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INTRODUCTION

"Everything depends on everything else."

(Translated credo of the Haida people of the Pacific Northwest)

All life on the planet is connected, but these connections go mostly unseen. As you read this, for example, microbes covering much of the surface of your body—inside and out—are going about their business. In fact, the vast majority of living cells that make the ecosystem that is "you" are not human; the vast majority are microbial, and some are fungal.

It's a similar story with the tree outside your window, which is mostly of non-living tree cells; most of the living cells making up that tree are probably not tree or even plant cells. Endophytic organisms inside the plant's tissues are responsible for much of the hormonal control of the plant, determining its drought resistance, heat resistance, and toxin production in response to attack by pathogens or herbivory. Mycorrhizae of the tree's roots are responsible for the uptake of water and nutrients. These fungi are attached to adjacent and unrelated trees, and have fruitbodies that host fungi-eating (mycophagous) arthropods. These arthropods are in turn parasitized by nematodes, or by smaller arthropods, such as braconid parasitoid wasps. Those tiny parasitoid wasps rely on viruses to mask their invading parasite egg from the immune system of the host's larva, and so the connections go on.

What all of these living organisms have in common, though—indeed, what every living organism on this planet has in common—is a reliance on fungi. Yet even though fungi are all around us, they remain poorly understood. With our planet and natural resources under constant assault from an ever-shrinking habitat and a burgeoning human population that brings with it pollution, invasive species, and other manmade disasters, it is becoming increasingly important that we are aware of the natural treasures that exist all around us.

Mushrooms and other fungi are beautiful and interesting organisms, which I know is an opinion that is not shared by everyone. If considered at all, fungi are often seen as mere recyclers of nutrients and decomposers of organic matter in the environment—rotters of the once-living. However, recently developed methods to detect organismal DNA from the environment, improved microscopic techniques, and novel methods for culturing and cultivating,

are showing that fungi are much more ubiquitous than we thought. They are also revealing that fungi are much more important to the environment and, by extension, to ourselves.

Based on sheer mass and the number of species, fungi (along with insects) are likely the most common and most evolutionarily successful organisms on the planet. Fungi can be found thriving on all continents of Earth, from the loftiest peaks to the driest deserts, from the depths of the world's oceans to our own backyards. Nor do they stop at our doors—they can be found thriving (to the chagrin of most) within our own homes. With advances in modern microscopy we have come to know that molds and other fungi are found in just about every niche in the environment and that probably no plants—long considered the keystones of all habitats—can thrive for very long without their

↑ *Favolaschia calocera* is a beautiful rotter of wood that has recently been turning up in many new places and new habitats. A changing climate and international travel and trade are changing the mycological landscapes around us.

← Mushrooms are the reproductive structures of fungi and come in a bewildering assortment of shapes and forms. The Common Splitgill (*Schizophyllum commune*) is one of the most ubiquitous of all mushrooms, found on dead wood of every continent except Antarctica.

fungal partners. Obligately intertwined among roots as mycorrhizae, growing epiphytically on plant surfaces, and found within plant tissues as endophytes, fungi are the true puppet masters in nature. Conversely, fungi also cause the vast majority of disease among plant species, including those to which we owe our very survival as sources of food, fiber, and medicines; again, fungi pull the strings.

↑ Fungi come in a tremendous array of colors, their forms and shapes range from very simple to complex, and at times otherworldly. Their ecology and roles they play in the environment are every bit as diverse.

As a species, we humans have come to a crucial point in our history. About 2.5 billion people inhabited our planet when I was born, but by the early 1990s, when I was a graduate student studying mushrooms and other fungi, our population had increased to 5.3 billion. Now that number is 7.8 billion, which is projected to rise to 9.7 billion by 2050. These snowballing figures highlight the immense challenges we face when tackling global climate change and figuring out how, as a species, we can sustain the healthy ecosystems that we depend on for our existence.

There is no doubt that fungi will play an important role in this process, as humans have collected, used, and eaten mushrooms and other fungi for (arguably) as long as we have been human—most likely longer. Today, wild forest mushrooms are harvested on every continent except Antarctica, and many species can be

cultivated with relative ease. However, the most abundant edible mushrooms are ectomycorrhizal, which means that they symbiotically interact with tree roots. These species have sufficient ongoing supplies of nutrition from their tree hosts to support abundant annual fruiting, but forests around the world face tremendous pressure for other uses. This often results in deforestation or degraded forest ecosystems, with a direct impact on the fungi they host.

Yet as crucially important as they are to the planet, we pay the average fungus almost no attention as it goes about its business, even though fungi do things and live in ways that would seem otherworldly to most people (some fungi do things you probably could not imagine). Sometimes, though, if the conditions are just right, and you happen to be at exactly the right place at exactly the right time, you might witness a moment of magic as mushrooms emerge from the forest floor. Their amazing hydraulic strength betrays their presumed delicate mien as they push up debris and duff. One by one, their caps mature and open to release innumerable spores to the vagaries of the slightest breeze. There is no telling where those spores will alight, but if the conditions and substrate are favorable, the cycle will begin anew. But the mushroom is just the mycological tip of the iceberg, as the main body of the fungus remains hidden. Moreover, the fungi that produce macroscopic fruitbodies—mushrooms that are large enough for you to notice—form just a tiny fraction of all the fungi. So just what are fungi? What are they up to and what are they doing in the environment?

What are fungi?

Fungi comprise an entire kingdom of life, and just as members of the animal or plant kingdoms are very different from one another, so are members of the fungal kingdom. Their ways of obtaining nutrition, their defense mechanisms, genetics, reproduction, communication, and so on, are very different to the animalian ways that are familiar to most people.

↓ *Cordyceps militaris* in cultivation.

For most of scientific history, fungi were considered to be plants. Beginning with Aristotle, all living things were treated either as plants or as animals, depending on whether they could move or not. The system of classification that we use today—with ranks of relatedness such as kingdom, phyla, genera, and so on—was developed by Carolus Linnaeus in the eighteenth century. However, although it is more sophisticated, it didn't much change things for fungi, which were still thought of as plants. So it is more than a little ironic that today, with a much better grasp of the evolutionary relatedness of all life on the planet, it turns out that the organisms most closely related to fungi are not plant, but animals (including us).

If you encountered a mushroom in your local woods, you would of course recognize it. Likewise, holding a green leaf in your hand you would know that it came from a plant. But the vast majority of fungi do not make mushrooms, and what if the plant material were not green? How would you then know what you were looking at? For that matter, how is life classified? To answer such a fundamental question, you have to know a bit about biology and physiology.

The first rule of biology is that living things are made of cells; the cell is a collection of all the materials needed to conduct the life of that organism, contained within a semipermeable phospholipid membrane. However, as simple as this sounds, not all biologists agree—according to this definition, a virus would not be a living entity, but some scientists would argue otherwise.

At the simplest level, all life is divided into Prokaryotes and Eukaryotes. Prokaryotes are single-celled organisms (which include bacteria) that lack membrane-bound organelles and do not have a nucleus, and their DNA consists of a single, circular chromosome. In addition to a cell membrane, bacteria may or may not have a rigid cell wall, but that's about it.

In comparison, Eukaryotes are far more organized from a physiological standpoint. They feature membrane-bound organelles, such as mitochondria and a nucleus, and DNA that is organized as complex chromosomes. Eukaryotes include single-celled protists, plants, animals, and fungi.

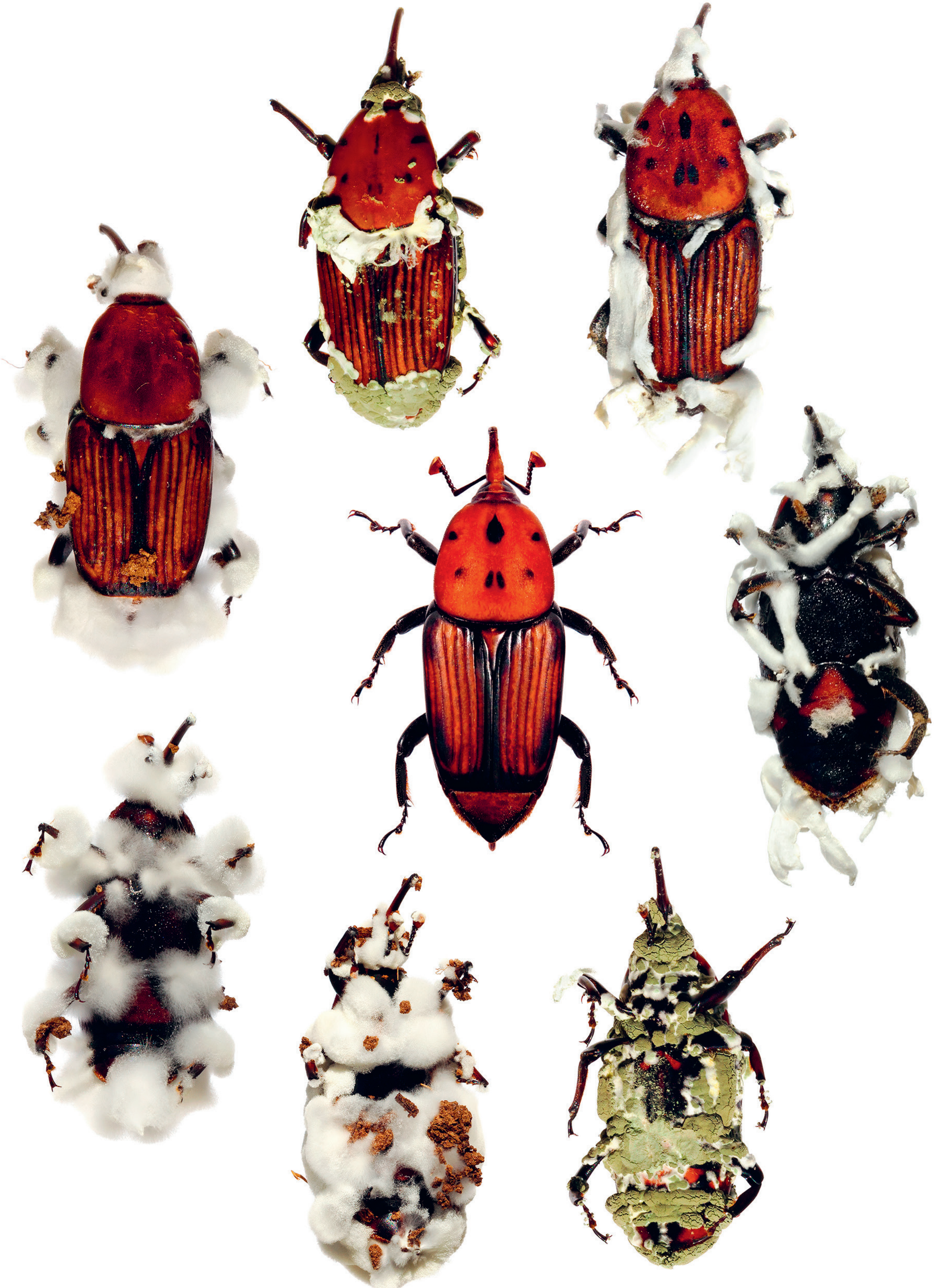
Fungi derive their energy from all heterotrophic means imaginable—and probably some fungi do things you could not imagine. Perhaps most fungi are parasites, and it is likely that all plants have species-specific fungal pathogens; many of our agricultural crop varieties have variety-specific fungal pathogens. Other fungi are saprobes (deriving their nourishment from decomposing dead organic matter), while some are mutualistic symbionts of other organisms, especially plants. A few fungi are carnivorous, trapping and killing their animal prey as a source of nitrogen.

What all fungi have in common, though, is cell walls composed of chitin, which gives the body of the fungus strength and flexibility. Chitin is somewhat similar to the cellulose found in plants, but is made of long chains of carbohydrates that are connected by a different specific chemical bond. In addition to fungi, chitin is found in the exoskeletons of insects and other arthropods; the group of protists most closely related to fungi also has cell walls of chitin.

Humans do not produce chitinases, which are the enzymes needed to degrade chitin. A popular misconception is that because fungi are composed of chitin, they're indigestible and not nutritious. However, although it is true that there is little nutrition to be had from chitin (or plant cellulose for that matter), there is plenty else within the cells of fungi and plants that is nutritious. Also, the chitin we ingest when we consume mushrooms and other fungi passes through us as fiber, in much the same way as plant cellulose. While it is indigestible, fiber has a beneficial role in our diets.

← Stinkhorns like *Aseroë rubra*, may look like some form of extraterrestrial life but are highly specialized for spore production and entice insects to do much of the work for them, in a similar fashion to insect pollination of plants.

→ Fungi are not always mutualists with insects. *Beauveria bassiana* and *Metarhizium anisopliae* are entomopathogenic (insect-killing) fungi and shown here on Red Palm Weevil (*Rhynchophorus ferrugineus*); by way of comparison, an uninfected specimen is shown in the center.



↑ Mushrooms often take on beautiful forms, sometimes resembling other organisms, like this coral mushroom, *Ramaria stricta*.

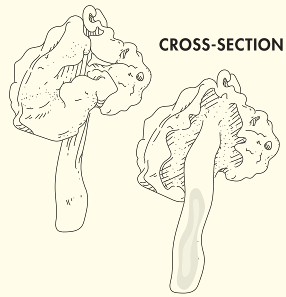
FORM AND FUNCTION

Fungal reproductive structures come in a wide array of sizes, shapes, and colors, but fruitbodies that are large enough to be called mushrooms are produced only by ascomycetes and basidiomycetes. Common fruitbody forms are often grouped as fruitbodies with gills, pores or tubes, teeth or spines (agarics and boletes); shelf-like mushrooms with pores or gills (polypores); bird's nest and cup fungi; puffballs and puffball-like fungi; jelly fungi; coral and club fungi; and truffles and truffle-like fungi.

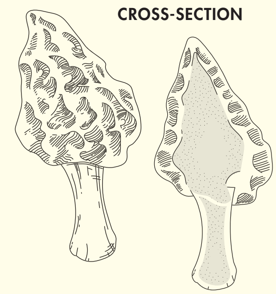
However, a similarity of fruitbody forms can be misleading and has led mycologists to disagree on classification schemes in the past. As a fascinating result of convergent evolution, ascomycete and basidiomycete fungi feature species that produce similar-looking mushrooms, such as cups, clubs, and truffles. Convergent evolution has driven groups within a phylum to produce similar looking forms as well. Thus we have several orders within the basidiomycetes that produce shelf-like fruitbodies, but not all of them are polypores. It is the environment and natural selection that drives the organism into a best fit for its situation, which is why we have many groups of basidiomycete fungi that produce truffle-like forms—this type of fruitbody is most suited to life in arid environments.

Diverse forms for reproduction
Fungi and fungi-like organisms produce reproductive structures in a wide array of sizes, shapes, and colors. Common forms feature gills, pores or tubes, teeth or spines; may be shelf-like with pores or gills; cup-shaped, coral or club-shaped; amorphous oozing or jelly-like; or round and spherical like a ball. Many tiny molds form no fruitbody at all, and simply create reproductive propagules from conidiophores.

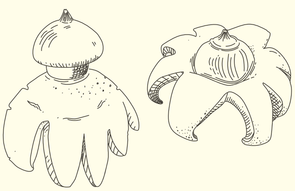
CHANTERELLES



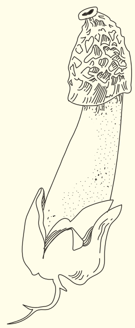
FALSE MORELS



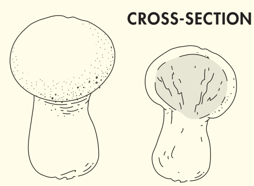
TRUE MORELS



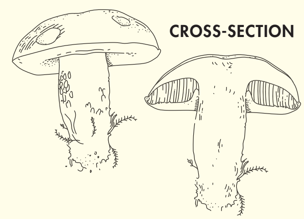
EARTH STARS



STINKHORNS



PUFFBALL

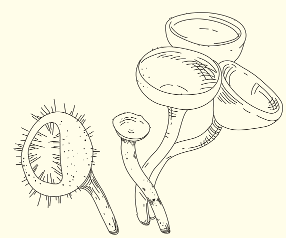


BOLETES

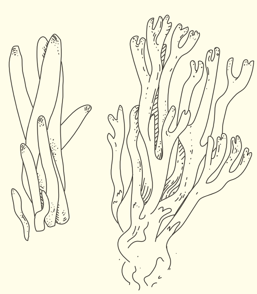
SIMPLE CONIDIOPHORES

SIMPLE CONIDIOPHORES

OOZING PLASMODIUM



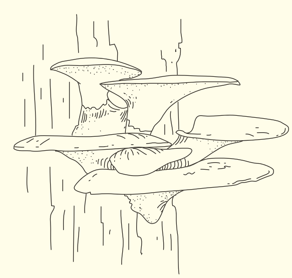
CUP FUNGI



CORAL FUNGI

GILLED FUNGI

TEETH FUNGI



POLYPORES

THE FUNGAL FOSSIL RECORD

Although soft fleshy fungi do not fossilize very well, we do have a fossil record for them. The first fungi undoubtedly originated in water, like much of the earliest life on Earth. Based on the fossil record, fungi are presumed to have been present in the Late Proterozoic, 900–570 million years ago (MYA), and maybe further back than that; the oldest "fungus" microfossils were found in Victoria Island shale and date to around 850M–1.4B years old, although the jury is still out on whether they are truly fungal. Whatever the precise date, the consensus seems to be that fungi probably arrived on land just ahead of the first terrestrial plants (which date to around 700 MYA), and paved the way for plants to move from a marine environment to ever-drier habitats.

The first "lichen-like" organisms we see in the fossil record date to around 600 MYA, and around 550 MYA the chytrids and higher fungi split from a common ancestor. The first taxonomically identifiable fungi are from 460 MYA, and seem similar to modern Glomeromycota. At about 400 MYA is when the Basidiomycota and Ascomycota split from a common ancestor. The first insects came on to the scene around 400 MYA; the first beetles and flies date to around 245 MYA.

Much of what we know of no-longer-extant fungi comes from specimens found in amber. Due to the preservative qualities of the tree resin, amber is one medium that preserves exquisite detail in delicate objects such as fungal bodies. Not only does the resin prevent air from reaching the fossils, but it also withdraws moisture from the tissue, resulting in a process known as inert dehydration. Furthermore, amber possesses antimicrobial compounds that kill any microorganisms that would decay organic matter, naturally embalming anything that gets trapped. Because of these properties a few fossilized mushrooms have been preserved beautifully in amber that dates from the Cenozoic and Cretaceous periods. The oldest mushroom is *Palaeoagaricites antiquus* (100 MYA), which resembles modern-day members of the family Tricholomataceae, while other species include *Archaeomarasmius legettii* (90 MYA), *Protomycena electra* (20 MYA), and *Coprinites dominicana* (20 MYA). The latter three all look pretty much the same as mushrooms you can find in woods today.

Mycorrhizal relationships are believed to have arisen more than 400 MYA, as plants began to colonize terrestrial habitats. These relationships are seen as a key innovation in the evolution of vascular plants. Recently, the first fossil ectomycorrhiza associated with flowering plants (angiosperms) was discovered. The fossils were found in a piece of Lower Eocene (52 MYA) Indian amber, from a time only 13 million years after the demise of the dinosaurs. Mycorrhizas are extremely rare in the fossil record.

↖ As discussed in the text, amber preserves entombed organisms exquisitely. Although very few fossils of mushrooms are known, organisms that feed on fungi are frequently found in amber, such as this mycophagous phorid fly.

→ The oldest known fungal fossil is *Ourasphaira giraldae* found in shale that formed between 900 and one billion years ago in what is now the Northwest Territories of Canada. Despite its age, the fossils are very well preserved. Spores of the fungus, clearly visible, are less than a tenth of a millimeter long and connect to one another by slender, branching hyphal filaments.

CLASSIFICATION AND TAXONOMY

At the time of writing there are around 100,000 species of named fungi, although it has been estimated that there are probably more like 1.5 million species in total, meaning the vast majority of fungi await discovery and description. The reason for this is because fungi are cryptic—the microscopic size of most of them makes them difficult to find, and those that elude culture often remain unknown. However, we know there are many unseen fungi out there because they leave their DNA behind in soil and other substrates.

The major groups of fungi have been classified according to characteristics of their sexual reproductive structures, which until recently meant that fungi were grouped into four classes: chytridiomycetes, zygomycetes, basidiomycetes, and ascomycetes. Although it is overly simplified, this taxonomic scheme is still a pretty useful system when it comes to understanding what these fungi are and how they reproduce.

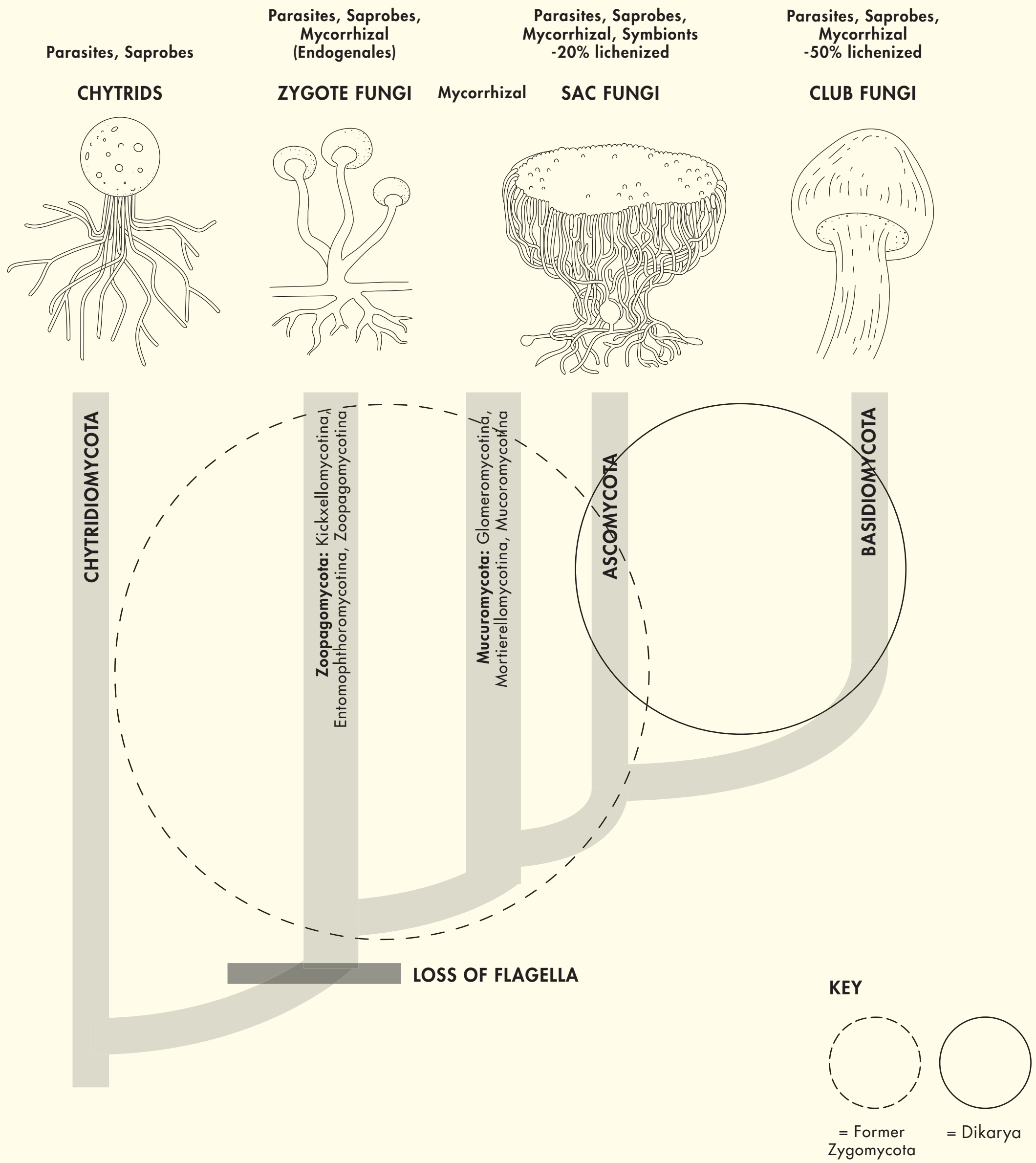
More recently developed classification schemes separate fungi into additional classes (or phyla), although not all scientists agree on the taxonomic hierarchies for some of the oddball groups. Formal phylum names are capitalized (Chytridiomycota, Glomeromycota Basidiomycota, and Ascomycota), while "Zygomycota" is often represented with quotations, as it is something of an artificial group of fungi that, together, are not monophyletic. Among these groups, basidiomycetes and ascomycetes fungi (or "basidios" and "ascos" as they are sometimes referred to by mycophiles) are collectively known as the "higher" fungi. Other than mycologists, most people are familiar only with the larger showy fungi of the basidiomycetes and a few ascomycetes.

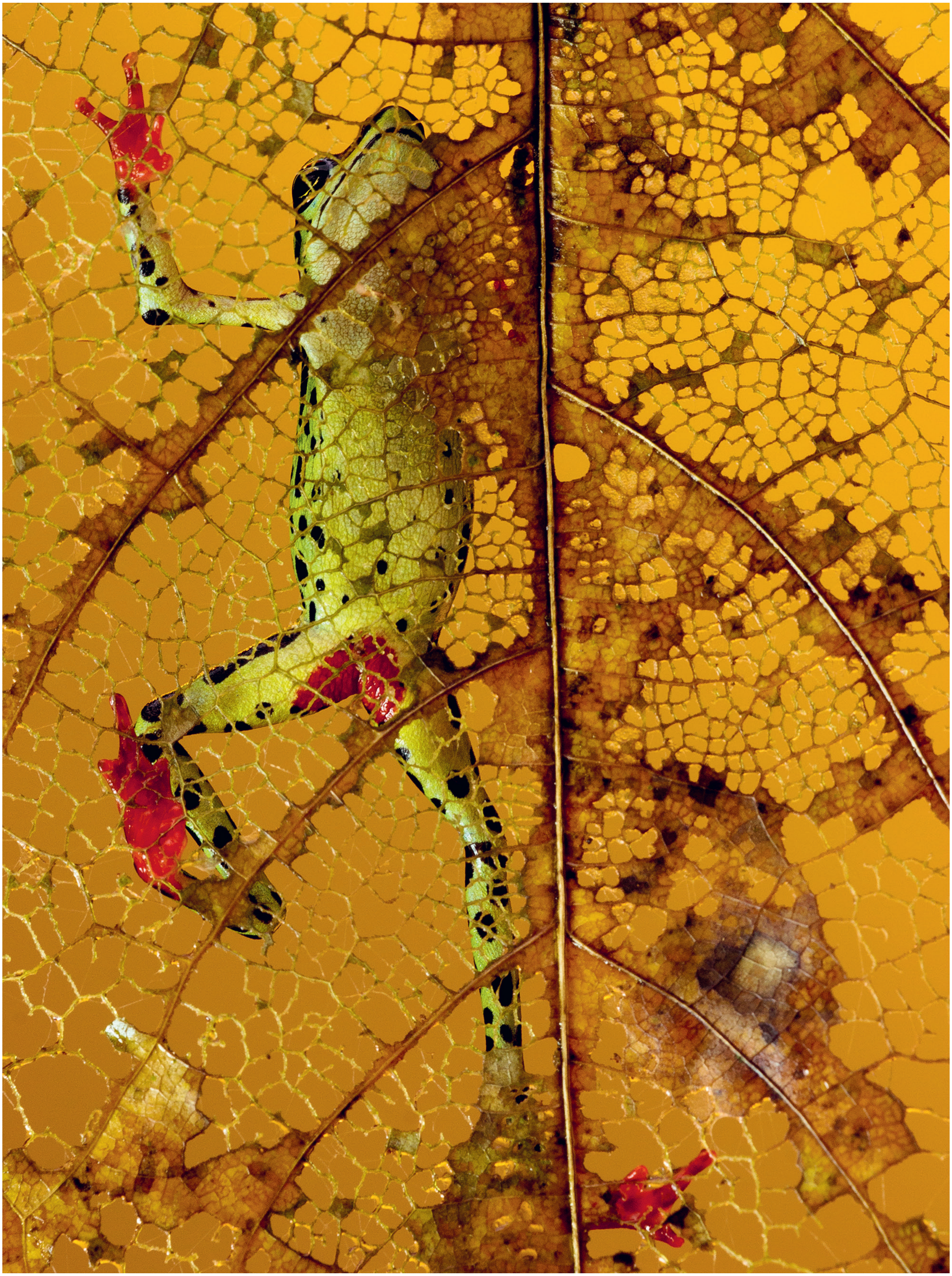
However, if fungi are classified on the basis of how they reproduce sexually (the teleomorphic or "perfect" life cycle state), what happens with asexual forms (the anamorphic or "imperfect" state)? A great many fungi are known only as anamorphs, and many of these are economically important—they cause damage to our crops, rot our stored foods, or cause mycoses. Such fungi are troublesome for the taxonomists whose job it is to come up with names for them, so in the past these "imperfect" fungi were simply lumped into one big group (the deuteromycetes or *fungi imperfecti*), regardless of their evolutionary relatedness. More recently, though, DNA sequence analysis has enabled researchers to finally determine the teleomorphic state, and thus teleomorphic name, for any fungus, without the need to attempt to get it to produce sexual spores in culture.

← Young oyster mushrooms (*Pleurotus* species) are a favorite culinary mushroom and easy to cultivate.

Fungal Phylogeny

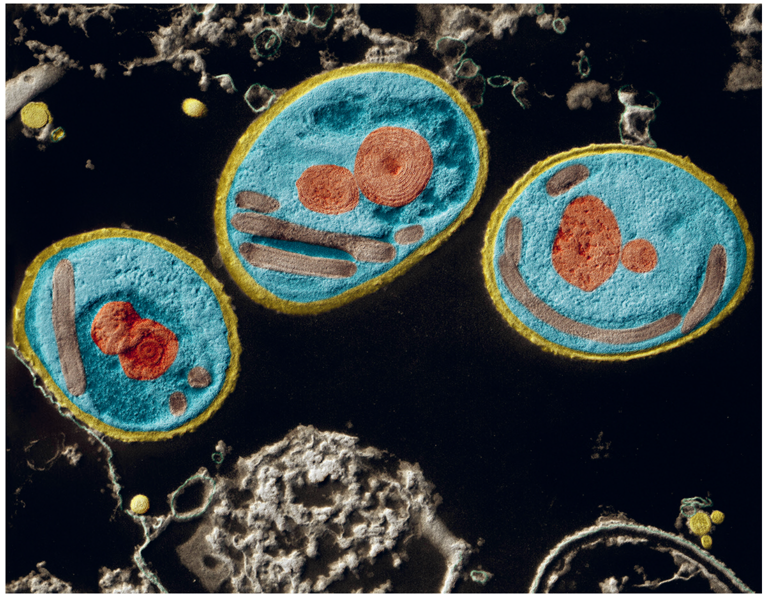
Modern classification schemes separate fungi into phyla Chytridiomycota, Glomeromycota, Basidiomycota, and Ascomycota, and the polyphyletic "Zygomycota" is slowly getting teased apart. The ecology of each group of fungi is also pointed out, as well as those that are motile.





← Chytrid fungi are infamous pathogens of amphibians like this infected Pebas Stubfoot toad (*Atelopus spumarius*) crawling over a leaf in Ecuador.

→ Some of the strangest and least known fungi are the Microsporidia, seen here at 58,000 X magnification using color-enhanced transmission electron microscopy (TEM). Microsporidia live entirely within the cells of their hosts and have extremely reduced physiologies and genomes.



DNA sequence analysis for some imperfect fungi has also led to some surprises. In the case of the *Aspergillus* (and this has been known for decades), it was confirmed that more than 300 species belong to no fewer than 11 teleomorphic genera. This was slightly problematic, as *Aspergillus* is an asexual name. So, in 2012, scientists changed the rules on how things are named, making allowances for well-established asexual names in cases where switching to the sexual name would be a major headache. Consequently, some *Aspergillus* species (including notorious mycotoxin producers such as *Aspergillus flavus*, *A. parasiticus*, and *A. ochraceus*) retain the anamorphic name, but when it's preferential to use teleomorphic names, as in well-established sexual genera like *Eurotium*, *Emericella*, and *Neosartorya*, those names are used instead.

Before we launch into a brief discussion of the "true" fungi, it is worth mentioning the newest group of fungi: the Microsporidia. Until 2006, this strange group of tiny organisms was thought to be protist, but it is now considered to be extremely simplified primitive fungi, or possibly just the nearest relatives to fungi—it's going to take further analysis to clarify the evolutionary relationships for this group. It's unlikely you will spy a microsporidian on your next foray in the woods, though, as Microsporidia are very tiny, unicellular parasites of animals (mostly insects, but a few are known parasites of humans). The entire life of a microsporidian, including replication, takes place within the cell of its host. If they came from a true fungal ancestor, they long ago gave up hyphal growth to live as endosymbionts. Microsporidians are some of the smallest known Eukaryotes and have the smallest Eukaryotic genomes.

While the microsporidians are the newest group, the chytridiomycetes have been long considered the most primitive of the "true" fungi. Found worldwide, most chytrids are saprotrophs, feeding on decomposing organic matter, although some species are parasites of plants and animals (as you will see later in this book, chytrids are linked to the worldwide die-off of amphibians). Chytrids are the only motile fungi, producing zoospores that are propelled by whip-like flagella; all fungi placed above chytrids on the fungal tree of life are nonmotile.

Our next group, the zygomycetes, was always a mixed bag of fungi placed together by virtue of having aseptate hyphae. Some well-known examples of zygomycete fungi include black bread mold *(Rhizopus stolonifer)*, and *Pilobolus* species (the Hat Thrower), which are capable of ejecting spores great distances.

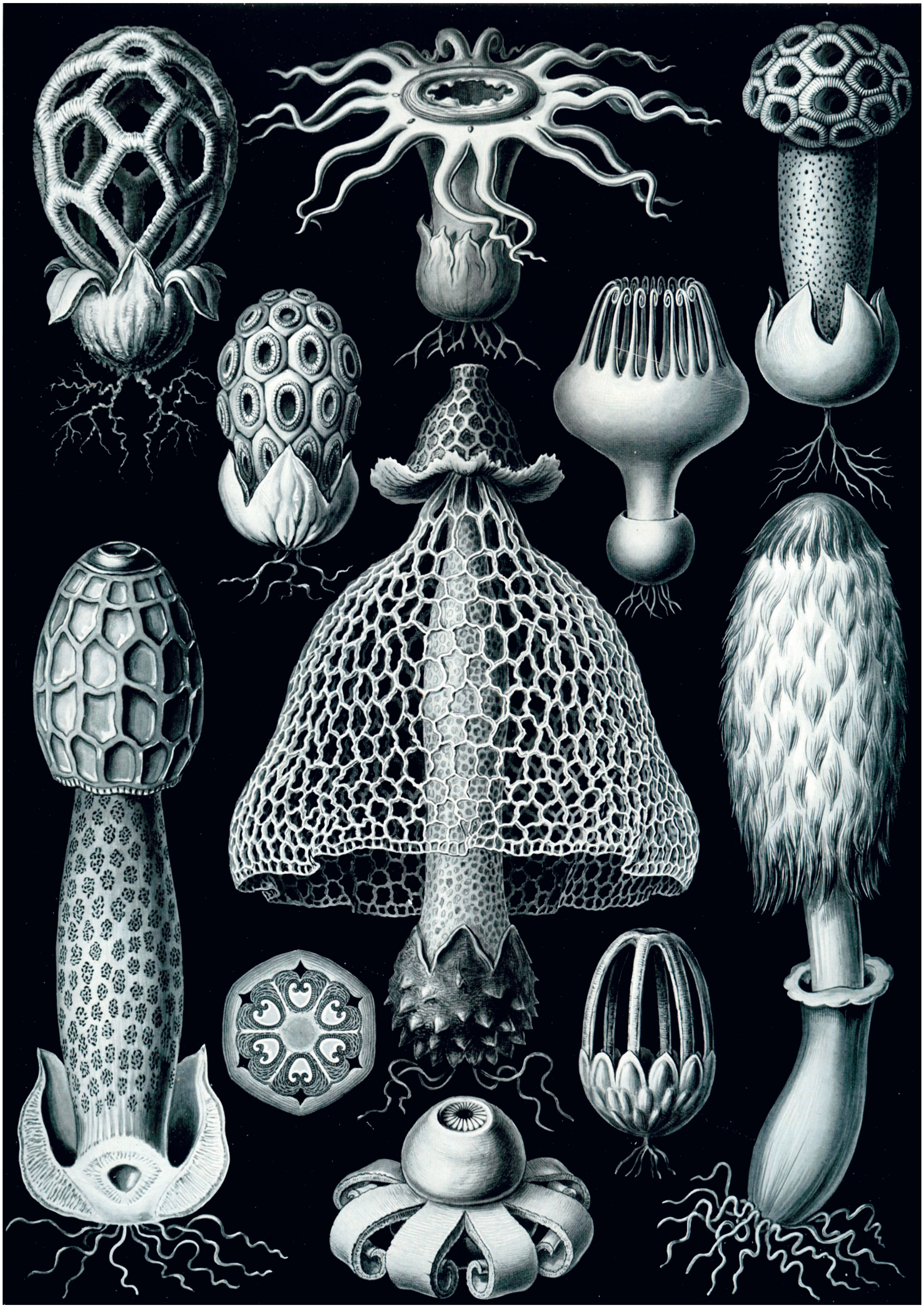
Glomeralean (also spelled glomalean) fungi were once part of the zygomycetes, but have now been elevated to their own phylum, the Glomeromycota. These fungi are poorly known, as few have been seen or cultured. Few (if any) have sexual reproduction; they form no obvious fruitbodies; some form clusters of asexual spores, and that's about it. We also know that glomeralean fungi are mutualistic symbionts of most plants, so they are likely the puppet masters of all life on the planet.

The most recently evolved of all fungi are the basidiomycete and ascomycete, which share a common ancestor. The basidiomycetes include most of the mushrooms people are familiar with and produce sexual spores on club-like stalks called basidia (giving them their alternative name, club fungi), while the ascomycetes (known as sac fungi) produce sexual spores in a special sac-like structure called an ascus. The ascomycetes are the largest group of fungi, and include morels, truffles, and yeasts.

Both groups grow by hyphae with septa, although some members grow as single-celled yeast, and they live as saprotrophs, parasites, or mutualistic symbionts.

↑ Some of the ascomycete fungi produce very colorful cup-shaped mushrooms like this pretty *Sarcoscypha coccinea*, the Scarlet Elf Cup.

→ In the 1800s, German naturalist Ernst Haeckel studied and illustrated numerous animals but a few fungi impressed him as well, notably the showy basidiomycetes.



FUNGAL PATHOGENS

Many of the fungi on the planet today—perhaps even the majority of them—are pathogens. But as with all life, fungi also have their own parasites and pathogens. In fact, there are many fungi that are parasites of other fungi. For example, the common jelly fungus *Tremella* (Witch's Butter) was long thought to be a saprobe of rotting wood, as it is often seen growing near species of *Stereum* (False Turkey Tail), which is another saprobe on fallen logs. However, it turns out that *Tremella* is a parasite of fungi like *Stereum* (and *Peniophora*).

Just like animals, fungi can be afflicted by viruses, virus-like pathogens, and even prions (scientists study the prions of yeast fungi to better understand how prions cause diseases in mammals, such as kuru of humans, scrapie of sheep, bovine encephalopathy of cattle, and chronic wasting disease of deer). Viruses are quite common in fungi and can cause economically important diseases like La France Disease in commercial mushroom farms. Fungal viruses are persistent, with transmission known to occur through anastomosis and via spores. As anastomosis occurs only between fungi of the same species (and usually the same strain), this method of transmission does not introduce viruses to new species.

In most cases, the role of viruses in the life of fungi is not known. However, in some plant pathogenic fungi the virus can act as a mutualist of the plant by reducing the effect of the pathology of the fungus. The best-studied example of this is Chestnut Blight, which is caused by the fungus *Cryphonectria parasitica*; when the fungus harbors Cryphonectria hypovirus, the pathology of the fungus on the plant is greatly reduced. This has

← Witch's Butter (*Tremella mesenterica*) is commonly seen on dead wood and often presumed a saprobe. In reality, this fungus is a parasite of other fungi growing within the rotting wood.

↗ Many different symbiotic organisms grow together. Each lichen is composed of several organisms, including fungi and photobionts.

been proposed as a method to rejuvenate the chestnut forests that once covered most of eastern North America. Other examples of hypovirulence-associated viruses in plant pathogenic fungi have also been found, including in *Ophiostoma ulmi*, the causative agent of Dutch Elm Disease.

Although not mutualists of their fungal hosts, these viruses are still beneficial for the plants that harbor the fungal pathogens. Indeed, in one instance, a fungal virus is an obligate partner in a complex three-way mutualistic symbiosis that allows plants to grow in geothermal soils in Yellowstone National Park, USA. *Dichanthelium lanuginosum* is a panic grass that grows in soils with temperatures of >122°F (>50°C), but to grow in these warm soils it requires a fungal endophyte (*Curvularia protuberata*) that is infected with Curvularia thermal tolerance virus. This is a clear mutualism, as the grass cannot survive without the fungus, and the fungus must also be infected with the virus—without that infection, no thermotolerance is conferred to the plants.

THE FUTURE AND FUNGI

It's an exciting time to be a scientist. Although we are finding out a lot of bad things about the state of our planet's health, which can be depressing, we can take some solace in the fact that our scientific sophistication is now allowing us to see and know this. We are now able to model and predict the outcome of taking steps (or not) to reverse our course, and scientists are better able to comprehend how complex ecosystems work. We are now able to inventory all life—even that which we cannot see—before any more of it vanishes.

Subsequently, it is likely that all humans alive on the planet today are part of the most crucial century of our long history, and our decisions will dramatically impact the future of humanity and the entire living planet. However, we are not alone in facing this challenge: all life in the ecosystem is connected, and everything depends on everything else. Underpinning many of these connections are fungi, which are some of the key decomposers, pathogens, and symbionts of this world. So prepare to enter a world that is very different from the one you're accustomed to: the (mostly) hidden world of fungi.

Mycologists (those who study fungi) have their own terminology for ways of describing fungi and their morphological features. Although this book presumes no prior scientific background, scientific terminology is inevitable in any text about natural history and living things, but do not be intimidated—a glossary at the end explains the technical terms used in this book.

← You've seen mushrooms in the environment. Once you learn about their ecology and what their role in nature is, you will see them in an altogether new light.

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