REVIEW



Predicting global numbers of teleomorphic ascomycetes

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Abstract

Sexual reproduction is the basic way to form high genetic diversity and it is beneficial in evolution and speciation of fungi. The global diversity of teleomorphic species in Ascomycota has not been estimated. This paper estimates the species number for sexual ascomycetes based on five different estimation approaches, viz. by numbers of described fungi, by fungus:substrate ratio, by ecological distribution, by meta-DNA barcoding or culture-independent studies and by previous estimates of species in Ascomycota. The assumptions were made with the currently most accepted, "2.2–3.8 million" species estimate and results of previous studies concluding that 90% of the described ascomycetes reproduce sexually. The Catalogue of Life, Species Fungorum and published research were used for data procurement. The average value of teleomorphic species in Ascomycota from all methods is 1.86 million, ranging from 1.37 to 2.56 million. However, only around 83,000 teleomorphic species have been described in Ascomycota and deposited in data repositories. The ratio between described teleomorphic ascomycetes to predicted teleomorphic ascomycetes is 1:22. Therefore, where are the undiscovered teleomorphic ascomycetes? The undescribed species are no doubt to be found in biodiversity hot spots, poorly-studied areas and species complexes. Other poorly studied niches include extremophiles, lichenicolous fungi, human pathogens, marine fungi, and fungicolous fungi. Undescribed species are present in unexamined collections in specimen repositories or incompletely described earlier species. Nomenclatural issues, such as the use of separate names for teleomorph and anamorphs, synonyms, conspecific names, illegitimate and invalid names also affect the number of described species. Interspecies introgression results in new species. while species numbers are reduced by extinctions.

Keywords Ascomycota · Estimates · Habitat diversity · Molecular techniques · Species concepts

Introduction

Ascomycota Caval-Sm. is the largest fungal phylum comprising around 93,000 extant species and are generally known as "sac fungi" (Bennett and Turgeon 2017; Clark et al. 2018; Catalog of Life 2021). Members of Ascomycota are ubiquitously spread in various terrestrial and fresh or marine ecosystems (Naranjo-Ortiz and Gabaldón 2019). Most ascomycetes are saprobes while some are soil or dung inhabitants (Richardson 2019). Some are animal, human and

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plant pathogens or parasites such as epiphytes or fungicolous fungi (Wu et al. 2011), while others are symbionts as endophytes, lichenicolous and mycorrhizae (Lawrey and Diederich 2003; Chomnunti et al. 2014; Kim et al. 2017; Sun et al. 2019; Hyde et al. 2020b). The sexual reproduction in ascomycetes often occurs as a response to adverse environmental conditions (Nieuwenhuis and James 2016) and it results high genetic diversity between species (Lee et al. 2010). Sexual reproduction helps to purge deleterious mutations and also selects beneficial mutations to adapt to a fluctuating environment (Otto and Lenormand 2002). Ascospores are more resistant to environmental stress and more widely dispersed than the conidia (Kirschner 2019).

Sexual reproduction in ascomycetes comprising the matingtype loci (MAT) which encodes key transcription factor genes that govern speciation (Paoletti et al. 2005). Two compatible partners fuse their genetic materials by recombination or crossing-over and also meiosis and mitosis to produce genetically diversified offspring (O'Gorman et al. 2009). Sexual reproduction occurs in the same mycelium (homothallic/self-fertile) or two different mycelia (heterothallic) and they produce spores in a sac-like structure called an ascus (Fig. 1). The sexual structures such as asci and ascospores are contained in fruiting bodies. Released ascospores from fruiting bodies germinate when contact with a suitable substrate and produce the mating



Fig. 1 Sexual reproduction of filamentous ascomycetes. **a** Reproduction cycle. **b** Ascus formation within fertilized ascogonium (drawn from Peraza-Reyes and Berteaux-Lecellier 2013)

type male (+) and female (-) mycelia (Taylor et al. 2006). The male mycelium produces an antheridium and the female produces an ascogonium, which are different reproductive organs.

Sexual reproduction in Ascomycota includes three stages as plasmogamy, karyogamy and meiosis (Wallen and Michae 2018). During the first step (plasmogamy), two haploid cells are fused and lead to a dikaryotic stage where two haploid nuclei coexist in a single cell. During the second step (karyogamy), the haploid nuclei of + and - mycelia fuse to form a diploid zygote nucleus. The diploid zygote nucleus produces unique haploid nuclei by meiosis and these haploid nuclei form haploid spores with mitosis and cell division within the sac-like structures called ascus. These ascospores are then released and germinate to form new hyphae in new environments. The production of these highly specialized sexual tissues is initiated and controlled by gene, protein, and secondary metabolite networks and those proteins regulate the expression of primary MAT genes (MAT1-1-1 and MAT1-2-1) (Dyer 2007). Both MAT genes are typically essential for successful fertilization and ascomatal development (Ferreira et al. 1998). Additionally, the MAT1-1-1 gene is also critical for ascospore production in some species (Debuchy et al. 2010) and alteration of both MAT genes results in failure to form even immature sexual structures (Lee et al. 2003).

Some anamorphic ascomycetes shuffle their genetic material by parasexuality. Parasexual reproduction results in recombination of genes from different individuals but does not involve meiosis and formation of a zygote by fertilization as in sexual reproduction. Parasexuality generates both genotypic and phenotypic diversity in species (Hirakawa et al. 2017). The variations in genotypes create by shuffling of different chromosome homologs, recombination between homologs and the generation of cells in various ploidy states with one or more supernumerary chromosomes (Forche et al. 2008). The mutations in genetic materials and haploidization occur inside the heterokaryotic hyphae prior to conidial formation (Becker and de Castro-Prado 2006). However, the mixing-up genetic materials without forming sexual structures does not discuss here and this study only estimates species formed by true sexual reproduction.

Teleomorphic ascomycetes are morphologically diversified (Fig. 2) and ubiquitous taxa that can survive in various ecological habitats in both terrestrial and aquatic ecosystems (Gould 2008; Schoch et al. 2009). Teleomorphic species are reported from only 17 classes in Ascomycota including all classes in subphylum Pezizomycotina and Neolectomycetes in subphylum Taphrinomycotina.

Why should we estimate the global species richness of teleomorphic ascomycetes?

In mycology, "species" is simply defined as a diagnosable cluster of individuals within a parental pattern of lineage displays a pattern of phylogenetic ancestry and descent among units and hence, it is valuable to give it a species name (Brown 2002; Aldhebiani 2018; Maharachchikumbura et al. 2021). Finalizing the global fungal inventory is a challenge due to their morphological, ecological and physiological diversity (Purvis and Hector 2000). Estimates of the total number of teleomorphic ascomycetes have major inferences for systematics, resource management and classification (Hawksworth 1991) as they play key roles in ecosystems as decomposers, mutualists and pathogens individually and with the interactions of each other (Schmit and Mueller 2007) and some of them in the plant rhizosphere protect root systems from pathogens (Mendes et al. 2013). Mutualistic ascomycetes are associated with their host without causing harm. It is a beneficial relationship for both fungi and the host (Volk 2013). Ascomycetes associate with algae or cyanobacteria to form lichens (Weber and Büdel 2011) and Arthoniomycetes, Dothideomycetes, Eurotiomycetes, Lecanoromycetes, Lichinomycetes and Sordariomycetes comprise the lichenized species (Grube and Winka 2002; Andersen and Ekman 2005). More than 40% of lichenized fungi are species in Ascomycota (Brodo et al. 2001; Schoch et al. 2009). Mycorrhizae are symbiotically associated with plant roots while endophytes are associated with living plants (Volk 2013).

There are numerous of plant pathogenic teleomorphic ascomycetes causing various diseases of economic crops and forest trees (Lu et al. 2003). The increasing number of virulent fungal infectious diseases is regarded as a worldwide threat to food security (Hyde et al. 2018). An unprecedented number of diseases caused by fungi including teleomorphic ascomycetes have resulted in some of the most severe diebacks in economic crops and wild species (Fisher et al. 2012; Hyde et al. 2019). Many species can be harmless endophytes in some plants, however cause severe damages in others (Hardoim et al. 2015; Terhonen et al. 2019; Song et al. 2021). Therefore, description and cataloging of teleomorphic ascomycetes helps to identify fungal pathogens and prevent future disasters.

The nutritional sources of the teleomorphic ascomycetes vary from dead organic matter to synthesized compounds by other organisms and they decompose litter, maintain the nutrient cycles and improve soil quality (Gams 2007; Gould 2008; Frac et al. 2018; Senanayake et al. 2020a). However, the mycota involved in decomposition incompletely known and there may be many species interactions (Frey-Klett et al. 2011; Volk 2013). Hyaloscyphaceae, Melanommataceae, Mytilinidiaceae and Savoryellaceae are some ascomycetous families which have many saprobic teleomorphic species (Hernández-Restrepo et al. 2017). Identifying and describing the teleomorphic ascomycetes involved in litter degradation is important in organic farming and fertilizer production (Peyvast et al.



Fig. 2 Diversity of fruitting bodies in teleomorphic Ascomycota. a, j, k, p, t, w, x, z Leotiomycetes, d Neolectomycetes, b, h, m, y Dothideomycetes, n, r Eurotiomycetes, e Geoglossomycetes, o Orbiliomycetes, q, v Pezizomycetes, c, f, g, i, l, s, u Sordariomycetes

2008). Isolation of those fungi and application to soil as a microbial assortment to enhance plant growth and yield is required (Khalid et al. 2017). Additionally, antibiotics, anticancer, anti-inflammatory and some medically important chemicals are extracted from teleomorphic ascomycete cultures (Rajamanikyam et al. 2018; Al-Fakih and Almaqtri 2019; Wu et al. 2019b). Many organic acids and enzymes such as citric acid, gluconic acid, amylases and proteases are produced by teleomorphic ascomycetes. Morels, truffles, *Hypomyces lactifluorum* are edible ascomycetes (Acton and Sandler 2008; Splivallo et al. 2010). Therefore, revealing the undescribed teleomorphic ascomycetes, estimating the species number and exploring their chemical and biological properties are important (Yang et al. 2018).

How many teleomorphic species in Ascomycota based on different estimation methods?

Estimated number of teleomorphic ascomycetes based on numbers of described fungi

Traditionally, taxonomic studies of teleomorphic ascomycetes were based mostly on morphological characters, subcellular arrangement, bio-chemical, physiological and ecological studies (Yang 2011; Maharachchikumbura et al. 2021). During 1960–2000, phenotypic taxonomic studies were improved by microscopy and in vitro culturing (Klopfstein 2016). Many groups of teleomorphic ascomycetes have been intensively studied (Todd et al. 2014) and simultaneously significant taxonomic monographs were published (Barr 1978, 1987; Kohlmeyer and Kohlmeyer 1979; Schmit and Lodge 2005; Senanayake et al. 2017, 2018). In the previous 20 years, molecular methods have modernized and studies are based on biogeography, phylogeny, population genetics, systematics and taxonomy (Yang 2011).

Since 1982, there has been a periodic update in the classification of taxa in Ascomycota especially in the *Journal Systema Ascomycetum*. The Species Fungorum database (http://www.speciesfungorum.org) has recorded the number of new species described each year. The taxonomy of the phylum Ascomycota has been updated at a fast pace over the last few years (Hyde et al. 2013, 2020a, b, c; Jaklitsch et al. 2016; Maharachchikumbura et al. 2016; Liu et al. 2017; Ekanayaka et al. 2018). Accepted families with descriptions and list of genera in the Ascomycota were provided by Jaklitsch et al. (2016). Currently there are 22 classes in the phylum Ascomycota as Archaeorhizomycetes, Arthoniomycetes, Candelariomycetes, Geoglossomycetes, Laboulbeniomycetes, Lecanoromycetes, Leotiomycetes, Lichinomycetes, Neolectomycetes, Orbiliomycetes, Pezizomycetes, Pneumocystidomycetes, Saccharomycetes, Sareomycetes, Schizosaccharomycetes, Sordariomycetes, Taphrinomycetes, Xylobotryomycetes and Xylonomycetes (Lumbsch and Huhndorf 2010; Voglmayr et al. 2019; Beimforde et al. 2020).

The "2.2-3.8 million" species estimate (Hawksworth and Lücking 2017) is considered as the most rational estimate by many mycologysts (Hyde et al. 2020b). There are approximately 150,000 extant fungal species (Roskov et al. 2019; Species Fungorum 2021), however this is only 15-26% of the estimated species (Hyde et al. 2020b). Early mycologists believed that only half of ascomycetes are meiosporic fungi which obligatory sexually reproduced and do not produce asexual spores (Reynolds and Taylor 1993). However, the rest are probably obligatory mitosporic or facultative mitosporic fungi with undetected teleomorphs (Nieuwenhuis and James 2016). Reynolds and Taylor (1993) showed that about 5% of obligatory anamorphic ascomycetes are known to be pleomorphic and thus discretionary sexually reproduce. However, the most accepted value is that may be the 90% of the described ascomycetes sexually reproduce (Judson and Normark 1996; Normark et al. 2003).

There are 92,725 described species in Ascomycota (Catalog of Life 2021; Species Fungorum 2021). Wijayawardene et al. (2017) listed 8897 species in Ascomycota with undetermined teleomorphs. There are 523 anamorphic ascomycetes with undetermined teleomorph have been introduced from 2018 to 2020 (31 December 2020) (Species Fungorum 2021). Hence, 9420 ascomycetous species are obligatory anamorphic species and therefore around 83,305 teleomorphic ascomycetes have been described. The reproduction arrangements appear to be similar across the phylum Ascomycota even though the life cycles among the major groups are different (Nieuwenhuis and James 2016). Hence, there should be 1.25–2.17 million teleomorphic ascomycetes based on described number of species considering the 2.2–3.8 million species estimate.

Estimated number of teleomorphic ascomycetes based on fungus:substrate or host ratio

The ratio of fungal species to each plant species was one of the key elements in estimating global species richness as 1.5 million (Hawksworth 1991) and this estimate was assumed from independent data sets which shown that the number of fungi in all environments was six times higher than the vascular plants present, inferred on a global scale. The "1.5 million estimate" was considered too low because, the number of plant species and the fungus: plant ratios were too conservative and many were collected from other substrata such as insects (Hawksworth 2001). The number of plant species has increased from 250,000 to 390,000 (Pimm and Joppa 2015) signifying that the estimated number of fungal species must rise to 2.4–3 million. Some authors also suggested that the ratio of fungi: plants is about 10:1, those found in soil, insects or lichen were excluded (O'Brien et al. 2005; Blackwell 2011). However, there are several complications in the fungus: plant ratio concept. The total inventory of species described in a particular area increases gradually, while the number of plant species remains more or less unchanged (Hawksworth and Lücking 2017). Therefore, the fungus: plant ratio decreases gradually with the description of new species.

Some studies based on meta-DNA sequencing of decaying litter samples showed that the fungus: plant ratio is 13:1 (Hawksworth and Lücking 2017). Therefore, the actual ratio in a particular area may be significantly higher than the ratio indicated by traditional inventory techniques. Further, the whole planet has not been screened evenly and known species number in some places is higher than in others. For example, fungal diversity in North America, Europe and Japan is well-studied compared to South Asia and Africa (Hawksworth 2001; Větrovský et al. 2019). O'Brien et al. (2005) noted that the fungus: plant ratios of two forests in North Carolina gave 19:1 and 13:1 suggesting that there may be 3.5 to 5.1 million species. Further, this ratio changes according to the substrata and Taylor et al. (2010) showed that fungus: plant ratio is 7.5:1 in forest soils in Alaska. Tedersoo et al. (2014) analyzed soil samples using meta-barcoding molecular methods and concluded that the number of species had been overestimated by 1.5 to 2.5 times from data based on plant: fungus species ratios.

Therefore, the estimates based on studies of fungus: plant/ insect/lichen/plant OTUs in soil ratios in a site, obtained by field survey and molecular approaches, have generated lower ranges from 0.42 to 3.5 million to (O'Brien et al. 2005; Tedersoo et al. 2014) an upper range from 0.6 to 5.1 million (O'Brien et al. 2005; Piepenbring et al. 2012) (Table 1). Considering the average of the upper and lower range of previous estimates, we estimated species number is 1.96–2.85 million based on fungus: host ratio. There are around 150,000 described species and 92,725 are ascomycetes, which is around 63.4%. Therefore, there should be about 1.11–1.62 million estimated teleomorphic ascomycetes (Table 1), excluding 10% obligatory anamorphic species (Normark et al. 2003).

The patterns of introducing new species are biased with more described from economically important plants (Cannon and Hawksworth 1995). Most early described species were collected from temperate floral communities and host specificity in tropical plants are not well-reported and new host records are not published (Tedersoo et al. 2010; Piepenbring et al. 2011). Therefore, fungus: plant/insect/substrate ratio is not an ideal method to estimate species numbers because of uneven exploration of global species in habitats.

Estimated number of teleomorphic ascomycetes based on ecological distribution

The traditional quantification approaches of teleomorphic ascomycetes are established on the opportunistic collections of specimens based on host, substrate, area and transects (Schmit and Lodge 2005). Opportunistic collecting requires highly trained collectors who can recognize taxa in the field without a bias. Some collectors only perceive favored particular groups of teleomorphic ascomycetes. Further, conspicuous species and more common species are often overlooked (Lodge et al. 2004). Teleomorphic ascomycetes produce fruit bodies in different types of substrata (Lodge 1996; Huhndorf and Lodge 1997; Schmit and Lodge 2005; Sainz et al. 2018). Some ascomycetes sexually reproduce rather dependably while others do so only occasionally, and therefore require long periods to be recorded from a particular area (Straatsma et al. 2001). Further, fruiting patterns, abundance and dispersion of ascomycetes differs among substrata (Lodge et al. 2004).

Some teleomorphic ascomycetes show a wide range of host and substrate variation and also different modes of life. *Daldinia eschscholtzii*, one of the common endophytes in

Ratio	Estimated species in millions	Host/substrate	References
N/A	~1.5	Fungi:insect	Hywel-Jones (1993)
8:1	~1.5	Fungi:plants	Hawksworth (2001)
13–19:1	3.5-5.1	Fungi:plants	O'Brien et al. (2005)
7.5:1	1.9–2.8	Fungi:plant OTUs in soil	Taylor et al. (2010)
6:1	0.8-5.1	Fungi:plants	Blackwell (2011)
1.8:1	0.45-0.6	Fungi:plants	Piepenbring et al. (2012)
17:1	1.5-6	Fungi:plant OTUs in soil	Taylor et al. 2014)
1.8:1	0.42-2.72	Fungi:plant OTUs in soil	Tedersoo et al. (2014)
50-53:1	0.9-0.95	Fungi:lichens	Zhang et al. (2015), Wang et al. (2016)
9.8:1	2.2-3.8	Fungi:plants	Hawksworth and Lücking (2017)

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on fung	us: host ratio	

plants (Stadler et al. 2014; Helaly et al. 2018) and marine algae (Tarman et al. 2012), has been reported as an endosymbiont of a mantis gut (Zhang et al. 2011), and a human pathogen (Chan et al. 2015). Further, Diaporthe sojae, a known pathogen of soybean, was also isolated from infected skin of an immunocompromised patient after kidney transplantation (Garcia-Reyne et al. 2011). Diaporthe toxica is a plant endophyte and occasionally a plant pathogen (Williamson et al. 1991) and produces secondary metabolites that result in toxicoses of animals such as liver disease known as lupinosis of sheep (Gardiner 1975; Allen and Wood 1979; Williamson et al. 1994). Therefore, it is necessary to understand the ecology and life strategies of teleomorphic ascomycetes before estimating the species number. Further, many endophytes do not sporulate in culture (Sun and Guo 2012) and some ascomycetes change colony morphology while growing and sub-culturing on different media (Senanayake et al. 2017). Some ascomycetes do not sexually reproduce or need specific conditions for sexual reproduction (Sun and Heitman 2011). Direct morphological examination of fruiting structures on substrata or media only is therefore biased in estimating number of teleomorphic ascomycetes (Guo et al. 2001; Promputtha et al. 2004).

Case studies from marine ascomycetes

Marine ascomycetes are recovered repeatedly from marine habitats, able to grow and/or sporulate on substrata in marine environments, form symbiotic relationships with other marine organisms, adapt and evolve at the genetic level or be metabolically active in marine environments (Pang et al. 2016). They are observed in a range of marine substrates, including mangrove plant wood and leaves, driftwood, saltmarsh plants, algae, dead coral, and sand grains on beaches (Gonçalves et al. 2021; Walker and Robicheau 2021), along with severe marine ecosystems such as deepsea trenches, hydrothermal vents, deep-sea subsurfaces, cold methane seeps and hypersaline, anoxic, and suboxic waters (Raghukumar and Ravindram 2012; Xu et al. 2018). Marine ascomycetes colonize a variety of substrata based on their ability to degrade complex substrata such as lignocellulose, keratin, chitin and calcareous structures and ascomycetes are the major decomposers in marine ecosystems (Kohlmeyer and Volkmann-Kohlmeyer 2001; Walker and Campbell 2010). Marine ascomycetes are also known as symbionts and pathogens of marine algae and marine fauna (Hyde et al. 1998).

The accessibility and the nature of substrate for colonization, competition, pH, temperature, and saltiness of water affect the diversity of marine ascomycetes (Jones 2000, 2011). Most marine fungi are recognized to have a cosmopolitan distribution (Pugh and Jones 1986). However, basic biogeographic diversity data are lacking for marine ascomycetes in most parts of the world (Walker and Robicheau 2021). Some marine fungi such as *Aniptodera chesapeakensis* Shearer & M.A. Mill., *Ceriosporopsis Halima* Linder, *Corollospora maritima* Werderm., *Lignincola laevis* Höhnk, *Savoryella lignicola* E.B.G. Jones & R.A. Eaton, and *Torpedospora radiata* Meyers have diverse geographic dispersion which is classified as tropical to subtropical while *Lulwoana uniseptata* (Nakagiri) Kohlm. et al. is reported from temperate habitats only (Torta et al. 2015; Tibell et al. 2020).

Mora et al. (2011) presented an approach to estimate species numbers on earth and ocean and predicted that 0.005 million species are marine. However, 91% of species in the ocean await description and increasing the sampling intensity is required to characterize the underexplored species of marine biodiversity (Walker and Robicheau 2021). It is estimated that more than 10,000 marine fungal species exist globally (Jones 2011; Walker et al. 2017) and only around 1000 have been described (Jones et al. 2015; Pang et al. 2016). Jones et al. (2019) listed 1257 marine species belonging to 539 genera and 943 of them are ascomycetes (Jones et al. 2009, 2015; Abdel-Wahab et al. 2010; Pang et al. 2010; Abdel-Wahab and Nagahama 2011; Dayarathne et al. 2016, 2019).

The number of species is estimated as 2.2–3.8 million (Hawksworth and Lücking 2017) while only around 150,000 species have been described (Species Fungorum 2021). If there are 943 described marine ascomycetous species, then it is predicted that 13,831–23,889 marine ascomycetes should be in oceans. However, considering only 90% of described ascomycetes are sexually reproduced (Judson and Normark 1996; Normark et al. 2003), then there are 12,448–21,500 marine, teleomorphic ascomycetes.

Case studies from freshwater ascomycetes

Freshwater ascomycetes are an ecological assortment rather than a taxonomic group and they reproduce sexually or asexually residing on sunken or partially submerged woody substrata in freshwater environments (Tsui et al. 2016; Calabon et al. 2021). In spite of their importance as decomposers and food sources in freshwater food webs, there has been little research on their global distribution, community structure and species diversity (Shearer et al. 2015). Freshwater ascomycetes occur on submerged or partially submerged substrata in lotic and lentic aquatic habitats. The teleomorphic ascomycetes are more dominant on submerged wood, while the anamorphic ascomycetes occur on submerged leaf litter (El-Elimat et al. 2021).

Phylogenetically, freshwater ascomycetes are grouped mostly throughout the class Dothideomycetes, Leotiomycetes and Sordariomycetes in Ascomycota (Shearer et al. 2009, 2014). They have soft fruiting bodies during teleomorphic stage with appendage baring ascospores (Hyde et al. 1998). Asci developed in ascomata possess pathways for efficient spore discharge and ascospores are frequently appendaged or have sheaths. The appendages facilitate spore dissemination and bonding to the substrata (Hyde and Goh 2003).

Freshwater ascomycetes are observed across the both lentic and lotic ecosystems, and they are commonly associated as endophytes and parasites on algae and aquatic macrophytes along with the saprobes on the dead plant matter (Lu et al. 2018). Many freshwater ascomycetes are believed to have evolved from terrestrial ancestors through a wide range of evolutionary pathways (Vijaykrishna et al. 2006; Grossart et al. 2019).

The number of aquatic species has been estimated as 0.5–10 million based on molecular data (Bass and Richards 2011; Blackwell 2011; Mora et al. 2011). A significant number of freshwater species are teleomorphic ascomycetes (Shearer et al. 2007; Hu et al. 2013; Shearer and Raja 2021). About 738 species of freshwater ascomycetes are known from their teleomorph, belonging to approximately 170 genera (El-Elimat et al. 2021; Shearer and Raja 2021). There are around 83,305 described teleomorphic ascomycetes (Species Fungorum 2021) and if there are 738 described freshwater teleomorphic ascomycetes, it is estimated that there are 19,490–33,664 aquatic teleomorphic ascomycetes based on "2.2–3.8 figure".

Case studies from insect-associated ascomycetes

Insects are an extremely diversified group of organisms in all ecosystems (Stork 1988) and include dragonflies, mayflies, grasshoppers, cockroaches, termites, stoneflies, true bugs, flies, beetles, butterflies, moths, ants, bees, and wasps (Stork et al. 2015, 2018). Insects and fungi share a long history of relationship in the similar habitats and (Bourtzis and Miller 2003) those interactions can be mutualistic or harmful. Insects involved in associations with fungi include members of the Coleoptera, Diptera, Homoptera, Hymenoptera, and Isoptera.

Fungal biotrophic parasites of insects are rare, except for the very successful associations of Laboulbeniomycetes (Blackwell et al. 2020; Haelewaters et al. 2021). Vega and Dowd (2005) highlighted the role of yeast-insect endosymbionts in supporting the digestion and detoxification of plant materials ingested by insects and discovered an enormous number of species of Saccharomycetes. Some fungi also interact with insects by providing nutritional supplements (Vega and Blackwell 2005). Suh et al. (2001) described around 200 new yeast species from the gut of beetles. It is suspected that these yeasts also might provide nutritional supplements.

Insect associated fungi were estimated to be 1.5 million (Hywel-Jones 1993) and Stork (2018) updated this to 5.5 million, while 1-2% of them may be cryptic species. Therefore, including the cryptic species, the consensus estimate of insect associated species ranges from 5.505 to 5.511 million. However, this is more deviated from currently estimated species numbers. The diversity of insect associated ascomycetes has been extensively studied (Aung et al. 2008; Mora et al. 2011; Hyde et al. 2018) and they are taxonomically distributed in Clavicipitaceae, Cordycipitaceae, and Ophiocordycipitaceae in Hypocreales, ambrosia fungi (e.g., Ceratocystis, Ophiostoma) in the Ophiostomatales, all families in Laboulbeniomycetes and some species in Saccharomycetes (Sung et al. 2007; Vega et al. 2012; Araújo and Hughes 2016; Maharachchikumbura et al. 2016; Wijayawardene et al. 2018). Mueller and Schmit (2007) estimated around 50,000 insect associated species, when there are 750 described species. However, currently, there are more than 4000 insect-associated species described (Species Fungorum 2021). Hence, there should be 52,800-91,200 insect associated teleomorphic ascomycetes according to "2.2-3.8 species estimate" and considering generally 90% of ascomycetes reproduce sexually (Judson and Normark 1996; Normark et al. 2003).

Case studies from coprophilous ascomycetes

Coprophilous fungi grow, sporulate and germinate on herbivore dung (Tretter et al. 2014; Lazarus et al. 2017) and they are specialized to survive in the harsh environment of the gastrointestinal tract of animals (Richardson 2001b; Bell 2005; Kirschner et al. 2015; De Souza et al. 2017; Lavrinienko et al. 2021). Coprophilous fungi recycle the nutrients in animal dung and release nutrients to the soil (Basumatary and McDonald 2017; Florenzano 2019).

Species richness and composition of coprophilous ascomycetes differ with abiotic and biotic factors. Intra- and inter-specific interactions in a dung pile affect fungal succession and species composition (Maynard et al. 2018; Lavrinienko et al. 2021). Many coprophilous ascomycetes are most common on only one or a few dung types (Lundqvist 1972) and dung from animals that live together generally show a similar species composition (Richardson 2001a).

However, the fungal community varied more between animal dung types than between the various grassland habitats (Angel and Wicklow 1983). Coprophilous ascomycetes can be found more frequently on dung of herbivores than carnivores (Lundqvist 1972; Richardson 2001a). In addition, they have seldom been reported on reptile or amphibian dung, indicating that coprophily in fungi developed among the warm-blooded animals (Webster 1970). Some ascomycetes are strictly coprophilous and they have a distinct lifecycle restricted to dung pile, plant surface and animal gut (Wicklow 1992). However, some spores disperse in soil. The spores of coprophilous ascomycetes are highly pigmented, with thick walls and are protected against the harmful ultraviolet sunlight (Ingold and Hudson 1993). Therefore, spores remain in soil alive and those species have been reported as soil fungi.

Kruys (2005) reported that many coprophilous ascomycetes belong to order Pleosporales in Dothideomycetes and three of the families are solely or mostly coprophilous, viz. Delitschiaceae, Phaeotrichaceae and Sporormiaceae. Calaça et al. (2015) listed 143 coprophilous ascomycetous species recorded from Brazil. Melo et al. (2020) studied the diversity and species richness of coprophilous fungi in Brazil. A total of 271 species are reported from dung substrata and among them, 70% of recorded species are ascomycetes. Most species are included in Sordariales, Hypocreales and Microascales and 9% of recorded species are anamorphic ascomycetes (Saumell et al. 1999, 2000; Saumell and Padilha 2000).

Calaça et al. (2020) listed the coprophilous species recorded in Brazil during 1900–2013 and 117 from 210 coprophilous species are ascomycetes. They were collected from 12 states of Brazil and total area of these 12 states is 303146 km². Therefore, one coprophilous ascomycetous species was collected from each 2591 km². If this value inferred for land area of earth, there should be 196,874 coprophilous ascomycetes. If 9% of recorded species are anamorphic species (Saumell et al. 1999, 2000; Saumell and Padilha 2000), then there should be 177,187 teleomorphic coprophilous ascomycetes. However, this value is 443,061 according to Melo et al. (2020). Therefore, it is assumed that there should be around 177,000–443,000 teleomorphic coprophilous ascomycetes.

Case studies from soil ascomycetes

Fungi occur in the soil or soil-associated environments at least for some stage in their life-cycle known as soil fungi (Bridge and Spooner 2001). They are active, freely growing fungi closely associated with other organisms or inactive dormant propagules (Rämä and Quandt 2021). The role of soil fungi are an extremely complex and are fundamental to the soil ecosystem (Hawksworth et al. 1995). Soil fungi carry out many different functions in soils such as the degradation of dead organic matter, binding soil particles to improve the aeration, water penetration, destroy soil pathogens, and improve soil health by formation of propagules (Zin and Badaluddin 2020; Jayaraman et al. 2021). Soil fungi can only be consistently identified if they produce fruiting bodies (Hibbett et al. 2016) and conventional techniques are unable to reliably identify the species that are assumed to be present in any given soil sample due to the fastidious nature of the great majority of species (Wardle and Lindahl 2014). Fungal communities in soil can be extremely species rich and patchy at small spatial scales (Taylor and Sinsabaugh 2015). High throughput sequencing of soil fungi in boreal forest sites revealed around 300 taxa in 0.25 g soil and the dominant taxa in the sites were quite distinct from each other (Taylor and Sinsabaugh 2015).

Around 80% of all soil-inhabiting taxa cannot be identified to species and 20% cannot be reliably assigned to known orders (Hawksworth 2001; Vartoukian et al. 2010; Tedersoo et al. 2014, 2017). The number of soil fungal species is considerably greater than the described amount and studies with the integration of molecular, genetic and ecological factors may reveal more species. The number of species identified by traditional culture dependent methods doubles when the same soil samples are analysed by culture-independent methods (Lord et al. 2002; Arenz et al. 2006; Malosso et al. 2006; Smith and Jaffee 2009; Zachow et al. 2009; Hirsch et al. 2013; Rodolfi et al. 2016).

There are no significant estimates of the number of species made for soil fungi. Gilman (1957) included around 700 fungal species which grew on only non-selective media by soil dilution method and many species were later included (Barron 1968; Domsch et al. 1993). Watanabe (1994) suggested that at least 1200 species have been isolated from soil. Pugh (1969) showed that only 17% of soil fungi can be readily grown in culture media. Therefore, Hawksworth (1991) estimated that around 7000 species could be considered as soil fungi based on Watanabe (1994). However, there are more than 80,000 fungal species so far named and described, and they are likely to occur in the soil environment at some stage in their life-cycle (Bridge and Spooner 2001). These species are mainly distributed in the subphylum Taphrinomycotina as the fission yeasts, animal and plant pathogens, the root-associated, sporocarp-forming, filamentous fungi (Schoch et al. 2009), while the Saccharomycotina includes the budding yeasts. Pezizomycotina contains lichen-forming fungi, mycorrhizal fungi, dark-septate endophytes, pathogens and saprotrophs. Further, Bridge and Spooner (2001) proposed that at least 10% of the described fungal species are obligatory soil fungi and around 75% of them are ascomycetes (Taylor and Sinsabaugh 2015). If this applies to 2.2-3.8 estimate considering 90% of them are teleomorphs (Normark et al. 2003), there should be 148,500-256,500 teleomorphic ascomycetes in soil.

Case studies from lichenized ascomycetes

Lichens are stable self-supporting associations of a mycobiont and a photobiont (Maria et al. 2021). They produce many secondary metabolites such as phenolic compounds, dibenzofurans, depsides, depsidones, depsones, lactones, quinones and pulvinic acid derivatives which are accumulated externally on the hyphae rather within the cells (Tehler and Irestedt 2007). These compounds are unique to each species and can be used as food, fodder, dyes, and pharmaceuticals. The lichens are the best bio-indicators of air pollution (Garty 2001). The mycobiont is usually an ascomycete but in a few cases it is a basidiomycete. The photosynthetic partners are generally green algae or cyanobacteria (Richardson 2002). The relationship between fungi and lichens can be endolichenic and lichenicolous (Tripathi and Joshi 2019).

Most of the endolichenic fungi and other accessory fungi reported from inside the lichen thalli are phylogenetically distinct from lichenicolous fungi (Miadlikowska et al. 2004) and more closely related to endophytic ascomycetes in vascular plants (Miadlikowska and Lutzoni 2004). Generally, most of the lichenized fungi belong to Ascomycota or rarely to Basidiomycota. Further, the ascolichens mainly belong to Sordariomycetes, Lecanoromycetes and Eurotiomycetes. The Lecanoromycetes is almost an entirely lichenized class comprising the remarkable population of lichen-forming species (Nash 2008).

A study of the diversity and distribution of the fungal communities that were associated with seven lichens in the Ny-Ålesund Region (Svalbard, High Arctic) using Roche 454 pyrosequencing method reported 370 OTUs of which 294 belonged to Ascomycota (Zhang et al. 2015). Among these, Leotiomycetes, Dothideomycetes, and Eurotiomycetes were the major classes, with Helotiales, Capnodiales, and Chaetothyriales as the dominant orders. Further, Wang et al. (2016) studied fungal diversity associated with a common lichen *Hypogymnia hypotrypa* in China and 28 were ascomycetes from 50 species. It is assumed roughly that lichen: fungi ratio as 1:45 (Fernández-Mendoza et al. 2011; Muggia and Grube 2018).

There are around 20,000 described lichen species (Çobanoğlu et al. 2010) and about 98% have an ascomycetous mycobiont (François et al. 2001). Therefore, there should be 19,600 endolichenic ascomycetous species. Further, about 40% of species in the Ascomycota are lichenized or lichenicolous fungi (Kirk et al. 2008). Currently, there are around 93,000 described species in Ascomycota and 40% is 37,200. However, excluding 10% obligatory anamorphic species, there are around 17,640–33,480 teleomorphic lichenized or lichenicolous species in Ascomycota.

Case study from ligninolytic ascomycetes

Fungi play a vital role in plant litter decomposition in ecosystems (Boddy et al. 2008; Watkinson et al. 2015; Baldrian 2017). They can degrade different types of organic compounds in the litter (Baldrian and Lindahl 2011), which other organisms are unable to degrade (de Boer et al. 2005). Ligninolytic fungi produce several kinds of extracellular enzymes that help to degrade cellulose and other organic compounds in litter and helps nutrient turnover (Sinsabaugh et al. 2002; Romaní et al. 2006). Most common extracellular enzymes produced by ligninolytic fungi are α -glucosidase, β -glucosidase, cellobiosidase, xylosidase, polyphenol oxidase, N-acetyl-polyphenol oxidase, N-acetyl- β -glucosaminidase and acid phosphatase (Marx et al. 2001; De-Forest 2009).

The majority of ligninolytic fungi are ascomycetes (Seena et al. 2019), that colonize during the early stages of decomposition (Aneja et al. 2006; Voříšková and Baldrian 2013; Prakash et al. 2015). It was proposed that ascomycetes dominate during the initial stages of litter decay presumably due to a superior ability to degrade cellulose (Weber et al. 2011) and decreases during the process of degradation as they are gradually replaced by other non-ascomycetous saprobes (Frankland 1998; Osono 2007). The classes Dothideomycetes, Eurotiomycetes, Saccharomycetes and Taphrinomycetes are the most ligninolytic species abundant classes in Ascomycota (Zhang et al. 2018). A few studies have denoted that endophytes living in plants shift their lifestyle to saprotrophs when the substrates die and they play a key role in early stage decomposition (Purahong and Hyde 2011; Fesel and Zuccaro 2015; Purahong et al. 2016; Szink et al. 2016). However, NGS data may partly reflect the fungal succession from ascomycetes to other fungi in early to later stages of litter decomposition and it does not clearly provide an idea about the species richness and abundance (Amend et al. 2010; Peršoh 2015).

Many studies have been revealed the species composition in decaying litter. However, the number of ligninolytic fungal species has not been estimated. Haňáčková et al. (2015) analyzed fungal species involved in decomposition of pine needle litter through culture dependent and culture independent methods. This study proved that the ratio of species recognition of culture dependent method to culture independent method is 1:2. Purahong et al. (2016) sampled leaf litter 473 times to study decomposing fungi and showed that the percentage of detection frequency of ascomycetes was 66–82%. Zhang et al. (2018) studied the ligninolytic fungal diversity in China and revealed 2621 fungal OTUs which mainly belong to Ascomycota, Basidiomycota and Zygomycota. Further, 75% are ascomycetes. Meanwhile, Seena et al. (2019) studied the ligninolytic fungal diversity in 19 globally distributed streams and the total number of fungal OTUs revealed in this study was 1311 with 79.7% being ascomycetes. Voříšková and Baldrian (2013) did a similar study and revealed that 71% of species are ascomycetes. Osono (2019) obtained 127 fungal species from 1133 leaf litter isolates and 95 are ascomycetes.

Based on the above studies, it is assumed that around 70–80% of ligninolytic fungi are ascomycetes and therefore, around 1045–1966 ligninolytic ascomycetes have been recorded in culture dependent and culture independent studies (Zhang et al. 2018; Seena et al. 2019). Further, Dashtban et al. (2010) reported that more than 14,000 fungal species produce ligninolytic enzymes and all litter degrading fungi must produce ligninolytic enzymes (Kumar and Chandra 2020). Assuming that 70–80% of above ligninolytic enzyme producing fungi are ligninolytic ascomycetes, there are around 10,500 described ligninolytic ascomycetes. If this applies to 2.2–3.8 estimate, considering 90% of them are teleomorphs (Normark et al. 2003), it is assumed that there are around 138,600–239,400 teleomorphic species of ligninolytic ascomycetes.

Case studies from endophytic ascomycetes

Endophytes are mutualists that colonize asymptomatically inside of any tissues of living plants at least in any phase in their life cycle (Singh and Dubey 2015). Bills (1996) proposed that some type of mycorrhizae such as ericoid mycorrhizae and pseudomycorrhizae can be endophytes. Endophytic colonization generally does not cause any damage to its host and does not produce any structures emerging from the external plant (Azevedo and Araújo 2007). Some endophytes can grow *invitro* in culture media.

Endophytes are ubiquitous and occur within a broad range of host plants, such as mosses, ferns, grasses, shrubs, deciduous and coniferous trees and lichens (Guo et al. 2008; Albrectsen et al. 2010; Mohamed et al. 2010; Su et al. 2010; Sun et al. 2011). Endophytes are an important component in natural ecosystems and they produce various bioactive chemicals, promote host growth, improve resistance to environmental stress and decompose litter (Aly et al. 2010; Saikkonen et al. 2010; Xu et al. 2010; Purahong and Hyde 2011; Tejesvi et al. 2011; Gouda et al. 2016).

Endophytic fungi have not been seriously considered in the estimation of fungal numbers (Hawksworth 1991). However, there could be more than 1 million endophytic fungal species based on ratios of vascular plants to fungal species of 1:4 (Petrini 1991). Dreyfuss and Chapela (1994) proposed that there should be 1.3 million endophytic fungal species. Most culturable plant endophytes are ascomycetes belonging to orders Amphisphaeriales, Capnodiales, Diaporthales, Hypocreales, Pleosporales, Sordariales, Trichosphaeriales and Xylariales (Guo et al. 2001; Crozier et al. 2006; He et al. 2012; Koukol et al. 2012).

Hamzah et al. (2018) revealed that the ratio of endophytic Ascomycota: Basidiomycota is around 25:1 and there are around 30,000 described, endophytic basidiomycetes species (Anke 1989; Anke and Steglich 1988). Hence, there should be 750,000 endophytic ascomycetes. Further, any vascular plant species can host somewhere 4–5 different endophytic fungal species (Sun and Guo 2012). There are 372,383 species of vascular plants and therefore, there could be 1.49 million endophytic fungal species. Hence, it is estimated that there are 675,000–1,341,000 endophytic teleomorphic ascomycetes excluding 10% obligatory anamorphs (Normark et al. 2003).

Case studies from epiphytic ascomycetes

Epiphytic fungi reside either permanently or casually on the surface of plants (Langvad 1980). They can multiply and grow on the surface of healthy leaves without any adverse effect to the host, while casual epiphytes land on the healthy leaf surface in the form of spores or mycelia but cannot grow like residents (Kharwar et al. 2010. The coexistence of epiphytic and endophytic microorganisms may play an important role for plant health and plant protection (Andrews and Harris 2000) as well as contributing to microbial biodiversity (Hawksworth and Rossman 1997).

Epiphytic fungi are dominant in Ascomycota and Basidiomycota with very few in other phyla and Sordariomycetes, Dothideomycetes and Eurotiomycetes are the most frequent among the all classes in Ascomycota (Dong et al. 2021). Among epiphytic fungi in the phyllosphere, 70–98% is ascomycetes while the rhizosphere comprises 73% of epiphytic species in Ascomycota (Oliveira et al. 2017). A comparative study of endophytic and epiphytic fungal association in leaves of Eucalyptus citriodora Hook. revealed 279 epiphytes out of 478 fungal isolates. This means number of epiphytic fungi is 1.4 times higher than endophytes. Further, Dong et al. (2021) analyzed the epiphytic and endophytic fungal communities of tomato plants and revealed 161 epiphytic fungal OTUs and 119 endophytic fungal OTUs. This suggested that the number of epiphytic fungi is around 1.4 higher than the endophytic fungi (Kharwar et al. 2010). In this study, we concluded that there should be 335,000-675,000 teleomorphic, endophytic ascomycetes and therefore, we suggest that there should be 469,000–945,000 teleomorphic epiphytic ascomycetes.

Based on the above case studies, it is estimated that there are around 1,710,000–3,405,000 teleomorphic ascomycetes in different ecological habitats and the average is around

2,558,000 species. However, all the predictions are based on the available data and some ecological groups are wellstudied while others are poorly examined.

Estimated number of teleomorphic ascomycetes based on meta-DNA and culture-independent studies

The identification of some teleomorphic ascomycetes such as fungal symbionts, endophytes, marine species associated with plants and green algae, and parasites is challenging due to their unculturable nature (Blackwell 2011). However, advanced molecular techniques facilitate the discovery of undescribed species from unculturable samples (Zhang et al. 2010; Blackwell 2011). The fungal diversity estimate increases with the advent of more uncultured fungi and fungi from environmental samples. Environmental DNA (meta-DNA) can be genetic material acquired directly from environmental samples, such as soil, sediment, water and others devoid of any clear signs of biological material is an effective, safe and quick standardized sampling method (Prosser and Hedgpeth 2018). The development of advanced molecular techniques such as high-throughput sequencing has greatly contributed in identification of undescribed species (Barnes and Turner 2015). More fungal species were identified by culture-independent approaches than by culture-dependent methods (Zhang et al. 2010) and the fungal species detected by one method is really different from other method, even for the dominant fungal species (Wu et al. 2019a).

Environmental DNA is a powerful tool to explore the hidden teleomorphic ascomycetes and it challenges understanding of global biodiversity (Venter et al. 2004). It was estimated that the number of fungal species on earth ranged between 3.5 and 5.1 million when considering the species recorded from environmental samples (Blackwell 2011). The class Archaeorhizomycetes in the sub-phylum Taphrinomycotina was introduced based on only environmental DNA, even its precise ecological niches and life cycle is unknown (Rosling 2011). Further, an unknown, basal clade of phylum Ascomycota which is characterized by unicellular zoospores with a single, non-chitin or non-cellulose-walled microtubular flagellum was described as *Cryptomycota* based on meta-DNA sequences (Jones et al. 2011).

Even though there is an argument as to use environmental DNA for nomenclature, Hawksworth and Rossman (1997) proposed to use this technique to explore the fungi existing in un-examined niches as well as known habitats. Therefore, the fungal species number could be much higher than the current reliable estimates of 2.2–3.8 million.

In a study based on fungal DNA assemblages and their spatial structure in river water using environmental DNA metabarcoding targeting of ITS locus revealed 985 fungal OTUs with 97% sequence similarity (Matsuoka et al. 2019). Totally, 770 OTUs were assigned as Ascomycota and it is 78.2% of total fungal OTUs. However, when there are 150,000 described fungal species, only 92,725 are ascomycetes and it is 61.8% in total. Therefore, environmental DNA metabarcoding method provides 16.4% additional amount of species and hence number of species in Ascomycota should be 117,325. If this applies to 2.2–3.8 estimate, considering 90% of them are teleomorphs (Normark et al. 2003), it is assumed that there are 1,548,690–2,675,010 species.

A study based on high-throughput sequencing of fungus: plant ratios revealed that the number of fungal species may be around 3.5-5.1 million species (O'Brien et al. 2005). Around 62% of described fungi are ascomycetes (Species Fungorum 2021) and if this applies to 3.5-5.1 estimate (O'Brien et al. 2005), considering 90% of them are teleomorphs (Normark et al. 2003), there should be 1,947,225-2,836,620 species. Here, we estimate around 1,747,958-2,755,815 teleomorphic species based on O'Brien et al. (2005), Hawksworth and Lücking (2017) and Matsuoka et al. (2019). Wu et al. (2019a) suggested that the range of species numbers based on environmental DNA is 8.8 times higher than the traditional culture dependent methods and this gives 11-19 million species for our estimate 1.25–2.17 million species based on described species in the data bases. This is quite large value and it is significantly different from other estimates in this study.

Estimated number of teleomorphic ascomycetes based on previous estimates of Ascomycota

De Meeûs and Renaud (2002) studied the phylogenetic relationship between the parasites and the eukaryotes. This study estimated that there should be 60,000 species in Ascomycota. Further, Aptroot (2001) studied fungal diversity of *Elaeocarpus* sp. and estimated that there should be 40,000–70,000 species of ascomycetes. However, these estimates were done two decades ago and more species have been introduced in last two decades. About 1900 fungal species were described per year over the past two decades (Hawksworth and Lücking 2017) and there should be around 38,000 more described species. Therefore, the updated estimate in Aptroot (2001) is 0.078–0.108 million. If 90% of described ascomycetes are teleomorphic species (Normark et al. 2003), it ranges for teleomorphic ascomycetes from 0.070 to 0.097 million with 0.084 million average.

Mueller and Schmit (2007) studied several groups of ascomycetes and estimated the species number. This study was based on Rossman (1994), Hawksworth et al. (1995) and data of the Dictionary of Fungi. They estimated species number for several groups in Ascomycota including Endomycetales, Helotiales, Hypocreales, insect-associated fungi, macrolichens, non-dematiaceous hyphomycetes and coelomycetes, other perithecioid ascomycetes, Pezizales and Xylariales. There were 40,706 described species in above groups and it was predicted as 694,000 species (Mueller and Schmit 2007) with the ratio of described species: estimated species as 1:17. If this ratio applys for the average of updated estimate in Aptroot (2001) (0.084 million), there should be 1,190,000–1,649,000 teleomorphic ascomycetous species.

Updated estimation of teleomorphic species number in Ascomycota

We evaluated species number for teleomorphic ascomycetes based on five approaches; number of described species in databases, fungus:substrate ratio, ecological distribution (Table 2), meta-DNA and culture-independent methods, and previous estimates by other authors (Table 3). The average of each method was used to propose the updated value for species number of teleomorphic ascomycetes and it is 1.86 million. The species number of teleomorphic ascomycetes ranges 1.37–2.56 million and the ratio between described teleomorphic ascomycetes to predicted teleomorphic ascomycetes is 1:22. Further, there should be 3.3 million fungi when 150,000 species has been described.

The estimates based on ecological distributions and environmental DNA analysis provide large numbers. It is suggested that one species can occur in several different

 Table 2
 Estimated
 species
 number
 for
 teleomorphic
 ascomycetes
 based
 on
 different
 ecological
 studies
 studies

Ecological group	Range of species number	Average of species number
Marine species	12,448-21,500	16,974
Freshwater species	19,490-33,664	26,577
Insect associated species	52,800-91,200	72,000
Coprophilous species	177,000-443,000	310,000
Soil inhabiting species	148,500-256,500	202,500
Lichenized species	17,640-33,480	25,560
Ligninolytic species	138,600-239,400	189,000
Endophytic species	675,000-1,341,000	1,008,000
Epiphytic species	469,000-945,000	707,000
Total fungal species	1,710,478-3,404,744	2,557,611

Table 3Updated estimatesfor number of teleomorphicspecies in Ascomycota based ondifferent approaches

habitats or in different life modes and counted several times as the different species. Additionally, environmental DNA reveal the hidden diversity in habitats and most unculturable species or species rarely produce teleomorph can be trace. Therefore, the species number in these two methods are higher than others (Fig. 3).

Limitations in estimation methods: Why estimating the species number of teleomorphic ascomycetes is challenging

The number of existing teleomorphic species in Ascomycota is not well-predicted and this estimation depends on the known number of species. So, what are the difficulties in knowing or describing teleomorphic ascomycetes? The diversity of teleomorphic ascomycetes is much higher due to their easily adaptable capability to different ecological conditions and therefore, in any given community or ecosystem, teleomorphic ascomycetes can be abundantly discovered (Berbee and Taylor 1992). A high level of reproductive plasticity and different life cycles with exciting teleomorphic and anamorphic reproduction mechanisms can be observed in ascomycetes due to their diversity (Wilson et al. 2019). These variations and diversity have led to a high level of species richness across different ecological niches.

There are three distinct phases in species introduction: an ascending phase in 1750s to 1860s, a steep phase in the 1870s to 1880s and a relatively constant phase from the 1890s to the present day based on publications (Hawksworth and Lücking 2017). However, the number of described species may be greater than this in ascending and steep phases. The internet was not previously available and most mycologists worked independently. Conferences, scientific meetings and societies were limited, and funding to attend was often unavailable. Most mycologists were unable to directly share their knowledge and experiences with others (Agerer et al. 2000). Further, scientific research was not done for commercial purposes. Most described species could not be published or published papers were destroyed during world wars. Additionally, studies in mycology and description of new fungal species decreased during the Second World War period (Hawksworth and Lücking 2017). Further, many books, notes, experimental observations and fungal specimens were

Method	Range	Average
Based on numbers of described fungi	1.25-2.17	1.71
Based on fungus:substrate ratio	1.11-1.62	1.37
Based on ecological distribution	1.71-3.40	2.56
Based on meta-DNA/culture-independent studies	1.74-2.80	2.25
Based on previous estimates of species in Ascomycota	1.19-1.65	1.42



 Based on numbers of described fungi
 Based on fungus: substrate ratio
 Based on ecological distribution
 Based on meta-DNA/culture- independent studies
 Based on previous estimations of species in Ascomycota
 Average of each approach Average of all approaches
 Range of each approach

Fig. 3 Estimated numbers of teleomorphic species in Ascomycota based on five different approaches. The range of each approach and their mean values are marked in black dots and blue diamonds,

destroyed and most mycologists had to move to other places or retired.

Recent intensive studies based on comprehensive inventories of ascomycetous genera and families have neglected morphology and are mostly based on molecular data (Senanayake et al. 2018). Over 90% of the collected specimens may constitute undescribed species (Hyde et al. 2018). The young mycologists and students are willing to describe new collections as novel taxa rather than assign them to existing species (Hawksworth and Lücking 2017). Further, it is required to combine the data on biogeographic distributions, levels of endemism and host specificity into the described species list when estimating the number of teleomorphic ascomycetes (Mueller and Schmit 2007). However, the number of described species has increased due to application of molecular techniques for species delimitation. There are up and downs in the number of described species after 2010. This may reflect the resolve of cryptic species, synonymize and link teleomorphs and anamorphs, rather than introducing new collections as new species.

The grid map-based method for predicting species richness introduced in Lücking et al. (2014) has been used to predict species richness in the lichenized family Graphidaceae in Ascomycota (Aptroot and Cáceres 2016; Cáceres et al. 2017; Mendonça et al. 2020). This method uses known occurrence records to provide a prediction and a precise estimate of species richness. Thus, to predict the species richness of a large group of teleomorphic species in Ascomycota, the accuracy of the used records is important. Errors during species introduction, incorrect nomenclature, misidentification of cryptic species or species complexes, fungi from understudied fungal habitats and hosts can be problematic. The correct estimates of teleomorphic species richness in Ascomycota can be a difficult task (Hyde et al. 2020b). There are several limitations of the species estimates as below.

respectively. The red dashed-line shows the average value for esti-

One name for one fungus (1N1F) for pleomorphic species

mated species number of the five approaches

The "One name = One fungus" system used nowadays has been effective in establishing standards for naming fungi in the scientific community. Before the 1N1F system came into effect, teleomorphs and anamorphs were given separate names depending on the circumstances from which they were discovered. Some ascomycetes produce an anamorph in their life cycle (Seifert and Samuels 2000) and the anamorph sometimes becomes the prominent, commonly available morph in nature (Li et al. 2020).

With the use of DNA sequence data for species identification, the accuracy in identification and linking teleomorphs and anamorphs of a species are important. Limitations in available DNA sequence data could however lead to erroneous identification. Recent studies have been resolved errors made when selecting one name for pleomorphic fungal genera (Hawksworth 2012, 2015; Réblová et al. 2016; May 2017; Taylor et al. 2016). There are plenty of teleomorphic species epithets in the species catalogs without linking to anamorphic species due to a lack of molecular data from ex-type and other authentic cultures or poor morphological descriptions (Seifert and Samuels 2000; Hawksworth et al. 2013). Most of the early introduced species do not have molecular data and species introduction was based on morphology (Vellinga et al. 2015; Koukol and Delgado 2021). Further, cultural studies not performed often and morphology of anamorph or teleomorph derived from pure cultures was not recorded. Therefore, recollection of earlier species or use fungarium materials to obtain DNA is required (Seifert and Rossman 2010; Aime et al. 2021).

Even after the implementation of 1N1F species system, certain research areas still predominantly use the older names in studies where the main focus is not related to taxonomy and nomenclature. The teleomorph of fungi are rarely encountered in plant pathology, thus plant pathologists tend to name the pathogenic species related to their anamorph, but the link between the two states was rarely established (Wingfield et al. 2012). These types of basic errors in species naming would hinder the possibility of accurate species estimates. Article F.8 for pleomorphic fungi in Shenzhen code states names proposed simultaneously for separate morphs (anamorph and teleomorph) of a taxon of non-lichen-forming Ascomycota and Basidiomycota are necessarily heterotypic and are not therefore alternative names (Turland et al. 2018). This code facilitates both teleomorphic and anamorphic names in the legitimate state and those legitimate names are treated equally when establishing priority to conserve the accepted name regardless of the lifehistory or stage of the type.

Rossman et al. (2015a, b) and Réblová et al. (2016) have provided recommendations for conservation or use of pleomorphic generic names in Dothideomycetes and Sordariomycetes. However, linking teleomorph and anamorph of species is challenging. Pure cultures obtained from single germinating ascospores often sporulate and anamorphs are formed (Senanayake et al. 2020a). Sometime, strains of pleomorphic species obtained from different specimens cluster together with strong support in phylogenetic trees (Karunarathna et al. 2017; Wanasinghe et al. 2018). The colony characters and nucleotide identity of molecular sequences should be checked even if cultures do not sporulate. Further, some unculturable ascomycetes that are only known from their teleomorph cannot be linked to the anamorph.

However, some other classes such as Orbiliomycetes, the generic names are much more complicated because of the names based on single morphological differences without molecular data (Baral et al. 2018). In Orbiliomycetes, a narrow concept has used for the demarcating the generic boundaries of the anamorphs, while a broad concept relies on the teleomorphs. Therefore, more generic names have been established for the anamorphs. Hence, it should be avoided to adopt a certain generic concept prematurely, as this may imply a lot of unnecessary name changes (Baral et al. 2018). Therefore, linking teleomorph and anamorph of

species is an important practice in nomenclature and it can affect species number.

Phenotypic plasticity

Phenotypic plasticity in fungi denotes that changes in morphology, behavior and physiology in response to the environmental variation (Price et al. 2003). Phenotypic plasticity allows teleomorphic ascomycetes to respond to climatic changes within their lifetime (Williams et al. 2008). This is important for species to survive as evolutionary responses for climatic changes by natural selection takes time to make any adaptation.

More than 40% of ascomycetes live in symbiosis as lichens (Kirk et al. 2008). Lichens show high phenotypic plasticity together with geographical distributions (Divakar et al. 2013; Muggia et al. 2014). Parmeliaceae is a hyper-lichenized fungal family mainly distributed in the tropics (Kraichak et al. 2015). The type genus *Parmelia* includes several distinct species by phenotypic plasticity (Valladares et al. 2007). *Parmelia discordans* and *P. omphalodes* were described based on morphological differences. However, molecular data showed that these two species are conspecific and phenotypic variations are made according to environmental changes (Divakar and Upreti 2005). *Nipponoparmelia pseudolaevior* and *N. laevior* show phenotypic plasticity in this family (Molina-Montenegro et al. 2016).

Phenotypic stasis

Phenotypic stasis is explained by natural selection and genetic drift, or by constraints imposed by mutation and recombination of standing genetic variation (Mallard et al. 2019). This is a basic method in speciation and genetic variations (Chethana et al. 2020). Gene variations formed by phenotypic stasis can completely disappear to reduce the genetic variation or initially rare alleles become much more frequent to dominant the gene variations (Mallard et al. 2019). However, the morphological variations formed by phenotypic stasis are retained in a population if only individuals survive and reproduce. Phenotypic stasis forms species morphologically similar, but genetically different. Therefore, species estimates must include these species.

Homoplasy

Homoplasy is a trait that has been gained or lost independently in separate lineages with evolution (Torres-Montúfar et al. 2018) and it can arise by selection pressures or genetic drift (Stearns and Hoekstra 2005; Hall and Colegrave 2008). Homoplasy mostly appears in similarity of morphological characters, but also in molecular sequences (Reece et al. 2011), life cycle (Silberfeld et al. 2010) and behavior (de Queiroz and Wimberger 1993).

Jiang et al. (2020) showed in a phylogenetic study of foliicolous lichens that a new lineage sister with Strigulaceae (Dothideomycetes) was formed, however morphologically similar to *Porina* (Lecanoromycetes). This new clade represents a monogeneric family Tenuitholiascaceae which is typified by *Tenuitholiascus* with a single species *T. porinoides*. This species is morphologically similar to the genus *Porina* in external morphology, ascospore type, the thin-walled asci and unbranched paraphyses. Further, Schmitt (2011) showed that homoplasy affects the evolution of fruiting body type and ascus at the class level within the phylum Ascomycota. This may increase the species number described if only based on phenotypic characters.

Synonyms and conspecific species

Synonym is a scientific name currently applies to a taxon that goes by a different scientific nameand synonyms form strong, monophyletic clades with currently applied taxon in phylogenetic trees. Therefore, these synonyms are known as conspecific species (Rossman et al. 2015a). Hence, there is often more than one scientific names for a single species and the morphs had been described in different genera (McNeill et al. 2006). Two or more names for different morphs of the same species are not accepted according to the Melbourne Code (McNeill et al. 2012). Hence, Wijayawardene et al. (2012), Rossman et al. (2015a,b), Réblová et al. (2016) have proposed recommendations to determine which name to conserve. Proposals were based on excluding synonymy, giving priority to basionyms, commonly used names or the commonly occurring morph in nature.

Conspecific species being identified as distinct species through morphological data, but with molecular data providing evidence for them being identical, has also led to incorrect species identification. Some sexually compatible conspecific fungal species can also produce new pathogens via interspecific hybridization and reproductive interference (Giordano et al. 2019). The genus *Diatrype* is typified by *D. disciformis* (Fries 1849). *Libertella betulina*, the type species of *Libertella*, is the anamorph of *Diatrype stigma* (Grove 1937; Kutorga et al. 2006), while *L. disciformis* is the anamorph of *D. disciformis*. *Diatrype disciformis* and *D. stigma* are conspecific (Trouillas et al. 2010). Further, *Libertella* is the older name as it was erected in 1830 while *Diatrype* was only erected in 1842, thus *Diatrype* and *Libertella* are synonyms. However, *Diatrype* has a great number of species including important plant pathogens. Hence, *Diatrype* was recommended for protection over *Libertella* (Réblová et al. 2016).

There are many recommendations proposed for taxa of Xylariaceae (Réblová et al. 2016). The genus *Daldinia* is typified by *D. concentrica* (Stadler et al. 2014). The monotypic genera *Annellosporium* which is typified by *A. nemorosa* and *Versiomyces* typified by *V. cahuchucosus* Whalley & Watling, have been synonymized under *Daldinia* as *D. nemorosa* based on the phylogeny and *D. cahuchucosa* based on morphology and chemotaxonomic evidences (Stadler et al. 2014). *Daldinia* is common with many species and has been recommended for use. Therefore, recognizing excluded synonyms is essential to estimate the actual number of fungi.

Illegitimate and invalid names

Published taxonomic names may be illegitimate and invalid. This means the species exist, but are nomenclaturally incorrect due to contravening some of the articles laid down by the nomenclature codes. If a published species name is not accepted as a proven valid species, then it can be superfluous as a synonym of a known species, non-compliant with nomenclature codes thus considered a "bad" name and doubtful name with insufficient study (Wang et al. 2019). The number of accepted names, synonyms, invalid or illegitimate names, and unstudied names has been compared by Wang et al. (2019). They found that accepted names increased markedly over time and increased significantly after the 1900s. The number of synonyms, invalid or illegitimate names increased slowly and it is evident that the quality of fungal taxonomic work has improved with the application of molecular techniques. The International Code of Nomenclature for Algae, Fungi, and Plants is updated every four years and proposes and regulates all the articles related to nomenclature (Turland et al. 2018).

Introgression and natural hybridization

Introgression means transfer and incorporates alleles from one species into the gene pool of another species by hybridization and backcrossing (Schardl and Craven 2003; Stukenbrock 2013, 2016; Restrepo et al. 2014). There are many occasions when genetic information can be transfered between closely related species and thus gene flow between cryptic species has frequently been found (Hawksworth 2001; Bickford et al. 2007; Hawksworth and Lücking 2017). Therefore, species boundaries in morphologically indistinct species and species complexes may be doubtful (Barton and Hewitt 1985; Barton and Gale 1993). If a portion of the introgressed gene pool of each of the hybridizing taxa remains constant and uncontaminated then different distinct gene pools can be recognized as new species.

Beneficial alleles tend to introgress easily for habitat adaptation or reproduction (Barton 1979). Thus, patterns of differential introgression across hybrid zones in genes or genome regions are important for habitat adaptation and speciation (Payseur 2010; Shaw and Mullen 2011; Nachman and Payseur 2012). Sometimes, the gene flow between species is limited or prevented in nature by a set of basic barriers. These limits control transfer of the genetic material which affects phenotypic variations between species and determines if species reproduce individually (Bouck et al. 2005; Lemmon et al. 2007; Roe and Sperling 2007; Wagner et al. 2013). However, the question is how many species evolves presently by introgression and hybridization? The answer is unpredictable. Therefore, this should be considered when estimate the teleomorphic species in Ascomycota.

"Man-made" or domesticated species

Adaptive hybridization is used to obtain industrially important species additionally to natural hybridization (Burgarella et al. 2019). Genetic materials are changed during domestication of wild species and new species or varities may form (Shibata et al. 2015). Industrial cultivation of some teleomorphic ascomycetes such as *Cordyceps*, morels, truffles requires hybrid varities to obtain high yield. However, the obtained number of hybrid species in a particular period is undetermined. Additionally, the behavior of hybrid species with the wild species gene pool is not well studied. Therefore, an idea of the number of domesticated species is needed to estimate the number of species in Ascomycota.

Polyphyletic genera and species

The polyphyletic nature of fungal genera derived from more than one common evolutionary ancestor or ancestral group cannot taxonomically be in the same genus. Sometime morphologically similar species cluster in different sub-clades in phylogenetic trees representing several distinct genera (Phookamsak et al. 2015, 2017; Konta et al. 2020). This affects the number of described species. Some studies have used slightly different morphological characters of taxa along with the phylogenetic analyses to introduce new genera (Hyde et al. 2020a).

Xylariaceae comprises several polyphyletic genera which are phylogenetically distantly related to each other (Peršoh et al. 2009; Senanayake et al. 2015). *Xylaria* is typified by *X. hypoxylon* (Schrank 1789; Greville 1824) and species in *Xylaria* are saprobes or endophytes (Thomas et al. 2016). Lumping and splitting of *Xylaria* species in phylogenetic trees forming unresolved lineages has occurred over time. Most phylogenetic analyses have shown that *Xylaria* species do not form a monophyletic clade and are scattered within Xylariaceae (Hsieh et al. 2010; Senanayake et al. 2015; Maharachchikumbura et al. 2016; Wendt et al. 2018). Few *Xylaria* species are clustered with *Amphirosellinia, Astrocystis,* and *Collodiscula* without strong statistical support (Wendt et al. 2018; Konta et al. 2020).

Generic polyphyly does not markedly change the number of existing species, but species polyphyly changes the number of species. The "special status" of a species comprises the unique, observable morphological characters (Queiroz and Donoghue 1988). It is implicitly assumed that species are monophyletic or at least paraphyletic. However, hybrid speciation arguably leads to polyphyletic species (Hörandl and Stuessy 2010). Hybrid species are a common phenomenon that allows for rapid speciation (Linder and Risenberg 2004) and polyphyletic species develop into different species later.

Extinct or endangered species

The evolution of fungi begun around 1.5 billion years ago (Wang et al. 1999; Brundrett 2002). There is evidence that fungal communities in Ascomycota were present in the Devonian period, 416-359 million years ago (Strullu-Derrien et al. 2018). Ascomycetes diversified rapidly in terrestrial environments and therefore, they occupied numerous ecological niches. However, teleomorphic ascomycetes are recently threatened by habitat loss, loss of symbiotic hosts, pollution, over exploitation of the animal and plants, destruction of ecosystems and climate change and they are also becoming extinct (Wang et al. 1999). However, the vast majority of teleomorphic ascomycetes have not been assessed. The IUCN has listed 280 threaten fungal species under several catogaries, such as critically endangered (CR, 15 species), endangered (EN, 59 species), vulnerable (VU, 90 species), near threatened (NT, 40 species), least concern (LC, 54 species) and data deficient (DD, 22 species). The IUCN Red List contains 46 threaten teleomorphic ascomycetes (Table 4) (IUCN 2021). The objective of the global IUCN red list of threatened fungal species is to determine conservation issues to the public and policy makers and help the international community decrease species decline and extinction (Lughadha et al. 2020). The IUCN Red List is the most comprehensive, objective global approach for evaluating the conservation status of fungal species. The largest number of threatened species is from Europe (IUCN 2021). IUCN organized three workshops in Chile, and the UK in 2020 and this effort will assess the conservation status of

 Table 4
 IUCN red-list category of teleomorphic species in Ascomycota issued by International Union for Conservation of Nature (IUCN)

CR Acomthothecis Jeucexonnthoides Stable Lecanoromycetes, Ostropales, Graphidaceae CR Acomthothecis Jeucetyora Stable Lecanoromycetes, Ostropales, Graphidaceae CR Buellia astrerella Decrensing Lecanoromycetes, Teloschistales, Physicaceae CR Hypocreopsis amplectors Decreasing Sordariomycetes, Peligerales, Pannariaceae CR Romalina portsonatana Decreasing Lecanoromycetes, Teloschistales, Physicaceae CR Rondin drysometeana Decreasing Lecanoromycetes, Teloschistales, Physicaceae CR Rundin drysometeana Decreasing Lecanoromycetes, Teloschistales, Physicaceae EN Arthonia kermesina Decreasing Lecanoromycetes, Lecanorales, Parmeliaceae EN Clutonia perforuta Utaknown Lecanoromycetes, Lecanorales, Chadoniaceae EN Gymouderna insular Decreasing Lecanoromycetes, Lecanorales, Chadoniaceae EN Romalina erosa Stable Lecanoromycetes, Lecanorales, Randiniaceae EN Romalina erosa Stable Lecanoromycetes, Peligerales, Pannariaceae EN Romalina erosa Stable<	Red-list category	Species name	Population trend	Classification
CR Acanthothecis paucipora Stable Lecanoromycetes, Teloschistales, Physicacae CR Buellia asterella Decreasing Lecanoromycetes, Teloschistales, Physicacae CR Hypocreopsis ampleterus Decreasing Sondariomycetes, Pethgerales, Physicacae CR Hypocreopsis ampleterus Decreasing Lecanoromycetes, Iecanorales, Ramalinaceae CR Ramalina portosantuna Decreasing Lecanoromycetes, Iecanorales, Pameliaceae CR Sulcaria islifiera Decreasing Lecanoromycetes, Iecanorales, Pameliaceae CR Sulcaria islifiera Decreasing Lecanoromycetes, Lecanorales, Cladoniaceae EN Cladonia perforat Unknown Lecanoromycetes, Lecanorales, Cladoniaceae EN Gamoiderma insulare Decreasing Lecanoromycetes, Lecanorales, Cladoniaceae EN Ramalina confertula Stable Lecanoromycetes, Lecanorales, Ramalinaceae EN Ramalina confertula Stable Lecanoramycetes, Petilgerales, Phasicaceae EN Ramalina consphpfula Decreasing Lecanoramycetes, Petilgerales, Phasicaceae EN Rinodnin brobdan Decreasin	CR	Acanthothecis leucoxanthoides	Stable	Lecanoromycetes, Ostropales, Graphidaceae
CR Buellia autentla Decreasing Lecanoromycets, Peltigenales, Physicaceae CR Hypocreapis amplecters Decreasing Scharlonycets, Hypocreales, Hypocreaceae CR Luxosporu asstaeguensis Stable Lecanoromycets, Icenorolis, Synamanaceae CR Ranulina portosantana Decreasing Lecanoromycets, Icenorolis, Stamalinaceae CR Ranulina portosantana Decreasing Lecanoromycets, Icenorolis, Arthoniaecae CR Sulcaria isfalifera Decreasing Lecanoromycets, Icenorolis, Arthoniaecae EN Arthonia kernenian Decreasing Lecanoromycets, Icenorolis, Arthoniaecae EN Catolinia peforata Unknown Lecanoromycets, Icenorolis, Cladoniaecae EN Gymnoderma insulare Decreasing Lecanoromycets, Icenorolis, Ranulinaceae EN Randlina insulare Stable Lecanoromycets, Peltigenies, Panariaecae EN Ranulina consa Stable Lecanoromycets, Peltigenies, Ranulinaceae EN Ranulina consa Decreasing Lecanoromycets, Peltigenies, Panariaecae EN Rindinia indudiana Decreasing Lecanoromycet	CR	Acanthothecis paucispora	Stable	Lecanoromycetes, Ostropales, Graphidaceae
CR Erioderma pedicellaram Decreasing Lecanoromycetes, Pediperales, Amporeaceae CR Hypocreoptis amplectens Decreasing Sordariomycetes, Incertas edits, Surameanaceae CR Ramalina portosantana Decreasing Lecanoromycetes, Lecanorales, Ramalinaceae CR Ramolina chryomelaena Decreasing Lecanoromycetes, Lecanorales, Ramalinaceae CR Sulcoria isidiffra Decreasing Lecanoromycetes, Lecanorales, Parmeliaceae EN Calenia perforata Unknown Lecanoromycetes, Lecanorales, Cladoniaceae EN Cladonia perforata Unknown Lecanoromycetes, Lecanorales, Cladoniaceae EN Ramalina confertula Stable Lecanoromycetes, Lecanorales, Cladoniaceae EN Ramalina confertula Stable Lecanoromycetes, Lecanorales, Cladoniaceae EN Ramalina confertula Unknown Lecanoromycetes, Pediparales, Cladoniaceae EN Ramalina conso Stable Lecanoromycetes, Pediparales, Cladoniaceae EN Ramolina confertula Unknown Lecanoromycetes, Pediparales, Cladoniaceae EN Stata diphomotina Decreasing	CR	Buellia asterella	Decreasing	Lecanoromycetes, Teloschistales, Physciaceae
CR Hypocreopsis amplecters Decreasing Sordarionycetes, Hypocreaces, Hypocreaces, CR CR Loxospora assateaguensis Stable Lecanoromycetes, Inceraorales, Ramalinaceae CR Rumalina portsantana Decreasing Lecanoromycetes, Lecanorales, Ramalinaceae CR Sulcaria isidifera Decreasing Lecanoromycetes, Lecanorales, Parmeliaceae EN Arthonia kermesina Decreasing Arthonia kermesina EN Cardionia perforata Unknown Lecanoromycetes, Lecanorales, Cladoniaceae EN Cladonia perforata Unknown Lecanoromycetes, Lecanorales, Cladoniaceae EN Ramalina confertula Stable Lecanoromycetes, Lecanorales, Ramalinaceae EN Ramalina confertula Stable Lecanoromycetes, Lecanorales, Ramalinaceae EN Ramalina timdaliana Unknown Lecanoromycetes, Lecanorales, Ramalinaceae EN Sulcaria badia Decreasing Lecanoromycetes, Lecanorales, Ramalinaceae EN Sulcaria badia Decreasing Lecanoromycetes, Lecanorales, Ramalinaceae EN Sulcaria badia Decreasing Lecanoromycetes, Le	CR	Erioderma pedicellatum	Decreasing	Lecanoromycetes, Peltigerales, Pannariaceae
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DD Thuemenidium sp. Unknown Geoglossomycetes, Geoglossales, Geoglossaceae	DD	Cordyceps kirkii	Unknown	Sordariomycetes, Hypocreales, Cordycipitaceae
	DD	Thuemenidium sp.	Unknown	Geoglossomycetes, Geoglossales, Geoglossaceae

CR critically endangered, EN endangered, VU vulnerable, NT near threatened LC least concern, DD data deficient

endemic species of three regions, South America, Europe and Southeast Asia.

However, the number of threaten teleomorphic ascomycetes is very low compared with the described number of teleomorphic species in Ascomycota due to the difficulties in screening fungal populations. Most teleomorphic ascomycetes are only visible when they produce fruiting bodies and may not be found in the same place every year (Senanayake et al. 2020a). Some early evolved teleomorphic ascomycetes have become extinct and there is no documentation for them.

Biodiversity hotspots

Only about 93,000 Ascomycota species have been introduced and documented even more are estimated (Roskov et al. 2019). Studying the fungi in biodiversity hotspots is important to determine the undescribed taxa (Hawksworth and Lücking 2017). Biodiversity hot spots and geographic and ecological habitats which are poorly or under-studied are major localities for these undescribed species. Biodiversity hot spots are designated by IUCN and they are conserved by government in located country (Marchese 2015). Biodiversity hotspots occupy approximately 1.4% of earth's land area, but 60% of Earth's biodiversity is gathered there (Possingham and Wilson 2005; Marchese 2015).

The global biodiversity hotspots are referred to as areas featuring exceptional concentrations of endemic species and experiencing exceptional loss of habitat (Myers et al. 2000). Most ascomycetous type collections were obtained from North America, Europe (France, Germany, Italy, Spain, Sweden, UK), Japan, India, China, Thailand, Philippines, Australia and Brazil (Species Fungorum 2021). Most of these countries are located in biodiversity hotspots, but the whole country has not been preserved as biodiversity hotspots (Matutea and Sepúlvedab 2019). Although many species have been collected from countries which are located in biodiversity hotspots, it does not mean that fungal diversity is restricted to the biodiversity hotspots (Marchese 2015). Generally, rules and regulations for entrance and utilization of reso urces are strictly controlled in these areas, even for scientific studies. This is one reason that mycologists could not estimate exact number of teleomorphic ascomycetes in hotspots. However, it is predicted that biodiversity hot spots have extremely favorable conditions for ascomycetes and thus production of sexual, thick-walled spores is not prominent. Therefore, species in Ascomycota may occur in vegetative phase or reproduce asexually.

Hidden species in niches

Morphologically, teleomorphs of ascomycetous fungi are only recognized when they produce sexual reproductive organs. Some ascomycetes occur in niches without forming any visible, distinct fruiting structures and are only obtained as hyphae (Schardl and Craven 2003). These species are ecologically cryptic and difficult to screen by traditional phenotypic approaches. Environmental DNA analyses can reveal such species (Wu et al. 2019a). Additionally, fungal succession may help to obtain those species separate. This has been defined as the sequential occupation of different ascomycetes or different associations of ascomycetes on the same substrate or site (Challacombe et al. 2019). This happens because of a sequence of sporulating fungi on a substrate by mycelium. However, replacement of one ascomycetous species by another is not necessary and some ascomycetes sporulate together on a substrate (Hyde and Jones 2002). Sometimes, incubation of fresh specimens is necessary to obtain maximum fungal diversity, especially rare or slow growing species.

Poorly-studied fields

Many terrestrial teleomorphic ascomycetes have been described, but fewer are known from aquatic habitats. Natural groundwater limestone aquifers are challenging and unexplored fungal habitats (Krauss et al. 2003; Lategan et al. 2012; Risse-Buhl et al. 2013). Mangrove and wetland associated teleomorphic ascomycetes are poorly known as compared to terrestrial taxa (Lee et al. 2019). Therefore, it is necessary to fully screen marine and aquatic habitats to explore the fungal diversity. Research on aquatic fungi in recent years have incorporated molecular techniques to achieve a better identification of taxa and many new species have been introduced (Zhang et al. 2017; Hyde et al. 2020a; Wei et al. 2020). Most of the earlier studies are based on observation of morphological characters and culturedependent techniques (Luo et al. 2019). There are unculturable freshwater ascomycetes and hence, culture-independent techniques need to be followed to understand the diversity among teleomorphic, freshwater ascomycetes (Hyde et al. 2020b). Clinical mycology is another field which has not been studied much with few human and animal pathogens reported (Homei 2006; Pihet et al. 2009; Köhler et al. 2015; Sullivan et al. 2015).

Less-studied sites in developing countries

Biodiversity hotspots in Asia (except Japan) and South America are generally poorly studied and not well-known (Hyde et al. 2020c). Most countries in these two continents are economically impoverished developing countries and lack resources and enough funding for fungal research (Subramanian 1986; Jones et al. 2007). Most developing countries are located in tropical and subtropical regions and fungi thrive in these countries due to the favorable habitat conditions. However, some species rich, biodiversity hotspots in these countries lack studies on species diversity and richness (Marchese 2015). In fact, the whole planet is not being evenly screened and therefore, many important teleomorphic ascomycetes may become extinct prior to description and documentation.

In 2017, 35% of the world's described fungal species were from Asia (Willis 2018). This may have increased within the last two years (Hyde et al. 2020c). Africa is very different from South America or Asia in biodiversity having dry climates and different geographical lands, while there are many rainforests and wet ecological sites in South America. Therefore, less-studied areas should be examined well to explore undescribed teleomorphic species in Ascomycota.

Unexamined collections in specimen repositories and missing specimen records

Traditionally, teleomorphic ascomycetes have been distinguished by different approaches and concepts such as morphology, physiology, biochemistry or reactions to chemical tests. Morphology was commonly used to introduce teleomorphic ascomycetes and it was improved with the innovation of the microscope. However, there are many poorly identified or superficially examined collections in fungaria (Senanayake et al. 2020a). Many reference specimens in fungaria and living cultures in fungal culture collections are not named to the species level, and in some cases not even to the generic level (Hawksworth and Lücking 2017).

Additionally, some collections and isolates are connected to existing species names without comprehensive specimen examination and sometimes it is possible to find different fungi in the same specimen if those specimens are examined carefully. It has been suggested that morethan 20,000 teleomorphic ascomycetes have been collected worldwide but not described yet (Hawksworth and Rossman 1997). Mycologists often have a large collection of material waiting for formal introduction and description. Some taxonomic records, descriptions and specimens have been lost in various situations before description (Senanayake et al. 2016). Therefore, re-visiting early-introduced ascomycetes which are only based on morphology is important (Ariyawansa et al. 2014).

Some monographic work and some journal issues that focus on exploration of global fungal biodiversity such as Mycosphere Notes (ZUAE, Guangzhou, China), Fungal Diversity Notes (Springer Nature, Switzerland) or Fungal planet description sheets (CBS, The Netherlands) describe hundreds of novel teleomorphic ascomycetes annually. However, some species are introduced only based on morphology and Mega-blast similarities in GenBank without phylogenetic analysis. Most of the new collections are described without re-visiting morphologically similar earlier species or genera. If a collection is from known host, then it is necessary to check previous species records on the host and locality (country or continent) prior to describing a new species (Senanayake et al. 2020b). Careless practices will result in proliferation of synonyms or invalid names leading to confusion and instability in nomenclature. Many described teleomorphic ascomycetes in the pre-molecular era are only based on morphology and there are older collections in repositories that need to be examined and described.

Incomplete descriptions of earlier described species

In earlier studies, specimens were examined by light microscope and 40 was the maximum magnification (Senanayake et al. 2020a). Lenses of light microscopes were calibrated manually (Zhang et al. 2016). One unit of the ocular micrometer disc is needed to calibrate against a known length and measurements were subjective from person to person. Newer technologies facilitate measurements directly when photographing and software is already calibrated. Hence, errors in measurements have been less in recent descriptions. Earlier prologues based on the limited characters and some important, inconspicuous characters were not examined or not mentioned (Senanayake et al. 2018). Therefore, new collections of existing species are mistakenly described as new species. A prologue should include information of examined materials (Seifert and Rossman 2010). However, some specimens lack these details or are incomplete. Earlier prologues usually do not contain culture characters. Therefore, incomplete descriptions of earlier introduced species make complications in species identification.

Synanamorphism

Synanamorphism is a teleomorphic species produces several morphologically distinct anamorphs and these synanamorphs have been often reported from cultural studies (Crous et al. 2009; Réblová et al. 2021). Before molecular data was available for taxonomic studies, species delimitation was based on the morphology of specimens and cultures. Pure cultures were used to obtain teleomorphs or anamorphs and then to describe the holomorph. However, some teleomorphic species produce several anamorphs and those anamorphs are described as different species. Molecular phylogenies of some studies proved that some teleomorphic species produce two or more anamorphs (Fan et al. 2018; Réblová and Štěpánek 2018). Therefore, it is assumed that some synanamorphic species might have been considered as separate species dueto their distinct morphologies and they should avoid from the unmber of known species.

Species in Cytosporina Sacc., Libertella Desm., and Naemospora Sacc. have been reported as anamorphs of diatrypaceous species (Glawe and Rogers 1984). However, the morphology of the anamorph is not useful when differentiating taxa in Diatrypaceae either at the genus or species level. There is indistinguishable morphology and many species produce different types of anamorphs in the same culture (Rappaz 1987). Additionally, different types of conidiogenesis have been reported in the same Diatrype strain (Glawe and Rogers 1982). Eutypella parasitica produces both pycnidia and acervuli on both natural substrata and cultures (Glawe 1983). Further, the anamorph of Hapalocvstis (Sydowiellaceae, Diaporthales) is reported as Stilbospora, Hendersonia or Dothiorella (Wehmeyer 1941; Castlebury et al. 2002), or as stilbospora-like taxa (Barr 1978). A phoma-like anamorph is reported for H. berkeleyi in culture (Glawe 1985; Liu et al. 2015; Senanayake et al. 2016).

Absence of molecular data for described species

Before the 1990s, fungal species were introduced based on morphology and there are no molecular data for many of those described species. Classification of those species is challenging without molecular data (Huang et al. 2021). Cryptic species, phenotypic plasticity, phenotypic stasis, pleomorphism, and homoplasy between teleomorphic ascomycetes are difficult to reveal without molecular data (Maharachchikumbura et al. 2014). Hence, the estimated number of teleomorphic species in Ascomycota should include those hidden species.

Addition to the phylogenetic relationships, molecular data reveals the character evolution of teleomorphic species in Ascomycota. Character evolution deals with the process of evolution of a trait along the branches over a period of time from a common ancestry (Hongsanan et al. 2018). This explains the history of life, the relationships among extant species and character states for each species (Vijaykrishna et al. 2006). Most character evolution studies were carried out after the 1990s (Liu and Hall 2004; Li

et al. 2005; Schoch et al. 2009; Schmitt 2011; Kumar et al. 2012) and these studies have not been obviously conducted on teleomorphic ascomycetes which lack sequence data. The unavailability of complete sets of sequence data is the major issue for absence of character evolution studies. These studies concur or argue against species delimitation. Hence, these studies influence the estimate number of teleomorphic species in Ascomycota.

Apothecia are the primitive fruiting body type of Pezizomycotina. However, the formation of perithecia and cleistothecia is still unclear (Hongsanan et al. 2018). The amyloid reaction of stromatic tissues occurs in some species in Sordariomycetes such as Hypocreaceae in Hypocreomycetidae, Xylariaceae in Xylariomycetidae and Cryponectriaceae in Diaporthomycetidae. However, the reason for the appearance and disappearance of the same character during evolution and when, how and why these characters evolved are unclear. If there is a complete set of molecular data, character evolution of teleomorphic species in Ascomycota can be predicted clearly and it provides additional taxonomic value for a species.

Molecular data unavailability for both teleomorph and anamorph of ascomycetes

Phenotypic species were previously introduced based on morphological characters and later, sequence data obtained for some of earlier described species. However, many species lack sequence data. If a culture of a teleomorphic Ascomycota sporulates then, the anamorph can be obtained and identified. These teleomorphs and anamorphs can be linked if they are derived from a pure culture. If a specimen contains both ascomata and conidiomata in close to each other, then cultures obtained from both ascospores and conidia should be further analysed for molecular and colony morphology. If the colony morphology in the same media and at the same maturity is similar and sequence data are identical, then the conidiomata are anamorph of teleomorphic fungi and it should be named as one species. However, colony characters and sequence similarity can be used if teleomorphs and anamorphs are described from different specimens. The sequence quality should be high and both forward and reverse directions are needed.

Senanayake et al. (2015) introduced the genus *Ciferriascosea* Senan., Bhat, Camporesi & K.D. Hyde with two teleomorphic species *C. fluctuatimura* Senan., Bhat, Camporesi & K.D. Hyde and *C. rectimura* Senan., Bhat, Camporesi & K.D. Hyde and they were accommodated in family Phlogicylindriaceae (Xylariales). The anamorph was not reported for this genus. Phlogicylindriaceae is typified by anamorphic genus *Phlogicylindrium* Crous, Summerb. & Summerell and teleomorph is not reported for this genus. Therefore, species in *Ciferriascosea* and *Phlogicylindrium* cannot be morphologically compared. Phylogenetically, species in these two genera clustered together with high bootstrap support. However, ITS loci of the type species of *Ciferriascosea*, *C. rectimura* showed 10.4% base pair differences from ITS loci of the type species of *Phlogicylindrium*, *P. eucalypti* (Jeewon and Hyde 2016). Further, 85 base pairs are missing in the ITS loci of *Phlogicylindrium eucalypti*. Additionally, *Ciferriascosea rectimura* was isolated from twigs of *Spartium junceum* L., while *Phlogicylindrium eucalypti* was collected from leaves of *Eucalyptus globulus* Labill. Therefore, Senanayake et al. (2015) proposed a new genus *Ciferriascosea* for this teleomorphic taxon instead of proposing it as the teleomorph of *Phlogicylindrium*.

Camarosporidiella caraganicola was introduced based on a strain derived from the anamorph that was described by Liu et al. (2015). Wanasinghe et al. (2017) has examined several specimens of the teleomorph of *Camarosporidiella caraganicola*. Phylogenetically, these strains clustered together with strong support. Both teleomorph and anamorph were collected from the same host (*Caragana frutex* (L.) K.Koch) in the Rostov Region, Russia. Therefore, Wanasinghe et al. (2017) linked these teleomorph and anamorph together as the holomorph of *Camarosporidiella caraganicola* by considering the host similarity and statistical support in phylogeny.

A teleomorph of an astragalicola-like taxon was collected and obtained in culture (MFLUCC 17-0832). The multigene sequence analyses showed that this isolate clusters with *Astragalicola amorpha* with strong support (Wanasinghe et al. 2018). However, *A. amorpha* is known from its anamorph and thus, it is not possible to compare their morphologies. A comparison of the ITS loci of these two strains revealed 2.12% nucleotide differences, which justifies these two isolates as two distinct taxa (Jeewon and Hyde 2016). Therefore, the new collection was introduced as *Astragalicola vasilyevae*.

The anamorph of *Wojnowiciella dactylidis* was illustrated in Liu et al. (2015) and molecular data was provided. Karunarathna et al. (2017) illustrated the teleomorph for this species. Both teleomorph and anamorph were collected from Italy on different host plants but colony characters of both strains are similar. Phylogenetically, both strains clustered together with strong support. The ITS sequences obtained from the teleomorphic strain was identical to anamorphic strain with 100% base pair similarity. Therefore, Karunarathna et al. (2017) linked these two strains as the holomorph of *Wojnowiciella dactylidis*.

Teleomorphic ascomycetes described based on only Internal Transcribed Spacer (ITS) region

The nuclear ribosomal internal transcribed spacer (ITS) region is located between the sequences encoding the small (SSU) and large (LSU) subunits of the ribosomal operon (White et al. 1990). The ITS region is the formal primary fungal barcode with the highest probability of correct species identification of a broad group of fungi (Horton and Bruns 2001; Bridge et al. 2005; Martin and Rygiewicz 2005; Seifert 2009; Bellemain et al. 2010; Schoch et al. 2012). More than 100,000 ITS sequences of teleomorphic ascomycetes are deposited in international nucleotide sequence databases (Baturo-Cieśniewska et al. 2020). Even though, many sequences of correctly identified species are deposited in databases, there are some sequences with technical errors, incorrectly named species, atypical chimeric ITS sequences, and sequences verified only at the generic level or above which makes reliable problems in species identification (Nilsson et al. 2009, 2014; Hongsanan et al. 2018). The ITS locus in species of some genera has minimal molecular variation (Andrew et al. 2009) and cannot resolve species (de Hoog and Horré 2002).

Further, the ITS region has additions and deletions in some groups of fungi and is not equally variable in all taxa (Nilsson et al. 2008). Most databases are improving sequence availability. The lack of sufficient ITS sequences especially in species-rich, morphologically indistinct genera, can therefore be problematic (Seifert 2009). A high-fidelity, universal primer pairs for amplification of the EEF1A1 gene has been developed as secondary DNA barcodes for the fungi (Stielow et al. 2015). However, the availability of deposited reference sequences of EEF1A1 gene in databases is poor (Meyer et al. 2019). Further, mycologists who have deposited sequences in the NCBI database determine the species name by themselves. The introduction of incorrectly identified sequences creates in errors because users adopt incorrect species names (Ko et al. 2011; Nilsson et al. 2012, 2019). In most species, the nucleotide composition of the ITS sequences in the single species is identical or slightly varied. The ITS locus has certain interspecific variations (Nilsson et al. 2008; Talgø et al. 2010). These interspecific variations in ITS sequences may be higher than 1% due to technical errors, may be evidence to be a new species (Jeewon and Hyde 2016).

As an example, 245 ITS sequences of *Diaporthe eres* obtained from GenBank and those sequences were aligned using default settings of MAFFT v.7 with *Diaporthella corylina* (CBS 121124) as the out group. Maximum like-lihood analysis was performed after excluding 105 identical sequences and then resulted in 14 different clades



Fig. 4 Phylogram generated from maximum likelihood analysis based on ITS sequence data of *Diaporthe eres*. The tree is rooted with *Diaporthella corylina* (CBS 121124) and ex-epitype strain of *D. eres* is in red bold. Subclades which are representing the different type of sequences are labeled \boldsymbol{A} to \boldsymbol{N}



Fig. 4 (continued)

(Fig. 4) representing 14 types of sequence patterns. The ex-epitype strain of *Diaporthe eres* (AR5193) clustered in clade A, while clades B-E showed around 1% base-pair difference with sequence pattern of clade A (A-B:1.1%, A-C: 1.3%, A-D:1.1% A-E:1.3%). However, clades F-N

showed more than around 1% base pair variation than clades A (A-F:4.0%, A-G:3.7%, A-H:3.9%, A-I:4.4%, A-J:4.4%, A-K:4.6%, A-L:5.2%, A-M:5.0%, A-N:5.4%). According to the guidence of Jeewon and Hyde (2016), 1% position ambiguities in ITS with 450 base pairs can be a

new species. In our analysis, B-E types of sequences show fewer base-pair differences than other patterns of sequence types showing certain interspecific variations (Nilsson et al. 2008; Talgø et al. 2010). However, clades F-N show more base-pair differences than the epitype strain due to technical errors of sequencing or misidentification of fungi. Therefore, newly obtained strains should always be compared with the sequences of ex-type strains and extype strains should be included in phylogenetic trees.

Further, ITS based species identification may not be suitable when interspecies nucleotide variations are less (Baturo-Cieśniewska et al. 2020). Sclerotinia sclerotiorum and S. trifoliorum are causative agents of clover rot disease and the symptoms are identical (Vleugels et al. 2012). ITS sequences of Sclerotinia species are almost identical (Freeman et al. 2002). Sclerotinia sclerotiorum differs from S. trifoliorum by one nucleotide, guanine or thymine in position 120 (Njambere et al. 2008; Baturo-Cieśniewska et al. 2017). Therefore, ITS based species identification is not suitable for this situation. Interspecific and intraspecific variation of ITS sequences is often low for some species. Phacidium fennicum differs from P. lacerum by two base pairs while others share identical ITS sequences but are morphologically distinct (Crous et al. 2014; Tanney and Seifert 2018). Therefore, use of ITS sequences together with morphology and at least a protein coding gene should be emphasized (Pryor and Michailides 2002; Schubert et al. 2007; Samson et al. 2014; Robbertse et al. 2017; Bensch et al. 2018).

Next generation sequencing (NGS) and meta-genomic DNA

NGS or high-throughput sequencing methods are the modern sequencing technologies (van der Heijden et al. 2008). These approaches have several advantages in that an initial knowledge of the genome or genomic features are not required, single-nucleotide resolution facilitates detection of related genes, alternatively spliced transcripts, allelic gene variants and requires less DNA/RNA as input and has higher reproducibility (Peršoh 2015). Diversity and distribution patterns of teleomorphic ascomycetes in ecosystems give important evidence on species number, ecosystem functions and stability (Schmit and Lodge 2005). Microscopic observations and culture-dependent approaches cannot efficiently calculate the number of teleomorphic species of Ascomycota in environmental samples such as soil, water, and air as the majority of them is generally complex, unculturable and not visible without a microscope (Mitchell and Zuccaro 2006; Stewart 2012; Hongsanan et al. 2018).

Authentic physical specimens do not exist for these species and they are therefore known as "dark taxa" (Tedersoo and Smith 2017; Ryberg and Nilsson 2018). There are no given any formal names to genus and species level, and hence types are not designated (Taberlet et al. 2012; Herder et al. 2014; Hawksworth et al. 2016). Article 40 (Valid publication of names; section 2: Names of new taxa) in Shenzhen Code states that a new taxon at the rank of genus or below published on or after 1st January 1958 is valid only when the type specimen of the name is indicated (Turland et al. 2018). Therefore, high-throughput sequencing approaches are needed to reasonably characterize and estimate those fungal communities.

However, there are some limitations in meta-DNA sequencing and many mycologists disagree with validating names. Concerns of the mycological community against the premature introduction of DNA-only based nomenclature have been presented (Hongsanan et al. 2018; Thines et al. 2018; Zamora et al. 2018). However, DNA meta-barcoding has the potential to provide a much better understanding the species diversity and richness in fungal communities (Heeger et al. 2018) and meta-genomic DNA has provided clues as to where and which teleomorphic ascomycetes can be found and this is applicable in estimation of the species number, but it cannot be used for classification.

Environmental samples are poorly linked to species-based databases (Hibbett et al. 2011). Therefore, errors in communication have occurred from one publication to another when using the system databases (Hibbett et al. 2011; Ryberg and Nilsson 2018). Thus, metagenomics DNA-based nomenclature can be accepted at least for species number estimations and fungal diversity studies (Hawksworth et al. 2016; Ryberg and Nilsson 2018). There is uncertainty when naming a species, if the morphology is indistinct or DNA sequences fail to resolve species relationships. Eventhough the species lack morphology, genomic and ecological significance supported this introduction. Khan et al. (2020) introduced two new species, Archaeorhizomyces victor and A. secundus (Archaeorhizomycetes, Taphrinomycotina, Ascomycota) based on the distinct base pairs comparison of the internal transcribed spacer region ITS1 and ITS2 with similar taxa obtained from environmental DNA.

Buèe et al. (2009) found 1000 operational taxonomic units (OTUs) in 4 g of soil. A study on litter decomposition in temperate forests based on meta-DNA confirmed that Ascomycota species have highest relative abundances in the later stages of decomposition (Voříšková and Baldrian 2013). Therefore, high-throughput sequencing methods can be used for fungal diversity estimates. Further, species estimates from different studies may not be compared directly due to differing laboratory standards, protocols and data processing methods (Lindahl et al. 2013; Purahong et al. 2017). However, determination of a common NGS platform, primer pairs and re-analyzation of missing or non-matching gene regions may allow comparison of the results of NGS across different studies and biomes (Nilsson et al. 2011).

How to avoid errors in species identification and estimation of teleomorphic ascomycetes

Species identification and description gives fundamental data for prediction of species number. Hence, documentation of species names in data bases without errors is important. Here we discuss some guidelines to improve this.

Documentation and personal errors

DNA sequences in public databases are annotated by the submitting authors and mostly, further validation by the curators in databases is not often. This approach creates erroneous taxonomic sequence labels (Kozlov et al. 2016). The novel sequences are annotated based on existing ones and mislabeled sequences induce downstream errors. Some sequences in databases are confusing because the same species are classified with different names (Ashelford et al. 2005). This may increase synonyms which are hidden under previous classifications (Bidartondo 2008; Nilsson et al. 2008; Robbertse et al. 2017). Therefore, the taxonomic credibility in sequence databases is with errors (Binder et al. 2005; Bridge et al. 2005; Nilsson et al. 2006). Blast similarities of sequences sometimes give uncultured or unverified sequences and names not identified to species level (Baturo-Cieśniewska et al. 2020). The major reason for these unidentified or insufficiently identified sequences in public databases is that most international journals require all sequences used in the manuscript to be deposited (Ryberg et al. 2008). Errors in protein coding gene sequences give wrongly translated protein sequences which are sometime named as "unverified". Further, all species in a genus necessary to form a well-supported, monophyletic clade with the type strain of the type species in the genus and the newly introduce species must be in this monophyletic clade without distantly cluster from generic type.

Senanayake et al. (2016) studied the taxonomy and phylogeny of phomatospora-like taxa and showed that *Paramicrothyrium chinensis* H.X. Wu & K.D. Hyde has 99% similarity to *Phomatospora biseriata*. Wu et al. (2011) introduced *Paramicrothyrium* based on *P. chinensis* using morphology and molecular data. However, the combined LSU and SSU analysis (Wu et al. 2011) showed *Paramicrothyrium chinensis* as morphologically close to *Microthyrium*, but phylogenetically distant from *Microthyrium*. Further, Singtripop et al. (2016) showed that *Paramicrothyrium chinensis* (IFRDCC 2258) clusters with *Chaetothyrina mangiferae* (Micropeltidaceae) with high support. Hence, these sequences might have some errors (Senanayake et al. 2016). Voglmayr et al. (2018) revealed problems in some xylarialean sequences. The LSU part included in the ITS sequences of KP297406 and KP297396 which were deposited as *Anthostomella helicofissa* and *A. forlicesenica* respectively, in NCBI searches show obvious variations in the sequence alignment. Further, the LSU sequence of KP340547 was revealed as xylarialean by BLAST searches; however, it has 60 nucleotides difference in LSU sequences with other *Anthostomella* species. A BLAST search of LSU and RPB2 sequence of KP340538 and KP340524 from MFLUCC 14-0007 (*A. forlicesenica*) revealed various pleosporalean taxa as the closest matches. Therefore, most scientific journals have recently made it a prerequisite that the sequence data and the alignments of novel taxa must be provided for review to have better quality control.

There is a 1% intra-species variation within Aspergillus niger (Henry et al. 2000). The ITS sequence of Aspergillus niger (MK461010) is identical to ITS sequences of Alternaria alternata (Baturo-Cieśniewska et al. 2020). Further, the ITS sequences of Aspergillus niger (MK461010) shows 10% inter-species variation of ITS sequences of other A. niger strains. This probably suggests a misnomer of the MK461010 sequence. This happens because the person who deposits sequences in the NCBI database determines the species affiliation. The deposition of incorrectly identified sequences creates errors and mistakes because users obtain incorrect species names (Ko et al. 2011; Nilsson et al. 2012). About 65% of the GenBank entries are mislabeled sequences or from poorly characterized vouchers (Leray et al. 2019).

Common, standard data base for taxonomic information of fungi

Recently, most scientific data are documented in websites (Hyde et al. 2020b). Websites gives quick and easy access, sorting and filtering facilities and safeness for data. Currently, there are several databases for molecular, taxonomic and ecological information of teleomorphic ascomycetes (Rossman 1994). There is no standardized protocol for introducing new teleomorphic species in Ascomycota (Seifert and Rossman 2010; Senanayake et al. 2020a). However, there are some formal requirements for proposing names that are imposed by the Nomenclatural Codes (Turland et al. 2018). All the taxonomic information must be available in public for future researchers including taxonomic characters, descriptions, prologues, sequence data, phylogenetic analysis, type specimens, ex-type cultures and ecological data. However, the mycologists have their own preferences and different policies when selecting databases to deposit taxonomic information. Therefore, taxonomic data are scattered in various databanks and this makes difficulties when comparing phenotypic characters. An introduction of "combined platform for taxonomic information of teleomorphic ascomycetes" with a unique identity number for each species is essential. Then, the entire phenotypic, genotypic, chemotaxonomic, ecological, evolutionary, biological and classification data of a teleomorphic species in Ascomycota can be obtained and compared easily. All the data of species can be updated with the newly obtain information. This kind of universal database would minimize errors due to poor updating and also personal arguments. Hibbett et al. (2016) listed commonly used databases and tools for fungal classification and identification.

The number of described, and accepted species in Ascomycota has been counted since 1943 through Ainsworth and Bisby's Dictionary of the Fungi and currently, the Catalogue of Life web site (https://www.catalogueoflife.org/index?taxon Key=F), which is updated annually through the Species Fungorum, The Integrated Taxonomic Information System and The Global Information System for Lichenized and nonlichenized Ascomycetes outputs.

A standard approach to demarcate species boundaries and describe teleomorphic species in Ascomycota

As there are different approaches to designate a species, mycologysts use different methods according to their requrements and those approaches demarcate species boundaries based on different criteria. Hence, the species numbers vary from one to another and this results complications in species identification and descriptions in Ascomycota (Maharachchikumbura et al. 2021). Therefore, it is necessary to designate a common criterion for species introduction and description (Pažoutová et al. 2013; Kamil et al. 2018). The number of described teleomorphic ascomycetes has increased with the use of molecular techniques for species delimitation. Most teleomorphic ascomycetes introduced earlier than the 1990s lack molecular data from their type collections (Wu et al. 2019a). Hence, it is impossible to compare genotypic characters of fresh collections with genotypic characters of available materials. Therefore, mycologists may misinterpret those collections as new species. Introduction of previously described teleomorphic ascomycetes as new species with molecular data has increased the number of teleomorphic species in the Ascomycota. Further, this value has accelerated with the ending of the separate naming of teleomorph and anamorph of the same species. Therefore, it is necessary to follow well-defined, sets of criteria when introducing a new species and obtain molecular data from the new collection revealing the genetically close taxa. Sequence data should be obtained from both conserved and variable gene regions and all the genes or loci are blasted with GenBank for base pair similarities. Morphological characters could be compared with all phylogenetically similar taxa to ensure that it is not an existing species and also it should be compare with all species in the genus which molecular data unavailable. Ecological data, colony characters, and secondary metabolites provide additional information. Sporulation or conidiation of cultures is important. Describing both teleomorph and anamorph characters and linked them as one is required.

Discussion and conclusion

Assessment of the actual number of teleomorphic species in Ascomycota and their diversity is important for systematics, resource utilization, industrial production and environmental management (Maharachchikumbura et al. 2021). Traditionally, species estimations were based on the numbers of fungi recorded on particular plants and insects. There are several estimations such as around 0.1 million by Bisby and Ainsworth (1943) to 2.2-3.8 million by Hawksworth and Lücking (2017). Traditional species estimation approaches have several drawbacks. The major limitation of these estimates is that they only focus on the fungi that either produces fruiting bodies, which can be identified using a microscope, or those that can be easily cultured on artificial media (Duong et al. 2006). Many ascomycetous endophytes do not sporulate in culture (White and Cole 1986), while some hostspecific species need host tissues to sporulate. Therefore, it is a bias estimate of teleomorphic ascomycetes based on microscopic examination of fruiting structures on substrata or media (Guo et al. 2001; Promputtha et al. 2004). Several studies have shown that most species are singletons found only once (Anslan et al. 2016) or found in only a few locations (Wu et al. 2013) however with plants and animals, some teleomorphic ascomycetes are endemic species. Even though fungi are ubiquitous, individual fungal species are restricted to a specific niche. Therefore, the distribution of teleomorphic ascomycetes is distinct and probably the fungal species number could be much higher than the current estimates (O'Brien et al. 2005; Blackwell 2011).

The development of molecular techniques, such as next generation sequencing has helped identify the previously undescribed diversity in the teleomorphic ascomycetes (Raja et al. 2017; Wilson et al. 2019). Obtaining molecular sequence data from environmental samples from a wide range of localities and substrata has generated a new source of data for estimating species numbers (Wu et al. 2013). The numerous sequences obtained through high-throughput sequencing do not have any close matches with described fungi in sequence databases (Lindahl et al. 2013) and this shows that the current estimated species number is too low. The occurrence of more uncultured teleomorphic ascomycetes also supports that the diversity of fungal species is in underestimation (Hawksworth 1991). However, the main problem in estimates is merging data obtained from traditional culture-based approaches with data obtained from high-throughput sequencing methods (Buée et al. 2009; Kubartová et al. 2012; Dissanayake et al. 2018). Several studies disagree to use sequences derived from high-throughput sequencing methods because of various reasons such as NGS detects only the predominant fungi in a sample instead of all available species (Dissanayake et al. 2018), specific PCR primers need to be developed for some ascomycetes, and the ITS locus is longer than the NGS sequences (Kruse et al. 2017). Further, many ascomycetous species are not well-separated into well-resolved species with a single gene region. Therefore, NGS are suitable to separate fungi only at the genus level (Purahong et al. 2017).

OTUs are also detected by other molecular approaches based on DNA sequence data such as TGGE (thermal gradient gel electrophoresis), DGGE (denaturing gradient gel electrophoresis), SSCP (single-strand conformation polymorphism), RFLP (restriction fragment length polymorphism), TRFLP (terminal restriction fragment length polymorphism), ARDRA (amplified ribosomal DNA restriction analysis), 454 pyrosequencing and illumina MiSeq sequencing can be used to establish a better estimate of species numbers (Hawksworth and Lücking 2017). These methods provide species-specific sequences and therefore, the OTUs generated in these methods reveal an enormous, unprecedented magnitude of fungal diversity.

Wu et al. (2019a, b) estimated that the total fungal diversity is about 12 million species based on meta-DNA and culture-independent methods. In culture-dependent methods, teleomorphic species in Ascomycota are mostly collected and isolated based on their conspicuous fruiting bodies. However, more fungal species are detected by cultureindependent approaches and the fungal species detected by culture-independent and culture-dependent approaches often do not overlap (Zhang et al. 2010). Therefore, cultureindependent methods are important in estimates of the teleomorphic species in Ascomycota. Hence, neither culturedependent nor culture-independent method can accurately determine the structure of a given community. Because of the intrinsic selectivity of each method, the probability of a given species being detected often differs with the method (Zhang et al. 2010).

The above-mentioned problems could be avoided with appropriate morpho-molecular phylogenetic approaches and proper taxon sampling. Furthermore, polyphasic taxonomy should be the preferred approach when introducing new teleomorphic species in Ascomycota, as the conclusions of one method may be eliminated or justified with evidence from the other methods (Maharachchikumbura et al. 2021). Furthermore, molecular data of more extype strains should be included in the phylogenetic analyses as these would provide more clarification where misidentified pleomorphic fungi could be correctly placed. This has not been followed universally by mycologists, thus leading to misidentifications of many fungal species. The best approach to avoid errors in future taxonomic studies of teleomorphic ascomycetes is to focus on increasing missing sequence data and linking those data to digital voucher specimens (Lücking et al. 2020; Jayawardene et al. 2021).

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Declarations

Conflict of interest The authors declare that there is no confict of interest.

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