

Synthesis of phylogeny and taxonomy into a comprehensive tree of life

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Reconstructing the phylogenetic relationships that unite all lineages (the tree of life) is a grand challenge. The paucity of homologous character data across disparately related lineages currently renders direct phylogenetic inference untenable. To reconstruct a comprehensive tree of life, we therefore synthesized published phylogenies, together with taxonomic classifications for taxa never incorporated into a phylogeny. We present a draft tree containing 2.3 million tips—the Open Tree of Life. Realization of this tree required the assembly of two additional community resources: (i) a comprehensive global reference taxonomy and (ii) a database of published phylogenetic trees mapped to this taxonomy. Our open source framework facilitates community comment and contribution, enabling the tree to be continuously updated when new phylogenetic and taxonomic data become digitally available. Although data coverage and phylogenetic conflict across the Open Tree of Life illuminate gaps in both the underlying data available for phylogenetic reconstruction and the publication of trees as digital objects, the tree provides a compelling starting point for community contribution. This comprehensive tree will fuel fundamental research on the nature of biological diversity, ultimately providing up-to-date phylogenies for downstream applications in comparative biology, ecology, conservation biology, climate change, agriculture, and genomics.

phylogeny | taxonomy | tree of life | biodiversity | synthesis

The realization that all organisms on Earth are related by common descent (1) was one of the most profound insights in scientific history. The goal of reconstructing the tree of life is one of the most daunting challenges in biology. The scope of the problem is immense: there are ~1.8 million named species, and most species have yet to be described (2–4). Despite decades of effort and thousands of phylogenetic studies on diverse clades, we lack a comprehensive tree of life, or even a summary of our current knowledge. One reason for this shortcoming is lack of data. GenBank contains DNA sequences for ~411,000 species, only 22% of estimated named species. Although some gene regions (e.g., *rbcL*, 16S, COI) have been widely sequenced across some lineages, they are insufficient for resolving relationships across the entire tree (5). Most recognized species have never been included in a phylogenetic analysis because no appropriate molecular or morphological data have been collected.

There is extensive publication of new phylogenies, data, and inference methods, but little attention to synthesis. We therefore focus on constructing, to our knowledge, the first comprehensive tree of life through the integration of published phylogenies with taxonomic information. Phylogenies by systematists with expertise in particular taxa likely represent the best estimates of relationships for individual clades. By focusing on trees instead of raw data, we avoid issues of dataset assembly (6). However, most

published phylogenies are available only as journal figures, rather than in electronic formats that can be integrated into databases and synthesis methods (7–9). Although there are efforts to digitize trees from figures (10), we focus instead on synthesis of published, digitally available phylogenies.

When source phylogenies are absent or sparsely sampled, taxonomic hierarchies provide structure and completeness (11, 12). Given the limits of data availability, synthesizing phylogeny and taxonomic classification is the only way to construct a tree of life that includes all recognized species. One obstacle has been the absence of a complete, phylogenetically informed taxonomy that spans traditional taxonomic codes (13). We therefore assembled a comprehensive global reference taxonomy via alignment and merging of multiple openly available taxonomic resources. The Open Tree Taxonomy (OTT) is open, extensible, and updatable, and reflects the overall phylogeny of life. With the continued updating of phylogenetic information from

Significance

Scientists have used gene sequences and morphological data to construct tens of thousands of evolutionary trees that describe the evolutionary history of animals, plants, and microbes. This study is the first, to our knowledge, to apply an efficient and automated process for assembling published trees into a complete tree of life. This tree and the underlying data are available to browse and download from the Internet, facilitating subsequent analyses that require evolutionary trees. The tree can be easily updated with newly published data. Our analysis of coverage not only reveals gaps in sampling and naming biodiversity but also further demonstrates that most published phylogenies are not available in digital formats that can be summarized into a tree of life.

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Data deposition: The Open Tree of Life taxonomy, the synthetic tree, and processed inputs are available from the Dryad database, [dx.doi.org/10.5061/dryad.8j60q](https://doi.org/10.5061/dryad.8j60q).

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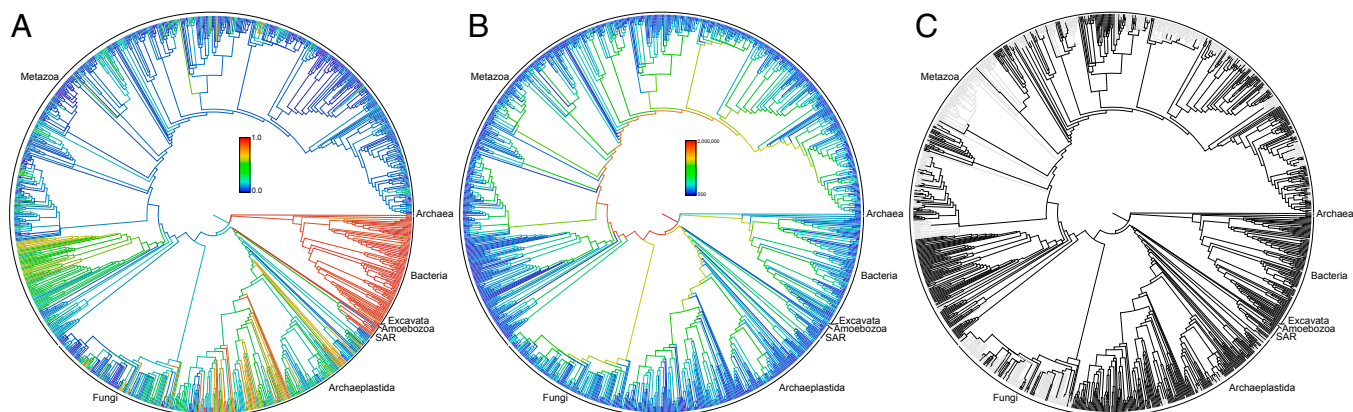


Fig. 1. Phylogenies representing the synthetic tree. The depicted tree is limited to lineages containing at least 500 descendants. (A) Colors represent proportion of lineages represented in NCBI databases. (B) Colors represent the amount of diversity measured by number of descendant tips. (C) Dark lineages have at least one representative in an input source tree.

published studies, this framework is poised to update taxonomy in a phylogenetically informed manner far more rapidly than has occurred historically (see Fig. S1 for workflow).

We used recently developed graph methods (14) to synthesize a tree of life of over 2.3 million operational taxonomic units (OTUs) from the reference taxonomy and curated phylogenies. Taxonomies contribute to the structure only where we do not have phylogenetic trees. Advantages of graph methods include easy storage of topological conflict among underlying source trees in a single database, the construction of alternative synthetic trees, and the ability to continuously update the tree with new phylogenetic and/or taxonomic information. Importantly, our methodology also highlights the current state of knowledge for any given clade and reveals those portions of the tree that most require additional study. Although a massive undertaking in its own right, this draft tree of life represents only a first step. Through feedback, addition of new data, and development of new methods, the broader community can improve this tree.

Results

Open Tree Taxonomy. To align phylogenies from different sources, the tips, which may represent different taxonomic levels, must be mapped to a common taxonomic framework (14). For synthesizing phylogenetic data, taxonomy also provides completeness and structure where phylogenetic studies have not sampled all known lineages (true of most clades). Available taxonomies differ in completeness and how closely the hierarchy matches known evolutionary relationships. The Open Tree Taxonomy (OTT) is an automated synthesis of available taxonomies, maximizing the number of taxa and preferring input taxonomies that better align to phylogenetic hypotheses in various clades (*Materials and Methods*). It contains taxa with traditional Linnaean names and unnamed taxa known only from sequence data. OTT ver. 2.8 has 2,722,024 OTUs without descendants and includes 382,564 higher taxa; 585,081 of the names are classified as non-phylogenetic units (e.g., *incertae sedis*) and were therefore not included in the synthesis pipeline. The taxonomy is available for download and through online services, including a taxonomic name resolution service for aligning other trees with our taxonomy (see *Data and Software Availability*, below).

Input Phylogenies. We built a user interface for collection and curation of potential trees for synthesis (<https://tree.opentreeoflife.org/curator>). The complete database contains 6,810 trees from 3,062 studies. At the time of publication, 484 studies in our database are incorporated into the draft tree of life. Our goal is to generate a best estimate of phylogenetic knowledge; based on our tests, we give several reasons not to use all available trees for synthesis. First, including trees that are incorrect does

not improve the synthetic estimate. In each major clade, expert curators selected and ranked input trees for inclusion based on date of publication, underlying data, and methods of inference (see *Materials and Methods* for details). These rankings generally reflect community consensus about phylogenetic hypotheses. Second, including trees that merely confirm, or are subsets of, other analyses only increases computational difficulty without significantly improving the synthetic tree. For example, although we have many framework phylogenies spanning angiosperms, we did not include older trees where a newer tree extends the same underlying data. Third, inclusion of trees requires a minimum level of curation; where most OTU labels have been mapped to the taxonomic database, the root is correctly identified, and an ingroup clade has been identified. This information is not in the input file and requires manual curation from the associated publication. Not all trees are sufficiently well-curved; at this point, we have focused curation efforts on trees that will most improve the synthetic tree. The full set of trees in the database is important for other questions such as estimating conflict or studying the history of inference in a clade, highlighting the importance of continued deposition and curation of trees into public data repositories. See *Dataset S1* for a list of input trees and metadata and see *Fig. S2* for size and scope of input trees.

A Draft Tree of Life. We constructed a tree alignment graph (14), the graph of life, by loading the Open Tree Taxonomy and the 484 rooted phylogenies into a neo4j database. The graph of life contains 2,339,460 leaf nodes (after excluding nonphylogenetic units from OTT), plus 229,801 internal nodes. It preserves conflict among phylogenies and between phylogenies and the taxonomy. To create the synthetic tree, we traversed the graph, resolving conflict based on the rank of inputs, and labeled accepted branches that trace a synthetic tree summarizing the source information. This method allows for clear communication of how conflicts are resolved through ranking, and of the source trees and/or taxonomies that support a particular resolution. The synthetic tree contains phylogenetic structure where we have published trees, and taxonomic structure where we do not. See the *Supporting Information*, including *Figs. S3–S6*, for details. The tree is available to browse and download, and online services allow extraction of subtrees given lists of species (see *Data and Software Availability*, below).

Coverage. Of the 2,339,460 tips in the synthetic tree of life, 37,525 are represented in at least one input phylogeny, with an additional 4,254 nonterminal taxa represented as tips in phylogenetic inputs (Fig. 1). In Bacteria, Fungi, Nematoda, and Insecta, there is a large gap between the estimated number of species and what exists in taxonomic and sequence databases (Fig. 2). In contrast, Chordata and Embryophyta are nearly fully sampled in

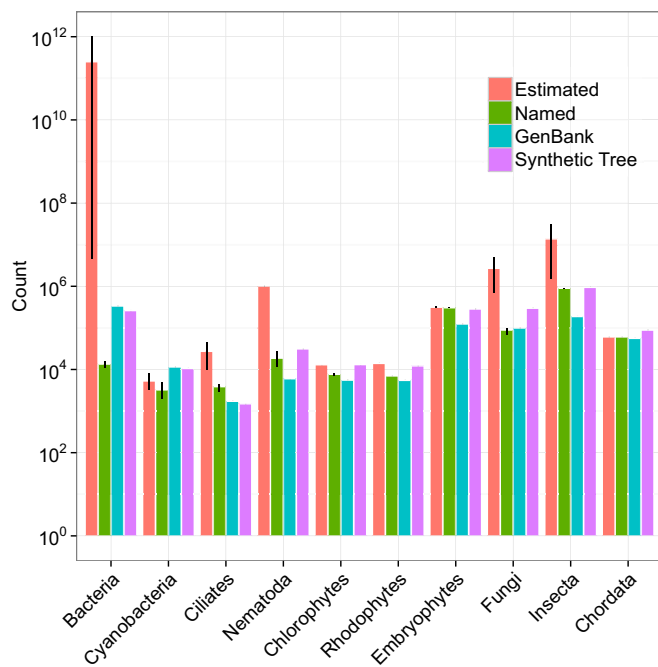


Fig. 2. The estimated total number of species, estimated number of named species in taxonomic databases, the number of OTUs with sequence data in GenBank, and the number of OTUs in the synthetic tree, for 10 major clades across the tree of life. Error bars (where present) represent the range of values across multiple sources. See [Dataset S2](#) for the underlying data.

databases and in OTT (Fig. 2). Poorly sampled clades require more data collection and deposition and, in some cases, formal taxonomic codification and identification to be incorporated in taxonomic databases. Most tips in the synthetic tree are not represented by phylogenetic analyses. The limited number of input trees highlights the need for both new sequencing efforts, additional phylogenetic studies, and the deposition of published tree files into data repositories.

Resolution and conflicts. The tree of life that we provide is only one representation of the Open Tree of Life data. Analysis of the full graph database (the graph of life) allows us to examine conflict between the synthetic tree of life, taxonomy, and source phylogenies. Fig. 3 depicts the types of alternate resolutions that exist in the graph. We recovered 153,109 clades in the tree of life, of which 129,778 (84.8%) are shared between the tree of life and the Open Tree Taxonomy. There are 23,331 clades either that conflict with the taxonomy (4,610 clades; 3.0%) or where the taxonomy is agnostic to the presence of the clade (18,721 clades; 12.2%). The average number of children for each node in the taxonomy is 19.4, indicating a poor degree of resolution compared with an average of 2.1 in the input trees. When we combine the taxonomy and phylogenies into the synthetic tree, the resolution improves to an average of 16.0 children per internal node. See the [Supporting Information](#), including [Fig. S7](#), for details.

Alignment of nodes between the synthetic tree and taxonomy reveals how well taxonomy reflects current phylogenetic knowledge. Strong alignment is found in Primates and Mammalia whereas our analyses reveal a wide gulf between taxonomy and phylogeny in Fungi, Viridiplantae (green plants), Bacteria, and various microbial eukaryotes (Table 1).

Comparison with supertree approaches. There were no supertree methods that scale to phylogenetic reconstruction of the entire tree of life, meaning that our graph synthesis method was the only option for tree of life-scale analyses. To compare our method against existing supertree methods, we used a hybrid MultiLevelSupertree (MLS) (15) plus synthesis approach (*Materials and Methods*). The total number of internal nodes in the

MLS tree is 151,458, compared with 155,830 in the graph synthesis tree, although the average number of children is the same (16.0 children per node). If we compare the source phylogenies against the MLS supertree and the draft synthetic tree, the synthesis method is better at capturing the signal in the inputs. The average topological error (normalized Robinson–Foulds distance, where 0 = share all clades and 100 = share no clades) (16) of the MLS vs. input trees is 31, compared with 15 for the graph synthesis tree. See the [Supporting Information](#) for details.

Discussion

Using graph database methods, we combine published phylogenetic data and the Open Tree Taxonomy to produce a first-draft tree of life with 2.3 million tips—the Open Tree of Life. This tree is comprehensive in terms of named species, but it is far from complete in terms of biodiversity or phylogenetic knowledge. It does not aim to infer novel phylogenetic relationships, but instead is a summary of published and digitally available phylogenetic knowledge. To our knowledge, this study represents the first time a comprehensive tree of life has been available for any analyses that require a phylogeny, even if the species of interest have not been analyzed together in a single, published phylogeny.

As a result of data availability, data quality, and conflict resolution, there are many areas where relationships in the tree do not match current phylogenetic thinking (e.g., relationships within Fabaceae, Compositae, Arthropoda). This draft tree of life represents an initial step. The next step in this community-driven process is for experts to contribute trees and annotate areas of the tree they know best.

Limitations on Coverage. Many microbial eukaryotes, Bacteria, and Archaea are not present in openly available taxonomic databases and therefore were not incorporated into the Open Tree Taxonomy and the synthetic tree. Most tips in the synthetic tree (98%) come from taxonomy only, reflecting both the need to incorporate more species into phylogenies and the need to make published phylogenies available. We obtained trees from digital repositories and also by contacting authors directly, but our overall success rate was only 16% (9). Many published relationships are not represented in the synthetic tree because this knowledge exists only as journal images. Our infrastructure allows for the synthetic tree to be easily and continuously updated via updated taxonomies and newly published phylogenies. The latter are dependent on authors making tree files available in repositories, such as TreeBASE (17) and Dryad ([datadryad.org](#)) or through direct upload to Open Tree of Life ([https://tree.opentreeoflife.org/curator](#)), and on having sufficient metadata for trees. We hope this synthetic approach will provide incentive for the community to change the way we view phylogenies—as resources to be cataloged in open repositories rather than simply as static images.

Conflicts in the Tree of Life. The synthetic tree of life is a bifurcating phylogeny (with “soft” polytomies reflecting uncertainty), but some relationships are more accurately described using reticulating networks. The Open Tree of Life contains areas with conflict (Fig. 3). For example, the monophyly of Archaea is contentious—some data-store trees indicate that eukaryotes are embedded within Archaea (18, 19) rather than a separate clade. Similarly, multiple resolutions of early diverging animal (20–23) and Eukaryotic (24–28) lineages have been proposed. Reticulations help visualize competing hypotheses, gene tree/species tree conflicts, and underlying processes, such as horizontal gene transfer (HGT), recombination, and hybridization, which have had major impacts throughout the tree of life [e.g., hybridization in diverse clades of green plants (29) and animal lineages (30), including our own (31), and HGT in bacteria and archaea (32–34)]. The graphical synthesis approach used here naturally allows for storage of conflict and non-tree-like structure, enabling downstream visualization, analysis, and annotation of conflict (Fig. 3) and highlighting the need for additional work in this area.

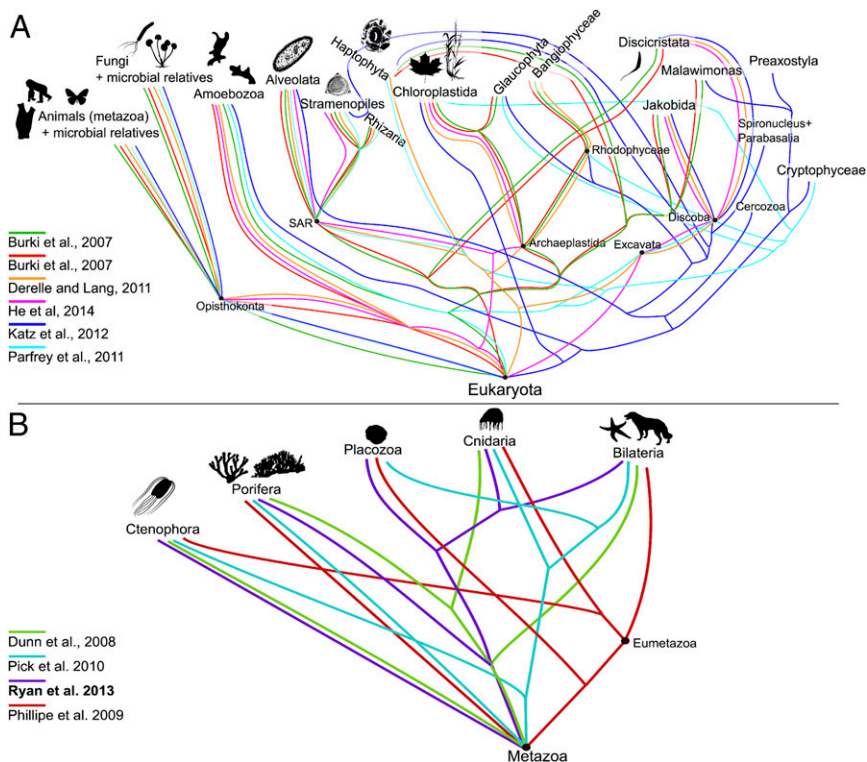


Fig. 3. Conflict in the tree of life. Although the Open Tree of Life contains only one resolution at any given node, the underlying graph database contains conflict between trees and taxonomy (noting that these figures are conceptual, not a direct visualization of the graph). These two examples highlight ongoing conflict near the base of Eukaryota (A) and Metazoa (B). Images courtesy of PhyloPic (phylopic.org).

Resolving conflict is a challenge in supertree methods, including our graph method. The number of input trees that support a synthetic edge may be considered a reasonable criterion for resolving conflict, but the datasets used to construct each source tree may have overlapping data, making them nonindependent. The number of taxa or gene regions involved cannot be used alone without other information to assess the quality of the particular analysis. Better methods for resolving conflict require additional metadata about the underlying data and phylogenetic inference methods.

Selection of Input Trees. We used only a subset of trees in the database for synthesis, filtering out trees that are redundant, are erroneous, or have insufficient metadata. Our current synthesis method relies on manual ranking of input trees by expert curators within major clades. The potential to automate this ranking, and to use metadata to resolve conflict, depends on the availability of machine-readable metadata for trees; such data currently must be entered manually by curators after reading the

publication. Additional metadata would allow a comparison of synthesis trees based on, for example, morphological versus molecular data, the inference method, or the number of underlying genes. Manual curation is time-consuming and labor-intensive; scalability would improve greatly by having standardized metadata (35) encoded in the files output by inference packages (e.g., in NeXML files) (36).

Source Trees as a Community Resource. The availability of well-curated trees allows for many analyses other than synthesis, such as calculating the increase in information content for a clade over time or by a particular project or laboratory, comparing trees constructed by different approaches, or recording the reduction in conflict in clades over time. These analyses require that tips be mapped to a common taxonomy to compare across trees. Our database contains thousands of trees mapped to existing taxonomies through the Open Tree Taxonomy. The data curation interface is publicly available (<https://tree.opentreeoflife.org/curator>)

Table 1. Alignment between taxonomy and phylogeny in various clades of the tree of life

Clade	Tips	Internal nodes	Nodes supported by		
			Taxonomy	Trees	Trees + taxonomy
Bacteria	260,323	11,028	8,454 (76.7%)	2,184 (19.8%)	390 (3.5%)
Cyanobacteria	10,581	788	678 (86.0%)	83 (10.5%)	27 (3.4%)
Ciliates	1,497	657	654 (99.5%)	1 (0.2%)	2 (0.3%)
Nematoda	31,287	3,504	3,431 (97.9%)	54 (1.5%)	19 (0.5%)
Chlorophytes	13,100	1,267	1,239 (97.8%)	20 (1.6%)	8 (0.6%)
Rhodophytes	12,214	1,292	1,278 (98.9%)	14 (1.1%)	0
Fungi	296,667	8,646	8,243 (95.3%)	383 (4.4%)	20 (0.2%)
Insecta	941,753	88,666	85,936 (96.9%)	2,205 (2.5%)	525 (0.6%)
Chordata	88,434	27,315	13,374 (49.0%)	11,689 (42.8%)	2,250 (8.2%)
Primates	681	501	129 (25.7%)	294 (58.7%)	78 (15.6%)
Mammals	9,539	4,433	1,645 (37.1%)	2,194 (49.5%)	594 (13.4%)
Embryophytes	284,447	32,211	22,400 (69.5%)	8,533 (26.5%)	1,271 (3.9%)

Table 2. Tree metadata, based on the MIAPA checklist (<https://github.com/miapa/miapa>)

Item	Description	Typically included in tree files	Use by Open Tree of Life
Topology	The topology itself, plus the type of tree (e.g., gene tree vs. species tree, type of consensus tree)	Topology, but not tree type	Yes, topology; tree type used by curators as criteria to rank trees
Root	Whether the tree is rooted, and the location of the root	Tree in file often rooted arbitrarily; different from in manuscript figures	Yes, requires manual checking by curator to match against manuscript
OTU labels	Labels on tips of tree should include (or be mappable to) a meaningful online identifier	Yes, but often do not map to online databases	Tip labels mapped through combination of automated and manual processes
Branch lengths	The length of each branch of the tree, and the units of measurement	Branch length sometimes included; units generally not present	Imported into database when present, but not included on synthetic tree
Branch support	Support values (e.g., bootstrap proportions or Bayesian posterior probabilities)	Often in files, but support type often not specified	Not in algorithm, but curators do examine branch support
Character matrix	The data used to infer the tree, including data type and source (e.g., GenBank accession or specimen)	Sometimes included with tree file, but often without sufficient metadata	Number and type of genes used by curators as criteria to rank trees
Alignment method	Method used to align sequence data	No	No
Inference method	Method used to infer tree from data	Usually no	Inference method used by curators as criteria to rank trees

We note whether the metadata is generally available in the tree file (as opposed to in the text of the article, if at all) and how the data are used by Open Tree of Life.

as is the underlying data store (<https://github.com/opentreeoflife/phylosystem>).

Dark Parts of the Tree. Hyperdiverse, poorly understood groups, including Fungi, microbial eukaryotes, Bacteria, and Archaea, are not yet well-represented in input taxonomies. Our effort also highlights where major research is needed to achieve a better understanding of existing biodiversity. Metagenomic studies routinely reveal numerous OTUs that cannot be assigned to named species (37, 38). For Archaea and Bacteria, there are additional challenges created by their immense diversity, lack of clarity regarding species concepts, and rampant horizontal gene transfer (HGT) (32, 39, 40). The operational unit is often strains (not species), which are not regulated by any taxonomic code; strain collections are not available to download, making it difficult to map taxa between trees and taxonomy and estimate named biodiversity. Open databases such as BioProject at the National Center for Biotechnology Information (NCBI) (www.ncbi.nlm.nih.gov/bioproject) have the potential to better catalog biodiversity that does not fit into traditional taxonomic workflows.

Materials and Methods

Input Data: Taxonomy. No single taxonomy both is complete and has a backbone well-informed by phylogenetic studies. We therefore constructed the Open Tree Taxonomy (OTT), by merging Index Fungorum (41), SILVA (42, 43), NCBI (44), Global Biodiversity Information Facility (GBIF) (45), Interim Register of Marine and Nonmarine Genera (IRMNG) (46), and two clade-specific resources (47, 48), using a fully documented, repeatable process that includes both generalized merge steps and user-defined patches (*Supporting Information*). OTT (ver. 2.8.5) consists of 2,722,024 well-named entities and 1,360,819 synonyms, with an additional 585,081 entities having nonbiological or taxonomically incomplete names (“environmental samples” or “incertae sedis”), that are not included in the synthetic phylogeny.

Input Data: Phylogenetic Trees. We designed and developed a user interface that saves phylogenetic trees directly into a GitHub repository (49) and used this interface to import and curate trees. We obtained published trees from TreeBASE (17) and Dryad and by direct appeal to authors. The data retrieved are by no means a complete representation of phylogenetic knowledge because we obtained digital phylogeny files for only 16% of recently published trees (9). Even when available (as newick, NEXUS, or NeXML files or

via TreeBASE import), trees require significant curation to be usable for synthesis. We mapped taxon labels (which often include laboratory codes or abbreviations) to taxonomic entities in OTT. We rooted (or rerooted) trees to match figures from papers. Because relationships among outgroup taxa were often problematic, we identified the ingroup/focal clade for the study. For studies with multiple trees, we tagged the tree that best matched the conclusions of the study as “preferred.” Then, within major taxonomic groups (eukaryotic microbial clades, animals, plants, and fungi), we ranked preferred trees to generate prioritized lists. In the absence of structured metadata about the phylogenetic methods and data used to infer the input trees, rankings were assembled by authors with expertise in specific clades and were based on date of publication, taxon sampling, the number of genes/characters in the alignment, whether the specific genomic regions are known to be problematic, support values, and phylogenetic reliability (agreement or disagreement with well-established relationships) (see Table 2 for details). In general, rankings reflect community consensus about phylogenetic hypotheses. As we collect more metadata—such as that described by the Minimum Information for a Phylogenetic Analysis (MIAPA) (35), either by manual entry into the system or by upload of tree files with structured, machine-readable metadata—automated filtering/weighting trees based on metadata will be possible.

Synthesis. The goal of the supertree (or “synthesis”) operation is to summarize the ranked input trees and taxonomy (with the taxonomy given the lowest rank). We used an algorithmic approach to produce the synthetic tree rather than a search through tree space for an optimal tree. Given a set of edges labeled with the ranks of supporting trees, the algorithm is a greedy heuristic that tries to maximize the sum of the ranks of the included edges. We summarize the major steps of the method here and provide details in the *Supporting Information*.

The first steps include preprocessing the inputs. We pruned nonbiological or taxonomically incomplete names from OTT and pruned outgroups and unmapped taxa from input trees. Removal of outgroups reduces errors from unexpected relationships among outgroup taxa. Finally, we found uncontested nodes across the taxonomy plus input trees and broke the inputs at these nodes into a set of subproblems. This divide-and-conquer approach shortened running time and reduced memory requirements.

We then built a tree alignment graph (14, 50), which we refer to as the graph of life. Tree alignment graphs allow for representation of both congruence and conflict in the same data structure, allow for nonoverlapping taxon sets in the inputs (as well as tips mapped to higher taxa), and are computationally tractable at the scale of 2.3 million tips and hundreds of

input trees. We loaded the taxonomy nodes and edges into the graph, and then each subproblem, creating new nodes and edges and mapping tree nodes onto compatible taxonomy nodes. We also created new nodes and edges that reflect potential paths between the inputs.

Once the graph was complete, generating the synthetic tree involved traversing the graph and preferring edges that originate from high-ranked inputs. We always preferred phylogeny edges over taxonomy edges. Given additional digitized metadata about trees, this system allows for custom synthesis procedures based on preference for inference methods, data types, or other factors.

As a comparison with this rank-based analysis, we also created a synthetic tree using MultiLevelSupertrees (MLS) (15), a supertree method where the tips in the source trees can represent different taxonomic hierarchies. We built MLS supertrees for the largest clades that were computationally feasible and then used these nonoverlapping trees as input into the graph database and conducted synthesis. Due to the lack of taxon overlap between each MLS tree, there was no topological conflict, and creating the final MLS supertree simply involved traversing the graph and preferring phylogeny over taxonomy.

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