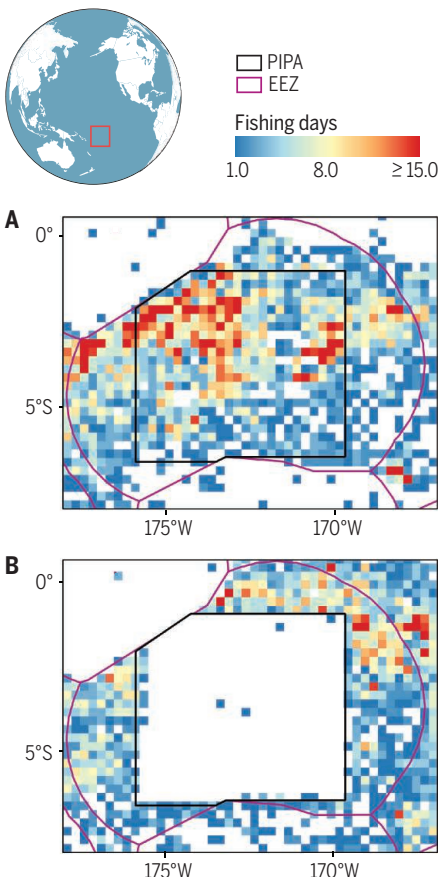


begin enforcing proper use of AIS. Simply having an AIS unit aboard a vessel, but failing to use it properly, can no longer be viewed as legal compliance. As noncompliance becomes better controlled, we also encourage that AIS data be more widely considered as admissible evidence in maritime judicial proceedings.

Evidence suggests that it is possible to equip all commercial fishing vessels in the world with AIS and enforce its use. About 75% of EU fishing vessels complied with 2014 AIS mandates within months (9). We estimated that 71% of large fishing vessels (>24 m) worldwide use AIS, and we observed a 17% increase in global AIS coverage for fishing vessels during 2014 (4). Closing remaining gaps among users resistant to compliance will be difficult but critically important.

Widespread implementation of publicly accessible AIS would effectively bring an end to the era of marine anonymity. There is growing awareness in marine and terrestrial sectors that benefits for human and environmental safety derived from



Observing marine protected areas from space.

Summary of long-line and purse seine fishing as measured using S-AIS data in PIPA during the 6 months before (A) and 6 months after (B) it was closed to commercial fishing by the Kiribati government on 1 Jan 2015 (4).

observation technologies outweigh costs of renegotiating the boundaries of industrial privacy. Recognizing these values, the marine shipping industry has almost universally adopted AIS, as well as supplemental data-sharing systems.

Reforms under way to begin managing the ocean at vastly larger and ecologically meaningful scales will only matter if we can see and act on what is happening in these spaces. Transparency is an extremely important part of this process. Parallel closed-access tracking systems can and should be linked to AIS to improve our view of vessel activity, but closed-access systems allow only part of the picture to be seen by few actors and, consequently, have more limited value to science and transboundary biodiversity management. Unfortunately, current lack of legislative support for AIS has stunted this system into a service that best observes vessels that don't mind being seen. Although the policy shifts we call for require brave revisioning of the primacy of privacy on the oceans, failure to close loopholes will continue to foster illegal activities that steal income and biodiversity from developing nations, promote social injustice at sea, and undermine efforts to cooperatively manage the sustained vitality of our shared marine resources. ■

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MICROBIOLOGY

The invisible dimension of fungal diversity

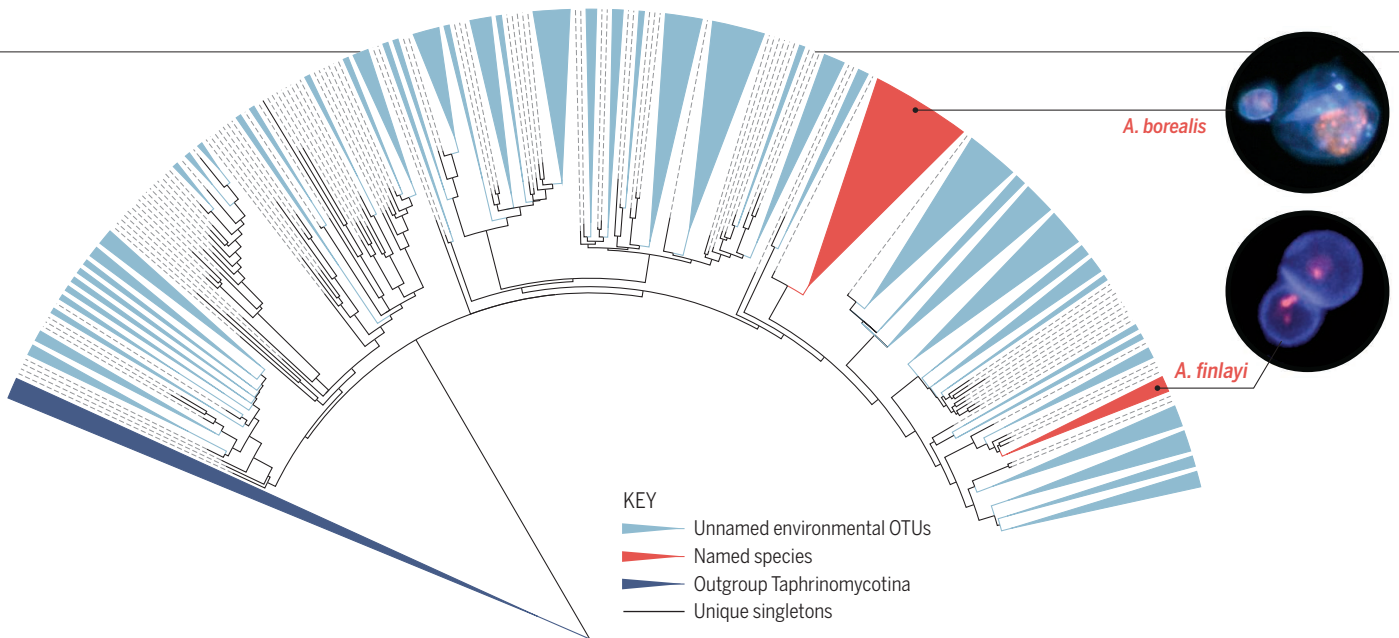
Can microbial taxa be defined from environmental molecular sequences?

By David Hibbett

Taxonomy plays a central role in understanding the diversity of life, translating the products of biological exploration and discovery—specimens and observations—into systems of names that capture the relationships between species. Taxonomic names facilitate communication among scientists and the public and provide conceptual handles for complex phylogenetic hypotheses. However, taxonomy can be challenging, particularly for fungi and other microorganisms, which are morphologically simple and extremely diverse (1). Molecular environmental surveys have revealed previously unknown branches of the fungal tree of life (2–5) and illuminated biogeographic patterns across all groups of fungi (6, 7). Yet the products of this research are not being translated into formal species names, in part because of the very rules designed to facilitate taxonomy.

Two recently recognized groups of fungi, Archaeorhizomycetes and Cryptomycota, illustrate the magnitude of ongoing molecular species discovery. Archaeorhizomycetes are root-associated soil fungi that have been found in more than 100 independent studies. When Menkis *et al.* (3) pooled environmental sequences of ribosomal internal transcribed spacer (ITS) genes, they found 50 lineages of Archaeorhizomycetes containing at least two independent sequences with 97% similarity, a standard cutoff for recognizing OTUs (operational taxonomic units, often equated with species). They also found 95 unique sequences (singletons). Thus, as many as 145 species of Archaeorhizomycetes have been discovered. But only two have been formally named, *Archaeorhizomyces finlayi* and *A. borealis*, based on the only live cultures obtained so far (see the figure).

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Visible and invisible diversity of Archaeorhizomycetes. Phylogenetic analysis of environmental DNA sequences resolves 50 species-level groups of Archaeorhizomycetes (3), but only two have been formally named. The existence of 95 unique singleton sequences suggests that there is much unsampled diversity. Archaeorhizomycetes is the most diverse class in the Taphrinomycotina, which include well-known plant pathogens and the model fission yeast. Tree topology from (3); micrographs by A. Rosling.

The aptly named Cryptomycota have also been detected repeatedly in molecular studies of soil, freshwater, and marine habitats (4, 5). Phylogenetic analyses suggest that Cryptomycota make up an ancient clade of fungi. Cryptomycota cells have been visualized in environmental samples with fluorescent tags, but these observations are not linked to cultures or specimens (4). Lazarus and James analyzed 109 environmental sequences of Cryptomycota and resolved 12 strongly supported groups (5). However, they could only assign three sequences to a formally named taxon, the genus *Rozella*, which includes endoparasites of protists and other fungi.

Molecular ecological studies have investigated fungal distributions on global (7) and local (8) scales. In one recent global survey, Davison *et al.* (6) analyzed the distribution of arbuscular mycorrhizal fungi, which form symbioses with about 80% of plants, but do not produce mushrooms and cannot be grown in pure culture. Using 18S ribosomal RNA gene sequences, the authors detected 246 OTUs, of which 93% occurred on multiple continents and 34% on six continents. This level of endemism is surprisingly low for fungi that do not produce airborne spores (6). However, the results provide limited information about distributions of known taxa, because only 41 of the OTUs (17%) include sequences from named species.

In the largest study of fungal diversity to date, Tedersoo *et al.* (7) analyzed 1.4 million ITS sequences from 365 sites worldwide and recovered ~45,000 OTUs represented by at least two sequences, with a further ~36,000 singletons. Only about one-third of the nonsingleton OTUs matched any sequences in public databases at the 97%

similarity cutoff. In other words, this study detected ~30,000 OTUs that could be new species—about 15 times the number of new fungal species descriptions published in journals and recorded in nomenclatural databases in the same year (1).

Environmental sequences have transformed understanding of the fungal tree of life, from its deepest roots to its finest branches. Why are these discoveries not being formalized in taxonomic names?

First, there are legitimate scientific concerns over the nature of evidence required to delimit species. Mycologists have selected ITS as the official barcode locus (9), but in some groups multiple species may have identical ITS sequences, whereas in other groups there may be multiple forms of ITS in a single genome. Single-cell genomics could provide multiple genes from individuals in environmental samples, but these technically demanding approaches are not yet widely applied in fungal ecology. Until they are, most studies will rely on single markers such as ITS, which can never reveal the patterns of gene flow that provide clues to the limits of reproductively isolated lineages.

Second, species names are no longer needed to test ecological or evolutionary hypotheses. Ecologists once relied on taxonomic resources to identify the species whose interactions they sought to explain; today, they use automated pipelines to cluster OTUs without reference to keys, vouchers, and monographs (10). Ecologists and evolutionary biologists do not need to undertake the tedious work of identification and formal taxon description to address the problems that motivate them. On the other hand, molecular ecological studies are providing un-

precedented resources for taxonomists, who could use the new data to describe new species or enhance existing descriptions with expanded geographic ranges and new insights into ecological roles.

Unfortunately, the rules that govern biological nomenclature prohibit formal naming of fungi and other microbial taxa based on environmental sequences. Physical type specimens are required by the botanical and zoological codes of nomenclature, which collectively determine conditions for valid publication of names of fungi and protists, and the bacteriological code requires type cultures. Classical taxonomy is thus cut off, by its own nomenclatural rules, from the major modes of discovery for microbial organisms. Working models for purely sequence-based delimitation of fungal taxa do exist (3, 6, 10, 11), but do not yet confer nomenclatural validity. Community standards for sequence-based taxon definition and revision of the codes of nomenclature are needed to make the products of molecular environmental surveys visible to scientific and lay communities. ■

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The invisible dimension of fungal diversity

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