

The promise of molecular identification of fungi to overcome the global challenges in plant biosecurity

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Abstract

Phytopathogenic fungi are a highly diverse group of eukaryotes with significant impact on natural ecosystems and cultivated lands, causing diseases on crops, ornamentals and forest trees. Historical outbreaks of invasive fungal pathogens on staple crops have caused severe food security threats to human populations. Therefore, accurate identification of pathogenic fungi has a great impact on global plant biosecurity and is considered to be crucial in this era of global exchange of horticultural products and plant germplasm. Although morphological features have traditionally been used in fungal identification, the past two decades have witnessed revolutionary changes with the implementation of DNA sequence data. The nuclear ribosomal internal transcribed spacer region (ITS), the standard fungal DNA barcode, is extensively used for a quick and often approximate identification. However, due to limitations of single DNA barcodes in fungal species discrimination and establishment of evolutionary relationships, multiple genomic loci have been utilized. The identification of fungi in plant biosecurity and quarantine practices are often based on morphology and tentative taxonomic assignments have increased the risk to regional and global plant biosecurity. This mini-review summarizes (1) the significance of precise naming of pathogenic fungi; (2) the incorporation of molecular data in the identification of emerging phytopathogens with a few examples; and (3) the need for paradigm shifts in global plant biosecurity practices. In addition, we urge the relevant agencies of the countries lacking organized plant biosecurity practices to recognize the need to confront the potential threats on their staple crops, ornamentals and forest trees and support appropriate research for DNA-aided identification and classification, and application of accurate names to high priority phytopathogens and emerging species. This will enable effective disease surveillance, prevent unnecessary trade restrictions for plant-based products and enhance biosecurity and quarantine efforts.

Keywords: Biological invasions, DNA barcoding, Emerging pathogens, Molecular phylogeny, Plant protection

Introduction

The kingdom of fungi constitutes a large, diverse group of eukaryotic, heterotrophic, ubiquitous microorganisms that play a significant role in human, animal and plant health, food security and ecosystem resilience on earth (Hibbett et al. 2007; Tedersoo et al. 2014). They are the dominant causal agents of a wide range of plant diseases (Udayanga et al. 2011; Dean et al. 2012). Saprotrophic fungi feed on dead plant tissues and parasitic fungi primarily live on or within living plants, causing various disease symptoms, whereas endophytic and mycorrhizal fungi exhibit a mutualistic association without causing apparent symptoms (McDonald & Stukenbrock 2016; Doehlemann et al. 2017).

Fungal diseases are threatening many commercially and socially valuable crops including cereals, fruits, vegetables, pulses, plantation and cash crops as well as ornamentals and forest trees (Park et al. 2000; Rossman et al. 2007). Emerging plant diseases, which may either be previously known or have recently shifted geographic regions or associated hosts have become a global challenge in crop biosecurity. The emergence of plant pathogens can be partly due to climate change, as well as the rapid development of international trade of horticultural products and other living plants (Elad & Pertot 2014). These emerging diseases are not only important in global crop production, but also pose severe risks on a local level, especially in export agriculture, plantation industry and small farms in developing countries. Invasive microorganisms, the species whose introduction or spread threatens human, animal, plant health, agricultural, environmental security or the economy are also one of the growing threats for plant biosecurity, human and animal health, and export agriculture worldwide (Paini et al. 2016; Stricker et al. 2016). The current inefficiencies of fungal identification, lack of

expertise as well as the minimum implementation of molecular data have aggravated the issues pertinent to global food security (Crous et al. 2016; McDonald & Stukenbrock 2016).

Some of the widespread fungal diseases are major threats to the most important crops such as rice, wheat and maize upon which humanity depends, whereas some of them may cause significant losses of crops that are the main means of revenue for some countries or serious threats to biodiversity (Couch & Kohn 2002; Godfrey et al. 2016). For instance, the rice blast pathogen, *Pyricularia oryzae*, formerly known as *Magnaporthe oryzae* is the most destructive pathogen of rice, the widely consumed staple food for a large part of the world's human population (Couch & Kohn 2002). Severe outbreaks of the rice blast disease are a recurrent problem in all rice-growing regions of the world where the disease is found to be difficult to control (Kahn et al. 2016; Nalley, 2016). Thus, rice blast that destroys up to 30% of the world's rice crop in each year is considered as a significant economic and humanitarian issue, especially in Asia (Savary et al; 2000; Saleh et al. 2014). Similarly, the coffee rust disease caused by the fungus, *Hemileia vastatrix*, has plagued coffee growers globally for more than a century (McCook 2006; Vandermeer et al. 2010, 2018). The fungus which is found to be with an East African origin turned into a destructive pathogen in the major coffee growing regions of Sri Lanka (then called Ceylon in 1867 and had ruined completely the celebrated coffee production in the Central Highlands of the country. After more than a century, the same fungus hit the renowned coffee-producing regions in Central America, causing a cluster of outbreaks since 2008. The succession of coffee rust outbreaks, termed “the big rust” by some biologists, begun in 2008 from Colombia, and then moved northward in 2012-2013, causing significant losses in parts of Central America and Mexico (McCook & Vandermeer 2015). Then it was reportedly shifted southward in 2014-2015 causing severe losses in Ecuador and Peru and again in 2018-2019 in Colombia, Honduras and throughout the region leading a massive hit on coffee-based economy (Ehrenbergerová et al. 2018).

Traditional species identification of fungi involved discovery, morphological descriptions, artificial system of classification and naming of fungal species (Rossman & Palm-Hernández 2008).

Similarly, morphological identification has been implemented for fungi in almost all phytopathological studies as well as to detect pathogens in biosecurity applications and quarantine (Burgess et al. 2016). In morpho-species recognition, the macroscopic and microscopic fungal structures of the sexual and asexual morphs of were compared using available taxonomic literature and preserved voucher specimens in fungal herbaria, which has been the basis for traditional system of identification (Cai et al. 2011; Hyde et al. 2013). The same methodical approach has been implemented in biosecurity and quarantine situations, primarily by authorities and specialists working on fungal identifications around the world. Nevertheless, the fungal identification solely based on morphology leads to numerous difficulties and failures, especially the species level classification (Crous et al. 2015; Raja et al. 2017). In some highly diverse genera of fungi, the species delimitation has been impossible even for well-experienced mycologists, trained to work on fungal identification by profession. Morphological crypsis, plasticity and limitations of distinguishing morphological characters among species often result misidentifications (Udayanga et al. 2011). Moreover, the pleomorphic fungi, which comprise two entirely dissimilar asexual and sexual morphs in the life cycle of the same fungus has confused early mycologists and were even given different scientific names until recently. Therefore, the phenotypic characters alone in fungi has been deemed to be obsolete for many of the genera. These common drawbacks of morphological species identification can be due to evolutionary consequences, including hybridization, cryptic speciation, and convergent evolution. As a consequence of failures in fungal morpho-species recognition, different species recognition criteria, including physiological, biological and biochemical species recognition criteria were used before the molecular identification of fungi become prominent (Udayanga et al. 2011; Hibbett et al. 2016). In this review, we consider the necessity for accurate identification, applications of molecular data in species-level fungal identifications with few recent examples. We urge for international agreements for fundamental changes in biosecurity and quarantine practices pertinent to trade-associated fungal plant pathogens based on standardized DNA-aided identification systems.

Significance of Precise Naming of Pathogenic Fungi

Among all taxa of the kingdom fungi, plant pathogens represent a relatively less number of species, however much diverse group of organisms (Figure 1). Scientific names of pathogenic fungi are the key to all accumulated knowledge and those are

the foundation for effective communication (Hawksworth 2001, 2015; Rossman et al. 2016). The names of fungi can be used to access the specific, scattered knowledge of the species identification, classification, geographic distribution, biochemistry and bioprospecting, biosecurity and quarantine, ecology, pathogenicity, virulence and fungal disease surveillance.

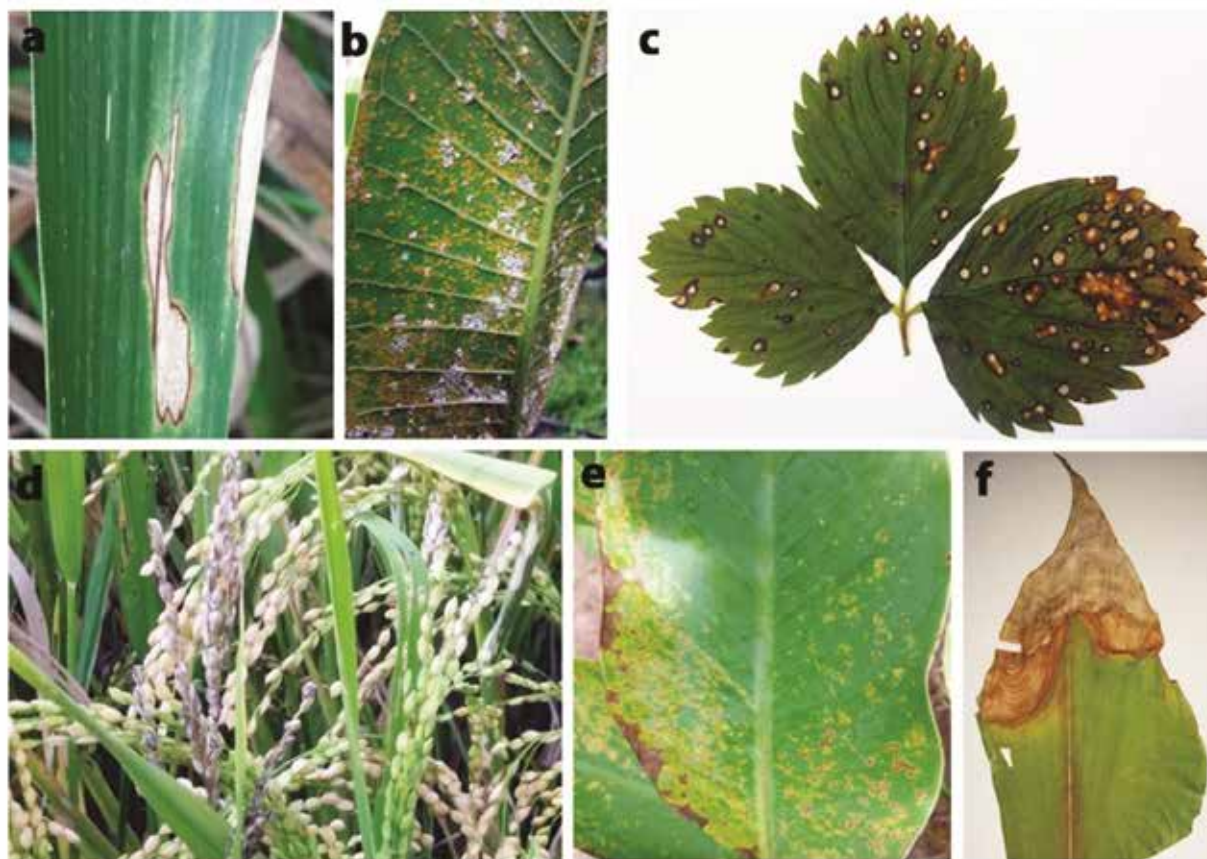


Figure 1: Diseases of a few economically important crops and ornamental plants.

a) Leaf spot of *Oryza sativa* (rice) –*Curvularia* sp. ; b) Rust on *Plumeria* (Frangipani) – *Coleosporium plumeriae* ; c) Purple leaf spot of *Fragaria* (strawberry) –*Ramularia grevilleana* ; d) Seed infections of rice –*Periconia* sp. ; e) Rust on *Canna* –*Puccinia* sp. ; f) Leaf blight of *Cucurma* (Turmeric) –*Diaporthe* sp.

Specifically, in biosecurity and quarantine, the name of the fungus of interest is paramount in the process of interception procedures or quarantine actions. For instance, the coffee rust pathogen, *Hemileia vastatrix* has been associated with coffee plant which is economically and socially important crop, for over 150 years (Cressey 2013; Avelino et al. 2015). The information linked with this scientific name, *Hemileia vastatrix* for decades, scattered globally, including disease reports, biological literature, specimens in fungal herbaria and intercepted

collections by biosecurity authorities. In the molecular era, numerous nucleotide sequence data as well as whole genome shotgun sequence data available in GenBank which provide crucial biological information associated with the fungus, and all facts are unified by this name (Carvalho et al. 2014).

The myrtle rust fungus, *Austropuccinia psidii* is considered to be an invasive species which has caused devastating effects in Australia in late 2018

and early 2019, since it has been first detected in Australia in 2010 on the NSW central coast (Morin et al. 2012). The myrtle rust formerly known as *Puccinia psidii* originates from South America and later become invasive infecting on several genera of Myrtaceae (e.g., Myrtle, pohutukawa, bay rum tree, clove, guava, acca) in Australia, causing emergency national action plans to mitigate the outbreak in January 2019. However, the taxonomic position and meaningful name for myrtle rust pathogen had been unclear until recently. Based on molecular phylogenetic analyses, Beenken (2017) showed that, it does not belong in the genus *Puccinia*, thus the new genus *Austropuccinia* was introduced to accommodate the myrtle rust fungus. Having a meaningful name for a fungus with greater impact on continent's major threat to biodiversity, allowed scientists to access more data and natural history information of the fungus that will be helpful to combat against this deleterious pathogen. This information will allow more precise risk assessments in support of scientifically sound plant quarantine decisions and policies that sustain world trade of agricultural commodities, while protecting the plant resources of individual countries.

According to the previous International Code of Botanical Nomenclature (ICBN), Article 59 permitted the application of different names to the different morphs of the same fungus, depending on whether a sexual (teleomorphic) or asexual (anamorphic) reproduction was involved (Norvell 2011). This dual nomenclature system, which allowed two or more names for the same species had resulted in significant failures in the consistency of identifying and naming species and no doubt on biosecurity and quarantine lists (Wingfield et al. 2012). Following the bold decisions taken by mycologists in "one-fungus one name" symposium and subsequent publication of the Amsterdam declaration of fungal nomenclature (Hawksworth et al. 2011), the International Botanical Congress held in Melbourne in 2011 (IBC-2011) approved several key resolutions that will affect fungal nomenclature (Norvell 2011; Taylor 2011). Accordingly, all

legitimate fungal names published prior to January 1, 2013 compete equally for priority, and the sole correct name is now the earliest legitimate name, regardless of the life history state of the type (Hawksworth 2011). However, this long awaited decision initially shocked plant pathological community who had their favorite names for different fungi, later embraced by them adjusting to more meaningful system in naming species (Geiser et al. 2013; Rossman et al. 2016). The changes of botanical code are widely implemented later in order to establish precise naming of fungi with greater importance in biosecurity in conjunction with the molecular phylogenetic results.

Incorporation of Molecular Data in the Identification of Emerging Phytopathogens with a Few Examples

The precise identification and molecular systematics fungi heavily utilize DNA sequencing and subsequent molecular phylogenetic analyses. The fungal DNA barcoding, which uses a standardized 500-800 bp sequence to identify species, has been a popular tool in both biodiversity and phytopathological studies as well as comparatively few cases in plant disease regulatory purposes. Recognition of the ribosomal Internal Transcribe Spacer region (ITS) as the standard DNA barcode for fungi, in 2012 is considered as a milestone in fungal studies with a greater scientific importance (Schoch et al. 2012). However, it should be noted that fungal species identification based on DNA sequence information from a single barcode locus, deviates from the current gold standard for fungal species recognition that utilizes the phylogenetic approach and is based on the concordance of multiple gene genealogies (Taylor et al. 2000). Today's molecular identification of fungi has evolved from DNA barcoding to DNA-aided taxonomy and phylogeny based on the premise of using the genetic variation inherent among sequences of different individuals to identify taxa (Figure 2).

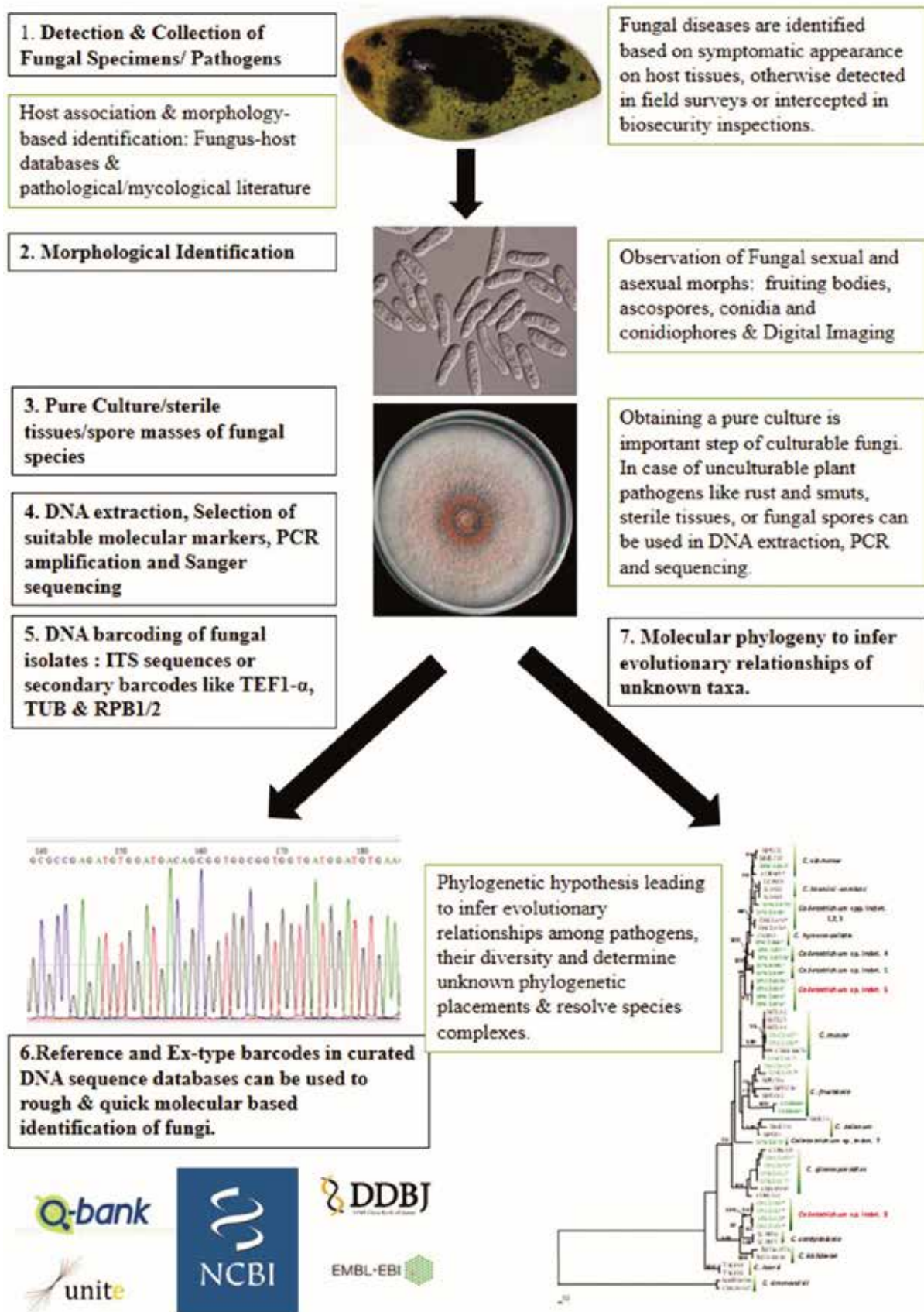


Figure 2: Diagrammatic illustration of the key steps of molecular identification of the plant pathogenic fungi.

The detection, morphological identification and generation of molecular data required skills and involvement of plant pathologists or mycologists. DNA barcodes generated should be carefully handled in order to maintain the quality standards. The International Nucleotide Sequence Database Collaboration (INSDC) is a long-standing foundational initiative that operates between DDBJ, EMBL-EBI and NCBI available for sequence similarity search. The Q-bank Fungi database contains curated DNA sequence data (barcodes), morphological, phenotypical and ecological data for approximately 600 species that are relevant to mycological phytopathology. The UNITE is a well-curated nucleotide database supported with ITS based Species Hypotheses (SHs), with collection of annotated ITS sequences. Phylogenetic reconstructions can be used to place unknown taxa within current classification system and predict relationships among them.

Phylogenetic species recognition of an unknown is established based on evolutionary hypothesis, thus advocating a robust biological basis for recognizing fungal species. For instance, the boxwood blight, caused by the ascomycetous fungus, *Calonectria pseudonaviculata*, is a recently known emerging disease, particularly in the USA infecting ornamental and native boxwood plants in the family *Buxaceae* (Ivors et al. 2012; Henricot & Wedgwood 2013). The disease has been first reported from a single location at a single nursery in southern England in 1994, and it is now known throughout Europe, Asia, New Zealand, and North America (Henricot & Culham 2002). The first documented and confirmed reports of the disease from USA were made from Connecticut and North Carolina in November 2011, followed by reporting in more than 10 other states and on alternative hosts within the United States (LeBlanc et al. 2018; Malapi-Wight et al. 2014). This disease has concerned the ornamental plant industry, due to severe threats to health and productivity of boxwood in both landscape plantings and nurseries (Gehesquière et al. 2016; LeBlanc et al. 2018). The studies on routine collections, molecular and morphological characterization as well as molecular markers aided studies of population structure have proven a substantial impact on the epidemiology and control of this destructive disease within United States and elsewhere in the world (Gehesquière et al. 2016).

Species of *Colletotrichum* are commonly encountered fungal pathogens associated with fruits

and a wide range of field crops and produce anthracnose symptoms and leaf spots, rots and seedling infections (Hyde et al. 2009; Cannon et al. 2012). Since the recommendations of polyphasic approach to study fungal pathogens, coupled with multi-locus phylogenetic reconstructions, the number of phylogenetic species within this genus has rapidly grown (Cai et al. 2009). Many species of *Colletotrichum* previously considered to be a single taxon have turned out to be “species complexes” consisting of multiple taxa. For instance, *Colletotrichum acutatum* is generally accepted to cause anthracnose of strawberries (*Fragaria × ananassa*) (Baroncelli et al. 2015; Damm et al. 2012). Damm et al. (2012), who performed a comprehensive molecular phylogenetic study, revealed that several species in the *C. acutatum* complex namely, *C. acutatum*, *C. fiorinae*, *C. nymphaeae*, *C. simmondsii*, *C. godetiae* and *C. salicis*, are associated with strawberry diseases. The anthracnose of banana is known to cause by *Colletotrichum musae*, which is commonly reported from tropical regions of the world where *Musa* species are widely grown (Ploetz, 1997). Multi-gene phylogenetic analysis revealed that *C. musae* groups in a distinct lineage within the *Colletotrichum gloeosporioides* species complex and is most closely related to *C. fruticola* (Su et al. 2011; Udayanga et al. 2013). This particular species exclusively found on banana species, and considered as a relatively host-specific pathogen, which is an aggressive, difficult to control postharvest disease (Priyadarshanie & Vengadaramana 2015). However, the recent studies of *Colletotrichum* species associated with banana particularly in tropics revealed that several species can be found associated with anthracnose, which make it more crucial in identifying, regulation and control (Vieira et al. 2017). For instance, latest reports of *Colletotrichum* species associated with banana anthracnose in Brazil confirmed the encounter of *C. chrysophilum*, *C. tropicale*, *C. theobromicola*, and *C. siamense* in association with the same disease along with *C. musae* (Vieira et al. 2017).

Fusarium oxysporum, is one of the most economically important and commonly encountered fungal species associated with plants, animals and human as both pathogenic and non-pathogenic strains (Al-Hatmi et al. 2015; Nirmaladevi et al. 2017; Gordon 2017). This species was originally described from Germany, causing dry rot of *Solanum tuberosum* (potato) (Von Schlechtendahl 1824). Subsequently, the use of sub-specific ranks

(special forms or *formae speciales*) in *F. oxysporum* has been popular practice among plant pathologists due to the broad morphological diversity and host range (Leslie & Summerell 2006). Some of the *formae specialis* of *F. oxysporum* cause noteworthy diseases on economically important crops worldwide. For instance, global banana production is seriously threatened by the Fusarium Wilt disease, caused by the soil-borne pathogen *Fusarium oxysporum* f. sp. *cubense* (*Foc*) and also known as “Panama disease” (Mostert et al. 2017). This disease wiped out the banana industry in Central America and the Caribbean, in the mid-twentieth century and is now reported from many of the banana growing tropical countries across the globe (De La Cruz & Jansen 2018). The previous system of special forms of *F. oxysporum*, has much confused the identification of this important fungal pathogen due to subjectivity of morphological identification and intricate genetic variations. Recently, considering the need to advance and stabilize the taxonomic position of *F. oxysporum*, an epitype originally collected from Germany from *Solanum* was designated for this species (Lombard et al. 2019). In the same study, a combined four gene phylogeny based on the loci *cmdA* (calmodulin), *rpb2* (DNA-directed RNA polymerase II), *tef1* (translation elongation factor -1) and *tub2* (tubulin-2) genes revealed that the isolates from *Musa* classified as *f. sp. cubense* belong in at least four different clades corresponding to distinct species, *Fusarium duoseptatum*, *F. nirenbergiae*, *F. odoratissimum* and *F. trachichlamydosporum* (Lombard et al. 2019). The designation of an epitype, supported by substantial molecular phylogenetic evidence, allows naming of the multiple cryptic species recognized in this species complex, thus plant pathologists as well as biosecurity officials can adopt robust standards in their decisions regarding regulations of pathogens (Wingfield et al. 2012).

Need for Paradigm Changes in Global Plant Biosecurity Practices

International trade of horticultural products and living plants has allowed the movement of plant associated fungi across the borders for centuries. The quick identification of an invasive species is a first line of defense; however, when it comes to fungi, accurate identification is often problematic with minimal macro-morphological features or microscopic observations. Many of the checklists and databases of invasive and quarantine fungi as well as disease compendia have become outdated

due to the identification of species merely based on morphology. To ensure the plant biosecurity of the country where sensitive cases of accurate fungal identification are vital, robust consolidated morphological and molecular based identification protocols should be followed (Aveskamp et al. 2008). This will not only assure the health of crops and natural ecosystems but also prevent unnecessary trade regulations for export-agriculture based economies. Almost all molecular plant pathology and phylogenetic studies of fungi frequently emphasize the significance of downstream utilization of their research outcome to ensure the sustainable plant health and global food security (Crous et al. 2016; Marsberg et al. 2017). However, much of the information available from research and thousands of DNA barcode sequences available in nucleotide databases may not be actually exploited for biosecurity purposes in many countries especially in highly vulnerable regions for severe food security issues. Although DNA sequencing technologies have become more accessible and affordable for the scientific community, the implementation of these golden tools in plant biosecurity, disease surveillance and quarantine are largely overlooked.

Apart from the dogma of taxon based identification and phylogenetics of plant pathogenic fungi, recent developments in research focused on genomes, transcriptomes, proteomes, and metabolomes of fungi in conjunction with biological information, can be used to determine whether a specific group of fungi poses a biosecurity risk (McTaggart et al. 2016). Fungal genomics can be used to predict the life modes of poorly known fungi, potential pathogenicity factors, including host target proteins and the presence of transposable elements with high mutation rates (McTaggart et al. 2016; Udayanga et al. 2017). Therefore, the biosecurity related decisions only based minimum morphological observations and tentative identifications, may largely underestimate the potential risks of high priority pathogens as well as other emerging species. Topics on biosecurity, plant disease surveillance and quarantine can be involved in a sequential approach of the awareness of the problem, involvement among plant pathologists and other experts, strong collaborative efforts and support from government agencies, the commercial sector, international organizations, research institutes and universities. We expect this article will stimulate further interest, research and discussion of this topic within scientific

communities, policy makers, other relevant authorities and the general public.

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