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The fungal rat race: mycophagy among rodent communities in eastern Australia

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ABSTRACT

Context. Rodents in many parts of the world perform an important ecosystem function as dispersers of mycorrhizal fungal spores. These fungi are vital to nutrient uptake in plant communities, but many of the fungal taxa that form these associations have fruiting bodies that are reliant on animals for their spore dispersal. **Aims.** Numerous studies have focused on the ecological importance of Australian marsupials (especially members of the Potoroidae) for the dispersal of these ecologically important fungi. We chose to focus this study on the role of murid rodents in the dispersal of these fungi in eastern Australia. **Methods.** To compare fungal taxa in murid diets, we trapped rodents in three regions of eastern Australia; our study sites spanned over 2000 km from temperate eucalypt forests to tropical eucalypt and tropical rainforest habitats. We performed microanalysis on all scats to determine whether fungi were consumed and which taxa were being eaten. Statistical analysis was conducted to investigate trends in levels of mycophagy among species and habitats. **Key results.** We examined 10 rodent species, and all were shown to ingest mycorrhizal fungi to varying degrees. The diversity, abundance and specific fungal taxa consumed varied depending on the site and forest type. In drier forests dominated by *Eucalyptus* spp., the fungal taxa consumed and dispersed were primarily ectomycorrhizal; in wetter rainforest habitats, the fungal diversity consumed was far lower and included primarily vesicular arbuscular fungi. We provide the first evidence of mycophagy by grassland melomys (*Melomys burtoni*) and Cape York melomys (*Melomys capensis*). **Conclusions.** Our findings highlight the importance of rodents as dispersers of mycorrhizal fungi across a variety of habitats from temperate to tropical forests of eastern Australia. **Implications.** This study increases the existing knowledge of rodent diets and habitat requirements. It also provides a new angle for mammal conservation efforts, given the vital nature of the ecosystem service provided by these small and frequently overlooked mammals.

Keywords: hypogeous fungi, mammal diets, mammal ecology, *Melomys*, mycorrhizae, *Pseudomys oralis*, *Rattus*, spore dispersal, *Uromys*, *Zyzomys argurus*.

Introduction

A wide array of vertebrates, including mammals, birds and reptiles, consume fungi and disperse fungal spores through their scats (Fogel and Trappe 1978; Claridge and May 1994; Nuske *et al.* 2017*a*; Elliott *et al.* 2019*a*, 2019*b*, 2022; Caiafa *et al.* 2021). Animal-facilitated fungal dispersal directly affects many aspects of ecosystems around the world in a variety of ways, including plant nutrient uptake, fungal community structure, selection of fungal fruiting morphologies, soil bioturbation, soil microbial community composition and overall nutrient cycling (Cázares and Trappe 1994; Johnson 1996; Maser *et al.* 2008; Elliott and Marshall 2016; Dundas *et al.* 2018; Valentine *et al.* 2018; Miranda *et al.* 2019; Nuske *et al.* 2019; Vašutová *et al.* 2019; Elliott *et al.* 2022). Many animals are capable of contributing to some or all of these ecosystem functions; however, certain groups are more ubiquitous and play a more significant role. Rodents are one such group. With 2590 species (Hamilton and Leslie 2021), rodents are the

most diverse and widespread order of mammals, and many of these species consume fungi. Rodents generally pass spores through their digestive systems quicker than do larger mammals and often have smaller home ranges/movement patterns (Danks 2012; Danks *et al.* 2020; Elliott *et al.* 2020). However, given their incredible abundance and adaptability to populate a multitude of habitats (Wilson *et al.* 2017), rodents have been found to be important fungal dispersers in most terrestrial ecosystems that have been studied (Elliott *et al.* 2022).

As a result of human modifications of ecosystems, many rodent species, particularly in Australia, have experienced population declines or extinctions (Smith and Quin 1996; Firth *et al.* 2010; Cove *et al.* 2017; Waller *et al.* 2017; Roycroft *et al.* 2021; Vernes *et al.* 2021). In some cases, introduced rodents have been shown to perform some of the fungal dispersal ecosystem services that were once provided by lost species (Vernes and McGrath 2009). In most systems, the full ecological effect of a loss in rodent diversity is not known in relation to its impacts on fungal dispersal. The significance of rodents as important fungal spore dispersers is gradually becoming more widely recognised, but it still remains incompletely studied. A recent global review indicated that more than 220 rodent species incorporate fungi into their diet (Elliott *et al.* 2022). Despite their ecological significance, threatened or extinct rodents rarely generate the same conservation attention as do larger, more charismatic animals.

Rodents eat many types of fungi, but sequestrate species are a particularly important food source for them (Fogel and Trappe 1978; Maser *et al.* 2008; Elliott *et al.* 2020; Stephens and Rowe 2020; Stephens *et al.* 2020; Elliott and Vernes 2021). Sequestrate fungi produce fruiting bodies that are enclosed in a skin (called a peridium), and they often fruit below ground. Unlike non-sequestrate fungi, it is usually impossible for sequestrate taxa to forcibly discharge their spores into air currents (Thiers 1984). At maturity, these fungi usually produce strong aromas that enable their detection by rodents and other animals (Stephens *et al.* 2020). After eating the fruiting bodies, these mycophagists subsequently disperse viable fungal spores through their scats (Vašutová *et al.* 2019; Elliott *et al.* 2022). Most sequestrate fungi also form mycorrhizal associations with plants and are essential to plant nutrient uptake (Tedersoo *et al.* 2010). Through these associations, mycophagous rodents are contributing to the health and diversity of fungal communities, the nutrient uptake of numerous plant species and the future food supplies of other vertebrates and invertebrates that also eat the fungi they are dispersing.

In Australia, much of the focus on these ecological associations has been directed towards mycophagous marsupials (Nuske *et al.* 2017*a*); however, this study focuses on the importance of ecosystem services provided by rodents. We investigate the levels of mycophagy across three disjunct rodent communities and measure differences among species, geographic region and habitat type. We also provide the first evidence of fungal consumption among two additional species of rodents.

Materials and methods

We selected study sites that had experienced low levels of recent disturbance, particularly in relation to land clearing. We also chose locations with relatively intact mammal communities that shared similar physiographic features despite the relatively large geographic distances between them.

At all trapping sites, we used a combination of Elliott and cage traps and followed standard live-trapping protocols approved by the University of New England Animal Ethics Committee (see AEC18-065, AEC09-129 and AEC12-114). Traps were set in the late afternoon and baited with peanut butter and vanilla paste that was either mixed with rolled oats or spread on bread. Traps were left overnight, after which we began checking for captures just before daylight the following morning. Any animals in traps were transferred to clean cloth bags to be examined, identified, weighed and sexed. To ensure identification of re-captures, we clipped a small patch of fur off the flank of each animal so that we would be able to determine whether we caught that individual in the future. The animal was photographed (Fig. 1) and then released. Scats were collected from within the trap and either placed in 70% alcohol or a paper envelope. Traps were cleaned after each capture to ensure that there was no contamination between captures. We had a total of 5181 trap-nights during this study.

Our southern-most site was on the New England Tablelands of north-eastern New South Wales, near Mount Hyland Nature Reserve (Fig. 2). Traps were at two sites, one within a 1 km radius of the central GPS point of 30°10′09″S, 152°28′13″E and the other within 800 m of 30°12′42″S, 152°26′05″E. Trapping at sites in New South Wales was conducted in June, August and November of 2009, April 2010 and February 2012 and between July and August 2019. During the 2009–12 trapping season in New South Wales, there was a total of 3450 trap-nights using Elliott Type A traps; in 2019, there were 820 trap-nights using Elliott Type A traps, 112 trap-nights using Elliott Type B traps and 10 trap-nights using cage traps. Combining all trap types during both trapping seasons, we had a total of 4392 trap nights in north-eastern New South Wales.

Two study sites were selected on the Atherton Tablelands of tropical Queensland (Fig. 2). The first site was located in Dinden National Park, and the second ran between Dinden and Davies Creek national parks. Traps were set at the first site along transects within 1.5 km of 17°06′42″S, 145°37′12″E and at the second site along transects within 2.5 km of 17°00′54″S, 145°34′59″E. Trapping at these sites was conducted in early August 2020. We used a combination of

Fig. 1. Images showing seven of the murid rodent species captured at our fieldsites during the course of this study. (*a*) *Rattus leucopus*. (*b*) *Rattus fuscipes*. (*c*) *Zyzomys argurus*. (*d*) *Melomys burtoni*. (e) *Melomys capensis*. (*f*) *Melomys cervinipes*. (*g*) *Uromys caudimaculatus*. Images © Todd F. Elliott.

Elliott A traps and cage traps. At the first site, there were 100 trap-nights using Elliott A traps and 27 trap-nights using cage traps; at the second site, there were 136 trap-nights using Elliott A traps and 69 trap-nights using cage traps. We had a total of 332 trap-nights across both sites on the Atherton Tablelands.

The third and most northern site was within Kutini-Payamu (Iron Range) National Park on the northern end of the Cape York Peninsula (Fig. 2). Traps were set along transects within a 2.5 km radius of the central GPS point 12°42′49″S, 143°17′15″E. Trapping at this site was conducted in late August 2020. There were 350 trap-nights with Elliott A traps and 107 trap-nights with cage traps. We had a total of 457 trap-nights on Cape York.

Scat samples were collected from each individual (multiple pellets were collected whenever possible and then mixed

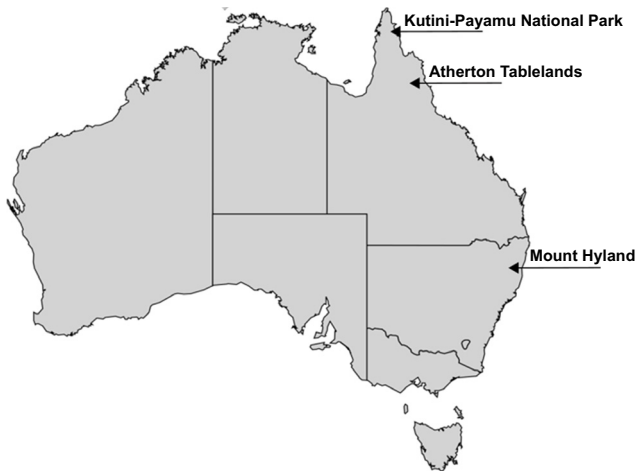

Fig. 2. Map illustrating the locations of our trapping sites.

to ensure accurate representation). Samples were either permanent-mounted or wet-mounted on glass slides and analysed at ×400 magnification to determine presence and species richness of fungal spores. To avoid reporting incidental consumption of spores that happened to be in the environment, only spores found to occur frequently (a minimum of five times) in each sample were considered, and these were identified on the basis of recognition of standard microscopic characters. Any ambiguous identities were confirmed through comparison with spores of identified fungal fruiting body collections made by the authors in the same or similar habitats. Given the large geographic range and the number of fungi in the region that remain undescribed, we did not attempt to refine the fungal identification beyond family or genus level. We would also prefer to underestimate, rather than overestimate, the significance of these animals as dispersers. Because we were focused on the diversity of fungi consumed by the rodents, we use some older nomenclatural concepts that help outline the diversity of taxa. For example, we mention the genera *Thaxterogaster* and *Quadrispora*. Taxonomic studies have shown that members of these historically sequestrate genera belong in *Cortinarius* (Gasparini 2014; Pastor *et al.* 2019; Nouhra *et al.* 2021). We agree with these taxonomic revisions, but in the context of this study, we mention these names in reference to spores that are members of the Cortinariaceae but have characters indicating that they are likely to belong to sequestrate taxa. The taxa that we list as *Cortinarius* could also be sequestrate, but we have no evidence to indicate their fruiting habits.

All analyses were performed in R ver. 4.0.3 (R Core Team 2020). Sites were designated as being either tropical (Atherton Tablelands and Kutini-Payamu) or temperate (New England Tablelands), and forest type was classed as either wet sclerophyll or rainforest. However, because forest type and latitude are interlinked, we combined these into a single factor ('habitat') that described both the forest type and its latitudinal position. For samples containing fungus, ANOVAs using the 'lmer' function in the packages lme4 and lmerTest were used to compare taxon richness per sample among rodent species and habitat (tropical wet sclerophyll forest, temperature wet sclerophyll forest and tropical rainforest). Season (summer, autumn, winter and spring, with each equinox/solstice marking seasonal cut-points) and year of collection were random effects in the model. *Post hoc* contrasts (Tukey) were performed using the package emmeans.

Multivariate analyses available in the package vegan (Oksanen *et al.* 2020) were used to explore trends in consumption of each individual fungal taxon among species, habitats and seasons. We first used the 'outlier' function to identify extreme outliers on the basis of nearest neighbour criterion (Wildi 2017); no outliers were identified. We then constructed a Bray–Curtis similarity matrix using presence–absence values for each of the 194 samples that contained fungi (rows) and the 29 taxa that occurred in the samples (columns) and applied non-metric multidimensional scaling (NMDS) to visualise and interpret these data. The NMDS was calculated using the function 'metaMDS' in the package vegan (Oksanen *et al.* 2020) within R (R Core Team 2020), using the Bray–Curtis dissimilarity matrix with weighted averages and a maximum number of 50 random starts. The function 'envfit' was then used to fit factors (species, season and habitat) to the ordination using 10 000 permutations, which showed associations between clusters of points and each factor. Data were plotted using the function 'ordellipse' that created ellipses encompassing the standard deviation of points coded by species, season and habitat, and 'ordspider' that overlaid a 'spider' diagram connecting each point to its group centroid (Oksanen *et al.* 2020).

To further visualise the differences in diet among species and habitats, we compiled a matrix of the percentage occurrence of fungal taxa in each mammal species × habitat combination, and then analysed these data by using hierarchical cluster based on Ward's minimum-variance method on a distance matrix computed using Euclidean distances. We used only winter (June–August) samples for this analysis, because winter captures contained the greatest diversity of fungus, and tropical sites were sampled only in winter. The results of the cluster analysis were displayed as an unrooted tree by using the function 'as.phylo' within the package 'Ape'.

Results

Patterns in dietary diversity

Across all sites, we had a total of 253 rodent captures, representing 10 rodent species. At sites in northern New South Wales, we trapped fawn-footed melomys (*Melomys*

cervinipes), bush rat (*Rattus fuscipes*), swamp rat (*Rattus lutreolus*) and Hastings River mouse (*Pseudomys oralis*). At the Atherton Tableland sites, we trapped fawn-footed melomys, house mouse (*Mus musculus*), bush rat, giant white-tailed rat (*Uromys caudimaculatus*) and common rock rat (*Zyzomys argurus*). At the sites in Kutini-Payamu, we trapped grassland melomys (*Melomys burtoni*), Cape York melomys (*Melomys capensis*), Cape York rat (*Rattus leucopus*) and giant white-tailed rat.

All species trapped in this study consumed fungi to varying degrees. We identified a total of 38 distinct spore types (taxa) across the sites (Table 1). Fungi were found to be an important dietary component; however, the levels of mycophagy and the taxa consumed depended on a combination of species of rodents and the habitat they occupied. Taxon richness per sample varied significantly with species ($F_{8,176}$ = 8.7, $P < 0.005$) and habitat ($F_{2,156}$ = 29.4, $P < 0.0001$). Species differences were driven by bush rats consuming significantly more fungal taxa than fawn-footed melomys ($P < 0.0001$), Hastings River mice ($P = 0.002$), swamp rats ($P = 0.02$) and common rock rats ($P = 0.005$), and rock rats consuming significantly more taxa than giant white-tailed rats ($P = 0.007$). Samples from rodents inhabiting tropical rainforest sites also contained fewer fungi than those from either tropical wet sclerophyll forest or temperate wet sclerophyll forest ($P < 0.0001$), and what fungi they did eat were predominately Glomeromycota. When members of the Glomeromycota were present in scats, they were usually in large numbers, which led us to believe that this represented deliberate consumption of this group. There was no significant difference in the number of fungal taxa per sample from rodents inhabiting either tropical or temperate wet sclerophyll forest ($P = 0.43$), and at these sites, ectomycorrhizal fungi were the most common fungi in rodent diets. The majority of fungal taxa consumed belong to groups that form sequestrate and/or hypogeous fruiting morphologies.

Non-metric multidimensional scaling (2D stress = 0.11) showed significant differences in dietary composition among the different species of rodents (r^2 = 0.28; $P < 0.001$; Fig. 3*a*), but the strongest differences were with season (r^2 = 0.42; $P < 0.001$; Fig. 3*b*), driven by winter diets being distinct from diets in other seasons (Fig. 3*b*), and habitat (r^2 = 0.33; $P < 0.001$; Fig. 3*c*), where there were clear differences among diets in the three habitat types (Fig. 3*c*).

Cluster analysis (which included only winter diets) identified several distinct clusters primarily on the basis of a combination of species and habitat (Fig. 4). The diet of bush rats, irrespective of habitat, clustered with temperate wet sclerophyll diets of Hastings River mice and fawn-footed melomys. Tropical wet sclerophyll diets and tropical rainforest diets formed largely distinct clusters, with the exception of Cape York melomys from rainforest clustering with tropical sclerophyll diets of other rodents.

Mycophagy by other mammals

In the process of conducting fieldwork, we also sampled seven additional mammals (all marsupials) as a result of accidental captures or finding roadkill. At the site in New South Wales, we sampled three brown antechinus (*Antechinus stuartii*; one individual consumed fungi), one long-nosed bandicoot (*Perameles nasuta*; consumed fungi), one red-legged pademelon (*Thylogale stigmatica*; consumed fungi) and one mountain brushtail possum (*Trichosurus cunninghami*; did not consume fungi). In northern Queensland, we sampled five northern bettongs (*Bettongia tropica*; all consumed fungi) and eight northern brown bandicoots (*Isoodon macrourus*; five consumed fungi). At the site on Cape York, we sampled one northern brown bandicoot (*I. macrourus*; consumed fungi) and one red-cheeked dunnart (*Sminthopsis virginiae*; did not consume fungi). We mention these incidental observations because they add to knowledge about mycophagy among Australian mammals and show that marsupials, alongside rodents, are mycophagists in these systems. Multiple previous studies have been conducted to investigate and/or review mycophagy among many of these taxa (e.g. Claridge and May 1994; Reddell *et al.* 1997; Vernes *et al.* 2015; Nuske *et al.* 2017*a*, 2017*b*; Elliott *et al.* 2022).

Discussion

Our study is the most comprehensive study to date of fungal consumption by rodents in Australia, both in terms of the number of rodent taxa studied and the geographical breadth covered by our sampling. The results showed that rodents are dispersing a great diversity of fungal spores in both tropical and temperate forest communities in eastern Australia, and that many different species of rodents are consumers of sequestrate fungi. For two of these, the grassland melomys and Cape York melomys, our work is the first to demonstrate fungal consumption. Some species such as the bush rat and fawn-footed melomys are widespread, and occurred at both our tropical and temperate study sites, in both wet sclerophyll forest and rainforest. These rodents demonstrated that fungi are eaten from temperate regions through to the tropics, but that consumption was strongly influenced by habitat type, with eucalypt-dominated forest returning much greater dietary richness of fungi than tropical rainforest.

Our study provided a snapshot of fungal consumption during the height of the 2019 and 2020 fruiting season. Fungal consumption by mammals in eastern Australia has been shown by multiple studies to vary among seasons, and to peak in winter (Taylor 1992; Vernes *et al.* 2001, 2015; Vernes 2014; Elliott *et al.* 2020). Cluster analysis of winter samples demonstrated a strong clustering of murid species on the basis of the habitat type from which they came, with clusters being most closely tied to forest type, rather than

Table 1. Percentage occurrence of fungal taxa in mammal diets from the three major habitat types (calculated from scats that contained fungus).

Fungal taxon	Habitat													
	Temperate wet sclerophyll				Tropical rainforest						Tropical wet sclerophyll			
	Mammal species													
	M. cervinipes (42)	*P. oralis* (10)	*R. fuscipes* (75)	*R. lutreolus* (17)	*M. burtoni* (9)	*M. capensis* (26)	*M. cervinipes* (4)	*R. fuscipes* (19)	*R. leucopus* (9)	*U. caudimaculatus* (9)	*M. cervinipes* (1)	*R. fuscipes* (4)	*U. caudimaculatus* (10)	*Z. argurus* (13)
Agaricoid	–	–	1.4	–	–	–	–	–	–	–	–	–	–	–
Amylascus	–	–	8.5	–	–	–	–	–	–	–	–	–	20.0	8.3
Mesophelliaceae	2.8	12.5	9.9	–	–	–	–	–	–	–	33.3	75.0	70.0	50.0
Aroramyces 1	–	–	1.4	–	–	–	–	–	–	–	33.3	–	20.0	41.7
Ascomycete (Dicina-like)	–	–	7.0	–	–	–	–	–	–	–	–	–	–	–
Austrogautieria	–	–	5.6	–	–	–	–	–	–	–	16.7	50.0	30.0	–
Boletoid	11.1	–	2.8	–	–	–	–	–	–	–	50.0	75.0	90.0	8.3
Cortinarius	13.9	–	12.7	–	–	–	–	5.9	–	–	–	–	–	–
Cortinarius (*Quadrispora*)	–	–	2.8	–	–	–	–	–	–	–	–	–	–	–
Cortinarius (*Thaxterogaster*)	33.3	12.5	16.9	–	–	9.1	–	–	16.7	–	–	–	–	–
Descomyces Cape York	–	–	–	–	–	9.1	–	–	–	–	–	–	–	–
Descomyces	16.7	62.5	43.7	72.7	100.0	–	–	–	–	–	–	–	10.0	–
Descomyces stolatus	–	–	1.4	–	–	–	–	–	–	–	–	–	–	–
Descomyces thick-walled	–	–	32.4	–	–	–	–	–	–	–	–	–	–	–
Descomyces 2 (skirt)	–	–	12.7	18.2	–	–	–	–	–	–	–	–	10.0	8.3
Descomyces 5 (short warty)	–	12.5	8.5	9.1	–	–	–	–	–	–	–	–	–	–
Entoloma	–	–	–	–	–	–	–	11.8	–	–	–	–	–	–
Dingleya	–	–	28.2	–	–	–	–	–	–	–	–	–	–	–
Elaphomyces	–	–	9.9	–	–	–	–	–	–	–	–	–	–	25.0
Glomeromycota	69.4	–	9.9	9.1	–	72.7	100.0	94.1	100.0	–	66.7	100.0	40.0	25.0

(*Continued on next page*)

Table 1. (*Continued*).

Fungal taxon	Habitat													
	Temperate wet sclerophyll				Tropical rainforest						Tropical wet sclerophyll			
	Mammal species													
	M. cervinipes (42)	*P. oralis* (10)	*R. fuscipes* (75)	*R. lutreolus* (17)	*M. burtoni* (9)	*M. capensis* (26)	*M. cervinipes* (4)	*R. fuscipes* (19)	*R. leucopus* (9)	*U. caudimaculatus* (9)	*M. cervinipes* (1)	*R. fuscipes* (4)	*U. caudimaculatus* (10)	*Z. argurus* (13)
Hydnangium	5.6	25.0	8.5	18.2	–	–	–	–	–	–	–	–	10.0	–
Hysterangium	44.4	–	43.7	–	–	–	–	–	–	–	66.7	50.0	90.0	83.3
Labyrinthomyces	–	–	4.2	–	–	–	–	11.8	–	–	16.7	50.0	30.0	–
Leucogaster	–	–	2.8	–	–	–	–	–	–	–	–	–	–	–
Octaviania	–	–	9.9	–	–	–	–	–	–	–	–	–	–	–
Rossbeevera	19.4	–	15.5	18.2	–	9.1	–	–	–	–	–	25.0	–	–
Russulaceae	8.3	37.5	74.6	54.5	–	18.2	–	5.9	–	–	16.7	25.0	50.0	–
Sclerogaster	2.8	–	1.4	–	–	–	–	–	–	–	–	25.0	–	–
Number of fungal taxa	11	6	26	7	1	5	1	5	2	0	8	9	12	8
% Occurrence of fungus	85.7	80.0	94.7	64.7	11.1	42.3	100.0	89.5	66.7	0.0	85.7	100.0	100.0	92.3

Total taxa in diets, and percentage occurrence of fungus in all scats are also shown. Numbers in parentheses indicates total number of samples analysed for each species in each habitat.

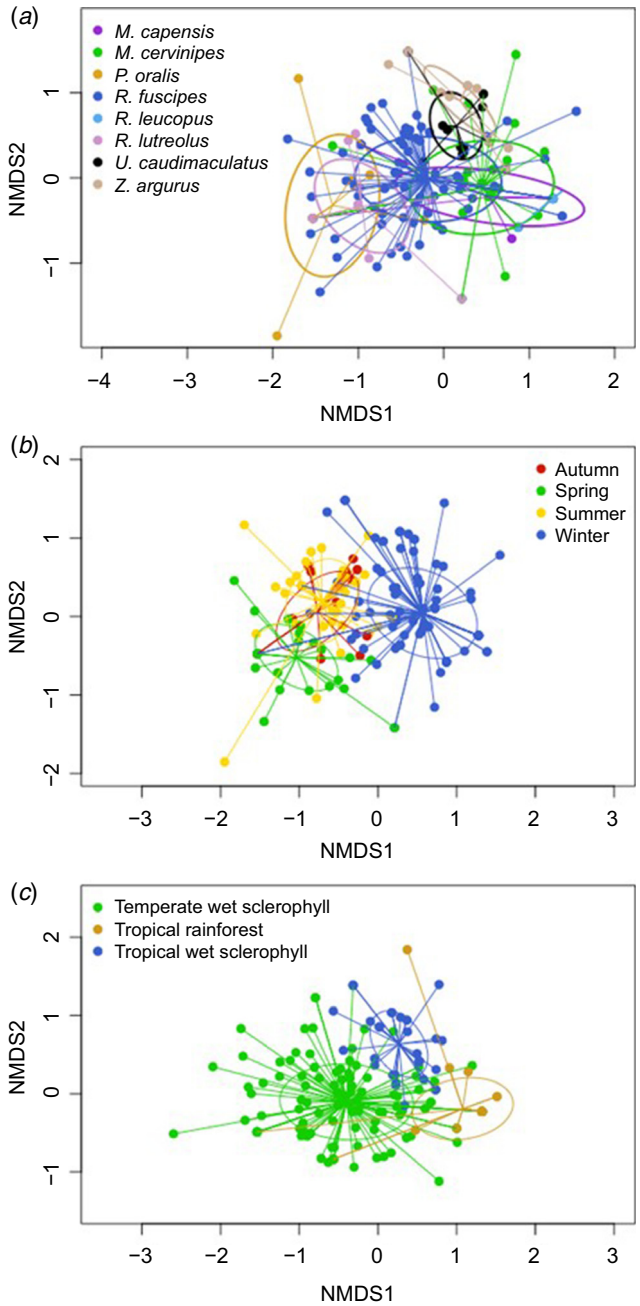

Fig. 3. Non-metric multidimensional scaling (NMDS) plot of Bray–Curtis dissimilarity coefficients for each sample of a rodent diet. Ellipses encompass the standard deviation of points coded by (*a*) rodent species, (*b*) season, or (*c*) habitat. Straight lines connect each point to its group centroid.

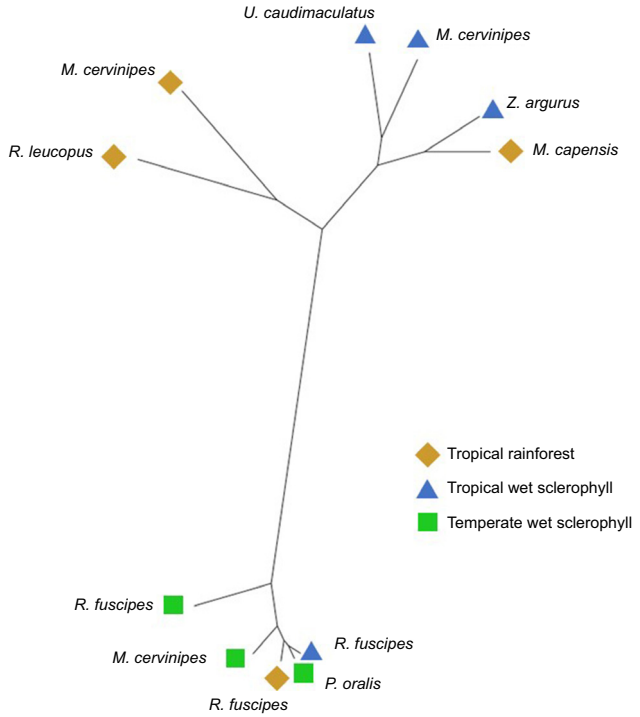

Fig. 4. Unrooted tree of winter rodent diets in different habitats using Euclidean distances. Each branch on the tree represents the percentage occurrence of fungal taxa in each mammal species × habitat combination.

species, or geographical location (i.e. temperate or tropical). However, there were some exceptions. Bush rats from tropical rainforest, tropical wet sclerophyll forest, and temperate wet sclerophyll forest clustered with other rodents from temperate wet sclerophyll forest, whereas the Cape York melomys (*M. capensis*) from tropical rainforest clustered with other rodents from tropical wet sclerophyll forest. These results indicated two things. First, bush rats are well known mycophagists, with several studies showing that they are probably among the most mycophagous of Australian rodents (Vernes and Dunn 2009; Nuske *et al.* 2017*b*). Because of the great diversity of taxa in their diet irrespective of habitat type, they clustered with rodents from the forest type that also collectively returned the greatest fungal diversity. Second, this observation is likely to indicate that both *R. fuscipes* and *M. capensis* had a relatively higher fungal consumption than did other rainforest rodents, and probably indicates that they foraged more widely than the other rainforest species, extending their movements into adjacent sclerophyll forest dominated by ectomycorrhizal taxa. Vernes and Dunn (2009) showed that in north-eastern New South Wales, *R. fuscipes* moved across rainforest boundaries and was spreading fungal spores through its mycophagous feeding habits.

Although difficult to prove within the context of this study, seasonal changes in fungal consumption are likely to be a reflection of food availability rather than preference. For example, the mammal community in Kutini-Payamu was the least mycophagous within our study. These differences could be due to seasonality, but we suspect that habitat is likely to be a more significant factor. We believe this in part because a long-term study of the long-nosed echymipera (*Echymipera rufescens*) in Kutini-Payamu

(Shevill 1999; Shevill and Johnson 2007) showed that fungal consumption by this species tended to peak in September.

There is substantial experimental data indicating that mycorrhizal fungal spores survive transit through the digestive system of various Australian murid rodents (McGee and Baczocha 1994; Reddell *et al.* 1997), as well as rodents in other regions of the world (Trappe and Maser 1976; Colgan and Claridge 2002; Caldwell *et al.* 2005; Ori *et al.* 2018; Elliott *et al.* 2022). We found no evidence in the literature that the digestive system of rodents or any other mammal prevents the germination of fungal spores. On the basis of our microscopic analysis of spores, we saw no evidence of spore degradation that would negatively affect spore germination rates. Three of the species we include in this study, fawn-footed melomys, bush rat and giant white-tailed rat, have been experimentally shown to pass viable mycorrhizal spores (Reddell *et al.* 1997) and it is highly likely that the other seven species share this ability.

The movement pattern and passage rate of an animal directly affect its spore dispersal potential. These factors inevitably vary among individuals and species, but larger mammals generally have greater movement patterns, larger home ranges and slower passage rates compared with smaller mammals (Swihart *et al.* 1988; Danks 2012). The giant white-tailed rat (*U. caudimaculatus*) was the largest species in our study; although we are unaware of any detailed studies examining the size of its home range, Wellesley-Whitehouse (1983) reported that an individual travelled 500 m overnight between trap sites. Further study of more individuals in more areas will likely show a greater range in movement patterns. The mean retention time of fungal spores for this species is 48.4 h, and some spores linger as long as 120 h in the digestive system (Comport and Hume 1998). Giant white-tailed rats have the potential to disperse fungal spores at least 500 m in a night, and depending on maximum retention times and movement patterns, they could likely disperse spores much farther over the 120 h window. More data are needed to accurately estimate maximum dispersal potential. Movement patterns and passage rates of the other rodent species in our study vary, but they are generally poorly studied. Smaller rodents would typically have faster passage rates, which would be likely to translate into smaller potential dispersal areas. However, the ecological importance of small versus large dispersal distances may balance out if estimates account for species abundance and distribution. The Hastings River mouse (*P. oralis*) was estimated to retain fungal spores up to 95–100 h after ingestion and to move spores as far as 1256 m (Elliott *et al.* 2020). It is important to remember that this does not mean 1256 m from the point of ingestion, but is within the species' home range. We suspect that given their slightly smaller size, the three *Rattus* species in this study would have a dispersal potential similar to but slightly smaller than what was calculated for *P. oralis*. The other five even smaller species we examined would be likely to have a dispersal potential smaller than that of the *Rattus* spp. More data on passage rates and movement patterns are needed to reliably estimate or model the dispersal potential of these rodents and their impacts on mycorrhizal fungal distribution.

Fungal spore dispersal distance has been modelled only for swamp wallabies (*Wallabia bicolor*); despite their much larger size, this species' maximum spore dispersal distance was estimated to be 1265 m from the point of ingestion (Danks *et al.* 2020). Regardless of the specifics of how far rodents are dispersing fungal spores, it is apparent that they are regularly moving mycorrhizal fungi at least hundreds of metres from where they are ingested. This is ecologically significant because many of the mycorrhizal fungi they eat form sequestrate fruiting bodies that are enclosed in a skin and often fruit below the soil surface (Maser *et al.* 2008). This fruiting habit makes the fungi reliant on animals for spore dispersal, and having their spores moved even a few metres from where they were fruiting is significant for their dispersal and the associated plant communities.

Our study highlights the importance of murid rodents in maintaining healthy mycorrhizal fungal communities through the consumption of a diversity of fungal taxa and subsequent dispersal of these fungi through their scats. With extinctions and/or losses in the abundance of many mycophagous marsupial communities (Nuske *et al.* 2017*a*), it is important to understand the key ecosystem services provided by Australian rodent communities. We urge researchers working with murids and other rodents in Australia and beyond to direct more attention toward understanding the fungal components of these animals' diets. In most regions of the world, only a handful of rodent species have been thoroughly studied and are recognised as being highly important mycophagous species and spore dispersers (Fogel and Trappe 1978; Elliott *et al.* 2022). There are hundreds of other rodent species that are likely to be equally important but remain unrecognised as spore dispersers. We hope this study of murid rodent mycophagy will stimulate more research interest into rodent mycophagy around the world.

References

Caiafa MV, Jusino MA, Wilkie AC, Díaz IA, Sieving KE, Smith ME (2021) Discovering the role of Patagonian birds in the dispersal of truffles and other mycorrhizal fungi. *Current Biology* **31**, 5558–5570.e3. doi:10.1016/j.cub.2021.10.024

Caldwell I, Vernes KA, Barlocher F (2005) The northern flying squirrel (*Glaucomys sabrinus*) as a vector for inoculation of red spruce (*Picea rubens*) seedlings with ectomycorrhizal fungi. *Sydowia* **57**, 166–178.

Cázares E, Trappe JM (1994) Spore dispersal of ectomycorrhizal fungi on a glacier forefront by mammal mycophagy. *Mycologia* **86**, 507–510. doi:10.1080/00275514.1994.12026443

Claridge AW, May TW (1994) Mycophagy among Australian mammals. *Australian Journal of Ecology* **19**, 251–275. doi:10.1111/j.1442-9993.1994.tb00489.x

Colgan W III, Claridge AW (2002) Mycorrhizal effectiveness of *Rhizopogon* spores recovered from faecal pellets of small forest-dwelling mammals. *Mycological Research* **106**, 314–320. doi:10.1017/S0953756202005634

Comport SS, Hume ID (1998) Gut morphology and rate of passage of fungal spores through the gut of a tropical rodent, the giant white-tailed rat (*Uromys caudimaculatus*). *Australian Journal of Zoology* **46**, 461–471. doi:10.1071/ZO98053

Cove MV, Simons TR, Gardner B, Maurer AS, O'Connell AF (2017) Evaluating nest supplementation as a recovery strategy for the endangered rodents of the Florida Keys. *Restoration Ecology* **25**, 253–260. doi:10.1111/rec.12418

Danks MA (2012) Gut-retention time in mycophagous mammals: a review and a study of truffle-like fungal spore retention in the swamp wallaby. *Fungal Ecology* **5**, 200–210. doi:10.1016/j.funeco.2011.08.005

Danks MA, Simpson N, Elliott TF, Paine CET, Vernes K (2020) Modeling mycorrhizal fungi dispersal by the mycophagous swamp wallaby (*Wallabia bicolor*). *Ecology and Evolution* **10**, 12920–12928. doi:10.1002/ece3.6873

Dundas SJ, Hopkins AJM, Ruthrof KX, Tay NE, Burgess TI, Hardy GESJ, Fleming PA (2018) Digging mammals contribute to rhizosphere fungal community composition and seedling growth. *Biodiversity and Conservation* **27**, 3071–3086. doi:10.1007/s10531-018-1575-1

Elliott TF, Marshall PA (2016) Animal-fungal interactions 1: notes on bowerbird's use of fungi. *Australian Zoologist* **38**, 59–61. doi:10.7882/AZ.2015.032

Elliott TF, Vernes K (2021) Notes on the diets of four rodent species from Goodenough Island. *Australian Mammalogy* **43**, 256–259. doi:10.1071/AM20022

Elliott TF, Jusino MA, Trappe JM, Lepp H, Ballard G-A, Bruhl JJ, Vernes K (2019*a*) A global review of the ecological significance of symbiotic associations between birds and fungi. *Fungal Diversity* **98**, 161–194. doi:10.1007/s13225-019-00436-3

Elliott TF, Bower DS, Vernes K (2019*b*) Reptilian mycophagy: a global review of mutually beneficial associations between reptiles and macrofungi. *Mycosphere* **10**, 776–797. doi:10.5943/mycosphere/10/1/18

Elliott TF, Townley S, Johnstone C, Meek P, Gynther I, Vernes K (2020) The endangered Hastings River mouse (*Pseudomys oralis*) as a disperser of ectomycorrhizal fungi in eastern Australia. *Mycologia* **112**, 1075–1085. doi:10.1080/00275514.2020.1777383

Elliott TF, Truong C, Jackson S, Zúñiga CL, Trappe JM, Vernes K (2022) Mammalian mycophagy: a global review of ecosystem interactions between mammals and fungi. *Fungal Systematics and Evolution* **9**, 99–159. doi:10.3114/fuse.2022.09.07

Firth RSC, Brook BW, Woinarski JCZ, Fordham DA (2010) Decline and likely extinction of a northern Australian native rodent, the Brush-tailed Rabbit-rat *Conilurus penicillatus*. *Biological Conservation* **143**, 1193–1201. doi:10.1016/j.biocon.2010.02.027

Fogel R, Trappe JM (1978) Fungus consumption (mycophagy) by small animals. *Northwest Science* **52**, 1–31.

Gasparini B (2014) *Cortinarius* (Agaricales) revised taxonomy: new species names or combinations. *Mycosphere* **5**, 541–544. doi:10.5943/mycosphere/5/4/6

Hamilton MJ, Leslie DM Jr (2021) Celebrating five decades of Mammalian Species, highlighted by the publication of the 1,000th account. *Journal of Mammalogy* **102**, 681–684. doi:10.1093/jmammal/gyab061

Johnson CN (1996) Interactions between mammals and ectomycorrhizal fungi. *Trends in Ecology & Evolution* **11**, 503–507. doi:10.1016/S0169-5347(96)10053-7

Maser C, Claridge AW, Trappe JM (2008) 'Trees, truffles, and beasts: how forests function.' (Rutgers University Press: New Brunswick, NJ, USA)

McGee PA, Baczocha N (1994) Sporocarpic Endogonales and Glomales in the scats of *Rattus* and *Perameles*. *Mycological Research* **98**, 246–249. doi:10.1016/S0953-7562(09)80193-7

Miranda V, Rothen C, Yela N, Aranda-Rickert A, Barros J, Calcagno J, Fracchia S (2019) Subterranean desert rodents (genus *Ctenomys*) create soil patches enriched in root endophytic fungal propagules. *Microbial Ecology* **77**, 451–459. doi:10.1007/s00248-018-1227-8

Nouhra E, Kuhar F, Truong C, Pastor N, Crespo E, Mujic A, Caiafa MV, Smith ME (2021) *Thaxterogaster* revisited: a phylogenetic and taxonomic overview of sequestrate Cortinarius from Patagonia. *Mycologia* **113**, 1022–1055. doi:10.1080/00275514.2021.1894535

Nuske SJ, Vernes K, May TW, Claridge AW, Congdon BC, Krockenberger A, Abell SE (2017*a*) Redundancy among mammalian fungal dispersers and the importance of declining specialists. *Fungal Ecology* **27**, 1–13. doi:10.1016/j.funeco.2017.02.005

Nuske SJ, Vernes K, May TW, Claridge AW, Congdon BC, Krockenberger A, Abell SE (2017*b*) Data on the fungal species consumed by mammal species in Australia. *Data in Brief* **12**, 251–260. doi:10.1016/j.dib.2017.03.053

Nuske SJ, Anslan S, Tedersoo L, Congdon BC, Abell SE (2019) Ectomycorrhizal fungal communities are dominated by mammalian dispersed truffle-like taxa in north-east Australian woodlands. *Mycorrhiza* **29**, 181–193. doi:10.1007/s00572-019-00886-2

Oksanen J, Guillaume Blanchet F, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Szoecs E, Wagner H (2020) vegan: community ecology package. R package version 2.5-7. Available at https://CRAN.R-project.org/package=vegan

Ori F, Trappe J, Leonardi M, Iotti M, Pacioni G (2018) Crested porcupines (*Hystrix cristata*): mycophagist spore dispersers of the ectomycorrhizal truffle *Tuber aestivum*. *Mycorrhiza* **28**, 561–565. doi:10.1007/s00572-018-0840-1

Pastor N, Chiapella J, Kuhar F, Mujic AB, Crespo EM, Nouhra ER (2019) Unveiling new sequestrate *Cortinarius* species from northern Patagonian Nothofagaceae forests based on molecular and morphological data. *Mycologia* **111**, 103–117. doi:10.1080/00275514.2018.1537350

R Core Team (2020) 'R: a language and environment for statistical computing.' (R Foundation for Statistical Computing: Vienna, Austria). Available at https://www.R-project.org/

Reddell P, Spain AV, Hopkins M (1997) Dispersal of spores of mycorrhizal fungi in scats of native mammals in tropical forests of northeastern Australia. *Biotropica* **29**, 184–192. doi:10.1111/j.1744-7429.1997.tb00023.x

Roycroft E, MacDonald AJ, Moritz C, Moussalli A, Portela Miguez R, Rowe KC (2021) Museum genomics reveals the rapid decline and extinction of Australian rodents since European settlement. *Proceedings of the National Academy of Sciences* **118**, e2021390118. doi:10.1073/pnas.2021390118

Shevill DI (1999) 'The ecology of the Rufus Spiny Bandicoot, Echymipera rufescens australis (Peters and Doria) (Marsupialia: Peramelidae) in Lowland Rainforest of Iron Range National Park, Cape York Peninsula.' (James Cook University, School of Tropical Biology)

Shevill DI, Johnson CN (2007) Diet and breeding of the rufous spiny bandicoot *Echymipera rufescens* australis, Iron Range, Cape York Peninsula. *Australian Mammalogy* **29**, 169–175. doi:10.1071/AM07021

Smith AP, Quin DG (1996) Patterns and causes of extinction and decline in Australian conilurine rodents. *Biological Conservation* **77**, 243–267. doi:10.1016/0006-3207(96)00002-X

Stephens RB, Rowe RJ (2020) The underappreciated role of rodent generalists in fungal spore dispersal networks. *Ecology* **101**, e02972. doi:10.1002/ecy.2972

Stephens RB, Trowbridge AM, Ouimette AP, Knighton WB, Hobbie EA, Stoy PC, Rowe RJ (2020) Signaling from below: rodents select for deeper fruiting truffles with stronger volatile emissions. *Ecology* **101**, e02964. doi:10.1002/ecy.2964

Swihart RK, Slade NA, Bergstrom BJ (1988) Relating body size to the rate of home range use in mammals. *Ecology* **69**, 393–399. doi:10.2307/1940437

Taylor RJ (1992) Seasonal changes in the diet of the Tasmanian bettong (*Bettongia gaimardi*), a mycophagous marsupial. *Journal of Mammalogy* **73**, 408–414. doi:10.2307/1382076

Tedersoo L, May TW, Smith ME (2010) Ectomycorrhizal lifestyle in fungi: global diversity, distribution, and evolution of phylogenetic lineages. *Mycorrhiza* **20**, 217–263. doi:10.1007/s00572-009-0274-x

Thiers HD (1984) The secotioid syndrome. *Mycologia* **76**, 1–8. doi:10.1080/00275514.1984.12023803

Trappe JM, Maser C (1976) Germination of spores of *Glomus macrocarpus* (Endogonaceae) after passage through a rodent digestive tract. *Mycologia* **68**, 433–436. doi:10.1080/00275514.1976.12019927

Valentine LE, Ruthrof KX, Fisher R, Hardy GESJ, Hobbs RJ, Fleming PA (2018) Bioturbation by bandicoots facilitates seedling growth by altering soil properties. *Functional Ecology* **32**, 2138–2148. doi:10.1111/1365-2435.13179

Vašutová M, Mleczko P, López-García A, Maček I, Boros G, Ševčík J, Fujii S, Hackenberger D, Tuf IH, Hornung E, Páll-Gergely B, Kjøller R (2019) Taxi drivers: the role of animals in transporting mycorrhizal fungi. *Mycorrhiza* **29**, 413–434. doi:10.1007/s00572-019-00906-1

Vernes K (2014) Seasonal truffle consumption by long-nosed bandicoots (*Perameles nasuta*) in a mixed rainforest–open forest community in north-eastern New South Wales. *Australian Mammalogy* **36**, 113–115. doi:10.1071/AM13040

Vernes K, Dunn L (2009) Mammal mycophagy and fungal spore dispersal across a steep environmental gradient in eastern Australia. *Austral Ecology* **34**, 69–76. doi:10.1111/j.1442-9993.2008.01883.x

Vernes K, McGrath K (2009) Are introduced black rats (*Rattus rattus*) a functional replacement for mycophagous native rodents in fragmented forests? *Fungal Ecology* **2**, 145–148. doi:10.1016/j.funeco.2009.03.001

Vernes K, Castellano M, Johnson CN (2001) Effects of season and fire on the diversity of hypogeous fungi consumed by a tropical mycophagous marsupial. *Journal of Animal Ecology* **70**, 945–954. doi:10.1046/j.0021-8790.2001.00564.x

Vernes K, Cooper T, Green S (2015) Seasonal fungal diets of small mammals in an Australian temperate forest ecosystem. *Fungal Ecology* **18**, 107–114. doi:10.1016/j.funeco.2015.09.015

Vernes K, Elliott TF, Jackson SM (2021) 150 years of mammal extinction and invasion at Koonchera Dune in the Lake Eyre Basin of South Australia. *Biological Invasions* **23**, 593–610. doi:10.1007/s10530-020-02387-2

Waller NL, Gynther IC, Freeman AB, Lavery TH, Leung LK-P (2017) The Bramble Cay melomys Melomys rubicola (Rodentia: Muridae): a first mammalian extinction caused by human-induced climate change? *Wildlife Research* **44**, 9–21. doi:10.1071/WR16157

Wellesley-Whitehouse H (1983) White-tailed rat *Uromys caudimaculatus*. In 'The Australian Museum complete book of Australian Mammals'. (Ed. R Strahan) pp. 371. (Angus and Robertson: Sydney, NSW, Australia)

Wildi O (2017) 'Data analysis in vegetation ecology.' 3rd edn. (CABI: Wallingford, UK)

Wilson DE, Lacher TE, Mittermeier RA (Eds) (2017) 'Handbook of the mammals of the world. Vol. 7. Rodents II.' (Lynx Editions: Barcelona, Spain)

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