolla*, *Scolecofusarium*, *Stylonectria* and *Xenoacremonium*) evolved from a mycophilic ancestor according to both methods; however, with clearly defined transitions to plant pathogen, insect symbiont or endophyte for the most recently diverged taxa (*Macroconia*, *Microcera* and *Scolecofusarium*, respectively).

The lifestyles of the ancestors of the primarily saprotrophic genera *Bisifusarium* and *Rectifusarium* remain ambiguous, resolved as either plant associates, plant pathogens or saprotrophs by ML. The same nodes were mapped by Parsimony as either plant pathogens or saprotrophs as equally parsimonious states.

The ancestral states of several fusarioid genera basal to *Fusarium s. str.* (the ancestors of *Luteonectria* and *Cyanonectria*, the common ancestor of *Geejayessia* and *Nothofusarium*, the latest common ancestor of *Albonectria* and *Setofusarium*, and its earlier common ancestor with *Neocosmospora*) were all resolved as plant associates with high PL by ML. Nevertheless, Parsimony identified plant pathogenicity as the ancestral state for all the ancestors of *Albonectria*, *Cyanonectria*, *Geejayessia*, *Neocosmospora*, *Nothofusarium*, *Setofusarium*; while the ancestor of *Luteonectria* was mapped as either a plant associate, plant pathogen or saprotroph. A variety of lifestyles coexists in all the above-mentioned genera, including mostly endophytes, plant associates and pathogens, and rare animal and human pathogens. Notably, an insect symbiont lifestyle is a derived character present exclusively in a particular subclade of *Neocosmospora*. By contrast, the endophytic lifestyle seems to have evolved (or equally probable to have reversed to) several times from plant pathogens in fusarioid and cylindrocarpioid genera, although it is far more common in *Fusarium s. str.*, according to our data.

The ancestors of *Calonectria*, *Coccinonectria*, all the cylindrocarpioid genera, *Pseudonectria*, as well as *Fusarium s. str.* (node F3) and several of its species complexes (SC) included here (*F. torreyae* SC, *F. buharicum* SC, *F. oxysporum* SC, *F. sambucinum* SC and *F. lateritium* SC) were plant pathogens, as determined by both ML and Parsimony methods. Moreover, with exception of the ancestral states of *Aquanectria* and *Cinnamomeonectria*, both derived from either a plant pathogen in ML, or a saprophyte according to Parsimony; plant pathogen is the main lifestyle for nearly all terminal taxa and reconstructed hypothetical ancestral taxa of cylindrocarpioid genera, *Calonectria* and the *Fusarium* SC mentioned above,

Discussion

Phylogenetic backbone

Phylogenetically, the present study separated *Fusarium s. str*. from other fusarioid genera, which is in agreement with multigene phylogenetic analyses by Crous et al. (2021), and phylogenomic analyses of Hill et al. (2022), Han et al. (2023), Chen et al. (2023), and Gomez-Chavarria et al. (2024). Rokas et al. (2003) estimated that at least 20 unrelated and unlinked genes, or 8 000 randomly selected orthologous nucleotides would be required to establish a stable systematic framework for fungi, which is well exceeded in our study.

The phylogenetic backbone for *Fusarium s. str.* was in agreement with the morphology, biology and phylogeny published by Crous et al. (2021). Although the phylogenomic study of Hill et al. (2022) did not focus on separating genera of fusarioid fungi, they did conclude that the divergence between *Fusarium s. str*. and other fusarioid taxa was associated with positive selection on a considerable number of core genes, an upwards shift in translational selection, and distinct patterns in codon usage bias, signalling a “larger and more abrupt” divergence between *Neocosmospora* and *Fusarium s.str*. than between species within the same genus, thus contrary to the wider definition of *Fusarium s. lat*. advocated by O'Donnell et al. (2020) and Geiser et al. (2021). This was also the conclusion of a similar study on *Fusarium* and allied genera by Han et al. (2023), and a subsequent revision of the *Sordariomycetes* by Chen et al. (2023), who included nine additional fusarioid genera (*Albonectria*, *Bisifusarium*, *Cyanonectria*, *Geejayessia*, *Luteonectria*, *Neocosmospora*, *Nothofusarium*, *Rectifusarium*, and *Setofusarium*), and found them to represent well-supported phylogenetic nodes, which are also morphologically and biologically distinct from *Fusarium.*

A recent phylogenomic study by Gomez-Chavarria et al. (2024) concluded that *Fusarium s.str.* genomes within the F3 hypothesis clade demonstrated a notably higher level of feature conservation than the various basal genera (F1 hypothesis). Furthermore, the branch lengths observed in their phylogenomic tree indicated a wider evolutionary divergence between the "allied" genera compared to the species within the F3 node (*Fusarium s. str.*). They also found that earlier-diverging fusarioid genera had higher GC content ratios (> 50%), while most groups in the F3 clade have shown a reductive trend, with values dropping to 47–48% in most *Fusarium* species complexes. They concluded that the groups diverging before the F3 clade exhibited a significant evolutionary distance from *Fusarium s. str.* (F3 node).

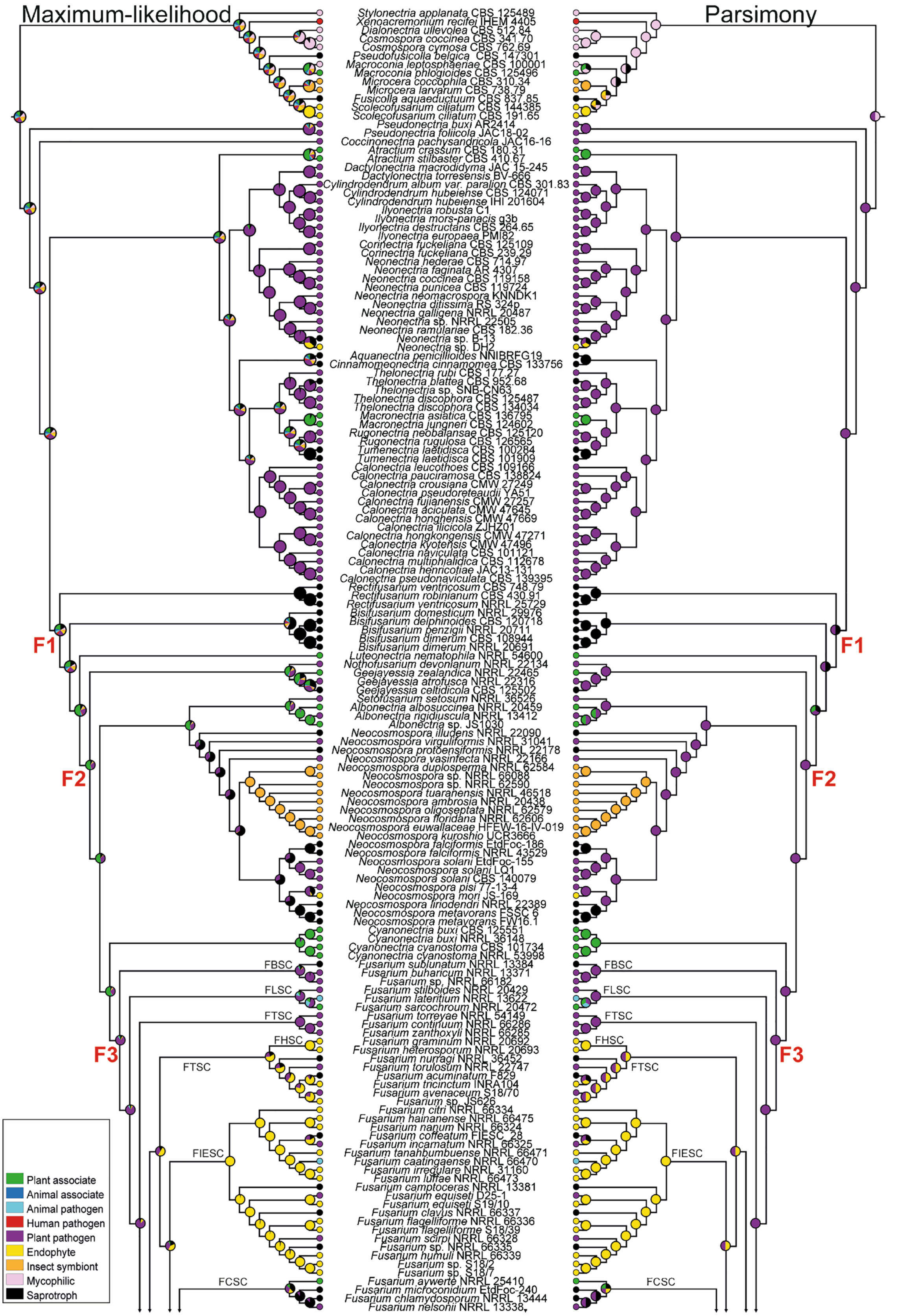
Fig. 2 Ancestral character state reconstruction of main (primary) ▶ lifestyles of fusarioid and cylindrocarpon-like fungi. Confronted maximum likelihood (left cladogram) and maximum parsimony (right cladogram) ancestral character reconstruction based on concatenated 263 BUSCO genes from 283 taxa. Coloured terminal circles represent observed character states for extant species. Reconstructed character states and their estimated proportions are shown at internal nodes. *Fusarium* species complexes (SC) are indicated at their respective nodes as: FBSC: *F. buharicum* SC, FBurSC: *F. burguesii* SC, FCSC: *F. chlamydosporum* SC, FFBSC: *F. falsibabinda* SC, FFSC: *F. fujikuroi* SC, FHSC: *F. heterosporum* SC, FIESC: *F. incarnatum-equiseti* SC, FLSC: *F. lateritium* SC, FNSC: *F. nisikadoi* SC, FOSC: *F. oxysporum* SC, FRSC: *F. redolens* SC, FSAMSC: *F. sambucinum* SC and FTSC: *F. tricinctum* SC

Lifestyles

Species of *Fusarium* and allied fusarioid genera have diverse lifestyles, which we classified here as animal or plant associates, animal, plant or human pathogens, endophytes, saprophytes, insect symbionts, and mycophilic, *i.e*. growing on other fungi (Table 1). By performing ancestral state reconstructions, we attempted to determine the evolution of their lifestyle, although some species seem to be multifunctional and up to eight different lifestyles have been linked to a single species in literature. Fungal species, for instance, have proven able to transition from an endophytic to a plant pathogenic lifestyle, and vice versa (Buijs et al. 2022; Liu et al. 2022). Hill et al. (2022) reported a significant difference in the candidate secreted effector protein content between saprophytes and endophytes, suggesting that fusarioid endophytes are more likely to be latent pathogens than inactive saprophytes waiting for a natural plant death.

In the present ancestral state reconstruction, the most early-diverging clade was inferred to have probably evolved from a mycophilic ancestor, and contains some very specific fungicolous genera such as *Dialonectria* (Lechat et al. 2021b), and members of *Cosmospora* and *Stylonectria* (Lechat et al. 2021a). Human pathogenicity is very rare, and appears only as a secondary, tertiary or additional lifestyle, suggesting these taxa to be opportunists.

Both ML and Parsimony analyses showed some uncertainty regarding the ancestral lifestyle of fusarioid and cylindrocarpioid genera in *Nectriaceae* (Supplementary Fig. S1). However, the Parsimony analysis suggested a plant parasitic ancestral state for cylindrocarpioid genera, while for fusarioid genera subtending F1, both a saprotrophic and a plant parasitic ancestral state were inferred to be equally parsimonious (Fig. 2). Considering the very low number of small secreted proteins and low number of CAZymes in the earliest-diverging genus of that clade, the saprotrophic genus *Rectifusarium*, and the also still comparatively low number of such genes in the genus diverging next, the saprotrophic



- 🟩 Plant associate
- 🟦 Animal associate
- 🟦 Animal pathogen
- 🟥 Human pathogen
- 🟪 Plant pathogen
- 🟨 Endophyte
- 🟧 Insect symbiont
- 🟪 Mycophilic
- ⬛ Saprotroph

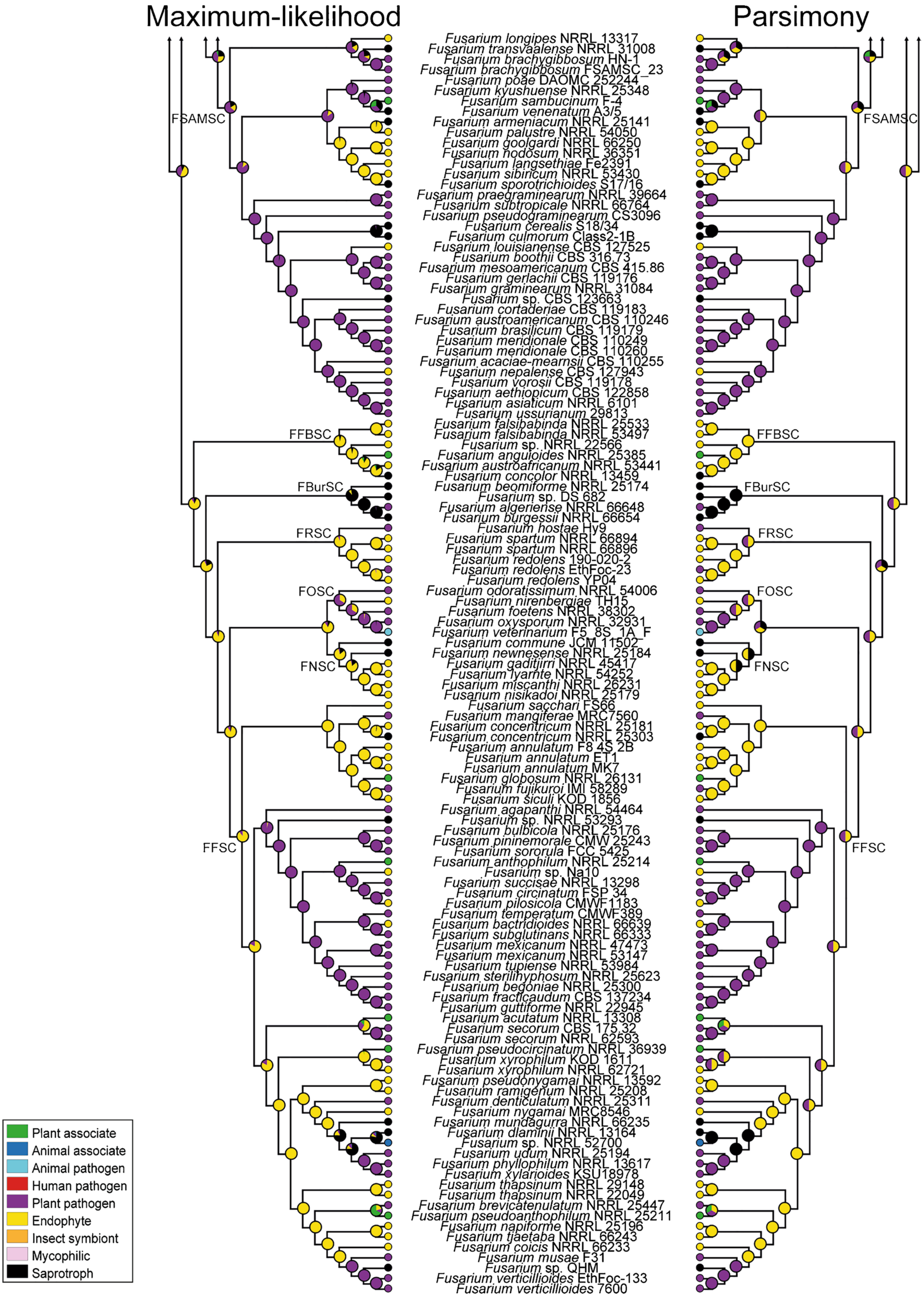


Fig. 2 (continued)

genus *Bisifusarium*, it seems likely that that root of the fusarioid genera lies in saprophytes rather than plant pathogens. Saprotrophism or a life as a plant-associate appears to be the ancestral state for *Neocosmospora*, *Bisifusarium* and *Rectifusarium* based on the ML reconstruction, but the Parsimony analysis contradicts this, identifying plant pathogenicity as the ancestral state, in line with the genomic content of these genera. The various cases of species of *Fusarium* that have been suggested to be saprophytes need to be revisited, as their genome content suggests that they are rather plant pathogens, considering that their genomic features, especially with respect to CAZYmes and small secreted proteins match those of well-known plant pathogens. This is also true for the symbiotic species of *Neocosmospora* and various species in *Fusarium* that have been classified as plant associates. This suggest that the ecological niche of *Nectriaceae* might be more complex than previously thought and that a thorough investigation might reveal yet unknown plant-pathogenic associations of those species.

The common ancestor of *Fusarium* (node F3) was most likely a plant pathogen. However, except for the most early-diverging clades of *Fusarium* (*F. buharicum*, *F. lateritium* and *F. torreyae* species complexes) all the other major clades are inferred to have likely evolved from an endophytic or plant pathogenic lifestyle, with plant pathogenic species present throughout the genus. The reason for this might be the ambiguity between the two lifestyles. Many studies have shown that fungi can switch between their growth as an asymptomatic endophyte and a virulent pathogen depending on environmental conditions (Kogel et al. 2006; Fesel and Zuccaro 2016; Rai and Agarkar 2016). Based on these data, it is apparent that in *Fusarium s. str.*, most plant pathogens will also be isolated as endophytes, and that its species have adaptable lifestyles, underlining their potential to act as generalists and opportunists in various niches. Furthermore, definitions of lifestyles are known to be too rigid, and frequently cannot incorporate the flexibility as observed in nature (Buijs et al. 2022). For fusarioid fungi specifically, in line with our conclusions, Hill et al. (2022) therefore suggested that multiple lifestyle hypotheses need to be considered to incorporate their various interactions, which depend on host, climate and environment. Thus, especially the classification into endophytes *vs* pathogens should be considered ambiguous.

Endophytism appears to be a lifestyle derived from plant parasitism, and vice versa. Both lifestyles have evolved in many separate occasions in most genera included here. Endophytism is however markedly more common in *Fusarium*, but it also appears as a more recent evolutionary event, or as secondary lifestyle in *Calonectria*, *Corinectria*, *Cylindrodendrum*, *Dactylonectria*, *Ilyonectria*, *Neocosmospora*, *Neonectria*, *Scolecofusarium* and *Thelonectria*.

Genomic content

The genomic content is in line with the reported lifestyles, with saprotrophs or plant associates featuring lower numbers of small-secreted proteins, CAZymes and biosynthetic gene clusters than plant pathogenic, endophytic or symbiotic species (Haridas et al. 2020). However, there are some hints of hidden lifestyles in the *Nectriaceae*, *e.g.* the number of small-secreted proteins and CAZymes in *Bisifusarium* suggests that there is a pathogenic lifestyle apart from the known role as saprotroph. Similarly, two of the three species of *Albonectria* included are characterised as plant associates, while their genome content, with a large secretome and a high number of small-secreted proteins is similar to the species classified as plant pathogens, suggesting that they are in fact plant pathogens rather than plant associates.

Interestingly, in contrast to a previous study (Hill et al. 2022), the broad sampling of high-quality genomes of *Nectriaceae* revealed higher support values for most *Nectriaceae* genera, both for genera proposed for inclusion in *Fusarium* (Geiser et al. 2021) and genera branching earlier than node F1. Apart from the morphological, biological and ecological differences previously used to circumscribe these genera in *Nectriaceae*, they also appear to have pronounced differences in their genomic makeup.

However, there are also a few genera branching below the F1 node that should be reconsidered, as their phylogenetic and genomic differentiation was not obvious, *e.g.* for the genera *Corinectria* and *Neonectria*, which were highly similar in terms of genome properties, as well as for the genera *Ilyonectria*, *Cylindrodendrum* and *Dactylonectria*. Given the fact that the morphological differentiation between these genera is also narrow, further research should be conducted with an even wider sampling to determine if they should be retained as separate or be fused.

It is noteworthy that within in the genera studied, there are some species that diverge from the overall properties with the genus, reflecting innovations in their lifestyle. A striking example for this is the species *Fusarium xyrophilum*, which differs from other *Fusarium* species by having evolved the ability to produce pseudoflowers on *Xyris* species (Laraba et al. 2020). This remarkable adaptation is paralleled by the pseudoflowers incited by some rust species (Roy 1993), which also use insect vectors to disperse their propagules. In pseudoflower-inducing rusts and in floricolous downy mildews, the adaptation to insect vectors as dispersers has led to a significant diversification of the pathogens (Pfunder and Schürch 2001; Thines and Kummer 2013), and it seems possible that additional species with the ability to produce pseudoflowers will be discovered in the hardly explored ecosystems of northern South America. In any case, it can be expected that such a huge innovation in the lifestyle will have a major impact on the genome of the pathogen, as it requires to keep the host competitive in its fitness over a long time, so it can successfully form pseudoflowers for its dispersal. In line with this, the genome of *Fusarium xyrophilum* codes for less than half the amount of CAZymes, similar to the situation in downy mildews, which, exemplary for biotrophic pathogens, also feature a significantly reduced set of cell-wall degrading enzymes (Baxter et al. 2010). Interestingly, also the overall secretome and even more so the small secreted proteins that are putative effector candidates have been drastically reduced, a development that is again similar to the situation in downy mildews and probably a sign of a high degree of specialisation (Baxter et al. 2010).

In addition, some other species also have significantly diverging genomic properties from the vast majority of species in the same genus, e.g. the endophytic species *Neocosmospora mori*. However, unlike *Fusarium xyrophilum*, where the innovation that led to the genomic anomalies is obvious, only deep genomic analyses that were out of the scope of the present study could reveal the hidden innovations causing this divergence. Such studies are highly warranted in future, as they promise to shed light on the ecological differentiation of *Nectriaceae* and the innovations that led to radiations of distinct species groups now recognisable as genera.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s11557-024-02025-4.

Acknowledgements We are thankful to Roy van Doorn for isolation of the genomic DNA used for whole genome sequencing. Funding for MT in the framework of the LOEWE Centre for Translational Biodiversity Genomics funded by the LOEWE excellence initiative of the government of Hesse and by the BLE in the Framework of AGRIFUTURE is gratefully acknowledged.

Authors' contributions PC and MT conceived the study. MSD, JZG, MMC, and SP conducted laboratory experiments, BU and BM performed genome assemblies and annotations, BU an MSD analysed the data, BU, MSD, JZG, MMC, PWC, and MT interpreted the data. BU, MSD, JZG, PWC, and MT wrote the manuscript with contributions from all authors. All authors agreed with the submission of the manuscript.

Funding Open Access funding enabled and organized by Projekt DEAL. This study was supported by the government of Hesse in the Framework of the Centre for Translational Biodiversity Genomics (TBG), and the Federal Ministry for Agriculture and Food (BLE) in the Framework of AGRIFUTURE.

Data availability Sequence Data have been deposited in GenBank. [### Numbers will be added to Table S2 upon revision. ###].

Declarations

Ethics approval and consent to participate Not applicable.

Consent for publication Not applicable.

Competing interests MT is the Editor-in-Chief of Mycological Progress, but was not involved in the editorial processes associated with handling this manuscript.

References

Akhmetova GK, Knapp DG, Özer G et al (2023) Multilocus molecular phylogenetic-led discovery and formal recognition of four novel root-colonizing *Fusarium* species from northern Kazakhstan and the phylogenetically divergent *Fusarium steppicola* lineage. Mycologia 115:16–31. https://doi.org/10.1080/00275514.2022.2119761

Al Yazidi LS, Huynh J, Britton PN et al (2019) Endobronchial fusariosis in a child following bilateral lung transplant. Med Mycol Case Rep 23:77–80. https://doi.org/10.1016/j.mmcr.2019.01.002

Al-Hatmi A (2016) Phylogeny, diagnostics and antifungal susceptibility of clinically relevant *Fusarium* species. Dissertation. University of Amsterdam

Aoki T, Kasson MT, Berger MC et al (2018) *Fusarium oligoseptatum* sp. nov., a mycosymbiont of the ambrosia beetle *Euwallacea validus* in the Eastern U.S. and typification of *F. ambrosium*. FUSE 1:23–39. https://doi.org/10.3114/fuse.2018.01.03

Aoki T, Smith JA, Kasson MT et al (2019) Three novel Ambrosia *Fusarium* clade species producing clavate macroconidia known (*F. floridanum* and *F. obliquiseptatum*) or predicted (*F. tuaranense*) to be farmed by *Euwallacea* spp. (*Coleoptera*: *Scolytinae*) on woody hosts. Mycologia 111:919–935. https://doi.org/10.1080/00275514.2019.1647074

Aoki T, Liyanage PNH, Konkol JL et al (2021) Three novel Ambrosia *Fusarium* Clade species producing multiseptate "dolphin-shaped" conidia, and an augmented description of *Fusarium kuroshium*. Mycologia 113:1089–1109. https://doi.org/10.1080/00275514.2021.1923300

Bartoszewicz JM, Nasri F, Nowicka M et al (2022) Detecting DNA of novel fungal pathogens using ResNets and a curated fungi-hosts data collection. Bioinf 38:ii168–ii174. https://doi.org/10.1093/bioinformatics/btac495

Baxter L, Tripathy S, Ishaque N et al (2010) Signatures of adaptation to obligate biotrophy in the *Hyaloperonospora arabidopsidis* genome. Science 330:1549–1551. https://doi.org/10.1126/science.1195203

Benyon FHL, Burguess LW, Sharp PJ (2000) Molecular genetic investigations and reclassifcation of *Fusarium* species in sections *Fusarium* and *Roseum*. Mycol Res 104:1164–1174. https://doi.org/10.1017/S0953756200002914

Bhattacharjee A, Anderson LN, Alfaro T et al (2021) Draft genome sequence of *Fusarium* sp. strain DS 682, a novel fungal isolate from the grass rhizosphere. Microbiol Res Ann 10:e00884-e920. https://doi.org/10.1128/MRA.00884-20

Bhunjun CS, Chen YJ, Phukhamsakda C et al (2024) What are the 100 most cited fungal genera? Stud Mycol 108:1–411. https://doi.org/10.3114/sim.2024.108.01

Blin K, Shaw S, Kloosterman AM et al (2021) antiSMASH 6.0: improving cluster detection and comparison capabilities. NAR 49:W29–W35. https://doi.org/10.1093/nar/gkab335

Bolger AM, Lohse M, Usadel B (2014) Trimmomatic: a flexible trimmer for Illumina sequence data. Bioinf 30:2114–2120. https://doi.org/10.1093/bioinformatics/btu170

Booth C (1971) The genus *Fusarium*. Commonwealth Mycology Institute, Kew. England

Buijs VA, Groenewald JZ, Haridas S, et al. (2022) Enemy or ally: a genomic approach to elucidate the lifestyle of *Phyllosticta citrichinaensis*. G3 12: 061. https://doi.org/10.1093/g3journal/jkac061

Bushnell B (2021) BBMap short read aligner. Available from: http://sourceforge.net/projects/bbmap/

Cabral A, Groenewald JZ, Rego C et al (2012) Cylindrocarpon root rot: multi-gene analysis reveals novel species within the *Ilyonectria radicicola* species complex. Mycol Prog 11:655–688. https://doi.org/10.1007/s11557-011-0777-7

Cantarel BL, Korf I, Robb SMC et al (2008) MAKER: an easy-to-use annotation pipeline designed for emerging model organism genomes. Gen Res 18:188–196. https://doi.org/10.1101/gr.6743907

Capella-Gutiérrez S, Silla-Martínez JM, Gabaldón T (2009) trimAl: a tool for automated alignment trimming in large-scale phylogenetic analyses. Bioinf 25:1972–1973. https://doi.org/10.1093/bioinformatics/btp348

Chaverri P, Salgado C, Hirooka Y et al (2011) Delimitation of *Neonectria* and *Cylindrocarpon* (*Nectriaceae*, *Hypocreales*, *Ascomycota*) and related genera with *Cylindrocarpon*-like anamorphs. Stud Mycol 68:57–78. https://doi.org/10.3114/sim.2011.68.03

Chen YP, Su PW, Stadler M et al (2023) Beyond observation: genomic traits and machine learning algorithms for predicting fungal lifestyles. Mycosphere 14:1530–1563. https://doi.org/10.21203/rs.3.rs-3118609/v1

Crous PW, Lombard L, Sandoval-Denis M et al (2021) *Fusarium*: more than a node or a foot-shaped basal cell. Stud Mycol 98:100116. https://doi.org/10.1016/j.simyco.2021.100116

Damm U, Mostert L, Crous PW et al (2008) Novel *Phaeoacremonium* species associated with necrotic wood of *Prunus* trees. Persoonia 20:87–102. https://doi.org/10.3767/003158508x324227

de Beer ZW, Duong TA, Barnes I et al (2014) Redefining *Ceratocystis* and allied genera. Stud Mycol 79:187–219. https://doi.org/10.1016/j.simyco.2014.10.001

de Beer ZW, Procter M, Wingfield MJ et al (2022) Generic boundaries in the *Ophiostomatales* reconsidered and revised. Stud Mycol 101:57–120. https://doi.org/10.3114/sim.2022.101.02

de Hoog S, Gené J, Ahmed S et al (2020) Atlas of clinical fungi, 4ª. Hilversum

Dean R, Van Kan JAL, Pretorius ZA et al (2012) The top 10 fungal pathogens in molecular plant pathology. Mol Plant Pathol 13:414–430. https://doi.org/10.1111/j.1364-3703.2011.00783.x

Farr DF, Rossman AY, Castlebury LA (2021) United States National Fungus Collections Fungus-Host Dataset. Ag Data Commons. https://agdatacommons.nal.usda.gov/articles/dataset/United_States_National_Fungus_Collections_Fungus-Host_Dataset/24855585/1. Accessed December 2023

Fesel PH, Zuccaro A (2016) Dissecting endophytic lifestyle along the parasitism/mutualism continuum in *Arabidopsis*. Curr Op Microbiol 32:103–112. https://doi.org/10.1016/j.mib.2016.05.008

Gargouri S, Balmas V, Burgess L et al (2020) An endophyte of *Macrochloa tenacissima* (esparto or needle grass) from Tunisia is a novel species in the *Fusarium redolens* species complex. Mycologia 112:792–807. https://doi.org/10.1080/00275514.2020.1767493

Geiser DM, Aoki T, Bacon CW et al (2013) One fungus, one name: Defining the genus *Fusarium* in a scientifically robust way that preserves longstanding use. Phytopathol 103:400–408. https://doi.org/10.1094/phyto-07-12-0150-le

Geiser DM, Al-Hatmi AMS, Aoki T et al (2021) Phylogenomic analysis of a 55.1 kb 19-gene dataset resolves a monophyletic *Fusarium* that includes the *Fusarium solani* species complex. Phytopathol 111:1064–1079. https://doi.org/10.1094/phyto-08-20-0330-le

Gerlach W, Nirenberg HI (1982) The genus *Fusarium* – a pictorial atlas. Mitteilungen der Biologischen Bundesanstalt Für Land- und Forstwirtschaft Berlin-Dahlem 209:1–406

Giraldo A, Crous PW (2019) Inside *Plectosphaerellaceae*. Stud Mycol 92:227–286. https://doi.org/10.1016/j.simyco.2018.10.005

Gomez-Chavarria DA, Rua-Giraldo AL, Alzate JF (2024) An evolutionary view of the *Fusarium* core genome. BMC Genomics 25:304. https://doi.org/10.1186/s12864-024-10200-w

González CD, Chaverri P (2017) *Corinectria*, a new genus to accommodate *Neonectria fuckeliana* and *C. constricta* sp. nov. from *Pinus radiata* in Chile. Mycol Prog 16:1015–1027. https://doi.org/10.1007/s11557-017-1343-8

Gräfenhan T, Schroers H-J, Nirenberg HI et al (2011) An overview of the taxonomy, phylogeny, and typification of nectriaceous fungi in *Cosmospora*, *Acremonium*, *Fusarium*, *Stilbella* and *Volutella*. Stud Mycol 68:79–113. https://doi.org/10.3114/sim.2011.68.04

Gräfenhan T, Johnston PR, Vaughan MM et al (2016) *Fusarium praegraminearum* sp. nov., a novel nivalenol mycotoxin-producing pathogen from New Zealand can induce head blight on wheat. Mycologia 108:1229–1239. https://doi.org/10.3852/16-110

Han S, Wang M, Ma Z et al (2023) *Fusarium* diversity associated with diseased cereals in China, with an updated phylogenomic assessment of the genus. Stud Mycol 104:87–148. https://doi.org/10.3114/sim.2022.104.02

Haridas S, Albert R, Binder M et al (2020) 101 *Dothideomycetes* genomes: a test case for predicting lifestyles and emergence of pathogens. Stud Mycol 96:141–153. https://doi.org/10.1016/j.simyco.2020.01.003

Hawksworth DL, Crous PW, Redhead SA et al (2011) The Amsterdam declaration on fungal nomenclature. IMA Fungus 2:105–112. https://doi.org/10.5598/imafungus.2011.02.01.14

Hill R, Buggs RJA, Vu DT et al (2022) Lifestyle transitions in fusarioid fungi are frequent and lack clear genomic signatures. Mol Biol Evol 39:msac085. https://doi.org/10.1093/molbev/msac085

Jacobs-Venter A, Laraba I, Geiser DM et al (2018) Molecular systematics of two sister clades, the *Fusarium concolor* and *F. babinda* species complexes, and the discovery of a novel microcycle macroconidium-producing species from South Africa. Mycologia 110:1189–1204. https://doi.org/10.1080/00275514.2018.1526619

Jiang N, Fan X, Tian C et al (2020) Reevaluating *Cryphonectriaceae* and allied families in *Diaporthales*. Mycologia 112:267–292. https://doi.org/10.1080/00275514.2019.1698925

Kasson MT, O'Donnell K, Rooney AP et al (2013) An inordinate fondness for *Fusarium*: phylogenetic diversity of fusaria cultivated by ambrosia beetles in the genus *Euwallacea* on avocado and other plant hosts. Fun Gen Biol 56:147–157. https://doi.org/10.1016/j.fgb.2013.04.004

Katoh K, Standley DM (2013) MAFFT multiple sequence alignment software version 7: improvements in performance and usability. Mol Biol Evol 30:772–780. https://doi.org/10.1093/molbev/mst010

Kim HS, Lohmar JM, Busman M et al (2020) Identification and distribution of gene clusters required for synthesis of sphingolipid metabolism inhibitors in diverse species of the filamentous fungus *Fusarium*. BMC Gen 21:510. https://doi.org/10.1186/s12864-020-06896-1

Klaubauf S, Tharreau D, Fournier E et al (2014) Resolving the polyphyletic nature of *Pyricularia* (*Pyriculariaceae*). Stud Mycol 79:85–120. https://doi.org/10.1016/j.simyco.2014.09.004

Kogel KH, Franken P, Hückelhoven R (2006) Endophyte or parasite–what decides? Curr Op Pl Biol 9:358–363. https://doi.org/10.1016/j.pbi.2006.05.001

Laraba I, Kim HS, Proctor RH et al (2020) *Fusarium xyrophilum*, sp. nov., a member of the *Fusarium fujikuroi* species complex recovered from pseudoflowers on yellow-eyed grass (*Xyris* spp.) from Guyana. Mycologia 112:39–51. https://doi.org/10.1080/00275514.2019.1668991

Laurence MH, Summerell BA, Burgess LW et al (2011) *Fusarium burgessii* sp. nov. representing a novel lineage in the genus *Fusarium*. Fun Div 49:101–112. https://doi.org/10.1007/s13225-011-0093-1

Laurence MH, Walsh JL, Shuttleworth LA et al (2016) Six novel species of *Fusarium* from natural ecosystems in Australia. Fun Div 77:349–366. https://doi.org/10.1007/s13225-015-0337-6

Lechat C, Fournier J, Chaduli D et al (2021) *Dialonectria favaceae*, a new species from France, and *Dialonectria magnusiana* comb. nov. for *Nectria magnusiana*. Ascomycete.org 13:75–82. https://doi.org/10.25664/art-0320

Lechat C, Fournier J, Hairaud M et al (2021) Two new species of *Stylonectria* (*Nectriaceae*) from the French Alps. Ascomycete.org 13:49–53. https://doi.org/10.25664/ART-0316

Leslie JF, Summerell BA (2006) The Fusarium laboratory manual. Blackwell Publishing Professional, USA

Liu F, Ma ZY, Hou LW, Diao YZ et al (2022) Updating species diversity of *Colletotrichum*, with a phylogenomic overview. Stud Mycol 101:1–56. https://doi.org/10.3114/sim.2022.101.01

Liu XF, Tibpromma S, Hughes AC et al (2023) Culturable mycota on bats in central and southern Yunnan Province, China. Mycosphere 14:497–662. https://doi.org/10.5943/mycosphere/14/1/7

Lombard L, van der Merwe N, Groenewald JZ et al (2014) Lineages in *Nectriaceae*: re-evaluating the generic status of *Ilyonectria* and allied genera. Phytopathol Mediterr 53:340–357. https://doi.org/10.14601/Phytopathol_Mediterr-14976

Lombard L, van der Merwe NA, Groenewald JZ et al (2015) Generic concepts in *Nectriaceae*. Stud Mycol 80:189–245. https://doi.org/10.1016/j.simyco.2014.12.002

Lombard L, Houbraken J, Decock C et al (2016) Generic hyperdiversity in *Stachybotriaceae*. Persoonia 36:156–246. https://doi.org/10.3767/003158516x691582

Lombard L, Sandoval-Denis M, Lamprecht SC et al (2019a) Epitypification of *Fusarium oxysporum* - clearing the taxonomic chaos. Persoonia 43:1–47. https://doi.org/10.3767/persoonia.2019.43.01

Lombard L, van Doorn R, Crous PW (2019b) Neotypification of *Fusarium chlamydosporum* - a reappraisal of a clinically important species complex. FUSE 4:183–200. https://doi.org/10.3114/fuse.2019.04.10

Lu T, Yao B, Zhang C (2012) DFVF: database of fungal virulence factors. Database 2012:bas032. https://doi.org/10.1093/database/bas032

Maddison WP, Maddison DR. (2023) Mesquite: a modular system for evolutionary analysis. Version 3.81. http://www.mesquiteproject.org

Manni M, Berkeley MR, Seppey M et al (2021) BUSCO update: novel and streamlined workflows along with broader and deeper phylogenetic coverage for scoring of eukaryotic, prokaryotic, and viral genomes. Mol Biol Evol 38:4647–4654. https://doi.org/10.1093/molbev/msab199

Maryani N, Lombard L, Poerba YS et al (2019a) Phylogeny and genetic diversity of the banana *Fusarium* wilt pathogen *Fusarium oxysporum* f. sp. *cubense* in the Indonesian centre of origin. Stud Mycol 92:155–194. https://doi.org/10.1016/j.simyco.2018.06.003

Maryani N, Sandoval-Denis M, Lombard L et al (2019b) New endemic *Fusarium* species hitch-hiking with pathogenic *Fusarium* strains causing Panama disease in small-holder banana plots in Indonesia. Persoonia 43:48–69. https://doi.org/10.3767/persoonia.2019.43.02

McNeill J, Barrie FR, Buck WR, et al. (2012) International Code of Nomenclature for algae, fungi, and plants (Melbourne Code) adopted by the Eighteenth International Botanical Congress Melbourne, Australia, July 2011. [Regnum Vegetabile No. 154.] Königstein: Koeltz Scientific Books

Na F, Carrillo JD, Mayorquin JS et al (2018) Two novel fungal symbionts *Fusarium kuroshium* sp. nov. and *Graphium kuroshium* sp. nov. of Kuroshio shot hole borer (*Euwallaceae* sp. nr. *fornicatus*) cause fusarium dieback on woody host species in California. Pl Dis 102:1154–1164. https://doi.org/10.1094/PDIS-07-17-1042-RE

O'Donnell K, Sutton DA, Fothergill A et al (2008) Molecular phylogenetic diversity, multilocus haplotype nomenclature, and in vitro antifungal resistance within the *Fusarium solani* species complex. J Clin Microbiol 46:2477–2490. https://doi.org/10.1128/jcm.02371-07

O'Donnell K, Humber RA, Geiser DM et al (2012) Phylogenetic diversity of insecticolous fusaria inferred from multilocus DNA sequence data and their molecular identification via FUSARIUM-ID and Fusarium MLST. Mycologia 104:427–445. https://doi.org/10.3852/11-179

O'Donnell K, Ward TJ, Geiser DM et al (2004) Genealogical concordance between the mating type locus and seven other nuclear genes supports formal recognition of nine phylogenetically distinct species within the *Fusarium graminearum* clade. Fun Gen Biol 41:600–623. https://doi.org/10.1016/j.fgb.2004.03.003

O'Donnell K, McCormick SP, Busman M et al (2018) Marasas et al. 1984 "Toxigenic *Fusarium* Species: Identity and Mycotoxicology" revisited. Mycologia 110:1058–1080. https://doi.org/10.1080/00275514.2018.1519773

O'Donnell K, Al-Hatmi AMS, Aoki T et al (2020) No to *Neocosmospora*: Phylogenomic and practical reasons for continued inclusion of the *Fusarium solani* species complex in the genus *Fusarium*. mSphere 5:e00810-20. https://doi.org/10.1128/msphere.00810-20

Otero-Colina G, Rodríguez-Alvarado G, Fernández-Pavía S et al (2010) Identification and characterization of a novel etiological agent of mango malformation disease in Mexico. *Fusarium mexicanum* sp. nov. Phytopathol 100:1176–1184. https://doi.org/10.1094/PHYTO-01-10-0029

Pfunder M, Schürch S (2001) Sequence variation and geographic distribution of pseudoflower-forming rust fungi (*Uromyces pisi* s. lat.) on *Euphorbia cyparissias*. Mycol Res 105:57–66. https://doi.org/10.1017/S0953756200003208

Rai M, Agarkar G (2016) Plant–fungal interactions: what triggers the fungi to switch among lifestyles? Crit Rev Microbiol 42:428–438. https://doi.org/10.3109/1040841x.2014.958052

Rokas A, Williams BL, King N et al (2003) Genome-scale approaches to resolving incongruence in molecular phylogenies. Nature 425:798–804. https://doi.org/10.1038/nature02053

Rossman AY, Samuels GJ, Rogerson CT et al (1999) Genera of *Bionectriaceae*, *Hypocreaceae* and *Nectriaceae* (*Hypocreales*, *Ascomycetes*). Stud Mycol 42:1–248

Rossman AY, Seifert KA, Samuels GJ et al (2013) Genera of *Bionectriaceae*, *Hypocreaceae* and *Nectriaceae* (*Hypocreales*) proposed for acceptance and rejection. IMA Fungus 4:41–51. https://doi.org/10.5598/imafungus.2013.04.01.05

Roy BA (1993) Floral mimicry by a plant pathogen. Nature 362:56–58. https://doi.org/10.1038/362056a0

Salgado-Salazar C, Rossman AY, Chaverri P (2016) The genus *Thelonectria* (*Nectriaceae*, *Hypocreales*, *Ascomycota*) and closely related species with cylindrocarpon-like asexual states. Fungal Div 80:411–455. https://doi.org/10.1007/s13225-016-0365-x

Samuels GJ, Doi Y, Rogerson CT (1990) *Hypocreales*. Mem New York Bot Gard 59:6–108

Samuels GJ, Lu B-S, Chaverri P et al (2009) *Cyanonectria*, a new genus for *Nectria cyanostoma* and its *Fusarium* anamorph. Mycol Prog 8:49–58. https://doi.org/10.1007/s11557-008-0577-x

Sandoval-Denis M, Crous PW (2018) Removing chaos from confusion: assigning names to common human and animal pathogens in *Neocosmospora*. Persoonia 41:109–129. https://doi.org/10.3767/persoonia.2018.41.06

Sandoval-Denis M, Guarro J, Cano-Lira JF et al (2016) Phylogeny and taxonomic revision of *Microascaceae* with emphasis on synnematous fungi. Stud Mycol 83:193–233. https://doi.org/10.1016/j.simyco.2016.07.002

Sandoval-Denis M, Guarnaccia V, Polizzi G et al (2018) Symptomatic *Citrus* trees reveal a new pathogenic lineage in *Fusarium* and two new *Neocosmospora* species. Persoonia 40:1–25. https://doi.org/10.3767/2Fpersoonia.2018.40.01

Sandoval-Denis M, Lombard L, Crous PW (2019) Back to the roots: a reappraisal of *Neocosmospora*. Persoonia 43:90–185. https://doi.org/10.3767/persoonia.2019.43.04

Sangalang AE, Summerell BA, Burgess LW et al (1995) Taxonomy of *Fusarium*: characterization of *Fusarium avenaceum* ssp. *aywerte* and *Fusarium avenaceum* ssp. *nurragi*. Mycol Res 99:287–290. https://doi.org/10.1016/S0953-7562(09)80901-5

Santos ACDS, Trindade JVC, Lima CS et al (2019) Morphology, phylogeny, and sexual stage of *Fusarium caatingaense* and *Fusarium pernambucanum*, new species of the *Fusarium incarnatum*-equiseti species complex associated with insects in Brazil. Mycologia 111:244–259. https://doi.org/10.1080/00275514.2019.1573047

Savary O, Coton M, Frisvad JC et al (2021) Unexpected *Nectriaceae* species diversity in cheese, description of *Bisifusarium allantoides* sp. nov., *Bisifusarium penicilloides* sp. nov., *Longinectria* gen. nov. *lagenoides* sp. nov. and *Longinectria verticilliforme* sp. nov. Mycosphere 12:1077–1100. https://doi.org/10.5943/mycosphere/12/1/13

Schroers HJ, Gräfenhan T, Nirenberg HI et al (2011) A revision of *Cyanonectria* and *Geejayessia* gen. nov., and related species with Fusarium-like anamorphs. Stud Mycol 68:115–138. https://doi.org/10.3114/sim.2011.68.05

Secor GA, Rivera-Varas V, Christ DS et al (2014) Characterization of *Fusarium secorum*, a new species causing Fusarium yellowing decline of sugar beet in north central USA. Fun Biol 118:764–775. https://doi.org/10.1016/j.funbio.2014.06.001

Stamatakis A (2014) RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. Bioinf 30:1312–1313. https://doi.org/10.1093/bioinformatics/btu033

Taylor LH, Latham SM, Woolhouse ME (2001) Risk factors for human disease emergence. Phil Tr R Soc b: Biol Sci 356:983–989. https://doi.org/10.1098/rstb.2001.0888

Teufel F, Almagro Armenteros JJ, Johansen AR et al (2022) SignalP 6.0 predicts all five types of signal peptides using protein language models. Nature Biotechnol 40:1023–1025. https://doi.org/10.1038/s41587-021-01156-3

Thines M, Kummer V (2013) Diversity and species boundaries in floricolous downy mildews. Mycol Prog 12:321–329. https://doi.org/10.1007/s11557-012-0837-7

Torbati M, Arzanlou M, Santos ACDS (2021) Fungicolous *Fusarium* species: ecology, diversity, isolation, and identification. Curr Microbiol 78:2850–2859. https://doi.org/10.1007/s00284-021-02584-9

Triest D, De Cremer K, Piérard D et al (2016) Unique phylogenetic lineage found in the *Fusarium*-like clade after re-examining BCCM/IHEM fungal culture collection material. Mycobiol 44:121–130. https://doi.org/10.5941/MYCO.2016.44.3.121

Villani A, Proctor RH, Kim HS et al (2019) Variation in secondary metabolite production potential in the *Fusarium incarnatum-equiseti* species complex revealed by comparative analysis of 13 genomes. BMC Gen 20:314. https://doi.org/10.1186/s12864-019-5567-7

Walsh JL, Laurence MH, Liew ECY et al (2010) *Fusarium*: two endophytic novel species from tropical grasses of northern Australia. Fun Div 44:149–159. https://doi.org/10.1007/s13225-010-0035-3

Wang MM, Chen Q, Diao YZ et al (2019) *Fusarium incarnatum-equiseti* complex from China. Persoonia 43:70–89. https://doi.org/10.3767/persoonia.2019.43.03

Wardeh M, Risley C, McIntyre MK et al (2015) Database of host-pathogen and related species interactions, and their global distribution. Sci Dat 2:150049. https://doi.org/10.1038/sdata.2015.49

Waterhouse RM, Seppey M, Simão FA et al (2018) BUSCO applications from quality assessments to gene prediction and phylogenomics. Mol Biol Evol 35:543–548. https://doi.org/10.1093/molbev/msx319

Wollenweber HW (1931) *Fusarium* – Monographie. Fungi Parasitici Et Saprophytici Z Parasitenk 3:260–516

Xia JW, Sandoval-Denis M, Crous PW et al (2019) Numbers to names - restyling the *Fusarium incarnatum-equiseti* species complex. Persoonia 43:186–221. https://doi.org/10.3767/persoonia.2019.43.05

Xiang T, Li J, Bao S et al (2021) Digital RNA-seq transcriptome plus tissue anatomy analyses reveal the developmental mechanism of the calabash-shaped root in *Tetrastigma hemsleyanum*. Tree Physiol 41:1729–1748. https://doi.org/10.1093/treephys/tpab024

Yilmaz N, Sandoval-Denis M, Lombard L et al (2021) Redefining species limits in the *Fusarium fujikuroi* species complex. Persoonia 46:129–162. https://doi.org/10.3767/persoonia.2021.46.05

Zerbino DR, Birney E (2008) Velvet: algorithms for de novo short read assembly using de Bruijn graphs. Gen Res 18:821–829. https://doi.org/10.1101/2Fgr.074492.107

Zhang H, Yohe T, Huang L et al (2018) dbCAN2: a meta server for automated carbohydrate-active enzyme annotation. NAR 46:W95–W101. https://doi.org/10.1093/nar/gky418

Zhu H, Zhu L, Ding N (2020) Genomic insights into the aquatic *Fusarium* spp. QHM and BWC1 and their application in phenol degradation. Curr Microbiol 77:2279–2286. https://doi.org/10.1007/s00284-020-02050-y