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MDPI

Data Descriptor

Linking Fungal Genomics to Thermal Growth Limits: A Dataset of 730 Sequenced Species

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Abstract: The response of fungal species to changes in temperature is of theoretical and practical importance in a world of changing temperatures, ecologies and populations. Genomic sequencing to identify fungal species and their potential metabolic capabilities is well established, but linking this to growth temperature conditions has been limited. To that end, I describe a dataset that brings together the maximum and minimum temperature growth limits for 730 species of Fungi and Oomycetes for which genome sequences are available, together with supporting proteome and taxonomic data and literature references. The set will provide an entry for studies into how genomic structure and sequence can be used to predict the potential for growth at low or high temperatures, and hence the potential industrial use or pathogenic liability of existing or new fungal species.

Dataset: Available in Supplementary Information to this paper.

Keywords: fungi; growth; temperature; genome; proteome

1. Summary

This paper describes a compilation of information on fungal species for which genome sequences and growth temperatures are known. The data were collected as part of a project to explore the genomic and proteomic parameters that relate to the maximum temperature at which eukaryotic life can flourish.

Organisms are known that can grow at 120 °C [1–3], but no eukaryote is known that can grow above 65 °C [4] (although many can withstand higher temperatures for a short period, or as dormant forms). In particular, fungi show a range of optimal growth temperatures from below 15 °C to 60 °C, and some can grow below 0 °C [5–8]. Exploring what sets these limits is of fundamental interest to understanding the limits of life on Earth, and may inform whether complex life could evolve on other worlds with substantially different surface temperatures from Earth [9]. It is also of substantial practical importance. Enzymes from thermophilic organisms are widely used in industrial processes [10–14]. Of medical relevance, fungi are particularly difficult infectious agents to treat because they share substantial biochemical similarity to mammals, unlike bacteria or protozoa [15], and fungal infections cause over 1.5 million deaths a year [13]. However the majority of fungi cannot grow above around 32 °C, and so cannot colonize mammalian hosts [13,16]. If any organism, including fungi but also other classes, can adapt to higher temperatures, then they become potential opportunistic pathogens [13,17]. This has already been observed with *Candida albicans*, a commensal organism that historically has been identified as only

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growing in human body niches that maintain a temperature well below 37 °C, such as the vaginal passage, where it causes thrush [18], but increasingly has been suggested to be adapting to the higher-temperature bloodstream and causing systemic infection [19], and for *Cryptococcus gattii*, which occupies an ecological niche in rotting trees but in recent decades has become an increasingly frequent pathogen in humans [20]. With global climate change resulting in some entire ecosystems shifting to higher maximum temperatures, there is concern that the adaptation of previously benign fungal species to new temperature regimes could result in 'new' infectious species [21–24].

Therefore, there are several reasons to want to understand the causes of the temperature limits of fungal growth, and how temperature limits might change under selection for growth at higher temperatures. The dataset reported here was conceived as a basis for the exploration of whether genome structure and function are related to the maximum and minimum growth temperatures of fungi, so that the potential for a species to evolve a higher (or lower) growth temperature limit could be inferred without the need for long-term in vitro evolution experiments [25]. While a number of such studies have been performed (e.g., [26–30]), they all relate to specific groups of fungi or to very limited comparisons between related species. Extensive databases of genome sequences are available (referenced below in Section 2), but there is no comprehensive listing of species for which growth temperature limits have been reported in the literature.

I therefore sought to identify all the fungal species for which growth temperature limits and genome sequences are known. To that end, an extensive literature search identified 699 fungal species for which both maximum and minimum growth temperatures and genome sequences are available. This substantially extends the previous compilation of fungal cardinal temperatures. I have also included 31 Oomycetes in the dataset as an outgroup. While morphologically similar to fungi, Oomycetes are taxonomically distant from the opisthokonts (fungi, animals and related taxa), and so probe whether patterns seen might be fungi specific.

This paper describes this dataset in the hope that other researchers can bring their own analytical methods to bear on the question of what limits eukaryotic growth temperature, for basic and applied goals.

This is a preliminary version of this dataset. In particular, it assumes that the growth temperature limits of a fungal species are characteristic of that species, as they are of mammals and birds. However, different isolates of the same fungus can show different maximum growth temperatures (e.g., [13,31–33]), and maximum growth temperature can depend on growth conditions [13,34] and whether bimorphic species' growth as a yeast or hyphal form is considered [13]. I have taken the highest recorded maximum temperature (and the lowest minimum temperature) here as representing the limits for any species, but a future dataset could probe the growth temperatures of each isolate under a range of conditions and compare them to the genome sequence of that isolate.

2. Data Description

The data comprise genome and growth temperature information on 699 fungal and 31 Oomycete species, of which 505 have translated proteomes available. The data are available as an Excel spreadsheet, with columns as described in Table 1. The spreadsheet file has five sheets: a 'Read Me', one sheet containing the data as listed in Table 1, one sheet implementing the growth model as described in Section 3.4, one sheet with the references for Table 1 and one for the compiled and processed Togashi dataset [35,36]. This last sheet is included for 'future proofing' for future genome project outputs. A 'Read Me' summarizes this information, and provides detail on how to run the temperature estimate model.

Table 1. Data columns in the dataset.

Group	Column	Description	Values
SPECIES	Name from Fungal Names	Uniform name from Fungal Names (https://nmdc.cn/fungalnames/)	Text
	Source name	Name of species as described in the source material	Text
	Other name(s)	Other names by which this species is referred to in the relevant literature, if any	Text
GENOMES	Genome length	Reported length of the genome, in megabases	Real number
	Protein number	Reported number of proteins in the genome annotation	Integer
	GC content	G+C percentage of the genome	Percentage number
	Reference	Literature reference for additional genome data, if not included in NCBI or Mycocosm databases	Text
PROTEOMES	Proteome file source	Source of the full proteome file, if one is available: Uniprot reference dataset, and, if not available there, the NCBI genome resource, and, if not available there, the JGI Mycocosm database	Text
	number of proteins	Number of proteins in the proteome file	Integer
	total number of amino acids	Total number of amino acids in the proteins in the proteome file	Integer
TEMPERATURE RANGE	Min	Minimum growth temperature as reported in the literature, as °C	Real number
	Max	Maximum growth temperature as reported in the literature, as °C	Real number
	Basis	Basis for estimating minimum and maximum temperature (see Section 3.5)	Text
	Reference	Reference for source of minimum and maximum growth temperature	Text
TOGASHI TEMPERATURE RANGE	Min	Minimum growth temperature as reported in the Togashi database, as °C	Real number
	Max	Maximum growth temperature as reported in the Togashi database, as °C	Real number
	Number of entries in Togashi db	Number of entries in the Togashi database from which minimum and maximum growth temperatures were educed	Integer

Table 1. *Cont.*

Group	Column	Description	Values
COMBINED TEMPERATURES	MIN	Minimum of the estimates of minimum growth temperature, as °C	Real number
	MAX	Maximum of the estimates of maximum growth temperature, as °C	Real number
TAXONOMY	Complete taxonomy	Complete taxonomic description as listed in NBCI Taxonomy database	Text
	Clade	Top-level clade	Text
	Subkingdom	Subkingdom (for fungi)	Text
	Division	Division (for fungi)	Text
	Order	Order where specified (for fungi)	Text

The downloaded proteome and genome sequence files are not provided here, as they are the property of other institutions. However, they can easily be downloaded from the websites listed in Table 2 using the species names given.

Table 2. Sources of data used.

Source	Relevant Data	URL	Access Dates
Google Scholar	Research-specific search engine	https://google.scholar.com	Varied dates in 2023 and 2024
NCBI Genome database	Data on genome sequence and coding capacity, proteomes	https://www.ncbi.nlm.nih.gov/datasets/ (used to be https://www.ncbi.nlm.nih.gov/genome/)	Varied dates in 2023 and 2024
Uniprot proteome database	Reference proteome data	https://ftp.uniprot.org/pub/databases/uniprot/current_release/knowledgebase/reference_proteomes/Eukaryota/	20 June 2024
JGI Mycocosm	Fungal genome statistics, proteomes	https://mycocosm.jgi.doe.gov/mycocosm/home	Varied dates in 2023 and 2024
Fungal names	Fungal names and synonyms	https://nmdc.cn/fungalnames/	Varied dates in 2023 and 2024
Undermind	AI-enabled literature search engine	https://www.undermind.ai/	27 December 2024
Togashi database	Detailed database on growth temperatures of fungi	https://datadryad.org/stash/dataset/doi:10.5061/dryad.tqjq2bvw6	28 August 2024

Data are only for species for which there is a literature citation for the maximum and the minimum growth temperature and extensive genome sequence data. I note that data on the rate of growth of fungal species at different temperatures probably exist for many more species than I have been able to include here. Many papers report that they grew a fungal species at many temperatures, but only report the temperature for optimal growth, not what the growth rate was at other temperatures. Future work could attempt to contact the many hundreds of workers reporting data in this way to extend the dataset. For other species, no growth data were traceable at all. For example, of the 59 species analyzed

from [37], 41 had no traceable growth temperature data. Future experimental programmes might rectify this gap.

Species are listed by their names as listed in nmdc.cn/fungalnames. This is not to claim that this source of nomenclature is authoritative, but is simply used to remove duplications in the dataset, as fungi can be known by several names, either because the classification of the species has changed with greater knowledge or because, for historical reasons, the same organism in different parts of its life cycle has acquired different names. Alternative names are listed in the dataset for search purposes.

All species have genome sequence data available, and the size, fraction of the bases in the genome that are Guanine or Cytosine (GC content) and (where annotated by the genome sequence depositor or by NCBI) number of coding sequences are described. For species where the complete proteome is available for download, the source of that proteome is listed. Summary proteome characteristics computed from these files are provided.

The maximum and minimum temperatures have been identified either from the literature search or from the Togashi database [35], as updated and digitized by [36]. Togashi entries are listed separately, and, if temperature estimates from both the literature and Togashi are present, the minimum and maximum temperatures are shown in the summary column.

A summary of higher-level taxonomic classification is also provided.

The sources of the data are summarized in Figure 1. Note that the 'Uniprot' set and 'Literature set' (species identified through searching Uniprot fungal species and those identified through the literature search) are mutually exclusive, as any species identified by the literature search was then not searched as part of the Uniprot search (see Methods below for more details).

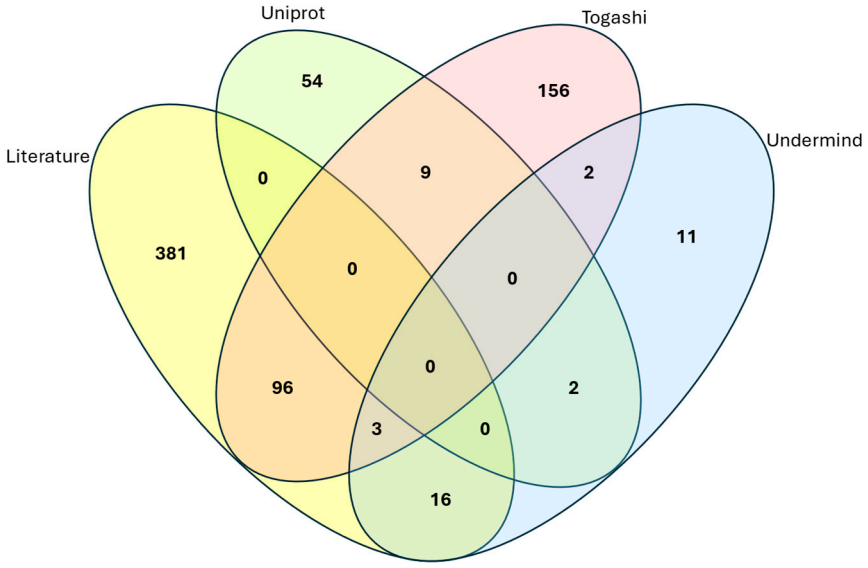

Figure 1. Sources of data for entries in the dataset. Shown are the number of entries identified by the literature search ("Literature"), those not identified by the literature search but that were identified by searching for Uniprot species names ("Uniprot"), those identified from the Togashi dataset ("Togashi") and those identified by an AI-assisted search using Undermind ("Undermind").

The taxonomic distribution of species is summarized in Figure 2. The study included a small number of Oomycetes, which have a morphology and lifestyle similar to some fungi but are actually quite distantly related (fungi are more closely related to animals than to Oomycetes).

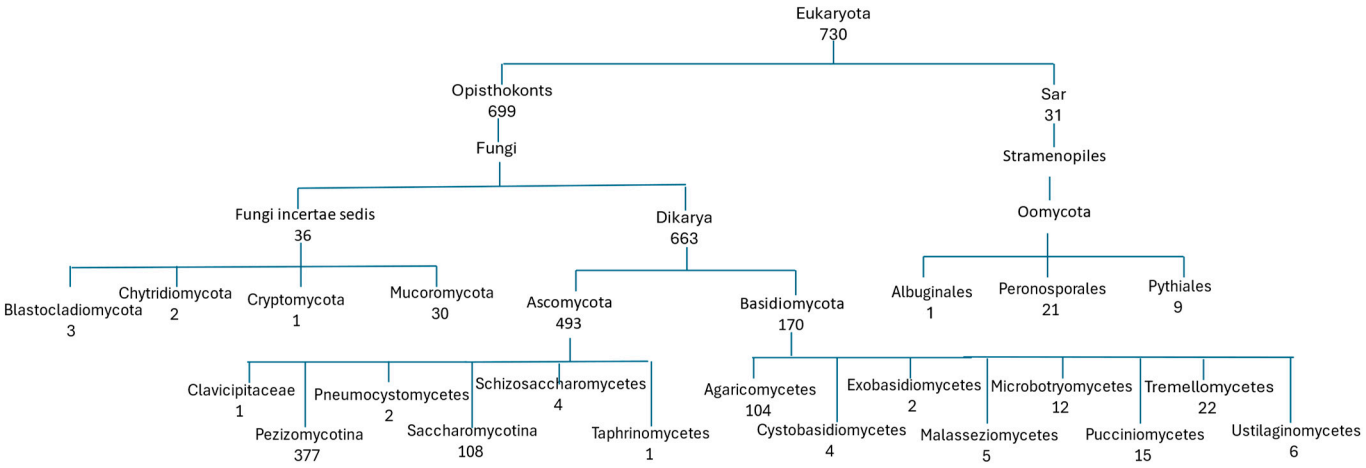

Figure 2. Taxonomic distribution of the species included in the dataset. The numbers under each taxonomic class show the number of species in that class in the database. Note that the majority of the fungi are in the Sacchaomycotina (yeasts), Pezizomycotina and Agaricomyces orders, reflecting both larger number of species and greater industrial interest in these groups of organisms.

The relative numbers of species in the different classification groups shown in Figure 2 roughly match the known number of genera of fungi identified from large-scale genomic comparisons [38].

Some summary statistics on the dataset, broken down by classification category, are provided in Appendix A.

3. Methods

Data were collected through three routes: a literature search, a Uniprot search and a Togashi dataset analysis. Sources for the data are listed in Table 2.

3.1. Literature Search

The primary source of growth temperature data was a literature search. The literature was searched for papers through a search of Google Scholar using the keyword combinations in Table 3. The term 'cardinal temperature' is used in the literature for the range of temperatures over which a phenomenon is observed. In the study reported here, the phenomenon being observed at different temperatures was the rate of growth of mycelia. All hits identified by Google Scholar search where the full text was available to the author (around 95% of the references were accessible) were then searched for any data relevant to the rate of growth of the organism reported in the paper.

Table 3. Search terms used in Google Scholar.

Search Type	Relevant Data
Literature first	("fungi" OR "fungal") AND "mycelial growth" AND ("maximum temperature" OR "minimum temperature" OR "cardinal temperature")
	("fungi" OR "fungal") AND ("maximum growth temperature" OR "minimum growth temperature")
Uniprot first	[fungal name] AND ("growth temperature" OR "cardinal temperature")
Genome	[fungal name] AND "genome sequence"

For a broad search for any data on any fungal species for which growth temperature was known, the 'Literature first' search strategy was adopted. For a narrower search for growth temperatures for fungi whose proteome was in the UniProt reference collection or for which genome data were available, the 'Uniprot first' and 'Genome' strategies were adopted. The same search strategy of reading accessible papers for temperature information was used in these searches.

Papers identified by any of these searches were then searched for relevant data, and, regardless of whether they contained such data, were searched for references to other papers on fungal growth, and the citations to that paper as identified in Google Scholar were also searched for potential data. This process was repeated until no new papers could be found.

3.2. Genome Data Search

For every fungal species identified through searching for temperature data, the NCBI Genome data resource and the JGI Mycocosm portal were searched for genome sequence information. If no entries were found in those resources, or if the data were incomplete (for example, lacking GC content or coding region data), the literature was again searched for genome sequence data on that species. The concern of this project was not for a complete, gap-free, chromosomal-level sequence assembly, but for a sufficiently complete set of genome sequence data to be listed in the NCBI or JGI as a genome sequence, or to be reported as a draft sequence in the literature.

3.3. Undermind Search

The manual search of the literature was complemented with a search using the AI search tool Undermind. Undermind is an AI-enabled literature search engine that takes a search query, uses a language model to recognize key concepts in the search query and in an initial literature search, and then uses the concepts educed from that analysis to perform repeated searches, adapting its search strategy as the repeated searches are conducted. In this, it claims to mimic how a human researcher would search the literature. Within the study reported here, the search phrase used at the start was "Synthesizing a dataset of fungal species by integrating genome data (from any source, with preference for genomes annotated with coding regions numbers) with experimentally determined minimum and maximum growth temperatures, prioritizing completeness across fungal diversity and actively seeking extremophilic species". This identified a few additional species for which both temperature and genome data were available.

3.4. Uniprot Search

As one goal of the overall project was to compare the proteomes of species with different temperature tolerances, I downloaded all the reference proteomes from the Uniprot database and identified fungi in this set, as these all have extensive genome sequence information listed by NCBI in their 'genomes' datasets or in JGI in the Mycocosm portal. I then searched the literature for growth temperature data using the more relaxed 'Uniprot Search' criteria shown in Table 3.

3.5. Maximum and Minimum Temperature Estimate

The way that growth is reported varies hugely in different studies. For those that show a detailed curve of growth rate vs. temperature, the maximum growth temperature is easily identified, and the minimum is either clear or is the temperature at which growth is <0.05 times the peak growth rate. A number of papers stated the maximum and minimum growth temperatures but without providing supporting data, and these values were transcribed directly into the database. However, a number of papers reported growth at a

number of temperatures which included a temperature above the maximum growth temperature (at which no growth happens) but not one approaching the minimum. For these papers, the parameters in Equation (1) were optimized to fit the observed growth data.

$$G = \text{Maximum}\left\{0, [Q_{10} \cdot k \cdot T] \cdot \left[e^{\frac{A}{T^f}}\right]\right\} \quad (1)$$

where G is the growth rate (in arbitrary units), Q_{10}, k, A and f are arbitrary constants to be optimized and T is the temperature in degrees Celsius. The predictions from Equation (1) are scaled so that the maximum growth rate is the same as the maximum growth rate as reported in the literature report, so the two can be compared. The equation assumes that growth rates below zero are meaningless, so a minimum rate of 0 is imposed on the calculation.

The formula is derived empirically, derived from two parts. The first set of square brackets is from the observation that the growth rate of a wide range of fungi for which detailed growth vs. temperature curves are available is linearly proportional to temperature (not, as might be expected, exponentially proportional) for temperatures well below their maximum growth temperature. The second term in square brackets is derived from the exponential decrease in growth rate at greater-then-optimal temperatures, caused by increased protein denaturation, metabolite reaction and other processes that limit cellular viability.

Note that this is not meant to be a 'model' of fungal growth. Rather, it is a numerical match for empirical observations about the shapes of the growth rate vs. temperature curves for those species where such curves were reported.

The methods are summarized in Table 4, together with the code used in the dataset, to show which method was used.

Table 4. Maximum and minimum temperature identification method.

Search Type	Relevant Data
Graph	Read from a graph of growth vs. temperature provided in the paper
Stated	Maximum and minimum growth temperature stated in a paper, with or without accompanying graphical data
Model	Temperature limits derived from Equation (1), as described above
Togashi	Identified from the Togashi dataset, as described in Section 3.5

3.6. Togashi Analysis

Kogo Togashi compiled a set of individual observations of the growth temperatures of fungi and oomycetes that are pathogens in plants in 1949 [35] from a manual reading of the primary literature. Ref. [36] has digitized and extended this dataset, and their digitized version was further analyzed for this study. The set of species reported in [36] was searched for species for which a maximum temperature and a minimum growth temperature were recorded. All species for which a maximum and a minimum were recorded were then searched in NCBI and JGI for genome information, and those with genome information were added to the dataset reported here.

Where growth temperatures were available from both the literature and the Togashi dataset, a 'Combined Data' temperature was calculated as the lower of the two minimum growth temperature and the higher of the two maximum growth temperatures. The reason for this is that if one study does not find growth at a specific temperature but another does, then that species has been demonstrated to grow at that temperature under at least one set of circumstances.

3.7. Naming and De-Duplicatiom

Because the same fungus can appear in the literature under several names, the name by which a species was reported in the literature was searched in the Fungal Names database, and the name listed as 'Current name' in the Fungal Names database was extracted. This name was used as a unique identifier for the species to ensure a unique species per row.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/data10040042/s1.

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Data Availability Statement: All data developed in this study are available for download, as above.

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Conflicts of Interest: The author declares no conflicts of interest.

Appendix A

In this Appendix I provide some summary statistics for the dataset, to illustrate the breadth and limitations of the data.

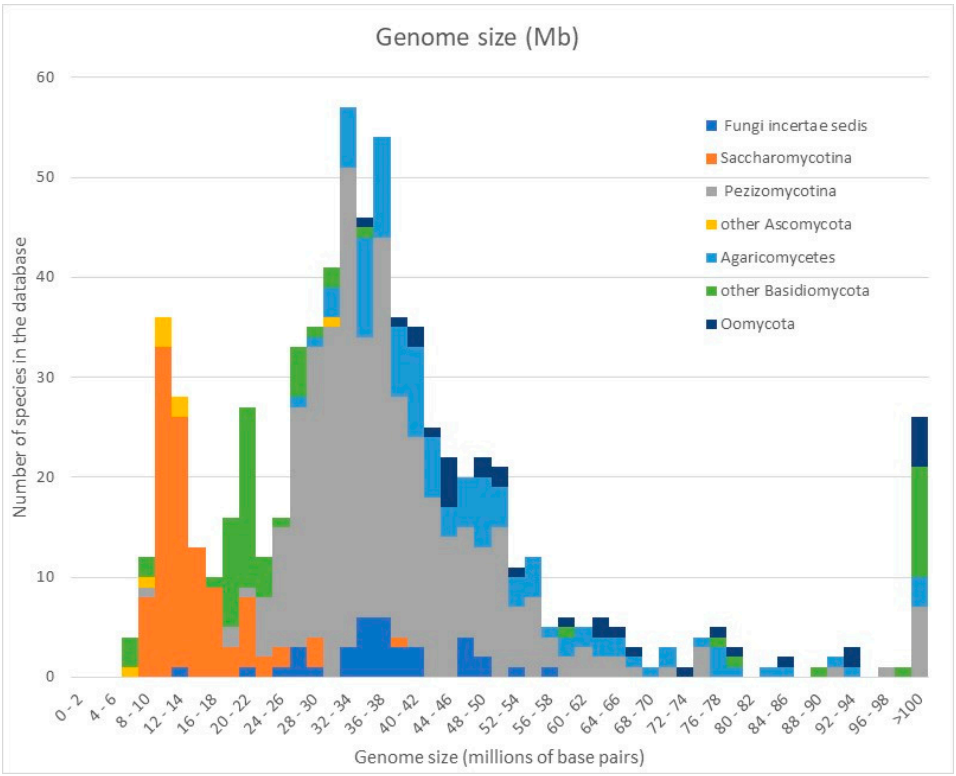


Figure A1. Frequency distribution of genome sizes in the database. X axis: genome size in 2 megabase increments. Y axis: number of entries in the database with that genome size. The major categories of taxonomy as described in Figure 2 of the main text are colored separately. Note that the yeasts (Saccharomycotine) have much smaller genomes than other fungi, but they are not uniquely small.

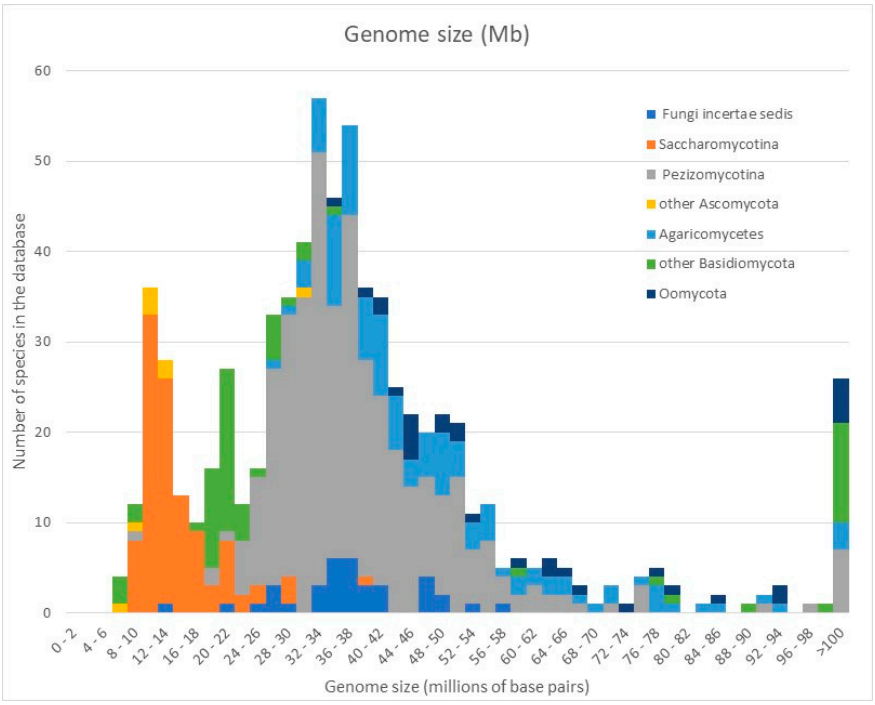


Figure A2. Frequency distribution of proteome sizes in the database. X axis: genome size in 500 amino acid increments. Y axis: number of entries in the database with that genome size. The major categories of taxonomy as described in Figure 2 of the main text are coloured separately. Note that the yeasts (Saccharomycotine) have much smaller proteomes than other fungi, in line with their smaller genomes, but not uniquely small.

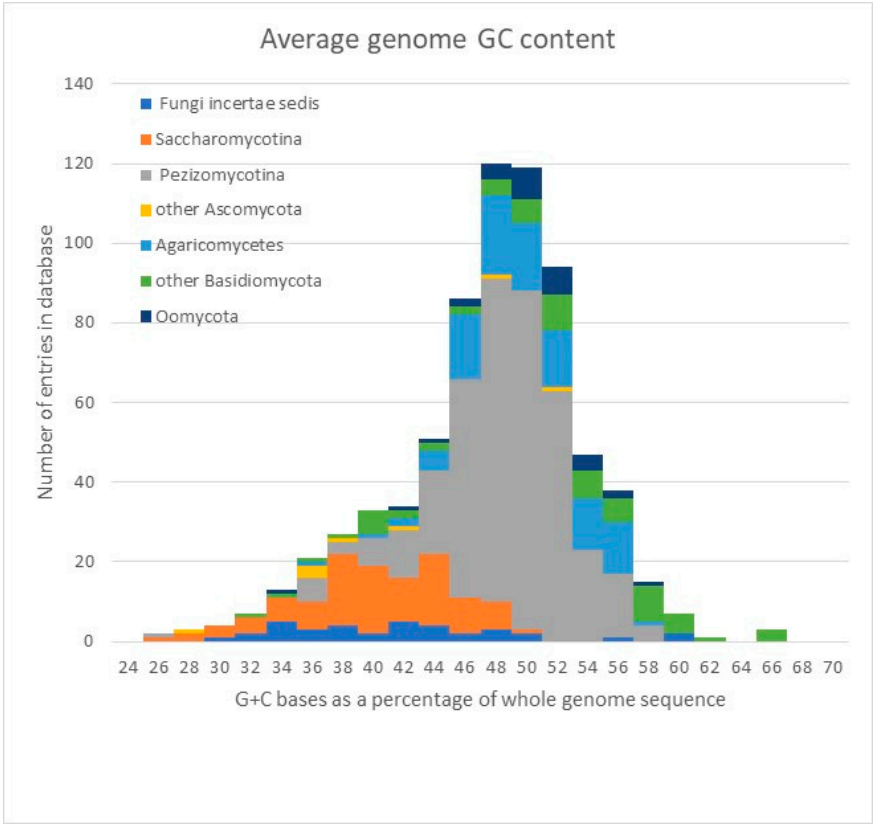
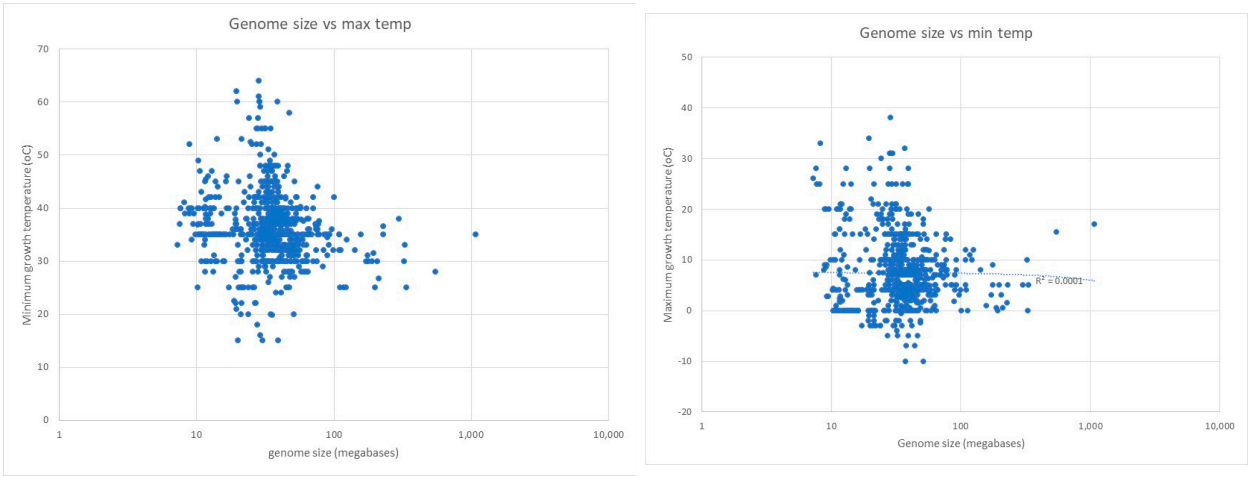


Figure A3. Frequency distribution of genome G+C content in the database. G+C content as a percentage of bases in the genome. Y axis: number of entries in the database with that genome size. The major categories of taxonomy as described in Figure 2 of the main text are colored separately.



(**A**) (**B**)

Figure A4. Plot of genome size vs. temperature limits for the species in the dataset. Y axis: genome size in megabases, plotted on a log scale. Y axis: (**A**) minimum growth temperature. (**B**) maximum growth temperature. There is a weak tendency for the largest genomes to belong to mesophilic fungi (i.e., species minimum growth temperatures between 0 °C and 20 °C and maximum growth temperatures between 25 °C and 40 °C), but the linear correlation coefficients ($R^2 = 0.016$ for maximum temperature and $R^2 = 0.001$ for minimum temperature) are not significant.

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