Fungal Diversity (2021) 109:239–266
https://doi.org/10.1007/s13225-021-00484-8

REVIEW

What is a species in fungal plant pathogens?

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Received: 30 March 2021 / Accepted: 21 July 2021 / Published online: 11 August 2021

Abstract

Scientific names are crucial for communicating knowledge concerning fungi and fungus-like organisms. In plant pathology, they link information regarding biology, host range, distribution and potential risk to agriculture and food security. In the past, delimitation among pathogenic taxa was primarily based on morphological characteristics. Due to distinct species sharing overlapping characteristics, the morphological identification of species is often neither straightforward nor reliable. Hence, the phylogenetic species concept based on molecular phylogenetic reconstructions gained importance. The present opinion discusses what a fungal species is and how identification of species in plant pathology has changed over the past decades. In this context, host-specialization and species complexes are discussed. Furthermore, species concepts in plant pathology are examined using case studies from *Bipolaris*, *Colletotrichum*, *Curvularia*, *Diaporthe*, *Diplodia*, *Meliola*, *Plasmopara*, rust fungi and *Trichoderma*. Each entry contains a brief introduction to the genus, concepts used in species identification so far and the problems in describing a species followed by recommendations. The importance of correctly naming and identifying a species is addressed in the context of recent introductions, and we also discuss whether the introduction of new species in pathogenic genera has been overestimated. We also provide guidelines to be considered when introducing a new species in a plant pathogenic genus.

Keywords Dual nomenclature · Host-specificity · Polyphasic approach · Pathology · Phylogeny · Species delimitation · Systematics

Handling Editor: Sajeewa Maharachchikumbura.

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Table of contents

Introduction

The fungal kingdom is thought to comprise between 2.2 and 3.8 million species, with 2–3 million yet to be discovered (Hawksworth and Lucking 2017; Hyde et al. 2018a, 2020). Fungi have endophytic, parasitic, saprotrophic or mutualistic relationships with plants (Zeilinger et al. 2016; Jayawardena et al. 2018). Fungal plant pathogens potentially incite devastating ecological and economic damage to agriculture and forestry, and can also cause severe damage to natural ecosystems (Fisher et al. 2012; Hyde et al. 2018b). The development of plant disease is a result of the tripartite interaction of host, pathogen and environment. Accurate identification and understanding of these factors are imperative for early pathogen detection, disease prevention, and management (De Wolf and Isard 2007). Control and management strategies may vary with the fungal species. Thus accurate identification and nomenclature for each of these species is an essential prerequisite.

The species is a fundamental category in biology. However, this term carries different meanings for scientists in different fields and can also vary with the group of organisms studied (Samarakoon et al. 2016). Over the past century, different kinds of species concepts have been proposed and applied to define a fungal species viz morphological, phylogenetic, evolutionary and reproductive species concepts (Cai et al. 2011a,b). As different groups are often defined based on different traditions and species concepts, comparative studies among fungal groups are often difficult to perform. Along with the challenges of delimitation of taxa described below, the species concept used will be central to clearing ambiguity in the accurate and specific naming of fungi.

Only two decades ago, delimitation among pathogenic taxa was primarily based on their morphological characteristics, but with the increasing availability of sequence data, which brought about detailed molecular phylogenetic investigations, it became clear that in many groups the conventionally used morphological features were insufficient for this purpose (Hyde et al. 2009; Thines 2014; Crous et al. 2015; Jayawardena et al. 2020). Classification of plant pathogens is not only crucial for identification, but also carries information regarding their diversity and potential functions. Thus, scientific names for a species often contain key information on the respective host range, distribution, as well as biological, ecological and associated disease risk (Crous et al. 2015). A major obstacle to bridging the gap between systematic mycologists and applied plant pathologists is often fundamental differences in the definition of the term 'species' and methods used for identifying species (Taylor et al. 2000). Molecular phylogenetics have begun to pave the way for clearing up the ambiguity (Wingfield et al. 2012; Crous et al. 2015), but there is still a long way to go until all plant pathogenic fungi and oomycete species and species complexes have been resolved.

The advent of molecular phylogeny has greatly helped in resolving the dual nomenclature of pleomorphic fungi which had been a concern of plant pathologists and fungal taxonomists alike. Scientists have thus mutually benefitted from resolving the “One fungus one name” paradigm of the Amsterdam declaration (Hawksworth et al. 2011), which heralded the end of dual nomenclature for fungi. However, given the huge number of broad and narrow species concepts and multiple synonyms with unclear typification, plant pathologists and taxonomists are often confronted with

ambiguity for newly identify pathogens. Pathologists must choose a name for a pathogen of interest, while taxonomists constantly find signatures of evolutionary divergence within species groups. As a result, pathologists could be naming a single species that taxonomists later break into two or more species based on evidence of divergence (Cai et al. 2011a, b). This is further complicated by global trade, which has led to the emergence of several new plant pathogens in crops over the past decades, which were often misidentified at first (Thines and Choi 2016) The same group of organisms may be classified differently when using different sets of criteria for species delimitation or species concepts (Singer 1986; Kwon-Chung et al. 2017). As a result, taxonomic revision with the aim to resolve monophyletic groups is a common feature in the current taxonomic literature, often involving moving organisms to different or new genera and even families (Cai et al. 2011a,b).

Fungal taxonomists frequently arrive at results that necessitate taxonomic revision of economically important groups (Crous et al. 2021). This can lead to changes of familiar names of plant pathogenic fungi, complicating the work of plant pathologists. Thus, such changes should always be very carefully initiated, considering also the possibility of nomenclatural conservation, to keep changes of names of pathogens for ornamentals and crops at a minimum. However, the rapid progress in fungal taxonomy has apparently eroded the stability of fungal names (Glawe 2003). Nevertheless, at the pace at which fungal systematics is currently progressing, it seems conceivable that within the next decade an era of higher stability can begin. The short-term instability resulting from regrouping species based on their taxonomy should result in a more stable and accurate nomenclature in the long-term (Crous et al. 2021).

Wingfield et al. (2012) pointed to the fact that most plant diseases are caused by ascomycetes. Their taxonomy has been problematic ever since they were recognized, especially as many of them have both sexual and asexual morphs, which were often described as independent species. Dealing with pleomorphic fungal pathogens is, thus, one of the most difficult aspects of fungal plant pathology. Moreover, dual naming is a critical issue especially for plant fungal pathogens, where the same species can be treated differently as a result of it bearing two different names (Carnegie et al. 2010). Contrary to the increase in names because of dual naming, there have been many cases where several fungal taxa had been lumped and treated as one species for convenience, mostly due to reliance on overlapping morphological characteristics. However, molecular phylogenetic analyses have shown that in most cases the narrow species concept is more appropriate and that they are actually well-resolved species (Bensch et al. 2010; Crous and Groenewald 2005; Thines and Choi 2016). The consequences of such lumping can be drastic in terms of disease identification, prevention and management (Carnegie and Cooper 2011; Thines et al. 2009; Görg et al. 2017).

To outline this issue and discuss potential ways towards a solution, the present review discusses aspects of defining a species, how the species was identified in the pre- and post-molecular era, and how species concepts in fungal pathology can be harmonized by using examples from some important plant pathogenic genera, namely, *Bipolaris*, *Colletotrichum*, *Curvularia*, *Diaporthe*, *Diplodia*, *Meliola*, *Plasmopara*, rusts and *Trichoderma*. In this context, we also discuss whether too many new species are currently being introduced in error and provide guidelines for consideration when introducing a new species in a plant pathogenic genus. The use of taxa below the species level is not considered here and is dealt with by Manawasinghe et al. (2021) in this special issue.

Species concepts and species recognition criteria

There are over 30 species concepts in the biological literature (Crous et al. 2015; Zachos 2016), common ones that have been applied to delineate fungal species include the morphological, ecological, phenetic, biological, evolutionary, and phylogenetic species concepts. Morphological and phenetic concepts especially rely on often overlapping characteristics of organisms. A species concept is a description of the kind of entity that constitutes a species, while a species criterion is the practical standard used to judge or recognize whether individuals should be considered members of the same species (De-Queiroz 1998). These two terms are related, however, the distinction between them is critical and a misunderstanding could result in ambiguity. A problem could arise if a particular species criterion is the basis of species delimitation under a certain concept and yet in a different setting the introduction of a species might be considered incorrect, if the species criterion was formulated differently (Hey 2006; Taylor et al. 2000). In other words, agreement on the species concepts applied is critical to unambiguously determining novel species.

The term biological species concept is often used to emphasize the criterion of inter-sterility. The morphological species concept, on the other hand, emphasizes the criterion of morphological similarity, while the ecological species concept emphasizes adaptations to a particular ecological niche. Unlike the previous concepts, the phylogenetic species concept highlights the divergence of nucleotides between monophyletic lineages (Giraud et al. 2008; Taylor et al. 2000). Even though these concepts may converge (Cai et al. 2011a,b), each of them uses different criteria for delimitating species. According to Giraud et al. (2008), species criteria that mycologists adopt cannot be universal.

Hence, it is impossible to have a single species criterion that is applicable in all cases. Therefore, to be useful, criteria for the recognition of species need to be tailored to the type of organism, history of speciation and the degree of divergence.

For example, criteria used to identify species in the plant pathogenic genera *Colletotrichum* and *Fusarium* are different from that of identifying a species belonging to *Botryosphaeriaceae*. In all three groups, morphological and phylogenetic species concepts are used. However, when defining a species in *Colletotrichum* or *Fusarium* genealogical concordance for phylogenetic species recognition is of great importance, due to the morphological similarity of many species. Different genera will therefore likely require a different accordance of species concepts to be applied. In this paper a deep discussion of species concepts is not provided as Chethana et al. (2021) dealt with what is a species concept, importance and the conflicts among each concept in this special issue.

Pre-molecular era species definition in plant pathology

Fungi occurring as pathogens of plants were historically separated by morphology and also on host association (Cai et al. 2011a, b; Wingfield et al. 2012; Hyde et al. 2014). However, this has often led to ambiguity and misidentifications (Jayawardena et al. 2016a). The decision on which characteristics are essential is mostly subjective and does not need to mirror evolutionary relationships.

Microscopic techniques were actively applied to study microscopic features of fungi from the seventeenth century onwards. The pioneering work of de Bary (1863) was influential for modern plant pathology, and led to the widespread recognition of fungi as plant pathogens (Berbee and Taylor 1992). In the mid-nineteenth century taxonomists discovered that fungi can have different stages in their life cycles with different morpho-types. However, as the link between the different morphs was often not obvious, a dual nomenclatural system was established, giving independent names to sexual and asexual morphs (discussed below). By the early twentieth century the micro-morphology of fungal structures such as size, shape, colour and shape of the spore-bearing structures, colour septation and dimension of the sexual and asexual spores were widely used in classification systems for both sexual and asexual morphs. In addition, physiological parameters such as growth rate were sometimes also used for species delimitation (Cai et al. 2009).

The biological species concept was introduced at the beginning of the twentieth century based on reproductive ability. The simpler version of Mayrs' definition is that a species can successfully interbreed and produce fertile offspring. However, they are incapable of successfully mating with other such groups (Bisby and Coddington 1995). Many cryptic species have been recognized with inter-sterility criterion, a derivative of the biological species definition criteria (Anderson and Ullrich 1979; Cai et al. 2011a,b). The scarcity of morphological characteristics of fungi led many mycologists to use tests for inter-sterility and gene flow to identify potential species (Harrington and Rizzo 1999). However, most fungi cannot be tested in vitro for compatibility. This is due to either the species not forming meiotic spores in the laboratory or because they are asexual. For example, this cannot be applied to homothallic or asexual fungi (Taylor et al. 2000). However, tests for inter-sterility have proven valuable in pointing where to look for phenotypic differences between species that are difficult to separate. For instance, delimitation of pathogenic mushroom species in *Armillaria* (Korhonen 1978b) and *Heterobasidion* (Korhonen 1978a), was greatly facilitated by sexual compatibility tests. Many *Armillaria* species occur sympatrically and occasionally, several species can be found on the same host substrate (Rizzo and Harrington 1993; Jayawardena et al. 2020). Until recently, the morphologically similar *Armillaria* species were considered to be part of a single, variable species, *Armillaria mellea*, even though virulence, basidiome morphology, rhizomorph production, and intraspecific variation were noted (Morrison and Pellow 2002). Since tests for inter-sterility have been applied, eight additional species in the *A. mellea* complex have been described and some others were newly introduced on the basis of classic morphological characteristics (Bérubé and Dessureault 1989; Jayawardena et al. 2020). Specific genes important for inter-sterility have been identified in the *Heterobasidion annosum* complex (Chase and Ullrich 1990; Jayawardena et al. 2020). However, as sexual reproduction is rare in artificial conditions and sometimes even in nature, mating experiments are often not feasible.

In the early decades of the twentieth century, another practice that was developed and became common was naming a species based on host association. Separate scientific names were given to fungi and oomycetes that were morphologically similar but found on different plant genera or species (e.g. in the genera *Cercospora*, *Colletotrichum* and *Peronospora*). In addition, minor differences in spore sizes were often considered. Plant pathologists supported this with the evidence from inoculation experiments that revealed that many morphologically indistinguishable taxa infect only one plant species and cannot occur on any other. However, as these relations were not always clear-cut and necrotrophic species did often show wider host ranges, there were also doubts regarding the separation of new species according to host associations. Thus, species shown to be experimentally host-restricted, but morphologically indistinguishable were often identified as forms (giving *formae* (abbreviation f.)) or special forms (giving *formae speciales* (abbreviation f. sp.)), e.g. *Colletotrichum capsici* f. *cyamopsidicola*,

Colletotrichum graminicola f. sp. *sorghi*, *Fusarium album* f. *album*, *Fusarium heterosporum* f. sp. *aleuritidis*. In some instances, the species were identified as varieties (abbreviation var.) which are dealt with in Manawasinghe et al. (2021) in detail. However, molecular phylogenetics has generally favored the recognition of specialized species (see below).

A range of chemical and biomolecular approaches, such as thin-layer chromatography and isozyme profiling appeared promising in distinguishing plant pathogens in the 1960s and 1970s. During cultivation studies, it was also discovered that the population structure of a fungus could be analysed using vegetative compatibility groups. For some plant pathogens, vegetative compatibility groups could be defined reasonably easily on agar in Petri-dishes. Nit (nitrate) mutants were, for example, applied to recognize vegetative compatibility pathogenic *Fusarium* groups (Leslie 1993). Morphological, phenotypic, chemical and biomolecular patterns were used for cladistic character analyses that came to use in the mid-1970s (Tehler 1993). Even though interpretation of the results was often difficult, these represented the early stage approaches for polyphasic taxonomy as practiced today.

Thus, species recognition based on microscopic features, sometimes combined with host ranges, continued to be the most important aspect for species recognition throughout the 1970s and 1980s. However, even though light microscopy techniques had improved significantly by the 1980s, especially with the application of Nomarski differential interference contrast, the separation of almost identical fungi often remained problematic. Thus, fungal classification during this period was controversial and debated between the two different arguments; those preferring the recognition of many host-specialized species (e.g. Gäumann 1918, 1923), or those recognizing only a few pathogenic species per host family, with many specialized forms. For example, Yerkes and Shaw (1959) did not reflect the desired level of classification needed by plant pathologists. However, this was set to change in the twentieth century when phylogenetics based on DNA sequences became common and easy to use.

DNA-guided species delimitation in plant pathology

The earliest techniques based on DNA, such as randomly amplified polymorphic DNA (RAPD) and restriction fragment length polymorphisms (RFLPs) were applied for fungal identification (Gil-Lamaignere et al. 2003). Amplified fragment length polymorphism (AFLP) markers have commonly been used to differentiate closely related species in pathogenic genera such as *Colletotrichum* and *Fusarium* (Cannon et al. 2012).

Phylogenetic inference based on DNA sequence data analyses radically changed fungal taxonomy since the turn of the millennium. This methodology has been responsible for identifying a large number of cryptic species in recent years (Schubert et al. 2007; Damm et al. 2009, 2012a,b, 2013, 2014, 2019; Wulandari et al. 2009; Aveskamp et al. 2010). Sequence-based phylogenetics relies on the analysis of variable characters, usually DNA or derived protein sequences of selected genes or genomes. Since the late 1990s, phylogenetic analyses based on DNA sequences (at one or multiple loci) in defining fungal species, has become widespread enabling a broad application in numerous taxonomic groups (Taylor et al. 2000; Schoch et al. 2012; Hyde et al. 2014; Jayawardena et al. 2016b, 2018, 2019, 2020). This approach has led to the identification of a large number of new and cryptic species amongst previously recognized fungal taxa. For example, *Colletotrichum gloeosporioides* was thought to be a single species. However, with the use of DNA sequence data of seven loci (ITS, *gapdh, chs, act, tub2, cal* and *gs*), this single species was identified as a species complex with 22 species (Weir et al. 2012; discussed below). Matute and Sepulveda (2019) reviewed 16 diverse genera from 51 studies and showed that each of the originally described single species represented an average of three cryptic species. In this sense technology can be used to greatly expand our ability to identify extant species. Importantly, the approach used and the genes analyzed could result in entirely different identifications.

At present, there is no standard as to which gene(s) should be analyzed, how much sequence divergence is needed, and what statistical support is required at both the individual locus and the combined concatenated sequence levels to determine whether different strains belong to different species (Lücking et al. 2020). However, there have been some universal barcoding loci suggested for both fungi (Schoch et al. 2012) and oomycetes (Robideau et al. 2011; Choi et al. 2015). Pathogenic genera such as *Neopestalotiopsis*, *Pestalotiopsis* and *Pseudopestalotiopsis* (pestalotiod fungi) use a three loci combination in species delimitation (Maharachchikumbura et al. 2014). Similarly, the amount of sequence divergence and statistical support separating closely related species based on individual genes varies significantly among groups. Besides, some taxonomic studies and new species descriptions rely on relatively few samples. In recent years, many species have been introduced based on a single strain. Further analyses of some of the closely related DNA sequence-based "phylogenetic or genotypic cluster species" with larger sample sizes revealed abundant signatures of recombination among them (Liu et al. 2016a). This indicates that some of these species belong to the same reproductive group in nature. Their separate species designations are mainly due to inadequate sampling (Liu et al. 2016a).

For all molecular approaches, DNA is most easily recovered from living cultures. Direct extraction of DNA from herbarium or dried specimens (e.g. Thines et al. 2009)

has also made it possible to revise major groups of obligate fungi that cannot be cultivated, such as rusts, smuts, downy mildews and white blister pathogens (Choi et al. 2010; Thines et al. 2009; Shivas et al. 2014). Other than for taxonomy, this approach has also made it possible to track invasive species of plant pathogens (Groenewald et al. 2007). Sequence variation in nineteenth-century samples of the pathogen (*P. infestans*) responsible for the Irish potato famine of 1845–1847 (Martin et al. 2013) has been identified by whole-genome sequence analyses of old herbarium specimens, leading to the identification of the pathogen lineage that triggered the famine (Yoshida et al. 2013, 2014).

In recent years, the Genealogical Concordance Phylogenetic Species Recognition criterion, which is an adaptation of the phylogenetic species concept, has been used widely (Taylor et al. 2000; Cai et al. 2011a,b; Crous et al. 2015). Genealogical Concordance Phylogenetic Species Recognition uses the phylogenetic concordance of multiple unlinked genes to indicate a lack of genetic exchange and therefore evolutionary independence of lineages. Species lacking distinguishing morphological characters or exhibiting incomplete inter-sterility can still be identified based on Genealogical Concordance Phylogenetic Species Recognition, given enough independent samples per lineage are included. Among the numerous complexes of sibling species recently uncovered using the Genealogical Concordance Phylogenetic Species Recognition criterion, some have typical allopatric divergence, as the cryptic species occupy non-overlapping areas separated by geographic barriers (Taylor et al. 2006). This is the case for some species in the species complexes *Fusarium graminearum* (O'Donnell et al. 2004) and *Armillaria mellea* (Anderson et al. 1980). Adaptation to a new host can, in these cases, be sufficient to restrict gene flow in sympatry, without requiring active assortative mating (Giraud 2006; Thines 2019). In such cases, closely related species may remain inter-fertile for some time, making in vitro crosses a poor criterion for recognizing species. Multiloci phylogenetic analyses of worldwide samples of *Ascochyta* revealed that each of these can be resolved into distinct species (Peever 2007) and experimental inoculation showed that infections are strongly host-specific, while in vitro mating tests showed that the species are infertile (Schirrmann and Leuchtmann 2015).

Even though there are many advantages to Genealogical Concordance Phylogenetic Species Recognition, its limitations also need to be considered. Crous et al. (2015) mentioned that the more loci or gene regions that are used to assess phylogenetic relationships, the more likely the results will reflect reality. Right now there are only 3–8 loci used in combination for distinguishing species in plant pathogenic genera. The information content of different loci can be quite different, as shown by Bhunjun et al. (2020) in *Bipolaris* and Bhunjun et al. (2021) in *Colletotrichum* species delimitation by phylogenetic analyses, automatic barcode gap discovery and object clustering. Therefore, the resulting trees are only as informative as the specific loci chosen for sequencing and the alignment used as input data (Aguileta et al. 2008; Cai et al. 2011a,b; Crous et al. 2015).

While individual approaches have merits and complexities, using a polyphasic approach to identify species by combining morphological, ecological, and phylogenetic data has been widely used in the taxonomy of plant pathogenic genera such as *Alternaria*, *Bipolaris*, *Colletotrichum* and *Diaporthe* (Cai et al. 2009; Cannon et al. 2012; Udayanga et al. 2013; Bhunjun et al. 2020). Quaedvlieg et al. (2014) referred to the polyphasic approach for identifying species as the consolidated species concept, but it needs to be emphasized that there are no well-defined criteria to weigh the different components considered in reaching species hypotheses.

A species based on host relation and specificity

Most plant pathogenic fungi cause diseases when infecting a narrow range of hosts, with strong specificity often at the host species level. However, some pathogenic species may have a broad host ranges, such as *Albugo candida*, *Colletotrichum acutatum, C. siamense, Fusarium oxysporium*, and *Pseudoperonospora cubensis* (Runge et al. 2011; Borah et al. 2018; Jayawardena et al. 2021). Interestingly, within these broad host range species, there seems to be some specialization, as some studies have shown that individual strains of *F. oxysporum* infect one or a few plant species only (Pietro et al. 2003). This is in line with host-specificity factors located on auxiliary chromosomes in this species (Vlaardingerbroek et al. 2016). Strains of different hosts within such a fungal species are commonly classified into different pathotypes or *formae speciales* (see Weir et al. 2012 for the *Colletotrichum gloeosporioides* species complex). Sometimes these *formae speciales* are further divided into different races depending on the particular cultivar that they can infect, which is referred to as 'host cultivar specificity' reflected by pathotypes. For example, based on host cultivar specificity, the tomato infecting strain of *F. oxysporum* is divided into three pathotypes, often referred to as "races" (Takken and Rep 2010). Naming below species in plant pathology is discussed in Manawasinghe et al. (2021).

The assumption that plant pathogenic species are host-specific may be artificial because of incomplete sampling, limitation of the sampling to economically important crops, and incomplete knowledge factors contributing to pathogenicity (Cannon et al. 2012). There are fewer studies concerning forest pathogens and aquatic plant pathogens due to limited sampling from these ecosystems. Many pathogens are obligate biotrophic and, thus, cross-pathogenicity tests to confirm host-specificity are difficult to perform as axenic cultures are lacking. In these cases, collections from the

same host from different localities and of related species on other hosts from the same areas should be investigated to confirm specificity.

Occasionally, a pathogen occurring on a certain host species can also occur on related hosts in the same area. For example, Mackenzie et al. (2007) demonstrated gene flow between populations of *C. acutatum* from native plants and those from adjacent strawberry crops. In addition, many pathogens can be isolated as endophytes and saprobes from the same host on which they might cause disease. This has led to the assumption that they can switch their lifestyle depending on the physiological condition of the host plant, genotype, and environmental factors (da Silva et al. 2020). Liu et al. (2015) isolated and identified six *Colletotrichum* species from both symptomatic and asymptomatic leaf tissues of *Camellia sinensis*. They assumed that the endophytic phase of these species can switch to pathogens when conditions are right. In any case, pathogenicity assays are necessary to confirm that the isolated fungal endophytic fungi are not pathogenic variants.

A hallmark of the evolution of plant pathogenic fungi is host jumping. Host jumping is a process by which pathogens occasionally settle on new host groups, which enables them to persist over a long evolutionary time scale, even if resistance leads to their extinction on the original host group (Thines 2019). Thus, by jumping hosts they escape the extinction on a particular group of hosts. Compatible microbiomes and similar physiology favour host jumping among fungal pathogens (Thines 2019). Support for this hypothesis has been observed in several plant pathogenic fungi and oomycetes, e.g. *Bremia* (Choi and Thines 2015). In *Puccinia* rusts, host jumping to geographically associated hosts were a more likely explanation for diversification than co-speciation and coevolution with the hosts (Roy 2001). Examples of recent host jumping occurrences include *Cronartium ribicola*, an Asian Pine rust, which jumped to a new *Pinus* species in Europe and North America, causing a devastating epidemic (Kinloch Jr 2008). *Fusarium circinatum* resulted in the pitch canker disease epidemic on *Pinus radiata* in California, following its introduction into that area from native Mexican pines (Gordon et al. 2001). The rust pathogen *Puccinia psidii* jumped from native *Myrtaceae* to introduced *Eucalyptus* trees in South America (Coutinho et al. 1998).

As host jumping can lead to subsequent parasitic radiation, a clear demarcation between specialist pathogens that can only infect one or a few closely related host species and generalists that can infect more than a hundred unrelated host species (Barrett et al. 2009) is difficult. The start of these radiation processes can be highly specialized in species that develop an important adaptation in an effector targeting a conserved core plant defense mechanism. This then enables a widening of the host range by a host jump to an unrelated plant species (Thines 2019). Thus, host-specialization is often considered as an evolutionary dead end (Moran 1988), as gene losses are usually irreversible and may limit specialist lineages transitions back to generalism (Day et al. 2016). Successful pathogen lineages however are thought to overcome these limitations via plastic genomes. Such plasticity enables adaptations that help to enable the survival of the species (Thines 2019). Evidence for the transitions from specialist to generalist pathogens can be found in various obligate biotrophic pathogens. An illustrative example for this is *Pseudoperonospora cubensis*, which causes downy mildew in a wide range of cucurbits (Lebeda and Cohen 2011), but has evolved from a species specialized in infecting hops (Runge et al. 2011). In necrotrophic and hemibiotrophic pathogens such patterns can be found, e.g. in *Sclerotiniaceae*. In this group, the dominant mode of association with plants is the parasitic radiation on distant hosts which may or may not result in specialized species, depending on the speed of host switching (host jump or duplication events) (Navaud et al. 2018).

It has long been believed that new species evolve mostly through allopatric divergence (Mayr 1963), i.e. due to the extrinsic barriers obstructing gene flow. Even though airborne fungal pathogens may disperse over very long distances (Brown and Hovmoller 2002), a large proportion of fungal pathogens appear to have evolved in a manner consistent with allopatric divergence by occupying non-overlapping areas separated by geographical barriers (Taylor et al. 2006). However, sympatric speciation can occur despite inter-fertility when host-specialization limits gene flow between different strains. This has likely happened during wheat domestication, and in the sympatric differentiation of *Zymoseptoria* pathogens of natural and domesticated grasses (Stukenbrock et al. 2007).

Based on the above facts, it is clear that the host association (ecological concept) of a species alone cannot be applied in the delimitation of a fungal species.

Dual nomenclature and one name one fungus

Pleomorphism, which means that species have different morphotypes for sexual and asexual propagation, can be observed in many important plant pathogenic fungi (Wingfield 2012). Common examples are *Calonectria* (sexual) and *Cylindrocladium* (asexual), *Elsinoe* (sexual) with *Sphaceloma* (asexual), *Gibberella* (sexual) and *Fusarium* (asexual) morph, *Glomerella* (sexual) and *Colletotrichum* (asexual) and the families *Botryosphaeriaceae* and *Mycosphaerellaceae* with a large number of very different asexual morphs (Cannon et al. 2012; Wingfield et al. 2012; Hyde et al. 2013; Phillips et al. 2013; Dissanayake et al. 2016; Jayawardena et al. 2019). In many plant pathogenic ascomycetes, the

asexual morph is most commonly found in nature. However, in many basidiomycetes, such as the smut fungi, the sexual state is more prominent, but in some genera, such as *Moesziomyces*, the asexual, saprotrophic morph is also frequently isolated from various substrates (Kruse et al. 2017). Sexual morphs often produce long-lasting, overwintering structures that initiate a new infection (Schubert et al. 2003; Jayawardena et al. 2019, 2020). Fungal taxonomists tried to link different morphological forms of plant pathogens, which was challenging, as in many cases only one of the morphs was known.

Saccardo (1904) introduced a dual system for naming fungi as a solution to this problem. The dual naming approach was considered by the International Botanical Congress and was included in the International Code of Botanical Nomenclature (Briquet 1905, 1912; Taylor 2011). This resulted in different but valid names for sexual and asexual morphs of the same fungus. Whenever an asexual morph was discovered, a new and independent name was given, even though it was known to be a morph of a known species. In many cases, in this naming system the same fungus may have not only had different generic names, but also different species' epithets, e.g. *Botryosphaeria rhodina* is the sexual morph of *Lasiodiplodia theobromae* (Alves et al. 2008). As sexual morphs were treated with priority after a link was established, many name changes for economically important plant pathogens occurred, which led to challenges in applied plant pathology, as communication was impaired by unclear synonymies. For example, the causal agent of Cylindrocladium pod rot of peanut *Cylindrocladium parasiticum* was linked to *Calonectria ilicicola* (Crous et al. 1993), while *C. ilicicola* was shown to be the asexual morph of *Ca. lauri* (Lechat et al. 2010).

The use of two different names also led to confusion with quarantine regulations. In the quarantine lists, some countries listed the names of asexual morphs, while other countries listed the names of sexual morphs, which confused export–import quarantine measures. Needless to mention, the species concepts for sexually and asexually typified names often differed, adding to the complexity of the situation. Another recent example of this confusion is the myrtle rust caused by *Uredo rangelii* in Australia (Carnegie et al. 2010). Due to incongruent species concepts for sexual and asexual morphs, it was unclear if the myrtle rust is the serious quarantine organism *Puccinia psidii*, the causal agent of eucalypt rust (Glen et al. 2007; Carnegie and Cooper 2011). To reduce the confusion arising from dual nomenclature, plant pathologists and mycologists generally agreed in 2005 not to assign names to newly discovered asexual morphs of fungi that were known in their sexual state (McNeill et al. 2006).

With the increasing availability of DNA sequence data, more and more sexual and asexual morphs could be linked, giving rise to the one fungus one name (1F = 1N) concept. In the Amsterdam declaration (Hawksworth et al. 2011), an international assemblage of mycologists opted for the application of priority in determining the only name to be applied to a fungal species, irrespective of the type of morph, except when there was a much more widespread name in use. For example, based on the precedence to date (*Fusarium* over *Giberella*, *Diaporthe* over *Phomopsis*) and younger, more commonly used names (*Colletotrichum* over *Glomerella*, *Elsinoe* over *Sphaceloma*) were fixed, accordingly. However, the confusion of the situation for plant pathology and quarantine regulations will most likely take a longer transition phase to be resolved, as, e.g. diseases caused by *Diaporthe* are commonly still known as Phomopsis dieback, blight, fruit rots (Moreira et al. 2020; Wrona et al. 2020). Similarly, rot caused by *Fusarium graminiearum* is often referred to as Gibberella ear rot (Machado et al. 2021).

However, it seems likely that with the increasing stability gained by the end of dual nomenclature, the use of traditional names in conflict with current naming of fungi will be discontinued after a phase of transition.

Cryptic species in plant pathology

The statement by Shivas and Cai (2011) that "Unmasking and understanding cryptic species is one of the major challenges for mycologists and plant pathologists in the next decade" has come true. Cryptic species are referred to as morphologically indistinguishable species that have been revealed by molecular phylogeny and can only be recognized by their DNA sequence data (Shivas and Cai 2011). Knowledge of these species is important to plant pathologists as they may show a significant difference in the host associations, geographical distribution as well as in disease severity. With the use of DNA sequence data and Genealogical Concordance Phylogenetic Species Recognition (GCPSR) concept a rapid increase in the number of cryptic species can be seen during the past decade (Damm et al. 2012a,b; Weir et al. 2012; Udayanga et al. 2014a,b; Norphanphoun et al. 2020). It has come to light that many common current names of widespread pathogens mask complexes of cryptic species (Shivas and Cai 2011).

Colletotrichum is one of the best examples of cryptic species in plant pathogens. Cannon et al. (2012) identified nine major clades that comprise cryptic species based on DNA sequence data. *Colletotrichum gloeosporioides* was associated with more than 400 different host genera and was believed to be a common tropical fruit pathogen causing anthracnose (Canon et al. 2012). However, Weir et al. (2012) showed that the single species *C. gloeosporioides* is a species complex with 22 different species based on DNA sequence data. Currently, this species complex consists of 52

closely related species (Jayawardena et al. 2021). It was also recognized that *C. gloeosporioides* is not a common pathogen that occur on tropical fruits (Phoulivong et al. 2010). The most common pathogens associated with many tropical fruits are *C. fructicola* and *C. siamense* (Bhunjun et al. 2021; Jayawardena et al. 2021). Other species identified in this complex can be associated with one or several hosts. *Colletotrichum acutatum* is another important fruit pathogen that causes anthracnose. This species is also associated with more than 200 different host genera (Damm et al 2012b). Damm et al. (2012b) identified this species to consist 31 separate taxa based on DNA sequence data. Currently, the acutatum species complex consists of 40 species associated with fruit rots (Jayawardena et al. 2021). Fourteen species complexes within *Colletotrichum* have been identified based on DNA sequence data and different molecular approaches such as coalescent-based species delimitation, general mixed Yule-coalescent method and Poisson tree processes (Bhunjun et al. 2021; Jayawardena et al. 2021).

Phyllosticta is another pathogenic genus with cryptic species. It is an earlier name of the asexual morph *Guignardia* (Viala and Ravaz 1892). Similar to other plant pathogenic fungi *Phyllosticta* species have overlapping morphological traits, which make it difficult to identify to species. Wikee et al. (2013) recognized 170 species names based on multilocus analysis in *Phyllosticta*. Norphanphoun et al. (2020) introduced six species complexes with cryptic species to resolve the genus using five loci.

Fusarium is a ubiquitous group of fungi that consists of plant pathogens causing blights, cankers, rots and wilts (O'Donnell et al. 2018; Jayawardena et al. 2019). In this genus there are 20 monophyletic species complexes that include numerous cryptic species and several taxonomic/classification systems, sometimes resulting in erroneous and confusing application of species names to toxigenic and pathogenic isolates (Geiser et al. 2004; Jayawardena et al. 2019). Several economically important *Fusarium* species lack living ex-type cultures which make it difficult to clarify the taxonomic positions.

Diaporthe eres which is identified as a weak to moderate pathogen was associated with approximately 70 different hosts based on morphological study and *D. eres* was regarded as a species complex (Wehmeyer 1933). Udayanga et al. (2014a) revised the section *D. eres* based on a polyphasic approach and identified 11 closely related but phylogenetically distinct lineages.

Neopestalotiopsis, *Pestalotiopsis* and *Pseudopestalotiopsis* were recognized based on DNAsequence data (Maharachchikumbura et al. 2014). These three genera can be distinguished based on morphological characters mentioned in Maharachchikumbura et al. (2014). However, within this genus species identification is difficult due to the overlapping morphological characters. In *Neopestalotiopsis*, a huge genetic variation is observed in the same species from different hosts, even though the morphology remains the same (Huanraluek et al. 2021).

Rusts are another important group of plant pathogens that may show cryptic diversity. Taxonomists have long recognized the likelihood of cryptic speciation in several of the rust complexes such as *Puccinia* (Hyde et al. 2014). A recent study on *Cyperaceae-Juncaceae* rusts suggested the existence of many cryptic species in North America (Léveillé-Bourret et al. 2021). This study was based on next generation sequence data which estimated that between 5 and 24 potential cryptic species could exist within each of the four most common and abundant north American species aggregates namely *Puccinia angustata*, *P. caricina*, *P. dioicae* and *P. urticata* on *Carex*, *Scirpus* and *Eriophorum*.

The concept of cryptic species defines closely related populations that have recently been separated and their genetic differences may contain significant information that needs to be identified. However, only accurate and unambiguous pathogen names can lead to reliable disease management and bio-security decisions. The dawn of DNA barcoding methods may have provided an evaluation of the incidence of cryptic species amongst plant pathogenic fungi. Previous plant pathology research may need to be revisited, as it is not clear which species have been extensively studied due to wrong naming. Many of the country-wise plant pathogenic records may be outdated and need to be reassessed. It is important to assess the host range, pathogenicity and the distribution of these cryptic species to determine the agricultural and environmental importance.

Why is correct naming important for plant pathology?

Names are the foundation of concise exchange of information concerning an organism (Jayasiri et al. 2015). These can either be common names, which often vary from place to place and among different languages (Rossman and Plam-Hernández 2008), or scientific names, which define an organism uniquely and are the key for concise communication of information regarding a particular organism (Hawkswoth 2011). Fungal pathogens are ubiquitous and diverse, with both ecological and economic significance due to the evolution of several successful strategies to infect plants (Doehlemann et al. 2017). Fungal plant pathogens have devastating effects on both food security and the natural ecosystem. For example, rice blast disease, caused by the ascomycete *Pyricularia oryzae* (earlier known as *Magnaporthe oryzae* Couch and Kohn 2002), is one of the most economically important diseases (Wilson and Talbot 2009). Between 2001 and 2005, an estimate of 5.7 million hectares of rice was damaged in Korea, Japan, Vietnam, and the

United States by rice blast disease alone (Wilson and Talbot 2009). Given the great economic relevance of this species, the application of the correct name is crucial to avoid misconceptions, which could arise if the species was named *P. grisea*, which is a closely related species that can also cause infections in rice, but leads to less yield losses than *P. oryzae*. A better knowledge of the biology of the species is vital to predict future outbreaks (Liang et al. 2018) as well as plant quarantine and phytosanitary measures. A correct naming is of even greater importance, if a disease is emerging. Emerging pathogens are those affecting hosts previously not known to carry the pathogen group, or manifesting in a completely novel environment, e.g. due to a jump to an introduced host, acquisition of new virulence genes, hybridization, or other evolutionary events (Ghelardini et al. 2016; Fones et al. 2017). In such cases, incorrect naming can lead to a critical delay in imposing phytosanitary and quarantine measures, such as in the case of *Peronospora belbahrii* (causing downy mildew of basil), which, on the basis of a broad species concept, was assumed to be *P. lamii*, which is a common pathogen in Europe (Thines et al. 2009). At the time it was shown that the species causing basil downy mildew was described as independent, it had already spread to almost all areas in which basil was cultivated (Thines et al. 2009).

Thus, correct placement and naming of a particular taxon are fundamental for disease diagnosis, eventually helping to understand the mechanisms of disease formation. These are preliminary steps to designing management strategies and update quarantine measures (Wingfield et al. 2012). Accurate communication of names among researchers consequently allows understanding the life-style and mode of infection of a pathogen better, which helps in implementing control strategies. For instance, *Colletotrichum fructicola* was initially recorded from coffee berries from Thailand (Prihastuti et al. 2009). However, later it was observed from many hosts, such as apple, avocado, and grapes (Weir et al. 2012; Peng et al. 2013). However, some pathogenic species may occur only in a restricted region, such as *C. kahawae*. This species is a significant pathogen on coffee plants in the African continent. An inaccurate identification of a pathogen during export may result in inappropriate or insufficient control measures resulting in the spread of this devastating pathogen (Crous et al. 2015).

In order to avoid import and export of diseases, country-specific inventories of plant pathogenic fungi with accurate and accepted names are essential (Hyde et al. 2010b). These are necessary for the development of effective biosecurity, trade policies, tests for plant resistance, as well as for the preservation of biodiversity and ecosystem function (Hyde et al. 2010a). In addition, these inventories also aid in the early identification of invasive fungal pathogens and allow the timely application of appropriate disease control measures (Rossman and Palm-Hernández 2008). Thus, an accurate identification of fungal species is critical in the establishment of quarantine regulations.

Quarantine regulations have been established based on extant plant pathogen names that are mostly morphology based and have affected specific hosts globally (McTaggart et al. 2016). However, correct naming of new taxa alone does not resolve all issues. The estimated number of fungi worldwide is 2–3 million, of which only 5–10% have been described (Hawksworth 2012; Hyde et al. 2020). As only described species can be effectively regulated, undiagnosed fungal taxa remain a serious threat to food production (McTaggart et al. 2016). This also applies to post-harvest disease agents capable of producing toxins. For instance, several species of *Aspergillus* can produce aflatoxins (Katsurayama et al. 2018). These taxa can grow on corn and fill the seeds with toxins. These toxins can attack the liver and are one of the deadliest carcinogens known to date (Martínez-Martínez et al. 2021). Therefore, correct naming of fungi is crucial for food security and human health.

Case studies

Herein we have taken eight important plant pathogenic genera and rust fungi as case studies to discuss the concepts that have been used in defining a species, problems of these concepts and recommendations to follow in future.

Bipolaris

Bipolaris is a genus of great importance both economically and to human health. Originally introduced by Shoemaker (1959) with *B. maydis* as the type species, *Bipolaris* species have been recorded as pathogens, saprobes, or endophytes of a wide range of hosts (Ellis 1971; Sivanesan 1987; Hyde et al. 2014; Manamgoda et al. 2014; Tan et al. 2016; Jayawardena et al. 2019). *Bipolaris* was previously classified in *Helminsporium*, which was revised and separated into *Curvularia*, *Drechslera,* and *Exserohilum* (Sivanesan 1987). Manamgoda et al. (2012a, b) revised *Bipolaris* and *Curvularia*, with important plant pathogens included in *Bipolaris* and species known as human pathogens and some plant pathogens included in *Curvularia*. It is important to accurately identify species in *Bipolaris* as they have been used in bio-technological applications including genetic manipulation and also have been known to cause devastating plant diseases (Rossman and Palm-Hernández 2008; Hyde et al. 2010a; Hawksworth 2011). Accurate identification is also vital to access accumulated knowledge for effective control measures (Hyde et al. 2010b; Cai et al. 2011a, b; Hawksworth et al. 2011).

Critically, *Bipolaris* are of major importance as plant pathogens in part due to their worldwide distribution and history of causing devastating plant diseases. (Manamgoda et al. 2014). *Bipolaris oryzae* was responsible for causing extensive damage to rice cultivation in India, causing a famine during 1943–1944 (Scheffer 1997). *Bipolaris* species have been linked with several disease symptoms, including leaf spots, leaf blights, melting outs, root rots, and foot rots (Manamgoda et al. 2014). *Bipolaris* are often associated with high-value field crops in *Poaceae,* including rice, maize, wheat and sorghum (Manamgoda et al. 2014). As pathogens and saprobes, they have been associated with over 60 plant genera in *Anacardiaceae*, *Araceae*, *Euphorbiaceae*, *Fabaceae*, *Malvaceae*, *Rutaceae* and *Zingiberaceae* (Manamgoda et al. 2011; Ariyawansa et al. 2015; Jayawardena et al. 2019; Bhunjun et al. 2020).

Despite their impact, accurate identification of *Bipolaris* has proved challenging. Species identification of this genus was previously based on morphology and host association (Jayawardena et al. 2019). The sexual morph of *Bipolaris* species is not common in nature and several *Bipolaris* species have overlapping morphology, which makes accurate identification based on morphology alone difficult. Some species of *Bipolaris* are morphologically similar to *Curvularia*, which makes distinguishing between these two genera problematic (Manamgoda et al. 2011, 2014). Previous studies have differentiated these two genera based on conidial morphology, although a less subjective approach will be required for a higher degree of precision (Ellis 1971; Sivanesan 1987; Manamgoda et al. 2012b). Therefore, molecular-based identification is vital for accurate species identification in morphologically conserved genera such as *Bipolaris*.

Accurate molecular identification in *Bipolaris* is hindered by the lack of ex-type or authenticated sequences (Cai et al. 2011a, b; Manamgoda et al. 2012b), and only 27 species have an ex-type sequence (Bhunjun et al. 2020). Manamgoda et al. (2014) clarified the taxonomy, host associations, geographic distributions and accepted 47 species. Marin-Felix et al. (2017b) accepted 40 species based on the phylogenetic analyses of ITS, *gapdh*, and *tef1*-α sequences. There are 137 species epithets listed in Index Fungorum (2021), but several of these epithets have been transferred to *Curvularia,* and only 45 species based on the phylogenetic concept are currently accepted in *Bipolaris* (Bhunjun et al. 2020).

Bhunjun et al. (2020) recommended a polyphasic approach to introduce new species or host records in *Bipolaris* based on morphological evidence, coupled with phylogenetic analyses based on a multi-loci dataset including the protein-coding region *gapdh* and other molecular-based approaches such as Automatic Barcode Gap Discovery or Objective Clustering methods. BLAST searches of GenBank to name species are not recommended as there is only a small number of reference sequences deposited in GenBank, and several of these sequences have been deposited with different species names (Bhunjun et al. 2020).

Bipolaris species have been isolated from several hosts and locations. Most studies have focused on high-value crops, and therefore we believe that extensive sampling of unstudied hosts and regions is likely to result in numerous new species, which should be carefully dealt with polyphasic approaches.

Colletotrichum

Colletotrichum is one of the most studied pathogenic fungal genus amongst the plant pathogens. Thegenus was recently revisited by Bhunjun et al. (2021) and Jayawardena et al. (2021). In the earliest studies, naming of species depended on morphological characters or host association (Canon et al. 2012). For many years, species of this genus were thought to be host specific which lead to the introduction of a large number of taxa which cannot be clearly distinguished by morphology and may have ended up by describing the same species on different hosts as different species (Cannon et al. 2012; Jayawardena et al. 2021). Between 1880 and 1900, 50 new taxa were described at the species level (or below) and by the time the first monograph of this genus was published, around 750 names existed (Cannon et al. 2012). Using the morphological concept, von Arx (1957) provided the first comprehensive monograph of *Colletotrichum* and he accepted 11 taxa (within a total of 23 specific and infraspecific taxa). He treated them as aggregates rather than individual taxa. For instance, *C. gloeosporioides* was merged into nine variant forms and were considered to be host-specific variants that cannot be distinguished based on morphology (Cannon et al. 2012; Jayawardena et al. 2016b). Sutton (1980) used morphological as well as cultural characteristics when accepting 22 species in the genus. Smith and Black (1990) emphasized the use of taxonomy and pathological data when defining a species. Hyde et al. (2009) provided the limitations of using morphological concept alone. Cai et al. (2009) recommended the use of polyphasic approach in identifying species of *Colletotrichum*.

Mills et al. (1992) and Sreenivasaprasad et al. (1992, 1996) provided the first studies with the use of DNA sequence data to distinguish species within the genus. Since then many studies have been carried out using the phylogenetic concept in identifying the species in *Colletotrichum*. Damm et al. (2012a,b) and Weir et al. (2012) revised the aggregates of *C. acutatum*, *C. boninense* and *C. gloeosporioides* respectively with the use of multi-gene phylogenetic analyses coupled with morphology. These resulted in identifying 31 species (21 new) in acutatum, 15 species (12 new) in boninense and 22 species (9 new species and a subspecies) in gloeosporioides species complexes. With the use of multi-gene phylogeny Cannon et al. (2012) showed that

majority of species in *Colletotrichum* fall into nine species complexes. Bhunjun et al. (2021) and Jayawardena et al. (2021) based on phylogenetic concept accepted 14 species complexes.

However, use of morphology and phylogenetic concepts are also not enough when defining a species in *Colletotrichum*. Weir et al. (2012) along with morphology and phylogeny used the GCPSR concept which provided better species delimitation along currently recognized lineages except *C. kahawae*. Liu et al. (2016a, b) used the GCPSR concept to test the null hypothesis that '*C. siamense* is a species complex' which lead to the rejection of the null hypothesis. Many studies have included the Pairwise homoplasy index test using the GCPSR model to determine the recombination level between taxa when describing new *Colletotrichum* species (Jayawardena et al. 2021). Haplotype and phylogenetic network analysis is another concept that mycologists have used in defining species in *Colletotrichum*. Liu et al. (2016a, b) based on this method, synonymized seven species to *C. siamense*. Bhunjun et al. (2021) recommended the use of coalescent based species delimitation (CBD), general mixed yule coalescent (GMYC) approach, poisson tree processes model (PTP) and species validation when defining species in *Colletotrichum*. All these approaches are tools of phylogenetic concept (or molecular approaches) which evaluate DNA sequence data on different criteria to give a better resolution for a species. For an example, based on morphology (apical appendage) and multigene phylogeny (ITS, *sod2*, *apn/Mat1*) Crouch (2014) introduced the caudatum species complex. However, with the addition of molecular approaches, such as CBD, GMYC and PTP, showed that this is a part (or a sub-clade) of the graminicola complex. Bhunjun et al. (2021) introduced a new species complex (agaves) based on phylogenetic and molecular clock data.

Pathogenicity data are only available for 108 species in the genus even though most of the species are described as pathogens associated with diseases (Jayawardena et al. 2020). It is very important to know whether a species can really cause a disease as a primary pathogen or is it a secondary pathogen in order to develop effective control measures in agriculture. It is also important to understand the life-mode and the host range of a species. In *Colletotrichum* some species may show a wide host range and some species may have all life modes in their life cycle (saprobic, endophytic and pathogenic) (Jayawardena et al. 2021). Cross pathogenicity data are also important for a pathogenic species. Conducting pathogenicity studies for every species that is uncovered associated with a disease is not always feasible. Hence the authors would like to recommend providing pathogenicity data when describing a *Colletotrichum* species associated with a disease whenever it is possible.

Colletotrichum is a complex and important plant pathogenic genus, and therefore it is recommended to use morphology, pathogenicity data, ecology as well as phylogeny with different approaches when defining a species.

Curvularia

As an example of the diversity and complexity of a genus causing confusion amongst taxonomists, the dematiaceous hyphomycete genus *Curvularia* comprises a large number of phytopathogens of grasses (*Poaceae*). There are 197 epithets of *Curvularia* are listed in Index Fungorum (2021). Species of *Curvularia* have been shown to be associated with plants in nature as pathogens (Khemmuket al. 2016; Liang et al. 2018; Raza et al. 2019), endophytes (Jena and Tayung 2013), epiphytes (Ávila-Díaz and Oyama 2007), and saprobes (Manamgoda et al.2012a). The majority, 38%, have been reported from poaceous hosts worldwide (Manamgoda et al. 2015; Tan et al. 2014, 2018; Marin-Felix et al. 2017a, 2020). Occasionally, *Curvularia* species have also been recorded from other plant families, including *Amaranthaceae*, *Amaryllidaceae*, *Araceae*, *Arecaceae*, *Asparagaceae*, *Asteraceae*, *Brassicaceae*, *Cactaceae*, *Cyperaceae*, *Euphorbiaceae*, *Fabaceae*, *Hypoxidaceae*, *Iridaceae*, *Lamiaceae*, *Lythraceae*, *Nyctaginaceae*, *Pandanaceae*, *Portulacaceae*, *Rubiaceae*, *Sapindaceae*, *Solanaceae*, and *Zygophyllaceae* (Sivanesan 1987; Manamgoda et al. 2015; Marin-Felix et al. 2017a, b).

Despite the fact that they are frequently encountered on plants, several studies have revealed them to also behave as opportunistic pathogens on immuno-compromised patients (Madrid et al. 2014; Danish et al. 2017; Bengyella et al. 2017; Chang et al. 2019; Tóth et al. 2020). Species such as *C. americana*, *C. chlamydospora*, *C. hominis*, *C. pseudolunata, C. pseudorobusta,* and the generic type, *C. lunata*, have been isolated from clinical specimens (Madrid et al. 2014). On the other hand, species initially isolated from clinical specimens such as *C. hominis* and *C. muehlenbeckiae* (Madrid et al. 2014) have later been found on herbaceous hosts (Manamgoda et al. 2015). The diversity of this genus and the potential for species to live on an array of hosts has been revealed through multiple approaches. Most recently, as will be discussed below, molecular approaches have been critical to clearing up ambiguity in the classification of *Curvularia.*

When considering the host association within the genus, the majority of the *Curvularia* species identified have been isolated from leaf spots on poaceous hosts, including *C. beasleyi* on *Chloris gayana*, *C. chiangmaiensis* on *Zea mays*, *C. warraberensis, C. petersonii* and *C. dactyloctenicola* on *Dactyloctenium aegyptium* (Marin-Felix et al. 2017a; Tan et al. 2018), *C. nodosa* on *Brachia riareptans*, *Chloris barbata*, and *Digitaria ciliaris* (Marin-Felix et al. 2017a), *C. nanningensis* on *Cymbopogon citratus* (Zhang et al. 2020) and *C. pseudobrachyspora* on *Eleusine indica*. Other than

leaf spots, some of the species have been reported from infected grains or inflorescences. For example, *C. kenpeggii* has been reported on moldy grain of *Triticum aestivum, C. eragrosticola* from inflorescence on *Eragrostis pilosa, C. beerburrumensis* on the blackened inflorescence of *Eragrostis bahiensis* (Tan et al. 2018), *C. ryleyi* on the inflorescence of *Sporobolus creber,* and *C. neergaardii* on the seeds of *Oryza sativa* (Tan et al. 2014). Moreover, *C. chonburiensis*, *C. pandanicola*, *C. thailandicum* and *C. xishuangbannaensis* have been recorded as saprobic on leaves of *Pandanus* sp. (Tibpromma et al. 2018). Raza et al. (2019) described 16 pathogenic species of *Curvularia* on *Saccharum officinarum. Curvularia* species have also been observed from grains and black kernels, seedling blight and leaf blight (Liang et al. 2018; Raza et al. 2019). Surprisingly, members of *Curvularia* survive both on commercially important crop varieties and their crop wild relatives in *Poaceae* (Manamgoda et al. 2011). For example, *C. asiatica,* which was originally reported as saprobic on *Panicum* spp., leaves of *Saccharum officinarum* (sugarcane), and grains of *Oryza sativa* (cultivated rice) had later been isolated as a foliar pathogen on *Oryza sativa* (Khemmuket al. 2016). Similarly, the holotype of *C. pseudobrachyspora* was reported on *Eleusine indica,* while recently, it has been reported from *O. sativa* (Marin-Felix et al. 2020). Even though *Curvularia* was found to be associated with many disease symptoms, the pathogenicity of only 20 *Curvularia* species have been demonstrated clearly following Koch's postulate. Some *Curvularia* species can be secondary pathogens or act as saprobes on dead tissue. Furthermore, *Curvularia* species exhibit the ability to switch from a saprobic life cycle to pathogenic or mild pathogenic to aggressive (Manamgoda et al. 2011). For example, *Curvularia alcornii,* first reported as saprobic on *Zea mays* (Manamgoda et al. 2012a), had recently been isolated as a foliar pathogen on rice (Khemmuk et al. 2016).

Morphological identification has been used to identify *Curvularia* species for the past 88 years, whereas molecular data for *Curvularia* identification was initiated during the last decade. Following a comprehensive phylogenetic and taxonomic reappraisal, Manamgoda et al. (2012b) and Tan et al. (2014), established a taxonomic guide for the genus. The majority of the recent publications on taxonomy of *Curvularia* have extensively utilized combined molecular phylogenetic approach while placing morphology as the base for taxonomy (Manamgoda et al. 2015; Tan et al. 2018; Raza et al. 2019; Marin-Felix et al. 2017a, 2020). Accordingly, 118 species are now accepted within the genus (Marin-Felix et al. 2020). However, considering the 197 epithets of *Curvularia* in Index Fungorum (2021), around 20% lack molecular data in public databases.

The phylogeny of *Curvularia*, revealed several closely related species without phylogenetic distance, such as *Curvularia harveyi* and *C. gudauskasii*, *C. borreriae,* and *C. pallescens* (Marin-Felix et al. 2020). Further investigations such as incorporating other gene regions or genomic data and more accessions will be needed to resolve their status as independent species or to provide evidence for conspecificity.

Extensive sampling and future studies regarding *Curvularia* provides insights into host ranges and ecological ranges (Tan et al. 2018), while studies on their virulence support the establishment of disease management strategies (Raza et al. 2019). However, a polyphasic approach should be always used when introducing new species in this genus.

Diaporthe

Diaporthe Nitschke comprises important plant pathogenic, endophytic, and saprobic species with a wide host range and a global distribution (Udayanga et al. 2011; Gomes et al. 2013; Hyde et al. 2014; Gao et al. 2017). The genus was originally introduced by Nitschke (1870) with the type species *D. eres*, which is placed in *Diaporthaceae*. Both generic names, *Diaporthe* and *Phomopsis* are nearly equally applied in mycological and phytopathological literature until recently. Therefore, approximately an equal number of *Diaporthe* and *Phomopsis* names exist in the available literature. The use of the older generic name *Diaporthe,* which has priority over *Phomopsis,* has been considered more favourable in moving towards one name for this pleomorphic genus (Rossman et al. 2015). Accordingly, *Diaporthe* was proposed as the name to be used, and *Phomopsis* is regarded as a synonym (Gomes et al. 2013; Udayanga et al. 2014a, b; Rossman et al. 2015). Currently, the Index Fungorum and MycoBank holds more than 1100 species under *Diaporthe,* while the number of species described in *Phomopsis* is nearly 1000.

Diaporthe spp. are well known causal agents of economically important plant diseases, including stem cankers, leaf and pod blights, leaf spots, root and fruit rots, dieback, seed decay, and wilts (Udayanga et al. 2011; Huang et al. 2013; Dissanayake et al. 2017; Guarnaccia and Crous 2017). In the past, *Diaporthe* species have been introduced predominantly based on the assumption that they are host-specific, which led to a proliferation of species names based on the hosts of which the fungus was isolated. In contrast, it has been now identified that *Diaporthe* contain several species with broad host ranges and a few relatively host-specific species (Udayanga et al. 2014a,b). Furthermore, a single host plant may harbour multiple distantly related species of *Diaporthe* (Brayford 1990; Rehner and Uecker 1994; Mostert et al. 2001). Few species such as *D. alnea* (on *Alnus* spp.), *D. ampelina* (on *Vitis* spp.), *D. citri* (on *Citrus* spp.) and *D. vaccinii* (on *Vaccinium* spp.) are recognized as relatively host-specific species to date (Udayanga et al. 2014a, b). The majority of the host-specific species are usually pathogens

causing mild to serious diseases on their respective host plants. In contrast, species occurring on an extensive range of host plants are mostly opportunistic pathogens causing mild to severe symptoms, often as secondary invaders. Some of the opportunistic species in the genus and their closely related taxa are regarded as species complexes (Gomes et al. 2013; Udayanga et al. 2014a). For example, the *Diaporthe eres* species complex is one of the prominent clades that consists of multiple species associated with woody plants in diverse families, including the *Ericaceae, Juglandaceae, Rosaceae, Sapindaceae, Ulmaceae, Vitaceae*, and others, both in temperate and tropical regions worldwide (Brayford 1990; Cline and Farr 2006; Udayanga et al. 2014a).

Species of *Diaporthe* are generally described in mycological literature as pathogens associated with diseases on their respective host plants, based on routine collections of symptomatic specimens. However, a few significant *Diaporte* species have been extensively studied by plant pathologists. For example, *Diaporthe* species associated with citrus, soybean, sunflower, and grapevine have been widely studied and their pathogenicity was confirmed by assays for disease incidence and virulence (Udayanga et al. 2011). In addition, the first disease reports published in phytopathology journals over the past two decades comprised numerous species of *Diaporthe*. In the journal of APS Plant Disease Notes, from 1998 to 2021, 61 first disease reports of well-identified *Diaporthe* species were reported affecting diverse hosts, confirmed by pathogenicity testing (accessed on 31st of January 2021). These studies have detailed the impacts of *Diaporthe* as a major ascomycete genus of fungi with a severe impact on crops, and ornamentals and as a result many species of *Diaporthe* are widely recognised.

Morphological species recognition has been considered inadequate in defining novel species because of the variability regarding changing environmental conditions. Therefore, it is now essential to use molecular data to define species in the genus (Udayanga et al. 2014a, b; Guarnaccia and Crous 2017; Gao et al. 2017; Guo et al. 2020). DNA sequence data of a few commonly used molecular markers have been promising tools for both identifications of *Diaporthe* species and inferring evolutionary relationships among them (Udayanga et al. 2012a,b). Multi-gene phylogenetic analyses of at least three or more of the gene markers are considered most effective for accurate reconstruction of species boundaries and relationships (Udayanga et al. 2012a; Gomes et al. 2013; Santos et al. 2017).

Considerable progress of the species identification of *Diaporthe* has been witnessed since the adoption of multigene phylogeny in species delimitation in 2012 (Udayanga et al. 2012a,b). Numerous novel taxa and new host records have been reported each year, and the number of species identified using molecular data continues to grow rapidly (Gao et al. 2017; Guarnaccia and Crous 2017; Dissanayake et al. 2017). The incorporation and rigorous analyses of molecular data in systematics have improved the current understanding of species limits within a genus. The adoption of GCPSR based on multiple gene genealogies is recommended to unravel cryptic species complexes of *Diaporthe* like *D. eres, D. foeniculina, D. rudis,* and *D. sojae* (Udayanga et al. 2012a, b; 2014a,b; 2015). The difficulties in resolving closely related phylogenetic species are likely due to the gene flow among species and recombination possibilities (Santos et al. 2011; Fan et al. 2018; Drenth et al. 2019). It has been observed that more genetic variability and conflicts occur in species delimitation within the minor or opportunistic pathogens, which infect an extensive range of hosts in wide geographic distribution (e.g. *D. eres*, *D. rudis,* and *D. foeniculina*). In contrast, relatively host-specific species (e.g. *D. vaccinii*, *D. ampelina*, and *D. citri*), which are usually serious pathogens, were clearly distinguished by gene genealogies making it relatively easy to delimit the species (Udayanga et al. 2014a,b).

With the existing total number of species names in *Diaporthe* and *Phomopsis,* which exceeds 1000 in public databases, the global diversity of the genus can be estimated as relatively high. The *Diaporthe*/*Phomopsis* names described earlier based on morphological characteristics can be either distinct or conspecific taxa occurring on a wide host range. However, the morphologically described species can only be accurately linked to the cultures and molecular data by the epitypification and comprehensive analysis of the names and their taxonomic affiliations (Udayanga et al. 2012a,b, 2014a, 2015; Gomes et al. 2013). Species that are revealed only by minimum DNA barcode data are not formally considered as species, unless they otherwise have been identified as a significant pathogenic species. Therefore, extended studies across the unexplored niches could reveal more undescribed species that can be encountered as saprobes and endophytes associated with a wide range of habitats.

With the high diversity of species within *Diaporthe* and the few clear-cut morphological characters for delimitation, the genus also has been shown to be polyphyletic within *Diaporthaceae*, based on the commonly used gene regions (Gao et al. 2017). However, the segregation of the genus into many genera based on the monophyletic groups is not the best option in this case, as the additional identification of morphological synapomorphy is difficult. No distinguishable morphological characters of either sexual or asexual morphs have been observed and the genus contains many polyphyletic groups, as discussed by Gao et al. (2017). Thus, rather than splitting *Diaporthe* into many small genera without a strong phylogenetic or morphological support, which would create further nomenclatural and taxonomic issues leading to the transfer of many names, the inclusion of some smaller genera with deviating morphology should be considered.

Due to the lack of type material for many species, epitypes of well-identified species of *Diaporthe* might be a potential solution, when fresh collections are available from suitable hosts and locations. A large numbers of sequences from the *Diaporthe* species have accumulated in public databases, but the interpretation of phylogenetic trees at the species level is subject to much confusion, especially in the taxa associated with broad host ranges (Udayanga et al. 2014a; Fan et al. 2018). This situation can only be resolved when ex-type sequence data has been established for the vast majority of species. The resulting data from this will not only be significant in biodiversity and evolutionary contexts, but also for when accurate identification of plant pathogenic species is required for quarantine and disease management.

Diplodia

Diplodia is a species-rich genus in *Botryosphaeriaceae*, with more than 1200 species epithets listed in Index Fungorum (2021). However, only a few species are widely recognized and have DNA sequence data available (Phillips et al. 2012, 2013; Alves et al. 2014; Pan et al. 2019). Members of *Diplodia* are pathogenic, saprobic, or endophytic and mainly occur on a wide range of woody hosts with a worldwide distribution (Phillips et al. 2008, 2013; Alves et al. 2014; González-Domínguez 2017; Hernandez-Escribano et al. 2018; Pan et al. 2019; Linaldeddu et al. 2020). The main pathogenic species include *D. corticola*, *D. fraxini*, *D. mutila*, *D. sapinea*, *D. seriata,* and *D. subglobosa*. *Diplodia mutila* causes black rot of apples and cankers of many woody plants, including *Chamaecyparis lawsoniana*, *Fraxinus* spp., *Malus* spp., *Populus* spp., *Taxus baccata* and *Vitis vinifera* (Phillips et al. 2013; Alves et al. 2014). *Diplodia seriata* causes frog-eye leaf spot, black rot, and canker of apples (Phillips et al. 2012) and is associated with a wide range of hosts, including *Fraxinus* spp., *Olea europaea* and *Vitis vinifera* (Phillips et al. 2012; Alves et al. 2014). *Diplodia subglobosa* has been reported on *Fraxinus* spp. and *Lonicera nigra* and is associated with cankers and dieback (Linaldeddu et al. 2020). Some species of *Diplodia* have shown possible host-specificity. *Diplodia sapinea* is known as the causal agent of crown wilt, dieback, pitch cankers, shoot and tip blight, and root disease on pines, and this species seems to have specificity towards *Pinaceae* hosts (Alves et al. 2014; Hernandez-Escribano et al. 2018). *Diplodia rosulata* has been found only on *Prunus* spp. as a seed-borne pathogen (Gure et al. 2005), while *Diplodia corticola* causes canker and dieback mainly on *Quercus* spp. (Alves et al. 2004; Phillips et al. 2013). *Diplodia fraxini* is always associated with cankers and dieback of *Fraxinus angustifolia* and *F. excelsior*.

Different *Diplodia* species and also strains of the same species show different degrees of virulence. Accurate species identification in *Diplodia* is difficult due to incomplete knowledge of the diversity and taxonomic state of the species in the genus (Phillips et al. 2012, 2013), also as a consequence of lack of sequence data. Recent studies have conducted pathogenicity tests for some *Diplodia* species identified based on DNA sequence data. These species include *D. alatafructa*, *D. eriobotryicola*, *D. fraxini*, *D. insularis*, *D. malorum*, *D. olivarum, D. sapinea, D. seriata,* and *D. subglobosa* (Linaldeddu et al. 2016, 2020; González-Domínguez 2017; Hernandez-Escribano et al. 2018). However, further investigations should be carried out to confirm the pathogenicity of other species, as the pathogenicity of the vast majority of species in this genus remains unresolved, an issue that concerns some recent introductions. For instance, Phillips et al. (2012) introduced *D. intermedia* from dead twigs of *Malus sylvestris,* and additional isolates of the species were obtained from fruit rot of *Malus domestica*, *Cydonia* sp. and canker of *Malus sylvestris*. However, pathogenicity was not tested, so the biology and potential aggressiveness of the isolates remain obscure. Also in the case of the study by Jami et al. (2012), who described *D. allocellula* from healthy tissues of *Acacia karroo*, and Pan et al. (2019), who described *D. quercicola* from branches of *Quercus variabilis* with symptoms of canker and dieback disease did not perform pathogenicity assays. Thus, pathogenicity of *D. allocellula* and *D. quercicola* could not be resolved.

Cryptic speciation is common amongst *Diplodia*, making species identification nearly impossible when based solely on morphological traits (Alves et al. 2014). However, two distinct conidial morphologies have been seen in *Diplodia* species, and these two groups were supported by phylogenetic reconstructions (Phillips et al. 2013). Furthermore, conidial dimensions sometimes could be used to distinguish species in the genus (Phillips et al. 2012, 2013). Nonetheless, most species cannot be resolved based on morphology, necessitating additional support from sequence analyses.

Thus, species identification in *Diplodia* should usually be guided by DNA sequence data, ideally based on multigene phylogenies. The majority of the recent studies have used ITS and *tef1–α* for this purpose (Phillips et al. 2012, 2013; Linaldeddu et al. 2016; González-Domínguez 2017; Pan et al. 2019). Dreaden et al. (2014) have developed an assay based on a PCR–RFLP detection method for the rapid and accurate detection of *D. corticola* and *D. quercivora,* which incite similar disease symptoms and can be directly applied to diseased plant tissues. However, further studies on this method using more strains are needed to evaluate the potential of transfer to other species.

In a recent study on *Diplodia* by Pan et al. (2019) 35 species with available ex-type strains were investigated. As most of the *Diplodia* species have not been recognized based on the DNA sequence data, further studies based on a much broader sampling of *Diplodia* species from a wider

geographical range are needed to infer the diversity of the genus and to establish species boundaries.

As mentioned earlier, more than 1250 species for *Diplodia* are accepted and approximately 35 species are known from a molecular basis. In addition, some of these species have been transferred to different genera based on modern taxonomic concepts. Therefore, the taxonomic resolution of the genus is still in a very preliminary state, necessitating recollection, epitypification, and molecular analysis to confirm the placement of doubtful species. This will also help to delimit species without adding novel species in error such as introducing the same species twice. These studies should also include pathogenicity tests to evaluate potential host ranges.

Meliola

Plants harbour diverse fungal communities on their surfaces, known as epiphytic fungi. *Meliola* commonly known as "black mildews" or "dark mildews" is the largest genus of *Meliolaceae* (Hongsanan et al. 2015; Zeng et al. 2017). *Meliola* species are commonly found in tropical and subtropical regions and mostly occur as biotrophic pathogens on leaves (Zeng et al. 2017). Some species occasionally also occur on petioles, twigs and branches (Hansford 1961; Mibey and Hawksworth 1997; Hosagoudar and Riju 2013). Species of *Meliola* form black, radiate, velvety colonies on the surface of a wide range of plants and are considered as minor plant pathogens as they do not cause extensive damage to the plants (Hongsanan et al. 2015; Jayawardena et al. 2020). However, due to the dark cover that the fungus produces, the photosynthetic area is reduced and respiration and temperature may increase (Hongsanan et al. 2015). Heavy infections by these species result in a dirty appearance of the plants, which can reduce the economic value of ornamentals. Even though this group of fungi also affects some crops, an in-depth study of *Meliolaceae* is still lacking (Hosagoudar and Riju 2013). Species of *Meliola* are believed to be host-specific, but there is little evidence to prove or disprove this notion. New species were often based primarily on host association, even if their morphology was very similar to existing species (Hongsanan et al. 2015). However, some species differ both in terms of morphology and in penetration mechanisms (Rodríguez-Justavino and Piepenbring 2007). To verify their host-specific nature, molecular investigation is needed, which is hampered due to their bio-trophic nature (Hongsanan et al. 2015).

Currently, *Meliola* comprises more than 2000 species (Zheng et al. 2017; Index Fungorum 2021). These species have mostly been introduced by host association, morphology and disease distribution (Mibey and Hawksworth 1997), making species identification almost impossible without first confirming the host identity (Hongsanan et al. 2015). Therefore, testing for host-specificity and phylogenetic investigation are needed in *Meliola* to accurately determine the species. The phylogenetic placement of *Meliola* in Sordariomycetes was inferred from DNA sequence data from fruiting bodies (Pinho et al. 2012, 2014; Hongsanan et al. 2015; Justavino et al. 2015). Even though there are 3063 species epithets in Index Fungorum (2021), less than 30 species have molecular sequence data in this genus, which are derived from direct sequencing of fruiting bodies and fresh mycelium (Pinho et al. 2012, 2014; Hongsanan et al. 2015; Justavino et al. 2015; Hyde et al. 2020). While *Meliola* is clearly polyphyletic (Hyde et al. 2020; Marasinghe et al. 2020; Zeng et al. 2020) the low amount of sequence data available for this genus prohibits clarifying relationships between species and genera in *Meliolaceae* (Hongsanan et al. 2015; Zeng et al. 2017).

It is essential to use not only morphology but also phylogeny combined together with ecological data when defining a species in this genus.

Plasmopara

Plasmopara is an obligate pathogen that belongs to oomycetes (fungi-like taxa), a diverse group of pathogens affecting a wide range of economically important plants (Thines 2014; Thines and Choi 2016). Downy mildews have evolved as filamentous, obligate biotrophic pathogens independent from the fungal lineage and belong to *Straminipila* (Thines 2014). There are 208 records under *Plasmopara* in Index Fungorum (2021). However, among them, 163 names are currently accepted as members of *Plasmopara,* including 34 forms and varieties. The disease name downy "mildew" refers to the typical symptom of cottony outgrowth appearing mainly on the lower leaf surfaces of infected plants (Jackson 2008). Prominent species of *Plasmopara* are *Pl. viticola*, causing downy mildew of grape, and *Pl. halstedii*, causing downy mildew on sunflower (Gascuel et al. 2015). Both species originate from North America and have been introduced into most areas in which their host plants are cultivated.

Downy mildew species are mostly strongly host-specific and exhibit pronounced virulence variation in their population. For example there are 18 downy mildew pathotypes associated with sunflower downy mildew. Also in *Pl. viticola* s.l., several lineages differing in pathogenicity have been found, which were classified as *P. viticola f. sp. riparia*, *P. viticola f. sp. aestivalis, P. viticola f. sp. vinifera,* and *P. viticola f. sp. quinquefolia* (Rouxel et al. 2013). However, it seems likely that several of these need to be characterized as new species (Schröder et al. 2011), as was recently implemented for *Pl. muralis*, the downy mildew of Boston ivy, which is morphologically and phylogenetically distinct from *Pl. viticola* (Thines 2011).

Generally, phylogenetic investigations have revealed that species are specific below the host genus level and that species traditionally accepted as broad range pathogens, such as *Pl. nivea*, *Pl. halstedii*, and *Pl. obducens*, indeed represent several phylogenetically independent species (Voglmayr et al. 2004; Choi et al. 2010; Görg et al. 2017). Even though closely related species are often morphologically similar, detailed morphological investigations have revealed that unambiguous identification is possible, when enough measurements are being performed (Thines 2011; Görg et al. 2017; Choi et al. 2020). Even though there are over a hundred names associated with this species in Index Fungorum, there are less than two dozen species available with sequence data. This is mostly because of the obligate biotrophic nature of the pathogen, which necessitates the use of historic herbarium specimens, and phylogenetic investigations. Such ambiguity further results in difficulties in obtaining specimens of rare species that are often known from only few collections on loan. However, a revision of some *Plasmopara* species complexes is under way, due to advances in DNA-extraction and PCR analysis of herbarium specimens (Telle and Thines 2008).

Apart from the few groups mentioned above, phylogenetic approaches have mainly been used for clarifying genus boundaries in the downy mildews with pyriform haustoria, of which *Plasmopara* is the largest genus (Göker et al. 2003; Voglmayr et al. 2004; Constantinescu et al. 2005; Thines et al. 2009).

Considering the strong host-specificity in *Plasmopara*, the correct identification to species level is crucial. Therefore, when defining a species in this genus it is recommended to use a polyphasic approach with morphology, phylogeny and ecological concepts.

Rust fungi

Many rust fungi produce five different spore types or stages in their lifecycles: pycniospores, aeciospores, urediniospores, teliospores and basidiospores (Lorrain et al. 2019). Some rust fungi can produce the five spore stages on a unique host (e.g. the flax rust fungus *Melampsora lini*; Lawrence et al. 2007). However, there are rust fungi that have different spore stages. *Puccinia malvacearum* and *P. heterogenea* are microcylic rusts with the shortest life cycles with only two spore types: basidiospores and teliospores, or pycniospores and teliospores (Demers et al. 2015). Demicyclic rust fungi lack the urediniospore stage and can be either autoecious or heteroecious such as *P. smyrnii* (Quilliam and Shattock 2003). Hemicyclic rust fungi such as *Melampsora pruinosae* and *M. microspora* exhibit only teliospores and urediniospores and are autoecious (Viale et al. 2013). For some rust fungi, the complete life cycles have never been observed (Lorrain et al. 2019). Best examples for this are the alternating hosts for two economically important species the soybean rust fungus *Phakopsora pachyrhizi* and the coffee rust *Hemileia vastatrix* (Slaminko et al. 2008; Talhinhas et al. 2017). The morphology of each of these stages is different making plant pathologists confused over the causal organism. Based on the morphology of different stages, and different hosts, one could assume that these fungi are different species. For example, there are 150 species epithets for *Phakopsora* and 5452 epithets for *Puccinia* in the Index Fungorum (2021).

However, two morphologically different fungi occurring on the same host or completely unrelated hosts can be the same species once the phylogenetic species concept is applied. Therefore, when defining a species in rusts a polyphasic approach should be always taken into consideration.

Trichoderma

Trichoderma is a pathogen on fruits, trees, and mushrooms and globally one of the most widespread fungal genera (Kredics et al. 2009). *Trichoderma*, causing green mold disease, is considered a serious threat for worldwide mushroom growers, causing diseases known as *Trichoderma* spot, *Trichoderma* blotch, and *Trichoderma* mildew (Sharma et al. 2007). Green mold disease has been recorded all over the world (Castle et al. 1998; Hatvani et al. 2007a,b, 2012; Jayalal and Adikaram 2007; Błaszczyk et al. 2013; Gu et al. 2020; Farr and Rossman 2021).

Trichoderma species associated with green mold disease have been isolated from both substrates and fruiting bodies of edible mushrooms such as *Agaricus bisporus*, *A. bitorquis*, *Calocybe indica*, *Ganoderma lucidum*, *Lentinus laedodes*, *Pleurotus eryngii, P. ostreatus, P. sajor-caju,* and *Volvariella volvacea* (Singh et al. 2006; Innocenti and Montanari 2014; Lee et al. 2020). It has been found that *Trichoderma pleuroticola* and *T. pleurotum* commonly cause green mold disease on oyster mushrooms whereas *T. aggressivum* and *T. harzianum* are the common causal agents on *A. bisporus* (Hatvani et al. 2012; Błaszczyk et al. 2013). However, species such as *T. atroviride*, *T. asperellum*, *T. harzianum*, and *T. longibrachiatum* have also been reported (Castle et al. 1998; Hatvani et al. 2007a). Furthermore, additional species have been reported as associated with the disease including *T. aureoviride*, *T. hamatum*, *T. inhamatum*, *T. koningii*, *T. lentinulae*, *T. polysporum*, *T. pseudokoningii*, *T. vermifimicola*, *T. virens,* and *T. viride* (Choi et al. 2003, 2010; Morris et al. 1995; Sharma et al. 2007; Gu et al. 2020). Among the species mentioned, *Trichoderma aggressivum* and *T. harzianum* have been identified as the most serious causal agents, resulting in considerable losses in worldwide mushroom cultivations (Seaby 1996; Baars et al. 2013).

Trichoderma species have been commonly isolated from soil and have been recorded as associated with different plant hosts (Farr and Rossman 2021). There are more than 400 species listed in Index Fungorum (2021) and 379 species listed in Species Fungorum (2021). Mushroom growers and plant pathologists face difficulties in identifying the species due to their overlapping morphological characters. Therefore, it is not recommended to use morphology alone in identifying *Trichoderma* strains. Sequence data play an important role in species identification (Baars et al. 2013; Gu et al. 2020; Inglis et al. 2020). Many attempts to develop molecular markers for rapid detection of *Trichoderma* pathogens on mushrooms were made (Hatvani et al. 2007b; Kredics et al. 2009; Lee et al. 2020), e.g. Hatvani et al. (2007b) developed a rapid method to detect *T. pleurotum*and *T. pleuroticola* using a polymerase chain reaction (PCR)-based technique without DNA sequence analyses. Lee et al. (2020) developed a molecular marker for the detection of a wide range of *Trichoderma* species based on ITS1 and ITS2 regions, which did not show any cross-reactivity with edible mushrooms.

In the Species Fungorum (2021) *Trichoderma lignorum* and *T. lignorum* var. *major* is recognized as *T. viride* while *T. lignorum* var. *narcissi* is recognized as *T. harzianum*. Unless the mushroom growers and plant pathologists have a sufficient knowledge concerning *Trichoderma* taxonomy, they will not be able to identify these two pathogens causing similar diseases. In *Trichoderma* the concept of biotypes (progeny developed by variant having similar heredity is called a biotype or a subgroup of individuals with in the species, usually characterized by the possession of single or few characters in common) can be observed. Castle et al. (1998) identified the biotype Th3 which was identified as a strain of *T. harzianum* was actually a strain of *T. atroviride*. Ospina-Giraldo et al. (1998) assessed the biotypes of *T. harzianum* (Th1, Th2 and Th4). The aggressive biotype in the North America (which was originally known as Th4) was renamed as *Trichoderma aggressivum* f. *aggressivum* (now known as *T. aggressivum*, Krupke et al. 2003). Use of biotypes and pathotypes in defining a fungal pathogen is not recommended due to the confusion that it can cause among pathologists and taxonomists.

As species of *Tricoderma* play different roles and are beneficial to humans, identification of species should always be based on a polyphasic approach (morphology, phylogeny, ecology, pathogenicity) whenever it is possible.

Are we introducing too many species?

Ignorance of morpho-species

Many species have been introduced as plant pathogens based on routine collections and phylogenetic reassessments of genera. Given the high number of newly described plant pathogenic species based on phylogenetic evidence over the past two decades, the question arises, if the newly introduced species are novel and unique or should be considered conspecific with species described earlier in the absence of molecular phylogenetic data. Indeed, it is a serious concern if new species are introduced from a host, for which there are previous records of a morpho-species (without molecular data). In these cases, the original morphological descriptions need to be evaluated carefully to avoid descriptions of superfluous taxa. For example, if a new *Diaporthe* species was introduced on grape (*Vitis* sp.), the morphology of the species should have been compared with *D. ampelina* and other well-known species reported from *Vitis*. However, sometimes, the original descriptions are of insufficient detail for unequivocal identification and type specimens are not available to compare the morphology. In these cases, epitypification can solve the situation. Hence, we recommend epitypification/neotypification of such morpho-species wherever possible. In addition, it needs to be considered that many species are not strongly host-specific, meaning that morpho-species from other hosts, especially in the same area could be potentially conspecific. Thus, especially in species-rich groups, new names should only be introduced after thorough morphological investigation, broad sampling and detailed literature research.

Taxon sampling

Related to the above issue, taxon sampling is important when introducing a new species in a genus. The larger the number of taxa used in phylogenetic analyses, the less misidentification and misinterpretation of species is prone to happen (Young and Gillung 2020). However, species recognition is often carried out based on the characteristics of a small group of individuals, while at the same time it is well established that in a particular species group, small sample size can lead to the incorrect assumption of uniformity and the synapomorphic trait of characteristics that in fact is polymorphic (Davis and Nixson 1992; Liu et al. 2016a). As a consequence, new species might be mistakenly introduced if two divergent populations have certain morphological or genetic distinctions (Goldstein et al. 2000), but without considering potential intermediate populations. *Colletotrichum* is a good example for wrong identification of "new" species based on the phylogenetic species concept. *Colletotrichum*

endomangiferae (Vieira et al. 2014), *C. hymenocallidis* (Yang et al. 2009), *C. jasmini-sambac* (Wikee et al. 2011) and *C. melanocaulon* (Doyle et al. 2013) were introduced as new species in the *C. siamense* species complex, in Sharma et al. (2015) based on phylogenetic concept. However, Liu et al. (2016a, b) adding more strains to the analyses demonstrated that the four species were in fact *C. siamense*. Thus, insufficient taxon sampling in conjunction with low phylogenetic resolution is one of the main reasons that lead to ambiguous species boundaries in plant pathogens. Therefore, it is strongly recommended to include multiple strains from diverse origins for delimiting species or introducing novel species and to investigate these with multiple loci to ensure sufficient phylogenetic resolution.

Misidentification and mistakes

In the last two decades, plant pathogenic species have been mainly identified based on a phylogenetic species concept and then described using a combination of assumed host range, morphology, physiology and phylogenetic independence. However, errors or mistakes in the sequence data can result in erroneous new species that do not actually exist in nature, and frequently, new species and names are introduced in a way that they do not adhere to the rules outlined in the International Code of Nomenclature for alge, fungi, and plants (ICNafp) and, thus, considered invalid.

For example, *Diaporthe pseudolongicolla* K. Petrović, L. Riccioni & M. Vidić was introduced as *nom. nov*. to replace the taxon *D. novem* J.M. Santos, Vrandečić & A.J.L. Phillips (Petrović et al. 2018). According to Petrović et al. (2018), the epithet 'novem' was not consistent with the International Code of Nomenclature in terms of a numerological classification that is not permissible (McNeill et al. 2011). However, the new name *D. pseudolongicolla* has been considered as invalid according to the Article 32.1 (a) of the ICNafp, which supports *D. novem* to be the appropriate name the name cannot be seen as a mere enumeration (McNeill et al. 2011). Another example of taxonomic confusion is *Diaporthe interrupta* Niessl, which was a homonym of *D. interrupta* (Mont.) Sacc. It has therefore been considered as invalid as per Article 53.1 of ICNafp (McNeill et al. 2011) and the adoption of a new name, *D. tecomae* Sacc. & P. Syd. was proposed for this taxon (Gomes et al. 2013). Similarly, *D. dorycnii* Dissan., Camporesi & K. D. Hyde has been mistakenly introduced with the same epithet as *D. dorycnii* (Mont.) Sacc. (Dissanayake et al. 2017).

In addition to these taxonomic confusions, mistakes in sequence editing, alignment and sequence concatenation can lead to the erroneous introduction of new species. For example, *Colletotrichum hymenocallidicola*, a singleton species was introduced based on a single strain using five loci (ITS, *gapdh, chs-1, act* and *tub2*; Ariyawansa et al. 2015). Based on a BLASTn search, Damm et al. (2019) noted that the placement of this species based on two gene regions (*act* and *tub2*) is differed from the placement based on the other three gene regions (ITS, *gapdh* and *chs-1*). These strongly divergent results likely reflect the result of mixing up the sequence data. Therefore, we strongly recommend to perform a cross-validation of each gene region with the original sequence data obtained, to blast each locus independently and to manually check the quality of chromatograms before conducting analyses.

Also the exclusion of information on the holotype or the correct deposition of strains has become a significant mistake during the past decades. For example, *Colletotrichum australisinense*, *C. bannanense*, *C. corchorum-capsularis*, *C. ledongense*, and *C. sichuanensis* were introduced without listing an authentic dried type specimen or a metabolically inactive culture, and a living culture was proposed as a holotype instead, which makes them invalid (Liu et al. 2016b, 2018). We recommend that authors should closely follow best practices when introducing new species, to avoid invalid publications and the introduction of superfluous names (Aime et al. 2021).

Poor documentation can lead to taxonomic instability. For example, Pérez et al. (2010) described *Diplodia pseudoseriata* from native *Myrtaceae* trees in Uruguay, while Mehl et al. (2011) introduced *D. alatafructa* from *Pterocarpus angolensis* in South Africa. Later, Phillips et al. (2012) stated that these two species appear to be morphologically identical and clustered in a single clade suggesting that they represent a single species. However, the ex-type sequences of these strains are different and indicate two separate species (Phillips et al. 2013; Alves et al. 2014) and Phillips et al. (2013) assumed that either cultures or sequences of the other isolates of these two species have been mislabelled, necessitating further scrutiny. Furthermore, species introduction with inadequate gene sequence data can also lead to an unclear separation among the strains used in the phylogenetic analyses. For instance, only ITS sequence data are available for the recently introduced *Diplodia huaxii*, *D. italica* and *D. pseudoplatani* (Wijayawardene et al. 2016). However, phylogenetic identification based on the ITS alone is not sufficient due to low resolution of data. In addition, *D. pseudoplatani* clustered in the *Diplodia pseudoseriata / D. alatafructa* clade further complicating the issue (Linaldeddu et al. 2016; González-Domínguez et al. 2017; Pan et al. 2019). Thus, the species in this clade need to be subjected to a more detailed study in order to determine whether they represent several species or not.

To conclude the authors would like to emphasise on the use of GCPSR concept when naming every new lineage in the phylogenetic or gene trees. When using the GCPSR it is recommended to use at least three strains in the data set. In cryptic species a close examination using GCPSR is

recommended to see whether the species are over-estimated. However, the known fungal species in the world is less than 5% of the total diversity. Therefore, describing new species especially from less-studied group of fungi is important as long as polyphasic approach (morphological, phylogenetic and GCPSR) in describing a species is used.

Guidelines for defining a species in plant pathology

To avoid an inflation of taxonomic issues with the introduction of invalid and unnecessary names we propose the following guidelines for the description of new species. However, when applying these guidelines, mycologists should be cautious as all guidelines cannot be applied to all existing pathogenic genera. Mycologists should try to avoid creating unnecessary confusions in fungal pathogen taxonomy and work together with plant pathologists to resolve the problems that already exist.

a. Sampling of strains and specimens should be as broad as possible, ideally from different cultivars, environments, and geographical areas.
b. During pathogen sampling, disease severity, plant growth conditions, or maturity status should be recorded wherever possible.
c. In the case of cultivable fungi, at least 2–3 independent strains (from different collections when possible) should be used for morphological and phylogenetic investigations to facilitate the detection of DNA sequencing errors and artifacts as well as to provide insights into intraspecific diversity.
d. At least two species recognition criteria should be used when identifying a species (e.g.: morphology and phylogeny).
e. Host association and pathogenicity criteria, when used for separating species should be supported by molecular evidence.
f. A plant pathogen should not be defined as host-specific, unless there are several collections from different geographic locations (with the same climate conditions) on the same host and collections of related species from the same localities. Pathogenicity studies should be conducted on a wide range of hosts. If the pathogen can cause disease on only one of many genera and families of hosts, then it can be deemed to be host specific.
g. The quality of sequences should be checked carefully and bi-directional sequencing should be performed when needed due to ambiguous base calls, e.g. as a result of homopolymers, to prevent sequence errors.
h. Phylogenetic reconstructions should be based on a combined phylogeny of phylogenetically informative markers to ensure sufficient phylogenetic resolution, e.g. ITS regions and one to several protein-coding genes, such as *tef1–α*, *rpb2*, or *tub2*. However, this depends on the genus itself.
i. Before combining different gene regions in the multi-loci phylogenetic analysis, congruence of the phylogenies from the single gene regions needs to be examined, to account for incomplete lineage sorting and to avoid artificially derived phylogenetic lineages.
j. Clade credibility of phylogenetic trees should be assessed by at least two independent phylogenetic methods.
k. A new species should not be introduced unless bootstrap support for monophyly is greater than 90% in two independent phylogenetic analyses and posterior probabilities are ≥ 0.99 in Bayesian Inference (when applicable).
l. Morphological characters of the subject species need to be compared carefully with species that do not have molecular data (morpho-species) but have been reported from the same regions, environments or hosts and should be treated with caution.
m. Phenotypic variation among species such as spore color, shape/size should be treated with caution. If there are only minor or insignificant variations it is not recommended to introduce a new species.
n. Comparison of phenotypic variations among sister taxa should be derived from cultures of a similar age and grown on the same medium at similar temperatures.
o. When dealing with cryptic species, the use of GCPSR approach combined with recombination analysis (PHI test) is recommended. In addition, the sequence differences need to be exactly defined on the basis of a deposited alignment (see Kruse et al. 2017 for an example).
p. When dealing with cryptic species complexes, the phylogenetic tree for the specific species complex should be established with at least three strains per species, whenever possible.
q. New disease report identification should be made based on multi-locus phylogenies instead of using ITS barcodes alone, whenever ITS sequences of related species are more than 99% similar.
r. In order to confirm the pathogenicity of a species, Kochs' postulates should be fulfilled. Both spore suspensions and mycelium plug inoculations should be considered. Ideally, infection trials should be carried out with both complete plants (whenever possible) and detached plant parts in the manner used as a standard for a specific group (e.g. with our without prior wounding). The results of these tests should be analyzed using statistical software to confirm whether there are significant differences.

Conclusion

A polyphasic approach for the accurate identification of pathogenic species is needed when new species causing plant diseases are introduced. Only by careful, combined investigation of morphological, ecological, biological, and phylogenetic data will introduction of stable names, that are essential for clear communication concerning plant diseases, become established (Kuhnert et al. 2017; Aime et al. 2021). The application of a polyphasic approach in plant pathology is, thus, essential for the accurate identification of fungal pathogens, and their naming, leading to advances in management and control of currently known and newly emerging diseases.

Acknowledgements This project is funded by National Research Council of Thailand (NRCT). Ruvishika S. Jayawardena would like to thank the National Research Council of Thailand, Grant for new researcher NRCT5-TRG630010-01, entitled "Biodiversity, taxonomy, phylogeny and evolution of Colletotrichum in northern Thailand". We would like to thank the Thailand Research Fund, Grant RDG6130001 entitled "Impact of climate change on fungal diversity and biogeography in the Greater Mekong Subregion". Kevin D Hyde thanks Chiang Mai University for the award of a Visiting Professor. Authors would like to thank Mushroom Research Foundation and Mae Fah Luang University.

Declarations

Conflict of interest The authors declare the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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