Fungal Ecology 27 (2017) 1–13

Contents lists available at ScienceDirect

Fungal Ecology

journal homepage: www.elsevier.com/locate/funeco

Redundancy among mammalian fungal dispersers and the importance of declining specialists

S.J. Nuske [a, *], K. Vernes [b], T.W. May [c], A.W. Claridge [d, e], B.C. Congdon [a], A. Krockenberger [f], S.E. Abell [a]

[a] *College of Science and Engineering, Centre for Tropical Environmental and Sustainability Science, James Cook University, Cairns QLD 4878 Australia*
[b] *Ecosystem Management, University of New England, Armidale NSW 2351 Australia*
[c] *Royal Botanic Gardens Victoria, Melbourne, VIC 3004 Australia*
[d] *Office of Environment and Heritage, NSW National Parks and Wildlife Service, Nature Conservation Section, P.O. Box 733, Queanbeyan, NSW 2620, Australia*
[e] *School of Physical, Environmental and Mathematical Sciences, The University of New South Wales at Canberra, Northcott Drive, Canberra, ACT 2600, Australia*
[f] *Division of Research and Innovation, James Cook University, Cairns QLD 4878 Australia*

ARTICLE INFO

Article history:
Received 8 June 2016
Received in revised form
10 February 2017
Accepted 22 February 2017
Available online 15 March 2017

Corresponding Editor: D. Jean Lodge

Keywords:
Diet
Ectomycorrhizae
Functional redundancy
Fungal generalist
Mycophagy
Potoroidae
Sequestrate fungi
Spore
Truffle-like fungi
Rat-kangaroo

ABSTRACT

Hypogeous sequestrate (truffle-like) fungi rely primarily on consumption by mammals for dispersal. Most truffle-like fungi are ectomycorrhizal, making mammalian dispersers essential to the maintenance of plant-fungal relationships, soil fungal diversity and ecosystem functioning. Australia has the highest current global rate of mammalian extinctions, including important fungal specialists within the family Potoroidae. Knowing the relative importance of different mammal species as dispersers helps us to understand how this loss in mammal diversity could affect plant-fungi interactions and fungal diversity. Despite detecting a sampling bias in the literature, our 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.

1. Introduction

Dispersal is an important mechanism influencing community assemblage and gene flow. For many fungi, dispersal can occur through wind, water or soil movement, or a combination thereof (Reddell and Milnes, 1992; Peay et al., 2012). Hypogeous sequestrate (truffle-like) fungi rely on dispersal by animals, particularly mycophagous mammals, as they form fruit bodies below-ground and do not have an alternative dispersal mechanism (Maser et al., 1978; Claridge et al., 1992; Claridge and May 1994). Truffle-like fungi form a highly diverse group, most of which are ectomycorrhizal (ECM). This group plays a key role in many ecosystems globally (Tedersoo et al., 2010, 2014). Ectomycorrhizal fungi also associate mutualistically with a diverse array of globally important plants (Brundrett, 2009). In exchange for carbohydrates, ECM fungi transport nutrients to the plant. As such ECM fungi are vital components of forest ecosystems (Buscot et al., 2000; van der Heijden et al., 2015). It is expected that mammals, as dispersers of spores of ectomycorrhizal fungi, are essential to the maintenance of fungal 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

* Corresponding author.
E-mail address: susan.nuske@my.jcu.edu.au (S.J. Nuske).

http://dx.doi.org/10.1016/j.funeco.2017.02.005
1754-5048/

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 most 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 (CI: 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; Bentley, 2008; Marchesan and Carthew, 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 rat-kangaroos in Australia (e.g. *Bettongia gaimardi* and *Bettongia tropica*) 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, the swamp wallaby, *Wallabia bicolor*, 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 rat-kangaroos 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 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 no studies that specifically address functional redundancy between specialist and generalist mammalian fungal dispersers, and data on mycophagy is scattered throughout the literature. Additionally, 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, we bring together data on fungal diets of mammals to infer their potential functional role as fungal dispersers. To be able to undertake valid comparative analyses between published studies we also developed selection criteria on dietary sampling methods that reduced bias and the under-detection of dietary fungi.

We used data on Australian mammals 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 et al., 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., mouse-sized insectivorous antechinus, *Antechinus stuartii* and medium-sized, omnivorous northern brown bandicoots, *Isoodon macrourus;* 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 diversity and fungal-plant interactions particularly pertinent for this continent.

From a dietary perspective, six out of eight extant Australian rat-kangaroo species within the family Potoroidae are viewed as fungal specialists and we hypothesise that they perform a disproportionately important role in fungal dispersal. Australian rat-kangaroos 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 the long-nosed potoroo, *Potorous tridactylus*; this study). The two notable exceptions from this family are the rufous bettong (*Aepyprymnus rufescens*) and the burrowing bettong (*Bettongia lesueur*). 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 we examine the available information on mycophagy in mammals within Australia in terms of the abundance, frequency, seasonality and diversity of fungi consumed. From these data, we infer the relative importance of mammals as fungal dispersers and test the hypothesis that in Australia rat-kangaroos (members of Potoroidae and fungal specialists) contribute disproportionally more to the consumption of fungi than generalist mycophagous mammal species. We also examine whether there is likely to be functional redundancy among generalist mycophagous mammals in their fungal dispersal roles.

2. Materials and methods

2.1. 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