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.

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

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.
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 [3]. 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

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**Glossary**

**Cognition:** the mechanisms by which organisms acquire, process, store, and act on information from the environment, including memory and decision-making (modified from [87]).

**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).

**Myelium:** 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 effects 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...
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 Spitenkörper 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
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 [34,36], 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

<table>
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<tr>
<th>Table 1. Comparison of key features and abilities important for the behaviour of major fungal phyla, and comparable features of vertebratesa</th>
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<tbody>
<tr>
<td>Chytridiomycota</td>
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<tr>
<td>Proportion of species in Kingdom Fungi (approximate)</td>
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<td>Main habitat</td>
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<td>Spread of spores</td>
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<td>Reproduction</td>
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<td>Growth pattern: determinate, d; indeterminate, i</td>
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<tr>
<td>Specialised hyphae</td>
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<td>Yeast body form</td>
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<tr>
<td>Morphological switching</td>
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<tr>
<td>Cross walls in hyphae</td>
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<tr>
<td>Network formation</td>
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<tr>
<td>Complex multicellular, c; simple multicellular, s</td>
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<tr>
<td>Maximum size</td>
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<td>Maximum age</td>
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<tr>
<td>Movement of water/nutrients over long distances within the body</td>
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<td>Ability to use extremely complex molecules (e.g., lignin)</td>
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<td>Tropic/taxic responses</td>
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</table>

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.

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.

gCross-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.
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,
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 [40]. Chemicals are also produced by fungi to attract insects that will spread their spores [43], and contrasting 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 photosynthesate and chemical communication [51] as well as benefiting 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.
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Declaration of interests
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References


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