Are there any science books that you recommend? Yes, several. *Shadows of Reality*, by Tony Robbin (Yale University Press) is a beautiful book that addresses the problem of illustrating high-dimensional entities. The issue is central to the sorts of things we deal with in science today, especially so in my field. How do we think and make sense of abstract spaces? This book is a great introduction to the topic. It is beautifully illustrated — much like Edward Tufte's books — but also filled with interesting maths, physics, arts and history.

Sparse Distributed Memories by Pentti Kanerva (MIT Press) is a more technical monograph that talks about the structure and advantages of binary spaces. Kanerva is a computer scientist and his theoretical exploration arose from an interest in cerebellum architecture, very much like David Marr's early work. A very interesting book to start thinking about memory and representations.

Principles of Brain Evolution by Georg Streidter (Sinauer) is another. One cannot think about biology, or the brain, without considering evolution. I think that experimental systems neuroscientists are some of the biologists least ready to acknowledge the value of comparative approaches and the advantages of simpler systems. Our kind of neuroscience regrettably is a very parochial corner of biology. Reading comparative neuroanatomy reveals how much there remains to discover about brain evolution. The number of unresolved issues means that people fight over ideas. Reading Georg's book is a treat, and a rare one with anatomy books.

Walter Heiligenberg's *Neural Nets in Electric Fish* (MIT Press) is a fantastic little book, published before Walter's tragic death and sadly out of print when I last checked. It describes nearly all that was known about the jamming avoidance response of the electric fish Eigenmannia in 1990, and how one can go about understanding a neural system, from ecology to behavior, structure and computation. People call this neuroethology. I call it neuroscience, in its ideal form.

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Quick guide

Mycorrhizal networks

Anne Pringle

What is a mycorrhiza? A symbiosis between a plant and fungus (Figure 1A); these ubiquitous associations are found in your garden and in forests — anywhere there are roots and soil. In this mutualism a plant exchanges photosynthetically derived carbon for scarce resources, including nitrogen and phosphorus. Mycorrhizal symbioses may at times function as parasitisms. For example, when agricultural fields are heavily fertilized, crops will no longer require a fungus. The fungi cannot live independently of a plant and, if fungal individuals persist, they will continue to drain carbon from the crops. In at least one case, a mycorrhizal fungus now functions as a parasite and causes a stunt disease of tobacco. Understanding how to promote these mutualisms in agriculture is a focus of research because mycorrhizal fungi may offer a viable alternative to phosphorus fertilizers; as phosphorus becomes globally rare, alternatives to mined fertilizers will be critically needed. Frameworks adapted from economic models of trade are used to explore the contexts that may facilitate or limit the maintenance of cooperation among plants and fungi.

What are mycorrhizal networks? In nature, a plant will associate with multiple fungi and each fungal individual may associate with more than one plant. A fungal network that grows among different plants will link these plants to each other; the network may connect individuals of the same or different species. Mycorrhizal networks are not obvious to most because they are hidden in the soil.

Do these networks coordinate the exchange of resources among plants? The idea that a plant can direct its own carbon through the fungal network to another plant has captured the popular imagination, and some scientists think that a plant can use its mycorrhizal networks to 'nurse' its own seedlings. But this is a controversial subject; of course, fungal individuals will act in their own selfish interests. It is not clear why a fungus would ever let go of the carbon it has captured, although some carbon will move back to the plant if it is incorporated into amino acids made by the fungus to give to the plant. Others argue that by directing carbon to seedlings a fungus would be safeguarding its future; the logic is complicated by the fact that these systems involve dozens of plants and at least hundreds, if not thousands, of competing fungal individuals. It is not clear whether or how one fungal individual would begin to feed a seedling that will be a habitat for many other individuals, as well as itself, as opposed to letting others do the work. A different way to interpret carbon that may move from fungus to plant is as parasitism of a fungus by the plant.

Do other fungal groups form networks? Networks are a feature of most fungi, including the fungi that infect humans and cause disease, and the fungi that decompose wood and other substrates (Figure 1B). The *Saccharomyces cerevisiae* yeast most familiar to scientists does not form networks, but many other yeasts are dimorphic and form filamentous networks in specific contexts.

Can fungal networks fuse to form a single cooperative system? The idea that independent fungi can fuse to form a single cooperative individual has also captured the popular imagination, but fungi have genetic systems that enforce recognition of self and other and so although individuals do fuse, it seems that the genomes must be nearly identical for fusion to be successful. In the genetic model *Neurospora crassa*, recognition of other is mediated by at least 11 (and potentially more) loci scattered across 7 chromosomes. Expression of these loci is suppressed during mating but, otherwise, genetically different cells that grow towards each other and initially fuse will rapidly die, a kind of 'scorched-earth' policy adopted by the fungus to prevent foreign viruses and genetically different nuclei from invading. Alleles at these recognition loci present beautiful examples of balancing selection, because rare alleles will more efficiently recognize nonself and have an advantage over common alleles.

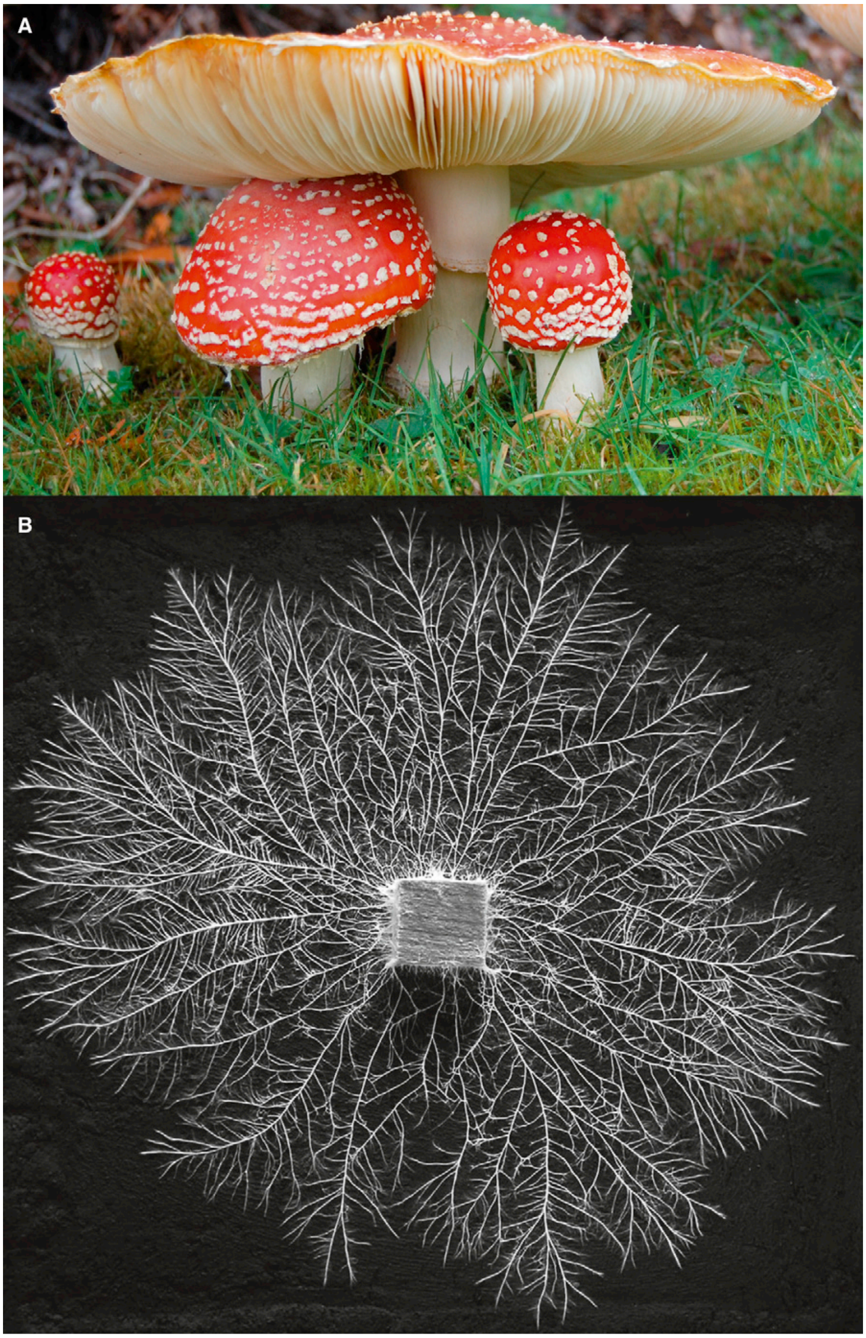

Figure 1. Mycorrhizal fungi and fungal networks.

(A) The mycorrhizal species *Amanita muscaria*. Mushrooms are typically found above ground but, within soil, all filamentous fungi form networks. (Photograph courtesy of Rytas Vilgalys.) (B) Pictured is a network formed across a petri dish by the saprotroph *Phallus impudicus*. (Photograph courtesty of Mark Fricker.)

Loci can also move among species, as demonstrated by the horizontal transfer of novel recognition loci to individuals of the Dutch Elm disease pathogen *Ophiostoma novo-ulmi*. Note that germinating asexual spores dispersed across a substrate can and do fuse, facilitating the capture of territory, and the capacity for asexual spores to cooperate and capture resources may be an unappreciated advantage of asexual propagation in these and other modular organisms.

Can these networks be manipulated to solve human problems? Yes, current research uses fungal networks to guide the design of efficient transport systems, for example, new paths for the often congested ring roads around London. In contrast to animal or plant networks, whose architectures are relatively invariant and controlled by universal scaling laws, fungal networks must continuously adapt and re-form in response to a heterogeneous and changing environment. Models inspired by fungal networks can be used to ask, what designs are robust to the temporary but damaging blocks caused by automobile accidents? Blocks caused by accidents and road closures sever connections among different parts of a transportation network, exactly analogous to the damage caused by an animal that digs in soil and breaks a fungal network.

How many species of fungi grow on earth? Conservative estimates suggest at least one million species of fungi; biologists have names for less than 100,000 of these organisms and a great deal of taxonomic work remains undone. Because fungal individuals are difficult to identify and count, data on whether or how species are coping with habitat loss and climate change are rare. Available evidence makes clear that mycorrhizal species are declining in the face of nitrogen pollution. Although fungi are central to earth's biogeochemistry and serve as key mutualists of plants in both natural ecosystems and within the context of organic agriculture, biologists rarely target fungal species as objects of conservation. It is likely that many species will go extinct before being identified.

Where can I learn more?

Bebber, D.P., Hynes, J., Darrah, P.R., Boddy, L., and Fricker, M.D. (2007). Biological solutions to transport network design. Proc. Biol. Sci. *274*, 2307–2315.

Déry, P., and Anderson, B. (2007). Peak phosphorus. Energy Bulletin at www.energybulletin.net/node/33164.

Glass, N.L., and Dementhon, K. (2006). Non-self recognition and programmed cell death in filamentous fungi. Curr. Opin. Microbiol. *9*, 553–558.

Hawksworth, D.L. (2001). The magnitude of fungal diversity: the 1.5 million species estimate revisited. Mycol. Res. *105*, 1422–1432.

Whitfield, J. (2007). Underground networking. Nature *449*, 136–138.

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