Spatial patterns in the distribution of truffle-like fungi, mutualistic interactions with mammals, and spore dispersal dynamics

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ABSTRACT

Truffle-like fungi play an important role in the health of forested ecosystems yet we know relatively little of spatial trends in their distribution and related dispersal processes. This thesis examines the spatial distribution of truffle-like fungi and mutualistic interactions with mammals across contrasting habitat types (rainforest, wet sclerophyll forest, dry open forest, and heathy woodland) on the New England Tablelands, north-eastern New South Wales, Australia. I also investigated whether mammal diets could be used as a surrogate method in detecting broad spatial patterns in fungal richness and composition. Spore dispersal dynamics in truffle-like fungi were explored by examining the relative role of different mammals as spore dispersal vectors with a specific focus on the mycophagist swamp wallaby *Wallabia bicolor*. Finally, the thesis reports on the discovery of microbats as a potential long-distance dispersal (LDD) vector for macrofungi and the novel observation of a fungus fruiting in a cave environment.

Spatial patterns in species diversity and assemblage structure inform our understanding of fungal dispersal dynamics and can be used to guide conservation management actions. Species richness of truffle-like fungi was found to vary among four sampled habitat types. Mammal diets indicated similar variation although the estimated gradient across habitats differed and suggested species richness in one habitat was potentially underestimated by sporocarp surveys. Both sampling techniques indicated wet sclerophyll forest supported higher species richness than heathy woodland. Taxon richness estimated from sporocarp surveys and observed in mammal diets was high by global standards, further confirming the extraordinary diversity of truffle-like fungi within Australia.

Broad habitat types were found to support different assemblages of truffle-like fungi based on the results of sporocarp surveys and analysis of mammal diets. Mammal diets indicated all three eucalypt-dominated habitats supported distinct assemblages. Both diets and sporocarp surveys suggested composition differences among habitats were complex and driven by numerous taxa. There was some correspondence between diets and sporocarp surveys in species and genera contributing most to differences between habitats, particularly in wet sclerophyll forest. Some taxa were strongly associated with specific habitat types while others were equally abundant across all habitats, suggesting some are habitat specialists while others utilise a range of habitats.

Dispersal plays a critical role in species distribution, community assembly, evolution, and biogeographic patterns. In the case of truffle-like fungi, dispersal dynamics are largely shaped by mutualistic interactions with animals which disperse their spores. Animals can differ in their
relative importance in this process by varying in the ‘quantity’ of dispersal provided, including the number and species diversity of spores dispersed. Results of the current study suggested mammals contributed differently to spore dispersal for assemblages of truffle-like fungi. The bush rat *Rattus fuscipes* was confirmed as a standard dispersal vector across all habitat types sampled, dispersing large numbers of spores representing a high diversity of fungal taxa. Bush rats also expanded the diversity of taxa consumed in accordance with availability, indicating the species is an important disperser across multiple habitat types and for different assemblages of fungi. Three other small mammal species and one macropod (swamp wallaby *Wallabia bicolor*) were also found dispersing spores of numerous taxa. Based on the frequency and taxon richness of fungal spores found in diets, swamp wallaby contribution to spore dispersal may differ by habitat type, being relatively more important in heathy woodland than in wet sclerophyll forest. Most mammal species differed in the taxon composition of spores they dispersed suggesting a diverse mammalian community may be important for maintaining dispersal services in fungal assemblages.

Animal spore vectors may differ in the ‘quality’ of dispersal provided to truffle-like fungi such as spore dispersal distances and patterns of deposition. To further understand dispersal dynamics in this group, mechanistic models were used to estimate spore dispersal distances and deposition patterns generated by the swamp wallaby. Although bush rats dispersed the greatest number of taxa, estimated spore dispersal distances facilitated by the swamp wallaby were considerable. Most (92%) spores were predicted to be dispersed >100m, many (60%) >250m and some >1000m from the source of origin. Models predicted an aggregated spatial pattern of spore deposition, which was strongly correlated with each animal’s space use. Clumped spore deposition could increase recruitment success through enhanced colonisation rates and may be influential in determining subsequent spatial patterns of recruitment.

Animal vectors can also differ in the degree to which they disperse spores to sites suitable for establishment. Swamp wallabies were estimated to frequently disperse spores across habitat boundaries, thereby facilitating the maintenance of ecotonal spore banks and the distribution of habitat generalists. LDD events facilitated by swamp wallabies were sufficient to disperse spores among distant patches of similar habitat within the study area. Fat-tailed kernels estimated for some animals suggested some animals may provide more frequent LDD events than others. Results also suggest swamp wallabies have the potential to facilitate the (re-)colonisation of disjunct suitable habitat patches by truffle-like taxa with more narrow niche ranges and also in gene flow among isolated populations. Spore dispersal distances facilitated by swamp wallabies also closely matched a frequency distribution of animal net displacement, evidence for movement
behaviour being an important determinant of spore deposition patterns.

Microbats may be important non-standard LDD vectors for truffle-like fungi, likely to facilitate greater dispersal distances than co-occurring mammals. Several microbat species were implicated in spore dispersal and considering their broad habitat range and tolerance of human-modified landscapes, may be important dispersal agents across a wide range of habitats including in those characterised by habitat fragmentation. Insect and microbat dispersal may have played important role in past biogeographic events and is one potential means for explaining the wide distributions of some truffle-like fungi lineages.

Spatial variation in sporocarp production and composition has important implications for the conservation management of truffle-like fungi and mycophagous mammal communities. Also, different spatial patterns in mycophagous habits of animals can influence their relative roles as spore dispersal vectors. Truffle diversity, abundance and aggregation were found to vary by habitat type. The gradient exhibited in sporocarp biomass followed that of species richness. There was some evidence that differences among habitats in the aggregation of fungal food resources may influence the mycophagous habits of mammals. An inverse relationship was observed between sporocarp consumption by the swamp wallaby and biomass in the soil, potentially driven by differences among habitats in feeding behaviour. Although the mycophagous habits of bush rats were found to be consistent across habitats, those of the swamp wallaby varied among habitats and may be comparatively less important as a spore vector in more mesic habitats.

The cryptic and ephemeral nature of truffles constitutes a significant challenge to the study of their spatial distribution and conservation requirements. Surrogate techniques for detecting spatial patterns in taxon richness and composition may assist in guiding broad-scale conservation measures for this group. Sampling of mammal diets provided contrasting estimates of species richness for one habitat (dry open forest) and correspondence in relative richness for the remaining eucalypt-dominated habitats based on sporocarp surveys. There was correspondence between bush rat, small mammal, and swamp wallaby diets in predicted total richness gradients. Bush rat and swamp wallaby diets exhibited distinct shifts in the composition of truffle-like taxa in response to habitat type, largely consistent with results of sporocarp surveys. Bush rat diets detected these differences at comparatively low sample size and may be a suitable surrogate for estimating broad spatial trends in taxon richness and composition. In all analyses, there was also close correspondence between (morpho)species and genus-level patterns among habitats in both taxon richness and composition, suggesting differences may occur at multiple taxonomic levels.
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**Table 5.1** Home range and core use estimates (in hectares) for swamp wallaby *Wallabia bicolor* individuals tracked continuously for more than one week. The 100% minimum convex polygon method (MCP100) provides a maximum estimate of home range size followed by the 95% (KDE95) and 75% (KDE75) isopleths of kernel density estimates. Core use area is represented by 50% isopleths of kernel density estimates (KDE50).

**Table 5.2** Statistics for spore-dispersal curves via swamp wallaby *Wallabia bicolor* zoochory and fitted gamma distributions.

**Table 5.3** Spatial analysis results including SADIE aggregation index (la) and simultaneous autoregression (SAR) results for spatial correlations between clustering patterns in 2D spore deposition models (Figure 5.7: column B) and space utilisation for each individual swamp wallaby *Wallabia bicolor*.

**Table 5.4** Average number (±SE) of daily habitat boundary crossings by swamp wallabies *Wallabia bicolor*, including values divided by relative habitat availability. Non-habitat refers to vegetation communities considered less likely to support truffle-like fungi (i.e. montane bogs and granite outcrops).

**Table 6.1** Number of samples containing spores of epigeous and truffle-like taxa for each of nine microbat species. Species were sampled from three sites on the New England Tablelands. Results from a combined sample from several microchiropteran species trapped in Gibraltar Range National Park is also shown.

**Table 7.1** Global and pair-wise results of one-way ANOSIM tests for differences among grids within each habitat. Shown with R-values and significance level where P<0.05. One-way ANOSIM tests for differences among grids were undertaken separately for each habitat. n.s.=non-significant result.