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Fungi species description rates confirm high global diversity and suggest half remain unnamed

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Abstract

Global estimates of the number of species of Fungi have ranged from 1.5 to 13.2 million, but have been based more on opinion and simple ratios than quantitative assessment. We analysed trends in the rate of description of fungal species over four centuries, noted the use of molecular methods in species delimitation, and used a statistical model designed for such data to predict future trends. A total of 144,035 fungal species were analysed, along with smaller species groups extracted from the core dataset that approximated biological and ecological traits. The groups explored included fungi of medical significance (728 spp), those associated with the marine environment (972 spp), rust and smut fungi (9,125 spp), arthropod ectoparasites of class Laboulbeniomycetes (2,376 spp), mushroom-forming fungi of class Agaricomycetes (37,717 spp), the budding yeasts of subphylum Saccharomycotina (1,165 spp), the class Dothideomycetes (30,912 spp), and lichenized fungi of classes Lecanoromycetes and Arthoniomycetes (12,154 spp). There was an acceleration in overall fungal description rates within the last two decades accompanied by the increased use of genetic data in new species descriptions. Mushroom-forming, lichenized, and plant-associated fungi were predicted to experience the greatest increase in new species. Increased description rates are supported by an increase in the number of authors describing species. However, the number of species described per author in a year has been declining since 1875. Because less than 10% of currently accepted fungal species have molecular data associated with corresponding type specimens, genetic data should not be used to discriminate new species without associated phenotypic information. An additional 68,750 species (48%) were predicted to be described this century, making Fungi the least well-described Kingdom assessed to date.

Highlights

- Global estimates of how many species may exist of fungi have ranged up to 13 million.

- We studied trends in the rate of description of 144,035 species, including those of medical significance, marine, rust and smuts, arthropod ectoparasites, budding yeasts, lichenised and mushroom forming fungi.

- The last two decades have seen a remarkable acceleration in rates of species description, primarily due to use of molecular data, and numbers of authors of new species.

- The use of genetics to discriminate new species is severely limited by the fact that less than 10% of described species have reference molecular information (so genetic data may belong to an already described species).

- Assuming the recent (molecular) species have not been previously described, we predict an additional 68,750 new species will be described this century, making Fungi the least well described Kingdom of life to date.

Keywords: biodiversity, description rates, diversity, fungi, molecular data, species concept, species richness, taxonomy.

Introduction

The number of species that may exist indicates how much we know and do not know about life on Earth at a most fundamental level, and thus has real-world implications for biodiversity and conservation science at a time when biodiversity loss has reached crisis status. Estimates of global species richness have become more robust with the availability of validated species inventories assisting in the resolution of synonyms to prevent inflation of known species numbers (Costello et al. 2012, 2013). The majority of recent assessments of how many species have been described indicate that over two-thirds of Earth's animal and plant species are described (Table 1). However, the diversity of Fungi remains a topic of debate (Costello & Chaudhary 2017).

Fungi have experienced a long history of varying global species estimates (Table 2). Hawksworth's (1991) estimate of 1.5 million has been widely cited but was based on a vascular plant to Fungi ratio extrapolated from Britain to the world, and later revised to between 2.2 and 3.8 million possible species (Hawksworth and Lücking 2017), while fitting a regression curve to described species yielded a prediction of 12 million species (Wu et al. 2017), and a recent synthesis of estimates suggests 2.5 million species (Niskanen et al. 2023). However, taxonomic ratios cannot be used for global estimates because taxa have not formed species at equal rates across habitats, environments, latitudes and geographically, as shown for marine taxa (Costello et al. 2010, Costello 2015), parasites (Costello 2016), and Fungi (Peay et al. 2010, Tedersoo et al. 2014, Senanayake et al. 2022). To date, estimates of the species richness of Fungi have lacked quantitative approaches and/or made misguided assumptions: see detailed review by Niskanen et al. (2023). A more robust approach is to apply statistical models to the trends in species description, because this builds on global scale data (rather than local), can account for variation in the rate of descriptions in new species, and considers how changes in diagnostic methods and taxonomic effort may affect the trend. To date, such a quantitative approach has not been attempted for Fungi (Niskanen et al. 2023).

Hawksworth and Lücking (2017) noted an increase in the number of newly introduced fungal species names post-2010, which they attributed to the increased use of molecular techniques in species delimitation. Description rates are also influenced by taxonomic effort, which can be estimated from the number of people involved in describing species and publications. While the field of taxonomy has been viewed as a diminishing practice anecdotally (Lee 2000, Hopkins & Freckleton 2002), the fact that the number of people describing species has increased over five-fold since the 1950s and continues to rise

Table 1: The proportion of species described across the range of global taxa (excluding fungi) listed chronologically with groups of how well-described the taxon was estimated to be.

Taxa	Proportion described	Reference
Butterflies	> 80%	Robbins and Opler 1997
Marine species in Europe		Wilson and Costello 2006
Birds		Bebber et al. 2007, 2014
Marine pinniped mammals		Woodley et al. 2008
Plants, amphibians, mammals in Brazil		Pimm et al. 2010
Flowering plants		Joppa et al. 2011
Land mammals		Giam et al. 2012
All land, freshwater and marine animals		Costello et al. 2012
All mammals		Burgin et al. 2018
Water bugs		Polhemus and Polhemus 2007
Extant and fossil bryozoans		Pagès-Escolà et al. 2020
Marine fish	> 70%	Eschmeyer et al. 2010,
All marine species in Europe		Costello and Wilson 2011
Sea anemones		Fautin et al. 2013,
Scale insects		Deng et al. 2016
Micro and macro algae	> 60%	Guiry 2012, DeClerck et al. 2013
All marine species		Appeltans et al. 2012
Neotropical catfish		Ota et al. 2015
All parasites		Costello 2016
All amphipod crustaceans		Arfianti et al. 2018
All polychaete worms		Pamungkas et al. 2019
Soil ciliates	> 50%	Chao et al.2006

Table 2: Past estimates of the number of fungi species that may exist and methods of determination (see also Wu et al. 2017).

Species estimate (*millions*)	Method	Reference
0.6	Higher taxonomic ratios	Mora et al., 2011
0.7	Ratio (vascular plant: fungi) accounting for geographic distribution & endemism	Schmit & Mueller, 2007
1.5	British vascular plant: fungi ratio applied globally	Hawksworth, 1991
1.5	Host specificity of tropical endophytes	Arnold et al., 2000
2.5		Niskanen et al. 2023
2.2 — 3.8	Ratio plant: fungi supplemented by DNA discoveries	Hawksworth & Lücking, 2017
3.5 — 5	Ratio of plant: fungi genetic diversity in local soil samples	O'Brien et al., 2005
12	Ratio of culture-dependent: culture-independent	Wu et al., 2019
165.6	Host-specificity assumptions (plant and animal)	Larsen et al., 2017

contradicts this (Joppa et al. 2011a, Costello et al. 2012, Costello et al. 2013b, Bouchet et al. 2016). It is possible that this increase in authors reflects relatively more part-time authors who may only describe one species, or shorter author-publication lifetimes, as may happen if they move out of taxonomy. However, analyses of authorship trends in animals found no evidence of changing proportions of part-time authors (Appeltans et al. 2012, Costello et al. 2012, 2013). Whether this applies to Fungi remains to be studied.

Using DNA sequences to describe and name new species can be problematic given the ongoing debates among mycologists regarding how these sequences relate to formal species or populations (Seifert 2017, Wu et al. 2019). In addition, equating novel sequences found in the environment to novel species, rather than belonging to already described species that have not yet been sequenced, means new species may turn out to be synonyms of previously described species currently without genetic data (Nagy et al. 2011). Despite such concerns, species delimitation of Fungi based solely on genetic information has been occurring (Dupérré 2020).

Here we examined and modelled trends in descriptions of all and sub-groups of 144,035 species of Fungi, changes in the numbers of authors that indicate effort, and availability of molecular data to distinguish species. Our modelling of species discovery uses a stochastic process model called the non-homogeneous renewal process. We separately analysed trends in sub-groups of economic and ecological importance, including medical, plant pathogens, arthropod ectoparasites, and mushrooms. While our analyses suggest more modest estimates of how many Fungi may exist, they also indicate a relatively higher proportion of undescribed species than for animals and plants.

Materials & Methods

Data Sources

Analyses were performed on data sourced from Index Fungorum (Royal Botanic Gardens Kew et al. 2019) and Species Fungorum (Kirk 2019) in September 2019. Data included categories for taxonomic rank, authorship details, publication dates, previously recognized fungal species' names, and the currently accepted species' names. Only unique, currently accepted species names and their most recent taxonomic ranks matched to the authorship and publication details of their earliest assigned name were retained for analysis to ensure an accurate representation of the first year a species was described. The final dataset consisted of 144,035 unique current species names (Cunningham 2020a). Details of data selection are in the supplementary data (Table S1) (Cunningham 2020c).

We expected some groups to be more comprehensively described due to their importance to society, such as being pathogenic to food plants, of popular interest as food, or of medical interest. Species lists for eight subgroups were extracted from the curated dataset based on higher taxonomic rankings that approximated biological and ecological traits according to literature, or group-specific databases:

1. 9,125 species of rust and smut Fungi (plant pathogens), namely Orders Pucciniales and Ustilaginales (Barnes 1979, Lorrain et al. 2019)

2. 2,376 species of arthropod ectoparasites, the Class Laboulbeniomycetes (Weir 2017)

3. 37,717 species of mushroom-forming Fungi, the Class Agaricomycetes (Hibbett 2007)

4. 1,165 species of budding yeasts, the subphylum Saccharomycotina (Nagy et al. 2017)

5. 12,154 species of lichenized Fungi, the Classes Lecanoromycetes and Arthoniomycetes (Tehler & Wedin 2008, Schoch & Grube 2015)

6. 30,912 species of diverse saprobes (saprotrophs) and plant-associated Fungi (including endophytes), the Class Dothideomycetes (Hyde et al. 2013, Goodwin 2014, Schoch & Grube 2015).

7. 972 species of marine-associated Fungi excluding microsporidia (Horton et al. 2019).

8. 728 species of medically significant fungi (Kidd et al. 2016, Westerdijk Fungal Biodiversity Institute 2019)

Due to the taxonomically diverse nature of both the marine-associated and medically significant fungal subgroups, additional sources were required to construct species lists found in Cunningham (2020a). Details of data selection for these groups are in the supplementary data (Tables S2 and S3) (Cunningham 2020c).

Data Analysis

The Non-Homogenous Renewal Process (NHRP) model of Wilson & Costello (2005) was fitted to the rate of species description data calculated for all Fungi and the eight subgroups using the following equation adopted from Arfianti et al. (2018):

$$\text{Number discovered by year } t = \frac{N}{1 + \exp\left(-N\beta\left(t - \alpha\right)\right)}.$$

Parameters:
N = Total number of species to be discovered
α = Year of maximum rate of discovery
β = Describes overall rate of discovery (larger β implies a faster rate)
exp = exponential

The equation for the number of species discovered follows an 'S'-shaped curve, with an initial slow rate of discovery that increases before levelling off as the majority of species in a group are described. The model has been used to estimate numbers of species across a diverse range of taxa such as bryozoans (Pagès-Esola at al., 2020), amphipod crustaceans (Arfianti et al., 2018) and isopod crustaceans (Hartebrodt et al. 2023) as well as making estimates of global marine (Appeltans et al., 2012) and all (Costello et al. 2012) species diversity. In contrast to more simplistic extrapolation methods which fit simple curves (and thus will not reach an asymptote), it provides 95% probability intervals based on the temporal variation in the number of species described. The model was applied to description data for all Fungi until 1990 and 2019 separately so as to note differences in predictions generated when including and excluding the molecular era.

The number of first authors for accepted species were counted as an indicator of taxonomic effort. Only the first author was counted to avoid the trend in recent decades for species to be described by multiple authors. Thus, our estimate of the number of people describing new species of fungi is an underestimate. Descriptions made in 2019 were excluded due to the incomplete data for that year. To detect changes in the trend of authors, we used breakpoint analysis in the segmented package (Muggeo 2008, Muggeo 2017) in R version 3.6.1 (R Core Team 2019). The increase in authors may be due to relatively more authors describing only one species over time (Appeltans et al. 2012, Costello et al. 2012). Therefore, the proportion of 'one-time' authors occurring within each decade was

calculated, as was Pearson's skewness coefficient for the number of species described by different authors per decade to explore changes in the distribution of estimated taxonomic effort over time.

Use of Molecular Data in Species Delimitation

The literature was sampled to denote changes in fungal species character descriptions and use of molecular techniques over the past 25 years. Since description methodologies vary between fungal groups, for example, lichenized fungi incorporate the characterisation of insoluble lichen pigments (e.g., van den Boom & Magain 2020) and budding yeasts use nutrient assimilation tests (e.g., Buchanan et al. 2017), it was decided to focus solely on the class Agaricomycetes (mushroom-forming fungi) due to its size and similar trend in description rates to that observed for the Kingdom.

SCOPUS was searched using the search-string '(new-speci* OR new-tax*) and (Polyporales OR Agaricales OR Cantharellales...) listing orders recognised within the Index Fungorum dataset. Search results were organised into five-year time periods including 2015 to 2019; 2010 to 2014; 2005 to 2009; 2000 to 2004 and 1995 to 1999. All bibliographic information for search results were exported as .csv files in March 2020 and saved as individual .xlsx files for each period. Entries were randomized within MS Excel and 180 taxonomic publications (36 per period) were selected for full-text review. Information collected included authors, publication date, source journal, number of novel species described and presence of phenotypic and genotypic character descriptions.

Analyses of the constructed dataset used the data analysis add-in package of MS Excel (2010) and IBM SPSS statistics V.23 (IBM Corp 2015). This included a Mann-Whitney U test on the number of species described per publication across categories of molecular consideration to identify if the use of molecular techniques could be contributing to increased species descriptions within publications. The constructed dataset and bibliographic data from which it was constructed are available in Cunningham (2020a).

A list of species type specimens with DNA data recorded in the National Centre for Biotechnology Information (NCBI) was downloaded in April 2020 from https://www.ncbi.nlm.nih.gov/nuccore. This was analysed within MS Excel (2010). The curated list included 12,996 unique names matching species names found within Index Fungorum and can be accessed at Cunningham (2020b).

Results

Description Rates

Periods of increased fungal species description occurred around the 1860s to early 1900s, followed by a noticeable dip around World War II (Fig. 1). Description rates subsequently recovered to early 20th Century levels over the 1950s and 1960s, remaining consistent until 2000. From the year 2000, fungal
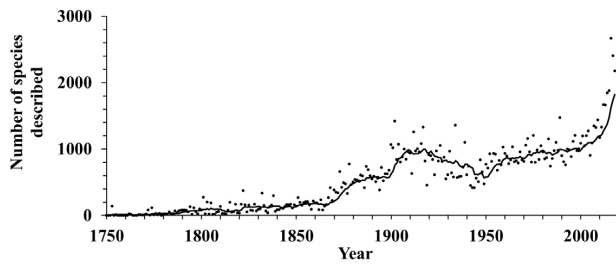
Figure 1. The number of all fungal species described per year for the Kingdom Fungi from dataset in Cunningham (2020a). Trend line displays a 10-year moving average.

species descriptions have notably increased. While an average of 925 fungal species were described per year from 1950 to 1999, an average of 1,510 species were described per year between 2000 to 2018.

The trends in description contrasted between the eight groups of Fungi analysed. Only 8% of all 'grouped' species were described before 1870 (Fig. 2). Peak rates of description for arthropod ectoparasites and rust and smut fungi occurred in the early 20th century and have since declined. All remaining groups experienced peak description rates within the last 20 years, apart from marine-associated fungi, which exhibited peak rates of description in the late 20th century.

Mushroom-forming and lichenized fungal groups both experienced substantial increases in species descriptions within the 21st Century (Fig. 2). The trend for new species descriptions occurring among the mushroom-forming, saprobes and endophytes, and medically important fungi was similar to the trend for all Fungi with a marked near-linear increase since 2010. However, mushroom-forming and medical fungi descriptions declined from the 1980s to 2010, and saprobes from the 1960s to 1990s. In contrast, the lichenized fungi and budding yeasts experienced no remarkable increases in species description until 2000, but after 2010 rates slowed. Description rates of the rust and smut fungi have been generally declining since 1910. The arthropod parasites had several peaks in species descriptions between 1900 and 1940, followed by a period of practically no new species descriptions until the 1970s (Fig. 2). A sharp decline in marine species descriptions was observed since 2000.
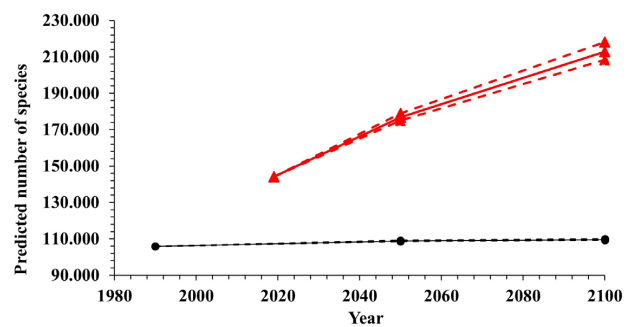
Future Predictions

The Non-Homogenous Renewal Process Model predicted, with 95% probability, 32,800 additional fungal species may be described by the year 2050, and 68,750 by 2100 based on data from 2018 (Table 3, Figure 3).

Based on the model prediction from 2019, a total of 212,785 fungal species may be described by the end of this century, increasing the number of species by 48% (Table 3). If the recent burst using molecular data is excluded by predicting from 1990, then only 109,601 species would be described by 2100 (an increase of only 4%). More species per sub-group were predicted when the model was extended from 2019 than 1990, except in the mushroom-forming,
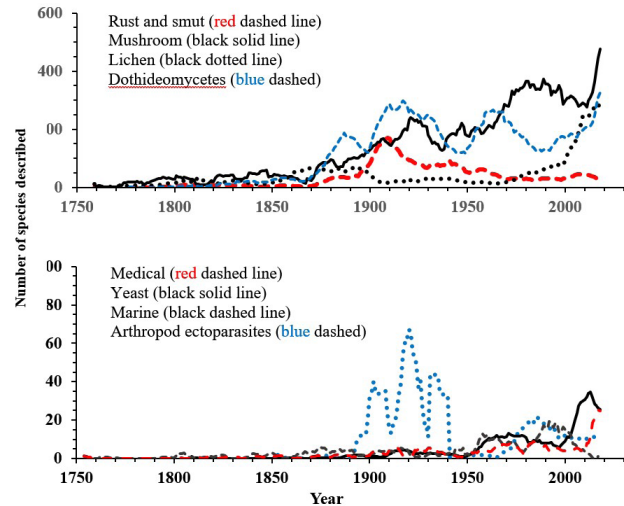
Figure 2. The number of fungal species originally described per year for ecological and taxonomic subgroups. Lines are a 10-year moving average.

Figure 3. A comparison of the effect of predicting future species descriptions from the number of accepted species recognised by 2018 (red) and 1990 (black) for all Fungi and their predicted median increase by the years 2050 and 2100 (solid line) with 95% probability intervals (dashed lines).

marine, and saprobic fungi (Table 3, Figure 4). With the exception of lichenized fungi and rusts and smuts, a similar number of species was predicted for 2100, regardless of whether the data to 1990 or 2019 were used.

While more species rich groups of Fungi generally had more species remaining to be described, the relative proportions varied greatly (Table 3). Budding yeasts, medical and lichenised groups would more than double in their number of species, while very few new arthropod parasite species were predicted. The mushroom-forming fungi, marine fungi, and rusts and smuts were predicted to increase by 46–62% (Table 3).

Author Trends

During the early stages of species discovery a few authors can describe many species. Thus, breakpoint analysis found that until 1875 the number of species described per number of authors for all Fungi was

Table 3: Median prediction of number of species to be described from 1990 and 2019 to the years 2050 and 2100, with expected proportional increase this century using the NHRP model. See Figure 3 for trends and confidence limits.

| Group	Named by		1990 to	2019 to	1990 to	2019 to	% increase by 2100	
	1990	**2019**	**2050**	**2050**	**2100**	**2100**	***1990**	***2019**
All Fungi	105,871	144,035	2950	32,800	3730	68,750	4	48
Mushroom forming	27,548	37,717	**16,200**	10,500	**23,900**	23,200	87	62
Diverse saprobes	24,131	30,912	**6,590**	5,000	7,950	9,100	33	29
Lichenized	6,572	12,154	2,260	4,300	3,610	12,600	55	104
Rusts & Smuts	8,148	9,125	270	2,000	300	4,200	4	46
Arthropod ectoparasites	2,040	2,376	12	100	13	160	1	7
Budding yeasts	562	1,165	515	750	649	1,570	115	135
Marine	744	972	**470**	260	**860**	570	116	59
Medical	468	728	320	340	460	910	98	125
Total sub-groups	**1842,439**	**1793,449**	**1612,05**	**1471,8**	**2317,46**	**1690,67**		
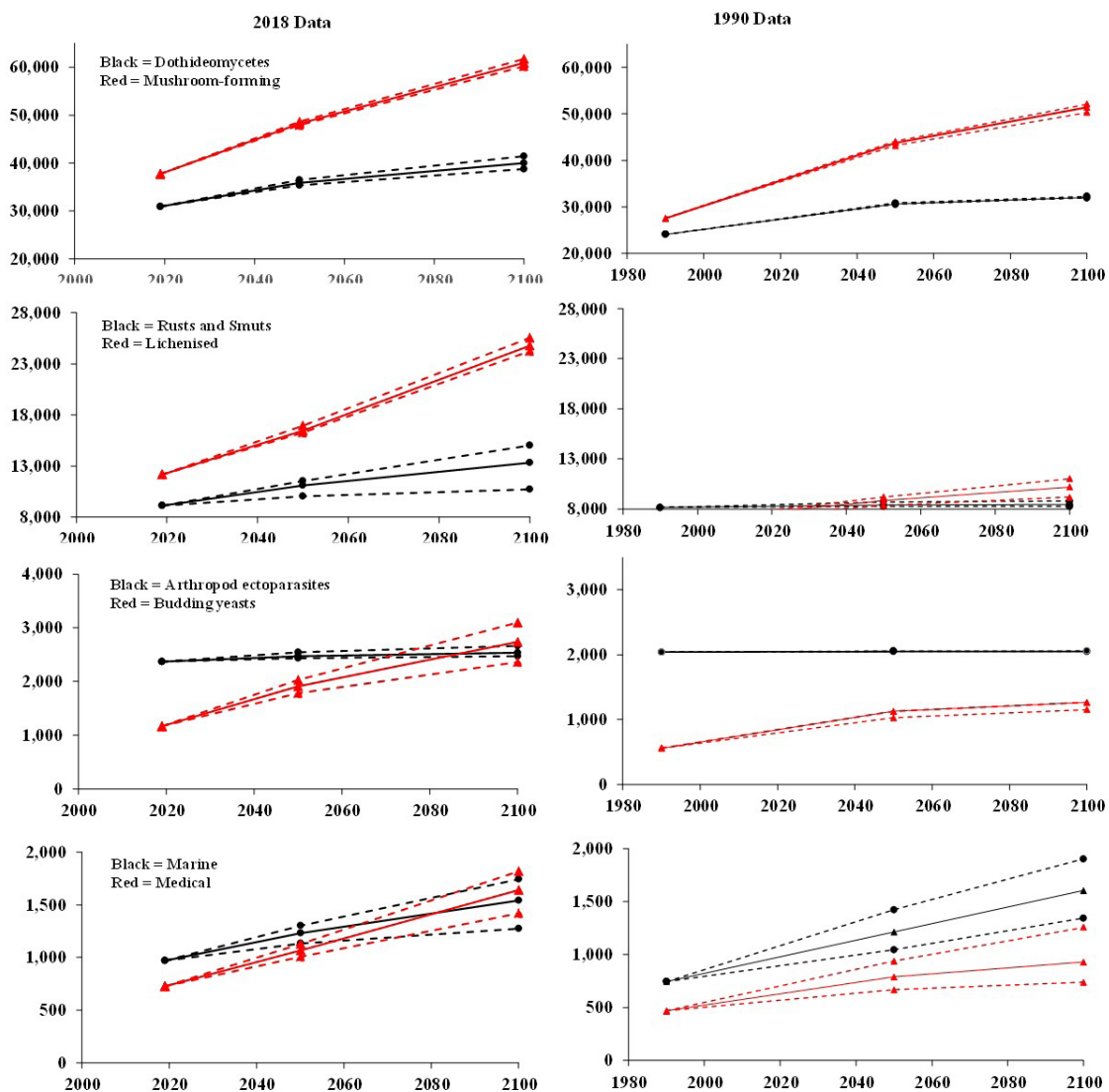
Figure 4. A comparison of the effect of predicting future species descriptions from the number of accepted species recognised in 2018 (left column) and 1990 (right column) for each subgroup and their predicted median increase by the years 2050 and 2100 (solid line) with 95% probability intervals (dashed lines). Note that the scales vary.

increasing, and since then has been decreasing ($R^2 < 0.5$, $P < 0.001$) (Fig. 5).

All fungal subgroups that underwent a recent increase in species description rates were accompanied by an increase in the number of unique first authors involved in species descriptions. These groups included the mushroom-forming fungi, lichenized fungi, saprobes, budding yeasts and fungi of medical significance (Fig. 5). The yeasts had a spike in unique first authors between 2000 and 2010, matching the period that the group

experienced increased description rates. Within these groups, the number of species described as a proportion of the total number of authors in a year declined except among the budding yeasts and medically significant fungal species. The two latter groups displayed an increasing trend in both the number of species described per number of authors and the number of unique first authors describing new species over time (Fig. 5).

No appreciable changes in one-time author descriptions have occurred, with proportions remaining
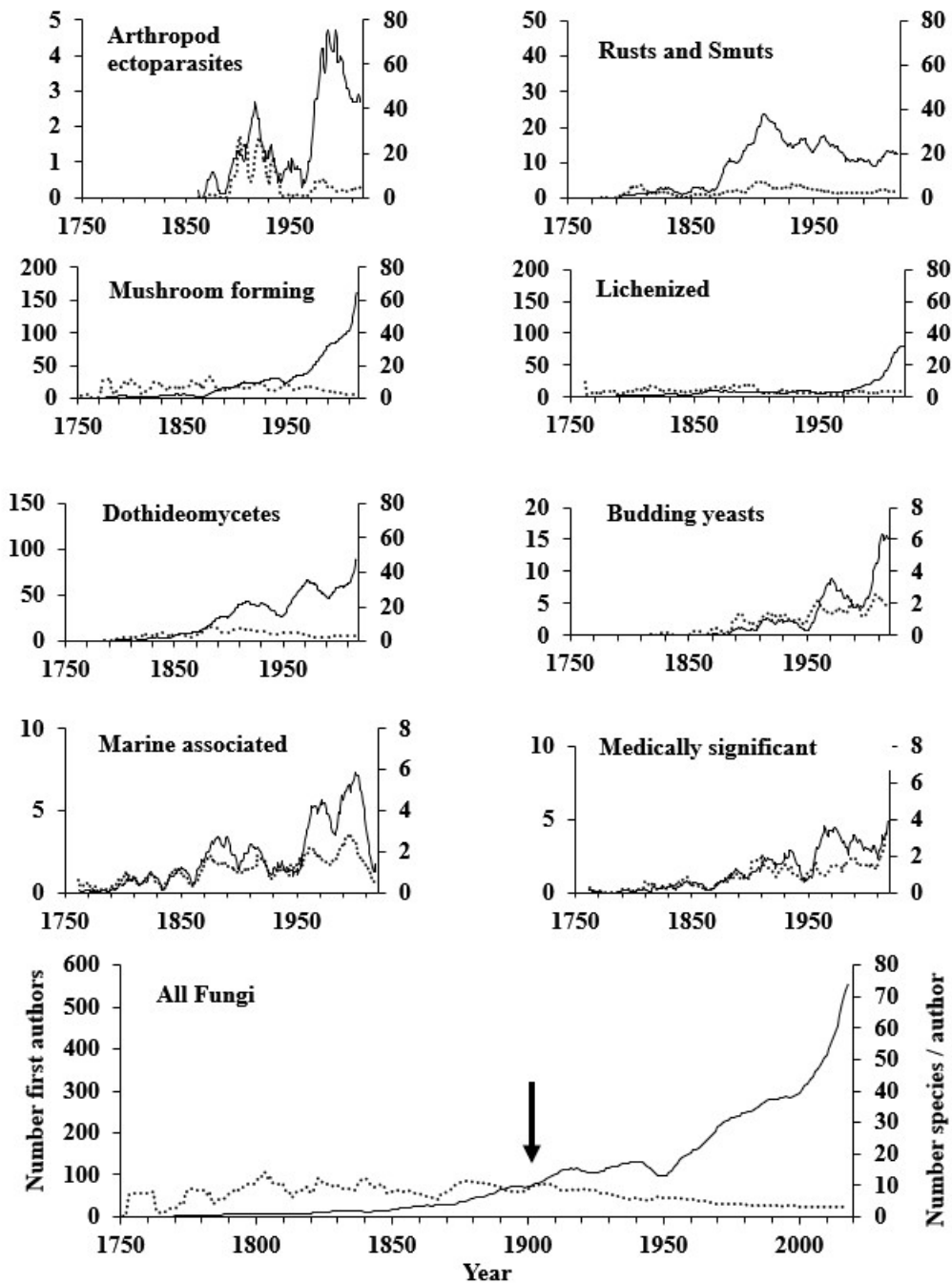
Figure 5. The number of first authors involved in the original description of species (solid line, left axis) and corresponding number of species described per number of authors in a year (dotted line, right axis), displayed as a 10-year moving average. Arrow indicating the break-point. Note scales vary.

between 37% and 42% over the last century exhibiting little variation (*CV* < 0.05) (Fig. S1) (Cunningham 2020c). The frequency distribution of species described among all first authors has been and remains positively skewed (Fig. S2) (Cunningham 2020c). This was highest in the earlier decades, where the 1750s and 1760s exhibited skewness coefficients of 1.40 and 1.76, respectively, thereby indicating that species description was strongly dominated by a few individuals. Since the start of the 20th century, skewness coefficients have remained below one, ranging between 0.57 and 0.86 (*CV* < 0.2).

Excluding all authors responsible for the naming of a single species, the average publication lifetime of an author involved in fungal species description was 13 years, but no significant relationship was determined between 'author publication lifetime' and the number of species described over time ($R^2 < 0.01$, $P > 0.05$) (Fig. S3) (Cunningham 2020c). A notable shift in citation practice from single to multiple authorships responsible for species description was observed during the 1990s (Fig. S4) (Cunningham 2020c). However, this has not affected the overall trends in this study because only the first authors were counted.

Use of Molecular Data

The inclusion of molecular data in publications describing new species has significantly increased over time ($P < 0.001$) (Table S4) (Cunningham 2020c). However, all incorporated a morphological description of the new species with discussion and comparison to known species.

Of the articles reviewed from 2010 to 2014 and 2015 to 2019, those including a molecular aspect made up 50% and 94%, respectively. These proportions followed 3% and 8% over 1995 to 1999 and 2000 to 2004, respectively (Fig. S5) (Cunningham 2020c). The Mann-Whitney U test revealed no significant change in the number of new species being described per publication whether molecular aspects were included or not ($P = 0.913$).

Most of the fungal species recognised within our dataset lacked sequenced type specimens when compared with the NCBI dataset (Fig. 6). Of the 144,035 currently recognised species, only 12,996 (9%) had type specimens with NCBI registered DNA sequences.
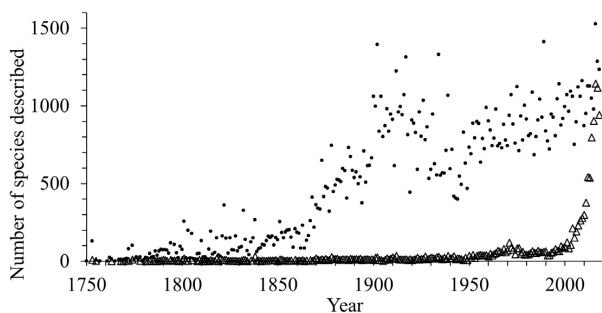
Figure 6. The number of fungal species described per year indicating species that have type genomic DNA sequences registered in NCBI (triangles) and the number that do not (points).

Discussion

Description Rates and Taxonomic Effort

Since 2010, we found that descriptions of fungal species have accelerated dramatically overall, as noted previously (Hawksworth & Lücking 2017, Lofgren & Stajich 2021). This trend is shared with spiders, amphibians, and freshwater bryozoans (Wang et al. 2019, Pagès-Escolà et al. 2020). However, this recent acceleration in descriptions of new fungal species in the past two decades contrasts with global trends for other taxa overall, which have either continued a previous increasing or decreasing trend (Costello et al. 2012, Costello 2016); as we found in the marine, arthropod ectoparasite, and rust and smut fungi.

The number of people involved in the description of Fungi has been steadily increasing over time but has sharply risen since the year 2000, thereby contributing to the overall increase in species description rates and further refuting previous claims that the field of taxonomy is in a state of decline (Burton 2003, Lücking 2008). Increasing numbers of individuals involved in the description of species has been well documented, along with the occurrence of fewer species being described per number of active authors (Joppa et al. 2011a, Joppa et al. 2011b, Appeltans et al. 2012, Costello et al. 2013b, Sangster & Luksenburg 2015, Arfianti et al. 2018, Pamungkas et al. 2019, Wang et al. 2019, Pagès-Escolà et al. 2020). Our study showed Fungi to be no different, exhibiting a decline in the number of species described per number of authors since 1875.

The decline in the number of fungal species described per authors could indicate increased difficulty in the discovery of new species (Costello et al. 2013b), or could be attributed to changing proportions of specialists in the field as suggested by Bouchet (2006) and Bouchet et al. (2016). This study provides evidence against the latter, showing no change in the proportion of 'one-time' author occurrences per decade over time. While Wang et al. (2019) plotted a recent increase in the proportion of authors responsible for describing only one new fungal species within their career dating back from 1750 to the 21st century, this increase is to be expected because new and upcoming taxonomists have not had as much time to describe more species and so single description careers would be more common in recent years. We also did not find a significant relationship between authors' publication lifetimes (careers) and the number of species described per year ($P > 0.05$). Thus, the increasing number of people describing new species of Fungi parallels trends across all other taxa and reflects the growth in science globally, and particularly in Asia and South America (Costello et al. 2013, Deng et al. 2019). That this increased number of first authors parallels the increase in new species descriptions and is a minimum because many papers have multiple authors we have not counted, supports an increased workforce contributing to the increase in species descriptions.

Economically Important Fungi

The medically significant and budding yeast fungal groups contradicted the overall trend among Fungi by presenting an increase in the number of species described per number of authors over time. Both groups had considerable overlap in species, some of the best-known belonging to the genus *Candida* (Berkow & Lockhart 2017). Similar trends in cyanobacteria and freshwater bryozoans were found to be insignificant ($P < 0.05$) (Nabout et al. 2013, Pagès-Escolà et al. 2020). The budding yeasts also differed from all Fungi in that the group experienced a sharp increase in description rates 10 years before most, around the year 2000. This has since declined, although description rates remain higher than ever experienced before the 21st Century. The analysis of all known ascomycetous yeasts using ribosomal DNA by Kurtzmann and Robnett (1998) likely brought a lot of attention to the group and contributed to increased descriptions. Additionally, species of medical significance to humans are likely to receive greater funding for research, ultimately fuelling greater species description rates through the use of better technologies and equipment (Gow et al. 2018). Certain yeast species are also economically important within the food industry due to the threats they pose to the agricultural sector, further justifying increased investment (Kurtzman & Sugiyama 2015). Therefore, larger investment within these two groups could explain the increase in the number of species described per number of active authors. Increased focus on the budding yeasts combined with the very recent decline in description rates could mean that most species have been described.

Marine Fungi

Fungi have exhibited far greater diversification on land than in the sea, as have insects and vascular plants (Grosberg et al. 2012). However, the evolutionary origins of Fungi have been linked to freshwater fungal forms possessing flagella, e.g., Chytridiomycota (James et al. 2006). The flagella are hypothesized to have dropped away in exchange for hyphae in the transition to land, subsequently resulting in extraordinary diversification (Naranjo-Ortiz & Gabaldón 2019a). The phylogeny of these early diverging clades, including chytrids, remains poorly resolved despite increased analyses using genomics and phylogenomics (Naranjo-Ortiz & Gabaldón 2019a, Naranjo-Ortiz & Gabaldón 2019b). Despite these uncertainties, the description of marine-associated fungi has been declining even though there has been increased interest in obtaining bioactive compounds produced by marine fungi for biotechnological applications (Shukla & Kin 2016, Giddings & Newman 2019, Keral et al. 2019). This contrasts with almost all other marine taxa, where marine species descriptions were higher in recent decades (Appeltans et al. 2012). This is not attributable to a delay in database record entry (Costello et al. 2012), because the decline began before the year 2000, and WoRMS (Costello et al. 2013, Horton et al. 2019) and Index Fungorum (Royal Botanic Gardens Kew et al. 2019) are continually updated.

The decline in the description of marine-associated species was accompanied by a decline in effort, where the number of active authors, as well as the proportion of species described per author, decreased. It thus appears that marine fungi have relatively few species and are well-described compared to terrestrial fungi. This supports previous studies which concluded that marine fungi were a relatively species- poor group (Kohlmeyer & Kohlmeyer 1979, Picard 2017).

Pathogenic Fungi

Apart from the marine fungi, the other two groups with declining global fungal species description rates were the rust and smut fungi and arthropod parasites. Both groups also exhibited declines in the number of first authors describing species and the number of species described per number of authors. A key commonality between species of these groups and marine species is their association as parasites or pathogens (Barnes 1979, Li et al. 2016, Scholz et al. 2016, Lorrain et al. 2019). At least half of all parasites may be described, and rates of description of terrestrial insect and marine crustacean and mollusc parasites have also been declining (Costello 2016). Previous host specificity assumptions used to estimate parasite richness may have been overestimated due to the under-sampling of hosts, vertebrate sampling bias (large bodies can host more parasites), and naming of species according to their host (Costello 2016). Parasitic species ultimately gain a greater survival advantage when capable of associating with multiple host species as increasingly seems to be the case (Costello 2016). Recent molecular phylogenetic analyses of rust fungi have revealed four previously recognised taxa as being a single species able to survive on multiple unrelated plant species (Padamsee & McKenzie 2017). Additionally, rusts are known to severely impact crops of agricultural value (Staples 2000). Because of this economic impact, it is likely that more time and resources have been focused on the group, as with yeasts, and that declining description rates could be indicative of the group's taxonomic completeness.

Impact of Molecular Techniques

The increased use of molecular techniques among the mushroom-forming fungi was clear in this study, and they were used in conjunction with morphological and other character descriptions. Thus, a holistic approach to taxonomy is being practised within mycology. Such an integrative approach applying 'traditional' methods of description complemented by 'next generation' approaches has been strongly called for among the mycological community (Truong et al. 2017, Chethana et al. 2020, Dupérré 2020, Vences 2020), and demonstrated here to be the case.

The inclusion of a molecular aspect within species descriptions may have helped taxonomists detect more subtle morphological differences following the discovery of phylogenetic differences (Accioly et al. 2019). Reports of fungal species being established without any morphological diagnoses (Dupérré 2020) are rare and likely not responsible for increased species

descriptions in recent years. Difficulties in applying a strictly morphological species concept within Fungi led to the early adoption of DNA based comparisons to aid in the resolution of fungal taxonomy (Chethana et al. 2020, Yahr et al. 2016). DNA "barcodes" were initially meant to be linked to inventoried and curated specimens but have unfortunately become increasingly decoupled with their physical counterparts within public sequence databases through additions of unnamed environmental sequences (Yahr et al. 2016). It is these unnamed sequences that have been equated to undiscovered species (Hawksworth & Lücking 2017). However, we found that 91% of described species lack associated sequence data sourced from type specimens. A similar problem has been found for marine animals, including amphipod crustaceans, where only about 10% of accepted species have genetic barcodes (Jażdżewska et al. 2021, Mugnai et al. 2021).

The lack of genetic sequences for about 90% of species, including Fungi, raises the concern that new species descriptions may be redescribing species previously named, although not so well described (Hofstetter et al. 2019). Thus, because any unrecognised sequences from environmental samples are more likely to belong to already described species rather than new ones the naming of new species based solely on DNA data is not helpful. Having molecular data on additional already-described species is necessary to realise its potential in characterising the diversity and phylogeny of Fungi.

Biogeography

Generally, geography plays less of a role in the distribution of microbes and fungi than for animals and plants; as expressed a century ago through the Baas-Becking hypothesis, "everything is everywhere but the environment selects" (Lumbsch et al. 2008, Tedersoo et al. 2014). Similarly, marine planktonic and nektonic species are relatively more cosmopolitan compared to the more species-rich seabed associated macrofauna (Costello & Chaudhary 2017, Costello 2023). As with bacteria and other micro-organisms and propagules, many Fungi benefit from high spore production and dispersal by air, water, and animals, and will have been spread by human activity. A global analysis found that the distribution of soil fungi was based more on the environment than geography by comparison with macro-organisms (Tedersoo et al. 2014). Patterns of species endemicity further support this. For example, < 20% of fungi are classified as endemic to New Zealand but 32, 34, and 68% of all terrestrial, freshwater, and marine biota are classified as New Zealand endemics (Costello 2023). Thus, taxonomic revisions will benefit from molecular data on previously described species because it is likely the same species may have been described based on geographic and ecological variants. In addition, the extraordinary ability of Fungi to swap genes with bacteria (Bruto et al. 2014), and possibly viruses and eukaryotes, further complicate assessments of genetic diversity of Fungi and how it can be used to define 'species', making holistic descriptions essential.

Predictions

In a recent special volume on the numbers of fungal species, eight studies used various methods of fungal diversity estimation, ranging from fungi to substrate ratios of described species, often based on previous estimates also based on ratios (e.g., of the number of species of fungi to plants), to available DNA barcode sequences. They all came to the conclusion that many more species are yet to be described (e.g., Boekhout et al. 2022, Phukhamsakda et al. 2022, Senanayake et al. 2022). However, one of the editors of this special issue concluded that although the authors intended to definitively estimate the number of Fungi there is further research needed (Hyde 2022). This is because inferring species richness from operational taxonomic units (when several may apply to one species), and accounting for synonyms, including when the sexual and asexual morphs of a species have been described as separate species, complicates knowing how to translate present names and molecular data to species (Baldrian et al. 2022, Boekhout et al. 2022, Wijayawardene et al. 2022, Niskanen et al. 2023). Moreover, these (e.g., Senanayake et al. 2022) and other (Costello 2016, Niskanen et al. 2023) studies show how the use of ratios, while popular, is misleading because: (a) the proportion of species within higher taxa is not the same geographically as shown by patterns of endemicity for species and higher taxonomic levels (e.g., for fungi see Niskanen et al. 2023); (b) increased sampling may increase one part of the ratio but not the other, e.g., fewer new species of plants are being described than fungi because the former are well described; (c) it is not justified to extrapolate from species richness in one locality or habitat to the world; typically, exceptionally species-rich places are used to extrapolate thereby exaggerating global richness; and (d) ratios of higher to lower taxa (e.g., phyla to species) are similarly flawed because reclassification and discrimination of new higher taxa is still occurring (e.g., in fungi Niskanen et al. 2023). Therefore, ratios of species richness patterns between taxa, geographic areas, and across higher taxa should not be used to estimate global species richness for any taxon.

Our analyses suggested that the Kingdom Fungi was predicted to see an additional 64,400–74,000 new species descriptions within this century, expanding by an average of 48% of what is currently recognised. Description rates for most groups showed no indication of reaching an asymptote, as previously pointed out by others (Bass & Richards 2011, Hawksworth & Lücking 2017, Niskanen et al. 2023). Our study demonstrated that the fungal groups expected to experience the greatest number of new species descriptions in the future include the 'mushroom-forming' fungi (Agaricomycetes), lichenized fungi (Lecanoromycetes and Arthoniomycetes), and various saprobic and plant-associated species within Dothideomycetes.

As for all studies assessing the number of known species, synonymy presents a problem contributing to potential overestimation. This was accounted for as best as possible by using only currently

accepted species names. At least 20% of all currently accepted species are likely to be later recognised as synonyms (Alroy 2002, May 2010, Costello et al. 2012, 2013). Among Fungi, known synonyms made up roughly 30% of fungal names at the start of the 20th century, decreasing to just under 20% a century later (Wang et al. 2019). Undoubtedly, more will be discovered with time. A particular problem among Fungi was the previous individual naming of sexual and asexual forms, but it's believed that most of the anamorph (asexual) – teleomorph (sexual) anomalies have been recognised (de Gruyter et al. 2013, Ertz et al. 2015, Jayasiri et al. 2015).

The marked acceleration of new descriptions since the 1990's, when the inclusion of molecular data in species descriptions became common, has greatly changed the trajectory of the rate of descriptions. Were molecular data not used, only 4% more species were predicted to be described by 2100, instead of 48% from 2019 (Table 3). Thus, without the use of molecular methods, the data would have suggested most Fungi have been described. Further research will need to determine whether the recent use of molecular data is really discovering new species, is double counting already described named species without molecular data, or, as seems likely, is a change in the application of the species concept. A recent review recommends a change in the concept of what determines a species of fungus to allow molecular driven species identification, but does not mention the absence of genetic data for most already described species (Niskanen et al. 2023). The data we presented indicates that this change in what discriminates species of fungi has been underway for two decades.

Conclusions

Fungi can be considered one of the least well-described taxa, with the number of global species described estimated to increase 45–51% this century assuming the species described in the last two decades, primarily based on molecular data, are the same as previously described species lacking molecular data. Overall fungal description rates are increasing, apart from the more economically important and marine groups which are relatively well known. The greatest number of new species discoveries are predicted to occur among terrestrial mushroom-forming, lichenized and plant-associated groups. The absence of genetic data for over 90% of current species compromises the use of DNA for species identification and means that some new species described based on genetic data may be synonyms of previously described species, and thus estimates of named and unnamed species are inflated. Obtaining genetic data for the already described species is thus at least as important as new species descriptions.

Acknowledgements

Data Availability Statement

Datasets and supplementary data can be accessed via Figshare following the below links:
Cunningham, J. A. (2020a) A dataset of 144,035 named species of fungi and associated species delimitation data. Dataset. https://doi.org/10.6084/m9.figshare.12649550.v3
Cunningham, J.A. (2020b) Dataset of fungi species with genetic data in NCBI, including their earliest associated description details. Dataset. https://doi.org/10.6084/m9.figshare.12661154.v2
Cunningham, J. A. (2020c). Supplementary Data_ Fungi species description rates confirm high global diversity and suggest half remain unnamed. Figshare https://doi.org/10.6084/m9.figshare.23498237.v1

Supplemental Material

The following materials are available as part of the online article at https://escholarship.org/uc/fb
Table S1. Initial data selection.
Table S2. Construction and data organization of marine-associated fungal species list.
Table S3. Construction and data organization of medically significant fungal species list.
Table S4. Cross tabulation with associated chi squared test for fungal species descriptions including a molecular aspect over time.
Figure S1. The percentage of one- time author occurrences per decade from 1750 until mid-2019.
Figure S2. Pearson's skewness coefficients calculated based on the frequency distribution of species described among all first authors within each decade with linear regression.
Figure S3. A linear regression of publication lifetime against the number of species described per year (total species described by author/ author's publication lifetime in years) for each author excluding all one–time authors.
Figure S4. Number of fungal species described by single (solid line) and multiple (dotted line) authors per decade.
Figure S5. The proportion of sampled articles including (dark) and excluding (clear) a molecular aspect.
This material is available as part of the online article from https://escholarship.org/uc/fb

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