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Opinion

Fungal behaviour: a new frontier in behavioural ecology

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As human beings, behaviours make up our everyday lives. What we do from the moment we wake up to the moment we go back to sleep at night can all be classified and studied through the concepts of behavioural ecology. The same applies to all vertebrates and, to some extent, invertebrates. Fungi are, in most people's eyes perhaps, the eukaryotic multicellular organisms with which we humans share the least commonalities. However, they still express behaviours, and we argue that we could obtain a better understanding of their lives – although they are very different from ours – through the lens of behavioural ecology. Moreover, insights from fungal behaviour may drive a better understanding of behavioural ecology in general.

Highlights

While there is increasing acceptance that non-neural organisms such as plants, slime moulds, and bacteria can perform behaviours, the vast kingdom of fungi is usually forgotten.

We argue that fungi can also be studied through the theoretical framework of behavioural ecology. This would benefit both fungal biologists – yielding a better understanding of the lives of fungi – and behavioural ecologists, providing access to model organisms that can help to explain the evolution of primary senses and potentially discover behaviours new to science.

Fungi have senses analogous to those of other organisms, they exhibit behaviour, and they have memory. This suggests a multitude of questions and new paths that could be taken to broaden our understanding of this forgotten and underestimated branch in the tree of life.

Can fungi be studied through the lens of behavioural ecology?

All organisms, be they prokaryotic or eukaryotic, macroorganisms or microorganisms, have to solve a similar set of basic problems to survive: how to obtain energy and nutrients, avoid being eaten or killed, and spread their offspring and how to partition resources between these activities [1]. To address these problems, they have all evolved different sets of solutions and behaviours (Figure 1 and Table 1).

Fungi constitute a vast kingdom of 2–6 million or more species [2,3] (Box 1 and Table 1), but despite our rapidly increasing understanding of fungal genetics, biochemistry, cell biology and physiology, there are a surprisingly large number of gaps in our basic understanding of their lives and behaviours. We believe that fungal ecology would greatly benefit from being studied under the framework of behavioural ecology and that behavioural ecology, in turn, will benefit from the challenges of including fungi.

Behaviour is not well defined in the literature, but broadly covers an organism's movements, interactions, **cognition** (see Glossary), and **learning**. Tinbergen introduced four classic ways of asking why an animal performs a certain behavioural act. How does the behaviour improve survival or reproduction? How has the behaviour changed over time? What factors lead to the behaviour seen in a specific instance? How does the behaviour in an individual change as it matures and which internal and external factors affect this? [4]. These questions are equally appropriate for fungi and through them we could gain a better understanding of the context in which fungi explore and forage for nutrients, interact with other organisms, and respond to their abiotic environment.

There are several reasons why fungal behaviour is less well understood than the behaviour of animals. Fungal **hyphae** are microscopic and usually live in opaque environments, such as the soil matrix or plant and animal tissues, making it difficult to observe fungal behaviour in real time. Movement is often considered an important aspect of behaviour, and fungi are frequently considered sessile [5]. However, movement can be defined as 'any translocation of biomass sustained by an organism's own energy resources, which is steered (navigated) in response to environmental

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cues and stimuli' [6]; thus, as **mycelia** are actually very dynamic and responsive, changing locations by growth and the reallocation of mycelial biomass [7,8] (see Figure II in Box 2), they clearly exhibit movement. A further hindrance is that fungal ecology is understudied and the pivotal roles of fungi in ecosystems, as the main decomposers and recyclers of dead organic matter and as mutualistic **mycorrhizas**, are largely overlooked [9]. However, despite this, major insights into mycelial behaviour (changes in its growth patterns, network architecture, spatial relationships, and function) and **decision making** have been gained, largely through soil microcosm studies of **cord**-forming fungi [7,8,10–12], and we now have the tools to study fungal behaviour over a range of spatial scales (Box 2).

Brainless behaviour: can an organism without a traditional brain behave?

One of the main obstacles to the discussion of fungal behaviour lies in the fact that fungi do not possess neurons or a brain in the classical sense. However, the concept of what constitutes a brain beyond the vertebrate paradigm is expanding [13,14]. Solé *et al.* [14] proposed that brains/cognitive networks need not just be static sets of linked neurons with a well-defined, physically persistent architecture (termed a 'solid brain'), but can include networks that exchange, process, and store information but do not have persistent, stable connections or static elements (termed 'liquid brains'). Moreover, cognitive processes (including **memory**, information processing, decision making, learning, and anticipation) occur in aneural organisms and even unicellular organisms have much of the molecular machinery associated with traditional brain-based cognition [15,16].

Dikarya fungi form large multicellular networks (Box 1), but, unlike the neuronal networks of animals or vascular systems of plants, a mycelial network is not part of the organism, it is the fungus. We provide evidence that fungi exhibit aspects of cognition, including **communication** and memory, within these networks. This leads to the suggestion that fungi could fit in the same category of brains suggested for invertebrates and plants, or even that of **eusocial organisms** [13], and that their hyphal networks constitute a 'liquid brain' [14]. While fungi were not considered in previous expanded concepts of brains [13,14], cognitive aspects of fungal activity have recently been raised [17,18]. Cognition in organisms with 'non-traditional brains' was considered in a recent journal special issue, arguing the need to start by understanding cognition in the smallest and simplest organisms before scaling up to examining and trying to understand cognition in more complex organisms [16]. While prokaryotes, single-celled eukaryotes, plants, and **slime moulds** were considered in detail, fungi were only briefly mentioned [15], highlighting the need for more fungal ecologists to engage with the discussion around how fungi fit into the fields of cognitive science and behavioural ecology.

Fungal senses: how do fungi sense and interact with their environment?

All organisms are able to sense their environment, both external and internal, major categories of stimuli being light, sound, chemicals, gravity/acceleration, position, motion, and temperature. In humans, these equate respectively to sight, hearing, smell/taste, balance, and touch. Other senses possessed by some organisms include magnetoreception, electroreception, and chronoception (passage of time). Fungi have analogues of the main senses (Figure 1) and in all fungal phyla there are species that can respond with positive or negative **tropisms** (as hyphae) or **taxes** (those that produce motile zoospores) to all of the main categories of stimuli (Table 1), perhaps even sound [19].

Decision making and motivation: how do fungi decide when to stay, grow, and reproduce?

There is a wealth of observational data describing behaviour of mycelia that: (i) grow out of food resources in search of new ones in soil [7,12,20]; (ii) are grazed on by invertebrates or damaged in other ways [8]; and (iii) interact with the mycelia of other species [7,12,20] (Figure 1). For example, responses to finding new resources include strengthening of mycelial interconnections between

Glossary

Cognition: the mechanisms by which organisms acquire, process, store, and act on information from the environment, including memory and decision-making (modified from [67]).

Communication: the ability to interact with other organisms or cells by forms of signalling (including chemical) initiating collective action.

Cords: macroscopic linear aggregates of hyphae.

Decision making: assessing two or more possible responses to a situation.

Dikarya: fungi that have dikaryotic hyphae (i.e., 'cells' with two different nuclei) at some point in their lives – Ascomycota and Basidiomycota.

Ecotype: a population adapted to local conditions.

Epigenetic changes: reversible changes to genetic material that do not alter the DNA sequence.

Eusocial organisms: species in which individuals live as a group and members of some castes lose some behavioural characteristics.

Fruit bodies: The large structures that bear sexual spores in Basidiomycota and Ascomycota (although microscopic in some).

Fungal traits: any morphological, physiological, or life history feature that an individual possesses.

Hyphae: narrow, walled tubes of cytoplasm that grow from the tip; the basic developmental unit of the mycelium.

Learning: the capacity to adapt behaviour to abiotic and biotic stimuli depending on past experience, by altering the nature of a response or the threshold at which a response occurs.

Memory: the capacity to retain information about the past (immediate or more distant).

Metabolic memory: the ability to start more rapidly to perform a specific metabolic/physiological process when it has been performed previously (e.g., due to the persistence of proteins or epigenetic changes).

Mycelium: the main body of most fungi, comprising a network of hyphae.

Mycorrhiza: symbiosis, usually mutualistic, between a plant root and fungal mycelium in which the fungus feeds water and mineral nutrients to the plant and receives sugars in return.

Non-neuronal memory: memory effected without neural networks.

resources, die back, and recycling of non-connected **mycelium**, renewed searching, and, sometimes, complete abandonment of a resource [7,10] (Box 2). The coordination and foraging patterns of hyphae within the mycelium have been likened to that of foraging ant and termite trails [21], potentially performing a multitude of behaviours at the same time in different locations. It is not known how these decisions are made or when nutrients are redirected elsewhere, nor how mycelial responses are co-ordinated [12]. The latter must involve long-distance communication through numerous cells, and there are several candidates for rapid long-distance signalling, including electrical impulses [12].

The main way in which fungi spread from one resource to another is by asexual and/or sexual spores. The types of spores, the timing of their production, and the extent to which mycelial biomass is converted to reproductive structures varies widely between taxa and depends on the nutritional status of the mycelium and the environmental conditions [22,23]. Some fungi with narrow enzymic abilities, poor combative ability, and low stress tolerance specialise in rapid colonisation of resources (feeding on simple compounds) and reproduction, often converting their whole biomass into spores before they are outcompeted by other fungi (r-strategists) [23]. Initiation of reproduction by these fungi is likely to be a simple response to depletion of resources, full occupation of territory, etc., with little decision making occurring. At the other extreme, basidiomycetes that decay the hearts of tree trunks (containing recalcitrant and inhibitory compounds) produce **fruit bodies** after many years of colonisation, and sometimes intermittently (K-strategists). Here it is likely that decisions have to be made to prioritise the use of resources for reproduction, further decomposition of the woody resource, expansion of territory, etc. Generally, behavioural responses are considered to provide organisms with long generation times a non-evolutionary way to improve their fitness [24]. By actively choosing or manipulating a habitat to match their phenotype, fungi could circumvent having to wait for natural selection to take its course.

Evolution, learning, and memory: can fungi learn behaviours?

Although **fungal traits** [25] and **ecotypes** [26] have been considered from an evolutionary perspective, mycologists have not previously distinguished behavioural traits (traits connected with performing behaviours). If a behaviour is linked to genes and affects fitness, the behaviour should evolve like other traits. We argue that there is a need to determine which traits could be considered behavioural traits to be able to distinguish between potentially learned behaviours and behaviours that have a genetic basis.

Animal behavioural ecologists distinguish between innate behaviours (reflexes and instincts) and learned behaviours (e.g., learning by imprinting or trial and error), which require memory. Learning refers to persistent and adaptive modifications of an organism's behaviour based on its experiences [27] and, controversially, it has been argued that even single-celled organisms and plants have the ability to learn behaviours [27,28].

In organisms without a central nervous system (i.e., liquid brains), memory has been categorised into: (i) external memory, achieved by depositing signals in the external environment; and (ii) somatic memory, resulting from epigenetic and/or non-genetic cell physiological changes [14]. Examples of external memory are provided by plasmodial slime moulds that navigate complex environments by avoiding areas where they have previously deposited extracellular slime [29] and by foraging ants, which deploy **pheromones** to attract other individuals of the same species to food trails [30].

There are indications of different types of fungal memory at the hyphal/mycelial level in terms of direction of growth, physiology, metabolism, and cell cycle events. Directional memory is evident

Pheromones: chemicals that act like hormones but outside the body.
Quorum sensing: coordinated behaviour and gene regulation mediated by the extracellular accumulation of small, diffusible signalling molecules.
Rhizomorph: a linear fungal organ containing many hyphae, the complete organ growing from the tip.
Slime moulds: informal name for several unrelated eukaryotic single-celled organisms. Most are less than a centimetre but some are large (>1 m^2) with thousands of nuclei.
Spitzenkörper: the organelle at the tips of hyphae that plays a central role in hyphal growth, direction, and morphogenesis.
Tropism/taxis: growth/body movement towards or away from an environmental stimulus. Tropisms are named after the stimulus (e.g., phototropism (light), thigmotropism (touch)).
Yeast: unicellular fungi, usually multiplying by budding.

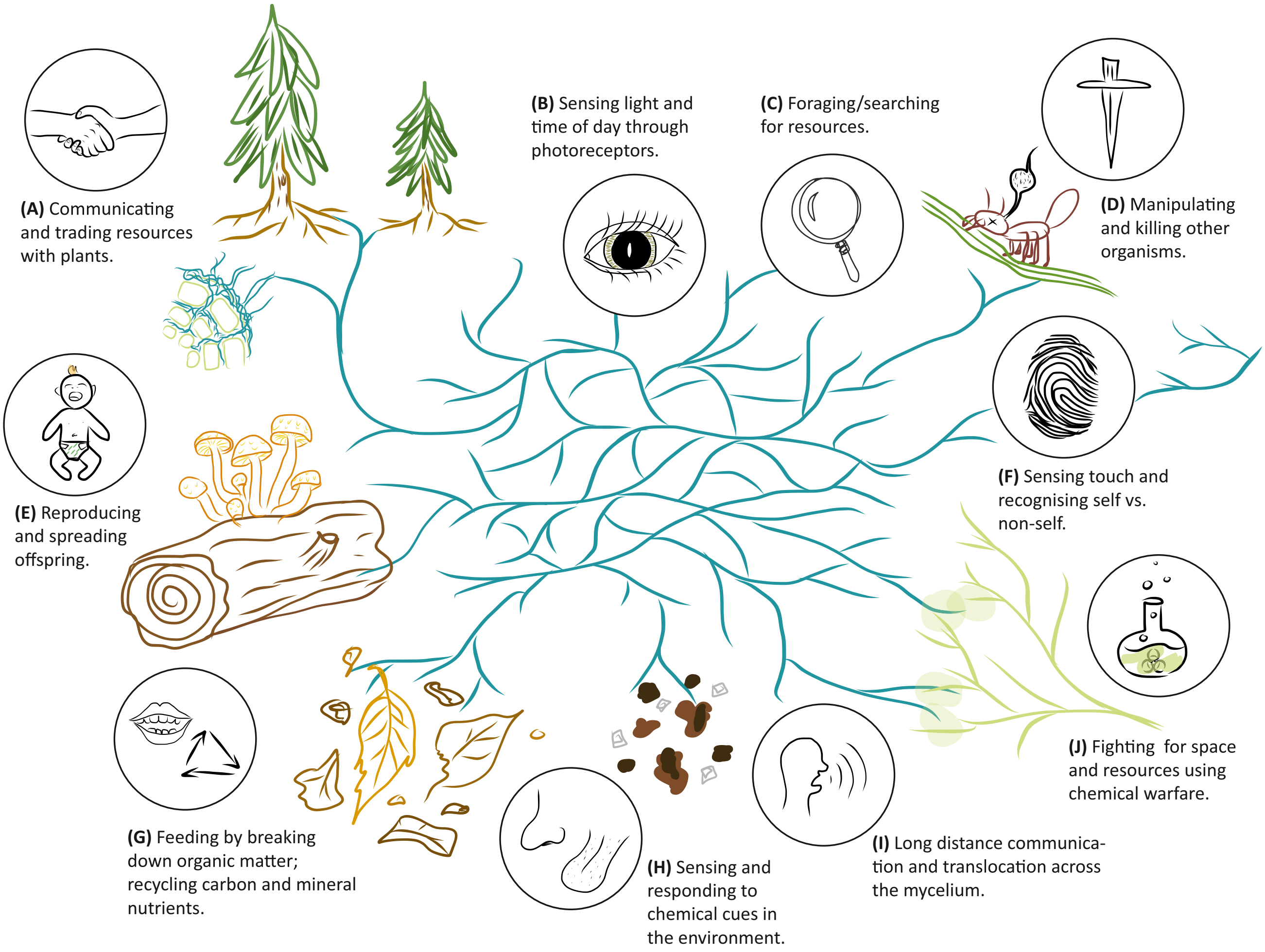

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Figure 1. Fungal senses and behaviours. Fungal mycelia are networks that experience a range of conditions at the same time in different places. Mycelial networks communicate and co-ordinate the movement of resources within the mycelium (G,I), between fungi and plants through the mycorrhizal mycelial network (A) [52,57], and between fungi and the plants and animals that they parasitize (D). The mycelium actively forages for nutrients in the soil (C) [21] and some have evolved the ability to break down complex organic molecules in nature (G) that few other organisms are capable of profiting from [40]. The mycelium can operate a wide range of behaviours by sensing and interacting with the biotic and abiotic environment, some analogous to but not necessarily homologous with animals. Tropisms are ubiquitous, including: (H) chemotropism – growing up or down gradients of volatile or diffusible chemicals [58]; (E) gravitropism – important in ensuring the vertical alignment of gills and pores for spore dispersal during reproduction [59]; (B) phototropism – possessing a range of photoreceptors that respond to light from UV to IR [53]; and (F) thigmotropism – particularly studied in pathogens that respond to surface contours to detect entry points into hosts [60]. When genetically identical mycelia meet, they fuse, recognise that they are self, and then continue to operate as a single individual (F) [40]. When mycelia of different species meet, there is considerable chemical interplay, first at a distance, and following contact, battles for territory ensue, using enzymes and volatile and diffusible chemicals (J) [61]. Illustrations © Kristin Aleklett.

at the mycelial level when fungi are foraging for nutrients [10,31] and in hyphae navigating through micrometre-wide channels [32,33] (Box 2), where the **Spitzenkörper** is thought to act as a gyroscope, allowing the hyphal tips to navigate past barriers and retain their growth direction [33]. There are several examples of **yeast** cell behaviour being influenced by past events (i.e., having memory). **Metabolic memory** occurs in the yeast *Saccharomyces cerevisiae*, where mother cells that have experienced fluctuating resources exhibit **epigenetic changes** that can be passed on to daughters cells [34,35]. Budding yeast also exhibit an adaptive response to pheromone-induced cell cycle arrest, which is effectively a memory of failed mating encounters and the learning of a different

Table 1. Comparison of key features and abilities important for the behaviour of major fungal phyla, and comparable features of vertebrates[a]

	Chytridiomycota	Zoopagomycota and Mucoromycota	Ascomycota	Basidiomycota	Vertebrates
Proportion of species in Kingdom Fungi (approximate)	<10	<15	45	25	NA
Main habitat	Aquatic/moisture films	Soil or on plants and animals	All	Terrestrial	Terrestrial/aquatic
Spread of spores	Swimming	Passive	Passive	Passive	NA
Reproduction	Asexual/sexual	Asexual/sexual	Asexual[b]/sexual	Asexual/sexual	Sexual
Growth pattern: determinate, d; indeterminate, i[c]	d/i	i	i	i	d
Specialised hyphae[d]	n	y	y	y	NA
Yeast body form	n	a few	y[e]	a few	NA
Morphological switching[f]	n		y	y	n
Cross walls in hyphae	n	n[g]	y	y	NA
Network formation	n	n/y[h]	y	y	internal
Complex multicellular[i], c; simple multicellular, s	A few s	s	s/c	c	c
Maximum size	<1 cm	<1 m?	Usually <1 m? Occasionally several metres	A few: many ha; >150 000 kg	150 000 kg
Maximum age	1 week?	<1 year	<50 years	A few >1000 years	200 years
Movement of water/nutrients over long distances within the body	n	n[j]	y	y	y
Ability to use extremely complex molecules (e.g., lignin)	n	n	A few	Some	n
Tropic/taxic responses	y	y	y	y	y

[a] The classification of fungi is still in considerable flux as genome sequencing is increasing. The number of phyla currently ranges between five and 12 depending on the author. Here we consider five from the JGI Mycocosm Fungal Genomics Resource (https://mycocosm.jgi.doe.gov/mycocosm/home). Numbers are approximate and details often uncertain. Only vertebrates are used for comparison as behavioural ecology has largely been developed based on them.

[b] Some are predominantly asexual.

[c] Body form is hyphal, but some form yeasts.

[d] Morphology of some hyphae are specialised for specific function.

[e] Subphylum Saccharomycotina contains about 1000 species, which are predominantly yeasts.

[f] Morphological switching includes the ability to change from hyphal to yeast form and vice versa or, in some, the production of different hyphal/mycelial forms with associated differing physiological activities.

[g] Cross-walls are produced to delimit reproductive structures and to block hyphae following damage.

[h] Some, for example, *Mortierella*, have anastomoses.

[i] Simple multicellular: all cells are in direct contact with the environment, while they are not in complex multicellular [62].

[j] Nutrient movement does occur within hyphae, but mycelia are relatively small.

response [36], and have memory of the experience of hyperosmotic stress, which is likely to result from changes to chromatin structure [37]. These examples indicate that fungi operate complex behavioural patterns beyond simply responding to the biotic and abiotic environment and other organisms on a ‘reflex basis’. Suggested mechanisms for **non-neuronal memory** in fungi and other organisms include epigenetic changes [34,35], chemical and bioelectricity gradients [38,39], and the uneven distribution of mycelial biomass within food resources [10].

Fungal interactions and communication: how do fungi interact with each other and other organisms/hosts?

Fungi do not live alone; they constantly interact with individuals of the same species, individuals of different species, and organisms from other kingdoms. This is a vast topic [40] and we provide only a few pointers to interactions of interest from a behavioural ecology perspective. Some

Box 1. Fungal characteristics relevant to behaviour

Fungi are one of the five main multicellular lineages in the tree of life. Like animals and plants, they possess the key traits of complex multicellularity: cell–cell communication, cell–cell adhesion, long-range transport, programmed cell death, and a developmental program [40]. However, they have fewer cell types (>12 compared with >100 in animals and ~30 in plants) with many different evolutionary origins [62]. Although some fungi have unicellular body forms (e.g., yeasts), most are multicellular and mycelial, comprising fine filaments [hyphae (Figure I)]. Hyphae grow by apical extension to explore the environment (Figure I), feeding by extracellular digestion (secreting enzymes to break down large molecules to smaller ones that can be absorbed). Tip growth, including direction, is controlled by a multicomponent organizing centre – the Spitzenkörper – near the tip [40]. Hyphae branch to form a fractal, tree-like system [63], and lateral branches often join adjacent hyphae resulting in indeterminate, adaptive networks [7,12,64] (Figure I).

In Dikarya (ascomycetes and basidiomycetes), hyphae are divided into compartments/cells by transverse partitions (septa), which extend from the wall inwards, leaving a small, central opening allowing cytoplasmic continuity and the passage of some organelles. Compartments commonly have two or more nuclei but the extent of co-ordination/competition is unclear [65]. Septal openings can be rapidly blocked off. This prevents loss of cytoplasm if a hypha is damaged and allows differentiation of morphology and activity, heterogeneous gene expression [65], the formation of large tissue-like structures, and dramatic behavioural responses.

Fungi are heterotrophs that obtain their food from dead organic matter, by killing other organisms/tissues/cells, from living cells either as parasites or mutualists (lichen and mycorrhizal fungi), or by a combination of these methods. Fungi live in environments where food sources and the microclimatic environments are spatially heterogeneous and everchanging temporally [7]. They spread to new resources in space and time by spores, which are commonly single cells. Some (e.g., cord- and **rhizomorph**-forming basidiomycetes), can grow through soil in search of new resources, operating foraging strategies [21], and some of these form the most extensive and persistent biological networks characterised to date [7,11,20].

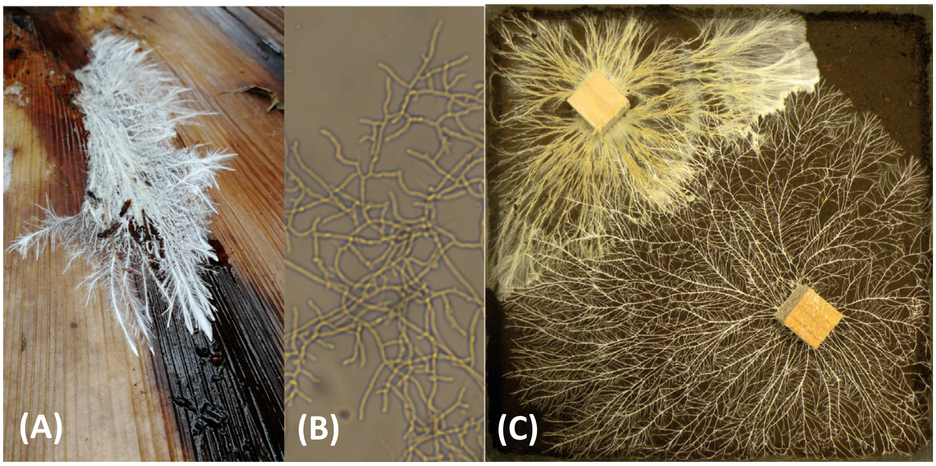

Figure I. Examples of hyphal and mycelial growth. (A) Unidentified hyphae growing at the surface of a leaf in Puerto Rico. (B) Hyphae of *Mycetinis scorodonius* seen through an inverted light microscope ×100. (C) Interacting mycelia of the basidiomycetes *Hypholoma fasciculare* (top) and *Phallus impudicus* (bottom) growing from wood blocks across the surface of compressed soil in a 24 × 24 cm tray. Photographs: (A,B) © Kristin Aleklett; (C) © Tim Rotheray.

effects of fungal interactions are indirect (e.g., altering habitat structure and accessibility for invertebrates and bacteria [41]), but many are direct. providing nutrition in numerous mutualisms with plants (mycorrhizas), vertebrates (in the rumen), and invertebrates (e.g., attine ants, Macrotermitinae, ambrosia and bark beetles) or by killing or parasitising plants, vertebrates, and invertebrates (Figure 1) [40].

Within microbial communities and in symbiotic associations involving hyphal entry into another organism, be they mutualistic or parasitic, there is continuous communication by chemical signalling,

Box 2. Methods and examples of fungal behaviour at varying scales

The behaviour of large mycelia operates, and must therefore be studied, at a range of scales from micrometres to many metres. Experimental setups can range from microfluidic chips at the hyphal scale, through laboratory microcosms of soil trays, to field systems. We present three case studies of directional memory at various scales (Figure II).

Microfluidic chips

Microfluidic chips, fabricated through a combination of computer design, soft lithography, and plasma bonding, contain microstructured environments of enclosed channels and chambers in a transparent and breathable material designed by the researcher (Figure IIA) [66]. These new techniques allow us to mimic the microscale structures of fungal environments (soil, plants, cells, etc.) [66] and to monitor fungal growth, behaviour, and decision making at the scale of individual hyphae, in real time with microscopic precision [32,33]. For example, directional memory was shown in the hyphal tips of the basidiomycete *Psilocybe* cf. *subviscida* when they were growing through such labyrinths, but could sometimes be lost or confused when the hyphae were forced to navigate 'roundabouts' [32] (Figure IIA).

Soil microcosms

Soil microcosms, comprising compressed, non-sterile sieved soil, are more controlled than the field situation but provide some spatial heterogeneity and are appropriate for larger mycelia of, for example, cord-forming wood-decay fungi (Figure IIB). Studies using these systems have revealed behavioural responses involving the reallocation of mycelial biomass when new resources are encountered [7], 'decisions' on when to grow out from a resource in search of new ones [7], 'decisions' on when to abandon a resource in favour of a new one [10], and 'memory' of the direction of a new resource relative to the original, when the original resource is severed from the network and placed on fresh soil [10] (Figure IIB). This memory might simply be achieved by the development of more mycelium in one part of the wood block than elsewhere.

Field systems

Mycelial systems can be mapped and manipulated directly in the field by adding new resources or relocating large sections of the mycelium to study behaviour (Figure IIC). The fairy-ring-forming fungus *Clitocybe nebularis* provides an example of a field-scale study of directionality. It grows through the forest floor in an ever-increasing circle as a 30–40-cm-wide annulus of mycelium (Figure IIC). When turves containing the width of the annulus were cut and reoriented, the mycelium continued to grow only at approximately 90° to the annulus, not in any other direction [31]. Mycelia of these fungi thus seem to be highly polar.

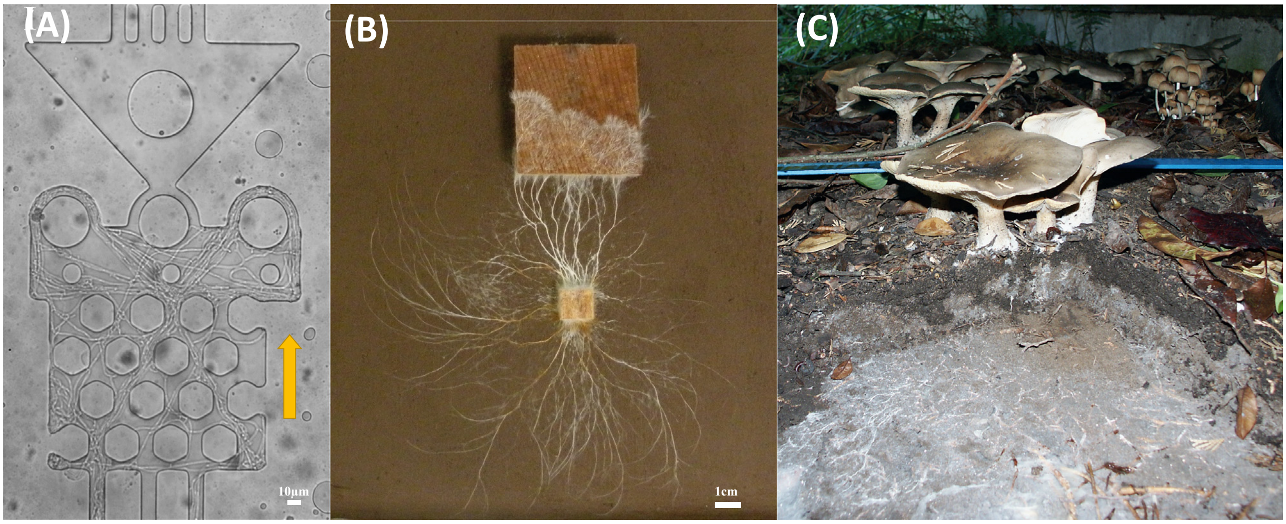

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Figure II. Examples of hyphal and mycelial growth. (A) Mycelium of *Psilocybe* cf. *subviscida* attempting to navigate through Obstacle Chip [32] and starting to grow back towards itself after passing a rounded corner. (B) The basidiomycete *Phanerochaete velutina* growing, across the surface of compressed soil in a 24 × 24 cm tray, from a small wood block to a large wood block. Following contact with the latter, mycelium not connected between the two woody resources has started to die back. (C) Fruit bodies and mycelium of the fairy-ring-forming basidiomycete *Clitocybe nebularis*. Photographs: (A) © Kristin Aleklett; (B) © Yu Fukasawa; (C) © David Moore.

with fungi producing a wide variety of signal molecules including hormones/pheromones, other small peptides, alcohols, lipids, and volatile compounds [40,42–44]. Coordination and communication between the cells in a fungus facilitate complex behaviours such as pathogen colonisation of a host [45]. **Quorum sensing** is one such mechanism and controls morphogenetic switches from unicellular (yeast) to multicellular (mycelial) forms – an important feature of some animal pathogens [46,47].

Fungi manipulate the organisms that they parasitise by diverting nutrients to hyphae [40]. The behaviour of invertebrates can even be altered by the fungi, such as infected ants socially distancing from non-infected ants, soil-dwelling moths moving close to the surface, and ground-dwelling ants climbing tropical forest shrubs [40,48]. These behaviours may be insects trying to prevent spread of the fungus to other individuals, but the behaviour of 'zombie-insects' is manipulated by fungally produced chemicals and mainly benefits the spreading of fungal spores [48]. Chemicals are also produced by fungi to attract insects that will spread their spores [43], and contrastingly are used by the fungi as grazing deterrents [49].

Some fungi eavesdrop on chemical signalling between other organisms and modify their own behaviour accordingly [50]. Due to their indeterminate body form [5], fungi, unlike many other organisms, can additionally modify their morphology appropriately. An example of both eavesdropping and the modification of body form is provided by some fungi that can produce trapping structures when they detect pheromones produced by nematodes [50]. In mycorrhizal associations, mycelial morphology and hyphal structure is modified within plant roots, allowing efficient exchange of resources and signalling. Moreover, mycorrhizal networks facilitate communication between plant hosts of the same and different species [28] (Figure 1), allowing the sharing of photosynthate and chemical communication [51] as well as benefitting the fungi as part of a nutritional trade market with the plants [52].

Fungi as a model system for behavioural ecology

Fungi clearly have senses and behaviours analogous to those of other eukaryotes (Figure 1). Moreover, some exhibit additional behavioural responses due to their indeterminate body form and, in some cases, their large size and age, which allows them to have different experiences in different parts of their systems at the same time. There may be many more eukaryotic behaviours to discover, and experiments on fungal behaviour could be the key to discovering them (see Outstanding questions).

The way in which fungal mycelia operate as networks and the ease with which we can manipulate them experimentally (Box 2) provide an excellent experimental system to test hypotheses concerning the physical, social, and physiological networks of other eukaryotes. Genetic transformation of fungi is possible, allowing the linking of gene functions to behaviour (e.g., the evolution of the molecular basis of vision [53]).

Behavioural ecologists have recently shown considerable interest in slime moulds (which, despite their name, are not fungi) as model study systems [54,55]. Many fungi are almost as easy to use experimentally, with the added advantage that they are multicellular and provide better opportunities to study more complex inter-and intraspecific fungal and interkingdom interactions.

Concluding remarks

Understanding how fungi navigate through their environment to find nutrients, how environmental changes affect their behaviour, and how they interact with each other and other organisms is essential for the promotion of agriculture, forestry, medicine, and human wellbeing [56]. We can address the many outstanding questions of fungal behaviour (see Outstanding questions) by studying fungi at a range of scales (Box 2). Moreover, fungi offer potential as model systems for behavioural ecology. By taking a mycocentric perspective when analysing fungal growth and activity, considering behavioural patterns with purposes and actions, we challenge the traditional view of fungi as sessile organisms without intent and purpose, and hope to inspire the development of a new branch of research in fungal ecology, that of fungal behaviour.

Outstanding questions

What types of behaviours do fungi express? Are these behaviours phylogenetically conserved and which are unique to fungi? It is essential to have an overall understanding of which behaviours all fungi express and which are more narrowly distributed. While some fungal behaviours may be analogous to behaviours in other organisms, fungi might also have unique behaviours due to their indeterminate network body form and, in some, their large size and age.

How can we integrate studies of fungal behaviour at different scales to draw conclusions about how the whole mycelium behaves? There has been extensive research on how hyphae grow and respond to environmental cues at the cellular level, quantitative measurements of network architecture/characteristics and dynamics, and predictive models of network function. The challenge now is to integrate this information from a wide range of spatial scales (e.g., Box 2) into a coherent explanation of fungal mycelial behaviour.

To what extent are fungi able to learn or remember behavioural patterns, and do different phyla behave differently? There are hints from experiments on basidiomycetes that fungi have a certain level of memory during foraging, but to what extent can fungi learn from experiences and become more adaptable to change? Is learning a widespread ability in fungi or is it conserved within a small group?

Are there behavioural differences between young and old fungi? One of the basic premises for learned behaviour is that the behaviours of an organism can change as it ages, either by learning behaviours from adults (imprinting) or from its own experiences. No studies have yet attempted to compare the behavioural patterns of mycelia of different ages. Could age be a determinant of which abilities and behaviours a fungus performs? Are there some behaviours that can be learnt by long-lived fungi?

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Declaration of interests

No interests are declared.

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