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Mammalian mycophagy: A global review of ecosystem interactions between mammals and fungi

T.F. Elliott[1*], C. Truong[2,3], S.M. Jackson[4,5,6], C.L. Zúñiga[3], J.M. Trappe[7], K. Vernes[1]

[1]Ecosystem Management, School of Environmental and Rural Science, University of New England, Armidale, NSW 2351, Australia
[2]Royal Botanic Gardens Victoria, Birdwood Ave, Melbourne, VIC 3004, Australia
[3]Instituto de Biología, Universidad Nacional Autónoma de México, Tercer Circuito s/n, Ciudad Universitaria, 04510 Ciudad de México, Mexico
[4]Australian Museum Research Institute, Australian Museum, 1 William St., Sydney, NSW 2010, Australia
[5]School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, NSW 2052, Australia
[6]Division of Mammals, National Museum of Natural History, Smithsonian Institution, Washington, DC 20013-7012, USA
[7]Department of Botany and Plant Pathology, Oregon State University, Corvallis, Oregon 97331, USA

*Corresponding author: toddfelliott@gmail.com

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Abstract: The consumption of fungi by animals is a significant trophic interaction in most terrestrial ecosystems, yet the role mammals play in these associations has been incompletely studied. In this review, we compile 1 154 references published over the last 146 years and provide the first comprehensive global review of mammal species known to eat fungi (508 species in 15 orders). We review experimental studies that found viable fungal inoculum in the scats of at least 40 mammal species, including spores from at least 58 mycorrhizal fungal species that remained viable after ingestion by mammals. We provide a summary of mammal behaviours relating to the consumption of fungi, the nutritional importance of fungi for mammals, and the role of mammals in fungal spore dispersal. We also provide evidence to suggest that the morphological evolution of sequestrate fungal sporocarps (fruiting bodies) has likely been driven in part by the dispersal advantages provided by mammals. Finally, we demonstrate how these interconnected associations are widespread globally and have far-reaching ecological implications for mammals, fungi and associated plants in most terrestrial ecosystems.

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INTRODUCTION

Fungi have many different strategies for spore dispersal. The most widespread mechanism among macrofungi involves liberating spores into air currents via forcible discharge (ballistospory among *Basidiomycetes* and bursting of the asci among *Ascomycetes*) (Buller 1909, Money 1998, Trail 2007). Other fungi rely on mutualisms with organisms that ingest their sporocarps as a food reward for subsequent dispersal. The term "mycophagy" refers to the consumption of fungi by vertebrates and invertebrates. Animals consume many groups of fungi that form macroscopic sporocarps both above ground (epigeous, *e.g.* mushrooms, brackets or cups) and below ground (hypogeous, *e.g.* truffles). These animals often act as important vectors for the spread of fungal spores across landscapes. Mammals, reptiles and birds are significant fungal dispersers (Fogel & Trappe 1978, Claridge & May 1994, Maser *et al*. 2008, Elliott *et al.* 2019a, b, Caiafa *et al.* 2021), but specialised dispersal associations have been most thoroughly studied among invertebrates (Fogel 1975, Hammond & Lawrence 1989, Schigel 2012, Kitabayashi *et al.* 2022). For example, in one of its developmental stages, the entomopathogenic fungal genus *Massospora* alters the behaviour of male cicadas by using cathinone (an amphetamine) and psilocybin (a tryptamine) to cause males to simulate the behaviour of sexually receptive females (Boyce *et al.* 2018, Cooley *et al.* 2018). This chemical manipulation causes males to attempt copulation with the infected pseudo-female, leading to further transmission of fungal spores. There are numerous other examples of specialised invertebrate-fungal associations. The polypore *Cryptoporus volvatus* has a veil enclosing its fertile surface; a diversity of insects live between these layers and disperse spores by entering and exiting via a portal hole through the veil (Ingold 1953, Kadowaki 2010, Elliott 2020). Members of the *Phallaceae* (stinkhorns and relatives) release pungent aromas that attract spore dispersing flies (Tuno 1998), while some shelf fungi (*e.g. Cerrena unicolor*) have incredibly specialised associations with wood-boring *Hymenoptera* that disperse spores as oidial inoculum transmitted into the wood via the wasp's ovipositors (Ingold 1953, Bunyard 2015). Other fungi (*e.g. Guyanagaster necrorhizus* as well as some members of the *Leucocoprineae, Lepiotaceae*, *Mycosphaerella*, *Phaeosphaeria*, *Termitomyces* and *Tricholomataceae*) rely entirely on termites, ants and snails for their dispersal (Chapela *et al.* 1994, Silliman & Newell 2003, Nobre *et al.* 2011, Koch & Aime 2018). In addition to the many specialised associations with invertebrates, fungi have also evolved a diversity of reproductive morphologies that are well adapted to mammalian dispersal. Although associations between fungi and vertebrates are not as specialised as those between fungi and invertebrates, many fungi consumed by mammals have evolved a sequestrate sporocarp morphology (spores are enclosed in a persistent skin called the pileus or peridium). This skin makes it difficult for the spores of sequestrate fungi to disperse without being eaten by animals. Sequestrate sporocarp morphologies include some epigeous fungi and a great diversity of hypogeous fungi (commonly referred to as truffles or truffle-like fungi) that have independently arisen in multiple fungal linages and have evolved more than 100 times (Bonito *et al.* 2013, Sheedy *et al*. 2015, Truong *et al.* 2017, Elliott & Trappe 2018, Elliott *et al.* 2020a, Palfner *et al.* 2020). While there is some debate about what evolutionary factors may have driven the rise of sequestrate morphologies (Sheedy *et al*. 2015), the high diversification of sequestrate species in many fungal groups may reflect the dispersal advantages of mycophagy and the major role that mammals played in the process (Trappe 1988, Trappe & Claridge 2005, Maser *et al.* 2008, Trappe *et al.* 2009, Beever & Lebel 2014).

Fungi with sequestrate sporocarp structures have numerous reproductive benefits, including substantial protection from extreme climatic conditions (temperature and humidity) and a reduced likelihood of being eaten by mammals before spores are mature (Maser *et al.* 2008, Beever & Lebel 2014). These factors have likely contributed to the loss of forcible discharge among sequestrate taxa and encouraged the transition away from producing a stalk (which is usually not composed of spore-bearing tissue). The loss of these traits allows sporocarps to optimise spore production in a larger percentage of reproductive tissue. On the other hand, trade-offs include susceptibility to saturated soil (*e.g.* rotting in place) and the reliance on other organisms to disperse spores. To remedy this, many sequestrate fungi have developed strategies to increase the probability of discovery by animals, such as the production of aromatic attractants (Maser *et al.* 2008). The mammals that excavate and consume hypogeous fungi will subsequently disperse spores through their faeces. Soil disturbance (bioturbation) from digging for hypogeous fungi increases fungal dispersal within the soil and improves soil aeration and organic matter decomposition (Fleming *et al.* 2014, Davies *et al.* 2018, Palmer *et al.* 2020).

Sequestrate fungi are predominantly ectomycorrhizal (ECM), so their successful dispersal is key to plant nutrition, regeneration and survival in many forest systems (Tedersoo *et al.* 2010). In exchange for a carbon source, these fungi form beneficial associations with the roots of their hosts and are vital to plant nutrient uptake and water movement (Allen 1991, 2007 Agerer 2001, Peay *et al.* 2008, Tedersoo & Smith 2013). In the rhizosphere, continuous mycelia of multiple ECM fungal species form a "mycorrhizal network" linking plants of the same or different species; within the network, fungal and plant species interact, compete and provide positive/negative feedbacks that can affect both plant and fungal communities (Gorzelak *et al.* 2015). Disruptions of mycorrhizal networks (*e.g.* through impacts on biodiversity that result in the loss of mammal dispersers) can therefore negatively affect regeneration of ECM plant species and forest resilience after disturbance (Dundas *et al.* 2018, Liang *et al.* 2020).

Previous work on animal-fungal interactions has provided in-depth study and/or reviews on the ecological impacts and importance of fungal consumption by birds (Elliott *et al.* 2019a, Caiafa *et al.* 2021), reptiles (Elliott *et al.* 2019b) and invertebrates (Fogel 1975, Hammond & Lawrence 1989, Schigel 2012). Given these previous works, we chose to focus this review on the associations between fungi and their mammal consumers and how these interactions are beneficial to fungal dispersal, mammal nutrition, host plant communities and overall ecosystem health. As highlighted below, these dispersal modes and their interconnected associations are widespread yet remain incompletely studied in comparison to other fields, such as pollination and seed dispersal ecology. Reproductive success often depends on interconnections between organisms, and these associations can range from specialist to generalist (Wheelwright & Orians 1982, Richardson *et al.* 2000, Schiestl 2004, Schupp *et al.* 2010). Ecosystem processes are complex and multifaceted, and there are inevitably multiple evolutionary factors – aridification in particular – that have contributed to the rise of sequestrate sporocarp morphologies. Considering the dispersal advantages facilitated by vertebrate vectors through the consumption of fungi, we argue that mammalian mycophagy has likely been a major contributing factor to the rise of a wide range of sequestrate sporocarp morphologies.

MATERIAL AND METHODS

This review is part of a series examining the associations between macrofungi and vertebrates; the two previous reviews examined interactions between fungi and birds (Elliott *et al.* 2019a) and between fungi and reptiles (Elliott *et al.* 2019b). In this study, we carefully reviewed references of relevant publications and conducted methodical searches in relevant journals, databases and search engines for publications detailing the behaviours and diets of hundreds of mammal species. We concentrated our search effort on dietary studies based on known behaviours of mammal species, including a focus on terrestrial rather than oceanic mammal groups. For practical reasons, we restricted our literature search to publications written in English, French, German, Portuguese and Spanish. Sources written in a few other languages were included when we were able to determine the mammal species reported to eat fungi, but we did not systematically review the literature beyond these five languages. We incorporated many of the references cited in the review of small mammal mycophagy by Fogel & Trappe (1978), but we could not locate all of the literature they cite. In total, we compiled 1 154 references published over the last 146 years (Fig. 1) reporting fungal consumption by 508 mammal species belonging to 15 orders (Fig. 2).

The number of publications on mammalian mycophagy is substantially greater than that on birds and reptiles combined. To make this review as comprehensive as possible in regard to the mammal species that eat fungi, we omitted imprecise notes (*e.g.* those that mention a "squirrel" or a "mouse" eating a mushroom) when we could not determine which mammal species was being discussed. Some publications (*e.g.* Berkeley & Broome 1887, Reess & Fisch 1887, Chatin 1892, Thaxter 1922, Zeller 1939, Dowding 1959, Hilton 1980) used general names like bandicoot, potoroo, shrew, mole, rock rabbit, dormouse, mouse, pine squirrel, jerboa, field mouse, chipmunk, wood rat,

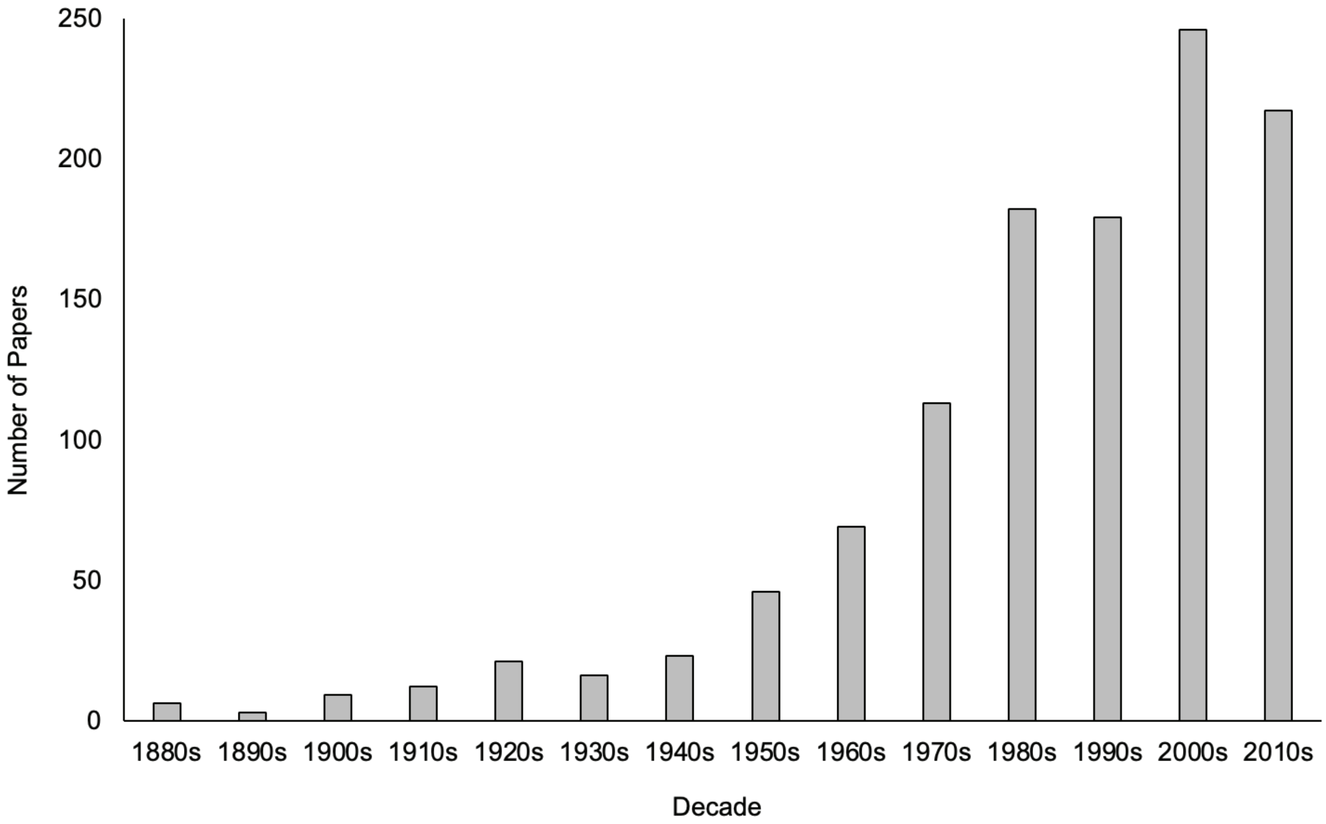

Fig. 1. Illustration of the number of publications reporting mammal mycophagy published each decade between 1880 and 2020.

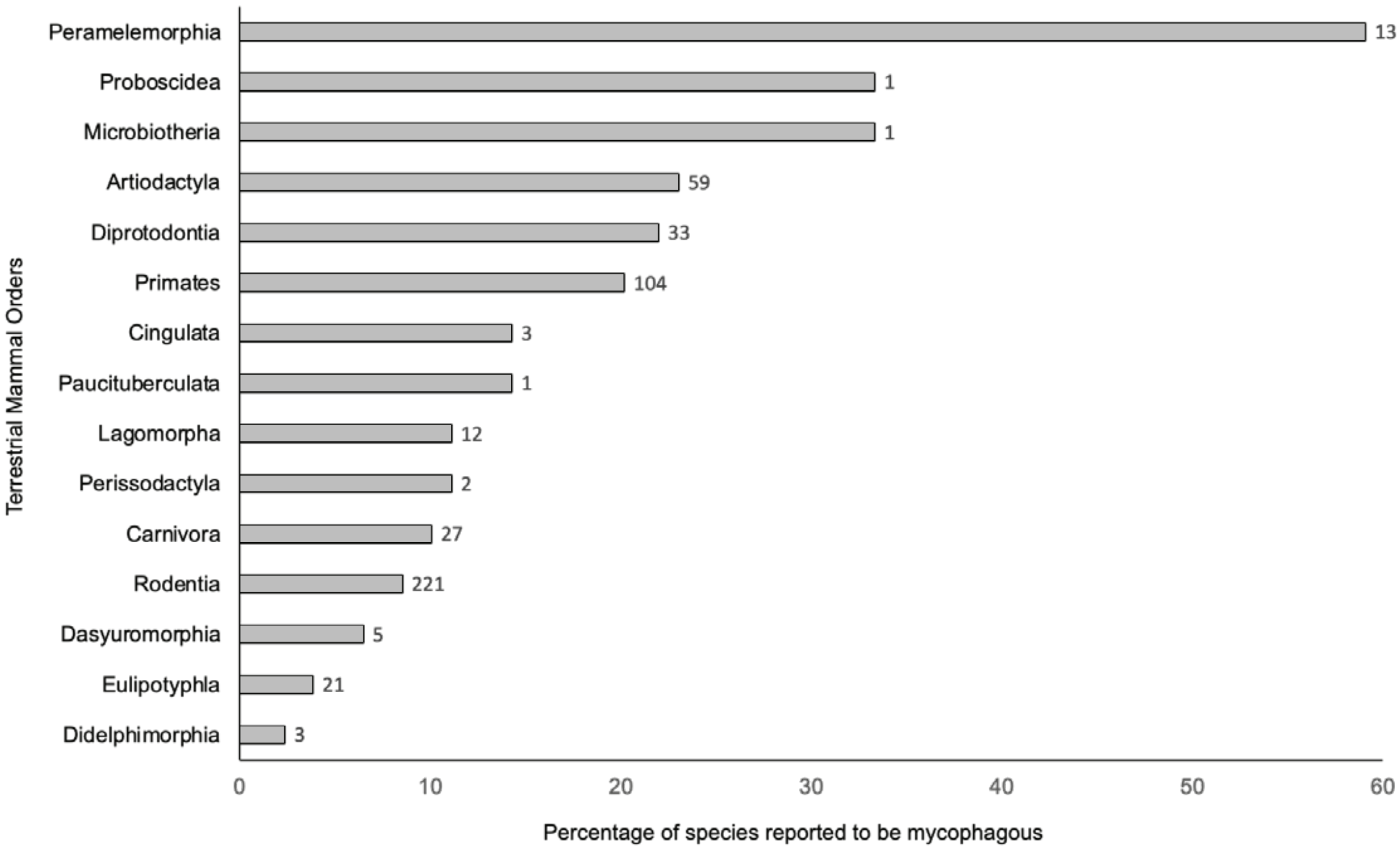

Fig. 2. Percentage of extant members of each order that has been reported to consume fungi. Numbers at end of graph bars indicate number of extant mycophagous species we found reported in the literature. Number of species in each order is based on Hamilton & Leslie (2021). Note that this figure only includes extant species. Two species that appear in the tables are not included in this graph and those are American mastodon (*Mammut americanum*) and neanderthal (*Homo neanderthalensis*).

deer and game animal. In these instances, we did our best to determine what mammal species the authors were referring to, but we sometimes disregarded reports due to lack of taxonomic clarity about the mammal species involved. Groups such as mice or squirrels are among the most thoroughly documented mycophagous mammals, so no value was lost by discarding imprecise species reports.

Where necessary, we updated names from their original citation to reflect current nomenclature. The taxonomy and common names of mammals included in this review follow the nomenclature of Wilson & Mittermeier (2009, 2011, 2014), Mittermeier *et al.* (2013), Jackson & Groves (2015), and Wilson *et al.* (2016, 2017, 2018, 2019). Total number of mammal species in each order is based on Hamilton & Leslie (2021). Rates of mycophagy may differ among subspecies, but we did not consider subspecies due to the large number of mammal species covered. In many instances, there was not enough information for us to determine which subspecies was involved and its taxonomic validity. Researchers interested in these particular issues can easily refer to the primary references provided under cited species in Supplementary Tables S1–S11.

Some mammalogists incorrectly assume that fungi are eaten mostly by rodents or other small mammals. This misconception led us to focus this review on the diversity of mammals that eat fungi rather than the diversity of fungal taxa eaten. Although some studies identify what fungi are eaten, most only mention “fungi” or “mushrooms” in the mammal diet. Terms used in cited references range from formal species names to general terms like toadstool, shelf mushroom, bracket fungus, truffle and puffball. When authors did provide identification, it was rarely possible to determine how accurately they had identified the fungal species; thus, it was not realistic for us to verify fungal identifications. We have not included lichens or myxomycetes in this review. We discarded the information from Maser *et al.* (1988) because they listed spores of three ECM truffle genera that were consumed by a range of mammals, but the habitats they sampled did not contain ECM host plants that are likely to associate with these fungi. Apart from this case, we have no reason to believe that the fungi and mammals reported were inaccurately identified. Researchers interested specifically in the diversity of fungal taxa eaten by mammals can consult the following reviews as starting points: Fogel & Trappe (1978), Claridge & May (1994), Claridge *et al.* (1996), Piattoni *et al.* (2016), and Nuske *et al.* (2017a, b). We also compiled a list of fungal species that are consumed and whose spores remain viable after passage through the gut of mammals (Table 2).

Our review does not include literature related to animal poisoning as a result of eating fungi. Although there is a substantial body of work in veterinary literature related to pet poisoning (*e.g.* Cleland 1934, Cole 1993, Naude & Berry 1997, Puschner *et al.* 2007, Beug & Shaw 2009, Bates *et al.* 2014, Möttönen *et al.* 2014, Bates 2016 and Seljetun 2017), this area of research has little relevance to mycophagy in wild animals. The behaviour and food choices of captive individuals does not necessarily represent their wild relatives, and we are unaware of any evidence of poisoning cases among wild individuals.

RESULTS

Diversity of mammal mycophagists by order

The following section provides tables listing a brief overview of the mammal groups that contain the 508 species reported to eat fungi. For anyone interested in the full lists and references for mammal mycophagy compiled by this review please also refer to the data provided in Supplementary Tables S1–11. Because we have updated the nomenclature to current taxonomy, names we list are not necessarily the same as in the cited references. This section is broken into subsections organised phylogenetically by mammalian order. Each of the 15 orders reported to eat fungi is briefly introduced. Any order containing three or more mycophagous species has a supplementary table where families, genera and species are organised alphabetically.

Mycophagy has been studied in great detail for some orders (*e.g.* rodents), whereas studies of other orders are limited. Likewise, some mammal species are included in numerous reports describing their roles as mycophagists and spore dispersal vectors, whereas other species have seldom or never been studied to determine whether or not they consume fungi. It is important to note that the number of cited references does not necessarily reflect the level of fungal consumption for a given species. There are undoubtedly many seldom studied species not on these lists that frequently eat fungi, and some of those may rely on fungi for a higher percentage of their diet than do the species for which we cite dozens of references. Some groups of terrestrial mammals with highly specialised diets, such as ant or termite feeding specialists (*e.g.* the families *Tachyglossidae*, *Myrmecobiidae*, *Manidae* and *Myrmecophagidae*), likely never deliberately consume fungi. It is also possible that some mammals – including species of cats (*Felidae*) – lack the ability to produce chitinases (Cornelius *et al.* 1975) that allow them to digest fungi, and this may lead to their avoidance of fungi as food. More studies are needed to understand the link between mammalian biosynthesis of chitinases and mycophagy.

In order to distinguish how important fungi are for mammal consumption, Claridge & Trappe (2005) proposed four categories of mammal mycophagists: obligate, preferential, casual or accidental. In the context of this review, we aimed to compile a comprehensive list of all mammal species that have ever been reported to utilise fungi as food. Unfortunately, the level of mycophagy of the vast majority of the 508 listed species has not been sufficiently studied for us to accurately classify most species we list within one of these four categories. With continued research, we hope it will become possible to classify more mammals within these categories; but in the context of this review, we use only the taxonomic categories listed below.

Marsupials

Didelphimorphia

The opossums are a relatively small order of marsupials native to the Americas. The diets of many members of the group are poorly studied, but we found reports of fungi in the diets of three species all within the family *Didelphidae* (Supplementary Table S1). Based on our review, we show that approximately 2.4 % of the extant members of this order have been shown to eat fungi (Fig 2).

Paucituberculata

The shrew-opossums of South America have been relatively poorly studied. To date, only the long-nosed shrew-opossum (*Rhyncholestes raphanurus*) has been reported to eat fungi (Meserve *et al.* 1988). Based on our review, we show that approximately 14.3 % of the extant members of this order have been shown to eat fungi (Fig. 2).

Microbiotheria

The Monito del Monte (*Dromiciops gliroides*) is one of three species in the order *Microbiotheria*. It is found in southern South America and has been reported to eat small amounts of fungi (Meserve *et al.* 1988). Based on our review, we show that at least a third of the extant members of this order have been shown to eat fungi (Fig. 2).

Dasyuromorphia

These carnivorous marsupials are endemic to Australia, New Guinea and several neighbouring islands and include animals such as: antechinus, dunnarts, the kowari, mulgaras, quolls and the Tasmanian devil. They are primarily carnivores or insectivores, but we found reports of fungi in the diets of five species in the family *Dasyuridae* (Supplementary Table S2, Fig 3D). Based on our review, we show that approximately 6.5 % of the extant members of this order have been shown to eat fungi (Fig. 2).

Peramelemorphia

The bandicoots and bilbies are endemic to Australia, New Guinea, and several surrounding islands. Although many of the New Guinean species remain poorly studied, most species in this order that have been studied have been shown to eat fungi. Some species that were once thought to have large geographic distributions have also been recently shown to be distinct species. We found reports of fungi in the diets of 13 species in three families (Supplementary Table S3). Based on our review, we show that approximately 59 % of the extant members of this order have been shown to eat fungi (Fig. 2).

Diprotodontia

The diprotodont marsupials are the largest and most diverse group of marsupial mammals and include koala, wombats, possums, gliders and macropods (the latter includes all kangaroos, wallabies, potoroos, bettongs, rat-kangaroos and their relatives). They are native only to Australia, New Guinea and several surrounding islands. This group has a diversity of dietary specialisations, and some members of the order rely heavily on fungi for large portions of their diet. We found reports of fungi in the diets of 33 species in eight families (Supplementary Table S4, Fig. 3C). Based on our review, we show that approximately 22 % of the extant members of this order have been shown to eat fungi (Fig. 2).

Placental Mammals

Cingulata

Armadillos are a relatively small order of placental mammals and are native to the Americas. There has been limited research on the overall importance of fungi in armadillo diets, but we found reports of fungi in the diets of three species in two families (Supplementary Table S5). Based on our review, we show that approximately 14.3 % of the extant members of this order have been shown to eat fungi (Fig. 2).

Proboscidea

The elephants comprise only three extant species that are restricted to Africa and southern Asia. The members of this group are primarily herbivores, with fungi playing only a very limited role in their diets. We only found mention of trace amounts of fungi in the diets of the living African Elephant (*Loxodonta africana*) (Paugy *et al.* 2004) and the extinct American Mastodon (*Mammut americanum*) that once occurred in North America (Newsom & Mihlbachler 2006). Given the size of both animals and the fungi that were reported, it is hard to definitively know if this represents deliberate mycophagy or incidental consumption of spores. But in this instance and until further studies are conducted on elephants, we are considering mycophagy to be any evidence of fungi in the diet. Based on our review, we show that approximately a third of the extant members of this order have been shown to eat fungi (Fig. 2).

Primates

Primates are a widely distributed and diverse group of placental mammals. If humans (*Homo sapiens*) are included, they can be found in virtually every habitat on Earth and are one of the most adaptable and successful species of mammals. Over the past hundred years, waste management systems used by many modern humans have changed our role as spore dispersers, but undoubtedly hardly more than 100 years ago, almost all humans that ingested fungi were playing a role in the dispersal of fungal spores. Although it has been shown that early humans and neanderthals (*H. neanderthalensis*) consumed fungi as food, their role as spore dispersers has not been as thoroughly studied as that of some other hominids (see Supplementary Table S6). Excluding all the plant pathogens and diseases that humans have accidentally spread, modern humans deliberately transport and cultivate numerous mycorrhizal and saprotrophic fungi as well as their associated plant species (Stamets 1993, Cotter 2014, Zambonelli *et al.* 2015, Guerin-Laguette *et al.* 2020). Modern humans have been documented to harvest more than 2 100 edible mushroom species both for personal use and commercial sale (Li *et al.* 2021), which is more species than has been documented by any other mammal in this review. In the process of picking, cleaning, carrying and sometimes shipping sporocarps, spores are inevitably being dispersed. There are obviously numerous ways - both positive and negative - that humans contribute to spore dispersal, and given that there have been hundreds of papers and books published about ethnomycology, this topic warrants a review of its own and is beyond the scope of this study. In Supplementary Table S6 we only cite a selection of papers that we think are most relevant to fungi consumption by humans, but it is important to note that this is the only mammal species that we have deliberately left incomplete.

There have been two previous reviews specifically relating to primate mycophagy. We encourage readers who are particularly interested in primate mycophagy to also refer to the earlier reviews by Hanson *et al.* (2003) and Sawada (2014). For our study, we found reports of fungi in the diets of 105 primate species in 13 families (Supplementary Table S6, Fig. 3B). This is more species than has been previously compiled. Hanson *et al.* (2003) reported just over 20 species, and Sawada (2014) showed nearly 60 species. Despite the diversity of primate species that consume fungi, they are frequently overlooked in primate dietary studies or are lumped in with plants, “other” or unidentified; this is the case even in major reviews on primate

Fig. 3. A selection of mycophagous mammals with fungal fruiting bodies. **A.** Mount Graham red squirrel with a partially dried fungus in its mouth on Mount Graham in Arizona, USA. **B.** In northwestern Cambodia, a Germain's langur holds a mushroom that it is eating. **C.** A northern bettong eats an unidentified truffle in northern Queensland, Australia. **D.** A brown Antechinus pauses near the fruiting body of a sequestrate species of *Descolea* (lower right corner of image) in eastern New South Wales, Australia. Image A © Eirini Pajak. Image B © Brenda de Groot. Image C © Stephanie Todd. Image D © Stephen Mahony.

nutrition and diets (*e.g.* Lambert & Rothman 2015). Unlike the majority of references, we cite that have reported mycophagy in other orders of mammals, almost all papers cited in this section are based on observational studies. There is much merit in observational methods to improve understanding of the biology and behaviour of mammals; but as has been shown with ornithological studies (Elliott *et al.* 2019a), using these methods in isolation makes it exceedingly easy to overlook, misidentify or underestimate the importance of the fungal components of diets. We suspect that if primate researchers employed the typical scat analysis methods commonly used in groups that are harder to observe, a far greater diversity of primates would be shown to utilise fungi for food and likely at a higher rate than is currently estimated among some species. Based on our review, we show that approximately 20.2 % of the extant members of this order have been shown to eat fungi (Fig. 2).

Lagomorpha
The hares, rabbits and pikas are a relatively small group of widely distributed placental mammals. They primarily eat plant material, but we found reports of fungi in the diets of 12 species in three families (Supplementary Table S7). Based on our review, we show that approximately 11.1 % of the extant members of this order have been shown to eat fungi (Fig. 2).

Rodentia
The rodents are a highly diverse and widespread order of placental mammals with native members found in most regions except the coldest portions of the Arctic and Antarctic and some islands (*e.g.* New Zealand). The members of this order are arguably some of the most important dispersers of fungal spores, and for some species, fungi represent large portions of their diet. We found reports of fungi in the diets of 221 species in 14 families (Supplementary Table S8, Fig. 3A). Based on our review, we show that approximately 8.5 % of the extant members of this order have been shown to eat fungi (Fig. 2).

Eulipotyphla
The *Eulipotyphla* are a diverse order of widely distributed placental mammals that includes hedgehogs, moonrats, shrews, moles and solenodons. They are often considered to be primarily insectivorous, but we found reports of fungi in the diets of 21 species in three families (Supplementary Table S9). Based on our review, we show that approximately 3.9 % of the extant members of this order have been shown to eat fungi (Fig. 2).

Carnivora
The carnivores are widely distributed, and while many members of this order are primarily carnivorous, a wide diversity of species augment their diet with many other food types. We found reports of fungi in the diets of 27 species in nine families (Supplementary Table S10). Based on our review, we show that approximately 10.1 % of the extant members of this order have been shown to eat fungi (Fig. 2).

Perissodactyla
The odd-toed ungulates of the order *Perissodactyla* are a relatively small order of placental mammals that are mostly grazers; the order includes horses, asses, zebras, rhinos and tapirs. Though they show little reliance on fungi, we found reports of fungi in the diets of the horse (*Equus caballus*) (Hastings & Mottram 1915, Cleland 1934) and the mountain tapir (*Tapirus pinchaque*) (Downer 1996, 2003). Other than these two species, we found no indication of fungi consumption by this order. Based on our review, we show that approximately 11.1 % of the extant members of this order have been shown to eat fungi (Fig. 2).

Artiodactyla
The even-toed ungulates are a diverse and widespread group of placental mammals (*e.g.* cattle, sheep, deer, pigs, giraffes, camels and llamas). Most species in this group are relatively large-bodied, so fungi often do not comprise a bulk of their diet; however, fungi do appear to be nutritionally important to them. We found reports of fungi in the diets of 59 species in seven families (Supplementary Table S11). Based on our review, we show that approximately 23 % of the extant members of this order have been shown to eat fungi (Fig. 2).

DISCUSSION

Feeding on fungi

Feeding preferences between fungal taxa, morphologies and portions of sporocarps
Several factors likely contribute to fungal food choices and species selection. It is possible that toxicity may be a factor in species selection, but there is very limited data on fungal toxins in relation to wild mammals. Sawada *et al.* (2014) studied fungal species preference in relation to their toxicity among Japanese macaques (*Macaca fuscata*) and found that this species of primate eats a diversity of fungi. They suggested that individuals use different methods to avoid poisonous mushrooms, including previous knowledge and on-site assessment of taste (but not smell). The macaques generally ate fungi without examining them; but when they were hesitant and tasted the sporocarps before eating, Sawada *et al.* (2014) determined the fungus was more likely to be a toxic species. Since almost all knowledge of fungal toxicity is in relation to humans and a few species of mammalian pets, it is difficult to determine the toxicity of fungi for specific mammal species. For the most part, what – if any – role fungal toxins play in food selection is still unknown.

Mammals are likely to prefer nutritionally rich fungal taxa that produce easily detectable aromas or colours. In response to these selection pressures, some fungi may produce chemicals and/or compounds to make certain parts of their sporocarps desirable. Even though mycophagy may have contributed to the success of certain fungal groups and sporocarp morphologies, there has been limited research that directly investigates the selection pressure from mammal food choices on fungal reproductive patterns and morphologies. Herbivores often selectively feed on certain species or parts of plants, sometimes preferentially selecting the tender new growth (Wilsey 1996, Pérez-Harguindeguy *et al.* 2003), and we suspect that preferential feeding strategies likely occur in fungi as well. There is evidence of different nutritional value within the sporocarps of some fungi. The chemical composition and nutritional value of desert truffles in the genera *Terfezia* and *Tirmania* vary between taxa and the different layers of sporocarps, depending upon whether or not the peridium (outer skin) of these truffles was removed or left on the exterior (Hussain & Al-Ruqaie 1999). Grönwall & Pehrson (1984) also found variation in nutritional value between the peridium and spores of the sequestrate ECM species *Elaphomyces granulatus*, while Vogt *et al.* (1981) detected differences in nutrient concentrations between mycorrhizal and decomposer fungal species.

Among the numerous members of the family *Russulaceae* that are important foods for mammals, some species/genera produce latex (including the genera *Arcangeliella*, *Lactarius*, *Lactifluus*, *Multifurca* and *Zelleromyces*), while members of the closely related genus *Russula* do not. The latex is produced in laticiferous hyphae, and in some species these hyphae also serve to store precursors of pungent dialdehydes (Camazine & Lupo 1984). The chemistry of the latex varies between species, and this may impact animal consumption. For example, the latex produced by *Lactarius volemus* contains polyisoprene, which is also found in rubber (Ohya *et al.* 1998) and appears to deter invertebrates from feeding. Therefore, invertebrates are less likely to feed on the latex-producing genus *Lactarius* than the closely related *Russula* species that do not produce latex (Taskirawati & Tuno 2016). Latex is most abundant in young sporocarps and deterred slugs in experimental feeding studies; once the sporocarp aged, latex production slowed or stopped and slugs ate *Lactarius* and *Russula* species at similar rates (Taskirawati & Tuno 2016). There may also be a finite number of latex-producing hyphae within each sporocarp, and as the sporocarp expands, it becomes more dispersed/diluted for the feeding animal. It is therefore possible that latex protects young sporocarps from being consumed by animals before spore maturation, at which point latex production is reduced and the sporocarps of lactating members of the family *Russulaceae* become more desirable to invertebrates. Latex production in fungi is restricted to a relatively small number of genera, so its impact on food preferences has limited relevance across the entire fungal kingdom. Nevertheless, we suspect a similar negative correlation between small mammal mycophagy and latex production.

Among many groups of animals, evidence suggests that the hymenium (spore-bearing surface) is preferentially selected for food instead of other portions of the sporocarp. Vogilino (1895) and Buller (1909) first suggested that gastropods preferentially eat gills/reproductive surfaces before other structures, an observation that we also made in slugs and other invertebrates (Fig. 4). Due to their large nature and faster movements (at least compared to slugs), mammals' feeding preferences are more difficult to observe. However, a few studies suggest that mammals also show a preference toward different portions of fungal sporocarps. For example, brown lemurs (*Eulemur* spp.) seem to preferentially eat the cap while discarding other parts of mushrooms (Overdorff 1993), and Humboldt's flying squirrels (*Glaucomys oregonensis*) preferentially feed on the reproductive tissues of epigeous fungi (Thysell *et al.* 1997). The volcano deermouse (*Neotomodon alstoni*) and the North American deermouse (*Peromyscus maniculatus*) are both known to eat entire fungal sporocarps but have a preference for the hymenium (Castillo-Guevara *et al.* 2012). Walton (1903) noted that North American red squirrels (*Tamiasciurus hudsonicus*) regularly ate the gills of mushrooms and rejected the rest of the sporocarp. Using camera trapping, Elliott & Vernes (2021a) showed that several species of Australian vertebrates (both mammals and birds) fed on *Amanita* mushrooms, with a preference for the caps of sporocarps. We observed that many small mammals (especially rodents) preferentially eat the hymenium before other portions of the fungal sporocarp (Fig. 5A–F), but larger mammals (*e.g.* deer) often ingest any parts they can find (Fig. 5G–H).

As outlined in the Introduction, sequestrate fungi have sporocarps with reproductive tissues enclosed within one or more layers of skin. In many cases, they are also hypogeous (*i.e.* sporulating below ground). It is not known when and where the first sequestrate fungi appeared, but estimates suggest that the first Australian sequestrate taxa emerged 34–13 million years ago during the Oligocene and Miocene, while many Australian mycophagous mammals appeared around 16 million years ago (Sheedy *et al*. 2015). In sequestrate basidiomycete species, the energy used for producing sporocarps with a stalk and cap can be relocated toward producing more sporocarps and/or spores; for cup fungi relatives (*Ascomycota*), the increased layering and folding of the hymenium increases the volume of spore-bearing tissue. Among these morphologies, spore dispersal relies heavily on animal consumption instead of air currents or water. Therefore, sequestrate sporulating morphologies likely evolved in partial response to feeding preferences toward different parts of the sporocarp. There are inevitably multiple factors that have contributed to the rise of sequestrate sporulating habits, *e.g.* as a response to major climatic changes such as aridification (Sheedy *et al*. 2016). Some groups, such as the *Mesophelliaceae*, predate the rise of mycophagy specialist mammals and may therefore have initially formed associations with early invertebrates or more generalist feeders (Sheedy *et al*. 2016).

Among sequestrate species with fleshy (non-powdery) sporocarps, the entire sporocarp is generally consumed; but in groups such as the genus *Elaphomyces* and the family *Mesophelliaceae*, powdery spores appear to be the least desirable portion (Figs 6, 7). Many small animals favour the exterior of *Elaphomyces* sporocarps by selectively eating the peridium (Fig. 6). Research on North American red squirrels by Vernes *et al.* (2014) showed that when *Elaphomyces* truffles are unearthed, the squirrel cleans the outer peridium by "shucking" adherent soil and mycelium from the truffle before it is eaten or cached (see Supplementary Video S1). Members of the family *Mesophelliaceae* differ in having a thin and non-nutritious outer layer surrounding a nutritious central core, with spores packed in between the two (Fig. 7). Animals typically peel the outer layer and focus on eating the central core; this is especially the case after fire when *Mesophelliaceae* truffles can become more fragrant and are often more easily discovered by foraging mammals (Trappe *et al.* 1996, Maser *et al*. 2008). Vernes (2000) noted that the discarded outer peridia and spore-bearing mass of *Mesophellia clelandi* littered the ground around bettong digs on burnt ground, but this was never recorded on unburnt ground. Spores of both *Elaphomyces* and *Mesophelliaceae* are common in faecal pellets of a broad range of mammals, and both groups are partly reliant on animals for their dispersal. Even though the spore-producing portions of sporocarps are not necessarily targeted, mammals inevitably ingest spores in the process and spill spores onto their fur. The leftovers of sporocarps are often left exposed on the ground or a log (Figs 6, 7), from where they can be carried away by wind or water.

Caching and hoarding of fungi

A diversity of mammal species cache and hoard foods to varying degrees (Vander Wall 1990). These behaviours have been arguably best studied among rodents, particularly in squirrels that bury nuts and/or cache cones. Fungal caching behaviours have been most frequently noted among North American red squirrels, but similar behaviours occur in rodents from other

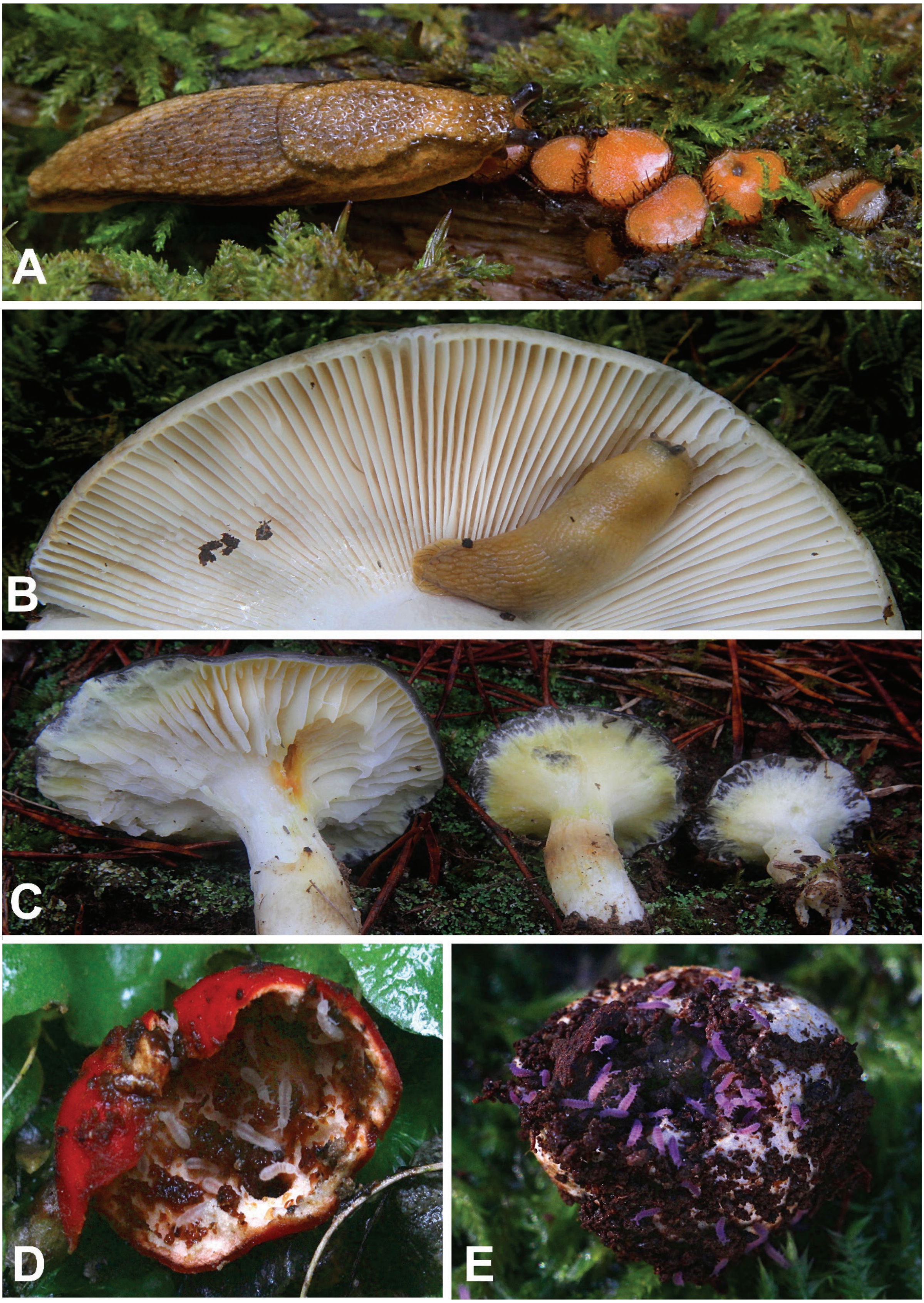

Fig. 4. Invertebrates display dietary preferences toward the reproductive portions of fungal fruiting bodies. **A.** *Arion subfuscus* feeds on the hymenium of several eyelash cups (*Scutellinia scutellata*) in Rusk County, Wisconsin, USA. Note the light-coloured sections of the fertile surface where the slug has eaten the reproductive tissues but not the rest of the fruiting body. **B.** An *Arion* sp. eats the gills on a *Russula* sp. in the Tucker County, West Virginia, USA. **C.** The gills of three *Hygrophorus hypothejus* fruiting bodies have succumbed to the feeding activities of a gastropod in Rutherford County, North Carolina, USA. The upper surfaces of the caps of these three fruiting bodies had been left untouched. **D.** Springtails hollowed out and ate the entirety of the spore-containing surfaces of the sequestrate fungus *Leratiomyces erythrocephalus* near Wellington, New Zealand. Note the visible brown line down the middle of the springtails that shows evidence of their digestive tracts filled with spores. **E.** The hollowed out skin of a sequestrate *Descolea* sp. that has had spores eaten by a lilac-coloured *Brachystomella* sp. in Barrington Tops National Park, New South Wales, Australia. Images © Todd F. Elliott.

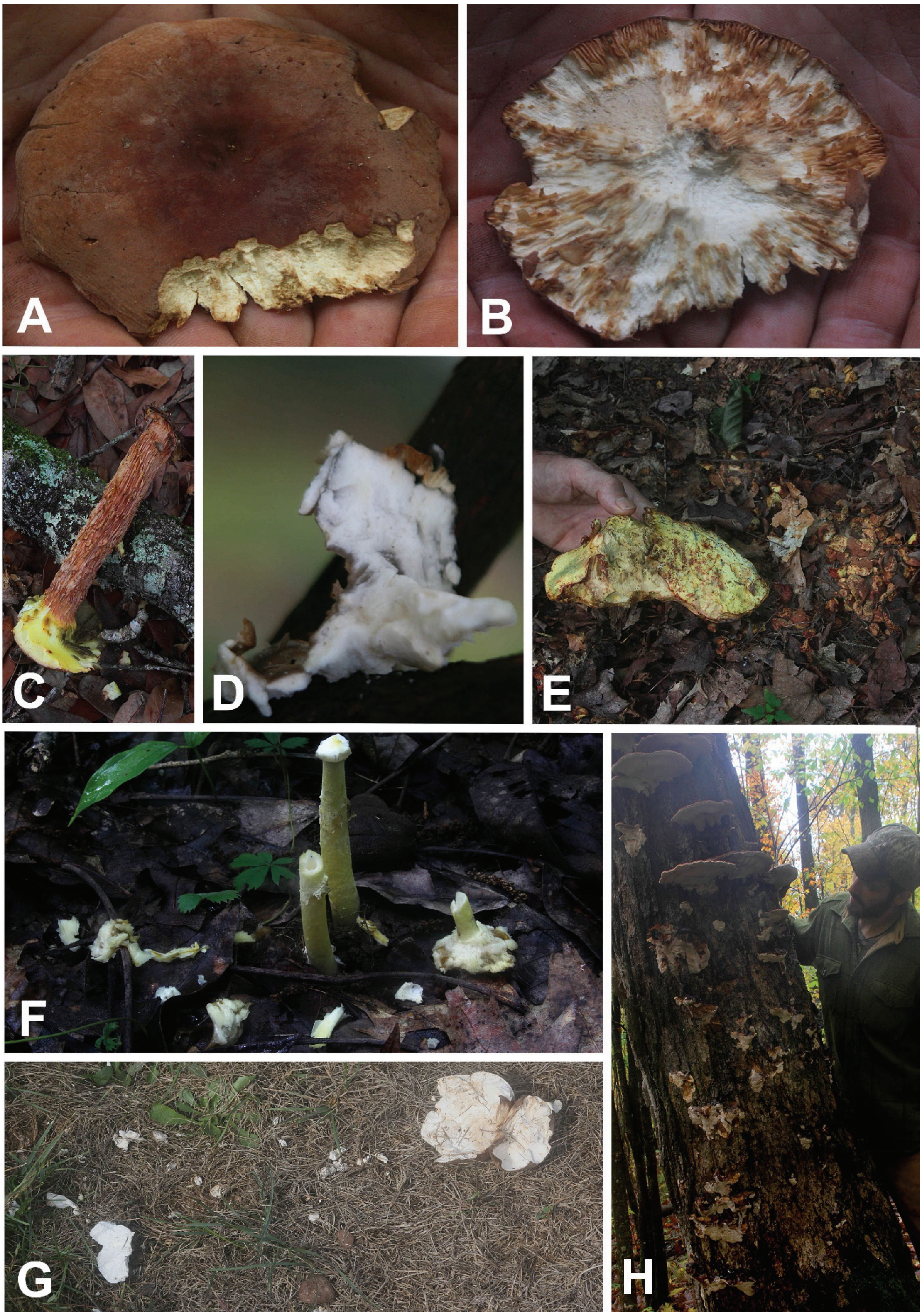

Fig. 5. Examples showing how mammalian mycophagists often selectively feed on the reproductive tissues of fruiting bodies. **A.** The upper surface of a *Lactarius corrugis* fruiting body from Buncombe County, North Carolina, USA. Note there is a little evidence of feeding on the margin of the cap. **B.** The same fruiting body as previous image but almost all of the gills have been removed by a feeding rodent. **C.** The remnants of a *Boletellus russellii* fruiting body left on a stick by a feeding rodent (likely a squirrel) Broward County, Florida, USA. The stem was virtually untouched, but all of the reproductive tissues and part of the cap were removed before the fruiting body was discarded. **D.** A *Russula* fruiting body with all of the gills removed by a feeding rodent in Randolph County, West Virginia, USA. Only part of the stem and a very thin section of the upper portion of the fruiting body remained. **E.** An unidentified bolete fruiting body ravaged by a feeding rodent in Tucker County, West Virginia. Most of the sterile portion of the cap remained, and the stem and other sterile portions were left in a chewed pile (visible in the right corner of the image). The rodent appeared to have ingested every bit of the pore surface. **F.** Stems and part of the cap surface of one fruiting body is all that remains of these two *Amanita jacksonii* fruiting bodies in Rutherford County, North Carolina. **G.** Immature *Calvatia craniiformis* fruiting bodies eaten before spore maturity by white-tailed deer in York County, Pennsylvania, USA. **H.** Entire *Ischnoderma resinosum* fruiting bodies eaten up to the maximum browse height of a white-tailed deer in Rusk County, Wisconsin, USA. Images © Todd F. Elliott.

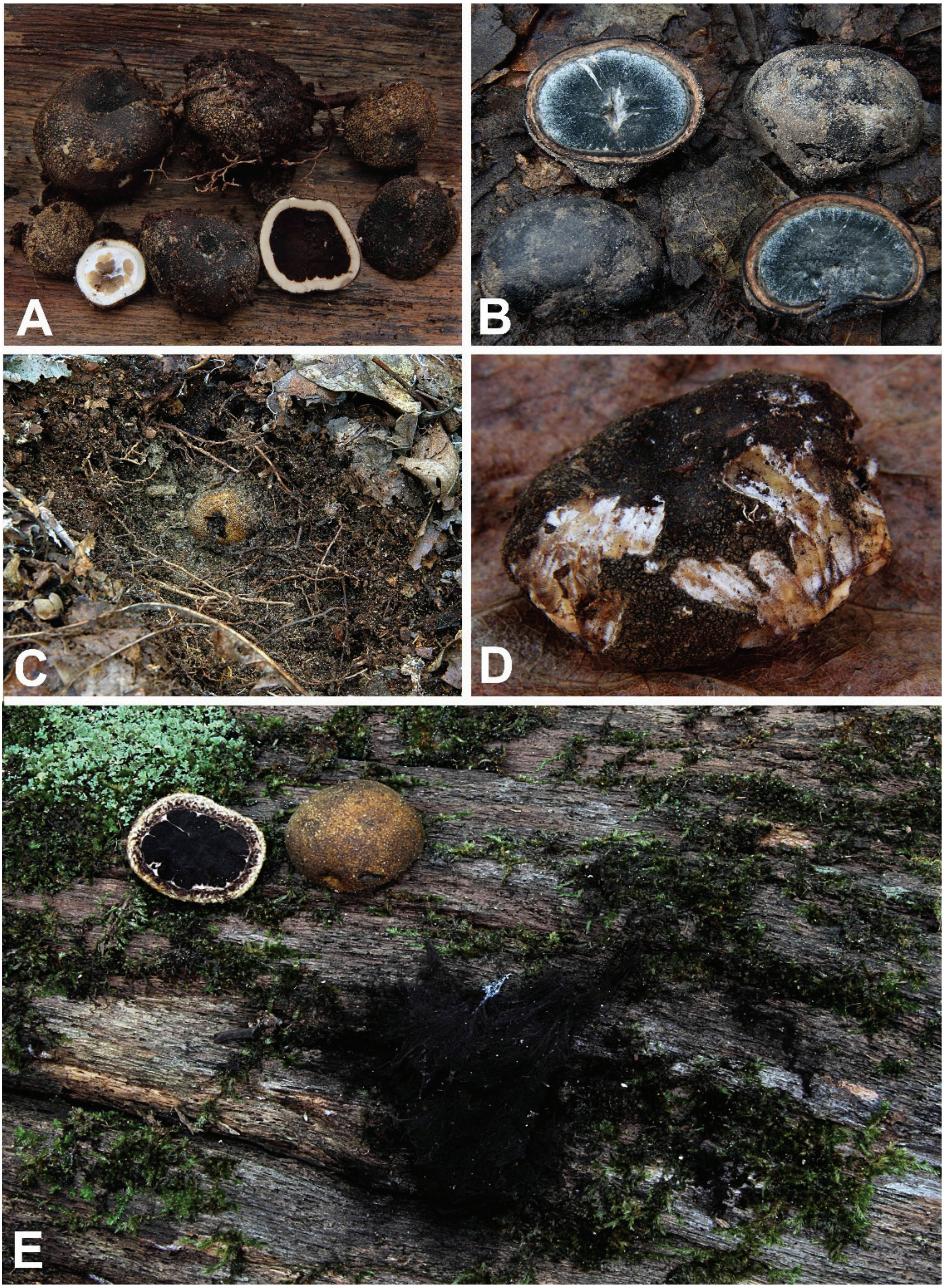

Fig. 6. The widely distributed sequestrate genus *Elaphomyces* is an important food source for mammals wherever it has been studied. **A.** The eastern North American endemic *E. macrosporus* and many other members of this genus have thick outer peridial layers that are sought out by mammals. **B.** *Elaphomyces favosus*, a tropical African species eaten by mammals that also illustrates the thick outer layers. **C.** An unidentified *Elaphomyces* sp. from Rutherford Coungy, North Carolina, USA that has been partially excavated by the foraging activities of a small mammal. Note the dark spot where several small bites have been taken. **D.** A single *Elaphomyces* fruiting body from Transylvania County, North Carolina that was excavated and partially eaten by a small rodent. Note the teeth marks on much of the peridium. **E.** While truffle hunting in Rutherford County, North Carolina, the first author encountered an area filled with extensive animal digs; a nearby log had this pile of powdery black *Elaphomyces* spores placed on top. Truffle raking near the digs uncovered this fruiting body of *E. americanum*, and microscopic examination revealed that the black spores left piled on the log matched those of the collected fruiting body. A chipmunk or squirrel was likely responsible for this tailings pile. Images © Todd F. Elliott.

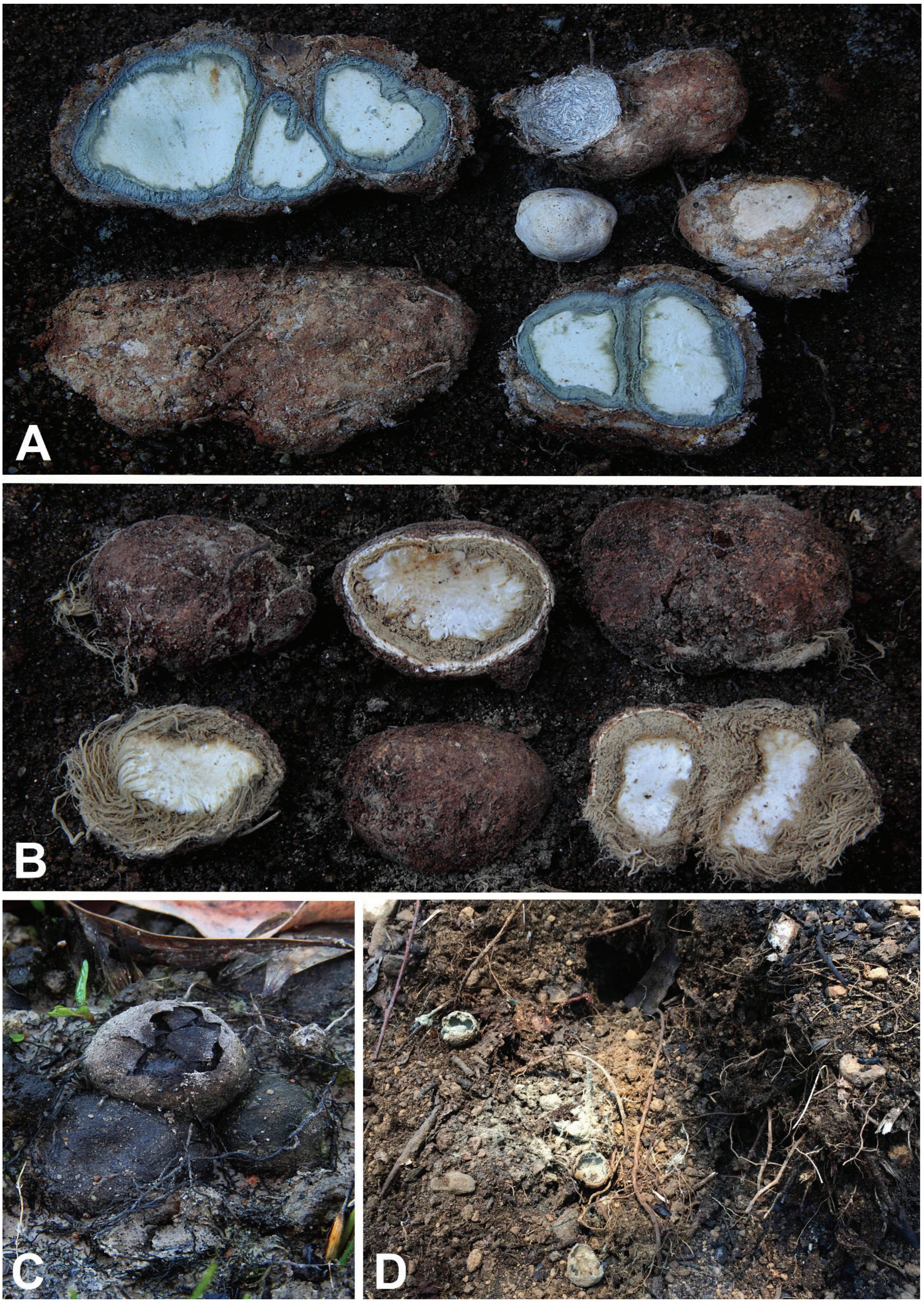

Fig. 7. Examples of members of the fire-adapted mycorrhizal family *Mesophelliaceae*. Widespread in *Eucalyptus* forests across Australia and an important food source for a diversity of mammals. **A.** *Mesophellia* (Reidsdale, New South Wales, Australia) fruiting bodies are often located deeper in the soil than other groups of sequestrate fungi and often grow in nearly confluent clusters. Note that the exterior of the fruiting body incorporates soil and mycorrhizal roots. The next layer is filled with powdery, greenish grey spores, and the central white core is the desired food of foraging mammals. **B.** *Andebbia pachythrix* (Braidwood, New South Wales), shares similar fruiting morphology and requires mammals to peel the exterior before they can eat the core. **C.** Three exposed fruiting bodies of a member of the *Mesophelliaceae* that were burned in a fire (Victoria, Australia). These fruiting bodies were close to the surface and exposed to excessive heat, which likely caused them to be overlooked by mammals foraging post fire. Fruiting bodies that are located deeper in the soil and are exposed to fire often produce a highly pungent aroma reminiscent of rotting onions. **D.** In the aftermath of the intense 2019/2020 Bee's Nest Fire near Dundurrabin, New South Wales, the first author was extinguishing a burning log and found the skins and spores of these three *Mesophellia* fruiting bodies in the tailings pile of a small mammal excavation approximately 20 m away from what was still burning. The mammal responsible for the tailings pile had successfully extracted the core and left behind the skin and spores. Due to the recent fire, there was little other food within several kilometers of this site, which highlights the importance of this family of fungi as post-fire food for Australian mammals. Images © Todd F. Elliott.

regions of the world that experience cold winters or other environmental/climatic factors that can lead to seasonal food shortages. Though their fungal caching behaviours have been far less thoroughly studied than nut/seed dispersal, rodents likely perform ecosystem functions that are of similar importance.

Early naturalists frequently wrote with amusement about the labours and physical feats of small squirrels as they built their fungal caches and struggled to haul large fungal sporocarps into the canopy to dry them for winter. Merriam (1884: 214) noted the following about a North American red squirrel:

> *"From his liking for mushrooms some would consider him an epicure, but in whatever light we regard this taste, it is a droll spectacle to see him drag a large 'toadstool' to one of his storehouses. If the 'umbrella' happens to catch on some stick or log and is broken from the stem, as is frequently the case, he is pretty sure to scold and sputter for a while, and then take the pieces separately to their destination".*

Most squirrels that have been studied were observed to dry fungal sporocarps on branches and later hide these in caches (Fig. 8). In some areas, squirrels dry so many mushrooms in tree branches that it has been described to look like a decorated Christmas tree (Odell 1925, Murie 1927). Some authors have reported only the drying behaviour, but given that squirrels are typically secretive about their caches, it is easy to overlook where they may have stored the dried mushrooms. It is also possible that in some regions or among some squirrel species, mushrooms are left in their original drying sites; however, further studies are needed to confirm this. Buller (1917, 1922) reported that North American red squirrels store dried sporocarps in hollow trees, crow nests, woodpecker nests and even boxes in old houses. Laursen *et al.* (2003) noted that in Alaska, northern flying squirrels and North American red squirrels hollowed out witches' brooms that were produced by spruce broom rust or yellow witches' broom rust (*Chrysomyxa arcotostaphyli*); the squirrels then used these cavities to raise their young and cache dried mycorrhizal fungi (both epigeous and hypogeous species). Jung *et al.* (2010) noted that North American red squirrels also used witches' brooms as nests, lining them with American bison (*Bison bison*) hair and storing dried fungi for the winter. Vernes & Poirier (2007) noted that a North American red squirrel filled a robin nest with more than 50 dried sporocarps from the hypogeous genus *Elaphomyces* (Fig. 8C). Caches made by North American red squirrels can often be quite large. Buller (1922) examined a box found in an abandoned house that was used as a North American red squirrel cache, and he reported it to weigh nearly 0.5 kg and contain 116 fungal sporocarps; another cache contained up to 300 sporocarps. Hardy (1949) studied a large North American red squirrel cache in a hollow tree containing 59 fungal specimens. He was able to identify at least 13 fungal species, most of which were ECM taxa; the most numerous species (30 specimens) was the sequestrate fungus *Hymenogaster tener*.

Kato (1985) noted that the Japanese squirrel (*Sciurus lis*) cached walnuts and pinecones in trees and underground, while fungi were only cached in trees. He also reported that underground food was eaten mainly in the spring. Foods stored below ground are naturally harder for thieves to find, but squirrels struggle to access them under deep snow. It is therefore usually important for squirrels to also cache food in elevated locations; however, Lampio (1967) reported that in Finland, Eurasian red squirrels (*Sciurus vulgaris*) dug cached fungi from under the snow. The amount of fungi and other foods cached likely correlates with climate and food availability in winter and inevitably varies between regions, habitats and species. Buller (1922) suggested that Great Britain's winters might be too wet for rodents to store fungi, and this may explain the higher frequency of reports on caching behaviours from the colder and drier parts of North America and Eurasia. In Scotland, for example, the Eurasian red squirrel was estimated to cache a minimum of 42 sporocarps across its home range (Lurz & South 1998); this is a much lower number than what has been generally reported among squirrel species in northern North America (Buller 1917, 1922, Dice 1921, Murie 1927, Hatt 1929, Hardy 1949, Smith 1965, 1968a). On the other hand, caches of Eurasian red squirrels in northern Finland have been estimated to contain approximately 440 stored fungi per hectare and possibly as many as 1 800 sporocarps per individual (Sulkava & Nyholm 1987). These studies show that caching rates vary both within the same species of squirrel from different latitudes and between squirrel species across the Northern Hemisphere, and may correlate with the length of winter, snow cover and other climatic conditions.

Fungi typically require air drying and subsequent storage in very dry caches (Fig. 8), while other foods preserve better in varying weather conditions. Despite the wide array of foods eaten by the North American red squirrel, their fungal caches typically do not contain other food items (Hardy 1949). Quality of drying and storage locations for fungi appear to be important to squirrels. Experimental studies suggest that most mushrooms stored in caches for a long period of time tend to lose nutritional value, particularly with exposure to freezing and thawing cycles (Frank 2009). This nutritional degradation may explain why squirrels are typically very diligent in making sure that stored fungi are dry, saving the driest and best insulated storage sites for fungi and/or to build their nests. Dice (1921) described a North American red squirrel nest on a shelf in an old Alaskan cabin where, by October, the squirrel had collected a large number of fungi. He reported that every open can was packed with dried mushrooms, while sporocarps that were not fully dry were spread out on the shelves. Hendricks & Hendricks (2015) observed that North American red squirrels in Montana preferred to dry/cache mushrooms on dead branches, possibly because they have better airflow.

Learning to dry a mushroom and cache it in an appropriate location for long-term storage is a relatively complex skill that squirrels progressively acquire with practice. Smith (1968a) observed that young North American red squirrels began to attempt this activity as early as three days out of the nest. He reported that in the first 10 days out of the nest, three young squirrels dropped 12 of the 32 fungi they attempted to hang on branches. They only dropped 10 out of 70 by their third week, while their mother only dropped three out of the 165 fungi that she hung to dry.

The full diversity of mammals that cache fungi is poorly known. As discussed earlier, most studies have focused on North American red squirrels, the Eurasian red squirrel and the Japanese squirrel, while there are few reports of other rodents caching fungi. Two studies reported the Siberian chipmunk (*Tamias sibiricus*) and the Uinta chipmunk (*T. umbrinus*) to cache fungi (Ognev 1966, Bergstrom 1986), but we were unable to find any additional information about other chipmunk species caching fungi. Most researchers who have studied the nests and behaviour

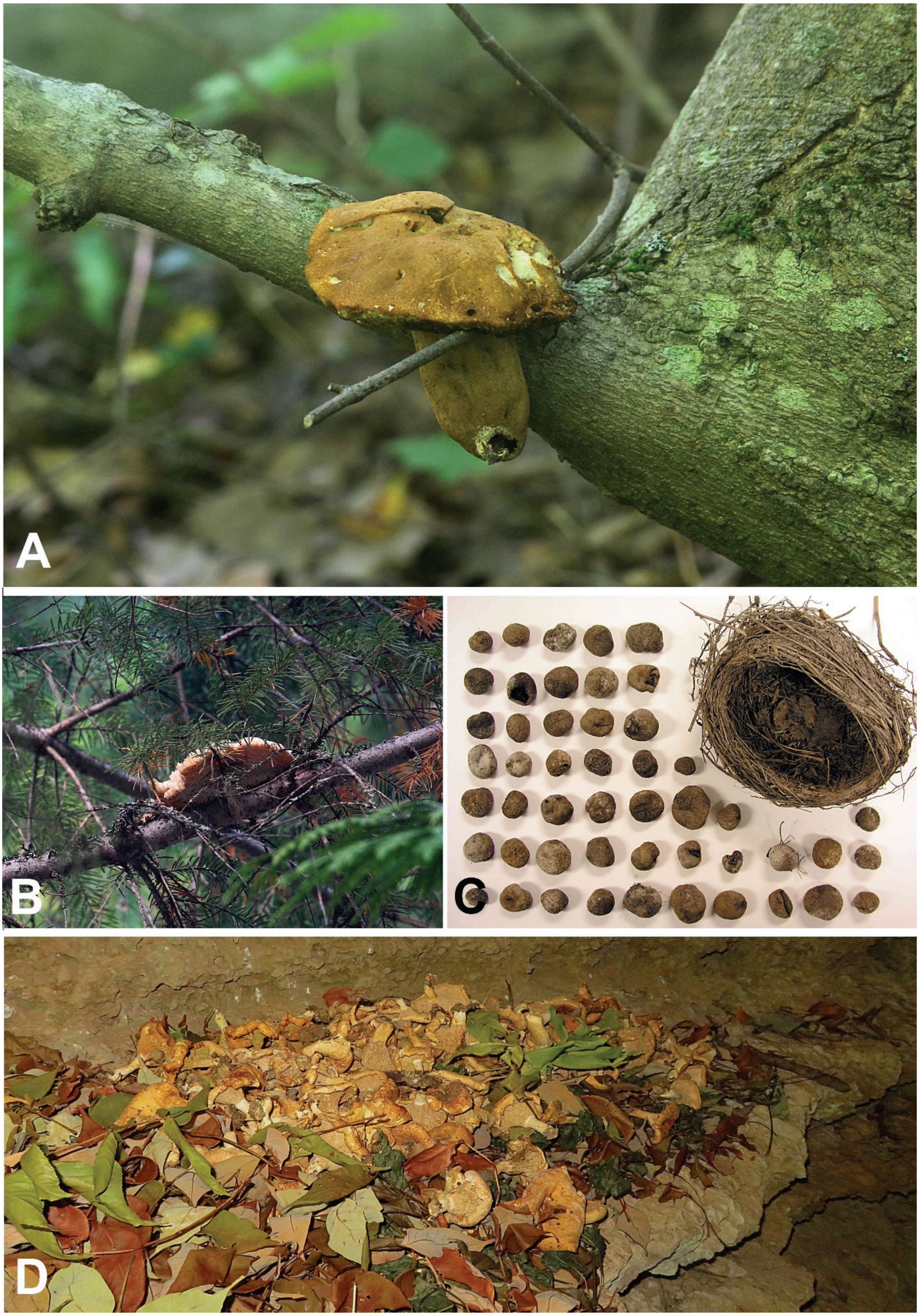

Fig. 8. Examples of fungi hung or cached by rodents. **A.** An entire bolete fruiting body carefully hung by a North American red squirrel in Tucker County, West Virginia, USA. **B.** A species of *Amanita* hung to dry by an unidentified squirrel (likely a Douglas's squirrel based on the species frequently observed in that area) in Chelan County, Washington, USA. **C.** A North American red squirrel in New Brunswick, Canada cached more than 50 *Elaphomyces* fruiting bodies inside of this abandoned robin nest (see: Vernes and Poirier 2007). **D.** A large Allegheny woodrat cache of dried fungi (likely mostly members of the *Russulaceae*) found inside of a cave in Adams County, Ohio, USA. Images A & B © Todd F. Elliott. Image C © Karl Vernes. Image D © Laura S. Hughes.

of various North American woodrats (*Neotoma* spp.) have reported that they frequently cache and collect fungi along with other seemingly random non-food objects (see papers reporting mycophagy for this genus in Supplementary Table S8 and Fig. 8D). *Neotoma* species, sometimes called pack rats, are notorious hoarders. They certainly use the stored fungi for food, but it is difficult to determine how reliant they are on the food value of cached fungi or whether this behaviour is simply an extension of their predisposition for hoarding random objects. Further study of fungal caching behaviours among various *Neotoma* species is needed to fully understand these interactions. Kangaroo rats frequently cache food, but we only found one study reporting fungi caching behaviours, and this was in the banner-tailed kangaroo rat (*Dipodomys spectabilis*) (Vorhies & Taylor 1922).

Species of the shrew family, *Soricidae*, have very fast metabolisms that require them to cache food (Moore 1943, Maser & Hooven 1974, Martin 1981, Robinson & Brodie 1982, Carraway 1985, Merritt 1986, Vander Wall 1990, Schwartz & Schwartz 2001, Rychlik & Jancewicz 2002, Urban 2016). Although this aspect of shrew biology remains relatively incompletely studied, many species are reported to eat fungi (Supplementary Table S9). Though we could not find any reports of caching fungi by shrews, further research may reveal such behaviour in some species. Some species of pocket mice (*Heteromyidae*), voles (*Cricetidae*), lemmings (*Cricetidae*) and gophers (*Geomyidae*) cache food (Vander Wall 1990, Schwartz & Schwartz 2001, Connior 2011), and members of these groups have been reported to eat fungi (Supplementary Table S8). However, we have so far been unsuccessful in locating explicit reports of these groups caching fungi, likely due to insufficient research having been undertaken on this topic.

Reports of fungal caching behaviours have focused on cold regions of the Northern Hemisphere. In regions where fungal caching does not occur, it is possible that fungi sporulate for a larger portion of the season, the climate is not conducive to fungal storage, or animals are adapted to seasonal fungal consumption and periodically rely on other food sources. It seems probable that mycophagous mammals in the Southern Hemisphere also cache fungi, though we could not find any evidence of such events even in the large volume of mycophagy literature published in Australia; we could also find no evidence in the literature for South America or Southern Africa. In Australia, some mycophagous mammals – including brush-tailed bettongs (*Bettongia penicillata*), musky rat-kangaroos (*Hypsiprymnodon moschatus*) and giant white-tailed rats (*Uromys caudimaculatus*) – have been reported to cache seeds (Forget & Vander Wall 2001, Theimer 2001, Theimer 2003, Murphy *et al.* 2005). Musky rat-kangaroos and giant white-tailed rats primarily reside in wet tropical habitats in northeastern Queensland, Australia. This type of wet tropical habitat is not conducive to storing fungi since they would quickly rot in humid warm conditions. Since brush-tailed bettongs reside in areas that would be better suited to storing fungi (compared to the tropics of northern Queensland), it is possible that they may be caching fungi on occasion or some fungi may be available throughout the season, but to our knowledge this has not been specifically studied. Further research may uncover that this behaviour is more widespread both geographically and among more mammal species.

For animals that store fungi, these caches provide an important food for seasons when the resource is less readily available. In addition to the species that make stores, other mammals and birds may depend on raiding the caches. For example, Andreev (1978) noted that Siberian jays (*Perisoreus infaustus*) survived Eurasian winters in part by feeding heavily on fungi stolen from rodent caches. Carey (1991) noted that during the night, Humboldt's flying squirrels raid caches of fungi made by diurnal squirrels. Stealing food from squirrel caches comes at a risk to the thief, since some squirrels can be violent (Seagears 1949–1950) and are usually highly defensive of their stores. Occasionally they have been reported to fight to the death over cache ownership (Smith 1968a). The diversity of mammals that cache fungi or raid these caches is still poorly understood, and more studies are needed to understand their importance as winter food.

The ecological implications of mammal caching behaviours for fungal dispersal are not fully understood. By placing fungi to dry several metres off the ground, rodents help with the release of fungal spores higher into air currents. Connor (1960) noted that North American red squirrels bury "small puffballs" in pits; he unfortunately did not identify the fungal species involved, but it is likely some type of hypogeous fungi. It is therefore possible that squirrels may dig hypogeous fungi in one location and bury them somewhere else. Regardless of whether squirrels really store fungi below ground or simply forget them, this behaviour has potentially important implications for fungal dispersal.

Nutritional advantage of fungi consumption

Since fungal cell walls are primarily composed of chitin (Cork & Kenagy 1989a, Balestrini *et al.* 2000) that is difficult for humans to digest when raw, there is a widespread myth that fungi are nutritionally insignificant; however, cooking fungi makes them highly digestible and nutritionally beneficial to humans (Wani *et al.* 2010). While cooking fungi is irrelevant in the context of wildlife nutrition, many mammals are capable of biosynthesizing chitinases and digesting raw fungal tissues to access nutrients (Cornelius *et al.* 1975, Boot *et al.* 2001, Wallis *et al.* 2012, Polatyńska 2014). The Abert's squirrel (*Sciurus aberti*) carries mushrooms to its nest as one of the first non-milk foods its young eat (Keith 1956), suggesting that fungi are highly digestible for this species. Fungi also do not require the processing often carried out on other foods (*e.g.* husking nuts, peeling fruit, extracting seeds). Young mammals such as the juvenile Tana River mangabey (*Cercocebus galeritus*) take advantage of this simple source of nutrition before they learn to process more energy intensive foods (Kivai 2018). Some arboreal mammals even risk predation by descending from the canopy to feed on highly desirable fungi. Germain's langurs (*Trachypithecus germaini*) have been found to come to the ground to pick fungal sporocarps and then immediately retreat into the trees to consume them (de Groot & Nekaris 2016; Fig 3D). Among other primates such as the grivet monkey (*Chlorocebus aethiops*), higher ranking members of troops tend to eat higher portions of fungi while lower ranking members eat more fruit (Isbell *et al.* 1999). The use of troop status to acquire fungi indicates that they are highly desirable; this is likely due to nutritional advantages, flavour or aroma. Japanese macaques (*Macaca fuscata*), which are known to eat at least 67 fungal species, can be so enthusiastic about fungi that fights frequently break out over possession and consumption of sporocarps (Sawada *et al.* 2014). Eastern gorillas (*Gorilla beringei*) apparently have similar disagreements within the troop over ownership of a highly valued species of *Ganoderma* fungus, as noted by Fossey (1983: 76) in the following:

> *"Still another special food is bracket fungus* (Ganoderma applanatum), *a parasitical tree growth resembling a large solidified mushroom. The shelflike projection is difficult to break free from a tree, so younger animals often have to wrap their arms and legs awkwardly around a trunk and content themselves by only gnawing at the delicacy. Older animals who succeed in breaking the fungus loose have been observed carrying it several hundred feet from its source, all the while guarding it possessively from more dominant individuals' attempts to take it away. Both the scarcity of the fungus and the gorillas' liking of it cause many intragroup squabbles, a number of which are settled by the silverback, who simply takes the item of contention for himself".*

Fungal biochemistry is complex and varies between taxonomic groups (Mendel 1898, Kinnear *et al.* 1979, Vogt *et al.* 1981, Blair *et al.* 1984, Grönwall & Pehrson 1984, Jabaji-Hare 1988, Hussain & Al-Ruqaie 1999, Claridge & Trappe 2005, Barros *et al.* 2007, 2008, Kalač 2009, Ouzouni *et al.* 2009, Wani *et al.* 2010, Wallis *et al.* 2012, Zambonelli *et al.* 2017, Lucchesi *et al.* 2021). The nutritional value for mammals also varies between fungal species and between different parts of the sporocarp. The nutritional role that fungi play in mammals' diets therefore varies between individuals, species, seasons, and the availability of other foods. Grönwall & Pehrson (1984) estimate that Eurasian red squirrels can reach up to half of their daily energetic requirements by eating fungi. As previous studies and reviews on mycophagy have typically shown, fungi are a significant source of nutrition and biomass for small mammals (Fogel & Trappe 1978, Claridge & May 1994, Claridge *et al.* 1996, Johnson 1996, Luoma *et al.* 2003, Polatyńska 2014, Nuske *et al.* 2017a, b, Zambonelli *et al.* 2017). Fungi are also important for some larger mammal species, including deer in the family *Cervidae* that rely heavily on fungi as a large portion of their diet (Strode 1954, Lovaas 1958, Kirkpatrick *et al.* 1969, Hungerford 1970, Launchbaugh & Urness 1992, also see Supplementary Table S11). The white-tailed deer (*Odocoileus virginianus*) has been reported to eat as many as 580 fungal species (Cadotte 2018). Ungulates generally eat larger fungal species, and since these taxa tend to sporulate most prolifically in the autumn and early winter, they are often more seasonally important. In cold regions of Eastern and Northern Europe, various ungulate species have been reported to excavate frozen mushrooms from under the snow (Blank 2003, Inga 2007).

Water constitutes up to 80–95 % of the biomass of fungal sporocarps (Claridge & Trappe 2005, Barros *et al.* 2007) and represents an important source of hydration for small mammals. In some cases, fungal sporocarps can be the major or only source of water for small mammals (Getz 1968). Using fungi as a water source therefore increase the adaptability of some mammals to marginal habitats where available surface water is scarce. This may explain the high diversity of mycophagous mammals in Australian dry woodlands and other similar environments around the world.

Fungal sporocarps generally contain more proteins and nutrients than plant material (Wallis *et al.* 2012) and can be an important source of essential amino acids (Blair *et al.* 1984). In larger mammals, fungi are not necessarily an important source of dietary biomass but can provide key nutrients that are often scarce or inaccessible in other food sources. Selenium, for example, is an important microelement in mammal diets that is found in relatively high levels in some fungi (Watkinson 1964, Quinche 1983a, b, Claridge & Trappe 2005, Falandysz 2008, Costa-Silva *et al.* 2011, Kabuyi *et al.* 2017). Selenium deficiency can lead to nutritional muscular dystrophy (white muscle disease), and many livestock feeding mixes include selenium supplements (Gupta & Gupta 2000, Claridge & Trappe 2005, Falandysz 2008). Fungi are likely one of the primary sources of selenium for wild mammals, thus making fungi an important food even if only small quantities are ingested.

In addition to selenium, fungi contain a wide array of essential amino acids, fats, fatty acids, carbohydrates, minerals, nutrients and proteins (Claridge & Trappe 2005). Some groups of fungi, including members of the families *Glomeraceae, Gigasporaceae* and *Mesophelliaceae*, also have high lipid and fatty acid content (Kinnear *et al.* 1979, Jabaji-Hare 1988). Many aspects of the chemical composition of various fungal species can boost animal health even in very small quantities. Studies on livestock and poultry feeds have experimentally shown the high value of fungi as a dietary supplement even in low dosages. When fungi were given to broiler chickens, for example, the chickens generally experienced increased weight gain and improved resistance to pathogens (Bederska-Łojewska *et al.* 2017). These benefits were detected even when fungi were added at levels of as low as 2 % in poultry diets. In addition to the use of sporocarps in the livestock feed industry, research has suggested that using mycelium as a fermenting agent can also provide antioxidants and improve the overall quality of livestock feeds (Ukpebor *et al.* 2007, Abdullah *et al.* 2016).

Most information about the nutritional composition of fungi is known from species cultivated for human or livestock feed, so there is very little information on the nutritional value of most wild fungal species. Deciphering the impacts of fungal consumption by wild animals is also more complex than in captive populations. Studies of wild populations of the heavily mycophagous eastern bettong (*Bettongia gaimardi*) suggested that an increase in fungi in the marsupial's diet correlated with an improved body condition (Johnson 1994b). Female eastern bettongs are more heavily mycophagous than males, and the growth rate of pouch young is positively correlated to the abundance of fungal sporocarps (Johnson 1994b). However, it remains difficult to measure the direct physiological impacts of fungal species in the diet of a given individual or species since there are many co-occurring variables. The idea of mammals "self-medicating" by using fungi and plants with certain pharmacological properties is still speculative, but research into some foods used by animals – including fungi – has uncovered compounds with promising pharmacological properties (Huffman 1997, 2003, Cousins & Huffman 2002). These studies compare some of the medicinal compounds found in pharmacological studies with food choice in primates; however, it is more difficult to relate medicinal compounds used for medical applications to the diets of mammals more distantly related to humans.

Fungi consumption has a variety of positive impacts for many mammals, but some fungal species are bioaccumulators that can absorb environmental toxins when they are growing in contaminated areas (Ernst 1985, Colpaert & Van Assche 1987, Gast *et al.* 1988, Brown & Hall 1989, Gadd 1994, Gonzalez-Chavez *et al.* 2004, Pokorny *et al.* 2004, Fomina *et al.* 2005, Soylak *et al.* 2005, Shavit & Shavit 2010, Dulay *et al.* 2015). Isotope studies in Europe have shown that fungi absorb radiocesium, which can be transmitted to animals that ingest contaminated sporocarps and then move up the food chain to eventually contaminate humans and other apex predators that have eaten these mycophagous game animals (Johnson & Nayfield 1970, Hove *et al.* 1990, Karlén *et al.* 1991, Fielitz 1992, Johanson 1994, Strandberg & Knudsen 1994, Avila *et al.* 1999, Zibold *et al.* 2001, Hohmann & Huckschlag 2005, Steiner & Fielitz 2009, Dvořák *et al.* 2010, Škrkal *et al.* 2015). Environmental contaminants are often the by-products of human activities such as agriculture, mining, bombing and manufacturing. The movement of these toxins through food webs from primary to secondary consumers is undoubtedly more widespread than is currently known, and further studies are needed to thoroughly understand the role that fungi play in the bioaccumulation and magnification of toxins through the food chain.

Evolutionary significance of mammal mycophagy

The role of mycophagy in fungal spore dispersal

Fungi disperse across ecosystems either vegetatively (through mycelium growth or asexual propagules) or sexually (via spore dispersal). Mycelium is the non-reproductive part of a fungus and is composed of a network of fine root-like filaments. In habitats with similar or compatible plant communities, mycorrhizal fungi commonly colonise seedlings through mycelial spread (Jonsson *et al.* 1999). In fragmented, highly disturbed or degraded areas, mycelial spread tends to be less effective, and spores are the primary means of establishment (Trappe & Strand 1969, Bruns *et al.* 2009, Okada *et al.* 2022).

Even though spores theoretically enable fungi to disperse over greater distances than mycelial spread does, only a small percentage of spores generally disperse successfully at significant distances. Many widespread mycorrhizal fungal species successfully disperse through air currents (Warner *et al.* 1987, Allen *et al.* 1989, Geml *et al.* 2008), but a high percentage of spores land very close to their source and very few spores are able to colonise new areas. Estimates suggest that only about 2 % of spores from wind-dispersed basidiomycete species travel beyond 5.2 m of the parent sporocarps (Li 2005), while about 5 % of spores travel beyond one metre (Galante *et al.* 2011). Among ectomycorrhizal fungi, density and diversity of wind-dispersed spores decrease with distance from forest edges, with few spores detected at distances over 1 km from the forest edge (Peay *et al.* 2012). Once landed, spores must find suitable substrates (for saprophytic species) or hosts (for mycorrhizal and parasitic species) to germinate. For sexual reproduction, individuals need to meet nearby compatible genetic strains. Therefore, spores landing closer to their parent sporocarps have a greater probability of finding suitable habitat and mating types (Kytöviita 2000, Peay *et al.* 2012, Horton 2017); however, proximity to the parent may also reduce the genetic diversity (thus the adaptability and resilience) of the species in the area. For example, low genetic diversity detected in populations of the hypogeous commercial truffle *Tuber melanosporum* is likely due to difficulties in long-distance spore dispersal (Taschen *et al.* 2016). Such genetic bottlenecks could be a result of too few animal dispersers.

Fungal sporocarps are often ephemeral and delicate, but their spores are far more resilient. Spores typically survive the enzymatic tribulations of the mammalian digestive tract and regularly germinate once deposited in scats (See next section and Tables 1, 2). Since mammals can eat entire sporocarps, mycophagy would account for the dispersal of a greater percentage of spores from a single sporocarp than would wind dispersal. Some rodents also co-disperse bacteria that interact with root-associated fungi and play important roles in nitrogen fixation (Li *et al.* 1986, Li & Maser 1986). Since an individual mammal often consumes multiple sporocarps, their scats may contain spores from multiple individuals and species of fungi that are deposited within close proximity to each other. Mycophagy is therefore an effective means of long-distance dispersal of fungal spores and improving genetic diversity within fungal populations.

Fungal spore dispersal through mycophagy can greatly impact the species composition, genetic diversity and adaptability of mycorrhizal fungal communities (Gehring *et al.* 2002, Nuske 2017, Dundas *et al.* 2018, Valentine *et al.* 2018, Miranda *et al.* 2019, Nuske *et al.* 2019). Mycophagous mammals may have played a role in the movement and recolonisation of mycorrhizal fungi under major climatic changes such as glaciation, with obvious impacts on the current distribution of fungal species and associated plants (Murat *et al.* 2004, Piattoni *et al.* 2016). It is difficult to estimate the long-term biogeographic impact of mycophagy at a global scale, but several studies have addressed these questions on a smaller scale, *e.g.* in degraded, newly forming or transitional systems. For example, mammals play a vital role in the transport of mycorrhizal inoculant into newly forming soils at the forefront of receding glaciers in the alpine zone of the North Cascades Mountains, USA (Cázares & Trappe 1994). Scats of mycophagous animals enable ectomycorrhizal tree establishment in nutrient-poor sandy dune environments in Oregon, USA (Ashkannejhad 2003, Ashkannejhad & Horton 2006). After the volcanic eruption of Mount Saint Helens in Washington, USA, the spore-containing scats of mammals served as vectors of mycorrhizal spores into newly formed sterile soils within the blast zone (MacMahon & Warner 1984, Allen 1987). In newly produced coal mine spoils, mycorrhizal spores can be dispersed by grasshoppers and rabbits (Ponder 1980). Small mycophagous mammals such as voles are key to habitat succession engineered by North American beavers (*Castor canadensis*), a species that causes more ecosystem-level change than any other non-human mammal. When beaver ponds eventually silt in, they become meadows dominated by herbaceous communities that typically associate with arbuscular mycorrhizal fungi, while the surrounding forests are dominated by ECM plants. Southern red-backed voles (*Myodes gapperi*) regularly eat hypogeous ECM fungi on the forested edges of beaver meadows and inadvertently carry spores into the meadows in their scats; this behaviour builds up a spore bank that assists ECM tree species in recolonising areas affected by beavers (Terwilliger & Pastor 1999). Similar meadow colonisation by ECM spores was observed in Oregon as a result of western pocket gophers (*Thomomys mazama*) depositing ingested fungal spores in below ground faecal chambers (Maser *et al.* 1978b). In regions where non-native pines (*Pinus* spp.) are farmed in plantations, a variety of mycophagous animals spread the spores of pine-associated mycorrhizal fungi outside the bounds of pine plantations, potentially contributing to the spread of these trees (Nuñez *et al.* 2013, Wood *et al.* 2015, Policelli *et al.* 2019, 2022, Aguirre *et al.* 2021).

Spore viability

Fungal spores tend to be very robust and remain viable after passage through the digestive system of a diverse range of invertebrates (Tuno 1998, Trappe & Claridge 2005, Kitabayashi & Tuno 2018, Vašutová *et al.* 2019, Ori *et al.* 2021) and birds (Caiafa *et al.* 2021).

Table 1. Mammal species experimentally shown to disperse viable mycorrhizal fungal spores.

Genus and species of mammals	Common Name	Method*	Viable	Rate*	Citation
Aepyprymnus rufescens	Rufous Bettong	IT	Yes	?	Reddell *et al.* (1997)
Bettongia penicillata	Brush-tailed Bettong	IT	Yes	+	Lamont *et al.* (1985)
Bettongia tropica	Northern Bettong	IT	Yes	?	Reddell *et al.* (1997)
Bison bison	American Bison	IT	Yes	?	Lekberg *et al.* (2011)
Callospermophilus saturatus	Cascade Golden-mantled Ground Squirrel	M	Yes	+	Cork & Kenagy (1989a)
Cervus canadensis	Wapiti/Elk	IT	Yes	?	Allen (1987)
Cervus elaphus	Western Red Deer	IT	Yes	?	Wood *et al.* (2015)
Ctenomys knighti	Catamarca Tuco-tuco	IT	Yes	?	Fracchia *et al.* (2011)
Glaucomys oregonensis	Humboldt's Flying Squirrel	M, IT	Yes	-	Colgan & Claridge (2002)
Glaucomys sabrinus	Northern Flying squirrel	IT	Yes	+	Caldwell *et al.* (2005)
Hystrix cristata	Crested Porcupine	M	Yes	?	Ori *et al.* (2018)
Isoodon fusciventer	Dusky-bellied Bandicoot	IT	Yes	+, ?	Smith (2018), Tay *et al.* (2018)
Isoodon macrourus	Northern Brown Bandicoot	IT	Yes	?	Reddell *et al.* (1997)
Lepus europaeus	European Hare	IT	Yes	?	Aguirre *et al.* (2021)
Loxodonta africana	African Elephant	IT	Yes	?	Paugy *et al.* (2004)
Melomys cervinipes	Fawn-footed Melomys	IT	Yes	?	Reddell *et al.* (1997)
Microtus oregoni	Creeping Vole	G	Yes	?	Trappe & Maser (1976)
Mus musculus	House Mouse	IT	Yes	+	Ori *et al.* (2021)
Myodes californicus	Western Red-backed Vole	M, IT	Yes	-	Colgan & Claridge (2002)
Myodes gapperi	Southern Red-backed Vole	IT	Yes	-	Terwilliger & Pastor (1999)
Neotomodon alstoni	Mexican Volcano Mouse	M	Yes	+, =	Castillo-Guevara *et al.* (2011, 2012), Pérez *et al.* (2012)
Odocoileus hemionus	Mule Deer	IT	Yes	?	Ashkannejhad & Horton (2006)
Perameles nasuta	Long-nosed Bandicoot	IT	Yes	?	McGee & Baczocha (1994), Reddell *et al.* (1997), McGee & Trappe (2002)
Peromyscus leucopus	White-footed Deermouse	IT	Yes	?	Rothwell & Holt (1978), Miller (1985)
Peromyscus maniculatus	North American Deermouse	IT, M	Yes	?,+,=	Rothwell & Holt (1978), Castillo-Guevara *et al.* (2011, 2012), Pérez *et al.* (2012)
Potorous tridactylus	Long-nosed Potoroo	IT	Yes	+	Claridge *et al.* (1992)
Proechimys semispinosus	Tome's Spiny-rat	IT	Yes	?	Mangan & Adler (2002)
Pseudalopex gymnocercus	Pampas Fox	IT	Yes	?	Aguirre *et al.* (2021)
Rattus fuscipes	Bush Rat	IT	Yes	?	Reddell *et al.* (1997)
Rattus rattus	Black Rat	IT	Yes	?	McGee & Baczocha (1994), McGee & Trappe (2002)
Reithrodontomys humulis	Eastern Harvest Mouse	IT	Yes	?	Rothwell & Holt (1978)
Rupicapra rupicapra	Alpine Chamois	IT	Yes	?	Wiemken & Boller (2006)
Sciurus aberti	Abert's Squirrel	IT	Yes	=	Kotter & Farentinos (1984)
Sus scrofa	Eurasian Wild Pig	M, IT	Yes	+,?	Nuñez *et al.* (2013), Piattoni *et al.* (2014), Livne-Luzon *et al.* (2017), Aguirre *et al.* (2021)
Sylvilagus floridanus	Eastern Cottontail	IT	Yes	+	Ponder (1980)
Tamias townsendii	Townsend's Chipmunk	M, IT	Yes	+	Colgan & Claridge (2002)
Thomomys talpoides	Northern Pocket Gopher	IT	Yes	?	Allen & MacMahon (1988)
Trichosurus vulpecula	Common Brush-tail Possum	IT	Yes	?	Wood *et al.* (2015)
Uromys caudimaculatus	Giant White-tailed Rat	IT	Yes	?	Reddell *et al.* (1997)
Two species of deer *Cervus elaphus* (Western Red Deer) *Dama dama* (Common Fallow Deer)		IT	Yes	?	Nuñez *et al.* (2013)

Table 1. (Continued).

Genus and species of mammals	Common Name	Method*	Viable	Rate*	Citation
Mixed scats from *Rattus fuscipes*, *R. rattus*, *R. villosissimus* and *Perameles nasuta* were shown to contain viable VAM spores, but it is unclear which species were actually tested for viability		IT	Yes	?	McGee & Baczocha (1994)
Ten species of small European mammals were examined in this study but it is unclear if viability was tested in all mammals		IT	Yes	?	Schickmann (2012)

A list of at least 40 mammal species that have been experimentally shown to disperse viable fungal spores through their scats. ***Method:** M: microscopic assessment, IT: Inoculation Trials, G: germination trial in vitro. ***Rate:** +: improved viability when consumed by animals compared to control, =: equal viability from scats to control, -: reduced viability compared to control, ?: no comparative viability data.

Table 2. Species of mycorrhizal fungi whose spores have been experimentally shown to remain viable after mammal consumption.

Fungal species	Method*	Viability	Rate*	Citation
Acaulospora morrowiae	IT	Yes	?	Lekberg *et al.* (2011)
Amphinema sp.	IT	Yes	?	Nuñez *et al.* (2013)
Archaeospora trappei	IT	Yes	?	Lekberg *et al.* (2011)
Densospora tubiformis	IT	Yes	?	McGee & Baczocha (1994)
Descolea angustispora	IT	Yes	?	Tay *et al.* (2018)
Elaphomyces granulatus	M	Yes	+	Cork & Kenagy (1989a)
Endogone aggregata	IT	Yes	?	McGee & Baczocha (1994)
Glomus atrouva	IT	Yes	?	McGee & Baczocha (1994), McGee & Trappe (2002)
Glomus australe	IT	Yes	?	McGee & Baczocha (1994)
Glomus fuegianum	IT	Yes	?	McGee & Baczocha (1994)
Glomus intraradices	IT	Yes	?	Lekberg *et al.* (2011)
Glomus macrocarpum	G, IT	Yes	?	Trappe & Maser (1976), Allen & MacMahon (1988), McGee & Baczocha (1994)
Glomus pellucidum	IT	Yes	?	McGee & Baczocha (1994), McGee & Trappe (2002)
Glomus spp.	IT	Yes	?	Allen (1987), McGee & Baczocha (1994)
Hebeloma mesophaeum	IT	Yes	?	Nuñez *et al.* (2013)
Laccaria trichodermophora	M, IT	Yes	+,-	Castillo-Guevara *et al.* (2011), Pérez *et al.* (2012)
Melanogaster sp.	IT	Yes	?	Nuñez *et al.* (2013)
Pyronemataceae	IT	Yes	?	Tay *et al.* (2018)
Rhizophagus fasciculatus	IT	Yes	?	Rothwell & Holt (1978)
Rhizopogon cf. arctostaphyli	IT	Yes	?	Nuñez *et al.* (2013)
Rhizopogon evadens	IT	Yes	?	Ashkannejhad & Horton (2006)
Rhizopogon fuscorubens	IT	Yes	?	Ashkannejhad & Horton (2006)
Rhizopogon occidentalis	IT	Yes	?	Ashkannejhad & Horton (2006)
Rhizopogon pseudoroseolus	IT	Yes	?	Aguirre *et al.* (2021)
Rhizopogon cf. rogersii	IT	Yes	?	Nuñez *et al.* (2013)
Rhizopogon roseolus	IT	Yes	?	Nuñez *et al.* (2013)
Rhizopogon salebrosus (group)	IT	Yes	?	Ashkannejhad & Horton (2006)
Rhizopogon truncatus	M, IT	Yes	?	Colgan & Claridge (2002)
Rhizopogon vinicolor	M, IT	Yes	varied	Colgan & Claridge (2002)
Rhizopogon spp. (3 unidentified species)	IT	Yes	?	Wood *et al.* (2015)
Russula aff. *cuprea*	M	Yes	=	Castillo-Guevara *et al.* (2012)
Suillus brevipes	IT	Yes	?	Ashkannejhad & Horton (2006)
Suillus granulatus	IT	Yes	?	Wiemken & Boller (2006), Aguirre *et al.* (2021)
Suillus luteus	IT	Yes	?	Nuñez *et al.* (2013), Wood *et al.* (2015)
Suillus tomentosus	M, IT	Yes	+	Castillo-Guevara *et al.* (2011), Pérez *et al.* (2012)

Table 2. (Continued).

Fungal species	Method*	Viability	Rate*	Citation
Suillus umbonatus	IT	Yes	?	Ashkannejhad & Horton (2006)
Thelephora americana	IT	Yes	?	Ashkannejhad & Horton (2006)
Thelephoraceae T73.1	IT	Yes	?	Ashkannejhad & Horton (2006)
Tomentella sublilicina	IT	Yes	?	Ashkannejhad & Horton (2006)
Tuber aestivum	M, IT	Yes	+	Piattoni *et al.* (2014), Ori *et al.* (2018, 2021)
Tuber borchii	IT	Yes	?	Livne-Luzon *et al.* (2017)
Tuber canaliculatum	IT	Yes	?	Miller (1985)
Tuber oligospermum	IT	Yes	?	Livne-Luzon *et al.* (2017)
Tuber shearii	IT	Yes	?	Miller (1985)
Tuberaceae	IT	Yes	?	Tay *et al.* (2018)
Unidentified (27 ECM taxa including *Ascomycetes* and *Basidiomycetes*)	IT	Yes	+	Claridge *et al.* (1992)
Unidentified taxa (including: *Elaphomyces* spp., *Glomus* sp., *Hysterangium separabile*, *Rhizopogon* spp., *Sclerogaster xerophilum* and *Sedecula pulvinata*)	IT	Yes (unclear which taxa)	=	Kotter & Farentinos (1984)
Colonisation by one or more of the following VAM taxa: *Glomus* spp., *Scutellospora gregaria* and *S. verrucosa*	IT	Yes (unclear which taxa)	?	Paugy *et al.* (2004)
A preliminary examination of the scats indicated that at least *Hysterangium*, *Descolea* and *Reddellomyces*, but a full list was beyond the scope of the study. Based on the results both ECM and VAM taxa remained viable	IT	Yes (unclear which taxa)	+	Smith (2018)
Dark septate endophytes and VAM fungi	IT	Yes	?	Fracchia *et al.* (2011)
Unidentified (at least 7 ECM taxa)	IT	Yes	+	Lamont *et al.* (1985)
VAM fungi	IT	Yes	+	Ponder (1980)
VAM fungi including *Glomus* spp. (3 unidentified species) and *Sclerocystis coremioides* unclear if all or some were viable	IT	Yes	?	Mangan & Adler (2002)
Unidentified ECM and VAM taxa	IT	Yes	?	Reddell *et al.* (1997)
Unidentified ECM fungi	IT	Yes	-	Terwilliger & Pastor (1999)
Unidentified ECM fungi	IT	Yes	?	McGee & Baczocha (1994)
Unidentified ECM fungi	IT	Yes	+	Caldwell *et al.* (2005)
Unidentified ECM fungi	IT	Yes	?	Schickmann (2012)

A list of at least 58 taxa of mycorrhizal fungi that have been experimentally shown to remain viable after passage through the digestive systems of mammals. ***Method:** M: microscopic assessment, IT: inoculation trials, G: germination trial in vitro. ***Rate:** +: improved viability when consumed by animals compared to control, =: equal viability from scats to control, -: reduced viability compared to control, ?: no comparative viability data, varied: different rates depending on mammal species. (Note: the names of the fungi listed in this table in some cases have been updated to reflect recent taxonomic/nomenclatural changes and may differ from the name listed in the original publication.)

Reess & Fisch (1887) and Hastings & Mottram (1915) first suggested that hypogeous fungi such as *Elaphomyces* may benefit from mammal dispersal, although they were not able to demonstrate spore viability. The concept of spore dispersal through mammal mycophagy assumes that spores remain viable after passage through the mammalian digestive system. To fully understand how frequently spores remain viable and among how many different mammal species, we reviewed the literature that tested spore viability in mammal faeces. Reess & Fisch (1887) tried multiple approaches with *Elaphomyces* spores extracted from scats of the common fallow deer (*Dama dama*), but both their controls and spores extracted from scats proved unsuccessful. Considering that mycorrhizae research was in its infancy in the 1880's, they were likely facing methodological limitations. Aside from this early attempt, we found multiple studies focusing on different groups of mycorrhizal fungi and using various microscopy techniques or inoculation/germination trials. These studies detected viable spores from more than 58 mycorrhizal fungal species after their passage through the digestive system of at least 40 mammal species (Tables 1, 2). We were unable to find any studies showing that fungal spores were no longer viable after ingestion by mammals.

Spore resilience may be due in part to melanins that limit the disintegration (lysis) of spore cell walls (Bloomfield & Alexander 1967, Zambonelli *et al.* 2017). Although further studies are needed to fully understand the relationship between melanins and mammalian digestive enzymes, the digestive enzymes of mammals appear to be no match for the melanins in fungal spores. It has been suggested that spores with ornamentation or thicker walls are more adept at surviving the digestive systems of animals (Korf 1973). Although there may be situations where this hypothesis holds true, there are fungi with smooth, thin-walled spores (*e.g.* the genera *Suillis* and *Rhizopogon*) that have been thoroughly documented to survive mammalian digestive systems (Table 2).

Although further empirical testing is needed, our review also revealed that at least 10 species of mammals may increase spore germination/viability after ingestion (Table 1). Colgan & Claridge (2002) suggested that several factors, such as body temperature, passage time and digestive anatomy, may impact spore viability. Nuñez *et al.* (2013) showed that twice as many seedlings inoculated with Eurasian wild pig (*Sus scrofa*) faeces formed mycorrhizal colonisation when compared with seedlings inoculated with western red deer (*Cervus elaphus*) and common fallow deer (*Dama dama*) faeces. The authors were unable to decipher whether these differences were due to the digestive system of deer decreasing spore viability, or if the digestive enzymes of wild pigs caused scarification that alleviates spore dormancy and increases germination. Scarification of fungal spores (*i.e.* erosion or breaking down of spore wall microstructures) after transit through mammalian digestive systems has only been studied in a few fungal taxa and is probably more common than presently known. For example, asci of *Tuber aestivum* break apart and the spore ornamentation is worn down after passage through digestive systems of Eurasian wild pigs (Piattoni *et al.* 2014, 2016). Despite this apparent damage, spores from faeces formed heavier mycorrhizal colonisation than non-ingested spores in inoculation trials. Different animals cause different amounts of spore scarification, and in general, longer passage rates among larger animals likely increase spore liberation from asci and/or scarification. For example, when comparing *Tuber* spores ingested by wild pigs with those ingested by the long-tailed field mouse (*Apodemus sylvaticus*), Zambonelli *et al.* (2017) suggested that the digestive system of the long-tailed field mice had liberated far fewer spores from their asci than did that of wild pigs.

There are likely situations where both seeds and associated fungal spores are dispersed in the same scat (Pirozynski & Malloch 1988), and it is possible that both are simultaneously being scarified, thus increasing their chance to match with suitable mycorrhizal symbionts. These studies are analogous to animal ingestion of fruits that can facilitate the disruption of seed dormancy and increases seed germination rates (Stiles 1992, Traveset *et al.* 2007). In mycology, similar studies remain scarce but are necessary to improve our understanding of these trophic interactions.

The role of aromas in mycophagy and fungal evolution

Evidence suggests that some bird species may encounter fungi simply by chance while others select them based on colour or aroma (Elliott & Marshall 2016, Elliott & Vernes 2019). Although terrestrial native mammals are absent from New Zealand, the country has a diversity of exceptionally colourful endemic truffles that may be a result of selective pressure from visually cued foraging birds (Beever & Lebel 2014, Elliott *et al.* 2019a). There are numerous reports of mammals eating epigeous fungi, but since these fungal sporocarps are easily visible above the surface of the soil, it is difficult to determine if mammals detect them by visual or olfactory cues or a combination of both. Fossey (1983: 131) provided an example of two young eastern gorillas named Pucker and Coco seeking out “bracket fungi” for food using what appears to be visual cues:

> *“One day while walking in a new area, Pucker suddenly ran toward a large cluster of* Hagenia *trees on the edge of the forest leading to the mountain. Coco leapt from my arms in rapid pursuit — which was unusual. I thought they were making a dash for the mountain and was hastily taking out the bananas when both infants halted below one of the larger trees. They peered up at the tree like children looking up a chimney on Christmas eve. I had never seen them so fascinated by a tree, nor could I determine what it was that so strongly attracted them. Suddenly the two began frenziedly climbing the huge trunk, leaving me even more puzzled. About thirty feet above the ground they stopped, pig-grunted at one another, and avidly started biting into a large bracket fungus. Previously I had noted these shelflike growths, which protrude from* Hagenia *tree trunks and rather resemble overgrown solidified mushrooms*[...] *Try as they might, neither Coco nor Pucker could pry the fungus from its anchorage on the trunk, so they had to content themselves with gnawing chunks out of it. A half-hour later only a remnant remained. Reluctantly they descended, but as we walked on they gazed longingly back at the tree with the fungus elixir”.*

The role of aroma is more obvious in hypogeous fungi, where the selective advantage of mycophagy contributed to the convergent rise of sequestrate sporulating morphologies in multiple fungal lineages (Sheedy *et al*. 2016, Truong *et al.* 2017, Elliott & Trappe 2018, Elliott *et al.* 2020a). Sequestrate sporocarps can be partially emergent or hidden entirely below the soil surface, placing the reproductive success of sporocarps and the species at the whim of animal detection. Many sequestrate fungi have lost their ability for the forcible discharge of spores (Thiers 1984) and therefore rely on the production of volatile olfactory cues to attract animal dispersers (Maser *et al.* 1978a, Talou *et al.* 1987, 1990, Donaldson & Stoddart 1994, Stephens *et al.* 2020).

Due to the culinary/economic importance of many members of the sequestrate genus *Tuber*, the chemistry of sequestrate fungal aromas has been most thoroughly studied in this genus (Splivallo *et al.* 2011, Molinier *et al.* 2015, Splivallo *et al.* 2015, Vita *et al.* 2018, Mustafa *et al.* 2020). Based on experiments with domestic dogs and pigs, Talou *et al.* (1990) suggested that dimethyl sulphide was the primary aroma responsible for the detection of mature *T. melanosporum* sporocarps. Dimethyl sulphide is also the primary odour that attracts truffle specialist arthropods (Pacioni *et al.* 1991). These relationships are analogous to plants attracting pollinators with nectar and seed dispersers with sugary fruits, but animal-fungal interactions remain less thoroughly studied. We argue that similarly interdependent associations have been developed by sequestrate fungi through the production of strong aromas that entice animals to find them when spores reach maturity. The level of specialisation and specificity in these aromas is still up for debate, and it is currently unknown whether some fungi can mimic pheromones to target certain species or sexes of mammalian dispersers. Claus *et al.* (1981) suggested that the ability of pigs to detect *T. melanosporum* may be linked to a steroidal pheromone (5α-androst-16-en-3α-ol) that is similar to sex chemicals produced by the mammal. Ultimately, it is hard to prove whether wild pigs are so passionately interested in truffles merely because they are tasty and nutritious or as a result of some sexual pheromonal trickery. Unlike analogous co-evolutionary associations involved in seed dispersal and pollination, we are unaware of any highly specialised associations that are exclusive between a mammal and a fungal species. However, it would be interesting to explore further whether the selective advantages offered by mycophagy could lead to more specialised dispersal associations.

There are many observational reports of mammals detecting hypogeous fungi by sense of smell, such as deer digging up hypogeous fungi hidden below the soil surface (Cowan 1945). Bermejo *et al.* (1994: 888) described a bonobo (*Pan paniscus*) seemingly using smell to locate an unidentified "truffle" species in the Democratic Republic of Congo:

> "…*standing quadrupedally, digs up the earth, first with one hand, then with the other, in search of subterranean truffles. She puts her face closer to the hole that she has dug and looks closely. Then she carefully puts one hand into the hole and withdraws it immediately, putting her fingers to her nose to detect the scent of truffles. She faithfully repeats this operation again and again"*.

This type of behaviour is not restricted solely to this species of primate. On multiple occasions, we have observed humans displaying nearly identical foraging behaviours while attempting to locate commercially valuable truffles in the wild and on cultivated truffle farms.

Smith (1968a) made extensive observations of the behaviour of young North American red squirrels in their first few days out of the nest as they learned what to eat. Smith (1968a: 42) described the following observation:

> *"On the third day one of the young travelled over 100 ft from the nest, at which point it sniffed along the ground and dug up a false truffle (*Hymenogastrales*). It ate all of the first false truffle, dug up another, and ate half of that before making an unsuccessful attempt to cache the rest in a tree".*

Based on this observation, squirrels appear to have an innate knowledge about using their sense of smell to detect hypogeous fungi and subsequently caching sporocarps. By making careful daylight observations from the day this squirrel was born, Smith (1968a) demonstrated that the behaviour of this young squirrel was truly innate and was not acquired from observing a parent or other individual (also see section: Caching and hoarding of fungi). He suggested that the young would gradually become more adept at this task, since it took over two minutes for this juvenile to dig up the first truffle and another nine minutes to eat it, while its mother could perform the same activity in approximately one minute.

Brown hyenas (*Hyaena brunnea*) in the southern Kalahari Desert are primarily scavengers of vertebrate remains, but they reportedly also use their acute sense of smell to detect and eat the hypogeous desert truffle *Kalaharituber pfeilii* (Mills 1978). Brown hyenas are heavily reliant on odours when foraging, and Mills (1978) reported in great detail how they utilised wind direction to detect and locate food, including desert truffles. In April of 1975, Mills reported brown hyenas picking up a scent on the breeze on 21 occasions, making upwind turns of up to 200 m and then digging for a few seconds in the sand before they uncovered specimens of *K. pfeilii*. We (TFE, JMT and KV) have observed similar behaviours among domesticated dogs trained to hunt *Tuber melanosporum, Lucangium carthusiana* and other commercially harvested truffles. On multiple occasions, we have seen highly trained truffle dogs step on partially emergent immature truffles, totally unaware of their presence, while signalling their handlers toward a ripe truffle nearby.

These examples suggest that aroma can be an important factor in controlling truffle consumption and preventing them from being discovered before spores are mature/ready to germinate. In western North America, the dusky-footed woodrat (*Neotoma fuscipes*) regularly eats hypogeous fungi of the genera *Gautieria* and *Hysterangium* (Parks 1919, 1922). Parks (1922) noted that in the process of digging up ripe sporocarps, woodrats often overlooked or even discarded unripe specimens. The more strong-smelling species were more regularly consumed, suggesting a preferential selection for mature hypogeous sporocarps likely due to the strength of the aromas. Parks (1922) also noted that when different hypogeous fungal species sporulated in close proximity to one another, dusky-footed woodrats preferentially ate more aromatic species and ignored other readily accessible taxa, even if they were significantly larger. The diversity and abundance of truffles (particularly the genus *Gautieria*) was also higher near dusky-footed woodrat nests, but without a randomised survey method it is not possible to prove if this is a meaningful correlation. Based on this early naturalist's observations, it is possible that when dusky-footed woodrats defecate in close proximity to their nests, they might inadvertently "farm" truffles close to the security and safety of their homes. More in-depth and rigorous studies are needed to follow up on Parks' observations.

These examples illustrate some of the reproductive and dispersal advantages of sequestrate fungi that produce aromatic compounds. How specialised these associations are and whether certain aromas are more appealing to different individuals, sexes or taxonomic groups of animals remains to be directly assessed. In a study investigating the interactions between sporulating depths, volatile production and rodent mycophagy of the genus *Elaphomyces*, Stephens *et al.* (2020) showed that deeper sporulating *Elaphomyces* species had distinct volatile organic compound profiles and produced significantly higher quantities of aromatic compounds compared to other members of the genus that sporulated closer to the soil surface. They also concluded that rodents were selecting for species that sporulated deeper in the soil but produced stronger volatiles. The aromas of some hypogeous fungi are potent enough to be detected with portable electronic gas detectors such as flame ionisation or explosimeters (Talou *et al.* 1988). Thus, some hypogeous species produce aromas that are so strong-smelling that they may be detected by animals that do not typically rely on olfactory abilities when foraging. Stronger aromas potentially translate into more frequent consumption and better dispersal, but more complex interactions also occur. Pacioni (1986) suggests that in Europe, domestic truffle dogs trained to detect white truffle species (*Tuber borchii* and *T. magnatum*) are less effective at finding black truffle species (*T. aestivum*, *T. brumale*, *T. macrosporum*, *T. melanosporum*, *T. mesentericum* and *T. uncinatum*), and *vice versa*. The aroma composition of these two groups differs only in the presence of one or more atoms of sulphur (Pacioni 1986), indicating that aromatic specialisation is possibly aimed at different animal dispersers. Donaldson & Stoddart (1994) showed that acetaldehyde, ethyl acetate, *n*-propyl acetate, isobutyl acetate, ethyl isobutanoate, ethyl butanoate and ethyl propanoate were the compounds responsible for eastern bettongs' attraction to and detection of species of *Mesophellia*. Ultimately, it is still unknown whether it is the combination of different aromatic compounds or the strength of the compounds themselves that is more impactful on mammalian sporocarp detection.

Mammal movements and impacts of primary versus secondary spore dispersal

Fungal spores ingested by mammals are generally only dispersed within the home range of an individual, and for most mammals, there is a direct relationship between larger body size and larger home range (Lindstedt *et al.* 1986, Swihart *et al.* 1988). The dispersal potential of any vertebrate species depends on three factors: passage rate (*i.e.* transit time through the animal's gastrointestinal tract); movement pattern (*i.e.* how far the individual will move as well as the size of its home range); and speed (*i.e.* how fast the animal will travel within its home range). These three factors are key to estimating the dispersal potential of fungi ingested by any animal.

Due to the small size and vast numbers of spores produced by fungal sporocarps, spores can linger in the mammalian gut for longer periods than other larger dietary components (Danks 2012). The passage rate of macrofungal spores has been directly studied in five mammal species: two Murids, one Sciurid, one Macropodid and domestic pigs (*Sus scrofa*) (Danks 2012, Piattoni *et al.* 2016). This small sub-sample does not reflect the large diversity of mammal mycophagists, and there is likely variability between species and individuals of the same species depending on weight, size, intestinal morphology, sex, age, health, movement, other dietary components and season/temperature (Cork & Kenagy 1989b, Comport & Hume 1998, Danks 2012, Piattoni *et al.* 2016, Elliott *et al.* 2020b). This area of research is still in its infancy in comparison to the extensive botanical research regarding vertebrate seed dispersal. More studies on spore passage rates in many groups of mammals are needed to better understand the processes behind fungal spore dispersal in various mammal species and to develop modelling applications similar to those widely used by plant ecologists. One modelling study showed that swamp wallabies (*Wallabia bicolor*) regularly disperse fungal spores hundreds of metres (in some instances up to 1 265 m) from where the sporocarp was initially ingested (Danks *et al.* 2020). Such long-distance dispersal events have strong ecological significance for fungal taxa, particularly those with sequestrate sporocarp morphologies. To our knowledge, this is the only study of its kind, and such modelling approaches show promise in their potential to demonstrate that a diversity of animal species carry spores for similar or even greater distances than does the swamp wallaby.

Secondary dispersal (diplochory) by predators that consume primary mycophagists is another important mode of fungal spore dispersal. This concept was first investigated more than a century ago in toads that dispersed viable fungal spores by eating slugs that had eaten fungi (Vogilino 1895, Buller 1909). Since then, very little modern research has directly investigated secondary dispersal, and it is still unclear how widespread it is. Numerous animals are likely playing a role, including the white-headed woodpecker (*Picoides albolarvatus*) that feeds on insects known to disperse spores of the veiled polypore (*Cryptoporus volvatus*) (Watson & Shaw 2018). These woodpeckers – as well as numerous other insectivorous birds and mammals – can inadvertently act as secondary dispersers of fungi. In most cases, secondary dispersal of fungal spores can greatly increase their dispersal distance, as insectivorous birds and mammals typically move over much larger distances than the primary consumers they prey upon (Schickmann 2012, Schickmann *et al.* 2012). Predators such as eagles, owls and hawks frequently prey on mycophagous rodents, and their aerial journeys inevitably disperse spores far more widely than those of the small earthbound mammals (Trappe 1988, Colgan 1997, Luoma *et al.* 2003, Halbwachs & Bässler 2015). Larger mammalian carnivores such as canids regularly feed on smaller mycophagous mammals. Because predators have much larger-scale movement patterns than their prey, these carnivores have the potential to provide a vital yet overlooked ecosystem function through secondary dispersal of mycorrhizal fungi. The pampas fox (*Lycalopex gymnocercus*) has been reported to disperse mycorrhizal fungal spores, but it is currently unclear if this is an example of primary or secondary dispersal (Aguirre *et al.* 2021). Many bats are also likely acting as secondary dispersers of fungi by ingesting insects that eat fungi (O'Malley 2013). New Zealand's flightless bats (*Mystacina*) may ingest fungi (Lloyd 2001); but this group of bats are atypical, and there is still insufficient data to confirm if they are fungal dispersers. Given the resiliency of fungal spores (see Tables 1, 2), it is unlikely that secondary dispersal negatively impacts their viability, but further studies are needed to address these questions.

When a scat is deposited by a primary or secondary disperser, it is not necessarily at the end of its journey. Numerous organisms interact with scats and may further impact spore dispersal. Some mammals eat scats (coprophagy) and may therefore further disperse spores or improve spore germination rates (Zambonelli *et al.* 2017). In many terrestrial ecosystems, scarab beetles move and bury animal dung, including that from mycophagous mammal species. Scarab beetles can further disperse or bury seeds (Vander Wall & Longland 2004), but very little research has assessed dung beetles as dispersal vectors of fungal spores in mammal scats. At least three species of scarab beetles (*Onthophagus ferox*, *O. rupicra* and *Thyregis* spp.) disperse spores from the brush-tailed bettong (*Bettongia penicillata*) after feeding on the scats of this mammal (Christensen 1980). Several Australian species of *Orthophagus* have claws on their legs that are modified for grasping the fur of mammals, including mycophagous wallabies and bettongs. This adaptation allows the beetle to cling to the animal until it defecates; upon defecation, the beetle drops from the animal and immediately buries the dung to use as a brood chamber for its larvae (Matthews 1972). Although it has yet to be directly studied, this behaviour in many scarab beetles likely improves the success of mycorrhizal fungal spores by burying them in the rhizosphere and thus facilitating mycorrhizal root colonisation.

Ecosystem implications of mammal mycophagy

Bioturbation resulting from mycophagy

The digging activities of animals excavating hypogeous fungi contribute to bioturbation (soil disturbance) and provide important soil aeration for water penetration and organic matter decomposition (Lamont 1995, Garkaklis *et al.* 1998, 2000, 2003, 2004, Newell 2008, James *et al.* 2009, Valentine *et al.* 2013, 2018, 2021, Fleming *et al.* 2014, Clarke *et al.* 2015, Davies *et al.* 2018, Palmer *et al.* 2020, 2021). Various mycophagous animals perform bioturbation to varying degrees, and the relative importance of animal-mediated soil turnover is also dependant on the region and soil type. In Australia, the role of mycophagous vertebrates in soil turnover has been relatively well studied in some regions. Many Australian forests are dominated by *Eucalyptus* species and their relatives (Holliday 1989). Leaves in these groups often contain high levels of oils that leach into the soil, creating a hydrophobic film on the soil surface that impairs water penetration (Garkaklis *et al.* 1998). The combination of soil dryness and oil concentration at the soil surface creates a layer of flammable material that increases the sensitivity of these forests to fires. In a healthy system, a multitude of vertebrates forage in the litter and dig down into the mineral soil in search of truffles and other subterranean foods. These activities contribute to the breaking up of the hydrophobic layer at the soil surface and create micro catchments, thus improving water penetration and assisting with organic matter decomposition (Lamont 1995, Garkaklis *et al.* 1998, 2000, 2003, 2004, Newell 2008, James *et al.* 2009, Valentine *et al.* 2013, 2018, Fleming *et al.* 2014, Davies *et al.* 2018, Palmer *et al.* 2020, Maisey *et al.* 2021).

The degree of bioturbation depends on the size of the animal and its foraging habits. Superb lyrebirds (*Menura novaehollandiae*) eat a diversity of hypogeous fungi (Elliott & Vernes 2019), and each individual is estimated to displace an average of 155.7 tonnes of soil per hectare per year (Maisey *et al.* 2021). Mammals typically turn over less soil than ground foraging birds, likely due to their keen olfactory abilities that allow them to pinpoint the locations of subterranean food (Elliott *et al.* 2019a). Ground foraging birds need to scratch larger areas to find food that they cannot necessarily detect by smell. Still, mammals contribute greatly to soil turnover. The brush-tailed bettong digs between 38 and 114 excavations per night, and each individual is estimated to displace an average of 4.8 tonnes of soil per year (Garkaklis *et al.* 2004). The southern brown bandicoot (*Isoodon obesulus*) has been estimated to dig about 45 foraging excavations per day and in the process displace about 10.74 kg of soil, resulting in a soil turnover of approximately 3.9 tonnes per year per individual (Valentine *et al.* 2013). Some of the larger desert species such as the greater bilby (*Macrotis lagotis*) and the burrowing bettong (*Bettongia lesueur*) are estimated to turn over approximately 30 tonnes of soil per year per individual (Newell 2008). These examples demonstrate the wide range in the rate/quantity of soil disturbance by various mammal species. Given that Australia is believed to have the greatest diversity of hypogeous fungi (Bougher & Lebel 2001, Claridge 2002) and is also home to numerous mycophagous mammal species, it is very likely that these interactions have coevolved.

In healthy systems, many individuals and species co-occur, and their combined foraging efforts are key to maintaining healthy forest soils. Due to the introduction of foxes and cats to Australia, many of these bioturbating mammals have disappeared from much of their historic ranges or became extinct (Bilney 2014, Fleming *et al.* 2014, Vernes *et al.* 2021). We suspect that the loss of mycophagous mammal species and the subsequent loss of their soil turnover capacities may be a contributing factor in the increased frequency/intensity of fires, as well as in the desertification of some regions of the continent. Though early foresters recognised the importance of well-aerated soil for the health of Australian forests and for the reduction of intense wildfires (Hutchins 1916), these aspects of forest ecology are unfortunately rarely considered in current forest management plans.

Ecosystem impact on below ground and above ground communities

The examples described in the previous section illustrate how mammal-mediated dispersal plays a major role in shaping the composition of soil-fungal communities. The mycorrhizal interactions between these fungi and plant roots can also directly impact plant community composition through plant-soil feedbacks (Liang *et al.* 2020) and have rippling impacts on overall ecosystem biodiversity. In the Mediterranean region, inoculation trials showed that the roots of *Pinus halepensis* seedlings inoculated with forest soil were dominated by the ectomycorrhizal fungus *Geopora* (Livne-Luzon *et al.* 2017); when faeces from Eurasian wild pigs were added to the inoculum, the ectomycorrhizal species composition shifted and became dominated by *Tuber* and other ECM species consumed preferentially by animals. The decline or extinction of mycophagous mammals may drastically affect mycorrhizal fungal diversity in soils and, in turn, directly impact the spore inoculum available to associated plants. In Western Australia, Dundas *et al.* (2018) showed that in conservation areas where mycophagous marsupials were protected within predator-proof fences, the mycorrhizal community was primarily composed of ectomycorrhizal hypogeous species that associated with the dominant tree *Corymbia calophylla*; in non-fenced areas where these mammals were virtually absent, arbuscular mycorrhizal fungi were four times more abundant. Since few species of arbuscular mycorrhizal fungi produce sporocarps that are large enough to be deliberately ingested by mammals, this suggests that mycophagy can generate fungal community shifts linked to selective pressure from mammal food choice toward specific fungal species or morphologies. Since different types of mycorrhizal fungi associate with different types of plant hosts (Trappe 1962, Brundrett & Tedersoo 2018), mycophagy likely affects the species composition of plant communities as well. For example, the biomass of *C. calophylla* seedlings inoculated with soil from fenced areas was significantly higher than when seedlings were inoculated with soil from non-fenced areas (Dundas *et al.* 2018). This suggests that the presence of mycophagous mammals likely affected the vegetation through plant-soil feedback, particularly in the ratio of ectomycorrhizal versus arbuscular mycorrhizal associations. The role of mammals as dispersal vectors of mycorrhizal fungi is likely of similar magnitude to the impact of mammals on seed dispersal in tropical forests, where a phenomenon described as “empty forests” occurs when mammal disappearance leads to significant plant biodiversity loss (Peres *et al.* 2016). It is therefore crucial to take these trophic interactions into account in conservation plans for mammals, fungi and plants.

Methodological considerations

This review highlights the ubiquitous nature of mycophagy, and yet the list we provide (Supplementary Tables S1–11) is undoubtedly far from complete. We have tried to be as comprehensive as possible and have considered all regions where terrestrial mammals are found, but there are undoubtedly species that we have overlooked or that remain unstudied. As with most reviews, this manuscript is biased toward regions and/or groups of mammals that have received more research attention. The highest diversity of mycophagous mammals has been documented in North America (Fig. 9), mostly due to the enormous diversity of rodent species recorded to consume fungi. Compared to North America, fewer rodents but a wider range of mammal orders have been recorded

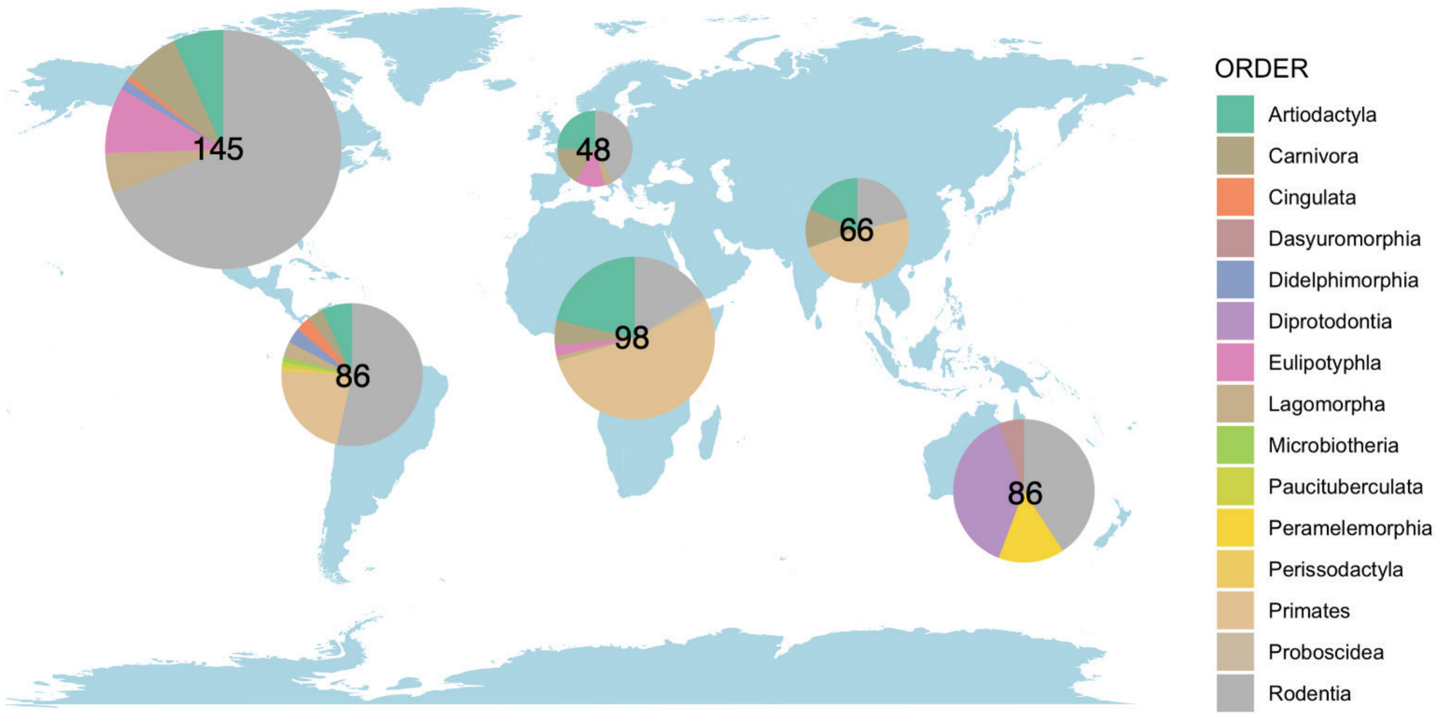

Fig. 9. Map depicting the number of mycophagous mammal species recorded per continent in North America, Central and South America, Europe, Africa, Asia (including Sulawesi) and Oceania. Colour-coded areas correspond to the number of recorded species from each mammal order. Extinct species (Neanderthals and American mastodon) have not been included. The native range of species is only considered in the context of this map. Widespread and/or exotic species (black rat, brown rat, cattle, dog, goat, grey wolf, horse, house mouse, human and sheep) have not been included given the difficulty in mapping their wild distribution and because it was not possible to determine if their mycophagous behaviour was also widespread.

to consume fungi in Central and South America, while mycophagy studies in Africa and Asia have primarily focused on primates (Fig. 9). Most studies from tropical regions, and especially Africa, are based on observational studies; very few use microscopic faecal analyses commonly applied in other regions. This likely explains why there are few reports of mycophagy among small mammals, and especially rodents, in Africa despite reports that truffles are used by traditional hunters as bait for trapping a diversity of small mammals (Kimura *et al.* 2015). It is thus highly probable that fungi are consumed as a highly desirable food by a diversity of small mammals in the region. In Oceania, endemic species of marsupials greatly contributed to the diversity of mycophagous mammals that have been documented; Europe unsurprisingly had the lowest diversity of mycophagous mammals, in correlation with the lower diversity of mammals (Fig. 9).

Language has also limited the comprehensiveness of this review. We focused on English, French, German, Portuguese and Spanish literature with a few additional works in other languages, but there are undoubtedly relevant references written in other languages that we have overlooked. This is particularly true for older references since it has only recently become more common to include English abstracts in non-English manuscripts. For example, we may have overlooked records of Asiatic mycophagous mammal species that were published in native languages; this may partially explain the lower number of mycophagous species recorded from Asia in comparison with other regions (Fig. 9).

Over the course of writing this review, we found little consistency in the way researchers refer to vertebrates eating fungi; a variety of terms were used, such as mycophagy, mycophagous, fungivory, fungivore, endozoochorous, mushroom eating or fungus eating. Some studies did not use any of these terms and only mentioned fungi in the diet list. This inconsistency in terminology hinders the development of a coherent body of knowledge about these associations. Therefore, we strongly encourage authors to use standardised terms: "mycophagy" for the action of eating fungi, with "fungus" (or "fungi") used to describe the dietary item(s). Whenever possible, we also recommend that researchers collect, voucher (deposit in a recognised herbarium) and identify (as specifically as possible) the fungi involved in the association. Adoption of these practices will allow a more comprehensive understanding of the impacts of mammals on fungal spore dispersal and the importance of different fungal species in mammal nutrition. We hope that this work will serve as a foundation for further research on mammal-fungi interactions, while also improving our understanding and awareness of these important associations.

Methods to aid fungal identification in mycophagy studies

Depending on the objectives of the study, several methods can be used to identify fungi in animal diets. Feeding behaviour has been reported through chance observations of feeding events among many animals, and systematic observational studies reporting mycophagy are particularly common in primate research. It is also possible to use camera traps to observe fungal feeding, although this can be difficult since most fungi sporulate and then decompose quite quickly. Camera trapping requires the researchers to either place fungi within the field of view of the camera or be very strategic and/or lucky with camera placement to actually capture fungal sporulation (Vernes *et al.*

2014, Vernes & Jarman 2014, Schmid *et al*. 2019, Ferkingstad 2020, Elliott & Vernes 2021a, see Supplementary Video S1).

The most common method used in the studies we reviewed is scat and/or stomach content analysis. It is rarely possible to identify fungi in the stomach of an animal using macro morphological characters, because most fungal tissues are soft and quickly become amorphous. Microscopic analysis of spores in stomach or faecal material is far more reliable. Gordon & Comport (1998) directly evaluated the effectiveness of different micro-analysis techniques, and we encourage future researchers to consider their work when selecting appropriate methods for their studies. In general, either a small subsample of stomach or faecal material is mounted on a slide, or the entire scat/stomach sample is sieved and only the fine fraction examined. The range of mounting mediums used in mycophagy studies includes KOH, water or alcohol at various percentages. Melzer's Reagent (Leonard 2006) is also used in studies focusing on fungal dietary components, since the spores of certain fungal groups produce reactions that are helpful in the taxonomic identification of spores. For best results, slide mount examination should be performed between 400 and 1 000× magnification. The accuracy of fungal species identification based on spores will vary depending on the existing background information available for fungal taxonomy in the region of interest. Ideally, fungal inventories have been performed in the area near where mammal samples were collected, allowing researchers to match spores from the mammal samples with collections of fungal sporocarps. When such information is not available, researchers depend on relevant fungal keys for the region where the study is being conducted. In this regard, Castellano *et al.* (1989) published a key that is specifically designed to identify the spores of hypogeous fungi from animal scats.

In recent years, new techniques have been developed to identify fungi in animal diets. Stable isotope signatures of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) can be used to decipher between fungi and various groups of plants in faecal samples, since ECM fungi (representing most of the fungi consumed by animals) have higher $\delta^{15}N$ values (Hobbie *et al.* 2017). Similarly, if fungal amino acids are incorporated into animal protein, the ratio of radiocarbon ($\Delta^{14}C$) in hair samples from mycophagous animals will be higher than in herbivores, since many fungi assimilate organic nitrogen from the soil with a higher $\Delta^{14}C$ than in the CO_2 incorporated by plants during photosynthesis (Hobbie *et al.* 2013). These methods are effective for deciphering fungi from plant diets but do not allow for the identification of specific fungal groups involved. There is a rise in the implementation of molecular-based approaches using DNA meta-barcoding of environmental samples (including faeces and gut contents), though they have not yet been widely employed in mycophagy studies (see: Nuske *et al.* 2019, Cloutier *et al.* 2019, Hopkins *et al.* 2021, Bradshaw *et al.* 2022). Detailed guidelines for fungal meta-barcoding are becoming abundant (see: Nguyen *et al.* 2015, Tedersoo & Lindahl 2016, Nilsson *et al.* 2019), and we strongly encourage researchers to standardise and publish detailed laboratory and bioinformatic protocols to make studies comparable between animal species and regions. Because of PCR biases toward certain fungal groups during the preparation of library amplicons, sequence abundance from next generation sequencing platforms is not directly equivalent to species, relative abundance and needs to be interpreted with caution (Pickles *et al.* 2020); this thus hinders detailed diet quantification. In addition, it is risky to base determination of mycophagy solely on these methods since the presence of fungal DNA does not necessarily indicate intentional fungal consumption nor that the fungus was "alive". We therefore encourage a rigorous and informative approach combining sequence data (with appropriate controls for DNA contamination) with microscopic examination to confirm the presence of ingested fungal material in the samples.

Finally, we wish to point out that many of the fungal groups that are frequently eaten by animals (particularly hypogeous taxa) are often inconspicuous and therefore difficult to survey. For example, States (1984) noted that the rare fungus *Sedecula pulvinata* was seldom collected during sporocarp inventories, but spores were frequently found in rodent scats in the survey area. Since *S. pulvinata* sporulates deeper underground than other hypogeous fungal species, it is frequently overlooked by humans that lack the ability of mycophagous mammals to detect its odours. Using molecular analyses of small mammal scats, Bradshaw *et al.* (2022) detected multiple species of *Rhizopogon* that were rarely collected in fungal surveys. This further highlights the potential application of animal scats as a tool in fungal surveys. Species that are rare or seldom collected may be more effectively found by foraging mammals than by scientists. This makes molecular and/or microscopic analysis of animal scats a viable surveying method to detect rare or overlooked species of fungi (Piattoni *et al.* 2016, Cloutier *et al.* 2019, Bradshaw *et al.* 2022).

CONCLUSIONS AND FUTURE DIRECTIONS OF RESEARCH

Mycophagy plays a major role in animal nutrition and fungal dispersal, with direct impacts on plant communities and overall ecosystem health. The selective pressures that mammals apply toward different fungal sporocarp morphologies, aromas, colours and habits most likely contribute to shaping fungal diversity, with critical consequences for mycorrhizal communities below and above ground. We hope that this review can serve as a foundation to inspire further research into these ecologically important yet understudied associations (Fig. 10) and their consequences for animals, fungi and plants. To expand our understanding of these associations, we highlight several key future directions of mycophagy research:

There is a need for baseline studies addressing whether fungi are a dietary component of many groups of mammals in understudied regions of the world. This is particularly true for small mammals in Africa and Asia (Fig. 9). Based on the application of inappropriate methods for determining mycophagy and the inconsistent geographic coverage of studies, it is likely that the 508 mammal species we report to consume fungi is a gross underestimation of the reality and Fig. 2 likely does not fully represent mycophagy across mammalian orders. Future studies need to take into consideration the application of appropriate methods (as outlined in the two previous sections) to determine if fungi are a component of mammal diets. The inclusion of these novel approaches would substantially improve our understanding of mammalian mycophagy globally. It would also be interesting to further investigate the diversity of mammals that practice fungal caching/hoarding behaviours and their role in fungal spore dispersal. Additionally, most research on the nutritional value of fungi has focused on cultivated mushroom species and their nutritional application for humans and/or livestock; we hope future studies will strive for a better

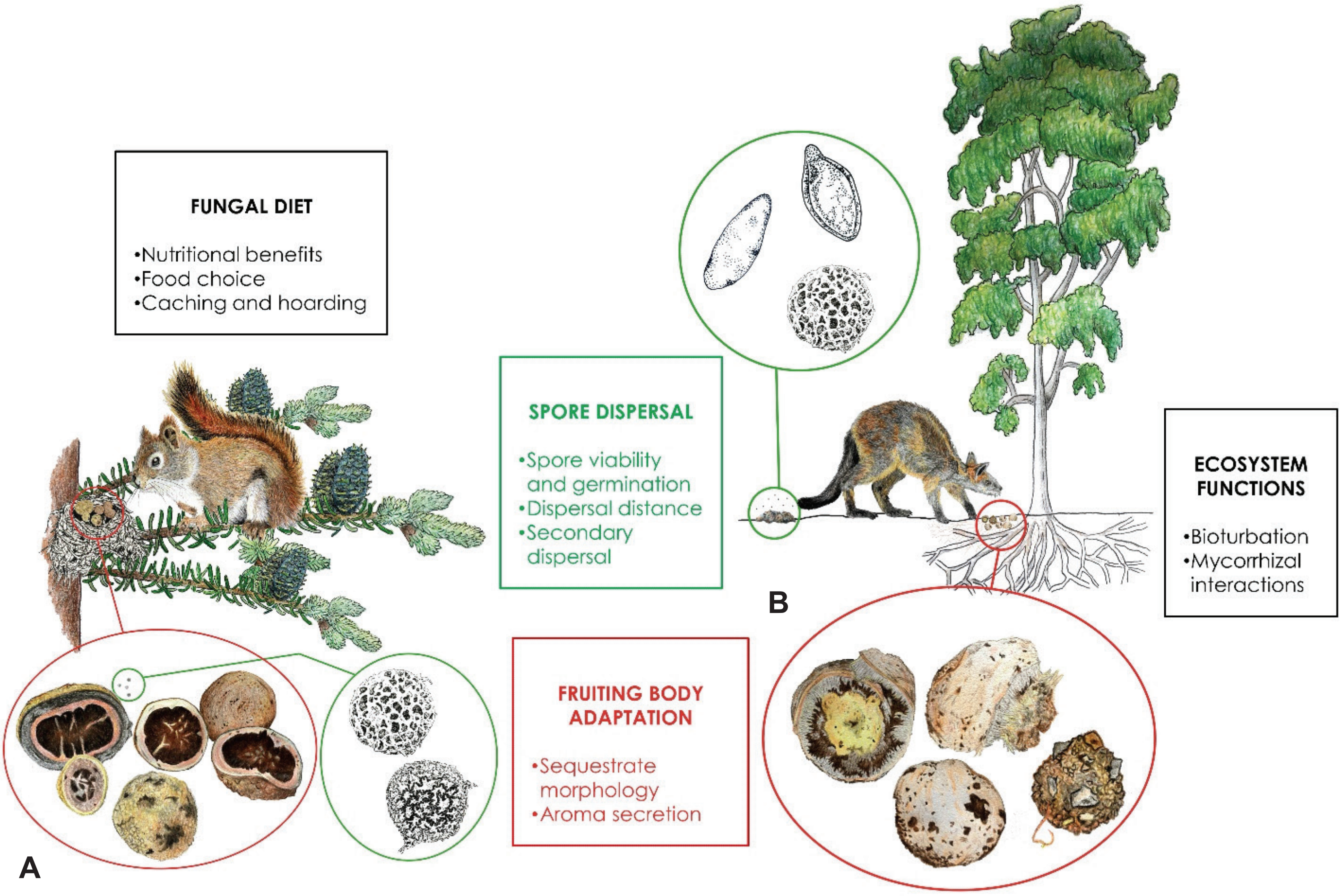

Fig. 10. Illustration representing the interactions between mammals, truffles and their ectomycorrhizal host plants. **A.** The left side of the illustration shows a North American red squirrel (*Tamiasciurus hudsonicus*) caching *Elaphomyces* truffles in an abandoned bird nest in a fir tree. **B.** In the right side of the illustration a swamp wallaby (*Wallabia bicolor*) can be seen digging for *Mesophellia* truffles at the base of an associated eucalypt tree. The wallaby also disperses fungal spores of several taxa in its scats. Illustration © PameFagus (Pamela Ciudad Martin).

understanding of the nutritional needs of wildlife consuming wild fungi, as well as preferences toward different portions of sporocarps.

To fully understand the role of mammals in spore dispersal, experimental studies on spore viability, passage rates and impacts of the presence of mycophagous mammals on soil-fungal communities need to be expanded to more mammal groups and wider geographic areas. The field of mycophagy would also benefit from a better understanding of spore enzymatic scarification in the digestive system of mammals, movement patterns combined with passage rates of different animals, and secondary dispersal by apex predators. Additionally, in order to understand the selective pressures that mammal mycophagy can apply toward the rise of certain sporocarp traits, such as sequestrate and/or hypogeous sporulating morphologies, experimental approaches are needed to determine feeding preferences toward certain traits (*e.g.* aromas, colours, shapes, nutritional components). Recent multi-gene and genome-wise molecular studies will allow researchers to determine more precisely the timing and diversification rate at which certain traits and species appeared in different groups of fungi (Varga *et al*. 2019, Sánchez-García *et al*. 2020). Coupled with predictive modelling, these studies can help to determine the role of co-occurring factors – such as past and future climate change – in the rise of certain fungal reproductive strategies.

Finally, mycophagy research needs to be considered in the wider context of the ecosystems in which these interactions occur. A handful of studies have focused on bioturbation by mammals foraging for hypogeous fungi and how mammal mycophagy contributes to the overall diversity of ectomycorrhizal fungal species, but these types of studies have so far been relatively geographically restricted. Extending these studies to other regions would significantly contribute to our understanding of the implications of mycophagy for soil aeration, water penetration, mycorrhizal plant communities and overall soil and ecosystem health.

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Supplementary Material: http://fuse-journal.org/

Table S1. The three members of the *Didelphimorphia* that have been reported to consume fungi.
Table S2. The five members of the *Dasyuromorphia* that have been reported to consume fungi.
Table S3. The 13 members of the order *Peramelemorphia* that have been reported to consume fungi.
Table S4. The 33 members of the *Diprotodontia* that have been reported to consume fungi.
Table S5. The three members of the *Cingulata* that have been reported to consume fungi.
Table S6. The 105 species in the order *Primates* that have been reported to consume fungi.
Table S7. The 12 members of the order *Lagomorpha* that have been reported to consume fungi.
Table S8. The 221 species within the order *Rodentia* that have been reported to consume fungi.
Table S9. The 21 members within the order *Eulipotyphla* that have been reported to consume fungi.
Table S10. The 27 members within the order *Carnivora* that have been reported to consume fungi.
Table S11. The 59 members within the order *Artiodactyla* that have been reported to consume fungi.
Video S1. When *Elaphomyces* truffles are unearthed, the North American red squirrel cleans the outer peridium by “shucking” adherent soil and mycelium from the truffle before it is eaten or cached (Vernes *et al.* 2014).