ResearchOnline@JCU

This file is part of the following reference:

Nuske, Susan Joy (2017) *The importance of declining mammalian fungal specialists for ectomycorrhizal fungal dispersal.* PhD thesis, James Cook University.

Access to this file is available from:

https://researchonline.jcu.edu.au/51587/

The author has certified to JCU that they have made a reasonable effort to gain permission and acknowledge the owner of any third party copyright material included in this document. If you believe that this is not the case, please contact ResearchOnline@jcu.edu.au and quote **https://researchonline.jcu.edu.au/51587/**

JAMES COOK UNIVERSITY AUSTRALIA

The importance of declining mammalian fungal specialists for ectomycorrhizal fungal dispersal

Thesis submitted by

Susan Joy Nuske BSc Hons University of Queensland

in October 2017

For the degree of Doctor of Philosophy

in the College of Science and Engineering

James Cook University

Declaration

I declare that this thesis is my own work and has not been submitted in any form for another degree or diploma at any university or other institution of tertiary education.

Information derived from the published or unpublished work of others has been acknowledged in the text and a list of references is given.

Every reasonable effort has been made to gain permission and acknowledge the owners of copyright material. I would be pleased to hear from any copyright owner who has been omitted or incorrectly acknowledged.

Signed, Susan Nuske.

Acknowledgements

This thesis is part of a larger project, working on the population status and conservation of northern bettongs (*Bettongia tropica*) in collaboration with James Cook University, Queensland Government (Queensland Parks and Wildlife Service, Department of National Parks, Sport and Racing; Threatened Species Unit, Department of Environment and Heritage Protection), and WWF-Australia. The project was funded through the Australian Government's Caring for Our Country grants program which was administered by WWF. There are also many other people and organisations that have contributed either monetarily or in-kind to this thesis. Without the combined, wonderful work of all these partners this thesis would not have been possible. As such, there are many people worthy of a very sincere thank-you.

Firstly, thank-you to my supervisors, Sandra Abell, Brad Congdon and Andrew Krockenberger for their countless hours of discussions, emails, laughs and occasionally, tears. Thank-you also to Jessica Koleck, WWF-Australia Bettong Project Coordinator, for your tireless work and keeping me sane in tough working conditions. Massive thank-you to the other students and techs who were fellow mid-night bettong trappers: Stephanie Todd, Naomi Bowie, Elise Chatterton, Jess Koleck (again) and Tegan Whitehead. Also, thank-you to the National Park rangers, Rob Miller, Lana Little, Jack Cosgrove, Karl Goetze, Chris White, Julie Bunny and Miki Bradley. Thank-you also to Jane McDonald from EHP for your insightful discussions and support.

Thank-you to Darren Crayn from the Australian Tropical Herbarium for your support and use of facilities. Thank-you to Melissa Harrison, ATH lab manager, for always allowing time for the simple questions and your valuable advice.

A huge thank-you to our collaborators from The University of Tartu, Estonia, Leho Tedersoo and Sten Anslan. Leho, thank-you for your invitation to work in your lab. Your advice and patience with my many questions was invaluable. Sten, thanks for tireless work in the field and invaluable bioinformatics expertise! Your offer of help with the bioinformatics saved me a massive learning-curve and a lot of time! Thank-you also to others from the lab at U of Tartu that made the experience productive, fun and unforgettable; Rebeca Casique, He Jin Jong, Elia Ambrosio, Heidi Tamm, Rasmus Puusepp, Sergei Polme, Ingrid Liiv, among others.

Thank-you to my co-authors for providing valuable advice and insights into this fascinating topic (Karl Vernes, Andrew Claridge and Tom May). Thanks again to Karl and Tom and to Chris Johnson for providing unpublished mycophagy data. Many thanks to Melissa Danks and Austin O'Malley for providing further details from their mycophagy studies to aid data collection for Chapter Two. Thank-you Jim Trappe for patiently answering many questions and being very welcoming into this mycological world.

Thank-you also to the wonderful people at the Wet Tropics Management Authority, the Australasian Mycological Society, the North Queensland Wildlife Trust and Skyrail Rainforest Fountain for providing minor monetary support throughout this project.

Many thanks to the tireless volunteers from all the field trips (in no particular order): Anton Moiseev, Megan Comerford, Sinead Bryant, Gabrielle Davidson, Sarah Hart, Di O'Rorke, Elliot Budd, Leanne Hales, Ori Albert-Mitchell, Marco Cucinelli, Maree

Baade, Mike Griggs, Paul Hales, Russell Best, Terry Purkiss, Elly Hetlam, Hiromu Nakamura, Umi Purnamasari, Raoul Alba, Rachel Barr, David Thomas, Hannah Thomas, Kath Kinneally, Andrew Krumins, Derek Preston, Vanessa Walker, Genevieve Buckton, Luke Windle, Elizabeth Lovett, Avril Underwood, Kaylene Bransgrove, Mark Bonner, Stu Biggs, Kelly Lambert, Annaliese Johnson, Melinda Greenfield, Claudia Paz.

Special thanks to Rhona Macdonald for sticking with me for the hot, humid and down-right ick conditions for almost two months! Thank-you also to the inspiring photographers Jurgen Freund and Stella Chiu-Freund who weren't afraid to dig in the dirt with me, was excited alongside me in finding truffles and saved us many hours of driving by allowing me to store soil samples in their freezer! I also thank Amberlee Hatcher and Harriet Allen for literally helping with the dirty work in the lab (yes, including the poo!).

Many people I would also like to thank for contributing to my ever-increasing knowledge of these beautiful ecosystems. Thank-you to David Tng, plant kingdom King, who taught me how to identify the trees and shrubs in my plots and elsewhere. A massive thank-you to Nigel Fechner, who contributed much to my understanding of fungi and their mysterious, elusive names (while never keeping a straight face). Thank-you to all the members of the Queensland Mycological Society (particularly, Pat Leonard, Fran Guard, Megan Prance and Susie Webster) who make fungi-finding fun, and welcomed a fellow myco-nerd in their mix. At the beginning of my adventure into fungi-world QMS provided valuable lessons at their workshops and forays.

A massive thank-you also to the council members of the Australasian Mycological Society (John Dearnaley, Julianne Djordjevic, Celeste Linde, Leona Campbell, Bevan Weir, Jeff Powell and Dee Carter). It was a fantastic experience to be the first Student Representative for the society. Thank-you especially to Past President, Diana Leemon who was instrumental in creating the role.

Humungous thanks to my friends (you know who you are), who provided me with much needed laughs and support throughout.

Last, but by no means least, massive and heart-felt thank-you to my partner, Mark Bonner and my family. You were there and continue to be so throughout this tumultuous journey. Thank-you for believing in me.

Northern bettong, *Bettongia tropica*, eating a truffle

Photo credit: Stephanie Todd.

Statement of the Contribution of Others

Item	Contribution	Name (affiliation)
Intellectual support	Proposal writing	**Dr. Sandra Abell** (primary advisor) **Dr. Brad Congdon** (secondary advisor) **Dr. Andrew Krockenberger** (third advisor)
	Statistical support	**Dr. Sandra Abell** **Dr. Brad Congdon**
	Editorial assistance	**Dr. Sandra Abell** **Dr. Brad Congdon** **Dr. Andrew Krockenberger**
	Co-authored accepted papers	**Dr. Karl Vernes**, Ecosystem Management, University of New England, Armidale NSW 2351 Australia **Dr. Tom May**, Royal Botanic Gardens Victoria, Melbourne, VIC 3004 Australia **Dr. Andrew Claridge**, Office of Environment and Heritage, NSW National Parks and Wildlife Service, Nature Conservation Section, P.O. Box 733, Queanbeyan, NSW 2620, Australia; School of Physical, Environmental and Mathematical Sciences, The University of New South Wales at Canberra, Northcott Drive, Canberra, ACT 2600, Australia **Dr. Brad Congdon** **Dr. Andrew Krockengerber** **Dr. Sandra Abell**
Data Collection	Provided unpublished data	**Dr. Tom May**, Royal Botanic Gardens Victoria, Melbourne, VIC 3004 Australia **Dr. Chris Johnson**, School of Biological Sciences, Zoology, University of Tasmania, Hobart, Tasmania 7001, Australia

		Dr. Karl Vernes, Ecosystem Management, University of New England, Armidale NSW 2351 Australia
	Field work – cage trapping and collection of scat samples and associated mammal identification data	**Jessica Koleck**, WWF-Australia **Tegan Whitehead**, JCU PhD Candidate **Stephanie Todd**, JCU PhD Candidate **Naomi Bowie**, JCU Research Assistant **Elise Chatterton**, JCU Research Assistant
Data Analysis	Bioinformatics (outlined in the 1st paragraph of Chapter Three, 3.3.3 Bioinformatics)	**Sten Anslan**, Institute of Ecology and Earth Sciences, University of Tartu; 14A Ravila; 50411 Tartu; Estonia
Facility Use	Laboratory	**Dr. Leho Tedersoo**, Natural History Museum and Institute of Ecology and Earth Sciences, University of Tartu, 14A Ravila, Tartu EE-50411 Estonia

Contribution of Co-authors on Publications

Chapter no.: Two

Details of publications on which the chapter is based:

Nuske*, S. J., K. Vernes, T. W. May, A. W. Claridge, B. C. Congdon, A. Krockenberger, and S. E. Abell. 2017. Redundancy among mammalian fungal dispersers and the importance of declining specialists. Fungal Ecology. 27: 1-13.

Nuske*, S. J., K. Vernes, T. W. May, A. W. Claridge, B. C. Congdon, A. Krockenberger, and S. E. Abell. 2017. Data on the fungal species consumed by mammal species in Australia. Data in Brief. 12: 251-260.

Nature and extent of the intellectual input of each author, including the candidate*:

Nuske, S. J.*: Formation of concept, collection of data, data analysis, writing of manuscript

Abell, S. E.: contribute to the formation of concept, support with data collection and analysis, editing early and final drafts of manuscript

Congdon, B. C.: contribute to the formation of concept, support with data collection and analysis, editing early and final drafts of manuscript

Krockenberger, A.: contribute to some of the formation of concept, editing final drafts of manuscript

May, T. W.: contribute unpublished data, lend expertise to process some data (fungal names), editing final drafts of manuscript

Vernes, K.: contribute unpublished data, support with data collection, editing final drafts of manuscript

Claridge, A. W.: editing final drafts of manuscript

Financial Support

Item	Fund	Principal Investigator
Field and laboratory research	Australian Government Caring for our Country 2 Target Area Grant 2013/14 (Project ID: TAG14-00542) *Bettongia tropica* population status, viability and impact of fire with project partners James Cook University, Queensland Parks and Wildlife Service, Department of Environment and Heritage Protection and WWF-Australia.	Primary Advisor: Sandra Abell
	North Queensland Wildlife Trust	Susan Nuske
	Wet Tropics Management Authority	Susan Nuske
	Australasian Mycological Society	Susan Nuske
	Skyrail Rainforest Foundation	Susan Nuske
Stipend	Australian Postgraduate Award	Susan Nuske

Abstract

Conservation is more than just preserving biodiversity but also preserving ecosystem processes. Understanding how loss of diversity can affect the functioning of ecosystems requires understanding of the system's functional redundancy. That is, how many species in the system perform similar roles and can compensate for the loss of similar species? In this thesis, I investigate the functional redundancy among mammal species involved in an important, yet poorly understood, interaction between three very different organisms; fungi, plants and mammals.

Mycorrhizal fungi associate mutualistically with the roots of many plant species. In exchange for nutrients accessed by the fungi, the plants provide the fungus with sugars (carbohydrates) from their photosynthesis. Many mycorrhizal species form below-ground fruit-bodies (truffles) that rely on mammals for spore dispersal. This interaction led to the hypothesis that mammals are important for fungal species diversity, plant-fungal interactions and ecosystem functioning. However, little is known about how truffles contribute to the structure of mycorrhizal communities. For instance, are truffle taxa that mammals disperse important components of the mycorrhizal community as a whole and thus, can mammals influence mycorrhizal community structure?

Globally, many different mammals are known to consume and disperse truffles, some to a much greater degree than others. For example, the term 'fungal specialists' is used for mammals that consume fungi for the majority of their diet (>50%, relative to other food types). Often as a consequence, fungal specialists can also consume (and disperse) a diversity of truffle species. Many mammals with generalist diets, on the other hand, frequently consume truffle fungi opportunistically. Hence, individual mammals with generalist diets often consume a lower diversity of truffle fungal species than mammals

with fungal specialist diets. However, currently it is unknown whether the combined fungal dispersal role of mammals with generalist diets equates to that of a specialist (i.e.: is there functional redundancy in the system?). In other words, if a fungal specialist were to become extinct in an ecosystem, is there enough functional redundancy that the dispersal roles for truffle fungi will be fulfilled by the remaining mammals with generalist diets?

Understanding this interaction is particularly relevant to Australian ecosystems. Unfortunately, Australia has the highest rate of mammal extinction and decline, including fungal specialists within the family Potoroidae. Additionally, the majority of Australia's native forests are dominated by woodland trees that host truffle-producing ectomycorrhizal (ECM) fungi (for instance, *Eucalyptus, Corymbia, Allocasuarina, Melaleuca*). In this thesis, I addressed a number of research questions aimed at better understanding how the loss of mammalian diversity could potentially impact on truffle populations and mycorrhizal communities. These research results pave the way to understanding how loss of mammal diversity could influence fungus-plant interactions and ecosystem functioning.

In Chapter Two, a meta-analysis brings together discordant data on fungal diets of mammals across Australia. These data were used to ask whether there is functional redundancy in fungal dispersal roles among mammalian fungal specialists and mammals with generalist diets. Despite detecting a sampling bias in the literature, on average, fungal specialists consumed fungi at a higher diversity and abundance, and more consistently across seasons than mycophagous mammals with generalist diets, indicating little functional redundancy in general. However, some generalist mammals ate a fungal species diversity on par with specialists (*Rattus fuscipes*, *Perameles nasuta*

and *Wallabia bicolor*) indicating that there may be functional redundancy in some systems. Studies presented in this meta-analysis utilised differences in morphological characters of spores to identify fungal species, however, this technique has limited resolution with some groups (e.g. Russulaceae). Additionally, much of the data could not be compared between studies because many taxa were undescribed (e.g. Unknown species 1).

Results from Chapter Two are built on in Chapter Three, by directly comparing fungal diets of a specialist and nine co-occurring generalist fungal diets using modern DNA sequencing techniques. This direct comparison eliminated the biases associated with using data collected from different studies and allowed a higher resolution of fungal species diversity to be measured. I found that the fungal specialist, *Bettongia tropica* (northern bettong), consumed a significantly higher diversity and more unique mycorrhizal and truffle fungal taxa than the combined diets of the generalists. *Bettongia tropica* also had a significantly different fungal community in their diets. These trends were consistent across sites and seasons. These data suggest that there is little functional redundancy in this ecosystem and indicates that truffle fungi populations may be detrimentally impacted by the loss of the endangered *B. tropica*.

To further understand whether potential loss of truffle taxa, via loss of specialists, would have detrimental impacts on fungal-plant interactions, a good understanding of the structure of the mycorrhizal community must first be obtained. Yet, particularly in Australia, little is known about the structure of mycorrhizal communities and how truffle diversity contributes to it. In Chapter Four, this knowledge gap was addressed by measuring the mycorrhizal community at different scales using molecular methods. I found that the dominant mycorrhizal fungal taxa associating with plant roots were

truffle taxa found in mycophagous mammalian diets. Over 80% of truffle taxa associating with roots were within the diet of the fungal specialist, and this percentage was just over half (52%) for generalist mammals. These data indicate that mammals, particularly those with specialist fungal diets, are important in shaping ECM fungal communities. This adds credence to the hypothesis that the loss of mammals could have detrimental effects on ECM communities and fungal-plant relationships.

Overall, my thesis addressed key knowledge gaps in the interactions between mycophagous mammals, ECM fungi and their host plants. This work also highlights previously overlooked ramifications of native mammal loss in Australia, drawing particular attention to specialist mycophagists whose role in maintaining the diversity of ECM truffle fungal taxa may be irreplaceable.

Table of Contents

List of Tables

List of Figures

List of Publications

Accepted manuscripts

Thesis Chapter Two

Nuske, S. J., K. Vernes, T. W. May, A. W. Claridge, B. C. Congdon, A. Krockenberger, and S. E. Abell. 2017. Redundancy among mammalian fungal dispersers and the importance of declining specialists. *Fungal Ecology*. 27: 1-13.

Nuske, S. J., K. Vernes, T. W. May, A. W. Claridge, B. C. Congdon, A. Krockenberger, and S. E. Abell. 2017. Data on the fungal species consumed by mammal species in Australia. *Data in Brief*. 12: 251-260.

Manuscripts from thesis in preparation

Thesis Chapter Three

Nuske, S. J., S. Anslan, L. Tedersoo, B. C. Congdon, and S. E. Abell. The consequences of losing the northern bettong, a fungal specialist, for the dispersal of ectomycorrhizal fungi. Submitted to *Molecular Ecology*.

Thesis Chapter Four

Nuske, S. J., S. Anslan, L. Tedersoo, B. C. Congdon, and S. E. Abell. Dominant root-associating ectomycorrhizal fungi are mammal dispersed. *In preparation.*

Other publications in preparation

Nuske, S. J., S. Anslan, L. Tedersoo, B. C. Congdon, and S. E. Abell. Seasonal diet of a fungal specialist; a molecular perspective. *In preparation.*

Nuske, S. J., S. Anslan, L. Tedersoo, B. C. Congdon, J. Kanowski, and S. E. Abell. Thinning and fire effects on soil fungal communities. *In preparation.*

Chapter One: Introduction

1.1 Functional redundancy

Ecosystems exist due to a myriad of interacting organisms. The type, quality and quantity of interactions between organisms influence the biology and ecology of their populations. How reliant a given population of an organism is on these interactions depends on the functional redundancy of the system (Brodie et al. 2014). For example, some plant species require the aid of animals to disperse their seeds. If the seed of a certain plant species is dispersed by many animal species, then the system is said to have more functional redundancy; i.e. the extinction of one animal species in the ecosystem would not affect the dispersal of its seeds. However, if a plant species is only dispersed by one or two animal species, then this system is less functionally redundant because the extinction of one or both animal species would disrupt the dispersal of the plant.

Understanding redundancy within an ecosystem for a given function can help elucidate when and why species are at risk due to the extinction of other organisms ('secondary extinction'; Brodie et al. 2014). Specialist organisms often perform unique roles in ecosystems, as their special requirements allow them to interact with other organisms in unique ways. Losing specialist organisms may or may not result in other species extinctions, depending on the redundancy of the system (Aizen et al. 2012, Colwell et al. 2012). Therefore, understanding the functional redundancy in ecosystems is a high priority when allocating resources for conservation. In this thesis, I examine the functional redundancy among the dispersal roles of mammals for important plant-symbiotic mycorrhizal fungi, including threatened mammals with specialist fungal diets.

1.2 The interactions

Mycorrhizal fungi are a diverse range of soil fungi that interact with a diverse range of plant species (Brundrett 2009). These fungi grow in and around plant roots, where they supply nutrients to the plants in exchange for carbon. This interaction is demonstrably beneficial for both partners (Hoeksema et al. 2010); plants exhibit increased growth and survival and mycorrhizal fungi receive carbon (e.g. carbohydrates) from the plant. Mycorrhizal fungi are therefore critical for ecosystem nutrient cycling (Hawkins et al. 2015, van der Heijden et al. 2015), plant health (Scott et al. 2012), and are an important component of many forest systems globally (Tedersoo et al. 2010, 2014). Many species of mycorrhizal fungi form hypogeous sequestrate fruit-bodies (truffles) (Bougher and Lebel 2001, Trappe et al. 2009), most of which are ectomycorrhizal (ECM), although some are arbuscular mycorrhizal (AM) or saprotrophic (Tedersoo et al. 2010, Tedersoo and Smith 2013). Truffles do not have an active spore-dispersal mechanism (cf. wind-dispersed mushroom species) and rely on animals for dispersal via consumption and deposition of spores in scats or from spores carried on body surfaces.

Among the animals recorded to consume and disperse truffle mycorrhizal fungi, mammals are the most prevalent and widely studied (e.g. Maser et al. 1978, Claridge and May 1994, Schickmann et al. 2012), although many other animals consume mycorrhizal fungi. There are a few records of reptiles and birds consuming soil fungi (Simpson 1996, 2000, Medway 2000, Jones et al. 2007, Cooper and Vernes 2011). However, truffle sporocarps of mycorrhizal taxa have rarely been observed as directly consumed by these animals. An exception is the ectomycorrhizal desert truffle *Picoa lefebvfei* (=*Phaeangium lefebvrei*) eaten by migratory birds (Alsheikh and Trappe 1983).

Invertebrates are also known to consume spores of mycorrhizal fungi (e.g. springtails: Collembola, beetles: Coleoptera and earthworms: Annelida) (Fogel and Peck 1975, Reddell and Spain 1991, Houston and Bougher 2010, Anslan et al. 2016), although whether this also contributes to dispersal depends on spore survival and animal movement. For some invertebrate species, few spores remain intact after gut passage (therefore, most are not viable for germination). For example, after passage through Collembola guts, the proportion of intact spores can be very low (<1-10%) (Nakamori and Suzuki 2005, 2010) and only 4% of truffle spores observed from beetle faeces appeared intact (Houston and Bougher 2010). Experimental evidence for mycophagous invertebrates to influence mycorrhizal colonisation shows either positive (Reddell and Spain 1991, Klironomos and Moutoglis 1999), negative (Pattinson et al. 1997) or neutral (Gormsen et al. 2004) directions, and this does not always seem to be associated with dispersal of propagules. Nevertheless, invertebrates have been shown to be dispersal vectors for other fungal taxa, for instance plant pathogens or saprotrophic fungi (Renker et al. 2005, Chen et al. 2014, Drenkhan et al. 2017).

Springtails and earthworms often only move short distances during foraging (centimetres to a few metres) and their short gut-retention times (<2 h) also mean that spores have less potential to move far from their origin (Nakamori and Suzuki 2010, Chauvat et al. 2014, Cameron and Bayne 2015). Mycophagous mammals, on the other hand, have much longer gut retention times (>20 h) (Danks 2012) and mammals can move from tens to hundreds of metres (Vernes and Haydon 2001, Pizzuto et al. 2007, Marchesan and Carthew 2008, Bentley 2008) or several kilometres (Morrant and Petit 2012, O'Malley 2012) during that time. Additionally, many studies have shown that mycorrhizal spores remain viable through the passage of mammalian guts (e.g. Lamont et al. 1985, Claridge et al. 1992, Reddell et al. 1997, Colgan and Claridge 2002,

Caldwell et al. 2005, Ashkannejhad and Horton 2006, Livne-Luzon et al. 2016). Mammals, therefore have a high probability to disperse intact, viable spores far from their origin. Consequently, current data shows that mammals are the main animals that influence the dispersal dynamics of mycorrhizal truffle taxa.

Many mammal species perform this dispersal role for truffle fungi (Maser et al. 1978, Claridge and May 1994). These interactions lead to the hypothesis that the productivity and diversity of plants is linked to mammals, via their mycorrhizal associations (Maser et al. 1978, Malajczuk et al. 1987, Johnson 1996, Vernes 2007). As a corollary, I hypothesise that for mammals to have an influence on both the mycorrhizal and plant communities, truffle taxa will need to form important components of mycorrhizal communities. For example, the higher the proportion of truffle taxa within the overall mycorrhizal community, either in terms of relative abundance or diversity, the higher the potential influence that mammalian spore dispersal has on the structuring of mycorrhizal and plant communities.

There are important differences in AM versus ECM fungi in ecology, distribution and diversity of truffle fungi. These differences are likely to impact the potential for mammals to influence mycorrhizal communities and, in turn, for their host plants. Even though AM fungi have a lower global diversity than other fungi, they associate with much of the global plant diversity and occur in almost every ecosystem where there are plants. At least two genera contain truffle-like sporocarps (Goto and Maia 2005); *Glomus* and *Acaulospora*. ECM associate with a smaller proportion of plant diversity (Brundrett 2009). However, ECM host plants can dominate forests in terms of biomass (for example, they associate with the majority of trees and shrubs in sclerophyll forest; Reddell et al. 1999) and ECM truffle diversity constitutes thousands of species (Bougher and Lebel 2001, Trappe et al. 2009). Therefore, truffles form a larger

contribution, in terms of species diversity, to ECM communities than to AM communities. Currently, we lack data on the influence of mammal mediated truffle dispersal for structuring of mycorrhizal communities and mycorrhizal/plant interactions.

Differences in the rates of mycophagy by mammals can influence their contribution to the dispersal of fungi. Fungal specialists, mammals that rely on fungi as a food source, consume and disperse a high quantity of fungi and often a higher diversity compared to mycophagous mammals with generalist diets. For example, squirrel species (*Glaucomys sabrinus, Spermophilus lateralis* and *Tamiasciurus douglasii*) in California, USA, consume and disperse truffle species more frequently and at a higher diversity than other small mammals in the same community (Pyare and Longland 2001). Similarly, the bank vole (*Myodes glareolus*) consumes a higher quantity and diversity of ectomycorrhizal fungal spores compared to other small mammals in central Europe (Schickmann et al. 2012). This suggests that the functional redundancy of these ecosystems may be low for fungal dispersal roles.

1.3 What we don't know

In many other ecosystems where mycorrhizal truffle fungi are important, we don't have enough data to make assessments about the functional redundancy of fungal dispersal roles. For instance, in Australia, there is much data on the fungal diets of fungal specialists within the mammalian family Potoroidae (Bennett and Baxter 1989, Taylor 1992, Johnson 1994a, Green et al. 1999, Vernes et al. 2001, Nguyen et al. 2005). However, within the same ecosystems, there is little comparable data on the fungal dispersal roles of mammals with generalist diets. There are only a few studies within Australia comparing fungal dispersal roles and they present conflicting results. Tory et al. (1997) found that the fungal diets of a fungal specialist, *Potorous tridactylus* (long-

nosed potoroo) and the generalist *Rattus fuscipes* (bush rat) had a similar composition and diversity in autumn and winter, indicating this system has some functional redundancy, at least seasonally. Whereas, the fungal specialist, *Bettongia tropica* (northern bettong) consumed a higher fungal abundance and diversity of fungal spores compared to other co-occurring mammal species (Reddell et al. 1997), indicating little functional redundancy.

Studying the functional role of mammals in dispersing these important mycorrhizal fungi is particularly pertinent for Australia, as this continent has the highest rate of mammal extinction and decline globally (Short and Smith 1994). This includes declines in fungal specialists (*Bettongia* and *Potorous* spp.) within the family Potoroidae (Seebeck and Rose 1989, Laurance 1997, Short 1998, Wayne et al. 2016). Historically, *Bettongia* and *Potorous* spp. had a wide distribution over much of the Australian continent and now reside only in fragmented populations (Claridge et al. 2007, Woinarski et al. 2014). We do not know how functionally redundant these systems are to the loss of mammal diversity, or fungal specialists. Can mycophagous mammals with generalist diets compensate for some, or all, of the role performed by a fungal specialist? Additionally, there is little known about the structure of mycorrhizal communities, particularly in Australian ecosystems. This data is essential to testing the hypothesis that mammalian spore dispersal influences the structuring of mycorrhizal and plant communities. The overall aim of this thesis is to determine the functional redundancy among mammalian fungal dispersers and examine the potential for mammals to influence the structure of mycorrhizal communities.

1.4 Data chapters

In Chapter Two of this thesis I address the question of functional redundancy in fungal dispersal by mammals by bringing together previously disjunct evidence from the

literature. Data on the fungal diets of mammals across Australia for variables including abundance, frequency, diversity and seasonality of fungi eaten was gathered. Using this data, I infer the relative importance of mammal groups to fungi dispersal and test the hypothesis that fungal specialists perform a disproportionate dispersal role compared to mammals with generalist diets.

Chapter Three builds on Chapter Two; in a field study, the functional redundancy among fungal dispersal roles of an endangered fungal specialist is compared to the co-occurring generalist mammal community. This direct spatial and temporal comparison removes any bias associated with using previously published literature to assess levels of redundancy. In this chapter, modern DNA sequencing technology to quantify mammalian fungal diets was used; a novel feat for mycophagy studies that allows a comparison at a higher resolution of diversity in these communities.

In Chapter Four I examine the mycorrhizal community structure from multiple sample types to assess the level of influence of mycophagous mammals. The mycorrhizal community and measured and compared from whole soil, plant-roots and mycophagous mammalian scats, using modern DNA sequencing technology. From these data, I infer the influence of mammals on mycorrhizal communities by quantifying the fruiting habits of the taxa and examining the overlap in mycorrhizal taxa between sample types.

Overall, the data and results from my thesis provide a new insight into this essential interaction in woodland forests. I demonstrate that these three diverse groups of organisms (mammals, fungi and plants) are tightly inter-connected and that disruption to these networks via loss of specialist mammalian fungal dispersers may have already caused detrimental, yet undocumented, declines of truffle fungi. My results also suggest that continuing declines are likely to have further significant implications for

ectomycorrhizal fungal communities, fungi-plant interactions and ecosystem functioning.

Chapter Two: Redundancy among mammalian fungal dispersers and the importance of declining specialists.

The content of this chapter adapted from published papers in *Fungal Ecology* (27: 1-13) and *Data in Brief* (12: 251-260) co-authored by K. Vernes, T. W. May, A. W. Claridge, B. C. Congdon, A. Krockenberger and S. E. Abell.

The entire chapter was written by Susan Nuske, with co-authors providing intellectual guidance in the design and implementation of the research and editorial contributions. Data collection, data analyses and production of tables and figures were conducted by Susan Nuske.

2.1 Abstract

Knowing the relative importance of different mammal species as dispersers helps us to understand how loss in mammal diversity could affect plant-fungi interactions and fungal species diversity. In this chapter, a meta-analysis of available data on the fungal diets of Australian mammal species was performed to infer the functional redundancy between fungal specialists and mammals with generalist diets. Despite detecting a sampling bias in the literature, the meta-analysis confirms that mammals with fungal specialist diets contribute disproportionally more to the potential dispersal of fungi than other mammals within Australia. Three mammal species with generalist diets also consumed fungi at comparable rates to fungal specialist species and, importantly, persist in many areas where fungal specialists are now absent. These results highlight the significance of mammals, particularly fungal specialists, for maintaining diverse ectomycorrhizal fungal communities.

2.2 Introduction

It is expected that mammals, as dispersers of spores of ectomycorrhizal fungi (ECM), are essential to the maintenance of fungal species diversity and ectomycorrhizal-host plant mutualisms and thus contribute to ecosystem functioning. For mammal species to positively affect fungal population diversity and gene flow via spore dispersal the spores need to both survive the mammalian gut and be deposited away from their point of origin. There are no published studies showing a reduction in ECM fungal spore viability associated with passage through mammalian guts. In contrast, several studies have successfully used scats from mycophagous mammals as ECM inoculum for bioassay seedlings (e.g. Lamont et al. 1985, Claridge et al. 1992, Reddell et al. 1997, Colgan and Claridge 2002, Caldwell et al. 2005, Ashkannejhad and Horton 2006,

Livne-Luzon et al. 2016). Consequently, current data suggest that ECM spores remain viable after passage through mammalian gut's and that, in general, consumption leads to dispersal opportunities.

The likelihood of spores dispersing away from their point of origin is an interaction between gut-retention time and movement of the animal. The average gut-retention time for mycophagous mammals is 26.9 h (95% confidence limits: 20-33.7 h), with maximum times up to 69 h (Danks 2012). Mammals can move from tens to hundreds of metres (Vernes and Haydon 2001, Pizzuto et al. 2007, Marchesan and Carthew 2008, Bentley 2008) or several kilometres (Morrant and Petit 2012, O'Malley 2012) during that time. Home range size in mammals is correlated with body size, with larger mammals generally having larger home range sizes (Tucker et al. 2014). However, there are exceptions. Highly mycophagous *Bettongia gaimardi* and *B. tropica* (Tasmanian bettong and northern bettong) in Australia have much larger home ranges than their body size would indicate (ca 60 ha for a 1-2 kg animal) (Taylor 1993, Vernes and Pope 2001). In contrast, *Wallabia bicolor* (swamp wallaby), a 10-20 kg animal has a smaller home range size (16-37 ha) (Troy and Coulson 1993, Di Stefano et al. 2011). It has been suggested that the large home range size of fungal specialists with the family Potoridae is related to their reliance on a fungal diet, as fungi are sparsely distributed but high quality food (Vernes and Pope 2001). Longer gut-retention times and larger home ranges increase the chance of long-distance dispersal of spores (Danks 2011, O'Malley 2012). Additionally, mammal species that consume higher amounts of fungi (in terms of quantity, frequency and diversity) are more likely to influence fungal communities via inoculum dispersal.

Globally, a diverse range of mammals consume fungi and thus potentially contribute to their dispersal. However, not all contribute equally. Often a few mammal species within

a community are more reliant on fungi (fungal specialists) and many other mammals only consume fungi seasonally, or as a supplementary food source (hereafter, fungal generalists) (Maser et al. 1978, Vernes and Dunn 2009, Schickmann et al. 2012). Mammals that consume a higher quantity of fungi typically also consume a higher diversity of fungal species (Maser et al. 1978, Claridge and May 1994) and are likely to contribute disproportionally more to fungal dispersal and ecosystem health. The resilience of both fungal and plant communities to the loss of these fungal specialists and their fungal dispersal roles is unknown. In the wake of ecosystem disturbance and species extinctions, it is unclear if a diverse group of mammalian fungal generalists can compensate for the loss of a single fungal specialist with respect to the community of fungi they disperse, and to what degree mammal diversity is important to fungal species diversity (Vernes 2007). To answer these questions, knowledge of functional redundancy is required. Put simply, do fungal generalists collectively disperse the same fungal community as fungal specialists? Are all fungal generalists functionally redundant, or do some generalists disperse more fungi (in abundance or diversity) than the average mycophagous mammal? The answers to these questions may have consequences for forest management and ecosystem health (Wayne et al. 2016).

Currently there are few studies that specifically address functional redundancy between specialist and generalist mammalian fungal dispersers. These studies suggest that systems have little functional redundancy. For instance, squirrel and vole species in North America and Central Europe consume higher abundance and diversity of mycorrhizal fungi than other mammals in the same communities (Pyare and Longland 2001, Schickmann et al. 2012). Other data on mycophagy is scattered throughout the literature and dietary studies on mammals often overlook fungi as an important dietary component (Vernes 2007), or use inappropriate methods to measure fungal abundance

in diets. Some authors even ignore and discard finer particles (Smith and Broome 1992, Evans and Jarman 1999) that potentially contain fungal spores and hyphae, resulting in an underestimation of fungal contribution to diets. In this meta-analysis, data on fungal diets of mammals are brought together to infer their potential functional role as fungal dispersers. To be able to undertake valid comparative analyses between published studies a selection criteria on dietary sampling methods was developed that reduced bias and the under-detection of dietary fungi.

Data on Australian mammals was used because Australia has a high diversity of truffle-like fungi (Lebel and Castellano 1999, Bougher and Lebel 2001), and mycophagy has been studied over a wide range of Australian mammal species (Claridge & May 1994; Vernes 2010; O'Malley 2012; Vernes, Cooper & Green 2015). For example, in a previous review Claridge and May (1994) recorded 37 native Australian mammal species across eight families having fungi in their diet, and more species have been added to the list since then (e.g. *Antechinus stuartii,* mouse-sized insectivorous antechinus, and *Isoodon macrourus,* medium-sized, omnivorous northern brown bandicoots) (Reddell et al. 1997, McIlwee and Johnson 1998, Vernes and Dunn 2009). Australia has also suffered from the highest rate of mammal extinction and decline of any continent (Short and Smith 1994, Woinarski et al. 2015), including some important fungal specialists within the family Potoroidae (rat-kangaroos) (Claridge et al. 2007). These fungal specialists previously occupied large areas of Australia, but today are restricted to fragmented populations mainly in coastal regions (Short 1998, Woinarski et al. 2014). This makes understanding how the loss of fungal specialists affects fungal species diversity and fungal-plant interactions particularly pertinent for this continent.

From a dietary perspective, six out of eight extant Australian Potoroid species are viewed as fungal specialists and I hypothesise that they perform a disproportionately

important role in fungal dispersal. Australian Potoroid mammals consume fungi as the majority of their diet (40-90%, depending on the season) (Scotts and Seebeck 1989, Taylor 1992, Claridge et al. 1993) and at a high diversity (cumulatively, 97 fungal taxa have been recorded in the diet of *P. tridactylus*; this study). The two notable exceptions from this family are *Aepyprymnus rufescens* (rufous bettong) and *B. lesueur* (burrowing bettong). Only about 23% or less of the diet of these two species is comprised of fungi; they rely mainly on other types of food (Wright and Hume 1984, McIlwee and Johnson 1998, Robley et al. 2001, Bice and Moseby 2008).

Specifically, in this meta-analysis the available information on mycophagy in mammals within Australia was examined in terms of the abundance, frequency, seasonality and diversity of fungi consumed. From these data, I infer the relative importance of mammals as fungal dispersers and test the hypothesis that in Australia, Potoroid mammals (members of Potoroidae and fungal specialists) contribute disproportionally more to the consumption of fungi than generalist mycophagous mammal species. I also examine whether there is likely to be functional redundancy among generalist mycophagous mammals in their fungal dispersal roles.

2.3 Materials and methods

2.3.1 Literature search

Searches were made for quantitative data on the occurrence of fungi within dietary studies of Australian mammal species. The following data were collected: the fungal taxa within each mammal species' diet, the abundance of fungi relative to other foodstuffs, the frequency of fungi across samples or individuals, and the abundance and frequency of fungi consumed across seasons.

The original location reported in each study was used as the lowest grouping variable within the dataset. To standardise the data and later compare potential dispersal events from populations of different mammal species that might overlap, data from locations were further pooled and averaged across sites if they occurred within 100 km of a random central point.

To locate dietary studies the following keywords were used alone, or in combination, to search Web of Science and Google Scholar databases: mycophagy, fungi, diet, mammal, Australia. Additionally, Australian mammal species names were searched combined with the word "diet". Unpublished theses were surveyed as well as relevant books. Methods within each study were examined for the inclusion criteria (see below) and added to the dataset if fungi were present. All references within an earlier review by Claridge and May (1994) were re-examined, except for 1 unpublished study (N. Baczocha) and 1 reference that could not be obtained (Stimson 1987).

Taxonomic names of Australian mammals followed Van Dyck et al. (2013) except for *I. obesulus peninsulae* which was considered separate from *I. obesulus* (southern brown bandicoot), as the populations that were studied are disparate (Keiper and Johnson 2004), and with the addition of *Pseudomys pilligaensis* (Pilliga mouse) (Tokushima et al. 2008). All bats were excluded (but see, O'Malley 2012).

2.3.2 Developing inclusion criteria

Fungal spores of the taxa most frequently encountered in diets (Basidiomycota and Ascomycota) are generally considerably smaller than most other dietary items (<20 μm). Consequently, authors may overlook such small particles in dietary analyses where particles are only examined at low magnification under a dissecting microscope. This is particularly likely for large-bodied mammals and predators, but may even occur

in small-bodied species, as for example with members of the genus *Antechinus* (mouse-sized insectivorous marsupials), where a lack of detection of fungal spores in dietary analysis (Allison et al. 2006) appears to be rectified when samples are examined at higher magnifications (Reddell et al. 1997, Vernes and Dunn 2009, O'Malley 2012, Vernes et al. 2015). Some authors ignore finer particles altogether (Evans and Jarman 1999), or sieve fine particles away without collecting and examining them (Smith and Broome 1992). This can also lead to underestimates of both the quantity and type of fungi eaten. For example Watts (1977) reported no fungi in the diet of *R. fuscipes*, contrasting with more methodologically appropriate studies reporting high levels of mycophagy for this species (Tory et al. 1997, Vernes and Dunn 2009, Vernes et al. 2015). Nevertheless, clumps of fungal hyphae may be visible at lower magnifications and are unlikely to pass through sieves. Therefore, it may still be possible to estimate the fungal portion of the diet even if fine particles are not examined (Scott et al. 1999).

For the purposes of the meta-analysis three methodological properties were considered important for being able to detect and/or estimate the abundance of fungi within mammalian diets: (1) examination of the 'fine fraction' or 'filtrate', if sieving techniques were used, (2) the smallest sieve size, and (3) the highest magnification. Out of the dietary studies examined in which the fine fraction was collected and inspected, the lowest magnification used that still reported fungi was 10x (Newell 2009). In those where the fine fraction was not inspected but fungi were still reported, the largest sieve size was 0.3 mm^2 and lowest magnification was 20x (Braithwaite and Griffiths 1996). Consequently, to reduce the likelihood of underestimating the abundance, frequency and seasonality of fungi within a specific mammal species diet, I excluded studies that used a minimum sieve size above 0.2 mm^2 and/or examined material at less than 40x magnification.

There were some studies that met the above criteria but did not mention fungi in their species diets (i.e. producing 'zero' data). These studies were not included in the dataset because I could not distinguish true absence from false negatives. For instance, even though fungi have been found to be a consistent part of the diet of *W. bicolor* (Claridge et al. 2001, Vernes 2010, Danks 2011, O'Malley 2012), some modern papers ignore fungi altogether (Green et al. 2014) (a possible false negative). Indeed, many other mammal species may not be included in the mycophagy data; for example, studies of *Petrogale* spp. (rock wallabies') diets met the above criteria but did not record fungi (Short 1989, Horsup and Marsh 1992), even though at least seven taxa of fungi were found in *Pe. penicillata* (brush-tailed rock-wallaby) scats in northern NSW (Vernes 2010). With these limitations in mind, the number of mammal species shown to consume fungi found by my literature search is considered to be conservative.

To identify fungal spores, specific techniques and expertise are needed. Spore characteristics can only be distinguished using at least 100x magnification (for Ascomycota and Basidiomycota). Even between comparable samples, fungal spore diversity may differ due to extraction methods (Gordon and Comport 1998). I used the following criteria to include studies within the diversity dataset: fine fraction material must have been examined (no sieving), samples must have been examined at 100x magnification or greater, and spores must have been identified by use of mycological literature and/or a mycological expert.

2.3.3 Compiling datasets

A list of fungal taxa consumed by different Australian mammal species was compiled. Each fungal taxon was listed to the nearest taxonomic level. If the author had question-marked or grouped fungal taxa (e.g. morpho-species), the next highest taxonomic level

was listed. Most often genus level was the lowest taxonomic level stated. Fungal taxonomic names followed Mycobank (http://www.mycobank.org/), except when more recent name changes have been published (T. May pers. comm.). Undescribed taxa ('Species 1' etc.) were provided with the author who introduced the name. Authors of publications on mycophagy (Claridge A W, O'Malley A, Danks M and Vernes K) provided details that allowed undescribed fungal species to be consistently matched between their publications. When comparing fungal taxa consumed between mammals, only published fungal names were used (i.e. not undescribed taxa).

If available, the abundance or frequency of fungi in mammalian diets was recorded by season. Only studies that examined all four seasons were included. Seasons were defined as summer (Dec-Feb), autumn (Mar-May), winter (Jun-Aug) and spring (Sept-Nov), except for studies that occurred in the tropics. These seasons were defined as 'early dry'(May-Jul = winter), 'late dry' (Aug-Oct = spring), 'early wet' (Nov-Jan = summer) and 'late wet' (Feb-Apr = autumn) (Johnson and McIlwee 1997, Vernes et al. 2001, Dennis 2002).

2.3.4 Data analysis

All statistical analyses were carried out in R (R Core Team 2012). Before each linear model was accepted I performed tests for normality, homoscedasticity of variance and linearity. Transformations were performed as appropriate if tests failed. Generalised linear models with quasi-binomial distributions were used to model differences between mammal families in: (1) percent abundance of fungi in mammal species diets' relative to other foodstuffs; (2) percent abundance of fungi in mammal species diets within each season between mammal families; and (3) percent frequency of fungi in mammal diets across samples. Differences in log-transformed fungal diversity (species-richness and

genera-richness) between mammal families' diets were compared using linear models. Pairwise differences in the fungal components of diet were compared statistically between mammal families for the abundance, frequency, diversity and seasonality of fungi using Tukey's Honest Significant Difference tests. Tests between mammal families were compared if *Ae. rufescens* and *B. lesueur* were excluded from analyses as they are not fungal specialists. If there were no differences, tests are shown with these species included. Data were graphed from logit back-transformed values predicted from linear models.

Correlations between the number of references or samples and the number of fungi species in a mammal species diet were investigated initially with linear models. Linear Mixed Effects Models (R package 'nlme', function 'lme') were used to investigate additional factors correlating with the number of fungal species recorded per mammal species' diet. The number of references, cumulative number of samples, mammal family and whether the aim of the published study included mycophagy were added as fixed effects. Location and published references were included as random effects. The intercept for fixed-effects was set to zero. Models were examined for normality, homoscedasticity of variance and linearity and model comparisons were performed using Analysis of Variance (ANOVA). Model selection was based on minimising AIC and maximising Pseudo-R^2 (function 'r.squaredGLMM' in R package 'MuMIn'), the latter of which accounts for the model variation and penalises for addition of variables (Nakagawa and Schielzeth 2013). Three locations (within 100 km of the random central point) in Australia contained data on several (>7) mycophagous mammals, and all other locations had data on 1-3 mammal species. Within these three locations, the identity of the fungi species was compared between mammal species' diets. One study was excluded from the mixed-effects model and comparison of the northern New South

Wales mammal community because Schlager (1981) was only able to identify one fungal taxa (*Rhizopogon sp.*) from the diet of *Ae. rufescens*, despite reporting 32 different spore types.

2.4 Results

Forty-four mammal species in the abundance dataset, 34 in the diversity dataset and a total of 53 mammal species (across nine families) were recorded to have consumed fungi in Australia. Within the Macropodidae, only seven of the smaller species (i.e. wallabies, pademelons and tree-kangaroos, not kangaroos) had fungi recorded in their diet (Table 2.1).

Table 2.1: Number of fungal species (*sp*) and genera (*g*) recorded in the diets of mammal species, mean ± SE. percentage of fungi in diet relative to other food stuffs (*A*), mean ± SE. percentage frequency of fungi eaten across samples (*F*), mean ± SE. percentage (frequency or presence) of fungi in diet in summer, autumn, winter and spring, respectively (*S*) and cumulative number of observations (*O*) across references in the abundance[A], frequency[F], diversity[D] and seasonality[S] data, respectively. Species marked with asterisk* are fungal specialists.

Mammal family	Mammal species	*sp*	*g*	*A*	*F*	*S*	*O*	References
Potoroidae (rat-kangaroos)	**Potorous tridactylus*	97	38	52.1 ± 7.95	100.0	41.6, 65.1, 69.8, 49.1	249[A], 159[F], 260[D], 209[S]	Bennett and Baxter 1989; Claridge et al. 1992, 1993; Tory et al. 1997; Vernes 2010
	**Potorous gilbertii*	65	18	75.3	100.0	74.5, 73.5, 75.0, 75.0	66[A], 8[F], 74[D], 66[S]	Nguyen et al. 2005; Bougher and Friend 2009
	**Potorous longipes*	63	35	82.6 ± 7.29	100.0	85.8, 91.9, 92.7, 89.2	283[A], 79[F], 202[D], 249[S]	Hill and Triggs 1985; Scotts and Seebeck 1989; Green et al. 1999; T. May unpubl. data
	**Bettongia gaimardi*	61	35	51.1 ± 14.25	100.0	57.3, 58.9, 63.6, 55.8	491[A], 400[F], 437[D], 491[S]	Taylor 1988, 1992; Johnson 1994a, 1994b; C. Johnson unpubl. data
	**Bettongia penicillata*	39	6	75.3	100.0		20[A], 78[F], 223[D]	Christensen 1980; Lamont et al. 1985; Zosky et al. 2010
	**Bettongia tropica*	30	27	48.3 ± 4.04	100.0	50.7, 49.7, 49.8, 52.2	240[A], 118 [F], 114[D], 210[S]	Johnson and McIlwee 1997; Reddell et al. 1997; McIlwee and Johnson 1998; Vernes et al. 2001; Weatherstone 2012
	Aepyprymnus rufescens	30	22	9.3	91.7 ± 8.35		32[A], 31 [F], 75[D]	Schlager 1981; Reddell et al. 1997; McIlwee and Johnson 1998; Vernes 2010
	Bettongia lesueur	5	1	10.8			10[A], 10 [D]	Robley et al. 2001

Muridae (rats and mice)	*Rattus fuscipes*	70	33	54.4	86.1 ± 10.68	11.0, 64.5, 79.7, 50.0	90[A], 227[F], 349[D], 228[S]	McGee and Baczocha 1994; Reddell et al. 1997; Tory et al. 1997; Vernes and Dunn 2009; O'Malley 2012; Vernes et al. 2015; T. May unpubl. data
	Melomys cervinipes	19	14		46.3 ± 6.43	(27.5, 44.0, 74.0, 27.5)	129[F], 76[D], 76[S]	Reddell et al. 1997; Vernes and Dunn 2009; O'Malley 2012; Vernes et al. 2015
	Uromys caudimaculatus	18	11	19.2	85.5 ± 10.45		143[A], 151[F], 159[D]	Reddell et al. 1997; Gordon and Comport 1998; Comport 2000
	Pseudomys fumeus	13	10	28.4			55[A], 57[D]	Ford et al. 2003; T. May unpubl. data
	Rattus rattus	8	4	90.0	100.0		3[A], 19[F], 41[D]	McGee and Baczocha 1994; Vernes and McGrath 2009
	Pseudomys shortridgei	6	5				1[D]	T. May unpubl. data
	Pseudomys pilligaensis	4	4	3.8	29.4 ± 9.42	0.0, 0.4, 3.1, 11.3	430[A], 435[F], 430[D], 430[S]	Jefferys and Fox 2001; Tokushima and Jarman 2010
	Pseudomys novaehollandiae	3	3	7.2 ± 3.54	70.6 ± 29.4		96[A], 24[F], 98[D]	Cockburn 1980; Wilson and Bradtke 1999; Vernes and Dunn 2009; O'Malley 2012
	Mus musculus	2	2	4.8 ± 4.42	9.2	0.5, 0.0, 0.3, 0.7	664[A], 651[F], 651[D], 651[S]	Cockburn 1980; Tann et al. 1991
	Pseudomys gracilicaudatus	1	1	19.5 ± 0.76		11.3, 20.7, 24.1, 22.0	249[A], 260[D], 209[S]	Luo et al. 1994; Luo and Fox 1996
	Pseudomys higginsi	1	1				1[D]	T. May unpubl. data

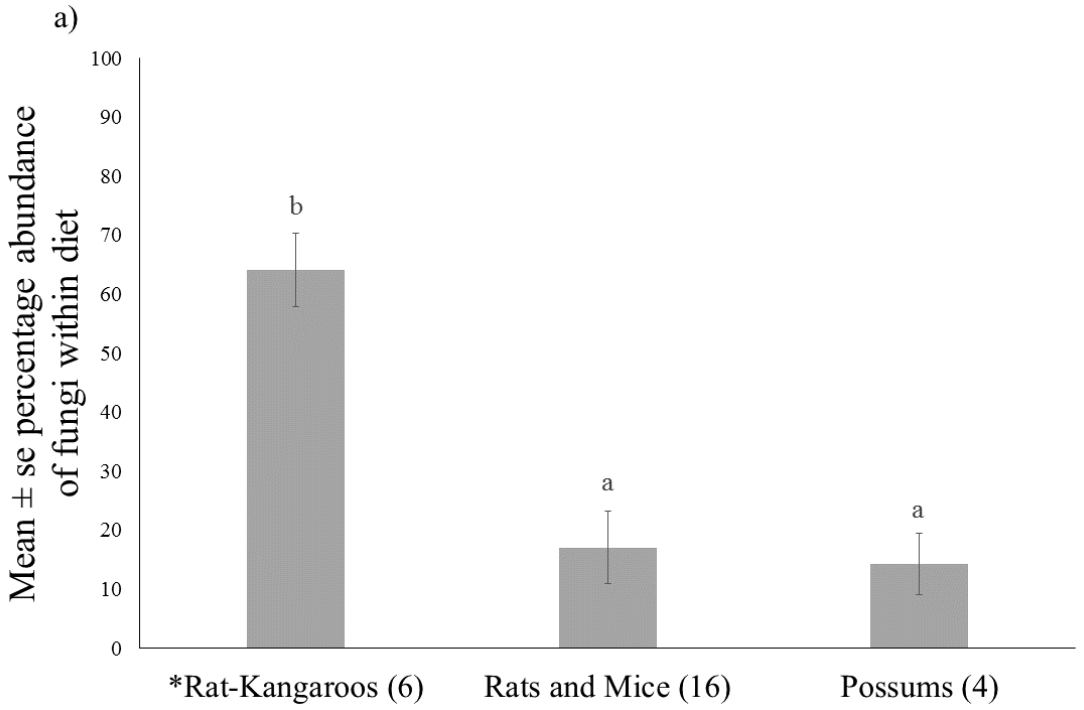
	Rattus villosissimus	1	1	0.8		9[D]	McGee and Baczocha 1994
	Rattus lutreolus			25.8	16.7	19.0, 37.5, 29.0, 17.5	38[A], 7[F], 38[S]	Luo and Fox 1996; Vernes and Dunn 2009
	Pseudomys oralis			1.9 ± 0.1			464[A]	Fox et al. 1994
	Pseudomys desertor			3.6			3[A]	Murray et al. 1999
	Pseudomys bolami			0.6			9[A]	Murray et al. 1999
	Pseudomys albocinereus			1.6			32[A]	Murray et al. 1999
	Leggadina forresti			1.5			1[A]	Murray et al. 1999
	Conilurus penicillatus			10.0	0.03 ± 0.00		28[A], 64[F]	Firth et al. 2005
	Rattus tunneyi				100.0		1[F]	Reddell et al. 1997
	Pseudomys hermannsburgensis				6.7		30[F]	Murray and Dickman 1994
	Notomys alexis				3.3		30[F]	Murray and Dickman 1994
Macropodidae (wallabies, pademelons and tree-kangaroos)	*Wallabia bicolor*	61	34		95.6 ± 3.59		353[F], 622[D]	Claridge et al. 2001; Vernes and McGrath 2009; Vernes 2010; Danks 2011; O'Malley 2012

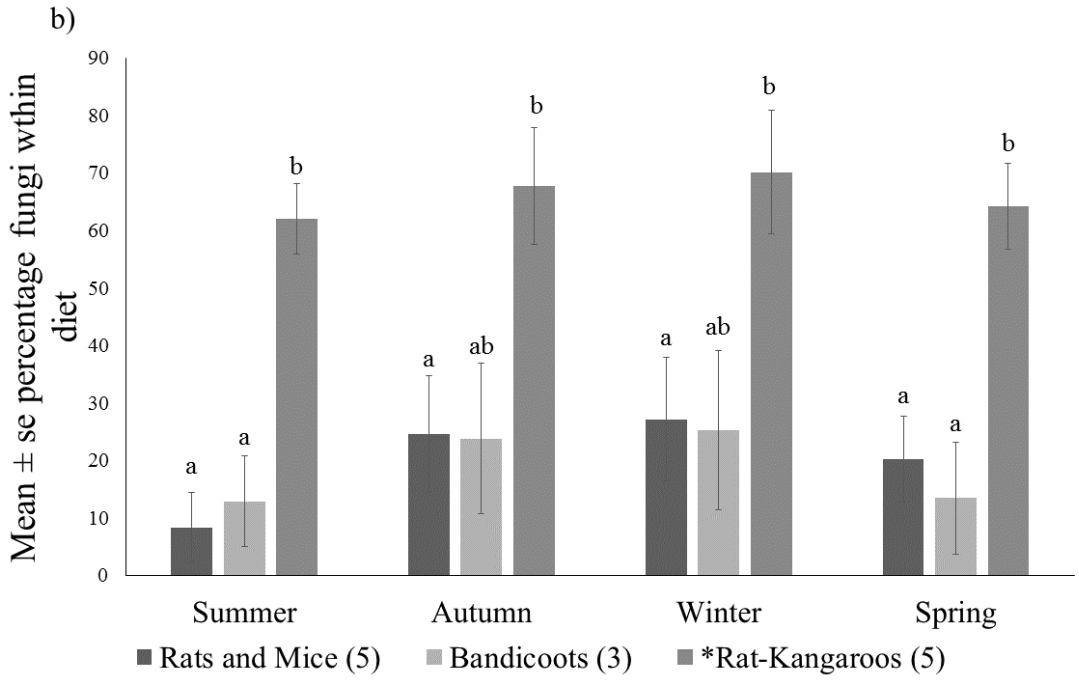
	Macropus parma	22	16				45[D]	Vernes 2010
	Thylogale thetis	21	16				124[D]	Vernes 2010
	Thylogale stigmatica	18	10		47.5 ± 13.77		33[F], 20[D]	Reddell et al. 1997; Vernes and Trappe 2007; Weatherstone 2012
	Petrogale penicillata	7	5				36[D]	Vernes 2010
	Setonix brachyurus			1.0			97[A]	Hayward 2005
	Dendrolagus lumholtzi				80.0		10[F]	Weatherstone 2012
Peramelidae (bandicoots)	*Perameles nasuta*	49	28	29.0 ± 12.8	67.8 ± 2.92	27.6, 51.2, 47.5, 17.9	141[A], 130[F], 223[D], 134[S]	Claridge et al. 1991; Claridge 1993; McGee and Baczocha 1994; Reddell et al. 1997; Scott et al. 1999; Thums et al. 2005; Shevill and Johnson 2008; Vernes 2014
	Isoodon obesulus	10	7				28[D]	Christensen 1980; Claridge et al. 1991; T. May unpubl. data
	Isoodon obesulus peninsulae	8	8	7.7		4.0, 7.0, 15.5, 0.0	48[A], 48[D], 48[S]	Keiper and Johnson 2004
	Isoodon macrourus	9	9	6.5	42.9		32[A], 7[F], 7[D]	Reddell et al. 1997; McIlwee and Johnson 1998
	Echymipera rufescens australis	3	3	14.2		7.3, 13.3, 13.0, 22.7	56[A], 56[D], 56[S]	Shevill and Johnson 2008
Phalangeridae (possums)	*Trichosurus caninus*	19	17		51.2 ± 7.61	(summer, autumn,	179[F], 138[D], 45[S]	Claridge and Lindenmayer 1993, 1998; Vernes et al. 2015

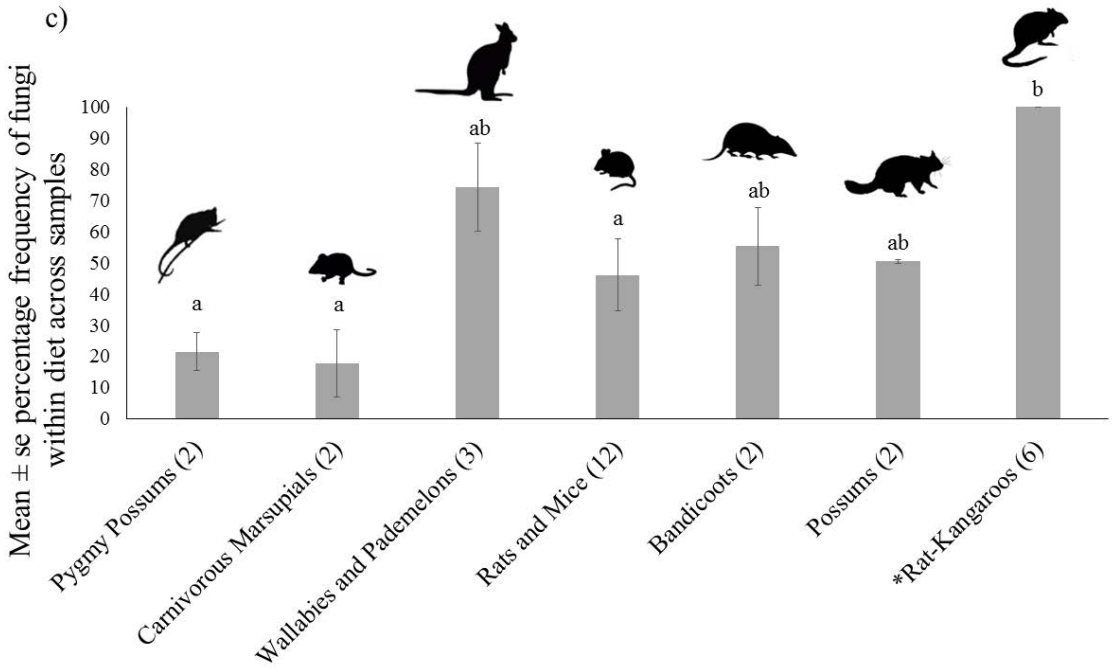
						winter, spring)		
	Trichosurus vulpecula				50.0		5 [F]	Reddell et al. 1997
Dasyuridae (carnivorous marsupials)	*Antechinus stuartii*	18	13		28.5 ± 8.69	(34.0, 20.0, 57.0, 37.5)	111 [F], 61[D], 61[S]	Vernes and Dunn 2009; O'Malley 2012; Vernes et al. 2015
	Antechinus godmani				7.1		14 [F]	Reddell et al. 1997
Thylacomyidae (bilbies)	*Macrotis lagotis*	2	2	0.6 ± 0.1	8.1		232[A], 206 [F], 26[D]	Gibson 2001; Navnith et al. 2009
Hypsiprymnodontidae (musky rat-kangaroos)	*Hypsiprymnodon moschatus*	1	1		67.5 ± 16.27	(42.0, 100, 18.0, 50.0)	171 [F], 2 [D], 165[S]	Reddell et al. 1997; Dennis 2002; Weatherstone 2012
Burramyidae (pygmy possums)	*Cercartetus concinnus*				15.4		39 [F]	Pestell and Petit 2007
	Cercartetus nanus				27.8		8 [F]	Vernes and Dunn 2009

2.4.1 Fungal abundance in mammalian diets relative to other foodstuffs

Fungal specialists (family Potoroidae, excluding non-specialists *B. lesueur* and *Ae. rufescens*) ate a significantly higher quantity of fungi (relative to other foodstuffs) than Muridae and Peramelidae (Figure 2.1a; pairwise comparisons Potoroidae and Muridae, $P < 0.001$; Potoroidae and Peramelidae, $P = 0.026$, respectively). When non-specialists (*B. lesueur* and *Ae. rufescens*) were included, Potoroid mammals were no longer significantly different from Peramelidae ($P > 0.1$) but were still significantly higher than Muridae ($P = 0.014$). The average fungal abundance for fungal specialists was greater than 48% and up to 82.6 ± 7.29% for *P. longipes* (long-footed potoroo; Table 2.1). Generalist mammal species that consumed comparable amounts of fungi were *R. fuscipes* (54.4%) and *R. rattus* (introduced black rat; 90%; Table 2.1).


a)
Mean ± se percentage abundance of fungi within diet
100
90
80
70
60
50
40
30
20
10
0
b
a
a
*Rat-Kangaroos (6)
Rats and Mice (16)
Possums (4)


b)
Mean ± se percentage fungi wthin diet
90
80
70
60
50
40
30
20
10
0
a
a
b
a
ab
b
a
ab
b
a
a
b
Summer
Autumn
Winter
Spring
Rats and Mice (5)
Bandicoots (3)
*Rat-Kangaroos (5)


c)
Mean ± se percentage frequency of fungi within diet across samples
100
90
80
70
60
50
40
30
20
10
0
a
a
ab
a
ab
ab
b
Pygmy Possums (2)
Carnivorous Marsupials (2)
Wallabies and Pademelons (3)
Rats and Mice (12)
Bandicoots (2)
Possums (2)
*Rat-Kangaroos (6)

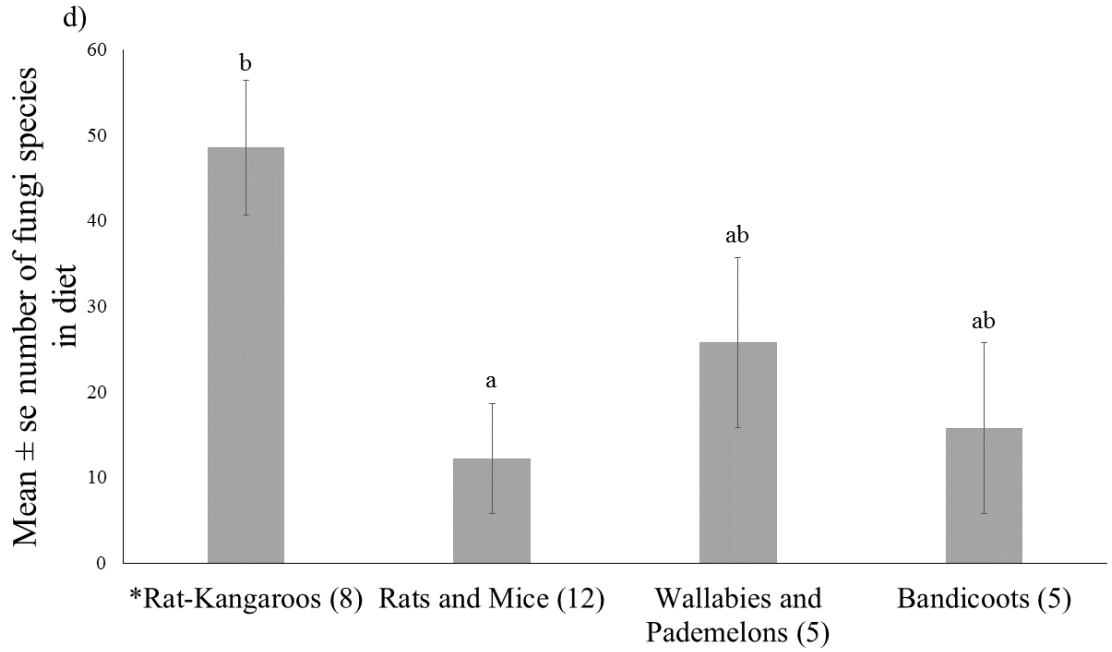

d)
Mean ± se number of fungi species in diet
60
50
40
30
20
10
0
b
a
ab
ab
*Rat-Kangaroos (8)
Rats and Mice (12)
Wallabies and Pademelons (5)
Bandicoots (5)

Figure 2.1: Abundance, frequency, diversity and abundance across seasons for fungal diets of different mammal families. a) Mean (± SE) percentage abundance of fungi relative to other food stuffs within diets of three mammal families, b) mean ± SE percentage abundance of fungi within diets of three mammal families across seasons, c) mean ± SE percentage frequency of fungi across samples within mammal family diets, d) mean ± SE number of fungal species within the diets of four mammal families. Different letters represent significant differences across mammal families or across mammal families within season (P <0.05). Number in parentheses are the number of mammal species represented. Families are as follows: pygmy possums are Burramyidae, carnivorous marsupials are Dasyuridae, wallabies and pademelons are Macropodidae, rats and mice are Muridae, bandicoots are Peramelidae, possums are Phalangeridae and rat-kangaroos are Potoridae. Rat-kangaroos include fungal specialists (*).

2.4.2 Frequency of fungi in mammalian diets across samples

All Potoroid species sampled were recorded to eat fungi (100% frequency) except for *Ae. rufescens* (91.7 ± 8.35% frequency, n = 31; Table 2.1). On average, across mammal families, the frequency of fungi in the diets of fungal generalists ranged between 21-74%. Generalised linear models were not significantly different between families for frequency data (Figure 2.1c). Despite the low average frequency for Muridae, three species were recorded to eat fungi at a frequency greater than 80% (*R. fuscipes*, *R. rattus,* and *Uromys caudimaculatus*; giant white-tailed rats). *Wallabia bicolor* and *Dendrolagus lumholtzi* (Lumholtz's tree-kangaroos) also ate fungi at a frequency greater than 80% (Table 2.1).

2.4.3 Seasonality of fungi in mammalian diets

When considering the presence/absence data across seasons, most mammal species ate fungi in all seasons (Table 2.1). Only two studies had data on frequency of individuals

consuming fungi across different seasons. Vernes et al. (2015) reported that all (100%) *R. fuscipes* individuals ate fungi all year, except in summer when fungi were present in 93% of individuals. Fewer individuals of *Melomys cervinipes* (fawn-footed melomys) and *A. stuartii* (brown antechinus) ate fungi year-round (mean ± SE across seasons: 43.2 ± 11.0% and 37.1 ± 7.6%, respectively). However, consumption by both species peaked in winter (74% and 57%, respectively) (Vernes et al. 2015). Dennis (2002) reported that on average 52.5% (± 17%) of individuals of *Hypsiprymnodon moschatus* (musky rat-kangaroos) ate fungi year-round and 100% of individuals consumed fungi in autumn.

Potoroid mammals ate significantly more fungi (relative to other food items) than Muridae in all seasons (Figure 2.1b). Potoroid mammals also ate more fungi than Peramelidae in all seasons but this was not significantly different between autumn and winter. The abundance of fungi always exceeded 41% for species within Potoroidae in all seasons. Other occurrences of a comparable amount of fungi in diets were *R. fuscipes* diets in autumn, winter and spring (>50%) and *Perameles nasuta* (long-nosed bandicoot) diets in autumn and winter (>47.5%; Table 2.1).

2.4.4 Fungal diversity within mammalian diets

Significantly more fungal species were recorded in the diets of Potoroidae when compared with Muridae (Figure 2.1d; $P = 0.00341$), but not when compared with Macropodidae or Peramelidae (Figure 2.1d). There was no significant difference between the fungal genera recorded in the diets of these four mammal families (7.4 ± 3.12, 11.0 ± 4.84, 16.2 ± 4.84, 22.4 ± 3.82 fungal genera recorded in Muridae, Peramelidae, Macropodidae and Potoroidae families, respectively). Except for *B. lesueur*, Potoroidae species had at least 29 fungal species recorded in their diets, with *P.*

tridactylus having the most fungal species recorded (97 species; Table 2.1; Nuske et al. 2017a). Generalist mammals with comparably diverse fungal diets are *R. fuscipes* (70 species), *W. bicolor* (61 species) and *Per. nasuta* (49 species; Figures 2.2 and 2.3).

There were significant linear relationships between the number of fungal species within a mammal species diet and the number of studies referenced ($R^2 = 0.783$, $P < 0.0001$; Figure 2.2) or the cumulative number of samples ($R^2 = 0.452$, $P < 0.0001$; Figure 2.3). However, the cumulative number of samples and number of studies did not differ significantly between mammal families for any of the data.

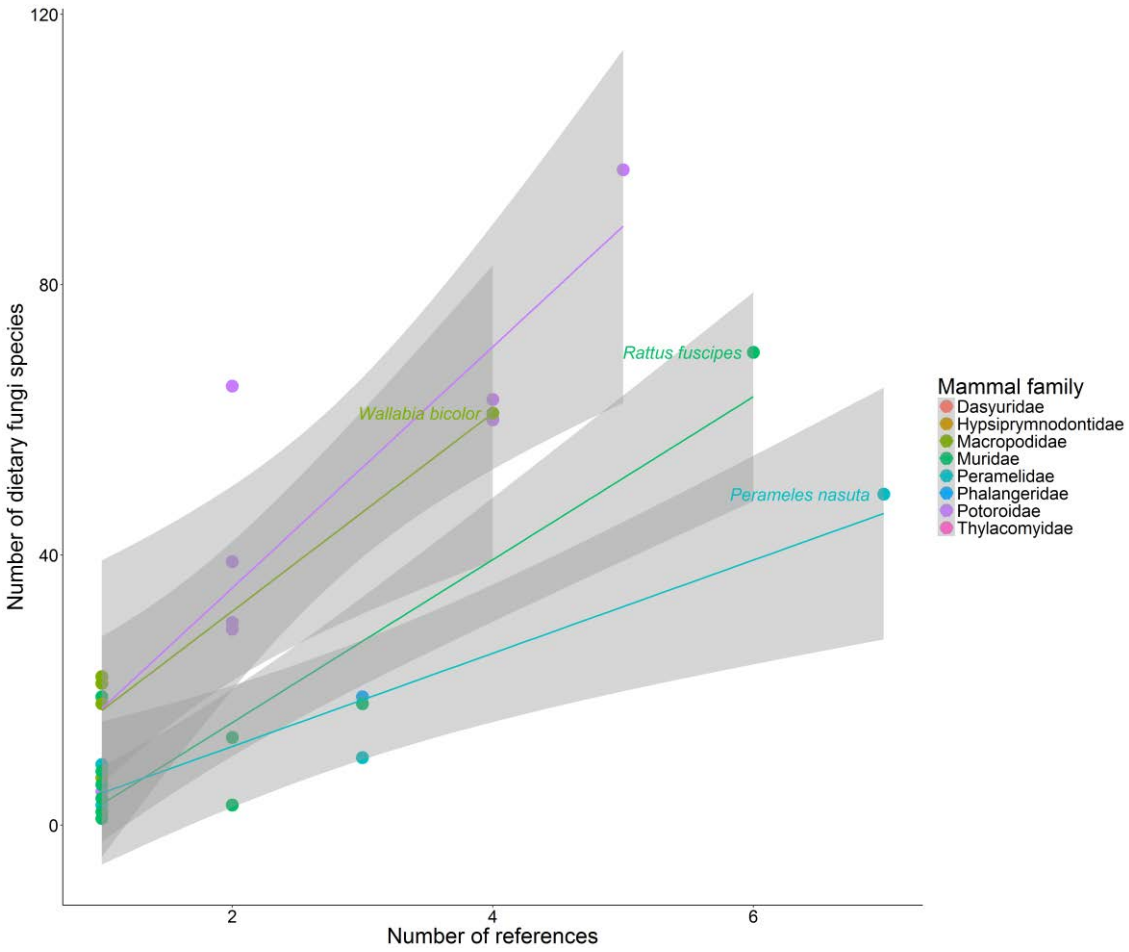


Figure 2.2: Number of references versus the number of fungal species recorded in each mammal species diet. Different colours represent different mammal families as per the associated legend. Lines represent linear models per mammal family ± SE. Generalist mammal species with diverse fungal diets (on par with specialists) are labelled: *Rattus fuscipes* (bush rats), *Wallabia bicolor* (swamp wallabies) and *Perameles nasuta* (long-nosed bandicoots).

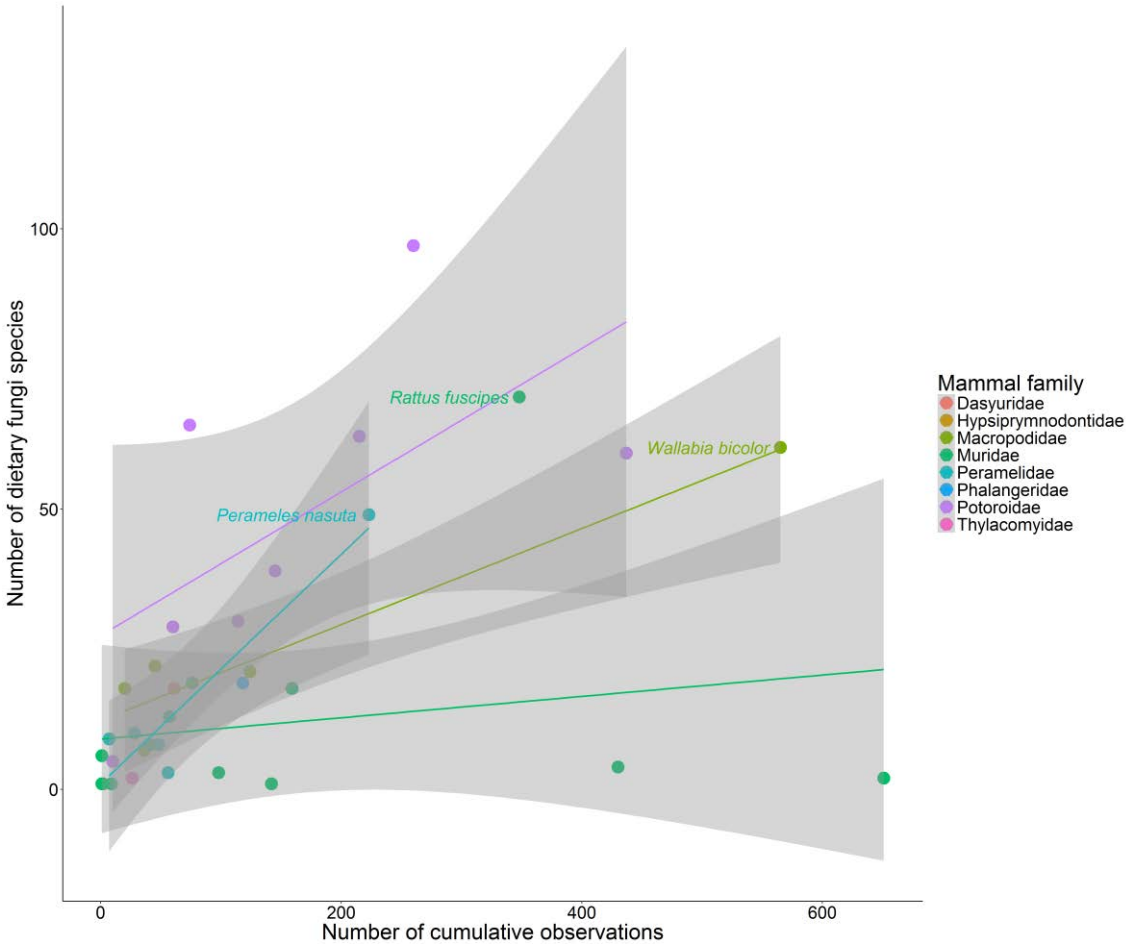


Figure 2.3: Number of cumulative observations versus number of fungal species recorded in each mammal species diet. Different colours represent different mammal families as per the associated legend. Lines represent linear models per mammal family ± SE. Generalist mammal species with diverse fungal diets (on par with specialists) are labelled: *Rattus fuscipes* (bush rats), *Wallabia bicolor* (swamp wallabies) and *Perameles nasuta* (long-nosed bandicoots).

Four variables within the selected linear mixed-effects model helped to explain the variation in the number of fungal species recorded between mammal species' diets: (1) whether the aim of the study included mycophagy, (2) cumulative number of samples, (3) number of references and (4) mammal family. With individual reference and location as random effects, the model explained 95.7% of the overall variation. Potoroid mammals significantly contributed positively to the slope of the model (Table 2.2). When the aim of the study was excluded only a marginal difference in explanatory power was observed ($P = 0.082$).

Table 2.2: Linear Mixed Effects Model with the number of fungal species in a mammal species diet as the response variable. Fixed effects are aim of the study, cumulative number of samples number of references and mammal family and reference and location are random effects. The model explained 95.7% of the variation. Significant values are in bold ($P < 0.05$). *Potoroidae include fungal specialists.

Variable		df	t-value	*P*-value
aim of study did not include mycophagy		41	-0.777	0.4416
aim of study included mycophagy		41	0.024	0.9807
number of samples		16	3.060	**0.0075**
number of references		16	11.832	**0.0000**
mammal family	Hypsiprymnodontidae (musky rat-kangaroos)	16	-0.381	0.7077
	Macropodidae (wallabies, pademelons and tree-kangaroos)	16	-0.093	0.9274
	Muridae (rats and mice)	16	-0.758	0.4595
	Peramelidae (bandicoots)	16	-2.029	0.0594
	Phalangeridae (possums)	16	-2.479	**0.0247**
	*Potoroidae (rat-kangaroos)	16	2.139	**0.0482**
	Thylacomyidae (bilbies)	41	-0.167	0.8684

Without considering fungal specialists, Potoroid mammals, other mycophagous mammals have considerable redundancy relating to the identity of the fungal species

eaten (Table 2.3; Appendix A). At two out of three locations in Australia where seven or more mammal species were studied within 100 km of each other, specialists (*Potorous* spp. and *B. tropica*) consumed a higher diversity of fungal species compared to generalist mammal species (Table 2.3). The exception was for Northern NSW, albeit where there was only one sample available for *P. tridactylus* due to their low capture rate (K. Vernes pers. comm.). *Potorous* spp. in the South-Eastern NSW mammal community consumed a much higher amount of unique mammal species than generalist mammals. An almost equal number of unique fungal species was recorded within *B. tropica* diets (12) compared to those found in *Thylogale stigmatica* (red-legged pademelon)*, I. obesulus peninsulae* and *U. caudimaculatus* diets combined (11) within the North Queensland mammal community.

Table 2.3: Number of fungal species recorded within mammal species diets within 100 km of the three given locations. N QLD: North Queensland on Atherton Tablelands (17° 16' 15.99' S, 145° 38' 2.00" E); N NSW: Northern New South Wales on Gibraltar Range (29° 32' 59.17" S, 152° 16' 0.50" E); SE NSW/E Vic: South Eastern NSW near Victorian border (37° 23' 30.00" S, 149° 49' 19.99" E). U: number of fungal species recorded within that mammal species' diet compared only to the mammal species' diets at the same location. S and NS are the fungi species recorded in that mammal species' diet and the others at the same location, or not recorded in that mammal species' diet but recorded in the others. *St* is the number of studies, *O* is the number of samples. Species marked with asterisk* are fungal specialists.

Site	Mammal species	U	S	NS	*St*	*O*
N QLD	**Bettongia tropica*	12	16	11	2	114
	Thylogale stigmatica	6	3	30	1	20
	Isoodon obesulus peninsulae	3	5	31	1	48
	Uromys caudimaculatus	2	8	29	3	159+
	Aepyprymnus rufescens	0	7	32	1	6
	Isoodon macrourus	0	8	31	1	7
	Perameles nasuta	0	4	35	1	3

N NSW	*Rattus fuscipes*	3	28	7	3	205
	Wallabia bicolor	3	22	13	2	350
	Antechinus stuartii	0	13	25	1	61
	Macropus parma	0	16	22	1	45
	Melomys cervinipes	0	13	25	1	76
	Perameles nasuta	0	17	21	1	45
	**Potorous tridactylus*	0	7	31	1	1
	Pseudomys novaehollandiae	0	1	37	1	18
	Thylogale thetis	0	16	22	1	124
SE NSW/E Vic	**Potorous spp.*	48	25	7	6	333
	**Potorous longipes*	20	26	34	3	173
	**Potorous tridactylus*	17	33	30	3	160
	Perameles nasuta	2	19	59	2	28
	Wallabia bicolor	1	5	74	1	19
	Trichosurus caninus	1	12	67	1	55
	Rattus fuscipes	1	1	78	1	1
	Pseudomys fumeus	0	5	75	1	55
	Isoodon obesulus	0	1	79	1	18

2.5 Discussion

Taking into account the higher number of references and samples for Potoroid mammals, these fungal specialists nevertheless consistently had a greater diversity of fungal taxa in their diets compared to generalist mammals. The cumulative data also showed that Potoroid mammals consistently ate fungi, at a higher abundance compared to other food, and consistently over seasons compared to generalist mammals. Therefore, fungal specialists (family Potoroidae, except *Ae. rufescens* and *B. lesueur*) can be considered to contribute disproportionally more to the potential dispersal of fungi than most other mammal taxa (i.e. there is little functional redundancy). *Potorous* spp. in the South-Eastern NSW mammal community consumed a much higher amount of unique fungal taxa than generalist mammals, providing more evidence that these species perform a unique and irreplaceable fungal dispersal role. Consequently, the loss of fungal specialists from such an ecosystem is expected to impact heavily on fungal dispersal dynamics. This may be particularly true for those fungal taxa only found in

Potorous diets in south-eastern NSW (48 taxa). This pattern of a few specialists and many fungal generalists is paralleled in other parts of the world, with species like the *Glaucomys sabrinus* (northern flying squirrel) and *Clethrionomys californicus* (red-back vole) in North America, and *Myodes glareolus* (bank voles) in Central Europe as the fungal specialists among a diverse array of generalist mammals known to consume fungi (Hayes et al. 1986, Malajczuk et al. 1987, Caldwell et al. 2005, Flaherty et al. 2010, Kataržytė and Kutorga 2011, Schickmann et al. 2012).

Fungal dietary values for Potoroid mammals were not significantly different from the average values obtained for Peramelidae; the Peramelidae values themselves being strongly influenced by high fungal consumption in *Per. nasuta*. Within Macropodids (wallabies, pademelons and tree-kangaroos), particularly *W. bicolor,* also consumed a comparable diversity of fungi at a similar frequency to Potoroid mammals. Despite the fact that, on average, Muridae species consumed significantly less fungi (in abundance, frequency, diversity and across seasons), *R. fuscipes* consumed comparable quantities to fungal specialists. *Rattus fuscipes* most probably contribute more to fungal dispersal than other small mammals. Several studies comparing *R. fuscipes* fungal diets directly to other small mycophagous mammals have found that they eat a higher diversity and abundance of fungi (Vernes and Dunn 2009, O'Malley 2012, Vernes et al. 2015), and their fungal diet can be as diverse as that of the specialist *P. tridactylus* (Tory et al., 1997). Therefore, there may be functional redundancy between the fungal dispersal roles of specialist and generalist mammal species within some communities.

The relationship between the number of fungi recorded in a mammal species' diet and the number of published references (likewise for number of dietary samples) suggests that for many mammals we have not yet come close to quantifying the total number of fungal species that are eaten and dispersed. Consequently, I cannot dismiss the

possibility that further mycophagy studies on fungal generalists would reveal more mammals to have comparable mycophagy rates to fungal specialists and so my conclusions here must be treated with caution. Indeed, *R. fuscipes*, *W. bicolor* and *Per. nasuta* also have a high number of references and replicates (>200) for diversity data. The conclusion that they contribute more to fungal dispersal than other fungal generalists deserves more study to further disentangle sampling bias. Nevertheless, the results show that those species are likely important fungal dispersers, particularly in areas where members of Potoroidae fungal specialists are locally extinct.

Most Potoroid mammals have larger home ranges than would be predicted from their size (Christensen 1980, Taylor 1993, Green et al. 1998, Vernes and Pope 2001). This large scale of movement adds to the unique nature of the specialists' fungal dispersal roles as it increases the chances of long-distance dispersal of spores. This is also the case for larger mycophagous mammals like *W. bicolor* (O'Malley 2012). As specialists, Potoroid mammals are very selective of the habitats they occupy (Norton et al. 2010). For instance, *B. tropica* distribution is restricted to a narrow strip (ca. 10 km) of relatively high-rainfall open-sclerophyll forest on the boundary of rainforest (Bateman et al. 2011). In contrast, some highly mycophagous mammals with generalist diets utilise a much wider range of habitats. For instance, in northern NSW, GPS data shows that *W. bicolor* utilise fragmented forest patches intermixed with pasture (Danks 2011). Coupled with gut-retention times, the predicted long-distance dispersal for spores ingested by *W. bicolor* was up to 1000 m (Danks 2011). Spore dispersal can also occur secondarily through the dynamics of food-webs. Predators consume smaller mycophagous animals (invertebrates or mammals) which then disperse spores over longer distances and over habitat boundaries (Jacobs and Luoma 2008, O'Malley 2012,

Lilleskov and Bruns 2013). This could be a particularly advantageous way for truffle fungi to disperse into new habitats.

The studies cited here show that Australian mammals consistently consume fungi year-round (more so for Potoroidae). The few studies on the seasonal abundance of truffle-like fungi in Australia show that, even though the abundance of truffles is reduced in drier months, truffles are rarely absent (Johnson 1994b, Claridge et al. 2000, Abell et al. 2006); a trend reflected in the continued consumption of truffle-like fungi by mycophagous mammals year-round (Taylor 1992, Vernes et al. 2001, Vernes 2014). Year-round consumption and thus dispersal of truffle-like fungi has also been recorded for mycophagous mammals in North America (North et al. 1997, Vernes et al. 2004, Meyer et al. 2005). This is an advantage of truffle-like fungi over epigeous taxa, which are more seasonal in their production (e.g. North et al., 1997).

The results reported in this meta-analysis are solely based on morphological identification of spores from within scat or stomach samples, which has known limitations for the resolution of many taxa (e.g. Russulaceae) but all literature to date has utilised this method. Barcode DNA regions are being developed that offer much promise for identification of environmental samples to species, or at least genus level (Schoch et al. 2012), especially when combined with modern high throughput sequencing technologies that sequence mixed DNA communities (Lindahl et al. 2013). However, such barcode regions need to be calibrated against robust multi-gene species delimitation on a lineage-by-lineage basis. For Australian species, for example, in *Cortinarius*, a genus that contains truffle-like species, the internal transcribed spacer (ITS) is an effective barcode (Stefani et al. 2014); while in *Laccaria*, also containing truffle-like species, ITS does not fully resolve all phylogenetic species (Sheedy et al. 2013). Application of barcode regions to identify fungal spores in mammal scats will

require comprehensive barcoding of authoritatively named reference collections of known species of fungi, along with means of designating those species yet to be formally named. Taxonomic assignment of sequences is continuing to become more accurate as online databases grow (Tedersoo et al. 2011, Kõljalg et al. 2013) and functional assignment of taxa is becoming possible (Nguyen et al. 2015b).

This meta-analysis confirms that mammals with fungal specialist diets contribute disproportionally more to the consumption and thus the potential dispersal of fungi than other mammals within Australia and so highlight the significance of mammals, particularly fungal specialists, for maintaining diverse ectomycorrhizal fungal communities. This chapter also highlights that significant gaps in knowledge remain about functional redundancy for fungal dispersal between mammals. For instance, in many areas of Australia there is not enough data to directly compare specialist and generalist fungal diets. Additionally, much of the data from the studies presented here could not be compared because many fungal taxa remain undescribed. Concurrent sampling of specialist and generalist fungal diets would help verify the accuracy of these results. This is the focus of my next chapter. Sequence-based isolation and identification of fungi was utilised as it is a more precise and comparable method of measuring diversity. This will permit further insight into the functional redundancy of fungal dispersal by specialists and generalists, and help to understand whether the loss of fungal specialists could potentially influence long-term forest health.

Chapter Three: The consequences of losing the northern bettong, a fungal specialist, for the dispersal of ectomycorrhizal fungi

3.1 Abstract

The level of functional redundancy between the dispersal roles performed by a fungal specialist, *Bettongia tropica* (northern bettong) and a combined suite of nine co-occurring fungal generalists was tested. *Bettongia tropica* consumed a significantly different fungal community with higher diversity and more unique taxa. Consequently, they performed a unique dispersal role for ectomycorrhizal and truffle fungi compared to the nine generalist mammal species examined; there was little functional redundancy. The endangered *B. tropica* is in decline and has already disappeared from the edges of its distributional range. These findings imply the loss of this species could have dramatic consequences for ectomycorrhizal fungal species diversity in these habitats. I conclude that conservation of fungal specialists is imperative to maintaining ectomycorrhizal fungal diversity and healthy plant-mycorrhizal relationships.

3.2 Introduction

Based on the existing literature, most members of the small marsupial family, Potoroidae, consume a higher abundance and diversity of fungi than do other Australian mammals (Nuske et al. 2017b; Chapter Two). This suggests that there is little or no functional redundancy associated with the dispersal of these fungal taxa by the Potoroidae. However, the literature upon which this conclusion is based also contains a significant taxonomic bias; *Potorous* spp. and *Bettongia* spp. (Potoroidae) having higher number of studies and samples than other mammal species (Nuske et al. 2017b). Additionally, some generalist mammals consumed a fungal species diversity on par with these fungal specialists, indicating that, at least in some systems, functional

redundancy may be higher. Therefore, in this current study, I aimed to remove the influence of this bias and re-examine functional redundancy in fungal dispersal by mammals, by explicitly comparing the fungal diet of an endangered fungal specialist, *Bettongia tropica* (Potoroidae), to that of other co-occurring mammal species within the same community.

Bettongia tropica is endemic to the Wet Tropics of North Queensland, Australia. The species is endangered and in decline, as it has already disappeared from a number of regions at the edge of its distributional range (Bateman et al. 2011). *Bettongia tropica* is described as an ecotonal specialist. Its distribution is restricted to wet open sclerophyll forest where the canopy is dominated by host plants that associate with ectomycorrhizal-truffle-bearing fungi that border rainforest (Vernes and Pope 2001, Vernes et al. 2001, Abell et al. 2006). *Bettongia tropica* diet consists mainly of a diverse range of (truffle) fungi consumed throughout the year (McIlwee and Johnson 1998, Vernes et al. 2001).

Definitions of fungal specialists and fungal generalists used here are as per Nuske et al. (2017b); the former being mammals that are reliant on fungi as a food resource and the latter as mammals that only consume fungi seasonally, or as a supplementary food source. I hypothesise that there will be little to no functional redundancy between a fungal specialist and the combined dispersal roles of fungal generalists within a given ecosystem. Specifically, I test the null hypothesis that *B. tropica* and co-occurring generalist mycophagous mammals disperse the same fungal taxa, with no differences in diversity and composition.

3.3 Methods

3.3.1 Field sampling

Mammal diets were examined by collecting scat samples from trapped individuals. Trapping and scat collection was carried out at three locations on the Lamb Range, North Queensland, Australia; Emu Creek (17°6'18.10"S, 145° 31'47.46"E), Danbulla State Forest near Tinaroo Dam (17°9’50.30"S, 145°32’11.56"E; now part of Danbulla National Park) and Davies Creek National Park (17°1’23.28"S, 145°34’55.71"E). These sites are roughly the same locations as used by previous studies on populations of *B. tropica* (Pope et al. 2000, Vernes et al. 2001). Elevation is between 600 and 900 m above sea level. The dominant ectomycorrhizal tree species are *Eucalyptus crebra, E. tindaliae, E. mediocris, Corymbia intermedia, Allocasuarina littoralis, Al. torulosa* and *Acacia flavescens*.

Seven or eight cage trap transects were set up in open forest at each location. Cage traps were spaced 100 m apart, 7-8 cages per transect totalling 53 cage trap locations per site. Three to four Elliot trap transects were also set with traps 50 m apart in each transect; totalling 50 Elliot traps/locations. Traps were baited with a mixture of peanut butter, oats, vanilla, honey and sardines. All traps were set at dusk. Cage traps were checked from midnight and Elliot traps one hour before dawn. Trapping was carried out across four consecutive nights at each site. Elliot trapping occurred within three weeks of cage trapping. Traps were set in three seasons; November-December 2014 (late dry), February-March 2015 (early wet) and May-June 2015 (late wet). However, due to logistic constraints Elliot traps were only set at Tinaroo Dam and Davies Creek, in the late dry and early wet seasons.

Each animal was handled according to James Cook University animal ethical guidelines (Approved ethics application A2044). Mammals were identified according to Van Dyck

et al. (2013) and marked by either removing a small patch of hair with scissors at the base of the tail or microchipping (*B. tropica* only; Minichips, Micro Products Australia, Canning Vale, WA or ISO FDX-B Microchips, OzMicrochips, Peakhurst, NSW). Scats were collected from the bottom of each Elliot trap or from plastic placed under each cage trap. All traps and plastic were initially cleaned with 70% ethanol and then re-cleaned subsequent to each animal being caught. Scats were stored on ice, or in a portable fridge (4 ºC) in the field and transferred to -20 ºC as soon as possible (≤ 4 days).

3.3.2 Laboratory Analysis

Scats were only used from the first capture of an individual per trapping session. The number of samples from each mammal species per site and season is listed in Appendix B. Obvious soil contamination was removed from each scat before processing. A small sample of faecal material was then taken from the inside of individual boluses for each scat sample. This material was homogenised manually with a sterilised blunt probe in a weight boat and 0.25 g of homogenate taken for DNA extraction.

DNA was extracted using PowerLyser PowerSoil DNA Isolation kit following the manufacturer's instructions (Mo Bio, Carlsbad, CA USA), except that the samples were lysed using a Qiagen Tissue Lyser for 2 x 30 secs at 30 Hz, swapping the position of the samples between runs. I included negative controls for all DNA extractions (without any material). These negatives were verified to have no measurable DNA on a NanoDrop (2000 Spectrophotometer, V1.0, Thermo Fisher Scientific, USA). DNA extracted from scat samples, as well as from other material (e.g. soil and roots) from multiple projects (including Chapter Four), were placed across six 96-well plates ensuring that no one replicate within mammal species, site or season was only on one plate. DNA was amplified with ITS3-Mix1-5

(5'CTAGACTCGTCANCGATGAAGAACGYRG-3') and barcoded ITS4ngs (5'-TCCTSCGCTTATTGATATGC-3') primers (Tedersoo et al. 2014). The primers were tagged with 10-11 base unique molecular identifiers (MID). DNA concentration was checked by running 5 µl of PCR product on 1% electrophoresis agarose gel for 20-30 min and PCR cycles adjusted as per Tedersoo et al. (2014). Negative controls for PCR extractions were included for all PCRs and checked on agarose gel. Positive controls for PCR reactions were included, which consisted of DNA from *Urnula craterium* (a European species, unlikely to show up in Australian samples) that consistently yielded bright bands on agarose gels. Three negative DNA extractions from batches extracted weeks apart were selected and sequenced with other samples to check for low levels of fungal contamination. Each plate of samples was sequenced with positive and negative controls. I used FavorPrep™ GEL/PCR Purification Kit (Favorgen Biotech Corp., Taiwan, China) to purify the amplicons, following manufacturer's instructions except two FADF Columns were used per plate, doubling the elution with milliQ water to 80 µl which I let stand for 5 mins. Normalized amplicons were subjected to ligation of Illumina adaptors using the TruSeq DNA PCR-free HT Sample Prep kit (Illumina Inc., San Diego, CA, USA). All 242 samples were sequenced in Illumina MiSeq 2×300 paired-end runs.

Because Australian truffle sequences are underrepresented in existing large-scale databases, I generated a reference sequence data set by sequencing representative specimens of multiple fungal species obtained from an extensive survey at Davies Creek (Abell-Davis 2008). The methods of DNA extraction, amplification and sequencing are described in Appendix C.

3.3.3 Bioinformatics

Bioinformatic analysis for the paired-end Illumina data were performed using PipeCraft (v1.0; http://dx.doi.org/10.15156/BIO/587450) as follows. Paired-end reads were merged and quality filtered using vsearch (v1.9.10; https://github.com/torognes/vsearch) with minimum overlap = 10, allowing no ambiguous base pairs and expected errors = 1. These high-quality sequences were allocated to samples (demultiplexed) based on MIDs using mothur (v1.36.1; Schloss et al. 2009), no primer or MID differences were allowed. Putative chimeric reads were detected and removed using *de novo* and reference database (UNITE uchime reference dataset v7.0; Abarenkov et al. 2010) based chimera filtering as implemented in vsearch (v1.9.10). Fungal ITS2 sequences were verified using ITS Extractor (v1.0.11; Bengtsson-Palme et al. 2013). Full ITS2 reads without flanking gene fragments were then clustered to Operational Taxonomic Units (OTUs) with CD-HIT (v4.6; Li & Godzik 2006) with 97% similarity threshold. Global singletons were removed from further analyses. Representative sequences were chosen using mothur abundance method and compared against UNITE (v7.0), GenBank ITS and my local truffle database to obtain taxonomic affiliation using BLASTn (Camacho et al. 2009).

I considered OTUs accurate at kingdom level if BLASTn matched to known species at <e-50, identity >75% and coverage >70% (Tedersoo et al. 2014). Other putatively non-fungal OTUs were removed from analyses. As predicted, positive controls consisted of an OTU that matched *Urnula craterium* at high read copies (between 7026 and >22000 copies) but also had OTUs present at low copy numbers (<21). These OTUs were also present in negative controls (at read copies never above 1110 in negative controls), suggesting a low level of contamination and tag-switching (i.e. where a MID on a sequence from a sample within a plate is switched to another sequence from another

sample, a common problem from amplicon high-throughput sequencing; Carlsen et al. 2012). As a precaution, I removed OTUs from samples if they were present in negative and positive controls. OTUs were further filtered manually based on BLASTn values. Taxonomic groups were assigned to functional categories using FUNGuild (v1.0; Nguyen et al. 2015). All Glomeromycota taxa were assigned as arbuscular mycorrhizal.

3.3.4 Statistical Analysis

OTU subsetting and multidimensional statistics were done using phyloseq package (McMurdie and Holmes 2013) in R (R Core Team 2012). Altogether 29 samples were removed from further analyses, because these comprised <500 filtered sequences (6 *B. tropica* samples and 18 samples from 6 generalist mammal species). Sequencing depth was not rarefied (McMurdie and Holmes 2014) but Hellinger-transformed before multidimensional statistics as this gives low weight to rare OTUs and offers good approximation to Euclidean distance (Legendre and Gallagher 2001). The fungal data were examined at three broad levels; at the whole OTU community level, only examining the ectomycorrhizal (ECM) fungal OTU's (4.1% of all taxa) and only examining truffle taxa (2.0% of all taxa). The ECM subset of the data included only taxa that were assigned as 'Highly Probable' and 'Probable' from the FUNGuild output (ECM taxa in Appendix E). Truffle fungi mature belowground (hypogeous with spore-bearing tissue completely enclosed), do not have an active dispersal mechanism and rely on animals for dispersal (truffle taxa listed in Table 3.1). Secotioid taxa and taxa listed with ambiguous fruiting habit because of uncertain taxonomic assignment (e.g. Russulaceae) were not included in the truffle fungi subset. Sporocarpic arbuscular mycorrhizal fungi were not included as truffle taxa. Only 4 OTUs of arbuscular mycorrhizal fungi could be distinguished to genus (3 matching sporocarpic *Glomus macrocarpus* and 1 matching *Scutellospora* sp.).

I compared fungal OTU richness per sample between *B. tropica* (n = 93) and all other mammal species combined as a representation of the rest of the mammal community (9 species, n = 120; Appendix B, thereafter referred to as generalist mammal species) using *Tukey* HSD tests. Linear models were used to examine the correlation between fungal OTU richness and fungal OTU sequencing depth per sample. These linear models were checked for normality, heteroscedasticity and outlier leverage using different transformations and data were best modelled with log-log transformation. ANCOVAs were performed to examine the effect of site (Davies Creek, Tinaroo Dam, Emu Creek), season (late dry, early wet and late wet) and mammal family on this correlation. Mammal families were only included if there was replication at each site and season. To estimate the accumulation of OTUs per sample, I created rarefied OTU accumulation curves for each mammal species and all samples using estimates and 95% confidence intervals from EstimateS 9.1.0 (Colwell 2013).

Multidimensional scaling (MDS, also known as Principal Coordinates Analysis; PCoA) were performed with Euclidian distances on Hellinger-transformed data and plotted to examine any structure in the community data. The MDS explained more variation in the first axes and modelled the groups in the data more efficiently than other non-constrained ordinations (Non-metric Multi-Dimenstional Scaling; NMDS or Redundancy analysis; RDA) on Chord or Hellinger-transformed data. Redundancy analysis and Correspondence Analysis (CA) with Hellinger-transformed data were used to examine the relationships between site, season and mammal species on the fungal community sequenced from the scats. Either RDA or CA was chosen to represent output based on which analysis had the highest fraction of explained variation (Legendre and Gallagher 2001). Partial-RDA or CCA (Canonical Correspondence Analysis) were used on the community data to partition out the variation within site and

season and to only examine the relationship between mammal species. Permutation Tests were used to establish the significance of the terms in constrained ordinations (function 'anova(ord)' in phyloseq which uses base vegan base functions; Anderson and Braak 2003, Oksanen 2015). Unique fungal OTUs within *B. tropica* and generalist mammal scats were examined by creating Venn diagrams using limma and VennDiagram packages in R.

3.4 Results

3.4.1 Total richness

There was a total of 7505 fungal OTUs across all 213 samples. Samples from generalist mammal species had a higher total OTU richness than *B. tropica* samples (Figure 3.1a). However, the accumulation curve for ECM OTUs predicts a higher diversity for *B. tropica* scats than for all generalists combined (Figure 3.1b). The number of OTUs obtained from the total number of samples sequenced did not reach an asymptote (Figure 3.1a), suggesting that more samples would be needed to fully characterise the fungal community within the scats; a common phenomenon with high throughput sequencing studies (Taylor et al. 2010, Anslan et al. 2016).

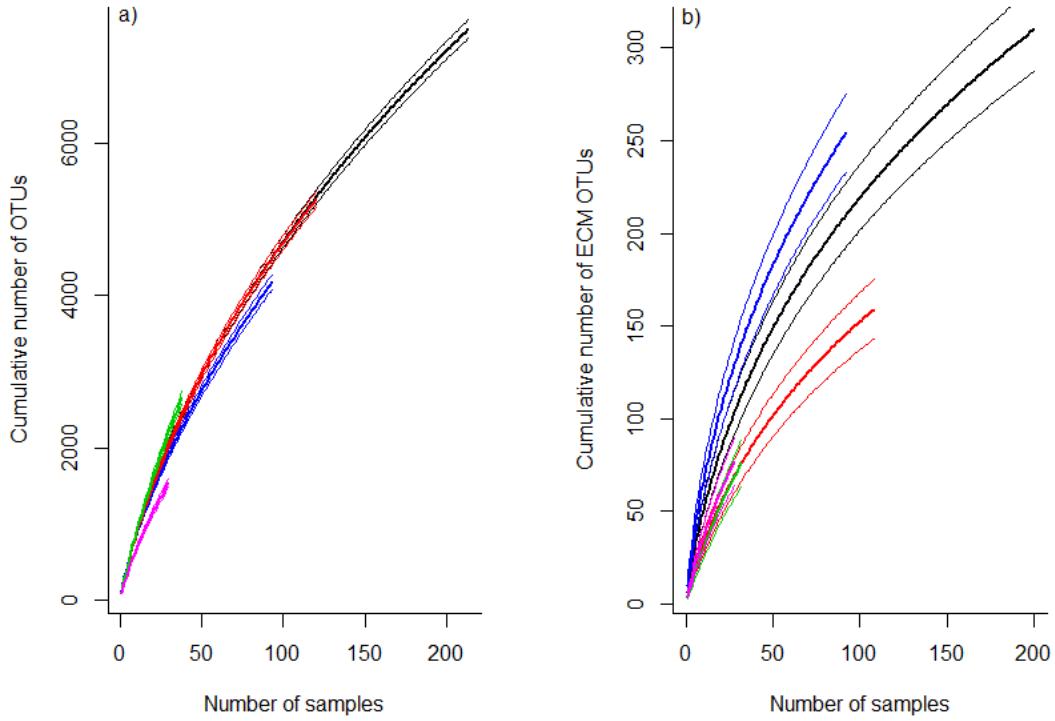


Figure 3.1: Rarefied accumulation curve for a) all OTUs and b) ectomycorrhizal (ECM) OTUs. Black lines are all scat samples (a: $n = 213$, b: $n = 200$), blue lines are *Bettongia tropica* samples (a: $n = 93$, b: $n = 92$), red lines are samples from nine generalist mammal species combined (a: $n = 120$, b: $n = 108$), green lines are *Isoodon macrourus* samples (a: $n = 38$, b: $n = 32$) and pink lines are *Uromys caudimaculatus* samples (a: $n = 30$, b: $n = 28$). Thin lines are 95% confidence intervals.

Only a small percentage of OTUs could be assigned to functional guilds by FUNGuild (20.4%). Of these the most diverse were undefined saprotrophs (728 OTUs, 9.7%), followed by ectomycorrhizal (323 OTUs, 4.3%). Many other functional groups were identified, including 199 OTUs of plant pathogens, 46 arbuscular mycorrhizal and 42 animal pathogens.

Only 150 OTUs could be assigned as truffle fungi (2.0%, 174 samples). Three hundred and six OTUs (4.1%) were assigned with ambiguous fruiting habit due to their uncertain taxonomic assignments (e.g. Russulaceae), or because they were secotioid

(Table 3.1). Most OTUs had unknown fruiting habit as the taxonomic assignment was at family level or higher (5416 OTUs, 72.2%). Twenty-one percent (1587 OTUs) were assigned as not truffles based on FUNGuild output or published literature.

Most (98.9%) of *B. tropica* samples and 90% of generalist mammal species contained ECM OTUs (Figure 3.2). Whereas the percentage of samples from generalist mammal species that contained known truffle OTUs was much less than *B. tropica* samples (70.8% and 95.7%, respectively).

3.4.2 Relative abundance of taxa

Truffle ECM OTUs had a higher relative abundance compared to other ECM OTUs for most mammal species (Figure 3.3), except *Antechinus flavipes* and *Isoodon obesulus*. Of all the known truffle genera in the scats, *Mesophellia* was the most OTU-rich (38.5% of all truffle OTUs, Table 3.1) and had the highest relative abundance in *B. tropica* scats. The second-most OTU-rich genus was *Hysterangium* (11.1% of all truffle OTUs, Table 3.1). Truffle families Hysterangiaceae, Mesophelliaceae and Tuberaceae also had many OTUs not matching published taxa (22, 12 and 15 OTUs, respectively; Table 3.1). *Mesophellia/Malajczukia* also had the highest relative abundance in *B. tropica, I. macrourus, Melomys, Uromys caudimaculatus, Trichosurus vulpecula* and *Zyzomys argurus* scats. Other relatively abundant ECM taxa were *Chondrogaster spB/spF* (in *B. tropica, Melomys, Rattus* and *U. caudimaculatus* scats), *Rhizopogon pseudoroseolus* (in *Perameles nasuta* and *U. caudimaculatus* scats) and *Russula* and Russulaceae (in *B. tropica, I. macrourus* and *U. caudimaculatus* scats). *Bettongia tropica* scats also had high relative abundance of OTUs matching *Scleroderma spB/spC, Cortinarius* spp., *Hysterangium* spp., *Lactarius romagnesii* and *Soliocassus polychromus.*

Table 3.1: Truffle taxa from scats and number of OTUs per taxon (OTU). Taxa in boldface are **truffles** and underlined are secotioid or taxa that have uncertain taxonomic assignments and contain truffle and/or secotioid species and epigeous mushroom/cup species. Taxa in grey font are not native to Australia (see footnotes).

Phylum	Family	Genus	Species	OTU
Ascomycota	Elaphomycetaceae			9
	Pezizaceae			1
	Pyronemataceae			7
		Paurocotylis		1
	Tuberaceae			15
		Dingleya	***D. spA***[a]	2
		Tuber[c]		1
			T. anniae[c]	1
			T. uncinatum[c]	2
Basidiomycota	Agaricaceae			17
	Amanitaceae			6
	Cortinariaceae			44
		Cortinarius		9
			C. globuliformis	5
			C. porphyroideus	1
	Entolomataceae			15
	Hydnangiaceae			3
	Hymenogastraceae	***Hymenogaster***	***H. glacialis***	1
	Inocybaceae			31
		Auritella		1
		Inocybe		5
	Physalacriaceae			1
	Strophariaceae			1
	Boletaceae			32
		Octaviania	***O. tasmanica***	1
		Solioccasus	***S. polychromus***	2
	Rhizopogonaceae			3
		Rhizopogon	***R. pseudoroseolus***[d]	1
	Sclerodermataceae			3
		Scleroderma	*S. spB/spC*[ab]	1
	Gomphaceae			4
		Gautieria	***G. amara***	1
	Gallaceaceae			2

	Austrogautieria	***A. macrospora***	1
Hysterangiaceae			22
	Hysterangium		5
		H. aggregatum	3
		H. cf gardneri[a]	7
Mesophelliaceae			12
	Chondrogaster		2
		C. spB/spF[ab]	1
	Gummiglobus	***G. joyceae/sp B***[ab]	1
	Malajczukia	***M. ingrattissima***	2
	Mesophellia		31
		M. glauca	16
		M. oleifera	5
Russulaceae			88
	Macowanites		1
		M. spC[a]	2
	Russula		22
	Zelleromyces	***Z. spE***[a]	2
Stephanosporaceae			1
	Stephanospora		3

[a] Morphological groups identified by Abell-Davis (2008).
[b] Morphological groups with <3% similarity at ITS2 (Appendix C).
[c] These OTUs possibly resulted from contaminant DNA or DNA from introduced taxa as *Tuber* are not native truffle species to Australia (Bonito et al. 2013) and consist of <0.5% of the relative abundance per sample (2-5 sequence copies) in 5 samples.
[d] These OTUs may represent contaminant DNA or DNA from introduced fungal species (*Rhizopogon* is not native to Australia but has been introduced with plantation tree species; e.g. Bell and Adams 2004). These OTUs are present in 4 samples, between 4-3190 sequence copies, which constitutes between 0.016 and 99.9% of the relative abundance per sample.

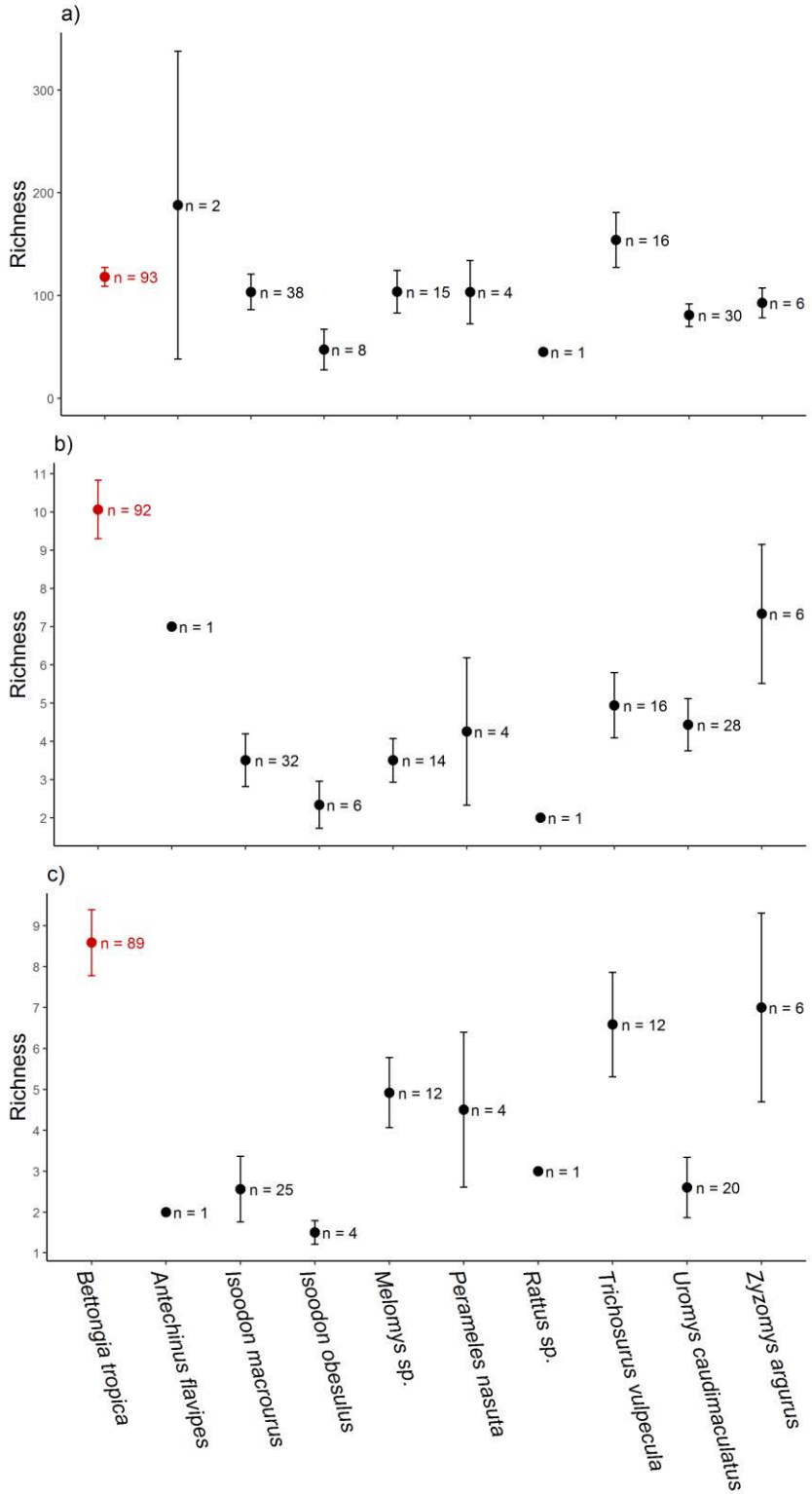


Figure 3.2: Mean ± SE OTU richness per sample for a) all OTUs, b) ectomycorrhizal OTUs and c) truffle OTUs for each mammal species. *Bettongia tropica* is the fungal specialist (points in red); all other species have generalist diets.

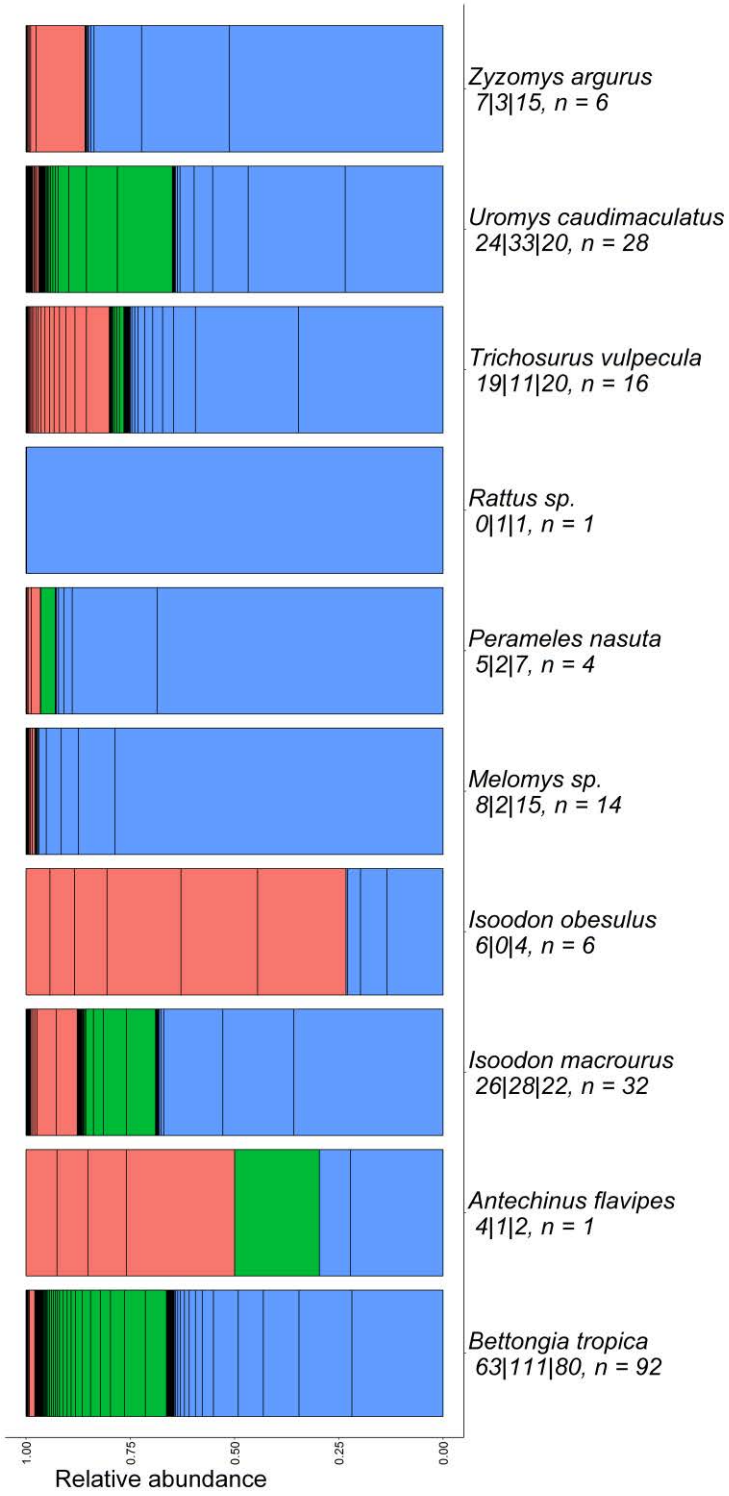


Figure 3.3: Relative abundance of ectomycorrhizal OTUs, for fruiting habits other than truffle (orange), uncertain fruiting habit (green) or truffles (blue), within a mammal species' scats. Numbers below mammal species names are total OTU richness for fruiting habits other than truffle (orange), uncertain fruiting habit (green) or truffles (blue) (*n* = number of replicates), respectively. Black are OTUs that have an abundance too low to display. *Bettongia tropica* (northern bettong) is a fungal specialist within the family Potoroidae.

3.4.3 OTU richness per sample

The fungal OTU richness per sample from *B. tropica* scats was significantly greater than in all generalist mammals combined (Table 3.2). This trend was most notable when only examining ECM OTUs or OTUs from truffle taxa (Table 3.2; Figure 3.2).

Log-log-scale richness correlated significantly with sequencing depth per sample at all subsets of the data. This correlation was influenced by mammal family (Potoroidae, Muridae and Peramelidae) and variation between sites and seasons (Table 3.3; Figure 3.4). *Bettongia tropica* (Potoroidae) positively influenced the correlation between richness and depth; for any given level of sequence depth in any season or at any site, *B. tropica* consumed a consistently greater level of OTU richness (Figure 3.4).

Table 3.2: Sample numbers (*n*) and mean ± SE OTU richness per sample (total OTU richness per mammal species) for the fungal specialist (*Bettongia tropica*) within Potoroidae and all non-bettong samples combined (generalists) across different subsets of the data (all OTUs, ectomycorrhizal OTUs and truffle OTUs).

	All OTUs		ECM OTUs		Truffle OTUs	
Mammal species	*n*	mean ± se (total)	*n*	mean ± se (total)	*n*	mean ± se (total)
Specialist	93	188.1 ± 9.34[b] (4176)	92	10.0 ± 0.75[b] (254)	89	8.6 ± 0.80[b] (135)
Generalists	120	101.2 ± 8.25[a] (5266)	108	4.1 ± 0.32[a] (159)	85	3.8 ± 0.44[a] (73)

[a,b:] Different superscript letters represent significant differences in *Tukey* HSD comparisons between *B. tropica* and generalist mammal species ($P < 0.05$).

Table 3.3: Results from type III ANOVA examining OTU richness per sample for different sections of the data and variation across OTU sequence count (depth) per sample, between sites (Davies Creek, Tinaroo Dam and Emu Creek), seasons (late dry, early wet and late wet) and mammal family (Potoroidae, *Bettongia tropica*, *n* = 93; Muridae, *Melomys sp.*, *n* = 15, *Rattus sp.*, *n* = 1, *Uromys caudimaculatus*, *n* = 30, *Zyzomys argurus*, *n* = 6; Peramelidae, *Isoodon macrourus*, *n* = 38, *I. obesulus*, *n* = 8, *Perameles nasuta*, *n* = 4). Significant *P*-values per variable are in bold. Richness and depth are transformed by natural log.

Dataset	Formula	Residual df	R^2_{adj}	Variable (df)	F	*P*-value
All OTUs	richness ~ depth + mammal family + site	189	0.975	depth (1)	43.5433	**<0.001**
				mammal family (3)	3.3311	**0.0207**
				site (2)	4.2571	**0.0156**
	richness ~ depth + site	191	0.975	depth (1)	55.3513	**<0.001**
				site (3)	7.2372	**<0.001**
	richness ~ depth + season	191	0.974	depth (1)	51.545	**<0.001**
				season (3)	4.3806	**0.005**
ECM OTUs	richness ~ depth + mammal family	179	0.902	depth (1)	163.1593	**<0.001**
				mammal family (3)	7.8732	**<0.001**
Truffle OTUs	richness ~ depth * season *mammal family	143	0.90	depth (1)	3.4437	>0.05
				season (3)	0.2219	>0.05

			mammal family (2)	0.5532	>0.05
			depth * season (2)	0.8218	>0.05
			depth * mammal family (2)	3.8854	**0.0227**
			season * mammal family (4)	1.1464	>0.05
			depth * season * mammal family (4)	0.6841	>0.05
richness ~ depth * mammal family + season	153	0.894	depth (1)	19.9355	**<0.001**
			mammal family (3)	0.7721	>0.05
			season (2)	10.7451	**<0.001**
			depth * mammal family	5.3764	**0.006**

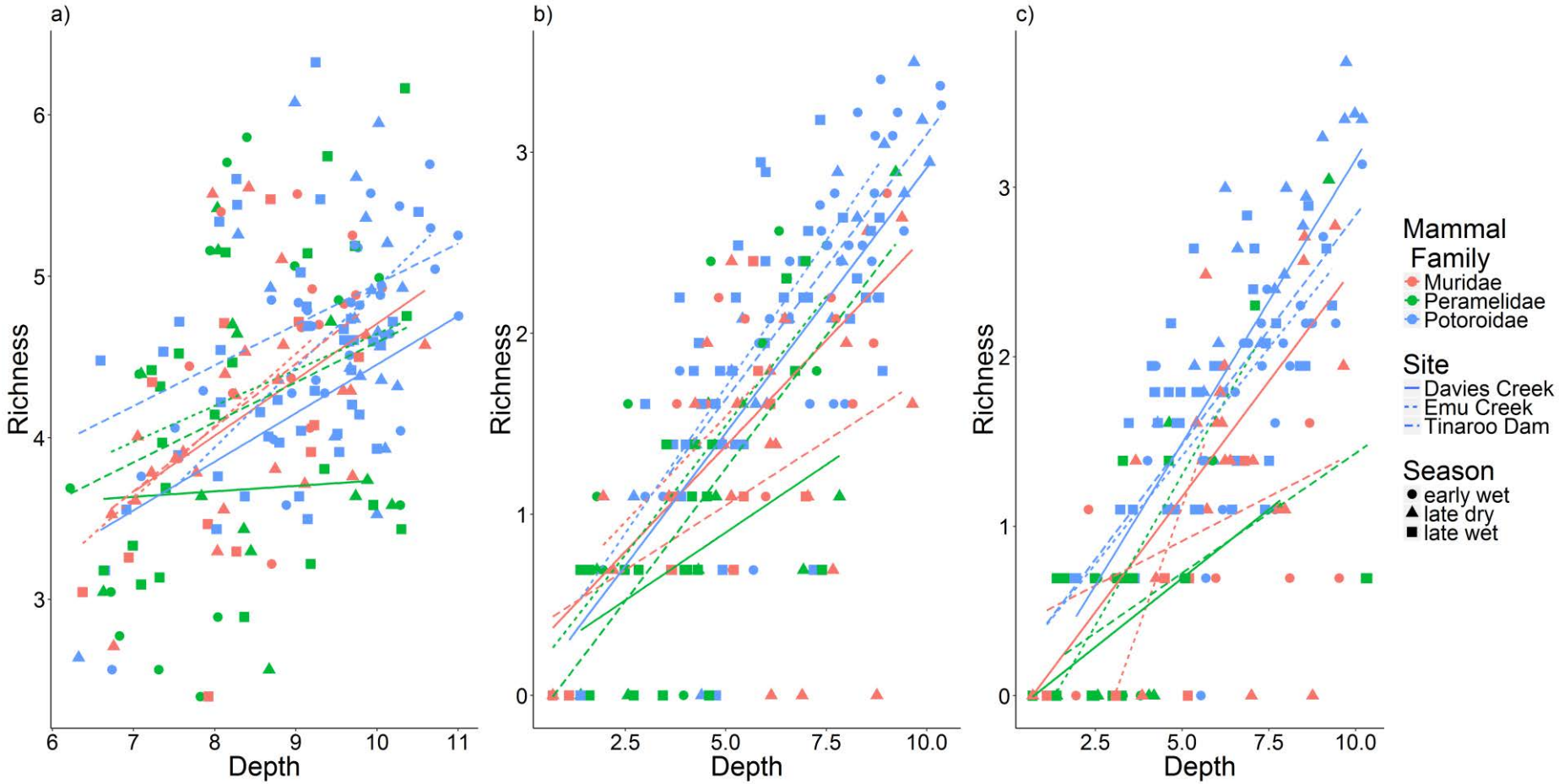

a)
b)
c)
Richness
Depth
Mammal Family
Muridae
Peramelidae
Potoroidae
Site
Davies Creek
Emu Creek
Tinaroo Dam
Season
early wet
late dry
late wet

Figure 3.4: OTU richness per sample versus sequence depth per sample in natural log-log-scale for a) all OTUs, b) ectomycorrhizal OTUs, and c) truffle OTUs across mammal families (colours), seasons (shapes) and sites (linear lines). See Table 3.3 for ANCOVA outputs. Mammal families for all OTU data are represented by *Bettongia tropica*, $n = 93$ for Potoroidae; *Melomys sp.*, $n = 15$, *Rattus sp.*, $n = 1$, *Uromys caudimaculatus*, $n = 30$, *Zyzomys argurus*, $n = 6$ for Muridae; and *Isoodon macrourus*, $n = 38$, *I. obesulus*, $n = 8$, *Perameles nasuta*, $n = 4$ for Peramelidae.

3.4.4 Unique OTUs

Bettongia tropica samples contained more ECM and truffle OTUs unique to these samples than generalist mammal species (Figure 3.5). However, when comparing the whole OTU dataset, there were more unique fungal OTUs in generalist mammal samples (Figure 3.5). Of all the truffle taxa matching the OTUs sampled from generalist mammal scats that were not in *B. tropica* scats, *Paurocotylis* sp. and *Gummiglobus joyceae/spB* were the only unique taxa.

3.4.5 Fungal community structure

Unconstrained multi-dimensional scaling ordinations (i.e. community analyses without *a priori* data structure) displayed distinct, but slightly overlapping, fungal communities between *B. tropica* and generalist mammal scats (Figure 3.6a). Nevertheless, as evidenced by the constrained RDA (Figure 3.6b) and permutation tests (Table 3.4), these communities were significantly different and there were significant interactions between site and season. Variation tended to be greater in fungal communities from the specialist than generalists (Figure 3.6). When site and season was conditioned out in a partial-RDA, *B. tropica* fungal diets were significantly different from all generalist mammal species combined (pseudo-$F_{1, 209} = 5.6108$, $P = 0.001$), although only 4.92% of the variation was explained by the axes (Figure 3.6c). The fungal diets of mammals

grouped within families (Figure 3.7) in partial-RDA constraining for mammal species and conditioning out site and season.

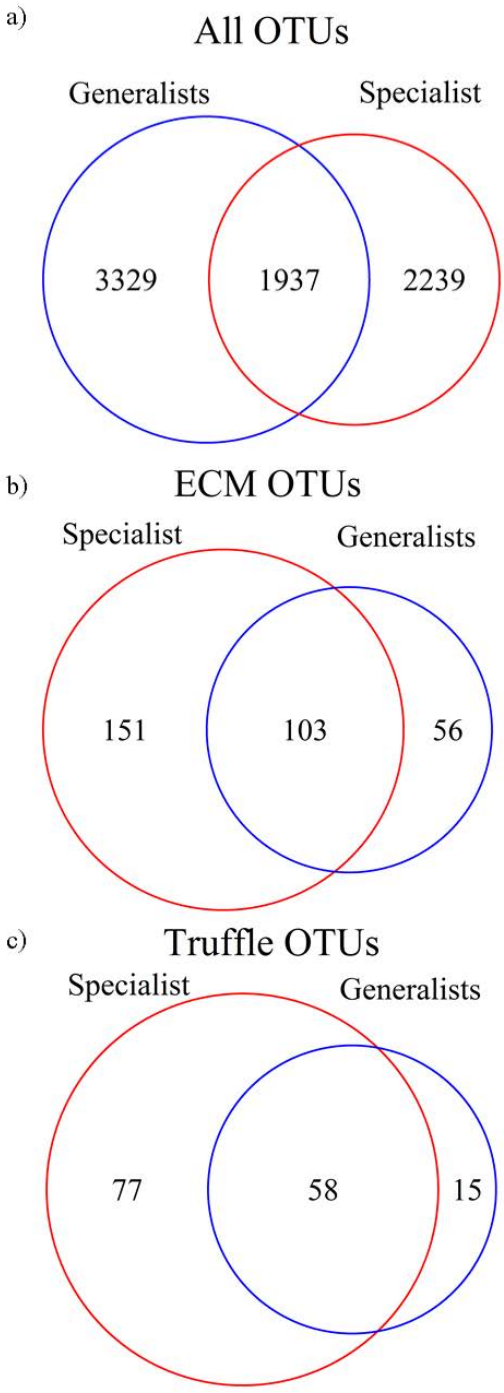


Figure 3.5: Venn diagrams comparing numbers of unique and shared OTUs from a fungal specialist (*Bettongia tropica*) and all fungal generalist mammal species' samples for a) all OTUs, b) ectomycorrhizal OTUs, and c) truffle OTUs.

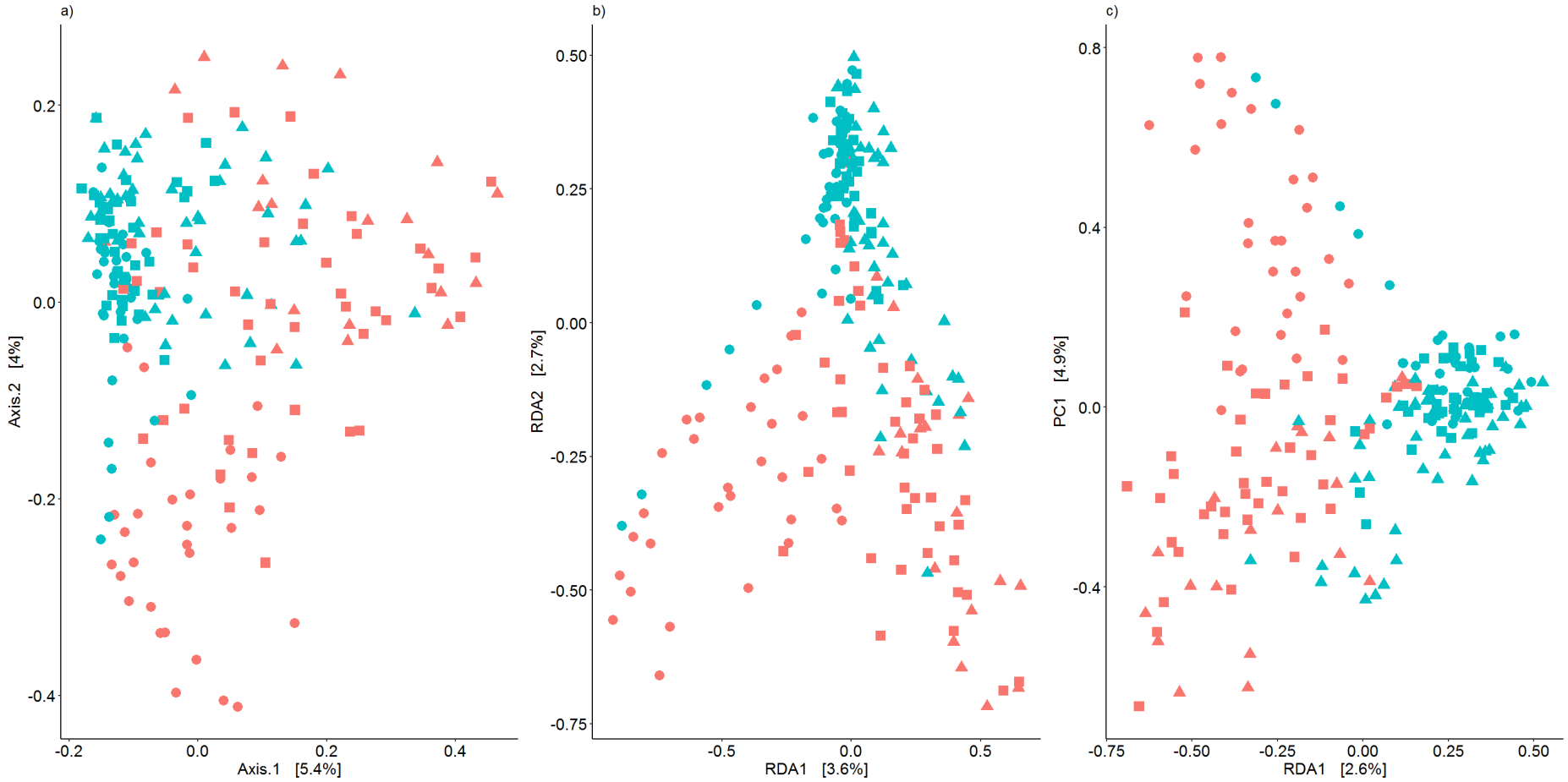

a)
Axis.2 [4%]
Axis.1 [5.4%]
b)
RDA2 [2.7%]
RDA1 [3.6%]
c)
PC1 [4.9%]
RDA1 [2.6%]

Figure 3.6: Ordination plots for the whole OTU dataset with Hellinger-transformed data on a) Multidimensional scaling with no data constraints; b) Redundancy analyses with interactions between mammal species (specialist vs generalists), site and season (RDA; fungal community ~ site*season*mammal species, 18.1% variation explained); c) Partial-RDA where variation of site and season are partitioned out (2.4% variation) and only mammal species examined (2.6% variation) (fungal community ~ mammal species + condition (site, season)). Fungal communities are significantly different between specialist and generalist scats ($F_{1, 209} = 5.611$, $P = 0.001$, c: partial-RDA). Red: specialist samples (*Bettongia tropica*), blue: samples from all generalists combined, diamonds: early wet season samples, triangles: late dry season samples, squares: late wet season samples.

Table 3.4: Results from Permutation Tests of a Redundancy Analysis examining the structure of the fungal community and interaction between sites (Davies Creek, Emu Creek and Tinaroo Dam), seasons (late dry, early wet and late dry) and 'bettong' (*Bettongia tropica* vs all generalist mammal species combined) for all OTU data (18.1% of the variation was examined by the axes).

Formula	Residual df	Variable (df)	Pseudo-F	*P*-value
Fungal community ~ site * season * bettong	195	Site (2)	2.8244	**0.001**
		Site (2)	4.4861	**0.001**
		Bettong (1)	6.1001	**0.001**
		Site*season (4)	1.9924	**0.001**
		Site*bettong (2)	1.8533	**0.001**
		Season*bettong (2)	2.1964	**0.001**
		Site*season*bettong (4)	1.5865	**0.001**

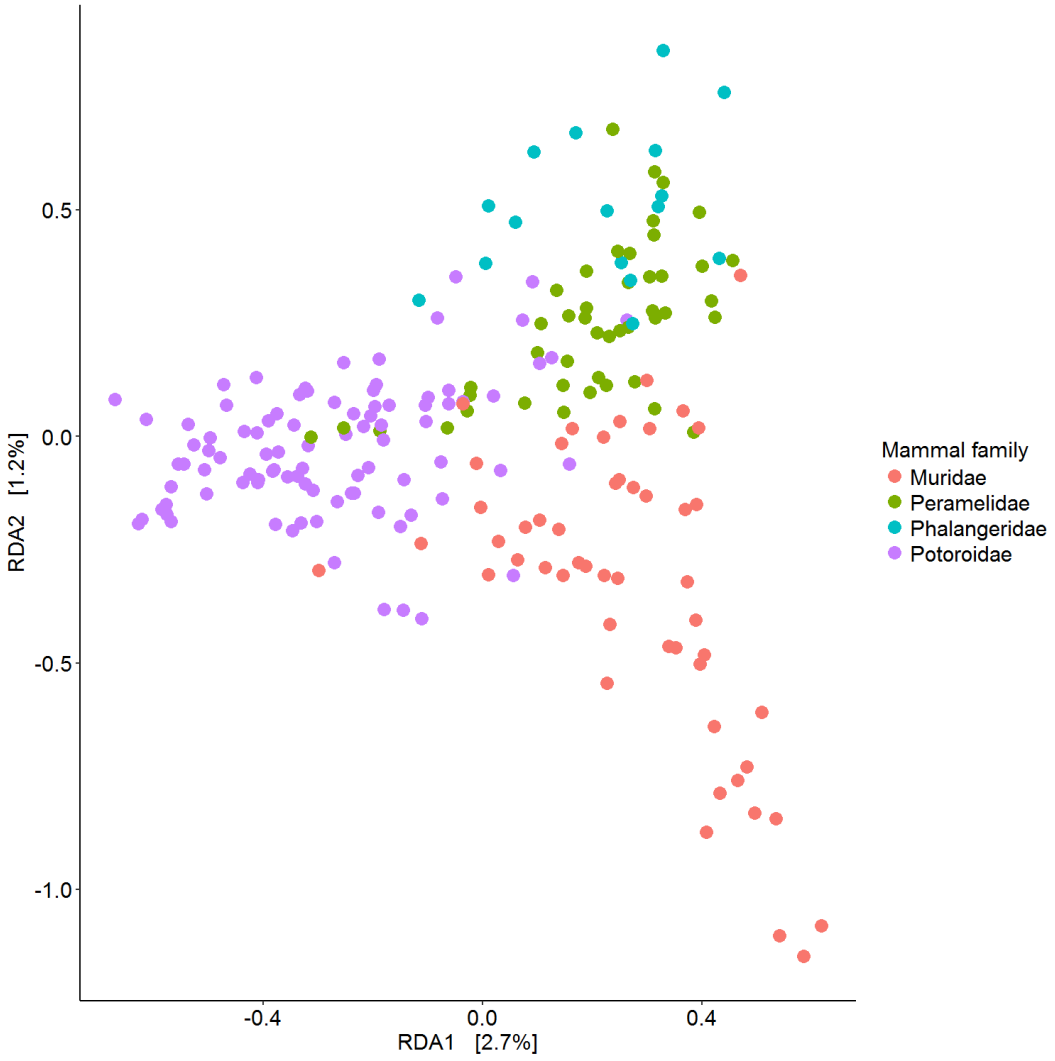


Figure 3.7: Ordination plot grouped by mammal family for the whole OTU dataset with Hellinger-transformed data for a partial-RDA where variation of site and season are partitioned out (2.45% variation) and only mammal species examined (6.36% variation) (fungal community ~ mammal species + condition (site, season)). Mammal families are represented by *Bettongia tropica*, $n = 93$ for Potoroidae; *Melomys sp.*, $n = 15$, *Uromys caudimaculatus*, $n = 30$, *Zyzomys argurus*, $n = 6$ for Muridae; *Isoodon macrourus*, $n = 38$, *I. obesulus*, $n = 8$ for Peramelidae; and *Trichosurus vulpecula*, $n = 16$ for Phalangeridae. Mammal species had significantly different fungal communities in their scats ($F_{6, 197} = 2.298$, $P = 0.001$).

3.5 Discussion

Bettongia tropica scats were found to contain a higher diversity of ECM and truffle fungal taxa and a significantly different community structure than the combined scats of the generalist mycophagous mammal species in the same community. These results are consistent with previous findings that, on average, Potoroid mammals (fungal specialists) consume a higher diversity of fungi than fungal generalists (Chapter Two; Nuske et al. 2017b). A higher number of unique ECM and truffle fungal taxa were found in *B. tropica's* diet than seen within the diets of all other mammal species combined. This third finding is contrary to previous results suggesting that *B. tropica* consumes roughly the same amount of unique species as seen in the combined diets of generalist mammals (12 vs 11) (Nuske et al. 2017b). It is likely this discrepancy is a consequence of the inconsistent methods used to identify fungal spores across the range of published studies presented in the Nuske et al. (2017b) meta-analysis, as only described fungal species could be compared. The consistency of methods used to identify fungal taxa across samples in this research alleviates any previous sampling bias and so adds to the validity of this new result. Additionally, these trends were consistent across all three sites and seasons. This suggests that *B. tropica* disperses more ECM truffle fungi than generalist mammals and supports the hypothesis that there is little functional redundancy in the fungal dispersal roles between specialists and generalists.

Even though just under half of the ECM taxa sampled from mammalian scats could be assigned as having a truffle fruiting habit, truffle taxa most often had the highest relative abundance in most mammal species' scats. This suggests that truffle taxa are consistently consumed by the mammals sampled and agrees with the literature on mycophagy in Australia (Claridge and May 1994). As truffle fungi rely on animals to

dig them up and disperse them away from where they form, it is likely that *B. tropica* and other mycophagous mammals heavily influence the gene flow and population structure of these fungal taxa (e.g. *Mesophellia/Malajczukia, Chondrogaster, Hysterangium, Soliocaccasus polychromus,* truffle taxa of *Russula* and *Cortinarius*). There is some evidence that among ectomycorrhizal fungi, truffle populations can be more genetically fractured than populations of epigeous wind-dispersed species at relatively small spatial scales (<10 km) (Grubisha et al. 2007). These effects may be exacerbated with the loss of mammal diversity or fungal specialists. However, these influences have not been measured yet for truffle taxa in Australia. Future studies on population genetics of truffle fungi in areas of differing mammal communities would verify the strength of the link between mycophagous mammals and truffle ECM communities.

The results revealed that many truffle OTUs unique to *B. tropica* scats (up to 77). In contrast, only 15 truffle OTUs were unique to generalist mammal scats that were not found in *B. tropica* scats. This suggests that if a fungal specialist, like *B. tropica,* were to become extinct, this could detrimentally impact gene flow among populations of many truffle taxa; much more than declines in generalist mammal populations. Indeed, such impacts may already be occurring as *B. tropica* has already disappeared from some regions of its range (Bateman et al. 2011). However, mammal species tend to consume fungi in proportion to their abundance (Johnson 1994a, North et al. 1997), suggesting that if a fungal specialist becomes locally extinct, generalist mammal species may simply increase their intake of those truffle fungi as they become more available. This hypothesis is yet to be tested. Given the relatively low fungal consumption by generalists shown here, a diverse range of mammals is likely to be necessary to conserve the diversity of truffle fungi in areas where fungal specialists have been lost.

Other members of the Potoroidae family in Australia (*Bettongia* spp. and *Potorous* spp.) and mammal species worldwide (e.g. flying squirrels, *Glaucomys sabrinus* in North America and bank voles, *Myodes glareolus* in Europe) are also considered fungal specialists (Meyer et al. 2005, Schickmann et al. 2012, Nuske et al. 2017b). Australia's history of mammal extinction and decline, including members of Potoroidae (Claridge et al. 2007), far exceeds other continents (Woinarski et al. 2015). Australia also has a high diversity of truffle species, most of which are endemic (Bougher and Lebel 2001). In terms of biomass and carbon stocks, ECM trees (especially *Eucalyptus* spp.) are dominant in much of Australia's forests (Reddell et al. 1999, Wood et al. 2015b) and reduced ECM abundance and diversity has been linked to declines in *Eucalyptus* tree health (Scott et al. 2012, Ishaq et al. 2013, Horton et al. 2013). Reduced spore dispersal from mycophagous mammals may, over time, reduce the species richness of truffle fungi, making this continent of particular concern for conservation of truffle fungi. The already substantial loss of *Bettongia* spp. and *Potorous* spp. throughout much of the Australian continent (Claridge et al. 2007) could have long-lasting detrimental, yet undocumented, consequences for the diversity of truffle fungi, tree health and ultimately ecosystem functioning.

Unexpectedly, some OTUs matched truffle sequences of non-Australian taxa (*Tuber* sp. and *Rhizopogon pseudoroseolus*). No *Tuber* species are known to occur natively in Australia on native flora (Bonito et al. 2013). Introduced *Tuber* species associate with introduced trees (mainly on *Quercus* and *Corylus*) in temperate regions of Australia (Linde and Selmes 2012, Thomas 2014) and are also known to associate with Pinaceae (Bonito et al. 2013). *Rhizopogon* species also associate with Pinaceae and other non-native Australian trees (Ivory and Munga 1983, Tedersoo et al. 2007) and have been recorded in Australian pine plantations (Bell and Adams 2004). Incidentally, there is a

plantation of *Pinus caribaea* ca. 10 km from one of the study sites (Tinaroo Dam) (Applegate and Nicholson 1988). *Rhizopogon* was found in highest abundance in *U. caudimaculatus* and *Per. nasuta* at Tinaroo Dam; both mammal species have been known to have home ranges within this distance (Scott et al. 1999, Streatfeild 2009). Therefore, it is possible that the OTUs matching *R. pseudoroseolus* or *Tuber* sp. resulted from native mammals consuming a non-native, introduced ectomycorrhizae associating with local *Pinus* plantations. Alternatively, they may have resulted from a contamination from laboratory processing. Nevertheless, five OTUs are unlikely to alter the main results of this study.

Whether reduction of mammal diversity results in compromised plant productivity via loss of truffle diversity has not yet been empirically shown, but has been suggested by many authors (Maser et al. 1978, Malajczuk et al. 1987, Johnson 1996, Vernes 2007). This link between mycophagous mammals and plant productivity assumes that altered mammal diversity influences population dynamics of truffle species, resulting in declines of truffle diversity. However, little is known about the structure of mycorrhizal communities. In the next chapter I address this knowledge gap by measuring the mycorrhizal community at different scales; whole soil and plant roots and comparing those taxa to the community of fungi that are present in mycophagous mammalian scats.

Chapter Four: Dominant ectomycorrhizal fungi on roots are mammal dispersed

4. 1 Abstract

Currently little is known about how truffles contribute to mycorrhizal community structure and its dependence on mycophagous mammals. At address this knowledge gap, the mycorrhizal community in a north-east Australian woodland, including the portion interacting with mycophagous mammals was quantified. The study area is core habitat of an endangered fungal specialist marsupial, *Bettongia tropica,* and as such provides baseline data on mycorrhizal fungi-mammal interactions in an area with no known mammal declines. The results revealed that the dominant root-associated ectomycorrhizal taxa (>90% sequence abundance) included the truffle taxa *Mesophellia, Hysterangium* and *Chondrogaster.* These same truffle taxa were present in mycophagous mammalian diets. Eighty-eight percent of truffle taxa associating with roots were shared with the fungal specialist diet and 52% with diets from generalist mammals. These data suggest that changes in mammal communities, particularly the loss of fungal specialists, could, over time, induce significant detrimental changes to truffle diversity, causing ectomycorrhizal communities to shift with possible negative impacts on plant and ecosystem health.

4.2 Introduction

Truffle mycorrhizal fungi are an important component of forest ecosystems and they rely on animals, particularly mammals, for their dispersal (Claridge and May 1994). This implies that truffle fungal diversity is likely linked to mammal diversity (Vernes 2007). Disruption to complex ecological networks, such as this mammal-fungi-plant interaction, can cause loss of biodiversity. For example, it is logical to assume that

reduced spore dispersal via loss of mammal abundance and diversity would reduce gene flow among truffle populations, resulting in undocumented impacts on truffle community structure and potential species extinctions. Loss of truffle diversity may in turn alter mycorrhizal communities, potentially impacting fungi-plant interactions.

Mammals are also thought to play a pivotal role in plant-mycorrhiza symbioses, and by extension, plant productivity, diversity and ecosystem health (Maser et al. 1978, Malajczuk et al. 1987, Johnson 1996, Vernes 2007). Such a hypothesis assumes that truffle taxa are important components of functioning mycorrhizal communities and that the higher the proportion of truffle taxa within the overall mycorrhizal community, either in terms of relative abundance or diversity, the higher the potential influence that mammalian spore dispersal has on the structuring of mycorrhizal and plant communities. Yet these assumed linkages remain largely untested.

To understand the strength of the relationship between total mycorrhizal communities, root-associating mycorrhizal communities and mycophagous mammals, first we must understand how important truffle taxa are to functioning mycorrhizal communities. Few studies have examined the structure of mycorrhizal communities or identified the fruiting habits of the various components of the fungal community (or presented data with enough resolution that this can be inferred *post hoc*; Appendix D). In three different studies of ECM sporocarps in Australia (Reddell et al. 1999, Lu et al. 1999, Adams et al. 2006), between 18 and 27% of taxa found were hypogeous (truffles). However, these three surveys are difficult to compare in terms of the richness of hypogeous versus epigeous species because the same methodology was not used for both groups.

It is important to make the distinction between ectomycorrhizal (ECM) and arbuscular mycorrhizal (AM) communities as the relative diversity of truffle species are quite different in these groups as are their distribution, ecology, and interactions with host plants. AM fungi associate with >80% of global plant diversity and occur in almost every ecosystem where plants are present, while ECM associate with a much smaller proportion (Brundrett 2009). However, ECM trees can dominate forests in terms of biomass (Reddell et al. 1999). The diversity of truffle-like (sporocarpic) AM fungi is much lower compared to ECM fungi; at least two AM genera contain truffle-like species (*Glomus* and *Acaulospora*; Goto and Maia 2005) while thousands of species of ECM truffle fungi are within Basidiomycota, Ascomycota and Zygomycota (Bougher and Lebel 2001, Trappe et al. 2009). Therefore, any influence that mammals may have on mycorrhizal communities will likely depend on the differences between these groups.

To my knowledge, only one study has quantified the truffle ECM community on plant host roots and compared this to mycophagous mammalian diets. Izzo et al. (2005) sampled roots from subtropical North America and found at least 21% of taxa were hypogeous (truffles) and between 25% and 40% of ECM dry root biomass were hypogeous taxa. However, they were limited to Sanger sequencing of DNA samples from mammalian scats and consequently only detected three hypogeous taxa in mammalian diets. Modern high-throughput sequencing technologies that amplify and sequence DNA from complex communities provide the necessary resolution to examine fungal communities from environmental samples like roots, scats and soil (Lindahl et al. 2013).

My aim was to address this knowledge gap in the structure of mycorrhizal communities, particularly the truffle community, by quantifying the relative proportion of the

mycorrhizal community that are interacting with mycophagous mammals. To do this, together with collaborators, I quantified the mycorrhizal community (concentrating on ECM fungi) using high throughput sequencing (Illumina MiSeq) across different sample types including plant roots, whole soil and scats from mycophagous mammals. The results were compared to ITS sequences of truffle morpho-species collected and characterised from an extensive survey undertaken at one of the studies sites (Abell-Davis 2008). Samples were also collected within the habitat of a fungal specialist (the northern bettong; *Bettongia tropica*) and other mycophagous mammals as this provides a baseline measurement of the interaction between root-associating mycorrhizal fungi and mycophagous mammals where limited known loss of mammal diversity has occurred.

4.3 Methods

4.3.1 Field sampling

Two locations on the Lamb Range in North Queensland in Australia were sampled in the early wet season (February to March): Danbulla National Park near Tinaroo Dam (17°9’50.30"S, 145°32’11.56"E) and Davies Creek National Park (17°1’23.28"S, 145°34’55.71"E). Additional sampling was carried out at Davies Creek in the late dry season (November to December). Six plots at each site were established at least 500 m apart around the trapping grid as per Chapter Three.

Topsoil cores (0-10 cm) were collected from 40 locations in each plot in a 12 x 20 m grid. The corers were cleaned with 70% ethanol between plots. Half of the samples per plot (6 x 20 m) were also used to collect putative ECM root associated taxa. The top 10 cm of soil was raked for 60 person-minutes and fine roots were collected. I found that it was too difficult to trace fine roots back to potential host plants as soil was often too

compacted and contained large rocks. Instead I collected all fine root material found (still connected to higher roots). When possible, grass roots were often eliminated from individual samples by tracing back to the grass plant. Preliminary work also suggested a higher volume of roots were collected with this more targeted approach compared to sieving roots from soil cores. A high volume of root tip material was necessary to obtain three DNA extraction subsamples per plot (3 x 0.25g of wet weight root tips). Soil and roots were refrigerated (-4ºC) within 24 hours of collection and placed into -20ºC freezer as soon as possible (up to 4 days).

Fungal diets of mammals were examined by collecting scat samples from trapped individuals. Each animal was handled according to James Cook University animal ethical guidelines (Approved ethics application A2044). Trapping methods and scat collection were carried out as per Chapter Three. Briefly, scat was collected from the bottom of Elliot traps or from plastic placed under each cage trap. All traps and plastic were initially cleaned with 70% ethanol and then re-cleaned if an animal was caught. Scats were stored on ice or in a portable fridge (4ºC) in the field and transferred to -20ºC as soon as possible (within 4 days).

4.3.2 Laboratory Analysis

Roots were cleaned of excess soil in reverse osmosis water. Fine roots were examined under a dissecting microscope. For each cluster of fine roots collected within a plot, the same volume of root tips of each mycorrhizal morphotype were placed into three subsamples (0.25g) for DNA extraction. Each soil core was homogenised and a small amount of fine powder from each was pooled and three subsamples were taken per plot for DNA extraction (0.25g). Scat samples were processed as per Chapter Three. Briefly, obvious soil contamination was removed from each scat sample, material was only

taken from the inside of each scat, samples were homogenised and 0.25g was taken for DNA extraction.

DNA extraction, PCR, sequences protocols and bioinformatics were performed as per Chapter Three. Briefly, DNA was extracted using PowerLyser PowerSoil DNA Isolation kit (Mo Bio, Carlsbad, CA USA). DNA was amplified with ITS3-Mix1 and barcoded ITS4-Mix1 primers (Tedersoo et al. 2012). I used negative (for DNA extraction and PCR) and positive controls (PCR) throughout the experiment. All samples were sequenced in seven Illumina MiSeq 2×300 bp paired-end runs.

4.3.3 Statistical Analysis

Operational taxonomic unit (OTU) subsetting and statistics were performed using the 'phyloseq' package (McMurdie and Holmes 2013) in R (R Core Team 2012). Altogether six samples were removed from further analyses, because these comprised a total of <500 filtered sequences. The fungal data was examined at three broad levels: at the whole OTU community level, only examining the mycorrhizal OTU's (8.4% of all taxa) and only examining truffle taxa (9.3% of mycorrhizal taxa). The mycorrhizal subset of the data included only taxa that were assigned as highly probable and probable, and as mycorrhizal from the FUNGuild (Nguyen et al. 2015b) output. Functional guilds are assigned to ECM status by FUNGuild based on genera, with the exception of Russulaceae. Russulaceae is also one of the most OTU-rich families in this dataset, therefore when comparing mycorrhizal taxa (e.g. as relative diversity as in Figure 4.2) Russulaceae are disproportionally over-represented. To make sure ECM taxa were evenly represented at the genus level, ECM OTUs based on Russulaceae at the family level were excluded from analyses (note: ECM OTUs based on genus and species within Russulaceae, for example *Russula*, were retained). Truffle taxa are listed in Appendix E.

The three subsamples per soil or root sample were pooled computationally by mean sequence abundance per OTU as this likely gives the best estimate of diversity (Song et al. 2015). To estimate the accumulation of OTUs per sample, I created rarefied OTU accumulation curves for each sample type with all OTU data and ECM OTU data using estimates and 95% confidence intervals from EstimateS 9.1.0 (Colwell 2013).

I compared mycorrhizal communities between sample types by tabulating the number of OTUs that were shared and not shared (using 'limma' and 'venneuler' packages in R). I ranked taxa according to their relative abundance per sample and considered the 'dominant' portion of the community to be the highest relative abundance that collectively accounted for >90% of the relative abundance. The dominant portion accounted for approximately 25% of the taxa present.

4.4 Results

4.4.1 Richness

Soil data were more OTU-rich than root data, and both were more OTU-rich than scat data (Figure 4.1a). There were a total of 9358 filtered OTUs from all samples. Most were not assigned a functional guild (7508 OTUs). Of those that were, most were symbiotrophic (805 OTUs, including 344 ECM OTUs and 428 AM OTUs) followed by saprotrophic (754 OTUs). For ECM OTUs at equivalent sample sizes the ECM OTU-richness of scats was ~67% of the root-associating taxa (Figure 4.1b).

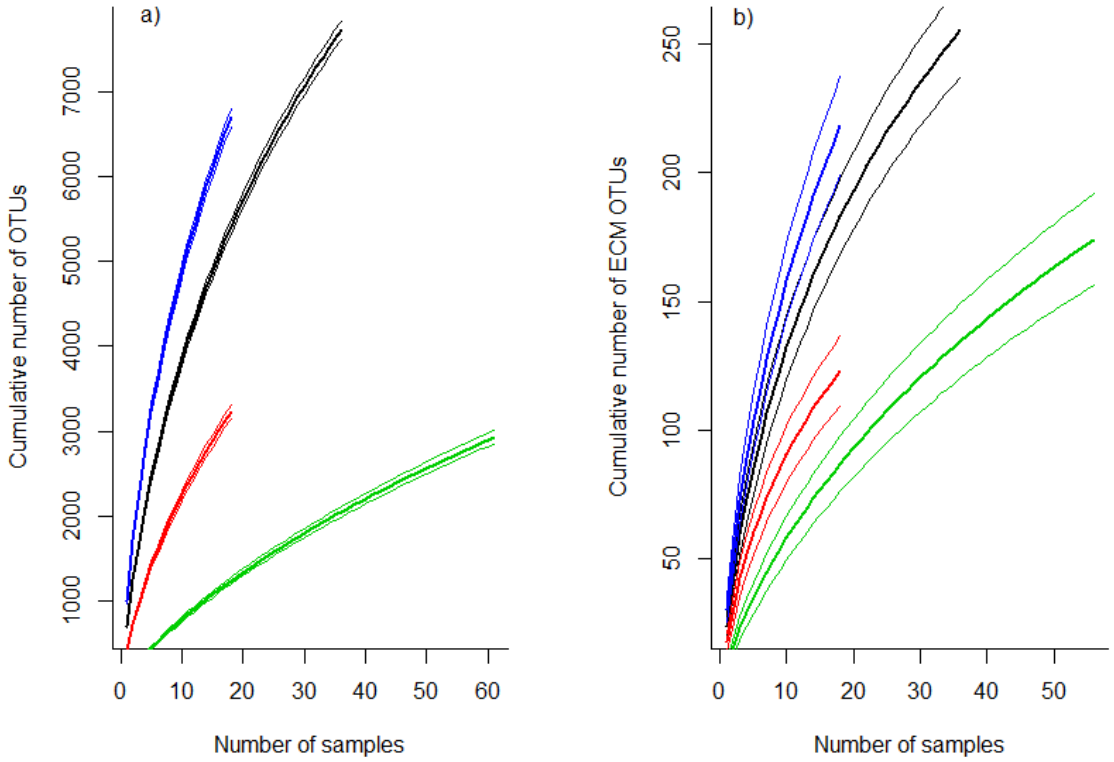


Figure 4.1: Rarefied accumulation curve for a) all OTUs and b) ectomycorrhizal (ECM) OTUs. Blue lines are soil samples (n = 36), red lines are root samples (n = 36), black lines are soil and root data combined (n = 72) and green lines are scat samples (n = 61). Thin lines represent 95% confidence intervals.

Both soil and root samples had AM fungi (Glomeromycota, Glomeraceae and Gigasporaceae) as the most OTU-rich mycorrhizal taxa. However, they made up <13% of the taxa in the mammalian scat samples (Figure 4.2, including Diversisporaceae) and constituted <0.01% of the relative abundance for all samples (Figure 4.3). The truffle family Mesophelliaceae was the most OTU-rich and highest relative abundance mycorrhizal taxon in mammalian scat samples (Figures 4.2 and 4.3).

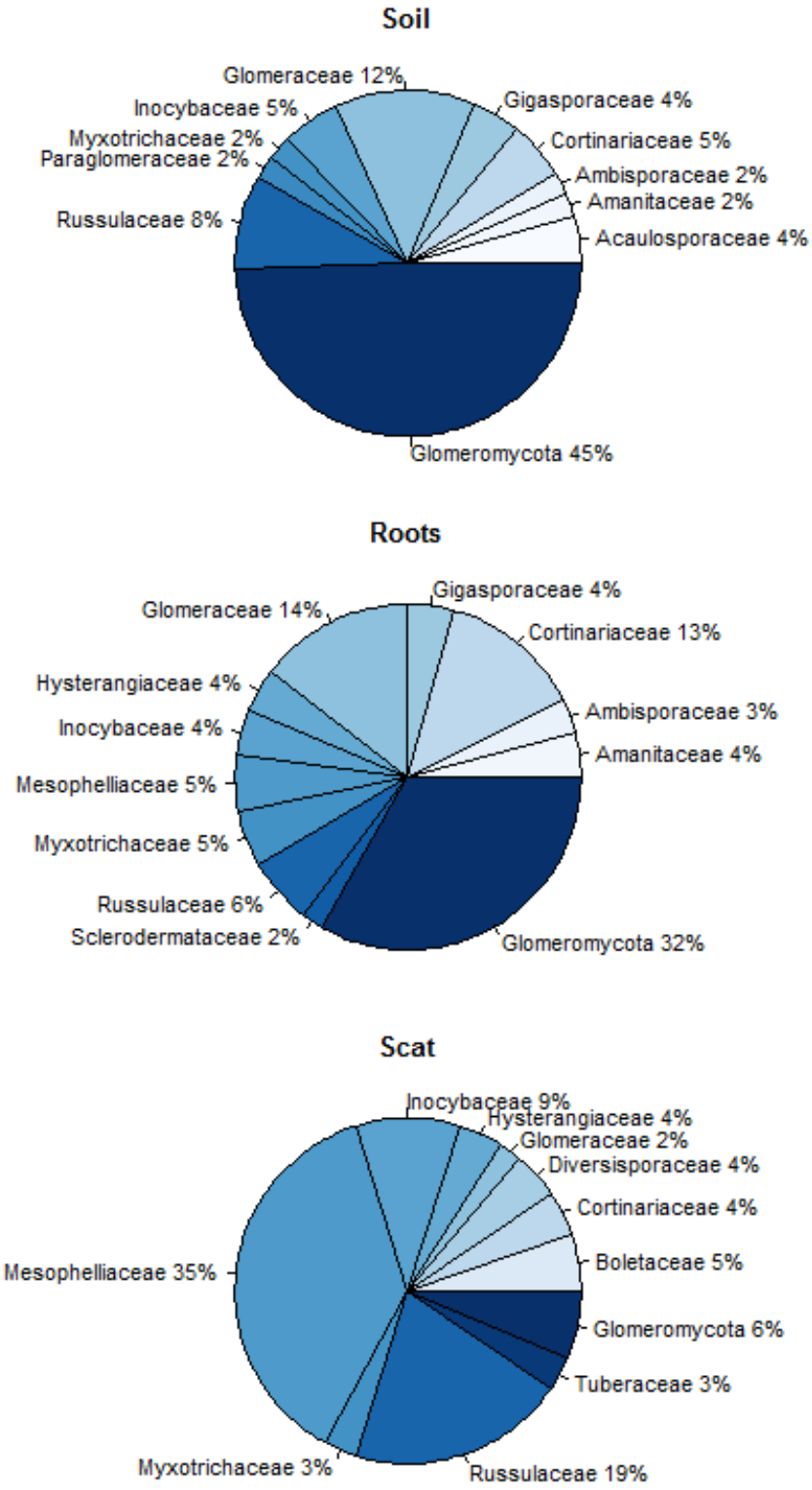


Figure 4.2: Relative diversity of mycorrhizal families in different samples (soil, roots and scats). Only taxa representing greater than 1% of the total OTU-richness are shown for clarity.

Overall, samples had 21.2% of ECM OTUs as truffle taxa (73 OTUs) and 54.1% as taxa with ambiguous fruiting habit (186 OTUs). Scat samples had a higher proportion of OTUs matching truffles than root or soil samples (30-90%, depending on site and season, compared to 17-23% for root samples and 7-8% for soil samples). Scat samples from the fungal specialist (*B. tropica*) had a higher proportion of ECM truffle OTUs (30-90%) than all other mammal species with generalist diets combined (18-73%).

4.4.2 Relative abundance

Truffle and secotioid taxa (e.g. Cortinariaceae and Hysterangiaceae) constituted higher proportions of the dominant mycorrhizal root-associating communities compared to soil communities (Table 4.1; Figure 4.3). Soil mycorrhizal communities were dominated by taxa with mixed fruiting habits (e.g. truffle taxa and mushroom taxa and *Russula* and *Cortinarius* that could represent truffle, secotioid or mushroom taxa Table 4.1, Figure 4.3). Of the dominant mycorrhizal OTUs associating with root samples, three out of four genera were truffles (*Hysterangium, Mesophellia* and *Chondrogaster*; Table 4.1). Four truffle OTUs were shared between dominant root taxa and mammalian diets and five dominant ECM OTUs were shared between soil and scat samples (Table 4.1). Within taxa comparisons showed that *Cortinarius* was more OTU-rich and more relatively abundant in roots and soil compared to scat samples, whereas *Malajczukia/Mesophellia* were more OTU-rich and relatively abundant in scat samples compared to soil and roots (Appendix E). *Hysterangium* and *Chondrogaster* were more relatively abundant in roots.

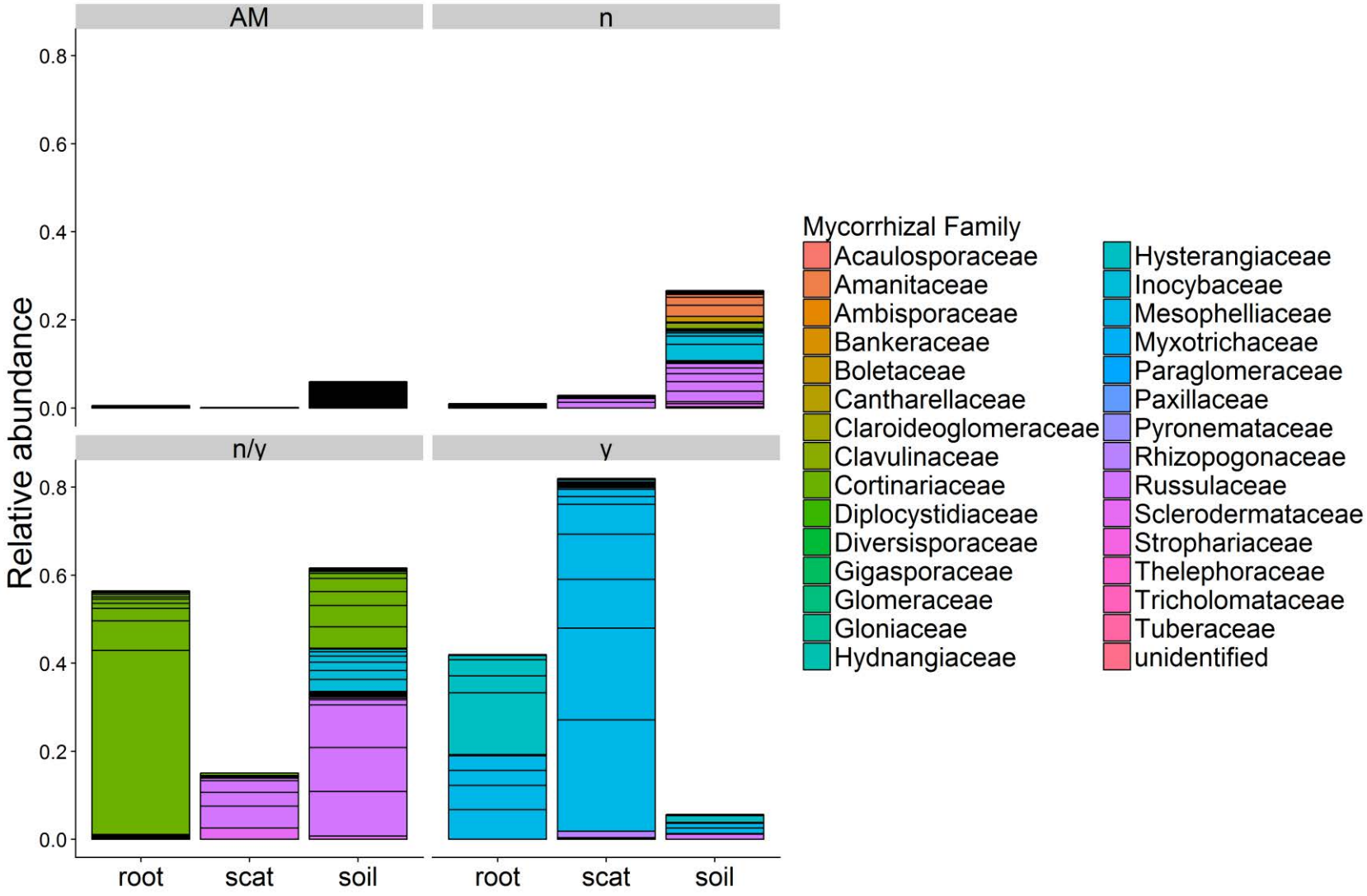

AM
n
n/y
y
Relative abundance
0.0
0.2
0.4
0.6
0.8
root
scat
soil
Mycorrhizal Family
Acaulosporaceae
Amanitaceae
Ambisporaceae
Bankeraceae
Boletaceae
Cantharellaceae
Claroideoglomeraceae
Clavulinaceae
Cortinariaceae
Diplocystidiaceae
Diversisporaceae
Gigasporaceae
Glomeraceae
Gloniaceae
Hydnangiaceae
Hysterangiaceae
Inocybaceae
Mesophelliaceae
Myxotrichaceae
Paraglomeraceae
Paxillaceae
Pyronemataceae
Rhizopogonaceae
Russulaceae
Sclerodermataceae
Strophariaceae
Thelephoraceae
Tricholomataceae
Tuberaceae
unidentified

Figure 4.3: Relative abundance of mycorrhizal families in different samples (soil, roots and scats) split by mycorrhizal type (AM = arbuscular mycorrhizal) and fruiting habit (n = fruiting habit other than truffle, n/y = unknown fruiting habit, y = truffle). Black are OTUs with a relative abundance to show.

Table 4.1: OTUs that make up the dominant proportion (cumulatively 90% of sequence abundance) of samples per site (DC = Davies Creek, TD = Tinaroo Dam), sample type and season, with number of replicates (*n*), total OTUs per sample (Total), percent relative abundance (RA), accession number, e-value, percentage similarity with database sequence (ID), percentage overlap with reference sequence (Cov) and OTU sequence length (SL). Taxa in boldface are **truffles** and underlined are secotioid or higher taxa that include truffle or secotioid taxa. When fruiting habit is listed at genus level it applies to the whole genus. Mycorrhizal status (Myc) is either ectomycorrhizal (ECM), ericoid mycorrhizal (ErM) or arbuscular mycorrhizal (AM). The mammalian specialist scats are from *Bettongia tropica*. The mammalian generalist scats are from *Isoodon macrourus, I. obesulus, Melomys sp., Trichosurus vulpecula, Uromys caudimaculatus* and *Zyzomys argurus.*

Site	Sample	Season	*n*	Total	RA	Fungal taxa	Myc	Accession	e-value	ID	Cov	SL
DC	roots	dry	6[b]	84	64.4	***Hysterangium aggregatum***	ECM	KY697566-7	2.21E-133	100	97.9	333
					17.2	*Cortinarius globuliformis*	ECM	AF325582	2.50E-141	99	100	350
					5.7	***Hysterangium aggregatum***	ECM	KY697566-7	2.16E-129	98	97.9	335
					5.3	*Cortinarius globuliformis*	ECM	AF325582	3.24E-142	99	100	349
	roots	wet	6[b]	102	44.1	*Cortinarius*	ECM	FR731477	1.53E-143	100	99.7	350
					12.5	***Hysterangium***[c]	ECM	KC222660	1.00E-144	94	100	340
					11.8	***Hysterangium cf gardneri***[a]	ECM	KY697590	3.96E-139	100	99.7	340
					11.4	***Hysterangium aggregatum***	ECM	KY697566-7	2.21E-133	100	97.9	333
					7.1	***Mesophellia oleifera***[c]	ECM	KY697602-3	4.15E-177	100	100	425
					3.9	*Cortinarius*	ECM	KJ421051	4.44E-112	91	100	358
TD	roots	wet	6[b]	99	53.1	*Cortinarius*	ECM	FR731477	1.53E-143	100	99.7	350
					12.5	***Mesophellia***[c]	ECM	GQ981511	2.00E-111	91	98	298
					12.4	*Cortinarius*	ECM	KF732610	5.34E-105	89	100	353
					9.3	***Mesophellia oleifera***[c]	ECM	KY697602-3	4.86E-166	97	100	420
					4.4	***Chondrogaster spB/spF***[a]	ECM	KY697582-5	4.75E-151	100	100	366
DC	specialist diet	dry	7	51	31.0	***Mesophellia***[c,d]	ECM	GQ981511	2.00E-111	91	98	298

					19.5	***Malajcukia ingrattissima*[d]**	ECM	KY697598	6.60E-156	100	100	377
					19.3	***Mesophellia oleifera*[c]**	ECM	KY697602-3	4.15E-177	100	100	425
					17.1	***Mesophellia glauca***	ECM	GQ981510	9.13E-147	98	99	376
					5.8	***Mesophellia glauca***	ECM	GQ981511	1.00E-162	97	99	354
	specialist diet	wet	6	24	34.7	*Russula*[d]	ECM	LC006943	3.99E-138	91	100	426
					32.9	***Mesophellia*[c,d]**	ECM	GQ981511	2.00E-111	91	98	298
					17.5	*Russula*	ECM	UDB016041	6.92E-129	93	100	376
					7.0	*Cortinarius*	ECM	FJ157098	8.08E-118	92	100	371
TD	specialist diet	wet	16	70	26.4	***Malajcukia ingrattissima*[d]**	ECM	KY697598	6.60E-156	100	100	377
					16.6	***Mesophellia*[c,d]**	ECM	GQ981511	2.00E-111	91	98	298
					15.2	***Mesophellia***	ECM	GQ981511	2.00E-110	91	99	295
					12.8	***Mesophellia glauca***	ECM	GQ981510	9.13E-147	98	99	376
					7.2	*Russula*[d]	ECM	LC008293	3.95E-138	91	100	422
					6.1	*Scleroderma spB/spC*[a,d]	ECM	KY697606-7	3.41E-146	100	100	355
					3.4	***Mesophellia oleifera*[c]**	ECM	KY697602-3	4.86E-166	97	100	420
					3.0	***Mesophellia oleifera*[c]**	ECM	KY697602-3	4.15E-177	100	100	425
DC	generalist diets	dry	11	27	68.8	***Malajcukia ingrattissima*[d]**	ECM	KY697598	6.60E-156	100	100	377
					18.7	***Mesophellia*[c,d]**	ECM	GQ981511	2.00E-111	91	98	298
					9.6	***Mesophellia***	ECM	GQ981511	2.00E-110	91	99	295
	generalist diets	wet	8	29	35.3	***Mesophellia***	ECM	GQ981511	2.00E-110	91	99	295
					30.0	*Russula*[d]	ECM	LC006943	3.99E-138	91	100	426
					16.8	*Russula*	ECM	UDB016041	6.92E-129	93	100	376
					11.5	*Lactarius rufus*	ECM	KT165272	4.86E-170	100	100	409
TD	generalist diets	wet	8	24	71.4	***Rhizopogon pseudoroseolus***	ECM	AJ810040	2.84E-168	100	100	405
					9.2	***Mesophellia*[c,d]**	ECM	GQ981511	2.00E-111	91	98	298

					7.9	***Malajcukia ingrattissima*[d]**	ECM	KY697598	6.60E-156	100	100	377
					2.6	***Hysterangium*[c]**	ECM	KC222660	1.00E-144	94	100	341
DC	soil	dry	6[b]	196	22.4	*Russula*	ECM	UDB016041	1.08E-122	92	100	370
					19.9	*Russula*[d]	ECM	LC006943	3.99E-138	91	100	426
					11.5	*Russula*	ECM	UDB016041	4.05E-127	92	100	373
					6.4	*Russula anthracina*	ECM	UDB011194	5.00E-151	97	100	382
					4.9	*Amanita*	ECM	KP071067	2.94E-126	94	100	356
					3.6	*Inocybe*	ECM	FJ904133	1.39E-100	88	100	344
					3.5	***Hysterangium aggregatum***	ECM	KY697566-7	2.21E-133	100	97.9	333
					3.1	*Russula*	ECM	EU019930.1	1.63E-104	93	80.4	382
					2.7	*Inocybe*	ECM	JQ085932	1.01E-91	87	100	346
					2.3	***Mesophellia*[d]**	ECM	GQ981511	2.00E-111	91	98	298
					2.1	*Lactarius*	ECM	HQ318282	2.43E-129	94	100	368
					1.3	*Inocybe*	ECM	JX178624	2.40E-98	86	100	359
					1.3	*Auritella serpentinocystis*	ECM	KJ729858	3.63E-150	100	100	364
					1.2	*Cortinarius globuliformis*	ECM	AF325582	2.50E-141	99	100	350
					0.9	*Russula*	ECM	UDB016041	2.40E-125	92	100	373
					0.8	***Hysterangium aggregatum***	ECM	KY697566-7	2.60E-122	97	97.9	330
					0.8	*Russula*	ECM	AB509981	3.49E-138	94	99.7	380
					0.7	*Cortinarius*	ECM	KR011131	2.92E-122	93	100	363
					0.6	*Cortinarius globuliformis*	ECM	AF325582	3.24E-142	99	100	349
	soil	wet	6[b]	251	24.8	*Russula*	ECM	UDB016041	4.05E-127	92	100	373
					13.7	*Cortinarius*	ECM	GU233352	1.41E-96	88	100	357
					9.6	*Russula*[d]	ECM	LC006943	3.99E-138	91	100	426
					8.0	*Auritella chamaecephala*	ECM	KT378201	9.00E-138	97	100	358
					7.5	*Inocybe*	ECM	JQ085932	1.01E-91	87	100	346

					4.7	*Cortinarius*	ECM	KJ421051	4.44E-112	91	100	358
					4.5	***Malajcukia ingrattissima***[d]	ECM	KY697598	6.60E-156	100	100	377
					2.5	*Russula*	ECM	UDB016041	1.08E-122	92	100	370
					2.3	*Lactarius*	ECM	HQ318282	2.43E-129	94	100	368
					1.8	***Mesophellia***[d]	ECM	GQ981511	2.00E-111	91	98	298
					1.5	*Amanita*	ECM	JF899547	4.64E-112	89	100	371
					1.1	*Cantharellus*	ECM	AB509732	8.03E-106	85	99.7	398
					0.9	*Russula*	ECM	UDB016041	3.12E-126	92	100	373
					0.8	*Auritella serpentinocystis*	ECM	KJ729858	3.63E-150	100	100	364
					0.7	*Russula*	ECM	KM373243	3.51E-134	93	100	391
					0.7	***Hysterangium aggregatum***	ECM	KY697566-7	2.21E-133	100	97.9	333
					0.6	*Scleroderma spB/spC*[a,d]	ECM	KY697606-7	3.41E-146	100	100	355
					0.5	*Oidiodendron*	ErM	AF062808.1	1.51E-105	95	100	291
					0.5	Glomeromycetes	AM	JF276264	4.84E-128	96	100	348
					0.4	*Auritella*	ECM	KT378201	4.51E-116	92	100	354
					0.4	Glomerales	AM	AY394681	3.63E-76	81	100	380
					0.3	Glomerales	AM	HE794042	2.00E-117	93	100	338
					0.3	Glomeraceae	AM	KM226647	1.20E-115	97	88.6	343
					0.3	*Inocybe*	ECM	JX178624	2.40E-98	86	100	359
					0.3	Glomerales	AM	KP235575	1.87E-101	90	97.5	354
					0.3	*Oidiodendron*	ErM	KX640607	3.00E-131	96	99.7	289
					0.2	*Russula*	ECM	UDB016041	8.38E-122	91	99.5	373
					0.2	Glomerales	AM	JX276895	4.56E-124	95	100	340
					0.2	Glomerales	AM	KM226647	3.30E-80	86	88.6	343
					0.2	Glomerales	AM	AY394681	1.72E-81	82	100	374
TD	soil		wet	6[b]	289	12.2	*Cortinarius globuliformis*	ECM	AF325582	6.96E-141	99	100	351

11.5	*Cortinarius globuliformis*	ECM	AF325582	3.24E-142	99	100	349
9.2	*Inocybe alienospora*	ECM	KP171105	1.88E-140	99	100	343
6.9	*Cortinarius*	ECM	FR731477	1.53E-143	100	99.7	350
6.5	*Amanita egregia*	ECM	KP012748	2.82E-134	100	100	328
5.6	*Lactarius*	ECM	AB509713	4.60E-112	90	99.7	369
5.0	*Inocybe*	ECM	KP308804	6.00E-135	89	94	359
4.8	*Inocybe*	ECM	KP308804	3.05E-99	87	100	352
4.4	*Lactarius eucalypti*	ECM	UDB002671	1.70E-162	96	100	420
3.2	*Clavulina*	ECM	JQ724058	3.49E-103	85	100	383
3.1	*Austroboletus subvirens*	ECM	KP242209	5.04E-155	100	100	375
2.8	***Zelleromyces spE***	ECM	KY697617-9	8.92E-153	96	100	399
2.6	*Lactifluus*	ECM	KM282287	1.36E-127	95	100	351
2.1	*Inocybe*	ECM	AM882711	2.72E-99	90	100	321
2.0	*Russula*	ECM	UDB016041	1.08E-122	92	100	370
1.5	*Scleroderma spB/spC*[a,d]	ECM	KY697606-7	3.41E-146	100	100	355
1.4	*Russula*[d]	ECM	LC006943	3.99E-138	91	100	426
1.1	*Pisolithus croceorrhizus*	ECM	JN847473	8.64E-157	100	100	379
0.8	*Inocybe violaceocaulis*	ECM	KP641643	4.75E-151	100	100	366
0.8	*Amanita*	ECM	GU222312	3.39E-111	92	94.1	356
0.6	*Pisolithus croceorrhizus*	ECM	JN847473	6.64E-156	99	100	379
0.5	*Cortinarius globuliformis*	ECM	AF325582	3.25E-142	99	100	350
0.5	*Amanita*	ECM	AB015702	8.29E-95	87	100	355
0.5	Glomerales	AM	JN195694	5.02E-132	96	100	350
0.5	***Mesophellia***	ECM	GQ981511	8.00E-116	92	97	301
0.4	*Russula*[d]	ECM	LC008293	3.95E-138	91	100	422

[a] indicates taxa that are indistinguishable from ITS2 sequences (within 3% similarity) from morphological groups identified in Abell-Davis (2008), Appendix C.
[b] includes 3 subsamples per sample pooled computationally.
[c] indicates OTUs that are shared between root and scat samples.
[d] indicates OTUs that are shared between scat and soil samples.

4.4.3 Shared taxa between samples

The percentage of shared taxa between fungal specialist diets and ECM communities on roots (36.6%) and in soil (28%) was slightly higher than that for fungal generalist diets (Figure 4.4; 26 and 14.7%, respectively). The percentage of shared truffle OTUs from roots and soil and fungal specialist diets was much higher (Figure 4.4; 87.5 and 78.8%, respectively). In contrast, just over half of the truffle taxa from root and soil samples overlapped with fungal generalist diets (52-53%). Arbuscular mycorrhizal (AM) diversity was highest from soil samples and AM communities from roots did not overlap significantly with mammalian scat samples (<1.8%; Figure 4.4).

Almost all Hysterangiaceae, Mesophelliaceae and Tuberaceae truffle taxa sequenced from roots and soil were also within mammalian scats (Figure 4.5). Hysterangiaceae and Mesophelliaceae made up between 28 and 71% of the ECM sequence abundance of root samples (depending on site and season; Table 4.1). Of the Russulaceae sequenced from root samples, over half (59%) were in scat samples, whereas this percentage was 20% for Inocybaceae and 7% for Cortinariaceae (Figure 4.5).

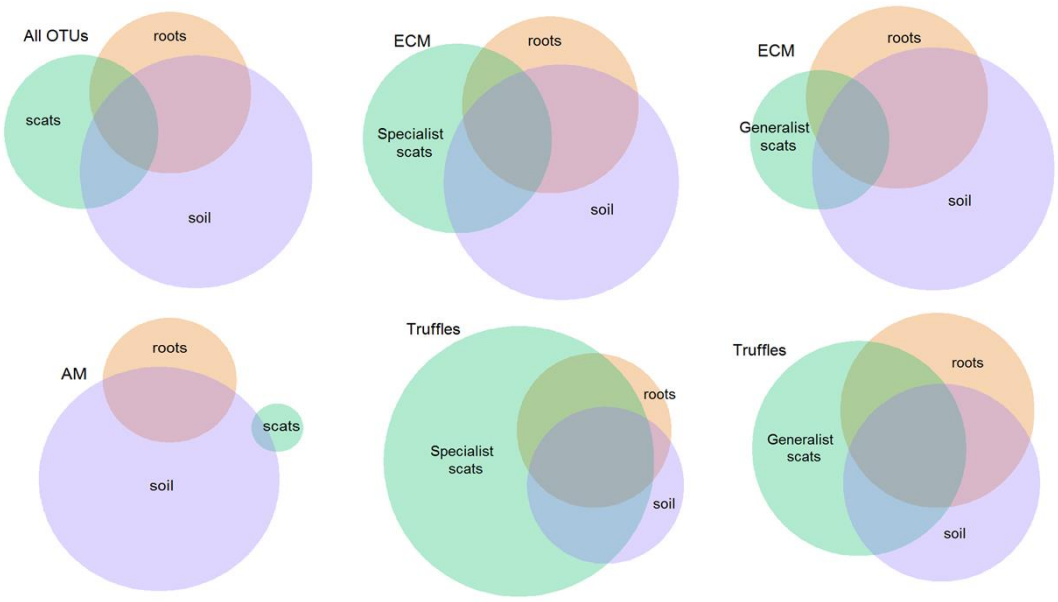


Figure 4.4: Venn diagrams where the size of a circle represents the relative OTU diversity of each sample type (soil, roots or scats) within each subsample of data (ectomycorrhizal = ECM, arbuscular mycorrhizal = AM, truffles and all OTUs). Overlapping areas represent the proportion of OTUs shared between sample types, whereas the non-overlapping areas represent OTUs unique to specified substrate. The total number of OTUs is 9358, 428 for AM fungi, 344 for ECM fungi and 116 for truffle fungi. Specialist scats are from fungal specialist *Bettongia tropica*, and generalist scats are from *Isoodon macrourus, I. obesulus, Melomys sp., Trichosurus vulpecula* (ECM only) and *Zyzomys argurus*. Note: For AM fungi, scats and roots shared 1.8% of taxa and scats and soil shared 0.8% of taxa and this is not shown because there were no taxa shared by all samples.

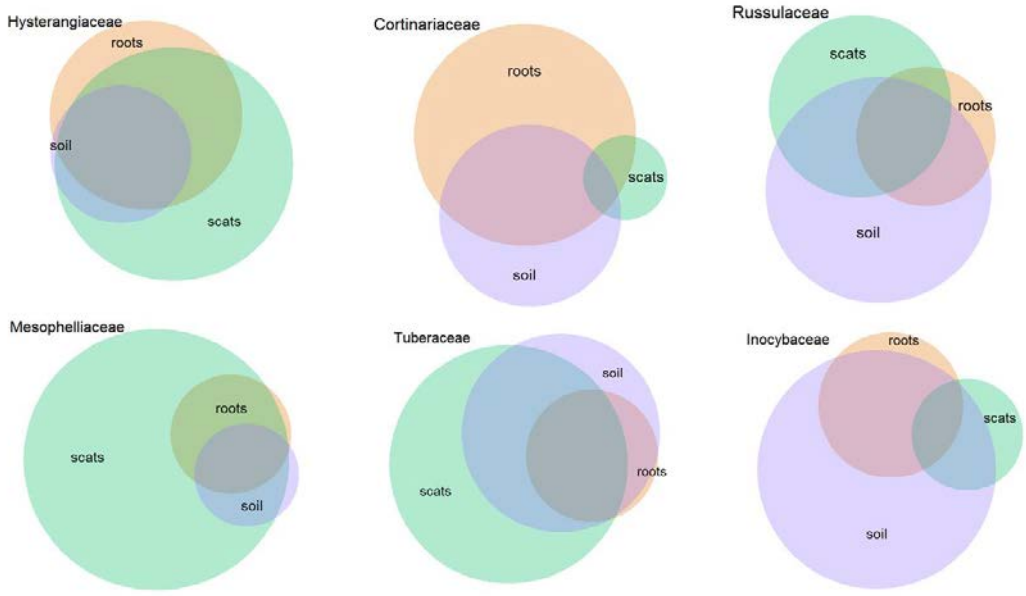


Figure 4.5: Venn diagrams where the size of a circle represents the relative OTU diversity of each sample type (soil, roots or scats) within each family of fungi (Hysterangiaceae [26 OTUs], Mesophelliaceae [59 OTUs] and Tuberaceae [15 OTUs] contain only truffle species; Cortinariaceae [128 OTUs], Russulaceae [159 OTUs] and Inocybaceae [132 OTUs] contain truffle and/or secotioid species as well as mushroom species). Overlapping areas represent the proportion of OTUs shared between sample types, whereas the non-overlapping areas represent OTUs unique specific substrate.

4.5 Discussion

The hypothesis that mammal communities are important for plant-mycorrhizal relationships, and indirectly are also contributing to the health of mycorrhizal host trees and nutrient cycling (Johnson 1996) assumes that mammal-dispersed truffles are an important part of mycorrhizal communities. Data from this chapter support this assumption in an ecosystem with the fungal specialist, *B. tropica*. Dominant components of the root-associating mycorrhizal community were ECM truffle taxa dispersed by mammals, indicating that, at least for these truffle taxa, *B. tropica* and other mammals can have a substantial influence on the functioning ECM community. Indeed, most truffle taxa associating with roots were within the fungal specialist's diet.

Reddell et al. (1999) also found truffle taxa (*Hysterangium* and *Nothocastoreum*) were included in the dominant tropical ECM communities as sporocarps and on roots. By moving a high diversity of ECM inocula, these mammals appear to indirectly contribute to plant productivity and nutrient cycling in these ecosystems.

The hypothesis linking mycophagous mammals to plant health and ecosystem functioning also implies that if the mammal community were to be altered, then the inoculum available for new colonising roots is also altered (lowering truffle diversity). This data provide support for such a connection in this study system. If dispersal of these taxa were reduced by changes to the mammal community, then the ECM community is likely to experience major shifts, with unknown consequences for plant health and nutrient cycling. Within Australia altered ECM communities and decreases in ECM colonisation rates have previously been associated with Eucalypt dieback and decreased crown health (Scott et al. 2012, Ishaq et al. 2013, Horton et al. 2013). Additionally, Australia has experienced high rates of mammal extinction and decline (Short and Smith 1994, Woinarski et al. 2015). Combined with these results, these observations raise concerns that major alterations to landscape-level ecosystem function may already be occurring, underscoring the need for further research. Further studies are needed to confirm whether this ECM community structure is typical for Australian woodlands. Future studies should utilise areas where fungal specialists have recently gone extinct or a reduction of mammal diversity has occurred, comparing to areas with higher mammal diversity to measure any changes in ECM communities. Additionally, studies are needed to investigate the functional redundancy of ECM taxa between truffles and epigeous taxa for aspects that interact with plant health and nutrient cycling.

Many mycophagy studies have found spores of sporocarpic (truffle-like) AM fungi in mammalian diets, mostly *Glomus* spp. (Janos et al. 1995, Vernes and Dunn 2009,

Nuske et al. 2017a). Indeed, these spores have been shown to be viable by inoculating bioassay seedlings with scats containing AM spores (McGee and Baczocha 1994, Reddell et al. 1997). However, these data from this chapter show that mammalian diets do not overlap significantly with AM fungi associating with roots or the general soil environment. This indicates that, at least in terms of species diversity, mammal dispersal of AM spores does not have a significant effect on the structure of AM communities in this system. Other mycophagy studies focusing on AM fungi, should test this hypothesis with more AM specific primers in order to place appropriate emphasis on these dispersal events for the whole AM community. Nevertheless, mammal dispersal may significantly affect the population structure of sporocarpic AM fungi like *Glomus* spp.

Previous ECM community studies in Australia classified between 3 and 27% of taxa as truffles (Appendix D). The percentage of truffle taxa from this study is within this range (21%). Additionally, the results reveal that truffles comprise dominant portions of the community. *Russula* and *Cortinarius* were the most OTU-rich taxa and were included in the relatively abundant groups from this sequencing and in other ECM surveys in Australia (Appendix D), although there was not enough taxonomic resolution to discern fruiting habit. This limits my capacity to draw conclusions about how truffle fungi form part of ECM diversity, and ultimately the overall influence of mycophagous mammals on the ECM community. It also emphasizes the need for further targeted truffle surveys and taxonomic work on these groups, coupled with continuous updating of online sequence databases.

While I took precautions in this study by removing OTUs present in negative and positive controls, contaminant DNA could still be present and errors in OTU assignment can occur via tag-switching (Carlsen et al. 2012, Nguyen et al. 2015a). For

this reason, I consider the proportion of overlapping taxa between sample types to be estimates. Also, taxa I observe at low relative abundances may be indistinguishable from contamination (e.g. the non-native *Tuber* spp., Appendix E). Amplicon sequencing data are considered 'semi-quantitative' in that relative abundances of sequences within rather than between taxa can be more meaningful as PCR procedures may selectively amplify certain taxa more than others (among other reasons) (Amend et al. 2010). Nevertheless, Nguyen et al. (2015a) argue that relative abundances of taxa may still have ecological value, provided the sequencing errors are appropriately handled and recognised. While I cannot verify whether dominant truffle taxa observed were selectively amplified, comparisons within truffle taxa (e.g. *Hysterangium*) show that they have a higher abundance in root associated communities. OTUs matching truffle taxa *Malajczukia/Mesophellia,* which have a high relative abundance in scats, are also present in root associating communities.

As the results were consistent across two sites and seasons, I consider my assessment of the ECM community structure sufficiently accurate to be confident in the conclusion that truffle taxa, and their mammalian dispersers, are important to ECM communities in this system.

Chapter Five: Discussion and Synthesis

The aim of this thesis was to understand the redundancy between mammal species in their roles as dispersers of mycorrhizal fungi and to determine the potential influence of mammals on the structure of mycorrhizal communities. Chapter Two's meta-analysis of the literature supported my hypothesis that fungal specialists within the mammalian family Potoroidae, consumed and potentially dispersed a significantly higher abundance and diversity of fungi than other mycophagous mammals with generalist diets (Nuske et al. 2017b; Chapter Two). This finding was further corroborated in a field study comparing the diet of a fungal specialist, *Bettongia tropica*, to that of other co-occurring mycophagous mammals. *Bettongia tropica* consumed a higher diversity and more unique species of ectomycorrhizal (ECM) truffle fungi than nine co-occurring mammal species (Chapter Three). Additionally, results from Chapter Four revealed that the dominant root-associating ECM taxa are also truffle forming fungi that are found within mammal diets and that specialist mammal diets overlapped with root-associating truffle taxa more than generalist diets. This implies that between specialist and generalist mammal species in Australia, there is little functional redundancy with respect to fungal dispersal. Taken together, the results of my thesis suggest that changes to mammalian communities, particularly the loss of fungal specialists, could, over time, induce significant detrimental changes to truffle diversity, shifting ECM communities with unknown consequences for plant health and nutrient cycling.

This thesis contributes to the growing body of evidence that altering mammal communities can influence mycorrhizal and plant communities. For example, changes to the mammal community by introducing non-native species (rats and rabbits) can affect soil fungal community structure (Peay et al. 2013, Clarke et al. 2015, Pansu et al. 2015). The removal of invasive mammals may not always result in the reversal of these

changes, particularly when vegetation has also changed and co-extinction of fungi and native mammals has occurred (Clarke et al. 2015, Pansu et al. 2015). So far, no experimental data exist that allow an examination of the changes that have occurred in ECM fungal communities with changes in native mammalian communities. However, the results from Chapter Four revealed that dominant root-associating fungi to be mammal dispersed, suggesting that changes in mammal communities could potentially shift the ECM community associating with plants, by lowering the diversity of truffle taxa. This shift may be exacerbated with the extinction of fungal specialists.

It is unclear at what time-scale the loss of mammalian fungal dispersers will impact on ECM fungal ecology and fungal-host dynamics. In a vertebrate removal experiment in an Australian rainforest, a decrease in arbuscular mycorrhizal (AM) colonisation, diversity and abundance was seen after only three years (Gehring et al. 2002). However, fungal spores can remain viable in the soil for a long time (years or decades) and even have long periods of dormancy (Bruns et al. 2009, Nguyen et al. 2012). These resistant propagules can form a 'spore bank' (analogous to seed banks; Long et al. 2015) which may be important after disturbance (Baar et al. 1999). While isolated trees, growing away from a forest and an established mycorrhizal network, and spore banks have been found to host a depauperate ECM community compared to intact forests (Peay et al. 2010, Glassman et al. 2015), in North America spore banks of ECM fungi are often dominated by truffle-like genera such as *Rhizopogon* and *Tuber* (Glassman et al. 2015). Little is known about how important direct spore colonisation is for the seasonal turnover of mycorrhizas, especially in tropical forests. Host trees may sustain their ECM partners, providing habitat for ECM fungi for some time. Therefore, we may not be able to fully understand or measure the cost to ecosystem health of losing

mammalian fungal specialists for decades or even centuries after their disappearance, as there may be an extinction debt to the fungal community (Kuussaari et al. 2009).

Certain mammals may play a role in distributing truffle taxa into fragmented areas of forest or across ecotones. Indeed, mammal dispersal of fungal spores has been shown to be critical for allowing seedlings of ECM plants to establish away from common mycelial networks of mature trees (Terwilliger and Pastor 1999, Ashkannejhad and Horton 2006, Frank et al. 2009, Wood et al. 2015a). For instance, in North America seedlings of ECM oak trees (*Quercus garryana*) growing away from mature trees in neighbouring shrub and grasslands were inoculated with truffle-like fungi by rodents via their scats (Frank et al. 2009). Within Australia, an analogue was found in *Rattus fuscipes* which consumed ECM fungi in sclerophyll forest and dispersed them into AM dominated rainforest (Vernes and Dunn 2009).

The results of this thesis suggest that a decline in mammals, which is common and particularly likely in increasingly fragmented and anthropogenically disturbed ecosystems, may lower the chances of truffle taxa contributing to the recovery of forested systems in fragmented areas (potentially lowering ECM diversity overall). If fragmentation were to occur in communities with truffle taxa as dominant components colonising plants (e.g. Chapter Four), and mammalian fungal specialist populations are detrimentally impacted, the shift in ECM community is likely to be more severe. Chapter Two of this thesis found that some generalist mammals, like the *Wallabia bicolor*, ate a high diversity of fungal taxa, similar to fungal specialists. *Wallabia bicolor* have also been shown to move between fragmented patches of forest through cleared areas (Danks 2011), hence may be especially important in those areas for maintaining truffle diversity and gene flow between populations within fragmented habitats.

5.2 Future research

5.2.1 Truffle population dynamics

Many populations of Australian fungal specialists (*Bettongia* and *Potorous*) were continuous and are now fragmented (Short 1998). For truffle species that rely on fungal specialists for dispersal, this fragmentation of disperser populations likely also results in fragmentation of truffle fungi populations. Clearing of habitat between populations also exacerbates the fragmentation of both fungal specialists and truffle fungi populations. Lower rates of dispersal of a particular fungus (due to loss of specialist mycophagists) may first affect the genetic population structure, prior and/or leading to local extinction of the fungus. Such effects would be testable but there are no data currently available.

Techniques to measure population dynamics of fungi are evolving and becoming increasingly efficient. Development of multiple species-specific markers (e.g. microsatellites, single nucleotide polymorphisms; SNPs) can be used to delineate individuals or populations and measure diversity, even from ECM roots or soil samples (Douhan et al. 2011). Additionally, new high throughput sequencing technology can sequence whole genomes or large numbers of restriction sites, allowing development of species-specific markers, mapping of coding genes or identify large numbers of SNPs (Wilson et al. 2015). Comparing population dynamics between areas of high mycophagous mammal diversity and low mycophagous mammal diversity could reveal lower genetic diversity and higher fragmentation for truffle fungi populations in the latter areas. Similarly, if the system holds little functional redundancy, lower population diversity for truffle taxa could be found in areas that have lost a fungal specialist compared to areas where specialists remain.

Alternatively, an increase in mammal diversity may have positive effects on truffle populations. There are many areas in Australia where native mammals, including fungal

specialists, have been reintroduced in predator-proof fences. For example, at Mulligans Flat, north of Canberra, the Tasmanian bettong (*B. gaimardi*) was reintroduced in 2012 (Portas et al. 2014, Batson et al. 2015). These areas and surrounding control sites would make ideal locations to study the effects of a fungal specialist on truffle fungi population dynamics.

5.2.2 Generalist foraging behaviour

One hypothesis that is yet to be tested is whether fungal generalists change their foraging behaviour when a fungal specialist becomes locally extinct. It is possible that generalists may increase the diversity of fungal species consumed once the competition for these resources reduces with the loss of a specialist. If this result is common, it will change the implications for many truffle populations. To test this hypothesis one would need to compare truffle consumption in relation to availability in areas with and without a fungal specialist. Ideally, the latter location will only have a recent extinction of a fungal specialist to limit the chances of any associated truffle population extinctions. For example, *B. tropica* has only recently become locally extinct at Mt Zero/Taravale. Comparing the truffle consumption of fungal generalist mammals at this location to that of *B. tropica* populations in the Lamb Range would make an ideal test of this hypothesis. Exclusion zones (fencing) can be used to compare the relative abundance of truffles available to those consumed by mammals (Johnson 1994a, North et al. 1997). If generalist mammals do not consume and disperse truffle taxa relative to their availability in the absence of a specialist, this would verify that there is little functional redundancy in their fungal dispersal roles. Such a result implies that the loss of specialists would have detrimental consequences for truffle diversity, altering ECM communities and plant-fungi interactions.

5.2.3 Climate change, mammals and fungi

Conservation of fungal specialists and mammal diversity is a priority, regardless of their roles in the environment. Fungal specialists rely on a high truffle abundance and diversity to maintain their populations (Johnson 1994c, Abell et al. 2006, Bateman et al. 2011). The abundance of truffles is strongly influenced by climatic variables, like precipitation and temperature (Claridge et al. 2000, Abell et al. 2006). Under current climate change models, temperature and CO_2 levels are predicted to increase, while changes in precipitation are expected but are more unpredictable (IPCC 2013). As climate change is likely to affect the production of their key resource, this makes fungal specialist populations, like those of *B. tropica*, particularly at risk and a high priority for future research to understand this dynamic.

There is currently not enough data to predict the direction of change to the abundance and diversity of truffles under climate change. As atmospheric CO_2 increases, theory predicts that trees will have increased rates of photosynthesis, which could lead to increased carbohydrate flow to ECM partners (Phillips et al. 2002, Wang et al. 2016). Increased CO_2 has been shown to increase the mycorrhizal colonisation of tree roots (Andrew and Lilleskov 2014, Wang et al. 2016). Some authors hypothesise that this may lead to increased production of fruiting bodies including truffles and mushrooms (although studies have mainly been on mushrooms) (Büntgen et al. 2012) while others predict a decrease (Ágreda et al. 2016). Experimental increases in CO_2 by Andrew et al. (2014) found that some species of ECM increase in mushroom biomass, while others decrease or exhibit no change. Indeed, most studies agree that changes in ECM-plant interactions under changes in CO_2, temperature or precipitation are species-specific (Andrew et al. 2014, Geml et al. 2015, Godbold et al. 2015). Simultaneous changes in CO_2, temperature and precipitation will also have confounding feedbacks which would

change the direction of some of the predictions. For instance, elevated CO_2 and temperature have interactive effects on plant-fungal dynamics; increases in temperature increases plant and fungal growth but this can be negated if CO_2 also increases (Hortal et al. 2016). Competitive interactions between mycorrhizas also complicate responses further (Hortal et al. 2016). Future research is needed to understand how the abundance and diversity of truffles is influenced by climate change.

5.2.4 Fungal conservation

Described as the third 'f' along with flora and fauna, fungi are typically a forgotten component of ecosystems (Pouliot and May 2010). Despite fungi performing vital roles in ecosystems we have little knowledge about the adequacy of current management practices for fungal conservation. My thesis highlights that, through the loss of mammalian fungal specialists, diversity of truffle fungi in Australia may be compromised. Within Australia there are only a few species listed by IUCN, including one sequestrate species (*Claustula fischeri*; http://iucn.ekoo.se). The vast majority of Australian fungal taxa remain 'not assessed' and few taxa match the data criteria to allow assessment (Dahlberg and Mueller 2011). Future research should concentrate on gathering of high-quality data combining fungal collections with environmental sequencing to allow accurate assessments of fungal population distributions. Additional actions are also needed to incentivise conservation of these essential organisms.

References

Abarenkov, K., R. Henrik Nilsson, K.-H. Larsson, I. J. Alexander, U. Eberhardt, S. Erland, K. Høiland, R. Kjøller, E. Larsson, T. Pennanen, R. Sen, A. F. S. Taylor, L. Tedersoo, B. M. Ursing, T. Vrålstad, K. Liimatainen, U. Peintner, and U. Kõljalg. 2010. The UNITE database for molecular identification of fungi--recent updates and future perspectives. New Phytologist 186:281–285.

Abell-Davis, S. E. 2008. Tropical hypogeous fungal sporocarp distribution in time and space. Implications for an endangered specialist mycophagous marsupial, *Bettongia tropica*. PhD thesis. School of Marine and Tropical Biology. James Cook University.

Abell, S. E., P. Gadek, C. Pearce, and B. C. Congdon. 2006. Seasonal resource availability and use by an endangered tropical mycophagous marsupial. Biological Conservation 132:533–540.

Adams, F., P. Reddell, M. Webb, and W. Shipton. 2006. Arbuscular mycorrhizas and ectomycorrhizas on *Eucalyptus grandis* (Myrtaceae) trees and seedlings in native forests of tropical north-eastern Australia. Australian Journal of Botany 54:271–281.

Ágreda, T., B. Águeda, M. Fernández-Toirán, S. M. Vicente-Serrano, and J. M. Òlano. 2016. Long-term monitoring reveals a highly structured interspecific variability in climatic control of sporocarp production. Agricultural and Forest Meteorology 223:39–47.

Aizen, M. A., M. Sabatino, and J. M. Tylianakis. 2012. Specialization and rarity predict nonrandom loss of interactions from mutualist networks. Science 335:1486–1489.

Allison, L. M., L. A. Gibson, and J. G. Aberton. 2006. Dietary strategy of the swamp

antechinus (*Antechinus minimus maritimus*) (Marsupialia: Dasyuridae) in coastal and inland heathland habitats. Wildlife Research 33:67–76.

Alsheikh, A. M., and J. M. Trappe. 1983. Taxonomy of *Phaeangium lefebvrei*, a desert truffle eaten by birds. Canadian Journal of Botany 61:1919–1925.

Amend, A. S., K. A. Seifert, and T. D. Bruns. 2010. Quantifying microbial communities with 454 pyrosequencing: Does read abundance count? Molecular Ecology 19:5555–5565.

Anderson, M., and C. T. Braak. 2003. Permutation tests for multi-factorial analysis of variance. Journal of Statistical Computation and Simulation 73:85–113.

Andrew, C. J., L. T. A. van Diepen, R. M. Miller, and E. A. Lilleskov. 2014. Aspen-associated mycorrhizal fungal production and respiration as a function of changing CO2, O3 and climatic variables. Fungal Ecology 10:70–80.

Andrew, C., and E. A. Lilleskov. 2014. Elevated CO2 and O3 effects on ectomycorrhizal fungal root tip communities in consideration of a post-agricultural soil nutrient gradient legacy. Mycorrhiza 24:581–593.

Anslan, S., M. Bahram, and L. Tedersoo. 2016. Temporal changes in fungal communities associated with guts and appendages of Collembola as based on culturing and high-throughput sequencing. Soil Biology and Biochemistry 96:152–159.

Applegate, G. B., and D. I. Nicholson. 1988. Caribbean pine in an agroforestry system on the Atherton Tableland in north east Australia. Agroforestry Systems 7:3–15.

Ashkannejhad, S., and T. R. Horton. 2006. Ectomycorrhizal ecology under primary succession on coastal sand dunes: interactions involving *Pinus contorta*, suilloid

fungi and deer. New Phytologist 169:345–54.

Baar, J., T. R. Horton, A. M. Kretzer, and T. D. Bruns. 1999. Mycorrhizal colonization of *Pinus muricata* from resistant propagules after a stand-replacing wildfire. New Phytologist 143:409–418.

Bateman, B. L., S. E. Abell-Davis, and C. N. Johnson. 2011. Climate-driven variation in food availability between the core and range edge of the endangered northern bettong (*Bettongia tropica*). Australian Journal of Zoology 59:177–185.

Batson, W. G., I. J. Gordon, D. B. Fletcher, and A. D. Manning. 2015. The effect of pre-release captivity on post-release performance in reintroduced eastern bettongs *Bettongia gaimardi*. Oryx 50:1–10.

Bell, T. L., and M. A. Adams. 2004. Ecophysiology of ectomycorrhizal fungi associated with *Pinus* spp. in low rainfall areas of Western Australia. Plant Ecology 171:35–52.

Bengtsson-Palme, J., M. Ryberg, M. Hartmann, S. Branco, Z. Wang, A. Godhe, P. De Wit, M. Sánchez-García, I. Ebersberger, F. de Sousa, A. Amend, A. Jumpponen, M. Unterseher, E. Kristiansson, K. Abarenkov, Y. J. K. Bertrand, K. Sanli, K. M. Eriksson, U. Vik, V. Veldre, and R. H. Nilsson. 2013. Improved software detection and extraction of ITS1 and ITS2 from ribosomal ITS sequences of fungi and other eukaryotes for analysis of environmental sequencing data. Methods in Ecology and Evolution 4:914–919.

Bennett, A. F., and B. J. Baxter. 1989. Diet of the Long-Nosed Potoroo, *Potorous tridactylus* (Marsupialia, Potoroidae), in Southwestern Victoria. Australian Wildlife Research 16:263–271.

Bentley, J. M. 2008. Role of movement, interremnant dispersal and edge effects in determining sensitivity to habitat fragmentation in two forest-dependent rodents. Austral Ecology 33:184–196.

Bice, J., and K. Moseby. 2008. Diets of the re-introduced greater bilby (*Macrotis lagotis*) and burrowing bettong (*Bettongia lesueur*) in the Arid Recovery Reserve, Northern South Australia. Australian Mammalogy 30:1–12.

Bonito, G., M. E. Smith, M. Nowak, R. A. Healy, G. Guevara, E. Cázares, A. Kinoshita, E. R. Nouhra, L. S. Domínguez, L. Tedersoo, C. Murat, Y. Wang, B. A. Moreno, D. H. Pfister, K. Nara, A. Zambonelli, J. M. Trappe, and R. Vilgalys. 2013. Historical biogeography and diversification of truffles in the Tuberaceae and their newly identified southern hemisphere sister lineage. PLoS ONE 8:e52765.

Bougher, N. L., and J. A. Friend. 2009. Fungi consumed by translocated Gilbert's potoroos (*Potorous gilbertii*) at two sites with contrasting vegetation, south coastal Western Australia. Australian Mammalogy 31:97–105.

Bougher, N. L., and T. Lebel. 2001. Sequestrate (truffle-like) fungi of Australia and New Zealand. Australian Systematic Botany 14:439–484.

Braithwaite, R., and A. Griffiths. 1996. The paradox of *Rattus tunneyi*: endangerment of a native pest. Wildlife Research 23:1–21.

Brodie, J. F., C. E. Aslan, H. S. Rogers, K. H. Redford, J. L. Maron, J. L. Bronstein, and C. R. Groves. 2014. Secondary extinctions of biodiversity. Trends in Ecology and Evolution 29:664–672.

Brundrett, M. C. 2009. Mycorrhizal associations and other means of nutrition of vascular plants: understanding the global diversity of host plants by resolving

conflicting information and developing reliable means of diagnosis. Plant and Soil 320:37–77.

Bruns, T. D., K. G. Peay, P. J. Boynton, L. C. Grubisha, N. A. Hynson, N. H. Nguyen, and N. P. Rosenstock. 2009. Inoculum potential of *Rhizopogon* spores increases with time over the first 4 yr of a 99-yr spore burial experiment. New Phytologist 181:463–70.

Büntgen, U., H. Kauserud, and S. Egli. 2012. Linking climate variability to mushroom productivity and phenology. Frontiers in Ecology and the Environment 10:14–19.

Caldwell, I. R., K. Vernes, and F. Bärlocher. 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.

Camacho, C., G. Coulouris, V. Avagyan, N. Ma, J. Papadopoulos, K. Bealer, and T. L. Madden. 2009. BLAST plus: architecture and applications. BMC Bioinformatics 10:421.

Cameron, E. K., and E. M. Bayne. 2015. Spatial patterns and spread of exotic earthworms at local scales. Canadian Journal of Zoology 93:721–726.

Carlsen, T., A. Bjørnsgaard Aas, D. Lindner, T. Vrålstad, T. Schumacher, and H. Kauserud. 2012. Don't make a mista(g)ke: Is tag switching an overlooked source of error in amplicon pyrosequencing studies? Fungal Ecology 5:747–749.

Chauvat, M., G. Perez, and J. F. Ponge. 2014. Foraging patterns of soil springtails are impacted by food resources. Applied Soil Ecology 82:72–77.

Chen, G., R.-R. Zhang, Y. Liu, and W.-B. Sun. 2014. Spore dispersal of fetid *Lysurus mokusin* by feces of mycophagous insects. Journal of Chemical Ecology 40:893–

899.

Christensen, P. E. S. 1980. The biology of *Bettongia penicillata* Gray, 1837, and *Macropus eugenii* (Desmarest, 1817) in relation to fire. Page (M. R. Lewis, Ed.). Bulletin 9. Forests Department of Western Australia.

Claridge, A. W. 1993. Fungal diet of the long-nosed bandicoot (*Perameles nasuta*) in south-eastern Australia. Victorian Naturalist 110:86–91.

Claridge, A. W., S. C. Barry, S. J. Cork, and J. M. Trappe. 2000. Diversity and habitat relationships of hypogeous fungi. II. Factors influencing the occurrence and number of taxa. Biodiversity and Conservation 9:175–199.

Claridge, A. W., and D. B. Lindenmayer. 1993. The mountain brushtail possum (*Trichosurus caninus* Ogilby): disseminator of fungi in the mountain ash forests of the central highlands of Victoria? Victorian Naturalist 110:91–95.

Claridge, A. W., and D. B. Lindenmayer. 1998. Consumption of hypogeous fungi by the mountain brushtail possum (*Trichosurus caninus*) in eastern Australia. Mycological Research 102:269–272.

Claridge, A. W., and T. W. May. 1994. Mycophagy among Australian mammals. Australian Journal of Ecology 19:251–275.

Claridge, A. W., A. McNee, M. T. Tanton, and S. M. Davey. 1991. Ecology of bandicoots in undisturbed forest adjacent to recently felled logging coupes: a case study from the Eden Woodchip Agreement Area. Pages 331–345 *in* D. Lunney, editor. Conservation of Australia's Forest Fauna. Royal Zoological Society of NSW, Mosman.

Claridge, A. W., J. H. Seebeck, and R. Rose, editors. 2007. Bettongs, Potoroos and the

Musky Rat-Kangaroo. First Edit. CSIRO Publishing, Collingwood, VIC.

Claridge, A. W., M. T. Tanton, and R. B. Cunningham. 1993. Hypogeal fungi in the diet of the long-nosed potoroo (*Potorous tridactylus*) in mixed-species and regrowth eucalypt forest stands in south-eastern Australia. Wildlife Research 20:321–337.

Claridge, A. W., M. T. Tanton, J. H. Seebeck, S. J. Cork, and R. B. Cunningham. 1992. Establishment of ectomycorrhizae on the roots of two species of *Eucalyptus* from fungal spores contained in the faeces of the long-nosed potoroo (*Potorous tridactylus*). Australian Journal of Ecology 17:207–217.

Claridge, A. W., J. M. Trappe, and D. L. Claridge. 2001. Mycophagy by the swamp wallaby (*Wallabia bicolor*). Wildlife Research 28:643–645.

Clarke, L. J., L. S. Weyrich, and A. Cooper. 2015. Reintroduction of locally extinct vertebrates impacts arid soil fungal communities. Molecular Ecology 24:3194–3205.

Cockburn, A. 1980. The diet of the new-holland mouse *Pseudomys novaehollandiae* and the house mouse *Mus musculus* in a Victorian coastal heathland. Australian Mammalogy 3:31–34.

Colgan, W., and A. W. Claridge. 2002. Mycorrhizal effectiveness of *Rhizopogon* spores recovered from faecal pellets of small forest-dwelling mammals. Mycological Research 106:314–320.

Colwell, R. K. 2013. EstimateS: Statistical estimation of richness and shared species from samples. Version 9.

Colwell, R. K., R. R. Dunn, and N. C. Harris. 2012. Coextinction and persistence of

dependent species in a changing world. Annual Review of Ecology, Evolution, and Systematics 43:183–203.

Comport, S. S. 2000. Habitat utilisation and dispersal of fungal spores by the White-tailed rat on the rainforest-wet sclerophyll boundary in the Wet Tropics. MSc thesis. Department of Zoology. James Cook University.

Cooper, T., and K. Vernes. 2011. Mycophagy in the larger bodied skinks of the genera *Tiliqua* and *Egernia*: are there implications for ecosystem health? Australian Zoologist 35:681–684.

Dahlberg, A., and G. M. Mueller. 2011. Applying IUCN red-listing criteria for assessing and reporting on the conservation status of fungal species. Fungal Ecology 4:147–162.

Danks, M. A. 2011. The swamp wallaby *Wallabia bicolor*: a generalist browser as a key mycophagist. PhD thesis. University of New England.

Danks, M. A. 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.

Dennis, A. J. 2002. The diet of the musky rat-kangaroo, *Hypsiprymnodon moschatus*, a rainforest specialist. Wildlife Research 29:209–219.

Douhan, G. W., L. Vincenot, H. Gryta, and M. A. Selosse. 2011. Population genetics of ectomycorrhizal fungi: From current knowledge to emerging directions. Fungal Biology 115:569–597.

Drenkhan, T., K. Voolma, K. Adamson, I. Sibul, and R. Drenkhan. 2017. The large pine weevil *Hylobius abietis* (L.) as a potential vector of the pathogenic fungus

Diplodia sapinea (Fr.) Fuckel. Agricultural and Forest Entomology 19:4–9.

Van Dyck, S., I. Gynther, and A. Baker, editors. 2013. Field companion to the mammals of Australia. New Holland Publishers, Sydney.

Evans, M. C., and P. J. Jarman. 1999. Diets and feeding selectivities of bridled nailtail wallabies and black-striped wallabies. Wildlife Research 26:1–19.

Firth, R. S. C., E. Jefferys, J. C. Z. Woinarski, and R. A. Noske. 2005. The diet of the brush-tailed rabbit-rat (*Conilurus penicillatus*) from the monsoonal tropics of the Northern Territory, Australia. Wildlife Research 32:517–523.

Flaherty, E. A., M. Ben-David, and W. P. Smith. 2010. Diet and food availability: implications for foraging and dispersal of Prince of Wales northern flying squirrels across managed landscapes. Journal of Mammalogy 91:79–91.

Fogel, R., and S. B. Peck. 1975. Ecological studies of hypogeous fungi. I. Coleoptera associated with sporocarps. Mycologia 67:741–747.

Ford, F., A. Cockburn, and L. Broome. 2003. Habitat preference, diet and demography of the smoky mouse, *Pseudomys fumeus* (Rodentia: Muridae), in south-eastern New South Wales. Wildlife Research 30:89–101.

Fox, B. J., D. G. Read, E. Jefferys, and J. Luo. 1994. Diet of the Hastings River mouse (*Pseudomys oralis*). Wildlife Research 21:491–505.

Frank, J. L., S. Anglin, E. M. Carrington, D. S. Taylor, B. Viratos, and D. Southworth. 2009. Rodent dispersal of fungal spores promotes seedling establishment away from mycorrhizal networks on *Quercus garryana*. Botany 87:821–829.

Gehring, C. A., J. E. Wolf, and T. C. Theimer. 2002. Terrestrial vertebrates promote arbuscular mycorrhizal fungal diversity and inoculum potential in a rain forest soil.

Ecology Letters 5:540–548.

Geml, J., L. N. Morgado, T. A. Semenova, J. M. Welker, M. D. Walker, and E. Smets. 2015. Long-term warming alters richness and composition of taxonomic and functional groups of arctic fungi. Federation of European Microbiological Societies Microbiology Ecology 91:1–13.

Gibson, L. A. 2001. Seasonal changes in the diet, food availability and food preference of the greater bilby (*Macrotis lagotis*) in south-western Queensland. Wildlife Research 28:121–134.

Glassman, S. I., K. G. Peay, J. M. Talbot, D. P. Smith, J. A. Chung, J. W. Taylor, R. Vilgalys, and T. D. Bruns. 2015. A continental view of pine-associated ectomycorrhizal fungal spore banks: a quiescent functional guild with a strong biogeographic pattern. New Phytologist 205:1619–1631.

Glen, M., N. L. Bougher, I. J. Colquhoun, S. Vlahos, W. A. Loneragan, P. A. O'Brien, and G. E. S. J. Hardy. 2008. Ectomycorrhizal fungal communities of rehabilitated bauxite mines and adjacent, natural jarrah forest in Western Australia. Forest Ecology and Management 255:214–225.

Godbold, D., M. Vašutová, A. Wilkinson, M. Edwards-Jonášová, M. Bambrick, A. Smith, M. Pavelka, and P. Cudlin. 2015. Elevated atmospheric CO2 affects ectomycorrhizal species abundance and increases sporocarp production under field conditions. Forests 6:1256–1273.

Gordon, V., and S. Comport. 1998. Comparison of three methods for extraction of spores of ectomycorrhizal fungi from mammal scats. Mycologia 90:47–51.

Gormsen, D., P. A. Olsson, and K. Hedlund. 2004. The influence of collembolans and

earthworms on AM fungal mycelium. Applied Soil Ecology 27:211–220.

Goto, B. T., and L. C. Maia. 2005. Sporocarpic species of arbuscular mycorrhizal fungi (Glomeromycota), with a new report from Brazil. Acta Botanica Brasilica 19:633–637.

Green, K., N. E. Davis, and W. A. Robinson. 2014. Does diet constrain the occupation of high elevations by macropods? A comparison between *Macropus rufogriseus* and *Wallabia bicolor*. Australian Mammalogy 36:219–228.

Green, K., A. T. Mitchell, and P. Tennant. 1998. Home range and microhabitat use by the long-footed potoroo, *Potorous longipes*. Wildlife Research 25:357–372.

Green, K., M. K. Tory, A. T. Mitchell, P. Tennant, and T. W. May. 1999. The diet of the long-footed potoroo (*Potorous longipes*). Austral Ecology 24:151–156.

Grubisha, L. C., S. E. Bergemann, and T. D. Bruns. 2007. Host islands within the California Northern Channel Islands create fine-scale genetic structure in two sympatric species of the symbiotic ectomycorrhizal fungus *Rhizopogon*. Molecular Ecology 16:1811–22.

Hawkins, B. J., M. D. Jones, and J. M. Kranabetter. 2015. Ectomycorrhizae and tree seedling nitrogen nutrition in forest restoration. New Forests 46:747–771.

Hayes, J. P., S. P. Cross, and P. W. McIntire. 1986. Seasonal variation in mycophagy by the western red-backed vole, *Clethrionomys californicus*, in Southwestern Oregon. Northwest Science 4:250–257.

Hayward, M. W. 2005. Diet of the quokka (*Setonix brachyurus*) (Macropodidae: Marsupialia) in the northern jarrah forest of Western Australia. Wildlife Research 32:15–22.

van der Heijden, M. G. A., F. M. Martin, M.-A. Selosse, and I. R. Sanders. 2015. Mycorrhizal ecology and evolution: the past, the present, and the future. New Phytologist 205:1406–1423.

Hill, F. A. R., and B. E. Triggs. 1985. Ecology and distribution of the Long-footed Potoroo (*Pototous longipes*) - a second preliminary examination. Department of Conservation, Forests and Lands. State Forests and Lands Service, Victoria.

Hoeksema, J. D., V. B. Chaudhary, C. A. Gehring, N. C. Johnson, J. Karst, R. T. Koide, A. Pringle, C. Zabinski, J. D. Bever, J. C. Moore, G. W. T. Wilson, J. N. Klironomos, and J. Umbanhowar. 2010. A meta-analysis of context-dependency in plant response to inoculation with mycorrhizal fungi. Ecology Letters 13:394–407.

Horsup, A., and H. Marsh. 1992. The diet of the allied rock-wallaby, *Petrogale assimilis*, in the wet-dry tropics. Wildlife Research 19:17–33.

Hortal, S., J. R. Powell, J. M. Plett, A. Simonin, and I. C. Anderson. 2016. Intraspecific competition between ectomycorrhizal *Pisolithus microcarpus* isolates impacts plant and fungal performance under elevated CO2 and temperature. Federation of European Microbiological Societies Microbiology Ecology 92:fiw113.

Horton, B. M., M. Glen, N. J. Davidson, D. A. Ratkowsky, D. C. Close, T. J. Wardlaw, and C. Mohammed. 2017. An assessment of ectomycorrhizal fungal communities in Tasmanian temperate high-altitude *Eucalyptus delegatensis* forest reveals a dominance of the Cortinariaceae. Mycorrhiza 27:67–74.

Horton, B. M., M. Glen, N. J. Davidson, D. Ratkowsky, D. C. Close, T. J. Wardlaw, and C. Mohammed. 2013. Temperate eucalypt forest decline is linked to altered ectomycorrhizal communities mediated by soil chemistry. Forest Ecology and Management 302:329–337.

Houston, T. F., and N. L. Bougher. 2010. Records of hypogeous mycorrhizal fungi in the diet of some Western Australian bolboceratine beetles (Coleoptera: Geotrupidae, Bolboceratinae). Australian Journal of Entomology 49:49–55.

IPCC. 2013. Climate change 2013: the physical science basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge, UK.

Ishaq, L., P. A. Barber, G. E. S. J. Hardy, M. Calver, and B. Dell. 2013. Seedling mycorrhizal type and soil chemistry are related to canopy condition of *Eucalyptus gomphocephala*. Mycorrhiza 23:359–71.

Ivory, M. H., and F. M. Munga. 1983. Growth and survival of container-grown *Pinus caribaea* infected with various ectomycorrhizal fungi. Plant and Soil 71:339–344.

Izzo, A. D., M. Meyer, and J. M. Trappe. 2005. Hypogeous ectomycorrhizal fungal species on roots and in small mammal diet in a mixed-conifer forest. Forest Science 51:243–254.

Jacobs, K. M., and D. L. Luoma. 2008. Small mammal mycophagy response to variations in green-tree retention. Journal of Wildlife Management 72:1747–1755.

Janos, D. P., C. T. Sahley, and L. H. Emmons. 1995. Rodent dispersal of vesicular-arbuscular mycorrhizal fungi in Amazonian Peru. Ecology 76:1852–1858.

Jefferys, E. A., and B. J. Fox. 2001. The diet of the Pilliga Mouse, *Pseudomys pilligaensis* (Rodentia: Muridae) from the Pilliga Shrub, Northern New South Wales. Proceedings of the Linnean Society of New South Wales 123:89–99.

Johnson, C. N. 1994a. Mycophagy and spore dispersal by a rat-kangaroo: consumption of ectomycorrhizal taxa in relation to their abundance. Functional Ecology 8:464–

468.

Johnson, C. N. 1994b. Fruiting of hypogeous fungi in dry sclerophyll forest in Tasmania, Australia: seasonal variation and annual production. Mycological Research 98:1173–1182.

Johnson, C. N. 1994c. Nutritional ecology of a mycophagous marsupial in relation to production of hypogeous fungi. Ecology 75:2015–2021.

Johnson, C. N. 1996. Interactions between mammals and ectomycorrhizal fungi. Trends in Ecology and Evolution 11:503–507.

Johnson, C. N., and A. P. McIlwee. 1997. Ecology of the northern bettong, *Bettongia tropica*, a tropical mycophagist. Wildlife Research 24:549–559.

Jones, S. C., W. J. I. Jordan, S. J. Meiners, A. N. Miller, and A. S. Methven. 2007. Fungal spore dispersal by the eastern box turtle (*Terrapene carolina carolina*). The American Midland Naturalist 157:121–126.

Kataržytė, M., and E. Kutorga. 2011. Small mammal mycophagy in hemiboreal forest communities of Lithuania. Central European Journal of Biology 6:446–456.

Keiper, P., and C. N. Johnson. 2004. Diet and habitat preference of the Cape York short-nosed bandicoot (*Isoodon obesulus peninsulae*) in north-east Queensland. Wildlife Research 31:259–265.

Klironomos, J. N., and P. Moutoglis. 1999. Colonization of nonmycorrhizal plants by mycorrhizal neighbours as influenced by the collembolan, *Folsomia candida*. Biology and Fertility of Soils 29:277–281.

Kõljalg, U., R. H. Nilsson, K. Abarenkov, L. Tedersoo, A. F. S. Taylor, M. Bahram, S. T. Bates, T. D. Bruns, J. Bengtsson-Palme, T. M. Callaghan, B. Douglas, T.

Drenkhan, U. Eberhardt, M. Dueñas, T. Grebenc, G. W. Griffith, M. Hartmann, P. M. Kirk, P. Kohout, E. Larsson, B. D. Lindahl, R. Lücking, M. P. Martín, P. B. Matheny, N. H. Nguyen, T. Niskanen, J. Oja, K. G. Peay, U. Peintner, M. Peterson, K. Põldmaa, L. Saag, I. Saar, A. Schüßler, J. A. Scott, C. Senés, M. E. Smith, A. Suija, D. L. Taylor, M. T. Telleria, M. Weiss, and K.-H. Larsson. 2013. Towards a unified paradigm for sequence-based identification of fungi. Molecular Ecology 22:5271–5277.

Kuussaari, M., R. Bommarco, R. K. Heikkinen, A. Helm, M. Pa, J. Krauss, R. Lindborg, E. Öckinger, M. Pärtel, F. Rodà, C. Stefanescu, T. Teder, M. Zobel, and I. Steffan-dewenter. 2009. Extinction debt: a challenge for biodiversity conservation. Trends in Ecology and Evolution 24:564–571.

Lamont, B. B., C. S. Ralph, and P. E. S. Christensen. 1985. Mycophagous marsupials as dispersal agents for ectomycorrhizal fungion *Eucalyptus calophylla* and *Gastrolobium bilobum*. New Phytologist 101:651–656.

Laurance, W. F. 1997. A distributional survey and habitat model for the endangered northern Bettong *Bettongia tropica* in tropical Queensland. Biological Conservation 82:47–60.

Lebel, T., and M. A. Castellano. 1999. Australasian truffle-like fungi. IX. History and current trends in the study of the taxonomy of sequestrate macrofungi from Australia and New Zealand. Australian Systematic Botany 12:803–817.

Legendre, P., and E. D. Gallagher. 2001. Ecologically meaningful transformations for ordination of species data. Oecologia 129:271–280.

Li, W., and A. Godzik. 2006. Cd-hit: A fast program for clustering and comparing large sets of protein or nucleotide sequences. Bioinformatics 22:1658–1659.

Lilleskov, E. A., and T. D. Bruns. 2013. Spore dispersal of a resupinate ectomycorrhizal fungus, *Tomentella sublilacina*, via soil food webs. Mycologia 97:762–9.

Lindahl, B. D., R. H. Nilsson, L. Tedersoo, K. Adarenkov, T. Carlsen, R. Kjøller, U. Kõljalg, T. Pennanen, S. Rosendahl, J. Stenlid, and H. Kauserud. 2013. Fungal community analysis by high-throughput sequencing of amplified markers–a user's guide. New Phytologist 199:288–299.

Linde, C. C., and H. Selmes. 2012. Genetic diversity and mating type distribution of *Tuber melanosporum* and their significance to truffle cultivation in artificially planted truffiéres in Australia. Applied and Environmental Microbiology 78:6534–6539.

Livne-Luzon, S., Y. Avidan, G. Weber, H. Migael, T. Bruns, O. Ovadia, and H. Shemesh. 2016. Wild boars as spore dispersal agents of ectomycorrhizal fungi: consequences for community composition at different habitat types. Mycorrhiza 27:165–174.

Long, R. L., M. J. Gorecki, M. Renton, J. K. Scott, L. Colville, D. E. Goggin, L. E. Commander, D. A. Westcott, H. Cherry, and W. E. Finch-Savage. 2015. The ecophysiology of seed persistence: a mechanistic view of the journey to germination or demise. Biological Reviews 90:31–59.

Lu, X., N. Malajczuk, M. Brundrett, and B. Dell. 1999. Fruiting of putative ectomycorrhizal fungi under blue gum (*Eucalyptus globulus*) plantations of different ages in Western Australia. Mycorrhiza 8:255–261.

Luo, J., and B. J. Fox. 1996. Seasonal and successional dietary shifts of two sympatric rodents in coastal heathland: A possible mechanism for coexistence. Australian Journal of Ecology 21:121–132.

Luo, J., B. J. Fox, and E. Jefferys. 1994. Diet of the eastern chestnut mouse (*Pseudomys gracilicaudatus*). I. Composition, diversity and individual variation. Wildlife Research 21:401–417.

Malajczuk, N., J. M. Trappe, and R. Molina. 1987. Interrelationships among some ectomycorrhizal trees, hypogeous fungi and small mammals: Western Australian and northwestern American parallels. Australian Journal of Ecology 12:53–55.

Marchesan, D., and S. M. Carthew. 2008. Use of space by the yellow-footed antechinus, *Antechinus flavipes*, in a fragmented landscape in South Australia. Landscape Ecology 23:741–752.

Maser, C., R. A. Nussbaum, and J. M. Trappe. 1978. Fungal-small mammal interrelationships with emphasis on Oregon coniferous forests. Ecology 59:799–809.

McGee, P. A., and N. Baczocha. 1994. Sporocarpic Endogonales and Glomales in the scats of *Rattus* and *Perameles*. Mycological Research 98:246–249.

McIlwee, A. P., and C. N. Johnson. 1998. The contribution of fungus to the diets of three mycophagous marsupials in *Eucalyptus* forests, revealed by stable isotope analysis. Functional Ecology 12:223–231.

McMurdie, P. J., and S. Holmes. 2013. Phyloseq: an R package for reproducible interactive analysis and graphics of microbiome census data. PLoS ONE 8:e61217.

McMurdie, P. J., and S. Holmes. 2014. Waste not, want not: why rarefying microbiome data is inadmissible. PLoS Computational Biology 10:e1003531.

Medway, D. G. 2000. Mycophagy by north island robin. Australasian Mycologist 19:102.

Meyer, M. D., M. P. North, and D. A. Kelt. 2005. Fungi in the diets of northern flying squirrels and lodgepole chipmunks in the Sierra Nevada. Canadian Journal of Zoology 83:1581–1589.

Midgley, D. J., J. A. Saleeba, M. I. Stewart, A. E. Simpson, and P. A. McGee. 2007. Molecular diversity of soil basidiomycete communities in northern-central New South Wales, Australia. Mycological Research 111:370–378.

Morrant, D. S., and S. Petit. 2012. Strategies of a small nectarivorous marsupial, the western pygmy-possum, in response to seasonal variation in food availability. Journal of Mammalogy 93:1525–1535.

Murray, B. R., and C. R. Dickman. 1994. Granivory and microhabitat use in Australian desert rodents: are seeds important? Oecologia 99:216–225.

Murray, B. R., C. R. Dickman, C. H. S. Watts, and S. R. Morton. 1999. The dietary ecology of Australian desert rodents. Wildlife Research 26:421–437.

Nakagawa, S., and H. Schielzeth. 2013. A general and simple method for obtaining R2 from generalized linear mixed-effects models. Methods in Ecology and Evolution 4:133–142.

Nakamori, T., and A. Suzuki. 2005. Spore-breaking capabilities of collembolans and their feeding habitat within sporocarps. Pedobiologia 49:261–267.

Nakamori, T., and A. Suzuki. 2010. Spore resistance and gut-passage time of macrofungi consumed by *Ceratophysella denisana* (Collembola: Hypogastruridae). Fungal Ecology 3:38–42.

Navnith, M., G. R. Finlayson, M. S. Crowther, and C. R. Dickman. 2009. The diet of the re-introduced greater bilby *Macrotis lagotis* in the mallee woodlands of

western New South Wales. Australian Zoologist 35:90–95.

Newell, J. 2009. The role of the reintroduction of Greater Bilbies (*Macrotis lagotis*) and Burrowing Bettongs (*Bettongia lesueur*) in the ecological restoration of an arid ecosystem: foraging diggings, diet, and soil seed banks. PhD thesis. School of Earth and Environmental Sciences. University of Adelaide.

Nguyen, N. H., N. A. Hynson, and T. D. Bruns. 2012. Stayin' alive: survival of mycorrhizal fungal propagules from 6-yr-old forest soil. Fungal Ecology 5:741–746.

Nguyen, N. H., D. Smith, K. Peay, and P. Kennedy. 2015a. Parsing ecological signal from noise in next generation amplicon sequencing. New Phytologist 205:1389–1393.

Nguyen, N. H., Z. Song, S. T. Bates, S. Branco, L. Tedersoo, J. Menke, J. S. Schilling, and P. G. Kennedy. 2015b. FUNGuild: An open annotation tool for parsing fungal community datasets by ecological guild. Fungal Ecology:1–8.

Nguyen, V. P., A. D. Needham, and J. A. Friend. 2005. A quantitative dietary study of the "Critically Endangered" Gilbert's potoroo *Potorous gilbertii.* Australian Mammalogy 27:1–6.

Nilsson, R. H., L. Tedersoo, K. Abarenkov, M. Ryberg, E. Kristiansson, M. Hartmann, C. Schoch, J. Nylander, J. Bergsten, T. Porter, A. Jumpponen, P. Vaishampayan, O. Ovaskainen, N. Hallenberg, J. Bengtsson, M. Eriksson, K.-H. Larsson, E. Larsson, and U. Koeljalg. 2012. Five simple guidelines for establishing basic authenticity and reliability of newly generated fungal ITS sequences. MycoKeys 4:37–63.

North, M., J. Trappe, and J. Franklin. 1997. Standing crop and animal consumption of fungal sporocarps in Pacific Northwest forests. Ecology 78:1543–1554.

Norton, M. A., K. French, and A. W. Claridge. 2010. Habitat associations of the long-nosed potoroo (*Potorous tridactylus*) at multiple spatial scales. Australian Journal of Zoology 58:303.

Nuske, S. J., K. Vernes, T. W. May, A. W. Claridge, B. C. Congdon, A. Krockenberger, and S. E. Abell. 2017a. Data on the fungal species consumed by mammal species in Australia. Data in Brief 12:251–260.

Nuske, S. J., K. Vernes, T. W. May, A. W. Claridge, B. C. Congdon, A. Krockenberger, and S. E. Abell. 2017b. Redundancy among mammalian fungal dispersers and the importance of declining specialists. Fungal Ecology 27:1–13.

O'Malley, A. 2012. Spatial patterns in the distribution of truffle-like fungi, mutualistic interactions with mammals, and spore dispersal dynamics. PhD thesis. School of Environmental and Rural Science. University of New England.

Oksanen, J. 2015. Multivariate analysis of ecological communities in R: vegan tutorial.

Pansu, J., R. C. Winkworth, L. Gielly, P. Taberlet, and P. Choler. 2015. Long-lasting modification of soil fungal diversity associated with the introduction of rabbits to a remote sub-Antarctic archipelago. Biology Letters 11:20150408.

Pattinson, G. S., S. E. Smith, and B. M. Doube. 1997. Earthworm *Aporrectodea trapezpodes* had no effect on the dispersal of a vesicular-arbuscular mycorrhizal fungi, *Glomus intraradices*. Soil Biology and Biochemistry 29:1079–1088.

Peay, K. G., I. A. Dickie, D. A. Wardle, P. J. Bellingham, and T. Fukami. 2013. Rat invasion of islands alters fungal community structure, but not wood decomposition

rates. Oikos 122:258–264.

Peay, K. G., M. Garbelotto, and T. D. Bruns. 2010. Evidence of dispersal limitation in soil microorganisms: isolation reduces species richness on mycorrhizal tree islands. Ecology 91:3631–3640.

Pestell, A. J. L., and S. Petit. 2007. Diet of the western pygmy possum, *Cercartetus concinnus* Gould (Marsupialia: Burramyidae), at Innes National Park, South Australia, and evaluation of diet sampling methods. Australian Journal of Zoology 55:275–284.

Phillips, R. L., D. R. Zak, W. E. Holmes, and D. C. White. 2002. Microbial community composition and function beneath temperate trees exposed to elevated atmospheric carbon dioxide and ozone. Oecologia 131:236–244.

Pizzuto, T. A., G. R. Finlayson, M. S. Crowther, and C. R. Dickman. 2007. Microhabitat use by the brush-tailed bettong (*Bettongia penicillata*) and burrowing bettong (*B. lesueur*) in semiarid New South Wales: implications for reintroduction programs. Wildlife Research 34:271–279.

Pope, L. C., A. Estoup, and C. Moritz. 2000. Phylogeography and population structure of an ecotonal marsupial, *Bettongia tropica*, determined using mtDNA and microsatellites. Molecular Ecology 9:2041–53.

Portas, T., D. Fletcher, D. Spratt, A. Reiss, P. Holz, K. Stalder, J. Devlin, D. Taylor, D. Dobroszczyk, and A. D. Manning. 2014. Health evaluation of free-ranging Eastern Bettongs (*Bettongia gaimardi*) during translocation for reintroduction in Australia. Journal of Wildlife Diseases 50:210–223.

Pouliot, A. M., and T. W. May. 2010. The third “F” — fungi in Australian biodiversity

conservation: actions, issues and initiatives. Mycologia Balcanica 7:41–48.

Pyare, S., and W. S. Longland. 2001. Patterns of ectomycorrhizal-fungi consumption by small mammals in remnant old-growth forests of the Sierra Nevada. Journal of Mammalogy 82:681–689.

R Core Team. 2012. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Reddell, P., V. Gordon, and M. S. Hopkins. 1999. Ectomycorrhizas in *Eucalyptus tetrodonta* and *E. miniata* forest communities in tropical northern Australia and their role in the rehabilitation of these forests following mining. Australian Journal of Botany 47:881–907.

Reddell, P., and A. V Spain. 1991. Earthworms as vectors of viable propagules of mycorrhizal fungi. Soil Biology and Biochemistry 23:767–774.

Reddell, P., A. V Spain, and M. Hopkins. 1997. Dispersal of spores of mycorrhizal fungi in scats of native mammals in tropical forests of northeastern Australia. Biotropica 29:184–192.

Renker, C., P. Otto, K. Schneider, B. Zimdars, M. Maraun, and F. Buscot. 2005. Oribatid mites as potential vectors for soil microfungi: Study of mite-associated fungal species. Microbial Ecology 50:518–528.

Robley, A. J., J. Short, and S. Bradley. 2001. Dietary overlap between the burrowing bettong (*Bettongia lesueur*) and the European rabbit (*Oryctolagus cuniculus*) in semi-arid coastal Western Australia. Wildlife Research 28:341–349.

Schickmann, S., A. Urban, K. Kräutler, U. Nopp-Mayr, and K. Hackländer. 2012. The interrelationship of mycophagous small mammals and ectomycorrhizal fungi in

primeval, disturbed and managed Central European mountainous forests. Oecologia 170:395–409.

Schlager, F. E. 1981. The distribution and status of the rufous rat-kangaroo, *Aepyprymnus rufescens*, and the Long-nosed Potoroo, *Potorous tridactylus*, in northern New South Wales. Report to the New South Wales National Parks and Wildlife Foundation by University of New England, Department of Ecosystem Management. Project Report No. 18.

Schloss, P. D., S. L. Westcott, T. Ryabin, J. R. Hall, M. Hartmann, E. B. Hollister, R. A. Lesniewski, B. B. Oakley, D. H. Parks, C. J. Robinson, J. W. Sahl, B. Stres, G. G. Thallinger, D. J. Van Horn, and C. F. Weber. 2009. Introducing mothur: Open-source, platform-independent, community-supported software for describing and comparing microbial communities. Applied and Environmental Microbiology 75:7537–7541.

Schoch, C. L., K. A. Seifert, S. Huhndorf, V. Robert, J. L. Spouge, C. A. Levesque, W. Chen, and Fungal Barcoding Consortium. 2012. Nuclear ribosomal internal transcribed spacer (ITS) region as a universal DNA barcode marker for Fungi. Proceedings of the National Academy of Sciences of the United States of America 109:6241–6246.

Scott, L. K., I. D. Hume, and C. R. Dickman. 1999. Ecology and population biology of long-nosed bandicoots (*Perameles nasuta*) at North Head, Sydney Harbour National Park. Wildlife Research 26:805–821.

Scott, P. M., B. L. Shearer, P. A. Barber, and G. E. S. J. Hardy. 2012. Relationships between the crown health, fine root and ectomycorrhizae density of declining *Eucalyptus gomphocephala*. Australasian Plant Pathology 42:121–131.

Scotts, D., and J. H. Seebeck. 1989. Ecology of *Potorous longipes* (Marsupialia: Potoroidae); and preliminary recommendations for management of its habitat in Victoria. Arthur Rylah Institute for Environmental Research. National Parks and Wildlife Division. Department of Conservation, Forest and Lands - Victoria. Technical Report Series No. 62 to Australian National Parks and Wildlife Service. Heidelberg, Victoria.

Seebeck, J. H., and R. W. Rose. 1989. 30. Potoroidae. Pages 1–45 *in* D. W. Walton and B. J. Richardson, editors. Fauna of Australia. Volume 1B. AGPS Canberra, Canberra.

Sheedy, E. M., A. P. Van de Wouw, B. J. Howlett, and T. W. May. 2013. Multigene sequence data reveal morphologically cryptic phylogenetic species within the genus *Laccaria* in southern Australia. Mycologia 105:547–63.

Shevill, D. I., and C. N. Johnson. 2008. Diet and breeding of the rufous spiny bandicoot *Echymipera rufescens australis*, Iron Range, Cape York Peninsula. Australian Mammalogy 29:169–175.

Short, J. 1989. The Diet of the Brush-Tailed Rock-Wallaby in New-South-Wales. Wildlife Research 16:11–18.

Short, J. 1998. The extinction of rat-kangaroos (Marsupialia: Potoroidae) in New South Wales, Australia. Biological Conservation 86:367–377.

Short, J., and A. Smith. 1994. Mammal Decline and Recovery in Australia. Journal of Mammalogy 75:288–297.

Simpson, J. A. 1996. Why don’t more birds eat more fungi? Australasian Mycologist 17:67–68.

Simpson, J. A. 2000. More on mycophagous birds. Australasian Mycologist 19:49–51.

Smith, A. P., and L. Broome. 1992. The effects of season, sex and habitat on the diet of the mountain pygmy-possum (*Burramys parvus*). Wildlife Research 19:755–768.

Song, Z., D. Schlatter, P. Kennedy, L. L. Kinkel, and H. C. Kistler. 2015. Effort versus reward: preparing samples for fungal community characterization in high-throughput sequencing surveys of soils. PLoS ONE 10:e0127234.

Stefani, F. O. P., R. H. Jones, and T. W. May. 2014. Concordance of seven gene genealogies compared to phenotypic data reveals multiple cryptic species in Australian dermocyboid *Cortinarius* (Agaricales). Molecular Phylogenetics and Evolution 71:249–260.

Di Stefano, J., G. Coulson, A. Greenfield, and M. Swan. 2011. Resource heterogeneity influences home range area in the swamp wallaby *Wallabia bicolor*. Ecography 34:469–479.

Stimson, N. W. 1987. A unpublished report on the feral pig (*Sus scrofa*) in the Alexandra Region, Department of Conservation, Forests and Lands, Victoria.

Streatfeild, C. 2009. The effects of habitat fragmentation on the demography and population genetic structure of *Uromys caudimaculatus*. PhD thesis. School of Natural Resource Sciences. Queensland University of Technology.

Tann, C. R., G. R. Singleton, and B. J. Coman. 1991. Diet of the house mouse, *Mus domesticus*, in the Mallee wheatlands of north-western Victoria. Wildlife Research 18:1–12.

Taylor, D. L., I. C. Herriott, K. E. Stone, J. W. McFarland, M. G. Booth, and M. B. Leigh. 2010. Structure and resilience of fungal communities in Alaskan boreal

forest soils. Canadian Journal of Forest Research 40:1288–1301.

Taylor, R. J. 1988. Ecology and conservation of the Tasmanian Bettong (*Bettongia gaimardi*). Consultancy Report to the Australian National Parks and Wildlife Service and National Geographic Society., Hobart, Tasmania.

Taylor, R. J. 1992. Seasonal changes in the diet of the Tasmanian bettong (*Bettongia gaimardi*), a mycophagous marsupial. Journal of Mammalogy 73:408–414.

Taylor, R. J. 1993. Home range, nest use and activity of the Tasmanian bettong, *Bettongia gaimardi*. Wildlife Research 20:87–95.

Tedersoo, L., K. Abarenkov, R. H. Nilsson, A. Schüssler, G.-A. Grelet, P. Kohout, J. Oja, G. M. Bonito, V. Veldre, T. Jairus, M. Ryberg, K.-H. Larsson, and U. Kõljalg. 2011. Tidying up international nucleotide sequence databases: ecological, geographical and sequence quality annotation of its sequences of mycorrhizal fungi. PLoS ONE 6:e24940.

Tedersoo, L., M. Bahram, S. Põlme, U. Kõljalg, N. S. Yorou, R. Wijesundera, L. V Ruiz, A. M. Vasco-Palacios, P. Q. Thu, A. Suija, M. E. Smith, C. Sharp, E. Saluveer, A. Saitta, M. Rosas, T. Riit, D. Ratkowsky, K. Pritsch, K. Põldmaa, M. Piepenbring, C. Phosri, M. Peterson, K. Parts, K. Pärtel, E. Otsing, E. Nouhra, A. L. Njouonkou, R. H. Nilsson, L. N. Morgado, J. Mayor, T. W. May, L. Majuakim, D. J. Lodge, S. S. Lee, K.-H. Larsson, P. Kohout, K. Hosaka, I. Hiiesalu, T. W. Henkel, H. Harend, L. Guo, A. Greslebin, G. Grelet, J. Geml, G. Gates, W. Dunstan, C. Dunk, R. Drenkhan, J. Dearnaley, A. D. Kesel, T. Dang, X. Chen, F. Buegger, F. Q. Brearley, G. Bonito, S. Anslan, S. Abell, and K. Abarenkov. 2014. Global diversity and geography of soil fungi. Science 346:125668-1-1256688–10.

Tedersoo, L., M. Bahram, M. Toots, A. G. Diédhiou, T. W. Henkel, R. Kjøller, M. H.

Morris, K. Nara, E. Nouhra, K. G. Peay, S. Põlme, M. Ryberg, M. E. Smith, and U. Kõljalg. 2012. Towards global patterns in the diversity and community structure of ectomycorrhizal fungi. Molecular Ecology 21:4160–70.

Tedersoo, L., T. Jairus, B. M. Horton, J. Abarenkov, T. Suvi, I. Saar, and U. Kõljalg. 2008. Strong host preference of ectomycorrhizal fungi in a Tasmanian wet sclerophyll forest as revealed by DNA barcoding and taxon-specific primers. New Phytologist 180:479–490.

Tedersoo, L., T. W. May, and M. E. Smith. 2010. Ectomycorrhizal lifestyle in fungi: global diversity, distribution, and evolution of phylogenetic lineages. Mycorrhiza 20:217–263.

Tedersoo, L., and M. E. Smith. 2013. Lineages of ectomycorrhizal fungi revisited: Foraging strategies and novel lineages revealed by sequences from belowground. Fungal Biology Reviews 27:83–99.

Tedersoo, L., T. Suvi, K. Beaver, and U. Kõljalg. 2007. Ectomycorrhizal fungi of the Seychelles: diversity patterns and host shifts from the native *Vateriopsis seychellarum* (Dipterocarpaceae) and *Intsia bijuga* (Caesalpiniaceae) to the introduced *Eucalyptus robusta* (Myrtaceae), but not *Pinus caribea* (Pinaceae). New Phytologist 175:321–333.

Terwilliger, J., and J. Pastor. 1999. Small mammals, ectomycorrhizae, and conifer succession in beaver meadows. Oikos 85:83–94.

Thomas, P. W. 2014. An analysis of the climatic parameters needed for *Tuber melanosporum* cultivation incorporating data from six continents. Mycosphere 5:137–142.

Thums, M., M. Klaassen, and I. D. Hume. 2005. Seasonal changes in the diet of the long-nosed bandicoot (*Perameles nasuta*) assessed by analysis of faecal scats and of stable isotopes in blood. Australian Journal of Zoology 53:87–93.

Tokushima, H., S. W. Green, and P. J. Jarman. 2008. Ecology of the rare but irruptive Pilliga mouse (*Pseudomys pilligaensis*). I. Population fluctuation and breeding season. Australian Journal of Zoology 56:363–373.

Tokushima, H., and P. J. Jarman. 2010. Ecology of the rare but irruptive Pilliga mouse, *Pseudomys pilligaensis*. III. Dietary ecology. Australian Journal of Zoology 58:85–93.

Tory, M. K., T. W. May, P. J. Keane, and A. F. Bennett. 1997. Mycophagy in small mammals: a comparison of the occurrence and diversity of hypogeal fungi in the diet of the long-nosed potoroo *Potorous tridactylus* and the bush rat *Rattus fuscipes* from southwestern Victoria, Australia. Australian Journal of Ecology 22:460–470.

Trappe, J. M., R. Molina, D. L. Luoma, E. Cázares, D. Pilz, J. E. Smith, M. A. Castellano, S. L. Miller, and M. J. Trappe. 2009. Diversity, Ecology, and Conservation of Truffle Fungi in Forests of the Pacific Northwest. Page General Technical Report. PNW-GTR-772. United States Department of Agriculture, Forest Service, Pacific Northwest Research Station. Portland, Oregon.

Troy, S., and G. Coulson. 1993. Home range of the swamp wallaby, *Wallabia bicolor*. Wildlife Research 20:571–577.

Tucker, M. A., T. J. Ord, and T. L. Rogers. 2014. Evolutionary predictors of mammalian home range size: body mass, diet and the environment. Global Ecology and Biogeography 23:1105–1114.

Vernes, K. 2007. Are diverse mammal communities important for maintaining plant-fungal associations and ecosystem health? Australasian Plant Conservation 15:16–18.

Vernes, K. 2010. Mycophagy in a community of macropodoid species. Pages 155–169 *in* G. Coulson and M. Eldridge, editors. Macropods: The Biology of Kangaroos, Wallabies and Rat-Kangaroos. CSIRO Publishing, Collingwood, Victoria.

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.

Vernes, K., S. Blois, and F. Bärlocher. 2004. Seasonal and yearly changes in consumption of hypogeous fungi by northern flying squirrels and red squirrels in old-growth forest, New Brunswick. Canadian Journal of Zoology 82:110–117.

Vernes, K., M. Castellano, and C. N. Johnson. 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.

Vernes, K., T. Cooper, and S. Green. 2015. Seasonal fungal diets of small mammals in an Australian temperate forest ecosystem. Fungal Ecology 18:107–114.

Vernes, K., and L. Dunn. 2009. Mammal mycophagy and fungal spore dispersal across a steep environmental gradient in eastern Australia. Austral Ecology 34:69–76.

Vernes, K., and D. T. Haydon. 2001. Effect of fire on northern bettong (*Bettongia tropica*) foraging behaviour. Austral Ecology 26:649–659.

Vernes, K., and K. McGrath. 2009. Are introduced black rats (*Rattus rattus*) a functional replacement for mycophagous native rodents in fragmented forests?

Fungal Ecology 2:145–148.

Vernes, K., and L. C. Pope. 2001. Stability of nest range, home range and movement of the northern bettong (*Bettongia tropica*) following moderate-intensity fire in a tropical woodland, north-eastern Queensland. Wildlife Research 28:141–150.

Vernes, K., and J. M. Trappe. 2007. Hypogeous fungi in the diet of the red-legged pademelon *Thylogale stigmatica* from a rainforest-open forest interface in northeastern Australia. Australian Zoologist 34:203–208.

Wang, X., E. Agathokleous, L. Qu, M. Watanabe, and T. Koike. 2016. Effects of elevated CO2 and O3 on the interaction between root of woody plants and ectomycorrhizae. Journal of Agricultural Meteorology 72:95–105.

Watts, C. H. S. 1977. The foods eaten by some Australian rodents (Muridae). Australian Wildlife Research 4:151–157.

Wayne, A. F., M. A. Maxwell, C. G. Ward, C. V Vellios, M. R. Williams, and K. H. Pollock. 2016. The responses of a critically endangered mycophagous marsupial (*Bettongia penicillata*) to timber harvesting in a native eucalypt forest. Forest Ecology and Management 363:190–199.

Weatherstone, C. 2012. The diversity of hypogeous fungi consumed by tropical Australian and Papua New Guinean Macropodoidae. MSc Thesis. School of Marine and Tropical Sciences. James Cook University.

White, T. J., T. Bruns, S. Lee, and J. Taylor. 1990. Amplification and Direct Sequencing of Fungal Ribosomal RNA Genes for Phylogenetics. Pages 315–322 *in* M. A. Innis, D. H. Gelfand, J. J. Sninsky, and T. J. White, editors. PCR Protocols A Guide to Methods and Applications. Elsevier Inc.

Wilson, A. W., N. J. Wickett, P. Grabowski, J. Fant, J. Borevitz, and G. M. Mueller. 2015. Examining the efficacy of a genotyping-by-sequencing technique for population genetic analysis of the mushroom *Laccaria bicolor* and evaluating whether a reference genome is necessary to assess homology. Mycologia 107:217–226.

Wilson, B. A., and E. Bradtke. 1999. The diet of the New Holland mouse, *Pseudomys novaehollandiae* (Waterhouse) in Victoria. Wildlife Research 26:439–451.

Woinarski, J. C. Z., A. A. Burbidge, and P. L. Harrison. 2014. The action plan for Australian Mammals 2012. CSIRO Publishing, Collingwood, Victoria.

Woinarski, J. C. Z., A. A. Burbidge, and P. L. Harrison. 2015. Ongoing unraveling of a continental fauna: Decline and extinction of Australian mammals since European settlement. Proceedings of the National Academy of Sciences of the United States of America 112:4531–4540.

Wood, J. R., I. A. Dickie, H. V Moeller, D. A. Peltzer, K. I. Bonner, G. Rattray, and J. M. Wilmshurst. 2015a. Novel interactions between non-native mammals and fungi facilitate establishment of invasive pines. Journal of Ecology 103:121–129.

Wood, S. W., L. D. Prior, H. C. Stephens, and D. M. J. S. Bowman. 2015b. Macroecology of Australian tall eucalypt forests: Baseline data from a continental-scale permanent plot network. PLoS ONE 10:1–24.

Wright, P. C., and I. D. Hume. 1984. Diet and some aspects of digestion in the rufous rat-kangaroo (*Aepyprymnus rufescens*). Bulletin of Australian Mammalogy Society 8:84.

Zosky, K., K. Bryant, M. Calver, and A. Wayne. 2010. Do preservation methods affect

the identification of dietary components from faecal samples? A case study using a mycophagous marsupial. Australian Mammalogy 32:173–176.

Appendix A: Fungal species consumed by mammal species in Australia

The following tables are supplementary tables for Chapter Two. The data was derived from the literature only (See Table 2.1 for citations). These tables are also published in *Data in Brief* (Nuske et al. 2017a).

Table A.1: Fungal species consumed by mammal species in North Queensland on the Atherton Tablelands. Taxa in boldface are **truffles** and underlined are secotioid or higher taxa that include truffle or secotioid taxa and normal text are non-truffles. Mycorrhizal status (Myc) is either ectomycorrhizal (ECM), putatively ectomycorrhizal (ECM?), other functional modes (N), unknown functional modes (?) or arbuscular mycorrhizal (AM; Tedersoo et al. 2010, Tedersoo and Smith 2013). These values are applied to the genera as a whole and/or species listed under a genus, unless otherwise specified. Fungal taxon names indicated by an asterisk* are only in the fungal specialist's, Northern Bettong's (*Bettongia tropica*) diet. Mammal species names are as follows; *Bt* is *Bettongia tropica*, *Ar* is *Aepyprymnus rufescens*, *Im* is *Isoodon macrourus*, *Iop* is *Isoodon obesulus peninsulae*, *Pn* is *Perameles nasuta*, *Ts* is *Thylogale stigmatica* and *Uc* is *Uromys caudimaculatus*.

Fungal taxa	Myc	*Bt*	*Ar*	*Im*	*Iop*	*Pn*	*Ts*	*Uc*	Total
***Amylascus sp.**	ECM?	1							1
***Aroramyces sp.**	ECM?	1			1				2
**** A. queenslandica**		1							1
***Austrogautieria sp.**	ECM				1				1
***A. amara**								1	1
***A. chlorospora**		1							1
***A. longispora nom. ined.**		1							1
***Beatonia sp.**	?	1							1
***Castoreum sp.**	ECM	1							1
***Chondrogaster sp.**	ECM	1		1					2
Cortinarius sp.	ECM	1			1				2
***Cribbea sp.**	N						1		1
***Descomyces sp.**	ECM	1							1
***Elaphomyces sp.**	ECM	1	1	1					3

Endogone sp.	ECM	1	1	1		1		1	5
****Gallacea sp.***	ECM?	1							1
Gautieria sp.	ECM	1			1		1		3
Glomus sp.	AM	1			1			1	3
Gummiglobus sp.	ECM	1	1	1		1		1	5
Gymnohydnotrya sp.	ECM						1		1
****Hydnangium sp.***	ECM	1							1
Hydnoplicata sp.	ECM						1		1
Hymenogaster sp.	ECM							1	1
Hysterangium sp.	ECM	1	1	1	1	1	1	1	7
****Hysterogaster sp.***	ECM?	1							1
Hysterogaster sp.	ECM?				1				1
Mesophellia sp.	ECM	1						1	2
Mycoamaranthus auriorbis	ECM?	1	1						2
Pogisperma sp.	?				1				1
Pseudohysterangium sp.	?	1	1	1		1		1	5
Rossbeevera sp.	ECM	1					1		2
****Royoungia boletoides***	ECM?	1							1
Scleroderma sp.	ECM	1		1				1	3
Sclerogaster sp.	?	1	1	1					3
Sphaerodes beatonii	N						1		1
Sphaerosoma sp.	ECM?						1		1
Stephanospora flava	N						1		1
****Timgrovea sp.***	ECM?	1							1
Zelleromyces sp.	ECM	1						1	2
Total		28	7	8	8	4	9	10	

Table A.2: Fungal species consumed by mammal species in Northern New South Wales on the Gibraltar Range. Refer to Table A.1 for annotation. Mammal names are as follows; *Pt* is *Potorous tridactylus*, *As* is *Antechinus stuartii*, *Mp* is *Macropus parma*, *Mc* is *Melomys cervinipes*, *Pn* is *Perameles nasuta*, *Pno* is *Pseudomys novaehollandiae*, *Rf* is *Rattus fuscipes*, *Tt* is *Thylogale thetis*, *Tc* is *Trichosurus caninus* and *Wb* is *Wallabia bicolor.*

Fungal taxa	Myc	*Pt*	*As*	*Mp*	*Mc*	*Pn*	*Pno*	*Rf*	*Tt*	*Tc*	*Wb*	Total
Agaricus sp.	N		1	1	1				1		1	5
Amylascus sp.	ECM?		1		1	1		1				4
Arcangeliella sp.	ECM							1			1	2
Aroramyces sp.	ECM?	1	1	1	1	1		1			1	7
Austrogautieria sp.	ECM		1	1	1	1		1	1		1	7
Boletellus sp.	ECM			1					1		1	3

Chondrogaster sp.	ECM							1			1	2
Cortinarius sp.	ECM	1	1	1	1	1		1	1	1	1	9
Densospora sp.	ECM										1	1
Descomyces sp.	ECM		1		1	1		1	1			5
D. stolatus						1		1	1			3
Dingleya sp.	ECM	1		1				1				3
Elaphomyces sp.	ECM	1		1		1		1	1	1	1	7
Endogone sp.	ECM						1	1				2
Gautieria sp.	ECM			1		1					1	3
G. monospora											1	1
Glomus sp.	AM				1	1		1	1			4
Hydnangium sp.	ECM				1	1		1				3
Hydnoplicata sp.	ECM							1	1			2
H. convolute			1			1		1			1	4
Hysterangium sp.	ECM	1	1	1	1	1		1	1		1	8
H. inflatum								1				1
Hysterogaster sp.	ECM?		1	1	1	1		1	1		1	7
Labyrinthomyces sp.	ECM	1	1	1				1	1		1	6
Leucogaster sp.	ECM				1	1		1				3
L. meridionalis		1									1	2
Mesophellia sp.	ECM			1				1			1	3
Octaviania sp.	ECM			1				1	1		1	4
Pogisperma sp.	?							1			1	2
Protubera sp.	ECM?					1		1				2
Rossbeevera sp.	ECM		1	1	1	1		1	1		1	7
R. vittatispora											1	1
Scleroderma sp.	ECM		1	1	1	1		1	1	1	1	8
S. tommayi			1	1				1			1	4
Sclerogaster sp.	?							1	1		1	3
Sphaerosoma sp.	ECM?							1			1	2
Stephanospora sp.	N							1				1
Timgrovea sp.	ECM?							1				1
Total		7	13	16	13	17	1	31	16	3	25	

Table A.3: Fungal species consumed by mammal species in South Eastern NSW near the Victorian border. Refer to Table A.1 for annotation. Fungal species indicated by an asterisk* are only in the fungal specialist's, *Potorous* spp., diets. Mammal names are as follows; *Pl* is *Potorous longipes, Pt* is *Potorous tridactylus, Io* is *Isoodon obesulus, Pn* is *Perameles nasuta, Pf* is *Pseudomys fumeus, Rf* is *Rattus fuscipes, Tc* is *Trichosurus caninus* and *Wb* is *Wallabia bicolor.*

Fungal taxa	Myc	*Pl*	*Pt*	*Io*	*Pn*	*Pf*	*Rf*	*Tc*	*Wb*	Total

***Acaulospora sp.**	AM	1							1
**Aleuria aurantia*	N	1							1
**Aleurina calospora*	ECM	1							1
**Amanita sp.*	ECM	1							1
** A. grandispora*			1						1
***Amarrendia lignicolor**	ECM?	1							1
***Amylascus tasmanicus**	ECM?	1	1						2
***Andebbia pachythrix**	ECM?		1						1
***Aroramyces gelatinosporus**	ECM?		1						1
***Austrogautieria costata**	ECM?	1	1						2
***Castoreum sp.**	ECM?		1		1				2
**** C. tasmanicum**			1						1
Cortinarius sp.	ECM	1	1				1		3
***C. atratus**	ECM		1		1				2
****C. leucocephalus**	ECM		1						1
****C. levisporus**	ECM		1						1
****C. oblongisporus**	ECM	1	1						2
****C. oleosus**	ECM		1						1
****C. piriformis**	ECM	1							1
***C. scabrosus**	ECM		1		1				2
****C. subviolaceus**	ECM	1							1
****Cystangium sp.**	ECM?	1							1
****C. phymatodisporum**		1							1
****C. rodwayi**		1							1
***Descomyces albellus**	ECM		1		1				2
***Descomyces albus**	ECM	1	1		1				3
****Dingleya tessellate**	ECM	1	1						2
***Endogone sp.**	ECM	1	1		1	1	1		5
Entoloma gasteromycetoides	ECM		1		1				2
***Gautieria sp.**	ECM		1		1		1		3
****G. albida**		1	1						2
***G. monospora**			1		1				2
**Geoglossum sp. sens. Lat.*	N	1							1
****Gymnohydnotrya echinulata**	ECM		1						1
***Gymnomyces sp.**	ECM							1	1
****G. pallidus**		1							1
****G. redolens**		1	1						2
****G. seminudus**		1							1
***Hydnangium sp.**	ECM				1				1
****H. archeri**		1	1						2
***H. carneum**							1	1	2
****Hydnoplicata convolute**	ECM		1						1
***Hymenangium album**	?					1			1

Hymenogaster sp.	ECM	1			1	1		1		4
****H. aureus***		1	1							2
H. inflatum					1					1
H. nanus			1		1					2
Hysterangium sp.	ECM	1	1			1			1	4
****H. affine***		1								1
****H. aggregatum***		1	1							2
H. inflatum		1	1				1			3
****H. salmonaceum***			1							1
****Hysterogaster fusisporus***	ECM?		1							1
Jafneadelphus sp.	ECM?		1		1			1		3
Labyrinthomyces sp.	ECM							1		1
L. varius		1	1		1					3
**Lamprospora sp.*	N	1								1
**L. crechqueraultii*		1								1
****Leucogaster sp.***	ECM	1								1
****L. meridionalis***			1							1
Mesophellia sp.	ECM	1	1	1	1	1		1		6
Octaviania sp.	ECM					1		1		2
O. tasmanica		1	1		1					3
Podohydnangium sp.	ECM?	1						1		2
****Richoniella sp.***	ECM?	1								1
Rossbeevera sp.	ECM	1	1		1				1	4
****R. mucosa***		1								1
****R. pachydermis***			1							1
R. vittatispora		1	1		1			1		4
Scleroderma sp.	ECM	1							1	2
****S. paradoxum***	ECM	1	1							2
**Sphaerodes beatonii*	N	1								1
Stephanospora flava	N	1	1					1		3
****Timgrovea macrospora***	ECM?		1							1
****Timgrovea reticulate***	ECM?		1							1
Zelleromyces sp.	ECM	1	1		1			1	1	5
****Z. australiensis***			1							1
Z. daucinus			1		1					2
****Z. malaiensis***			1							1
****Z. striatus***		1	1							2
Total		46	50	1	21	5	2	13	6	

Appendix B: Mammal species per site and season

Table B.1: Mean ± SE OTU richness per sample (total OTU number in parentheses), mean ± SE depth (sequence read copy) per sample (total in parentheses) and number of samples (*n*) per mammal species for each site and season (Late dry = Nov-Dec, Early wet = Feb-Mar, Late wet = May-Jun) for all OTUs. Generalists are all non-bettong samples combined.

		Season								
		Late dry			Early wet			Late wet		
Site	Mammal species	Richness	Depth	*n*	Richness	Depth	*n*	Richness	Depth	*n*
Davies Creek	*Bettongia tropica*	128 ± 46.0 (613)	24030 ± 815 (168210)	7	67.8 ± 17.7 (305)	19310 ± 9362.3 (115836)	6	72 ± 9.4 (439)	12730 ± 2409.6 (152753)	12
	Generalists	64 ± 12.8 (544)	10680 ± 3282.8 (128220)	12	110.3 ± 21.1 (937)	8771 ± 2181.2 (96482)	11	43 ± 7.3 (390)	3331 ± 1029.7 (36645)	11
	Isoodon macrourus	82 ± 45.9 (229)	8986 ± 5306.9 (26959)	3	18	3106	1	47 ± 10.4 (292)	2621 ± 1194.5 (18344)	7
	Uromys caudimaculatus	37	1120	1	157 ± 30.7 (497)	14880 ± 3405.8 (59515)	4	46 ± 13.5 (90)	6458 ± 3718 (12916)	2

	Melomys sp.	69 ± 28 (132)	24410 ± 15381.5 (48825)	2						
	Isoodon obesulus	24 ± 3 (46)	2706 ± 1949 (5412)	2	89 ± 46.7 (276)	1830 ± 501.6 (5491)	3	23 ± 5 (44)	2692 ± 1605.5 (5385)	2
	Zyzomys argurus	74 ± 12.3 (227)	11480 ± 3718.4 (45904)	4	131 ± 6 (249)	12310 ± 2388 (24618)	2			
	Antechinus flavipes				38	3752	1			
Emu Creek	*Bettongia tropica*	146 ± 58.5 (639)	15610 ± 1956.9 (93670)	6	130 ± 31.5 (708)	16750 ± 5879.2 (133965)	8	102 ± 42.2 (920)	7240 ± 1527.4 (86877)	12
	Generalists	144 ± 37.8 (1082)	7162 ± 2327.2 (78785)	11	111 ± 29.7 (1169)	9082 ± 2481.7 (118072)	13	106 ± 23.8 (1162)	6572 ± 1553.9 (92002)	14
	Isoodon macrourus	72 ± 32 (369)	9353 ± 4152.1 (56117)	6	144 ± 44.7 (979)	10620 ± 3690.0 (84944)	8	157.5 ± 56.7 (572)	4936 ± 2387.0 (19742)	4
	Uromys caudimaculatus	97	6933	1	65 ± 7 (127)	6690 ± 2968.5 (13381)	2	73 ± 41.9 (349)	4246 ± 1691.8 (21228)	5

	Trichosurus vulpecula	267 ± 78.1 (625)	4277 ± 1049.2 (12831)	3	75 ± 20.5 (146)	9412 ± 6462 (18824)	2	77 ± 27.8 (203)	10180 ± 4555.0 (30535)	3
	Melomys sp.	247	2904	1						
	Isoodon obesulus				16	923	1			
	Perameles nasuta							133 ± 46 (247)	10250 ± 6540.5 (20497)	2
Tinaroo Dam	*Bettongia tropica*	158 ± 30.7 (776)	13920 ± 4042.1 (97447)	7	138 ± 12.8 (1164)	21400 ± 3553.7 (342473)	16	125 ± 16.7 (1390)	10170 ± 2033.1 (193214)	19
	Generalists	104 ± 18.7 (1759)	5136 ± 1033.3 (123258)	24	101 ± 22.3 (771)	5295 ± 1681.7 (47658)	9	119 ± 30.0 (1317)	12330 ± 2886.7 (184974)	15
	Isoodon macrourus	109 ± 2.4 (279)	6702 ± 2882.2 (20106)	3	40	503	1	150 ± 85.5 (718)	14920 ± 5110.6 (74608)	5
	Uromys caudimaculatus	52 ± 7.4 (268)	6546 ± 2754.9 (39273)	6	89 ± 23.6 (454)	7124 ± 2155.8 (42745)	6	78 ± 33.5 (223)	4842 ± 1787.8 (14526)	3

	Trichosurus vulpecula	173 ± 61.9 (593)	2872 ± 595.1 (11488)	4	110	1186	1	161 ± 43.1 (433)	5097 ± 1818.2 (15292)	3
	Melomys sp.	87 ± 25.9 (675)	3009 ± 675.9 (27085)	9	221	3224	1	84 ± 6.5 (165)	9508 ± 8126.5 (19015)	2
	Perameles nasuta							74 ± 42.5 (131)	30770 ± 993.5 (61533)	2
	Antechinus flavipes	338	19024	1						
	Rattus sp.	45	6282	1						

Appendix C: Sequencing of local truffle database

Truffle sequences are not well represented on online databases. To address this I sequenced a local library of truffles of 33 morphogroups (Table B.1) from extensive truffle surveys of Davies Creek by Abell-Davis (2008). From a maximum of three specimens (independent collections) per morpho-group, a small section from the gleba of dried sporocarps was taken and DNA was extracted using DNeasy Plant Mini Kit following the manufacturer's instructions (Qiagen). Some specimens were harder to lyse because of their tough texture, therefore I performed additional steps of lysing with steps of freezing in liquid N between lysing. DNA was amplified using ITS1 or ITS5 forward primers and ITS4 reverse primer (White et al. 1990). The PCR cocktail consisted of 1.0 µl DNA, 0.4 µl each of the primers (10 µmol), 2.5 µl Kappa BufferB (Kapa Biosystems, Massachusetts, USA), 1 µl $MgCl_2$, 0.4 µl DNTPs, 0.4 µl BSA, 0.6 µl DMSO, 0.25 µl Taq (Kapa Biosystems) and made up to 20 µl with MilliQ water. PCR was carried out using the following thermocycling conditions: an initial 1 min at 95 °C, followed by 36 cycles at 94 °C for 1 min, 54 °C for 1 min, 72 °C for 1 min, and a final cycle of 8 min at 72 °C. The relative quantity of PCR products was estimated by running 3.5 µl amplicon DNA on 1% agarose gel for 20-30 min. The amplicons were visualised and cleaned with Exo-AP Mix (Enzyonmics, Daejeon, Korea). Amplicons were Sanger sequenced by AGRF or Macrogen.

The truffle sequences were processed using Geneious (v8-9.2), contigs were constructed from forward and reverse sequences when available. The quality of ITS sequences were checked using the guidelines outlined in Nilsson et al. (2012). If more than one specimen from one morphogroup successfully sequenced, a consensus sequence from the two-three specimens per morphogroup was extracted. If specimens within a morphogroups varied more than 3% across ITS then they were considered

separate ‘variants’ and the sequences were kept separate (Table B.1). Similarly, if more than one morphogroups within a genus varied less than 3% across ITS then they were considered one ‘species’ and lumped together. ITS2 sequences were extracted to construct the local database and BLASTed against Illumina sequences generated for Chapter Three and Chapter Four. Accession numbers for truffle sequences are in Table B.1.

Table C.1: Truffle taxa from Abell-Davis (2008) that formed part of the local database of ITS2 sequences.

Morpho-group	S. E. Abell specimen number	Accession Number
Aroramyces spA	S0159	KY686200
	S0187	KY686201
	S0160	KY686202
Castoreum sublaeve	S0342	KY697589
Chondrogaster spA	S0075b	KY697588
	S0096	KY697587
	S0076	KY697586
Chondrogaster spB/spF[a]	S0270	KY697583
	S0292	KY697585
	S0293	KY697584
	S0190	KY697582
Dingleya spA	S0055	KY697580
	S0071	KY697581
Dingleya spB	S0049	KY697578
	S0287	KY697579
Gautieria amara	S0259	KY697575
	S0365	KY697576

Gummiglobus joyaceae (variation 1)/spB[a]	S0063	KY697573
	S0291b	KY697572
Gummiglobus joyaceae (variation 2)	S0114	KY697574
Gymnomyces eildonensis	S0161	KY697571
Hysterangium affine	S0174	KY697570
	S0331	KY697568
	S0333	KY697569
Hysterangium aggregatum	S0278	KY697567
	S0279	KY697566
Hysterangium cf gardneri	S0246	KY697590
Hysterangium spA	S0295	KY697591
	S0301	KY697592
Hysterangium spB	S0234	KY697594
	S0256	KY697593
Labyrinthomyces spA (cf varius)	S0069	KY697595
Macowanites/Russula spA	S0149	KY697597
Macowanites/Russula spC	SM12	KY697596
Malajcukia ingrattissima	S0260	KY697598
Mesophellia clelandii	BB003	KY697600
	S0261	KY697601
	S0267	KY697599
Mesophellia oleifera	BB004	KY697602
	BB006	KY697603
Pogisperma spA	S0296	Unpublished[b]
	S0134	Unpublished[b]
	S0116	Unpublished[b]
Pogisperma spB	S0129	Unpublished[b]
	S0132	Unpublished[b]
	S0157	Unpublished[b]

Royoungia boletoides	S0309	KY697604
Scleroderma bougheri	S0125	KY697605
Scleroderma spB/spC[a]	Sm16a	KY697606
	SM30	KY697607
Sclerogaster spA	S0059	KY697609
	S0364b	KY697608
Stephanospora spA	S0107	KY697612
	S0322	KY697611
	S0328	KY697610
Zelleromyces spA	S0137	KY697614
	S0193	KY697613
Zelleromyces spC	S0192	KY697615
	S0370	KY697616
Zelleromyces spE	S0164	KY697619
	S0165	KY697617
	S0285	KY697618

[a] indicates taxa that are indistinguishable from ITS2 sequences (within 3% similarity).
[b] Manuscript genus (T. Lebel).

Appendix D: Ectomycorrhizal studies that sampled both epigeous and hypogeous taxa

Table D.1: Studies of Australian ectomycorrhizal fungi (ECM) that sampled both truffle and non-truffle taxa. Method of identification (S = Sanger sequencing, HTS = high throughput sequencing, M = morphological, RFLP = restriction fragment length polymorphism), number of replicates or sampling effort (*n*), dominant taxa by abundance[a] or diversity[d], total ectomycorrhizal diversity (ECM, Sp = sporocarps only), diversity of ectomycorrhizal truffles (T) and percent of truffle diversity (%). Taxa in boldface are **truffles** and underlined are secotioid or higher taxa that include truffle or secotioid taxa.

Study	Climate	Method	*n*	Dominant taxa	ECM	T	%
This study	Tropical; Lamb Range North Queensland	HTS	56 scats, 18[a] root samples, 18[a] soil samples (total 92)	Russulaceae*, Russula,* **Mesophelliaceae *Mesophellia, M. glauca*,** Cortinariaceae, *Cortinarius, C. globuliformis,* Inocybaceae, Amanitaceae [d]; ***Hysterangium, H. aggregatum, H. cf gardneri, Chondrogaster spB/spF, Mesophellia. M. oleifera,*** *Cortinarius, C. globuliformis* [a]	344	73	21
Adams et al. 2006	Tropical; Various sites in *E. grandis* habitat of North QLD	M	Sporocarps collected opportunistically	*Russula* [d]	29	6	21
Reddell et al. 1999	Tropical; Various sites in *E. tetrodonta* and *E. miniata* habitat	M	Hypogeous sporocarps searched for a total of 140 mins/2.3 hours (10 mins	Sporocarps: ***Nothocastoreum, Hysterangium,*** undescribed Boletaceae [a]; *Amanita* [d]	Sp: 73	Sp: 13	18

	North QLD and North NT		each site). Epigeous sporocarps collected when seen. Roots from bioassay	Roots: *Laccaria, Pisolithus* 1, ***Nothocastoreum*** [a]			
Tedersoo et al. 2008	Temperate; Mt Field NP, Tasmania	M; S	Roots collected from 5 cores each from 3 sites (total 15)	*Laccaria* sp1, *Lactarius eucalypti* [a]; *Cortinarius, Tomentella-Thelephora, Russula-Lactarius, Clavulina, Descolea (*incl. *Setchelliogaster* and ***Descomyces***), *Laccaria* [d]	123	4	3
Horton et al. 2013, 2017	Temperate; Tasmania	M; S	Roots: 10 cores each from 12 plots (120 total). Sporocarps: 15.5 person hours/plot split evenly searching for epigeous and hypogeous sporocarps	Cortinariaceae and Russulaceae [d]; Roots: *Laccaria* sp. 1, *Russula persanguinea, Discinella sp. 1, Lactarius eucalypti* [a]; Sporocarps: *L. eucalypti, Laccaria* sp. 1 and sp. 5, *Artomyces* sp. 1, *Cortinarius rotundisporus, C. magellanicus, C. tasmacamphoratus* [a]	175	21	12
Midgley et al. 2007	Subtropical; Northern-central NSW	RFLP	Soil from 12 cores each from 7 sites (84 total)	Thelephorales, *Pisolithus,* Cantharellales [d]	14		
Lu et al. 1999	Mediterranean; South-western WA	M	Sporocarps: 5 ha each site (n = 13) for epigeous and 5 random locations (5 m^2) in each site for hypogeous. Each site visited at least 4 times.	*Scleroderma cepa, Laccaria lateritia* [a]; *Russula, Cortinarius* [d]	44	12	27

Glen et al. 2008	Mediterranean; South-western WA	M; RFLP	Sporocarps: 90 person mins each plot (15 mins for hypogeous). Each plot (n = 54) was visited 3 times per year over 3 years (total 13.5 hours/plot). Roots: 5 cores per plot, 3 times a year, 2 years	Sporocarps: *Austropaxillus infundibuliformis, Laccaria* cf. *proxima, Ramaria ochraceosalmonicolor* [a] Roots: *Cortinarius* group 3, *Cortinarius* group 2 [a]	458

[a] 3 subsamples per sample pooled computationally

Appendix E: Ectomycorrhizal taxa sequenced from this study compared to previous studies at the same site

Table E.1: Relative abundance (as percentage) of ectomycorrhizal taxa from sequencing (Chapter Three and Chapter Four) within *Bettongia tropica* scat samples (Sp), generalist mammalian scat samples (G), root samples (R) and soil samples (S). Acc: Accession number for OTU; E: e-value, ID: percentage similarity with sequence from database, Cov: percentage coverage with sequence from database, SL: sequence length. Taxa in boldface are **truffles** and underlined are secotioid or higher taxa that include truffle or secotioid taxa.

OTU#	Phylum	Family	Genus Species	Acc	E	ID	Cov	SL	Sp	G	R	S
Otu01265	Ascomycota	Gloniaceae	*Cenococcum geophilum*	HM189724	1.E-119	100%	100%	295	0.01	0.50	<0.009	<0.009
Otu02870	Ascomycota	Gloniaceae	*Cenococcum geophilum*	KC967408	6.E-118	99%	100%	295	<0.009	0.10	<0.009	<0.009
Otu11512	Ascomycota	Helvellaceae	*Helvella leucomelaena*	UDB019754	2.E-140	99%	100%	344	<0.009	<0.009	<0.009	<0.009
Otu18766	Ascomycota	Helvellaceae	*Helvella leucomelaena*	UDB019754	1.E-139	99%	100%	344	<0.009	<0.009	<0.009	<0.009
Otu03336	Ascomycota	Pyronemataceae	*Geopora cervina*	JF908021	2.E-114	99%	98%	293	<0.009	0.05	<0.009	<0.009
Otu03503	Ascomycota	Pyronemataceae	*Otidea leporina*	KM010090	2.E-132	100%	100%	324	0.01	0.08	<0.009	<0.009
Otu19334	Ascomycota	Pyronemataceae	*Wilcoxina*	UDB007989	6.E-114	95%	100%	308	<0.009	<0.009	<0.009	<0.009
Otu01565	Ascomycota	Tuberaceae	***Dingleya spA***[a]	KY697580-1	1.E-145	98%	100%	364	0.05	0.05	<0.009	<0.009
Otu15874	Ascomycota	Tuberaceae	***Dingleya spA***[a]	KY697580-1	2.E-139	97%	100%	363	<0.009	<0.009	<0.009	<0.009
Otu20487	Ascomycota	Tuberaceae	***Tuber***	FM205679.1	4.E-146	98%	100%	366	<0.009	<0.009	<0.009	<0.009
Otu17159	Ascomycota	Tuberaceae	***Tuber anniae***	KT182909	2.E-141	99%	100%	346	<0.009	<0.009	<0.009	<0.009
Otu09671	Ascomycota	Tuberaceae	***Tuber rufum***	FM205609	2.E-140	99%	100%	344	<0.009	<0.009	<0.009	<0.009
Otu16959	Ascomycota	Tuberaceae	***Tuber uncinatum***	AJ492203	6.E-148	99%	99%	366	<0.009	<0.009	<0.009	<0.009
Otu20494	Ascomycota	Tuberaceae	***Tuber uncinatum***	AJ492203	6.E-148	99%	99%	366	<0.009	<0.009	<0.009	<0.009
Otu03799	Basidiomycota	Amanitaceae	*Amanita*	AB015702	8.E-95	87%	100%	355	<0.009	<0.009	<0.009	0.09
Otu04803	Basidiomycota	Amanitaceae	*Amanita*	AB015702	3.E-95	87%	100%	340	<0.009	<0.009	<0.009	0.06
Otu04421	Basidiomycota	Amanitaceae	*Amanita*	AY194981	6.E-113	89%	100%	367	<0.009	0.08	<0.009	<0.009
Otu07365	Basidiomycota	Amanitaceae	*Amanita*	AY194982	5.E-128	95%	100%	350	<0.009	<0.009	<0.009	0.01
Otu23498	Basidiomycota	Amanitaceae	*Amanita*	AY194982	6.E-109	90%	100%	362	<0.009	<0.009	<0.009	<0.009

Otu01409	Basidiomycota	Amanitaceae	*Amanita*	GU222312	3.E-111	92%	94%	356	<0.009	<0.009	0.10	0.14
Otu01478	Basidiomycota	Amanitaceae	*Amanita*	GU222312	3.E-126	95%	94%	371	<0.009	<0.009	<0.009	0.06
Otu01779	Basidiomycota	Amanitaceae	*Amanita*	JF899547	5.E-112	89%	100%	371	<0.009	<0.009	<0.009	0.30
Otu02090	Basidiomycota	Amanitaceae	*Amanita*	KF017932	1.E-115	88%	100%	391	<0.009	<0.009	<0.009	0.01
Otu00905	Basidiomycota	Amanitaceae	*Amanita*	KP071067	3.E-126	94%	100%	356	<0.009	<0.009	<0.009	0.85
Otu00351	Basidiomycota	Amanitaceae	*Amanita egregia*	KP012748	3.E-134	100%	100%	328	<0.009	0.12	0.02	1.22
Otu03083	Basidiomycota	Amanitaceae	*Amanita marmorata*	KP757875	2.E-136	98%	100%	349	<0.009	<0.009	0.01	<0.009
Otu00653	Basidiomycota	Amanitaceae	*Amanita roseolamellata*	KP866164	6.E-133	97%	100%	341	<0.009	<0.009	<0.009	<0.009
Otu04465	Basidiomycota	Amanitaceae	*Amanita submembranacea*	KM658287	1.E-123	100%	100%	304	<0.009	0.08	<0.009	<0.009
Otu05184	Basidiomycota	Amanitaceae	*Amanita xanthocephala*	AY194982	5.E-132	96%	100%	351	<0.009	<0.009	0.01	0.03
Otu09214	Basidiomycota	Amanitaceae	*Amanita xanthocephala*	AY194982	2.E-132	96%	100%	355	<0.009	<0.009	<0.009	0.01
Otu08648	Basidiomycota	Cortinariaceae	*Anamika angustilamellata*	AY575919	4.E-139	96%	100%	364	<0.009	<0.009	<0.009	<0.009
Otu00782	Basidiomycota	Cortinariaceae	*Cortinarius*	FJ157098	8.E-118	92%	100%	371	0.39	<0.009	<0.009	<0.009
Otu00004	Basidiomycota	Cortinariaceae	*Cortinarius*	FR731477	2.E-143	100%	100%	350	3.33	0.05	**40.68**	1.42
Otu00710	Basidiomycota	Cortinariaceae	*Cortinarius*	FR731477	9.E-138	98%	100%	351	<0.009	<0.009	0.52	<0.009
Otu04852	Basidiomycota	Cortinariaceae	*Cortinarius*	FR731477	7.E-141	99%	100%	350	<0.009	<0.009	0.02	<0.009
Otu11479	Basidiomycota	Cortinariaceae	*Cortinarius*	FR731477	5.E-132	96%	100%	355	<0.009	<0.009	<0.009	<0.009
Otu14791	Basidiomycota	Cortinariaceae	*Cortinarius*	FR731477	1.E-138	98%	100%	354	<0.009	<0.009	<0.009	<0.009
Otu20640	Basidiomycota	Cortinariaceae	*Cortinarius*	FR731477	9.E-138	98%	100%	353	<0.009	<0.009	<0.009	<0.009
Otu00321	Basidiomycota	Cortinariaceae	*Cortinarius*	GU233352	1.E-96	88%	100%	357	<0.009	<0.009	0.22	1.50
Otu04038	Basidiomycota	Cortinariaceae	*Cortinarius*	GU233352	2.E-94	88%	100%	359	<0.009	<0.009	<0.009	<0.009
Otu07485	Basidiomycota	Cortinariaceae	*Cortinarius*	JN114094	6.E-117	92%	100%	358	<0.009	<0.009	0.01	<0.009
Otu06578	Basidiomycota	Cortinariaceae	*Cortinarius*	JN942291	2.E-137	97%	100%	350	<0.009	<0.009	0.01	0.01
Otu00384	Basidiomycota	Cortinariaceae	*Cortinarius*	JX000356	1.E-115	93%	100%	347	0.96	<0.009	<0.009	<0.009
Otu11081	Basidiomycota	Cortinariaceae	*Cortinarius*	JX000369	2.E-128	95%	100%	354	<0.009	0.01	<0.009	<0.009
Otu20735	Basidiomycota	Cortinariaceae	*Cortinarius*	KF732282	1.E-119	93%	100%	350	<0.009	<0.009	<0.009	<0.009
Otu00076	Basidiomycota	Cortinariaceae	*Cortinarius*	KF732610	5.E-105	89%	100%	353	0.04	<0.009	6.50	<0.009
Otu00348	Basidiomycota	Cortinariaceae	*Cortinarius*	KJ421051	4.E-112	91%	100%	358	<0.009	<0.009	1.13	0.52
Otu07253	Basidiomycota	Cortinariaceae	*Cortinarius*	KJ635239	2.E-129	95%	100%	351	<0.009	<0.009	<0.009	0.01
Otu23626	Basidiomycota	Cortinariaceae	*Cortinarius*	KR011130	1.E-119	93%	100%	356	<0.009	<0.009	<0.009	<0.009
Otu01153	Basidiomycota	Cortinariaceae	*Cortinarius*	KR011131	3.E-122	93%	100%	363	<0.009	<0.009	<0.009	0.11
Otu11861	Basidiomycota	Cortinariaceae	*Cortinarius*	KR011131	2.E-121	92%	100%	363	<0.009	<0.009	<0.009	<0.009

Otu20787	Basidiomycota	Cortinariaceae	*Cortinarius anomalus*	UDB018302	4.E-143	100%	100%	348	<0.009	<0.009	<0.009	<0.009
Otu04855	Basidiomycota	Cortinariaceae	*Cortinarius ardesiacus*	AY669650	4.E-143	100%	100%	348	<0.009	<0.009	<0.009	0.06
Otu01860	Basidiomycota	Cortinariaceae	*Cortinarius badiolatus*	KF732612	5.E-128	96%	100%	349	0.05	0.02	<0.009	<0.009
Otu01945	Basidiomycota	Cortinariaceae	*Cortinarius betuletorum*	UDB018300	2.E-136	100%	100%	333	0.01	0.21	<0.009	<0.009
Otu11930	Basidiomycota	Cortinariaceae	*Cortinarius brunneoviolaceus*	KF732269	6.E-129	96%	100%	350	<0.009	<0.009	<0.009	<0.009
Otu12971	Basidiomycota	Cortinariaceae	*Cortinarius brunneus*	UDB020272	1.E-139	100%	100%	340	<0.009	<0.009	<0.009	<0.009
Otu04900	Basidiomycota	Cortinariaceae	*Cortinarius caesioarmeniacus*	KP137499	5.E-136	100%	100%	332	<0.009	0.06	<0.009	<0.009
Otu02534	Basidiomycota	Cortinariaceae	*Cortinarius clelandii*	JN942297	9.E-134	96%	100%	354	<0.009	<0.009	0.08	<0.009
Otu11489	Basidiomycota	Cortinariaceae	*Cortinarius collinitus*	UDB019897	2.E-144	100%	100%	351	<0.009	<0.009	<0.009	<0.009
Otu00901	Basidiomycota	Cortinariaceae	*Cortinarius flexipes*	AJ889972	2.E-137	100%	100%	335	<0.009	0.97	<0.009	<0.009
Otu00156	Basidiomycota	Cortinariaceae	*Cortinarius globuliformis*	AF325582	3.E-141	99%	100%	350	<0.009	<0.009	2.76	0.22
Otu00198	Basidiomycota	Cortinariaceae	*Cortinarius globuliformis*	AF325582	3.E-142	99%	100%	349	0.01	<0.009	0.91	2.28
Otu00308	Basidiomycota	Cortinariaceae	*Cortinarius globuliformis*	AF325582	7.E-141	99%	100%	351	<0.009	<0.009	0.51	2.29
Otu00415	Basidiomycota	Cortinariaceae	*Cortinarius globuliformis*	AF325582	4.E-143	99%	100%	350	0.02	<0.009	0.05	0.03
Otu00906	Basidiomycota	Cortinariaceae	*Cortinarius globuliformis*	AF325582	5.E-140	98%	100%	353	<0.009	<0.009	0.36	0.02
Otu02545	Basidiomycota	Cortinariaceae	*Cortinarius globuliformis*	AF325582	3.E-142	99%	100%	350	<0.009	<0.009	0.02	0.10
Otu03775	Basidiomycota	Cortinariaceae	*Cortinarius globuliformis*	AF325582	3.E-138	98%	100%	351	<0.009	<0.009	0.02	0.04
Otu05189	Basidiomycota	Cortinariaceae	*Cortinarius globuliformis*	AF325582	4.E-139	98%	100%	351	<0.009	<0.009	<0.009	0.05
Otu08179	Basidiomycota	Cortinariaceae	*Cortinarius globuliformis*	AF325582	5.E-140	98%	100%	351	<0.009	<0.009	<0.009	0.01
Otu08832	Basidiomycota	Cortinariaceae	*Cortinarius globuliformis*	AF325582	5.E-140	98%	100%	351	<0.009	<0.009	<0.009	0.01
Otu10451	Basidiomycota	Cortinariaceae	*Cortinarius globuliformis*	AF325582	3.E-141	99%	100%	350	<0.009	<0.009	<0.009	<0.009
Otu15974	Basidiomycota	Cortinariaceae	*Cortinarius globuliformis*	AF325582	1.E-138	98%	100%	350	<0.009	<0.009	<0.009	<0.009
Otu16067	Basidiomycota	Cortinariaceae	*Cortinarius globuliformis*	AF325582	2.E-132	97%	100%	342	<0.009	<0.009	<0.009	<0.009
Otu10445	Basidiomycota	Cortinariaceae	*Cortinarius globuliformis*	AY669602	1.E-138	98%	100%	350	<0.009	<0.009	<0.009	<0.009
Otu03800	Basidiomycota	Cortinariaceae	*Cortinarius globuliformis*	JN942291	2.E-140	98%	100%	350	<0.009	<0.009	0.04	<0.009
Otu18662	Basidiomycota	Cortinariaceae	*Cortinarius globuliformis*	JN942291	1.E-135	97%	100%	351	<0.009	<0.009	<0.009	<0.009
Otu17272	Basidiomycota	Cortinariaceae	*Cortinarius laniger*	UDB018661	1.E-138	100%	100%	338	<0.009	<0.009	<0.009	<0.009
Otu11505	Basidiomycota	Cortinariaceae	*Cortinarius multiformis*	KJ421137	1.E-142	100%	100%	347	<0.009	0.01	<0.009	<0.009
Otu03064	Basidiomycota	Cortinariaceae	*Cortinarius patrickensis*	KF732532	2.E-129	96%	100%	346	0.05	<0.009	<0.009	<0.009
Otu07885	Basidiomycota	Cortinariaceae	*Cortinarius porphyroideus*	JX178612	1.E-130	96%	100%	355	0.01	<0.009	<0.009	<0.009
Otu10477	Basidiomycota	Cortinariaceae	*Cortinarius roseoarmillatus*	HQ845117	1.E-138	99%	100%	340	<0.009	<0.009	<0.009	<0.009
Otu00625	Basidiomycota	Cortinariaceae	*Cortinarius splendidus*	AY669598	6.E-144	99%	100%	352	<0.009	<0.009	<0.009	<0.009

Otu20668	Basidiomycota	Cortinariaceae	*Cortinarius tillamookensis*	KP087981	1.E-138	98%	100%	354	<0.009	<0.009	<0.009	<0.009
Otu15182	Basidiomycota	Cortinariaceae	*Cortinarius viridirubescens*	KF732476	2.E-125	96%	100%	329	<0.009	<0.009	<0.009	<0.009
Otu12872	Basidiomycota	Hydnangiaceae	*Laccaria*	JQ670896	2.E-129	95%	100%	362	<0.009	<0.009	<0.009	0.01
Otu00328	Basidiomycota	Hydnangiaceae	*Laccaria bicolor*	KM067839	4.E-143	99%	100%	354	<0.009	<0.009	<0.009	<0.009
Otu08483	Basidiomycota	Hydnangiaceae	*Laccaria bicolor*	KM067839	7.E-141	98%	100%	354	<0.009	<0.009	<0.009	0.01
Otu06183	Basidiomycota	Hydnangiaceae	*Laccaria glabripes*	HQ533019	7.E-137	97%	100%	358	<0.009	<0.009	<0.009	0.03
Otu15910	Basidiomycota	Hydnangiaceae	*Laccaria glabripes*	HQ533019	3.E-138	97%	100%	358	<0.009	<0.009	<0.009	<0.009
Otu01834	Basidiomycota	Inocybaceae	*Auritella*	KT378201	5.E-116	92%	100%	354	0.09	<0.009	<0.009	0.07
Otu20658	Basidiomycota	Inocybaceae	*Auritella*	KT378201	3.E-107	89%	100%	354	<0.009	<0.009	<0.009	<0.009
Otu13453	Basidiomycota	Inocybaceae	*Auritella arenicolens*	KT382278	3.E-134	96%	100%	361	<0.009	<0.009	<0.009	<0.009
Otu00738	Basidiomycota	Inocybaceae	*Auritella chamaecephala*	KT378201	9.E-138	97%	100%	358	0.01	<0.009	<0.009	0.88
Otu09201	Basidiomycota	Inocybaceae	*Auritella chamaecephala*	KT378201	7.E-137	97%	100%	359	<0.009	<0.009	<0.009	0.01
Otu01633	Basidiomycota	Inocybaceae	*Auritella serpentinocystis*	KJ729858	4.E-150	100%	100%	364	<0.009	<0.009	<0.009	0.35
Otu00844	Basidiomycota	Inocybaceae	*Inocybe*	AM882711	3.E-99	90%	100%	321	0.01	<0.009	<0.009	0.48
Otu01028	Basidiomycota	Inocybaceae	*Inocybe*	FJ904133	1.E-100	88%	100%	344	<0.009	<0.009	<0.009	0.64
Otu02127	Basidiomycota	Inocybaceae	*Inocybe*	HQ201335	2.E-108	93%	89%	351	0.08	<0.009	<0.009	<0.009
Otu07478	Basidiomycota	Inocybaceae	*Inocybe*	HQ604347	7.E-110	91%	100%	363	<0.009	<0.009	<0.009	<0.009
Otu00484	Basidiomycota	Inocybaceae	*Inocybe*	JQ085932	1.E-91	87%	100%	346	<0.009	<0.009	0.28	1.30
Otu09226	Basidiomycota	Inocybaceae	*Inocybe*	JQ085932	8.E-91	86%	100%	346	<0.009	<0.009	<0.009	0.02
Otu01985	Basidiomycota	Inocybaceae	*Inocybe*	JX178624	2.E-98	86%	100%	359	<0.009	<0.009	<0.009	0.27
Otu00095	Basidiomycota	Inocybaceae	*Inocybe*	KJ756468	1.E-119	92%	100%	357	<0.009	<0.009	<0.009	0.01
Otu00448	Basidiomycota	Inocybaceae	*Inocybe*	KJ778856	2.E-94	91%	92%	326	<0.009	<0.009	<0.009	<0.009
Otu00876	Basidiomycota	Inocybaceae	*Inocybe*	KP308804	3.E-99	87%	100%	352	<0.009	<0.009	<0.009	0.91
Otu08329	Basidiomycota	Inocybaceae	*Inocybe*	KP641634	1.E-110	90%	94%	371	<0.009	<0.009	<0.009	0.01
Otu12516	Basidiomycota	Inocybaceae	*Inocybe*	KT329452	6.E-110	94%	100%	326	<0.009	<0.009	<0.009	<0.009
Otu00231	Basidiomycota	Inocybaceae	*Inocybe*	MF461618	4.E-136	90%	100%	417	0.03	<0.009	0.18	0.94
Otu04797	Basidiomycota	Inocybaceae	*Inocybe*	MF461618	2.E-133	90%	100%	404	<0.009	<0.009	<0.009	0.01
Otu04770	Basidiomycota	Inocybaceae	*Inocybe adaequata*	UDB023657	2.E-132	100%	100%	324	0.02	<0.009	<0.009	<0.009
Otu00450	Basidiomycota	Inocybaceae	*Inocybe alienospora*	KP171105	2.E-140	99%	100%	343	<0.009	<0.009	0.01	1.74
Otu04452	Basidiomycota	Inocybaceae	*Inocybe alienospora*	KP171105	1.E-130	96%	100%	342	<0.009	<0.009	<0.009	0.07
Otu03969	Basidiomycota	Inocybaceae	*Inocybe calamistrata*	UDB017941	8.E-138	99%	100%	340	<0.009	0.09	<0.009	<0.009
Otu04805	Basidiomycota	Inocybaceae	*Inocybe cincinnata*	FN550922	8.E-138	99%	100%	338	<0.009	0.07	<0.009	<0.009

Otu02947	Basidiomycota	Inocybaceae	*Inocybe cookei*	UDB018191	2.E-126	100%	100%	310	<0.009	0.15	<0.009	<0.009
Otu00362	Basidiomycota	Inocybaceae	*Inocybe dewrangia*	KP171114	2.E-137	98%	100%	345	<0.009	<0.009	<0.009	<0.009
Otu00480	Basidiomycota	Inocybaceae	*Inocybe dewrangia*	KP171114	2.E-137	98%	100%	345	<0.009	<0.009	<0.009	<0.009
Otu02086	Basidiomycota	Inocybaceae	*Inocybe erubescens*	UDB019503	2.E-133	100%	100%	326	<0.009	0.19	<0.009	<0.009
Otu08200	Basidiomycota	Inocybaceae	*Inocybe lasseroides*	KP171146	2.E-137	99%	100%	339	<0.009	<0.009	0.01	<0.009
Otu24507	Basidiomycota	Inocybaceae	*Inocybe mixtilis*	KP308781	1.E-131	99%	100%	328	<0.009	<0.009	<0.009	<0.009
Otu00704	Basidiomycota	Inocybaceae	*Inocybe obsoleta*	UDB015339	5.E-136	100%	100%	332	<0.009	1.25	0.02	<0.009
Otu13400	Basidiomycota	Inocybaceae	*Inocybe torresiae*	KP641634	6.E-136	97%	94%	373	<0.009	<0.009	<0.009	0.01
Otu00204	Basidiomycota	Inocybaceae	*Inocybe torresiae*	KP641634	1.E-141	98%	94%	382	<0.009	<0.009	<0.009	0.02
Otu01917	Basidiomycota	Inocybaceae	*Inocybe torresiae*	KP641634	3.E-145	99%	94%	380	<0.009	<0.009	<0.009	0.04
Otu00161	Basidiomycota	Inocybaceae	*Inocybe torresiae*	KP641635	2.E-125	98%	93%	345	<0.009	<0.009	<0.009	<0.009
Otu01397	Basidiomycota	Inocybaceae	*Inocybe violaceocaulis*	KP641643	5.E-151	100%	100%	366	<0.009	<0.009	0.04	0.17
Otu10738	Basidiomycota	Strophariaceae	*Hebeloma leucosarx*	KT218244	2.E-148	99%	100%	364	<0.009	0.01	<0.009	<0.009
Otu04929	Basidiomycota	Strophariaceae	*Hebeloma youngii*	KP012873	6.E-148	99%	100%	365	0.02	<0.009	<0.009	<0.009
Otu06491	Basidiomycota	Tricholomataceae	*Tricholoma*	AB036894	2.E-113	90%	100%	372	<0.009	<0.009	<0.009	0.03
Otu24128	Basidiomycota	Tricholomataceae	*Tricholoma fucatum*	UDB011591	4.E-139	99%	100%	341	<0.009	<0.009	<0.009	<0.009
Otu23826	Basidiomycota	Tricholomataceae	*Tricholoma inamoenum*	LT000173	4.E-143	99%	100%	350	<0.009	<0.009	<0.009	<0.009
Otu00457	Basidiomycota	Boletaceae	*Austroboletus subvirens*	KP242209	5.E-155	100%	100%	375	0.29	<0.009	0.26	0.59
Otu01722	Basidiomycota	Boletaceae	*Boletus*	KF442406	5.E-139	91%	100%	422	<0.009	<0.009	<0.009	<0.009
Otu06138	Basidiomycota	Boletaceae	*Boletus*	KP071065	4.E-108	94%	99%	312	<0.009	0.04	<0.009	<0.009
Otu08962	Basidiomycota	Boletaceae	*Boletus griseipurpureus*	KF442406	5.E-174	98%	100%	430	<0.009	<0.009	<0.009	<0.009
Otu22644	Basidiomycota	Boletaceae	*Phylloporus orientalis*	JQ003651	3.E-180	99%	100%	436	<0.009	<0.009	<0.009	<0.009
Otu00382	Basidiomycota	Boletaceae	***Solioccasus polychromus***	JX888459	4.E-173	99%	100%	422	1.00	0.01	<0.009	<0.009
Otu03626	Basidiomycota	Boletaceae	***Solioccasus polychromus***	JX888459	9.E-172	99%	100%	424	0.04	<0.009	<0.009	<0.009
Otu01169	Basidiomycota	Diplocystidiaceae	*Astraeus morganii*	DQ421111	5.E-159	99%	100%	386	0.03	0.34	<0.009	<0.009
Otu07049	Basidiomycota	Paxillaceae	*Paxillus involutus*	AY230243	5.E-159	100%	100%	384	<0.009	<0.009	<0.009	<0.009
Otu00261	Basidiomycota	Rhizopogonaceae	***Rhizopogon pseudoroseolus***	AJ810040	3.E-168	100%	100%	405	<0.009	4.90	<0.009	<0.009
Otu23627	Basidiomycota	Sclerodermataceae	*Pisolithus albus*	KP012747	3.E-145	99%	100%	357	<0.009	<0.009	<0.009	<0.009
Otu01002	Basidiomycota	Sclerodermataceae	*Pisolithus croceorrhizus*	JN847473	9.E-157	100%	100%	379	0.03	<0.009	0.06	0.33
Otu01469	Basidiomycota	Sclerodermataceae	*Pisolithus croceorrhizus*	JN847473	7.E-156	99%	100%	379	0.03	<0.009	0.03	0.21
Otu02320	Basidiomycota	Sclerodermataceae	*Pisolithus marmoratus*	AF270772	3.E-149	99%	100%	371	0.01	<0.009	0.05	0.01

Otu20719	Basidiomycota	Sclerodermataceae	*Scleroderma sinnamariense*	FM213356	1.E-139	98%	100%	351	<0.009	<0.009	<0.009	<0.009
Otu00079	Basidiomycota	Sclerodermataceae	*Scleroderma spB spC*[a]	KY697606-7	3.E-146	100%	100%	355	5.05	0.03	0.08	0.35
Otu05787	Basidiomycota	Suillaceae	*Suillus cothurnatus*	EF619769	1.E-153	98%	100%	383	<0.009	0.04	<0.009	<0.009
Otu11397	Basidiomycota	Suillaceae	*Suillus grevillei*	UDB023570	5.E-159	99%	100%	386	<0.009	0.01	<0.009	<0.009
Otu12813	Basidiomycota	Suillaceae	*Suillus luteus*	UDB024152	5.E-159	99%	100%	386	<0.009	0.01	<0.009	<0.009
Otu00025	Basidiomycota	Cantharellaceae	*Cantharellus*	AB509732	8.E-106	85%	100%	398	<0.009	<0.009	<0.009	0.12
Otu18282	Basidiomycota	Clavulinaceae	*Clavulina*	JN228221	2.E-140	94%	100%	389	<0.009	<0.009	<0.009	<0.009
Otu00576	Basidiomycota	Clavulinaceae	*Clavulina*	JQ724058	3.E-103	85%	100%	383	0.01	<0.009	0.02	0.61
Otu12324	Basidiomycota	Gomphaceae	***Gautieria amara***	KY697575-6	2.E-147	98%	99%	375	<0.009	<0.009	<0.009	<0.009
Otu05637	Basidiomycota	Gallaceaceae	***Austrogautieria macrospora***	GQ981492	1.E-123	98%	100%	322	0.01	<0.009	<0.009	<0.009
Otu00110	Basidiomycota	Hysterangiaceae	***Hysterangium***	KY697566-7	3.E-118	95%	98%	332	<0.009	<0.009	<0.009	<0.009
Otu18893	Basidiomycota	Hysterangiaceae	***Hysterangium***	KY697566-7	7.E-118	95%	98%	337	<0.009	<0.009	<0.009	<0.009
Otu13553	Basidiomycota	Hysterangiaceae	***Hysterangium***	KY697590	2.E-133	97%	100%	341	<0.009	<0.009	<0.009	<0.009
Otu16050	Basidiomycota	Hysterangiaceae	***Hysterangium***	KY697590	1.E-130	97%	100%	344	<0.009	<0.009	<0.009	<0.009
Otu18832	Basidiomycota	Hysterangiaceae	***Hysterangium***	KY697591-2	4.E-139	99%	100%	342	<0.009	<0.009	<0.009	<0.009
Otu00106	Basidiomycota	Hysterangiaceae	***Hysterangium***	KY697591-2	5.E-140	100%	100%	341	0.61	0.33	3.80	0.01
Otu00013	Basidiomycota	Hysterangiaceae	***Hysterangium aggregatum***	KY697566-7	2.E-133	100%	98%	333	1.49	0.13	**13.64**	0.70
Otu00300	Basidiomycota	Hysterangiaceae	***Hysterangium aggregatum***	KY697566-7	3.E-122	97%	98%	330	0.02	0.01	0.20	0.15
Otu00340	Basidiomycota	Hysterangiaceae	***Hysterangium aggregatum***	KY697566-7	2.E-129	98%	98%	335	0.13	0.02	0.92	<0.009
Otu12993	Basidiomycota	Hysterangiaceae	***Hysterangium aggregatum***	KY697566-7	1.E-123	96%	98%	333	<0.009	<0.009	<0.009	<0.009
Otu00111	Basidiomycota	Hysterangiaceae	***Hysterangium cf gardneri***[a]	KY697590	4.E-139	100%	100%	340	0.48	0.58	3.56	<0.009
Otu01691	Basidiomycota	Hysterangiaceae	***Hysterangium cf gardneri***[a]	KY697590	2.E-136	99%	100%	342	0.09	0.05	0.02	<0.009
Otu03026	Basidiomycota	Hysterangiaceae	***Hysterangium cf gardneri***[a]	KY697590	1.E-135	99%	100%	340	0.05	<0.009	<0.009	<0.009
Otu18876	Basidiomycota	Hysterangiaceae	***Hysterangium cf gardneri***[a]	KY697590	5.E-136	99%	100%	339	<0.009	<0.009	<0.009	<0.009
Otu18880	Basidiomycota	Hysterangiaceae	***Hysterangium cf gardneri***[a]	KY697590	4.E-135	98%	100%	339	<0.009	<0.009	<0.009	<0.009
Otu18881	Basidiomycota	Hysterangiaceae	***Hysterangium cf gardneri***[a]	KY697590	6.E-137	99%	100%	339	<0.009	<0.009	<0.009	<0.009
Otu21023	Basidiomycota	Hysterangiaceae	***Hysterangium cf gardneri***[a]	KY697590	5.E-136	99%	100%	339	<0.009	<0.009	<0.009	<0.009
Otu02643	Basidiomycota	Mesophelliaceae	***Chondrogaster***	KY697586-8	2.E-128	98%	100%	328	0.03	<0.009	<0.009	<0.009
Otu08687	Basidiomycota	Mesophelliaceae	***Chondrogaster***	KY697586-8	4.E-120	96%	100%	332	0.01	<0.009	<0.009	<0.009
Otu00021	Basidiomycota	Mesophelliaceae	***Chondrogaster spB spF***[a]	KY697582-5	5.E-151	100%	100%	366	1.65	**12.89**	3.31	0.01
Otu24017	Basidiomycota	Mesophelliaceae	***Gummiglobus joyceae spB***[a]	KY697572-3	1.E-139	99%	100%	345	<0.009	<0.009	<0.009	<0.009

Otu24496	Basidiomycota	Mesophelliaceae	***Malajcukia ingrattissima***	KY697598	1.E-95	100%	73%	331	<0.009	<0.009	<0.009	<0.009
Otu00011	Basidiomycota	Mesophelliaceae	***Malajcukia ingrattissima***	KY697598	7.E-156	100%	100%	377	**12.67**	**22.65**	<0.009	0.50
Otu03682	Basidiomycota	Mesophelliaceae	***Mesophellia***	GQ981510	7.E-152	91%	88%	410	0.04	<0.009	<0.009	<0.009
Otu06318	Basidiomycota	Mesophelliaceae	***Mesophellia***	GQ981510	4.E-154	93%	87%	435	0.01	<0.009	<0.009	<0.009
Otu12767	Basidiomycota	Mesophelliaceae	***Mesophellia***	GQ981510	5.E-160	94%	87%	441	<0.009	<0.009	<0.009	<0.009
Otu00003	Basidiomycota	Mesophelliaceae	***Mesophellia***	GQ981511	5.E-109	91%	68%	315	**21.87**	**14.69**	6.57	0.60
Otu00029	Basidiomycota	Mesophelliaceae	***Mesophellia***	GQ981511	6.E-108	91%	68%	310	6.00	**17.10**	0.18	<0.009
Otu00177	Basidiomycota	Mesophelliaceae	***Mesophellia***	GQ981511	2.E-113	92%	67%	318	<0.009	<0.009	<0.009	0.09
Otu00572	Basidiomycota	Mesophelliaceae	***Mesophellia***	GQ981511	1.E-109	91%	68%	317	0.15	1.28	<0.009	<0.009
Otu00656	Basidiomycota	Mesophelliaceae	***Mesophellia***	GQ981511	5.E-109	91%	68%	316	0.31	0.29	0.03	<0.009
Otu01096	Basidiomycota	Mesophelliaceae	***Mesophellia***	GQ981511	2.E-107	91%	68%	315	0.18	0.13	<0.009	<0.009
Otu01130	Basidiomycota	Mesophelliaceae	***Mesophellia***	GQ981511	3.E-149	94%	94%	385	0.21	<0.009	<0.009	<0.009
Otu01665	Basidiomycota	Mesophelliaceae	***Mesophellia***	GQ981511	1.E-149	94%	94%	382	0.13	<0.009	<0.009	<0.009
Otu02095	Basidiomycota	Mesophelliaceae	***Mesophellia***	GQ981511	3.E-106	91%	68%	314	0.07	0.05	<0.009	<0.009
Otu02356	Basidiomycota	Mesophelliaceae	***Mesophellia***	GQ981511	5.E-109	91%	68%	316	0.05	0.03	<0.009	<0.009
Otu04801	Basidiomycota	Mesophelliaceae	***Mesophellia***	GQ981511	6.E-102	89%	88%	367	0.01	<0.009	<0.009	<0.009
Otu04921	Basidiomycota	Mesophelliaceae	***Mesophellia***	GQ981511	1.E-104	90%	68%	311	0.01	<0.009	<0.009	<0.009
Otu06105	Basidiomycota	Mesophelliaceae	***Mesophellia***	GQ981511	1.E-147	94%	94%	386	0.01	<0.009	<0.009	<0.009
Otu07036	Basidiomycota	Mesophelliaceae	***Mesophellia***	GQ981511	7.E-107	91%	68%	320	<0.009	<0.009	<0.009	<0.009
Otu08302	Basidiomycota	Mesophelliaceae	***Mesophellia***	GQ981511	1.E-109	91%	68%	318	<0.009	<0.009	<0.009	<0.009
Otu10349	Basidiomycota	Mesophelliaceae	***Mesophellia***	GQ981511	3.E-118	93%	68%	315	<0.009	<0.009	<0.009	<0.009
Otu12763	Basidiomycota	Mesophelliaceae	***Mesophellia***	GQ981511	4.E-110	92%	68%	317	<0.009	0.01	<0.009	<0.009
Otu13920	Basidiomycota	Mesophelliaceae	***Mesophellia***	GQ981511	1.E-109	92%	68%	318	<0.009	<0.009	<0.009	<0.009
Otu15143	Basidiomycota	Mesophelliaceae	***Mesophellia***	GQ981511	4.E-104	91%	85%	322	<0.009	0.01	<0.009	<0.009
Otu15783	Basidiomycota	Mesophelliaceae	***Mesophellia***	GQ981511	7.E-145	93%	94%	390	<0.009	<0.009	<0.009	<0.009
Otu17264	Basidiomycota	Mesophelliaceae	***Mesophellia***	GQ981511	1.E-122	95%	85%	316	<0.009	<0.009	<0.009	<0.009
Otu18065	Basidiomycota	Mesophelliaceae	***Mesophellia***	GQ981511	6.E-108	91%	87%	365	<0.009	<0.009	<0.009	<0.009
Otu18131	Basidiomycota	Mesophelliaceae	***Mesophellia***	GQ981511	3.E-105	90%	69%	319	<0.009	<0.009	<0.009	<0.009
Otu20360	Basidiomycota	Mesophelliaceae	***Mesophellia***	GQ981511	2.E-153	95%	94%	391	<0.009	<0.009	<0.009	<0.009
Otu03414	Basidiomycota	Mesophelliaceae	***Mesophellia***	KY697602-3	7.E-113	95%	73%	442	0.04	<0.009	<0.009	<0.009

Otu09645	Basidiomycota	Mesophelliaceae	***Mesophellia***	KY775688-9	2.E-104	94%	84%	359	0.01	<0.009	<0.009	<0.009
Otu12387	Basidiomycota	Mesophelliaceae	***Mesophellia***	KY775688-9	1.E-111	96%	84%	360	<0.009	<0.009	<0.009	<0.009
Otu09401	Basidiomycota	Mesophelliaceae	***Mesophellia***	KY775688-9	4.E-142	96%	100%	378	<0.009	<0.009	<0.009	<0.009
Otu18398	Basidiomycota	Mesophelliaceae	***Mesophellia***	KY775688-9	7.E-133	93%	100%	376	<0.009	<0.009	<0.009	<0.009
Otu00042	Basidiomycota	Mesophelliaceae	***Mesophellia glauca***	GQ981510	5.E-179	98%	88%	436	8.55	0.57	0.04	0.01
Otu16736	Basidiomycota	Mesophelliaceae	***Mesophellia glauca***	GQ981510	2.E-164	97%	84%	418	<0.009	<0.009	<0.009	<0.009
Otu12991	Basidiomycota	Mesophelliaceae	***Mesophellia glauca***	GQ981511	1.E-112	98%	85%	339	<0.009	<0.009	<0.009	<0.009
Otu00339	Basidiomycota	Mesophelliaceae	***Mesophellia glauca***	GQ981511	5.E-160	97%	94%	386	1.17	<0.009	<0.009	<0.009
Otu02263	Basidiomycota	Mesophelliaceae	***Mesophellia glauca***	GQ981511	4.E-173	99%	94%	387	0.05	<0.009	<0.009	<0.009
Otu02493	Basidiomycota	Mesophelliaceae	***Mesophellia glauca***	GQ981511	1.E-173	99%	94%	386	0.06	0.01	<0.009	<0.009
Otu03665	Basidiomycota	Mesophelliaceae	***Mesophellia glauca***	GQ981511	1.E-166	98%	94%	386	0.04	<0.009	<0.009	<0.009
Otu04419	Basidiomycota	Mesophelliaceae	***Mesophellia glauca***	GQ981511	2.E-172	99%	94%	389	0.01	0.01	<0.009	<0.009
Otu06732	Basidiomycota	Mesophelliaceae	***Mesophellia glauca***	GQ981511	5.E-141	99%	68%	317	<0.009	0.02	<0.009	<0.009
Otu06746	Basidiomycota	Mesophelliaceae	***Mesophellia glauca***	GQ981511	4.E-167	98%	94%	385	0.01	<0.009	<0.009	<0.009
Otu06936	Basidiomycota	Mesophelliaceae	***Mesophellia glauca***	GQ981511	4.E-167	98%	94%	387	0.01	<0.009	<0.009	<0.009
Otu08963	Basidiomycota	Mesophelliaceae	***Mesophellia glauca***	GQ981511	1.E-129	96%	68%	312	<0.009	0.01	<0.009	<0.009
Otu14868	Basidiomycota	Mesophelliaceae	***Mesophellia glauca***	GQ981511	4.E-167	98%	94%	388	<0.009	<0.009	<0.009	<0.009
Otu20362	Basidiomycota	Mesophelliaceae	***Mesophellia glauca***	GQ981511	5.E-166	98%	94%	382	<0.009	<0.009	<0.009	<0.009
Otu20370	Basidiomycota	Mesophelliaceae	***Mesophellia glauca***	GQ981511	1.E-161	97%	94%	384	<0.009	<0.009	<0.009	<0.009
Otu24275	Basidiomycota	Mesophelliaceae	***Mesophellia glauca***	GQ981511	1.E-128	94%	88%	372	<0.009	<0.009	<0.009	<0.009
Otu17020	Basidiomycota	Mesophelliaceae	***Mesophellia oleifera***	KY697602-3	2.E-117	98%	91%	331	<0.009	<0.009	<0.009	<0.009
Otu00041	Basidiomycota	Mesophelliaceae	***Mesophellia oleifera***	KY697602-3	4.E-177	100%	100%	425	6.00	<0.009	3.21	<0.009
Otu00049	Basidiomycota	Mesophelliaceae	***Mesophellia oleifera***	KY697602-3	5.E-166	97%	100%	420	2.64	0.96	5.36	<0.009
Otu04710	Basidiomycota	Mesophelliaceae	***Mesophellia oleifera***	KY697602-3	1.E-172	99%	100%	424	<0.009	<0.009	0.02	<0.009
Otu22710	Basidiomycota	Mesophelliaceae	***Mesophellia oleifera***	KY697602-3	3.E-168	98%	100%	422	<0.009	<0.009	<0.009	<0.009
Otu00396	Basidiomycota	Russulaceae	*Lactarius*	AB509713	5.E-112	90%	100%	369	0.01	<0.009	<0.009	1.05
Otu01119	Basidiomycota	Russulaceae	*Lactarius*	HQ318282	2.E-129	94%	100%	368	<0.009	<0.009	<0.009	0.62
Otu05269	Basidiomycota	Russulaceae	*Lactarius camphoratus*	KR025610	1.E-169	100%	100%	408	0.01	0.03	<0.009	<0.009
Otu10998	Basidiomycota	Russulaceae	*Lactarius eucalypti*	EF634122	8.E-168	98%	100%	421	<0.009	<0.009	<0.009	0.01
Otu00848	Basidiomycota	Russulaceae	*Lactarius eucalypti*	UDB002671	2.E-162	96%	100%	420	0.01	<0.009	0.03	0.84

Otu07592	Basidiomycota	Russulaceae	*Lactarius glyciosmus*	KR090911	6.E-167	100%	100%	402	<0.009	<0.009	<0.009	<0.009
Otu00309	Basidiomycota	Russulaceae	*Lactarius romagnesii*	KF432964	7.E-152	98%	100%	382	1.29	<0.009	<0.009	<0.009
Otu00502	Basidiomycota	Russulaceae	*Lactarius rufus*	KT165272	5.E-170	100%	100%	409	0.02	1.98	<0.009	<0.009
Otu02732	Basidiomycota	Russulaceae	*Lactarius tabidus*	KR025582	1.E-176	100%	100%	424	0.01	0.16	<0.009	<0.009
Otu02791	Basidiomycota	Russulaceae	*Lactarius trivialis*	KT165317	6.E-167	100%	100%	402	0.01	0.13	<0.009	<0.009
Otu04789	Basidiomycota	Russulaceae	*Lactarius trivialis*	KT165317	5.E-166	99%	100%	402	0.01	0.02	<0.009	<0.009
Otu16784	Basidiomycota	Russulaceae	*Lactarius trivialis*	KT165317	4.E-165	99%	100%	402	<0.009	<0.009	<0.009	<0.009
Otu00082	Basidiomycota	Russulaceae	*Lactifluus*	KM282287	1.E-127	95%	100%	351	<0.009	0.06	<0.009	0.49
Otu02605	Basidiomycota	Russulaceae	***Macowanites***	KY697596	2.E-139	95%	100%	382	0.06	<0.009	<0.009	<0.009
Otu01773	Basidiomycota	Russulaceae	***Macowanites spC[a]***	KY697596	2.E-143	96%	100%	379	0.11	0.02	<0.009	<0.009
Otu23168	Basidiomycota	Russulaceae	***Macowanites spC[a]***	KY697596	5.E-143	96%	100%	378	<0.009	<0.009	<0.009	<0.009
Otu00863	Basidiomycota	Russulaceae	*Russula*	AB509526	1.E-141	94%	100%	388	<0.009	<0.009	<0.009	<0.009
Otu02775	Basidiomycota	Russulaceae	*Russula*	AB509981	3.E-138	94%	100%	380	<0.009	<0.009	0.01	0.14
Otu20588	Basidiomycota	Russulaceae	*Russula*	EU019918.1	2.E-116	96%	88%	359	<0.009	<0.009	<0.009	<0.009
Otu00869	Basidiomycota	Russulaceae	*Russula*	EU019930.1	2.E-104	93%	80%	382	<0.009	<0.009	0.16	0.55
Otu20178	Basidiomycota	Russulaceae	*Russula*	GU222265	1.E-137	95%	95%	403	<0.009	<0.009	<0.009	<0.009
Otu01387	Basidiomycota	Russulaceae	*Russula*	GU222285	2.E-105	85%	100%	418	0.15	<0.009	0.01	0.02
Otu02240	Basidiomycota	Russulaceae	*Russula*	JF834355	3.E-133	94%	100%	379	<0.009	<0.009	0.06	0.08
Otu10762	Basidiomycota	Russulaceae	*Russula*	JQ711921	5.E-116	91%	100%	355	<0.009	<0.009	<0.009	<0.009
Otu08327	Basidiomycota	Russulaceae	*Russula*	KF245487	2.E-135	94%	100%	372	<0.009	<0.009	<0.009	<0.009
Otu18383	Basidiomycota	Russulaceae	*Russula*	KF245487	3.E-138	95%	100%	373	<0.009	<0.009	<0.009	<0.009
Otu00361	Basidiomycota	Russulaceae	*Russula*	KJ748441	3.E-103	85%	100%	375	1.04	<0.009	<0.009	0.01
Otu08350	Basidiomycota	Russulaceae	*Russula*	KM085379	8.E-130	95%	100%	353	<0.009	0.02	<0.009	<0.009
Otu14039	Basidiomycota	Russulaceae	*Russula*	KM085422	3.E-114	91%	100%	358	<0.009	<0.009	<0.009	<0.009
Otu02052	Basidiomycota	Russulaceae	*Russula*	KM373243	4.E-134	93%	100%	391	<0.009	0.10	0.03	0.08
Otu00077	Basidiomycota	Russulaceae	*Russula*	LC006943	4.E-138	91%	100%	426	2.02	5.00	0.04	4.79
Otu00181	Basidiomycota	Russulaceae	*Russula*	LC008293	4.E-138	91%	100%	422	2.33	<0.009	<0.009	0.11
Otu00633	Basidiomycota	Russulaceae	*Russula*	LC008293	3.E-137	91%	100%	422	0.48	<0.009	<0.009	<0.009
Otu08454	Basidiomycota	Russulaceae	*Russula*	LC008293	1.E-141	91%	100%	419	0.01	<0.009	<0.009	<0.009
Otu13952	Basidiomycota	Russulaceae	*Russula*	UDB011108	4.E-150	94%	100%	409	<0.009	0.01	<0.009	<0.009
Otu07861	Basidiomycota	Russulaceae	*Russula*	UDB016041	8.E-122	91%	100%	373	<0.009	<0.009	<0.009	0.03

Otu14866	Basidiomycota	Russulaceae	*Russula*	UDB016041	7.E-106	86%	100%	375	<0.009	<0.009	<0.009	0.01
Otu00215	Basidiomycota	Russulaceae	*Russula*	UDB016041	1.E-122	92%	100%	370	0.05	0.05	0.14	4.57
Otu00225	Basidiomycota	Russulaceae	*Russula*	UDB016041	7.E-129	93%	100%	376	0.97	2.80	0.08	<0.009
Otu00234	Basidiomycota	Russulaceae	*Russula*	UDB016041	4.E-127	92%	100%	373	0.02	0.24	0.03	4.74
Otu02522	Basidiomycota	Russulaceae	*Russula*	UDB016041	3.E-126	92%	100%	373	<0.009	0.01	<0.009	0.17
Otu02713	Basidiomycota	Russulaceae	*Russula*	UDB016041	2.E-125	92%	100%	373	<0.009	<0.009	<0.009	0.16
Otu06651	Basidiomycota	Russulaceae	*Russula*	UDB016041	3.E-122	92%	100%	370	<0.009	<0.009	<0.009	0.03
Otu09857	Basidiomycota	Russulaceae	*Russula*	UDB016041	4.E-115	88%	100%	375	<0.009	<0.009	<0.009	0.02
Otu14040	Basidiomycota	Russulaceae	*Russula*	UDB016041	2.E-125	92%	100%	373	<0.009	<0.009	<0.009	0.01
Otu14863	Basidiomycota	Russulaceae	*Russula*	UDB016041	3.E-126	92%	100%	375	<0.009	<0.009	<0.009	<0.009
Otu14881	Basidiomycota	Russulaceae	*Russula*	UDB016041	1.E-127	92%	100%	372	<0.009	<0.009	<0.009	<0.009
Otu14885	Basidiomycota	Russulaceae	*Russula*	UDB016041	9.E-126	92%	100%	373	<0.009	<0.009	<0.009	0.01
Otu15803	Basidiomycota	Russulaceae	*Russula*	UDB016041	9.E-130	93%	100%	375	<0.009	<0.009	<0.009	<0.009
Otu16913	Basidiomycota	Russulaceae	*Russula*	UDB016041	2.E-125	92%	100%	373	<0.009	<0.009	<0.009	<0.009
Otu18380	Basidiomycota	Russulaceae	*Russula*	UDB016041	2.E-120	90%	100%	375	<0.009	<0.009	<0.009	<0.009
Otu20409	Basidiomycota	Russulaceae	*Russula*	UDB016041	5.E-120	91%	100%	371	<0.009	<0.009	<0.009	<0.009
Otu23234	Basidiomycota	Russulaceae	*Russula*	UDB016041	2.E-128	93%	100%	372	<0.009	<0.009	<0.009	<0.009
Otu23294	Basidiomycota	Russulaceae	*Russula*	UDB016041	1.E-114	89%	100%	370	<0.009	<0.009	<0.009	<0.009
Otu23306	Basidiomycota	Russulaceae	*Russula*	UDB016041	2.E-117	90%	100%	370	<0.009	<0.009	<0.009	<0.009
Otu23090	Basidiomycota	Russulaceae	*Russula*	UDB024048	6.E-140	95%	100%	383	<0.009	<0.009	<0.009	<0.009
Otu05978	Basidiomycota	Russulaceae	*Russula acrifolia*	KF850401	8.E-153	99%	100%	374	<0.009	0.05	<0.009	<0.009
Otu00748	Basidiomycota	Russulaceae	*Russula anthracina*	UDB011194	5.E-151	97%	100%	382	<0.009	<0.009	<0.009	1.12
Otu23110	Basidiomycota	Russulaceae	*Russula anthracina*	UDB011194	3.E-149	97%	100%	382	<0.009	<0.009	<0.009	<0.009
Otu03864	Basidiomycota	Russulaceae	*Russula betularum*	KT933969	1.E-169	100%	100%	408	0.01	0.07	<0.009	<0.009
Otu06478	Basidiomycota	Russulaceae	*Russula claroflava*	AY061665	7.E-171	99%	100%	421	<0.009	0.03	<0.009	<0.009
Otu02277	Basidiomycota	Russulaceae	*Russula congoana*	UDB016932	1.E-169	99%	100%	415	<0.009	0.05	<0.009	<0.009
Otu06240	Basidiomycota	Russulaceae	*Russula decolorans*	KT933992	8.E-172	100%	100%	413	0.01	<0.009	<0.009	<0.009
Otu20219	Basidiomycota	Russulaceae	*Russula pelargonia*	UDB011242	7.E-164	100%	100%	395	<0.009	<0.009	<0.009	<0.009
Otu20102	Basidiomycota	Russulaceae	*Russula vinosa*	UDB000902	2.E-171	99%	100%	419	<0.009	<0.009	<0.009	<0.009
Otu00058	Basidiomycota	Russulaceae	*Russula violeipes*	KF361784	2.E-144	96%	100%	378	<0.009	0.01	<0.009	<0.009
Otu18327	Basidiomycota	Russulaceae	*Russula violeipes*	KF361784	1.E-141	96%	100%	380	<0.009	<0.009	<0.009	<0.009
Otu03793	Basidiomycota	Russulaceae	unidentified	AB509815	2.E-140	95%	100%	375	0.03	<0.009	<0.009	<0.009

Otu07730	Basidiomycota	Russulaceae	unidentified	AB509815	1.E-150	99%	100%	373	<0.009	<0.009	<0.009	0.03
Otu02019	Basidiomycota	Russulaceae	unidentified	AB509909	6.E-144	94%	100%	401	0.09	<0.009	<0.009	<0.009
Otu00347	Basidiomycota	Russulaceae	unidentified	AB769905	5.E-124	93%	100%	368	<0.009	<0.009	<0.009	0.02
Otu22751	Basidiomycota	Russulaceae	unidentified	AB848534	7.E-156	95%	100%	418	<0.009	<0.009	<0.009	<0.009
Otu00956	Basidiomycota	Russulaceae	unidentified	AF448488	7.E-141	96%	100%	372	0.26	0.05	<0.009	0.02
Otu03435	Basidiomycota	Russulaceae	unidentified	AF448488	3.E-137	95%	100%	374	0.04	<0.009	<0.009	<0.009
Otu03887	Basidiomycota	Russulaceae	unidentified	AF448488	3.E-134	94%	100%	373	0.03	0.02	<0.009	<0.009
Otu07352	Basidiomycota	Russulaceae	unidentified	AF448488	1.E-138	95%	100%	373	0.01	<0.009	<0.009	<0.009
Otu15821	Basidiomycota	Russulaceae	unidentified	AF448488	3.E-130	93%	100%	371	<0.009	<0.009	<0.009	<0.009
Otu20176	Basidiomycota	Russulaceae	unidentified	AF506378	1.E-130	92%	98%	403	<0.009	<0.009	<0.009	<0.009
Otu11033	Basidiomycota	Russulaceae	unidentified	DQ178933	6.E-144	97%	100%	379	<0.009	<0.009	<0.009	<0.009
Otu00312	Basidiomycota	Russulaceae	unidentified	DQ178934	2.E-151	99%	100%	375	0.86	1.14	<0.009	<0.009
Otu11821	Basidiomycota	Russulaceae	unidentified	DQ388829	2.E-132	92%	100%	383	<0.009	<0.009	<0.009	<0.009
Otu11824	Basidiomycota	Russulaceae	unidentified	DQ388829	2.E-128	91%	100%	383	<0.009	<0.009	<0.009	<0.009
Otu00137	Basidiomycota	Russulaceae	unidentified	DQ388829	2.E-147	96%	100%	383	2.43	0.10	0.63	0.39
Otu00334	Basidiomycota	Russulaceae	unidentified	DQ388829	2.E-156	99%	100%	383	0.49	<0.009	0.06	0.25
Otu02349	Basidiomycota	Russulaceae	unidentified	DQ388829	5.E-155	99%	100%	384	<0.009	<0.009	<0.009	0.09
Otu06737	Basidiomycota	Russulaceae	unidentified	DQ388829	2.E-147	96%	100%	383	0.01	<0.009	<0.009	<0.009
Otu09391	Basidiomycota	Russulaceae	unidentified	DQ388829	8.E-145	96%	100%	383	<0.009	<0.009	<0.009	<0.009
Otu11822	Basidiomycota	Russulaceae	unidentified	DQ388829	1.E-146	96%	100%	383	<0.009	<0.009	<0.009	<0.009
Otu12304	Basidiomycota	Russulaceae	unidentified	DQ388829	1.E-142	95%	100%	387	<0.009	<0.009	<0.009	<0.009
Otu16859	Basidiomycota	Russulaceae	unidentified	DQ388829	1.E-145	96%	100%	383	<0.009	<0.009	<0.009	<0.009
Otu16861	Basidiomycota	Russulaceae	unidentified	DQ388829	2.E-147	96%	100%	383	<0.009	<0.009	<0.009	<0.009
Otu18311	Basidiomycota	Russulaceae	unidentified	DQ388829	2.E-147	96%	100%	383	<0.009	<0.009	<0.009	<0.009
Otu05231	Basidiomycota	Russulaceae	unidentified	DQ388830	8.E-133	92%	100%	400	<0.009	<0.009	<0.009	0.01
Otu00135	Basidiomycota	Russulaceae	unidentified	DQ388830	2.E-156	99%	100%	384	0.03	0.01	0.24	1.28
Otu07459	Basidiomycota	Russulaceae	unidentified	DQ388830	7.E-152	97%	100%	384	<0.009	<0.009	<0.009	<0.009
Otu00035	Basidiomycota	Russulaceae	unidentified	DQ388833	6.E-144	99%	100%	356	<0.009	<0.009	<0.009	0.01
Otu06247	Basidiomycota	Russulaceae	unidentified	EF619750	2.E-121	90%	100%	376	<0.009	0.04	<0.009	<0.009
Otu06560	Basidiomycota	Russulaceae	unidentified	EF619750	2.E-124	91%	100%	376	0.01	0.02	<0.009	<0.009
Otu18420	Basidiomycota	Russulaceae	unidentified	EF619750	6.E-113	88%	100%	370	<0.009	<0.009	<0.009	<0.009
Otu09376	Basidiomycota	Russulaceae	unidentified	EF685080	2.E-171	99%	100%	414	0.01	<0.009	<0.009	<0.009

Otu03815	Basidiomycota	Russulaceae	unidentified	EU569286	8.E-172	99%	100%	420	<0.009	0.09	<0.009	<0.009
Otu09597	Basidiomycota	Russulaceae	unidentified	FJ196956	7.E-156	97%	100%	399	<0.009	0.02	<0.009	<0.009
Otu18305	Basidiomycota	Russulaceae	unidentified	GQ219944	4.E-146	96%	100%	384	<0.009	<0.009	<0.009	<0.009
Otu20300	Basidiomycota	Russulaceae	unidentified	GQ219944	6.E-140	95%	100%	382	<0.009	<0.009	<0.009	<0.009
Otu00197	Basidiomycota	Russulaceae	unidentified	GQ268649	4.E-135	95%	100%	364	0.04	0.03	0.11	3.14
Otu08995	Basidiomycota	Russulaceae	unidentified	GQ268649	3.E-134	95%	100%	364	<0.009	<0.009	<0.009	0.02
Otu23193	Basidiomycota	Russulaceae	unidentified	GU184059	3.E-106	86%	100%	376	<0.009	<0.009	<0.009	<0.009
Otu14031	Basidiomycota	Russulaceae	unidentified	GU184059	2.E-121	90%	100%	375	<0.009	<0.009	<0.009	0.01
Otu14862	Basidiomycota	Russulaceae	unidentified	GU184059	4.E-123	90%	100%	376	<0.009	0.01	<0.009	<0.009
Otu06034	Basidiomycota	Russulaceae	unidentified	HE647707	6.E-144	97%	100%	378	0.01	<0.009	<0.009	<0.009
Otu00445	Basidiomycota	Russulaceae	unidentified	JF304418	5.E-147	95%	100%	402	0.20	<0.009	0.07	1.49
Otu02893	Basidiomycota	Russulaceae	unidentified	JF304418	1.E-145	94%	100%	404	<0.009	<0.009	<0.009	0.14
Otu03512	Basidiomycota	Russulaceae	unidentified	JF960807	1.E-165	99%	100%	405	0.01	<0.009	<0.009	0.01
Otu00175	Basidiomycota	Russulaceae	unidentified	JF960853	2.E-155	95%	100%	411	<0.009	<0.009	<0.009	0.02
Otu00378	Basidiomycota	Russulaceae	unidentified	JF960853	3.E-164	97%	100%	421	<0.009	0.02	<0.009	0.03
Otu00638	Basidiomycota	Russulaceae	unidentified	JF960853	2.E-159	96%	100%	413	<0.009	0.01	<0.009	<0.009
Otu00697	Basidiomycota	Russulaceae	unidentified	JF960853	3.E-156	96%	100%	411	<0.009	<0.009	<0.009	0.01
Otu00525	Basidiomycota	Russulaceae	unidentified	JQ279512	1.E-160	96%	100%	420	0.14	<0.009	0.03	0.74
Otu03415	Basidiomycota	Russulaceae	unidentified	JQ279512	1.E-168	98%	100%	420	<0.009	<0.009	<0.009	0.01
Otu04840	Basidiomycota	Russulaceae	unidentified	JQ279512	8.E-168	98%	100%	420	<0.009	<0.009	<0.009	0.01
Otu00399	Basidiomycota	Russulaceae	unidentified	JQ347192	1.E-138	92%	100%	402	0.04	<0.009	0.05	2.38
Otu05368	Basidiomycota	Russulaceae	unidentified	JQ347192	3.E-137	92%	100%	403	<0.009	<0.009	<0.009	0.05
Otu11803	Basidiomycota	Russulaceae	unidentified	JQ347192	2.E-140	93%	100%	402	<0.009	<0.009	<0.009	0.01
Otu00488	Basidiomycota	Russulaceae	unidentified	JQ396496	2.E-151	97%	100%	389	<0.009	<0.009	<0.009	0.02
Otu01267	Basidiomycota	Russulaceae	unidentified	JX425382	2.E-167	97%	100%	433	0.06	0.01	<0.009	0.28
Otu00562	Basidiomycota	Russulaceae	unidentified	JX456823	2.E-155	95%	100%	416	0.51	<0.009	<0.009	0.21
Otu00303	Basidiomycota	Russulaceae	unidentified	KC152217	6.E-136	93%	100%	392	<0.009	0.97	0.04	2.63
Otu00464	Basidiomycota	Russulaceae	unidentified	KC152217	6.E-136	93%	100%	391	<0.009	<0.009	<0.009	0.40
Otu17131	Basidiomycota	Russulaceae	unidentified	KC154104	5.E-109	90%	100%	349	<0.009	<0.009	<0.009	<0.009
Otu18671	Basidiomycota	Russulaceae	unidentified	KC154104	2.E-109	90%	100%	351	<0.009	<0.009	<0.009	<0.009
Otu00145	Basidiomycota	Russulaceae	unidentified	KF220110	5.E-128	95%	100%	361	<0.009	<0.009	<0.009	<0.009
Otu02484	Basidiomycota	Russulaceae	unidentified	KF220110	2.E-128	95%	100%	357	<0.009	<0.009	<0.009	0.19

Otu07254	Basidiomycota	Russulaceae	unidentified	KF220110	4.E-127	94%	100%	355	<0.009	<0.009	<0.009	0.03
Otu05370	Basidiomycota	Russulaceae	unidentified	KF245493	4.E-154	98%	100%	391	<0.009	0.06	<0.009	<0.009
Otu01064	Basidiomycota	Russulaceae	unidentified	KF245501	5.E-143	96%	100%	374	0.09	<0.009	<0.009	0.44
Otu02357	Basidiomycota	Russulaceae	unidentified	KM409436	7.E-175	100%	100%	420	0.01	0.14	<0.009	<0.009
Otu12296	Basidiomycota	Russulaceae	unidentified	KM576495	2.E-136	93%	100%	392	<0.009	0.01	<0.009	<0.009
Otu16771	Basidiomycota	Russulaceae	unidentified	KM576518	1.E-168	100%	100%	406	<0.009	<0.009	<0.009	<0.009
Otu00634	Basidiomycota	Russulaceae	unidentified	KM576559	3.E-149	97%	100%	380	0.01	0.20	0.10	0.90
Otu02910	Basidiomycota	Russulaceae	unidentified	KM594806	9.E-130	93%	100%	393	<0.009	<0.009	<0.009	0.14
Otu00439	Basidiomycota	Russulaceae	unidentified	KM658971	4.E-131	95%	100%	369	<0.009	0.26	0.02	1.94
Otu01135	Basidiomycota	Russulaceae	unidentified	KP012681	2.E-163	99%	100%	402	0.23	<0.009	<0.009	<0.009
Otu00059	Basidiomycota	Russulaceae	unidentified	KP012684	8.E-153	99%	100%	373	5.04	0.09	0.09	2.87
Otu23248	Basidiomycota	Russulaceae	unidentified	KP012684	2.E-147	98%	100%	373	<0.009	<0.009	<0.009	<0.009
Otu01378	Basidiomycota	Russulaceae	unidentified	KP012694	4.E-142	91%	100%	401	<0.009	<0.009	<0.009	0.46
Otu09858	Basidiomycota	Russulaceae	unidentified	KP012763	4.E-154	99%	100%	375	0.01	<0.009	<0.009	<0.009
Otu00453	Basidiomycota	Russulaceae	unidentified	KP012799	2.E-170	99%	100%	416	0.46	<0.009	0.01	0.87
Otu00394	Basidiomycota	Russulaceae	unidentified	KP012812	6.E-167	98%	100%	414	0.01	0.01	0.98	0.33
Otu01449	Basidiomycota	Russulaceae	unidentified	KP012812	9.E-153	95%	100%	412	0.15	<0.009	<0.009	<0.009
Otu00186	Basidiomycota	Russulaceae	unidentified	KP012851	1.E-160	98%	100%	406	0.04	<0.009	0.04	4.90
Otu09378	Basidiomycota	Russulaceae	unidentified	KP012851	2.E-144	93%	100%	406	<0.009	<0.009	<0.009	0.02
Otu13350	Basidiomycota	Russulaceae	unidentified	KP012851	9.E-153	96%	100%	405	<0.009	<0.009	<0.009	0.01
Otu23645	Basidiomycota	Russulaceae	unidentified	KP012857	3.E-142	99%	100%	356	<0.009	<0.009	<0.009	<0.009
Otu00020	Basidiomycota	Russulaceae	unidentified	KP012863	1.E-149	99%	100%	365	<0.009	1.34	<0.009	**10.29**
Otu05614	Basidiomycota	Russulaceae	unidentified	KP012863	7.E-141	96%	100%	365	<0.009	<0.009	<0.009	0.02
Otu16966	Basidiomycota	Russulaceae	unidentified	KP012863	2.E-143	97%	100%	365	<0.009	<0.009	<0.009	<0.009
Otu18494	Basidiomycota	Russulaceae	unidentified	KP012863	2.E-144	98%	100%	365	<0.009	<0.009	<0.009	<0.009
Otu13944	Basidiomycota	Russulaceae	unidentified	KP071079	2.E-154	91%	97%	401	<0.009	<0.009	<0.009	<0.009
Otu20289	Basidiomycota	Russulaceae	unidentified	KP071275	6.E-105	88%	100%	385	<0.009	<0.009	<0.009	<0.009
Otu00874	Basidiomycota	Russulaceae	unidentified	KP071315	3.E-145	96%	100%	377	<0.009	0.06	<0.009	0.63
Otu20377	Basidiomycota	Russulaceae	unidentified	KP071315	2.E-125	92%	100%	374	<0.009	<0.009	<0.009	<0.009
Otu00040	Basidiomycota	Russulaceae	unidentified	LC008298	3.E-137	91%	100%	418	<0.009	<0.009	<0.009	0.01
Otu00043	Basidiomycota	Russulaceae	unidentified	UDB013045	2.E-120	92%	100%	375	<0.009	<0.009	<0.009	<0.009
Otu00683	Basidiomycota	Russulaceae	unidentified	UDB013085	2.E-132	91%	100%	416	0.21	0.04	0.22	0.09

Otu00690	Basidiomycota	Russulaceae	unidentified	UDB013085	2.E-119	87%	100%	419	0.44	<0.009	<0.009	0.02
Otu08610	Basidiomycota	Russulaceae	unidentified	UDB013085	2.E-139	92%	100%	415	<0.009	<0.009	<0.009	0.02
Otu12772	Basidiomycota	Russulaceae	unidentified	UDB013085	8.E-133	91%	100%	412	<0.009	<0.009	<0.009	<0.009
Otu20101	Basidiomycota	Russulaceae	unidentified	UDB013085	2.E-140	92%	100%	420	<0.009	<0.009	<0.009	<0.009
Otu02288	Basidiomycota	Russulaceae	unidentified	UDB013103	6.E-152	99%	100%	370	<0.009	0.05	0.07	<0.009
Otu12284	Basidiomycota	Russulaceae	unidentified	UDB013216	4.E-165	99%	100%	402	<0.009	<0.009	<0.009	<0.009
Otu00112	Basidiomycota	Russulaceae	unidentified	UDB013241	1.E-150	99%	100%	369	<0.009	0.02	<0.009	0.01
Otu02499	Basidiomycota	Russulaceae	unidentified	UDB013250	3.E-137	96%	100%	368	<0.009	<0.009	<0.009	0.19
Otu00074	Basidiomycota	Russulaceae	unidentified	UDB013273	4.E-146	97%	100%	375	1.61	0.13	0.01	**10.80**
Otu00266	Basidiomycota	Russulaceae	unidentified	UDB013273	1.E-150	98%	100%	375	<0.009	0.03	<0.009	4.23
Otu00609	Basidiomycota	Russulaceae	unidentified	UDB013273	2.E-136	95%	100%	384	<0.009	1.60	<0.009	<0.009
Otu00635	Basidiomycota	Russulaceae	unidentified	UDB013273	2.E-144	96%	100%	375	0.01	<0.009	<0.009	1.37
Otu00796	Basidiomycota	Russulaceae	unidentified	UDB013273	3.E-145	97%	100%	375	0.21	0.15	<0.009	0.34
Otu00930	Basidiomycota	Russulaceae	unidentified	UDB013273	2.E-147	97%	100%	376	0.25	<0.009	0.06	<0.009
Otu01507	Basidiomycota	Russulaceae	unidentified	UDB013273	1.E-146	97%	100%	376	0.13	<0.009	0.02	<0.009
Otu01564	Basidiomycota	Russulaceae	unidentified	UDB013273	8.E-149	98%	100%	375	0.01	<0.009	<0.009	<0.009
Otu02606	Basidiomycota	Russulaceae	unidentified	UDB013273	3.E-145	97%	100%	375	0.02	<0.009	<0.009	0.11
Otu03582	Basidiomycota	Russulaceae	unidentified	UDB013273	2.E-151	98%	100%	375	0.02	0.06	<0.009	<0.009
Otu06036	Basidiomycota	Russulaceae	unidentified	UDB013273	2.E-147	97%	100%	376	0.01	<0.009	<0.009	<0.009
Otu10703	Basidiomycota	Russulaceae	unidentified	UDB013273	5.E-147	97%	100%	375	<0.009	<0.009	<0.009	0.01
Otu14874	Basidiomycota	Russulaceae	unidentified	UDB013273	5.E-147	97%	100%	375	<0.009	<0.009	<0.009	0.01
Otu16905	Basidiomycota	Russulaceae	unidentified	UDB013273	1.E-149	98%	100%	375	<0.009	<0.009	<0.009	<0.009
Otu18350	Basidiomycota	Russulaceae	unidentified	UDB013273	2.E-144	97%	100%	377	<0.009	<0.009	<0.009	<0.009
Otu20356	Basidiomycota	Russulaceae	unidentified	UDB013273	2.E-144	96%	100%	375	<0.009	<0.009	<0.009	<0.009
Otu14086	Basidiomycota	Russulaceae	unidentified	UDB013288	7.E-137	96%	100%	364	<0.009	<0.009	<0.009	<0.009
Otu00087	Basidiomycota	Russulaceae	unidentified	UDB013323	8.E-141	95%	100%	375	<0.009	<0.009	<0.009	0.02
Otu00381	Basidiomycota	Russulaceae	unidentified	UDB013323	5.E-155	100%	100%	375	0.05	0.01	0.12	0.58
Otu03921	Basidiomycota	Russulaceae	unidentified	UDB014176	3.E-142	98%	100%	356	0.02	0.02	<0.009	<0.009
Otu00061	Basidiomycota	Russulaceae	unidentified	UDB014226	1.E-127	92%	100%	378	<0.009	<0.009	<0.009	0.01
Otu00628	Basidiomycota	Russulaceae	unidentified	UDB014470	1.E-138	92%	100%	405	0.02	0.46	0.19	0.14
Otu00665	Basidiomycota	Russulaceae	unidentified	UDB014470	1.E-137	92%	100%	405	0.03	0.35	0.18	0.10
Otu00618	Basidiomycota	Russulaceae	***Zelleromyces spE***[a]	KY697617-9	2.E-167	99%	100%	406	0.12	0.06	<0.009	0.07

Otu01104	Basidiomycota	Russulaceae	***Zelleromyces spE***[a]	KY697617-9	9.E-153	96%	100%	399	0.01	0.01	<0.009	0.54
Otu06422	Basidiomycota	Bankeraceae	*Boletopsis leucomelaena*	UDB016050	8.E-130	96%	100%	354	0.01	0.01	<0.009	<0.009
Otu16123	Basidiomycota	Bankeraceae	*Phellodon*	GU222318	1.E-111	92%	100%	334	<0.009	<0.009	<0.009	<0.009
Otu23362	Basidiomycota	Thelephoraceae	*Thelephora*	JX630820	2.E-132	94%	100%	368	<0.009	<0.009	<0.009	<0.009
Otu13428	Basidiomycota	Thelephoraceae	*Thelephora atra*	KC152246	1.E-150	99%	100%	369	<0.009	<0.009	<0.009	<0.009
Otu01950	Basidiomycota	Thelephoraceae	*Thelephora palmata*	AJ537505	6.E-148	98%	100%	372	<0.009	<0.009	0.05	0.07
Otu02294	Basidiomycota	Thelephoraceae	*Thelephora palmata*	AJ537505	5.E-147	98%	100%	372	<0.009	<0.009	0.06	0.03
Otu20497	Basidiomycota	Thelephoraceae	*Thelephora terrestris*	KP814379	1.E-150	99%	100%	367	<0.009	<0.009	<0.009	<0.009
Otu04588	Basidiomycota	Thelephoraceae	*Tomentella*	EF507250	9.E-130	93%	100%	369	0.01	<0.009	<0.009	<0.009
Otu11854	Basidiomycota	Thelephoraceae	*Tomentella*	EF507250	4.E-127	93%	100%	369	<0.009	0.01	<0.009	<0.009
Otu03228	Basidiomycota	Thelephoraceae	*Tomentella asperula*	UDB018469	7.E-137	96%	100%	364	<0.009	<0.009	<0.009	<0.009
Otu12347	Basidiomycota	Thelephoraceae	*Tomentella lapida*	JQ724049	2.E-143	97%	100%	371	<0.009	0.01	<0.009	<0.009
Otu23299	Basidiomycota	Thelephoraceae	*Tomentella lapida*	JX630638	2.E-152	99%	100%	371	<0.009	<0.009	<0.009	<0.009
Otu14908	Basidiomycota	Thelephoraceae	*Tomentella muricata*	UDB014248	3.E-141	96%	100%	368	<0.009	0.01	<0.009	<0.009
Otu06109	Basidiomycota	Thelephoraceae	*Tomentella sublilacina*	UDB014056	8.E-149	99%	100%	367	0.01	0.03	<0.009	<0.009
Otu08985	Basidiomycota	Thelephoraceae	*Tomentellopsis zygodesmoides*	UDB011640	1.E-153	99%	100%	374	<0.009	<0.009	<0.009	<0.009

[a] indicates taxa from morphological groups identified in Abell-Davis (2008), Appendix C.