Chapter 5. Spatial patterns of fungal spore dispersal generated by a mammalian dispersal vector, the mycophagous swamp wallaby *Wallabia bicolor*

Introduction

Dispersal is an important demographic and biogeographic process that influences the colonisation of new habitats, genetic structure, population dynamics and patterns in species richness (Morales & Carlo 2006). Despite its potential importance, very little is known about spore dispersal for most ectomycorrhizal (EcM) or arbuscular mycorrhizal fungi (AM)(Douhan *et al.* 2011). As in most plants, spore dispersal may be an important process in spatial structuring of fungal populations, communities, and genetic variance but also those of their symbiotic plant hosts. Consequently, spore dispersal in mycorrhizal fungi may be a crucial spatial process not only for fungi but also for their symbiotic host-plant partners.

The two major modes of dispersal in fungi are wind and animal-mediated dispersal (zoochory) with the former thought to dominate in fungi producing epigeous sporocarps and the latter in fungi producing sequestrate and hypogeous sporocarps ('truffles' and 'truffle-like fungi')(Johnson 1996; Douhan *et al.* 2011). As most truffle-like fungi are sequestrate (i.e. producing 'truffle-like' sporocarps in which spores are enclosed within an outer layer called a peridium), they are considered largely reliant on animals to excavate their sporocarps and liberate spores. Through subsequent mechanical processing including ingestion, mycophagous vertebrates disperse spores by: 1) releasing them into the air (i.e. secondary wind-dispersal), 2) external attachment to their bodies (ectozoochory), and 3) ingestion and subsequent defecation (endozoochory) at a later time in faecal pellets (Claridge 2002). Mammals have been shown to disseminate viable spores after gut-passage (Cork & Kenagy 1989b) and in some cases increase spore viability through gut-treatment (Colgan III & Claridge 2002). Mycophagy has also received attention as a potentially important mode of dispersal for arbuscular mycorrhizal (AM) fungi (Gehring *et al.* 2002; Mangan & Adler 2002; Lekberg *et al.* 2011) and also EcM fungi with epigeous sporocarps (Galante *et al.* 2011).

Dependence upon mycophagous mammals for dispersal varies among truffle-like taxa based on the characteristics of spore-bearing fruiting-structures (sporocarps). Taxa producing deeper-fruiting sporocarps with hard outer shells (peridia), such as species belonging to the Australian endemic genus *Mesophellia* (Vernes & Lebel 2011), exemplify reliance on mammalian dispersal when

compared to soft-bodied, partially sequestrate, and subhypogeous ('erumpent') taxa such as some *Cortinarius* taxa (e.g. *C. globuliformis*)(see Johnson 1996 for illustrations of different forms of sporocarps). Specific adaptations to zoochory have led researchers to suggest co-evolution between many truffle-like fungi and their mammalian dispersers (Claridge & May 1994). Selection for the truffle-like form has been related to their obligate EcM associations with plant hosts and reliance on endozoochory. The aggregation of spores of several truffle-like fungi together in animal faecal pellets along with delivery of spores close to plant roots have been identified as important characteristics driving the truffle-host plant symbiosis (Bougher & Lebel 2001; Claridge 2002).

Where a species potential range, distribution, or gene flow is constrained by the process of seed or spore dispersal, it is considered dispersal restricted or limited. Dispersal limitation in micro-organisms, including AM and EcM fungi, has received recent attention as a potentially influential factor in determining observed spatial patterns in taxa, species richness, and community composition (Telford *et al.* 2006; Grubisha *et al.* 2007; Tedersoo *et al.* 2009b; Peay *et al.* 2010a; b). The spatial pattern of spore dispersal may be non-random, predictable, and largely determine subsequent patterns in spore survival. Dispersal of spores may also facilitate rapid migration and establishment as has been predicted for wind-dispersed AM fungi (Allen *et al.* 1989).

Long-distance dispersal (LDD) is a critical process to investigate in attempting to understand current biogeographic distributions of organisms. In biogeography studies LDD events often refer to transoceanic dispersal of propagules while in ecological studies LDD may refer to rare stochastic dispersal events of a smaller scale depending on the organism involved (>100m to several kilometres; Nathan 2006). While short-range dispersal may influence resource use, spatial patterns of recruitment, species co-existence, and small-scale metapopulation dynamics, LDD operates at a larger temporal and spatial scale in influencing spread and colonisation rates, gene flow, genetic structure, and species diversity (Higgins *et al.* 2003; Douhan *et al.* 2011). Relative to their frequency in time, LDD events contribute disproportionally to observed biogeographic events such as post-glacial migration rates of woodland herbs (Clark *et al.* 1998; Cain *et al.* 1998, 2000), re-colonisation of sterile (Allen 1987), disturbed or isolated habitats, maintenance of diversity, and the spatial dynamics of species and metapopulations (Soons & Bullock 2008). Consequently, describing the dispersal kernel (see Glossary) is crucial for understanding these ecological processes. The kernel tail is of most importance as it predicts the frequency of LDD events with fatter tails predicting more frequent LDD (Hirsch *et al.* 2012). Long-distance dispersal of spores has been previously implicated in *Pisolithus* species shared between Australia and New Zealand by Moyersoen *et al.* (2003)(but see Orlovich & Cairney 2004), the biogeographic history and global distribution of the truffle-like fungi genus *Elaphomyces* (Reynolds 2011), initial establishment of truffle-like fungi on islands (Grubisha *et al.* 2007), assemblage of arctic EcM basidiomycetes

(Geml *et al.* 2011), and the biogeography of Hysterangiales (Hosaka *et al.* 2008), the polypore fungus *Ganoderma applanatum* (Moncalvo & Buchanan 2008), and other basidiomycetes (Kauserud *et al.* 2006).

It has been suggested that in fungi producing epigeous sporocarps, few spores may escape from the parental vicinity (Li 2005) leading to limited spore dispersal and potential inbreeding. Shorter-distance dispersal also increases the likelihood of spores falling onto already exploited microsites. Rates of seed survival have been shown to increase with distance from the parent source, potentially due to density-dependent processes such as predation and competition (Howe & Miriti 2004). This may also be true for fungi where genets escape intraspecific competition with the parent fungi of a different genotype through greater spore dispersal distances (Kennedy 2010). Consequently, dispersal away from the parent may confer a greater relative survival probability.

Spore dispersal of EcM fungi also has important implications for the life histories of host plant species. From the perspective of EcM plant hosts, endozoochorous dispersal of spores has been implicated in promoting the establishment of EcM trees beyond parent trees through dispersing fungal inoculum (Frank *et al.* 2009). Due to the conferred benefits or obligate requirement of mycorrhizal colonisation, spore dispersal may also shape patterns of dispersal and recruitment in EcM or AM host plant species (Tedersoo *et al.* 2009b; Peay *et al.* 2010b). Conversely, where host specificity in a fungi species is present and the host plant is patchily distributed within a landscape, spore dispersal is likely crucial for the maintenance of the fungi populations and the exchange of genes (Peay *et al.* 2008, 2010b). Dispersal also maintains spore banks, allowing fungi species to reside in the spore bank between successional stages or disturbance events (Izzo *et al.* 2005a; Rusca *et al.* 2006). Mycophagous dispersers have been implicated in the maintenance of AM soil inoculum potential and associated mycorrhizal infection of host plants (Gehring *et al.* 2002). Through dispersing spores across habitat boundaries, mycophagous mammals have also been implicated in facilitating local expansion and contraction of plant communities in response to natural fire regimes and climatic cycles (Vernes & Dunn 2009).

Consumption of fungal sporocarps by mammals has been hypothesised to result in effective spore dispersal due to the large foraging ranges of animals implicated in dispersal (Johnson 1996) and delivery of large numbers of spores concentrated in animal faecal pellets (Miller *et al.* 1994; Colgan III & Claridge 2002). Resulting dispersal distances may facilitate outcrossing of EcM populations along with directed dispersal of spores to host plants. Secondary dispersal by dung beetles or water may subsequently move spores into the rhizosphere and into contact with host-plant root systems. Consequently, the consumption of truffle-like fungi by mammals (mycophagy) and subsequent dispersal of spores is considered a crucial ecological process for maintaining the symbiosis between many mycorrhizal fungi and their plant hosts. However, estimates of dispersal

distances for spores via endozoochory are lacking (Claridge & May 1994).

Determining the distance spores are dispersed is a basic question in the dispersal ecology of fungi. As with the seeds of plants, direct measurement of spore dispersal is difficult or impossible due to the challenges of tracking microscopic spores in three-dimensional space (Hirsch *et al.* 2012). Direct measurement of wind-dispersed basidiospores of epigeous fungi has only been undertaken previously for a small number of species and has focused on dispersal distances along a horizontal plane (Galante *et al.* 2011). Techniques employed for wind-dispersal of epigeous taxa include the use of spore traps radiating outwards from the sporocarps of fungi. Even where this direct measurement is possible, the tail of the dispersal curve will often be poorly estimated due to increasingly lower densities of spores with distance from the parent fungi and hence lower detectability by spore traps. As such, the frequency and extent of LDD can be poorly estimated by standard means of direct physical measurement (Nathan *et al.* 2003; Hirsch *et al.* 2012). Furthermore, as marking and remotely tracking spores remains challenging, dispersing fungal spores via endozoochory are difficult to follow. Consequently, we know little of dispersal dynamics in truffle-like fungi and the dispersal kernels produced by their mycophagous vectors.

Spatially explicit mechanistic models have helped quantify wind and zoochorous dispersal of seeds including LDD (Will & Tackenberg 2008) and are a promising tool for the study of fungal spore dispersal. In most cases, they constitute the only means to estimate the 'tail' of a dispersal kernel which describes the frequency and scale of LDD events. Limited use of simulation or mechanistic models has been made with wind-dispersed fungi (Bicout & Sache 2003; Galante *et al.* 2011) but none to date with zoochorous dispersal. The primary mechanisms underlying the dispersal of fungal spores by vertebrates are highly similar to those governing endozoochorous dispersal of plant seeds. Spore dispersal dynamics in truffle-like taxa are considered to be largely the product of the movement behaviours of the animal disperser combined with the rates of spore passage through their guts (Claridge & May 1994). These two principle mechanisms determine the scale and spatial pattern of spore deposition by a single disperser. Simulation or mechanistic models allow the relative importance of different processes to be explored along with providing predictions that can guide sampling of related processes or patterns. As such, they are an important tool for ecological research where few ecological processes or patterns can be measured directly. This is particularly the case with cryptic EcM fungi for which individual reproductive units are near impossible to measure in the field.

One-dimensional dispersal curves are commonly used to describe dispersal of seeds. They are typically described by a histogram of deposition probability or number of propagules dispersed at distance intervals or annuli (i.e. rings) removed from the parent source. These can be further described using a cumulative probability curve (Santamaría *et al.* 2007) or probability density

function (PDF). Two-dimensional spatially explicit models of zoochorous dispersal have in recent times been used to predict spatial patterns of seed rain generated by plants and animal dispersers. The latter provides a more detailed and realistic description of dispersal and provides predictions of deposition patterns in two-dimensional space, important to understanding processes that are spatial and anisotropic in nature (Santamaría *et al.* 2007; Savage *et al.* 2011). They also allow the query of other related variables which may influence the dispersal process (i.e. habitat structure) or subsequent recruitment patterns (Santamaría *et al.* 2007; Rodríguez-Pérez *et al.* 2012b).

The foraging range of animal dispersal vectors is important in determining the quality of dispersal offered and specifically, the scale of dispersal services provided. The quantity of dispersal relates to the proportion of spores dispersed by the mycophagous disperser while the quality of dispersal relates to how effective the dispersal agent is at dispersing viable spores to locations where subsequent recruitment is successful (Schupp *et al.* 2010). Another form of quality relates to the importance of the vector at larger spatio-temporal scales including biogeographic patterns and evolutionary processes. Differential contribution of vertebrate dispersers can occur due to variation in consumption, gut-passage, and movement rates as well as behavioural patterns including habitat selection (Jordano *et al.* 2007; Spiegel & Nathan 2007). The time in which propagules are consumed by the disperser can also influence the scale and quality of dispersal (Westcott *et al.* 2005; Kays *et al.* 2011).

Spore dispersal is the primary mode of dispersal limitation in fungi and may be crucial where host-specificity or narrow habitat requirements are present (Peay *et al.* 2008). An increasing appreciation of spatial structuring in fungal populations and communities and the importance of scale is leading many researchers to reassess the importance of spore dispersal in fungal ecology. Although dispersal dynamics are acknowledged as influential in fungal genetics and evolutionary ecology (Roy 2001; Grubisha *et al.* 2007), little is known of how they may influence ecological patterns. Basic information is needed on fungal spore dispersal to allow linking of dispersal to key ecological processes such as succession at a landscape scale. To gain an understanding of the scale and pattern of spore deposition I estimated spore dispersal kernels generated by the swamp wallaby *Wallabia bicolor*, investigated associations between predicted patterns in spore deposition and each animal's space utilisation, along with the species potential to disperse spores across vegetation boundaries.

Methods

Study area and species

Animal GPS telemetry was undertaken in Gibraltar Range National Park (-29.5214 S, 152.3548 W)

on the New England Tablelands of north-eastern New South Wales, Australia. Gibraltar Range NP forms part of a large (150,620 ha) contiguous wilderness area and includes one the largest areas on un-logged sclerophyll forest in New South Wales (Hunter & Sheringham 2008). The park is located between the New England Table bioregion and the Great Escarpment which forms part of the Great Dividing Range of eastern Australia. Altitude varies greatly within the park boundaries, ranging from 200m to 1175 m (NSW NPWS 2004) although mean elevation of the study site is approximately 950 m. Average rainfall on the central plateau can be high (>2000mm) with rainfall decreasing westward from the escarpment edge (NSW NPWS 2004; cited in Vernes *et al.* 2006). Recorded average annual rainfall at localities nearest the study site is between 1084mm to 1214mm (BOM 2012). Most of this rainfall occurs during the warmest months (November to March) that average around the high twenties (º Celsius), while winters are characterised by prolonged low intensity rainfall and comparatively cold temperatures (mean min/max range: -0.5º to 14.0º between June to August)(Hunter & Sheringham 2008; Bureau of Meteorology 2012). Shallow and nutrient poor granitic soils dominate within the study site.

The study site supports a variety of broad vegetation types including montane bogs and sedge heaths in low lying areas, wet sclerophyll on slopes, temperate rainforest in gullies, sparse shrublands and heaths on rock outcrops, and heathy woodlands on flatter terrain. Ecotonal boundaries are often narrow due to high topological relief at small spatial scales, particularly between heathy woodland, wet sclerophyll, and rainforest. The latter vegetation communities support different assemblages of native truffle species (Chapter 2) which is reflected in the diets of swamp wallabies (Chapter 4) and other mycophagous mammals (Chapter 3; Vernes & Dunn 2009).

Numerous mammal species are known to consume the sporocarps of native truffle-like species, including at least eleven recorded consuming and dispersing spores within the study area (Chapter 3; Vernes & Dunn 2009; Vernes 2010). Of these standard dispersal vectors, mycophagous macropods such as the swamp wallaby are likely to facilitate the greatest dispersal distances for fungal spores due to their relatively large foraging range and high mobility (Johnson 1996; Di Stefano *et al.* 2007). Swamp wallabies are a wide-spread species within the coast and ranges of eastern Australia and are found in a wide array of habitat types (Merchant 1995). The species mycophagous habits are well established with animals known to consume a wide variety of truffle-like taxa, with peak consumption occurring during winter months within the study area (Chapter 4, Claridge *et al.* 2001; Vernes 2010). Consequently, through the process of consumption and subsequent defecation of spores at distances removed from the parent source, the species is implicated as a major spore disperser for truffle-like taxa.

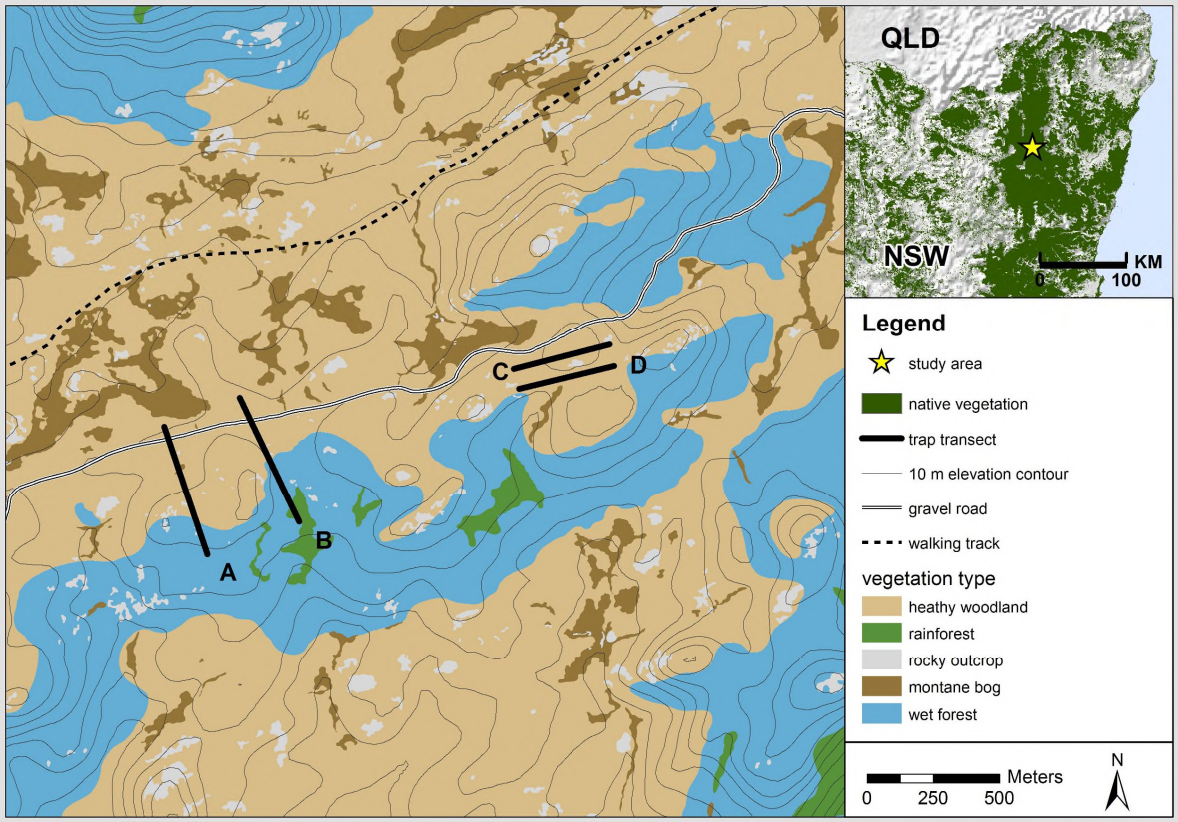


Figure 5.1 Location of the study site in heavily forested wilderness of the New England Tablelands, north-east New South Wales (NSW) (insert). Main window shows location of wallaby trap transects (A-D) and the general study area in which animals were tracked using GPS radio-telemetry. Shown with the distribution of broad vegetation types and elevation contours.

Sampling

Animals were captured using traps designed by the author (A.O.) similar to those previously reported in the literature for the safe trapping of wallabies (Pollock & Montague 1991; Di Stefano *et al.* 2005). Improved features included a more sensitive and safer treadle trigger mechanism, a tapered bag that restricted animal contact with any hard surfaces of the trap, and the ability to very quickly restrain the animal without direct physical contact between the researcher and animal (see Appendix D). There were no trap deaths or injuries to animals during the study. Four transects (350m-500m), each with 6 trap locations (n=24), were established in late 2006 with trapping sessions undertaken between late 2006 to early 2008 (Figure 5.1). Traps were wired open for several weeks prior to trapping sessions and baited with lucerne or apple. Captured animals were weighed, restrained, and subsequently lightly sedated with an intra-muscular injection of 1:1 tiletamine and zolazepam (Zoletil100©-Virbac) at a dosage of 10 mg kg−1 of body weight prior to processing. An intramuscular injection (I.M) of diazepam (Pamlin®) (0.5 mg kg−1) was also given as a skeletal muscle relaxant and when increased sedation was required (Cathy Herbert pers com.). Excess salivation due to this anaesthetic was controlled using a subcutaneous injection of atropine

sulphate (0.04 mg kg−1; see Holz 2005). Vitamin E/Selenium (Selevite-E®) was also administered (0.02 mL kg−1 I.M.) to counter potential deficiencies and reduce the likelihood of post-capture myopathy (Roberts 1997; Miller 2001). Animals were sexed, measured, micro chipped, fitted with GPS/radio-collars or backpacks, and checked for reproductive state and general physical condition. Blood, skin, and tissue samples were also taken. All points of skin breakage caused by processing were sprayed with an antibiotic aerosol (Terramycin® Pfizer Pty Ltd or Cetrigen® Verbac Pty Ltd) prior to release. All animals were protected from the elements during recovery by a blanket and overhead suspended tarpaulin. Animals and the trap area were continually checked at hourly intervals post processing. Only one capture resulted in a post-recovery period of >2hrs with the remainder of animals mobile within 60-90 minutes. No trap deaths or post-capture myopathy was observed. A number of animals were trapped several times over the course of fieldwork and no loss of weight or other signs of stress were observed in these animals.

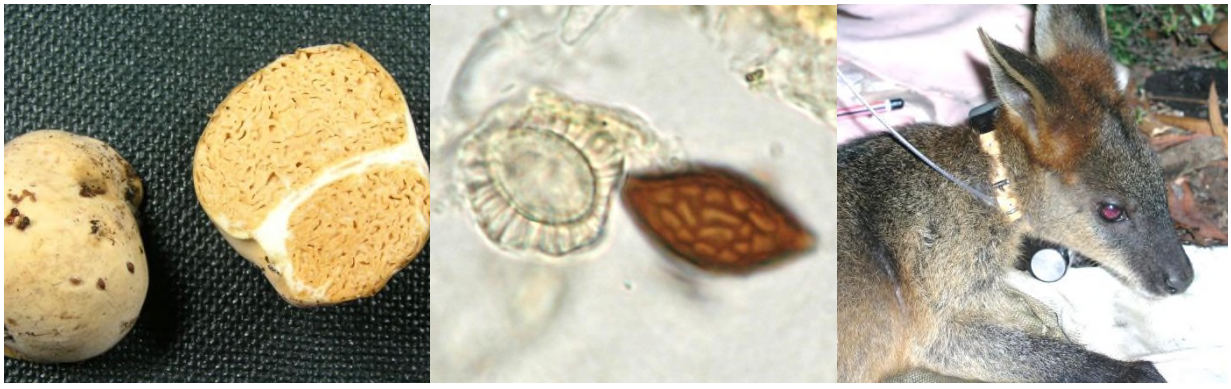


Figure 5.2 A truffle-like fungus sporocarp of an undescribed *Arcangeliella* sp. collected within the study area with the interior spore-bearing chambers exposed (left). The swamp wallaby *Wallabia bicolor* consumes a diverse array of truffle-like taxa which can be observed and identified by spores in their scats (centre). GPS radio-telemetry of swamp wallabies allows fine-scale movements to be recorded and spore dispersal distances estimated (right).

Sirtrack GPS collars and in-house built GPS backpacks (Appendix D) were used in the collection of GPS radio-telemetry data for swamp wallabies. Successful trapping and deployment of GPS collars occurred between early autumn (March) and winter (June). Twenty-eight captures of animals and fourteen deployments of GPS collars or backpacks were made over this time. Nine of these were recovered and found to have successfully recorded movements of swamp wallabies. Animals tracked for more than one week were all fitted with GPS collars. GPS units were programmed to capture high resolution movement data with fixes scheduled at 10 minute intervals. Eighty-eight percent (88%) of scheduled fixes were successful resulting in 15,686 GPS locations across all animals tracked and 13,020 locations for animals tracked more than one week. Mean and median HDOP (horizontal diffusion of position: accuracy estimate) values for fixes (3.4 ± 3.0 SD

and 2.6 respectively) were not greatly dissimilar to that for stationary GPS units (see below), although the reported relationship between HDOP values and true location inaccuracy varies among studies and was not considered robust in the present study. Erroneous outlier fixes were removed from datasets prior to analysis.

To assess GPS accuracy, un-deployed GPS collars and backpacks were positioned at 11 localities within the study area during the period of tracking. Units were positioned at a height above ground approximating swamp wallaby shoulder height. They were located in the three major habitat types of wet sclerophyll, heathy woodland and rainforest. The median centroid of fixes at each locality was used as a surrogate for true location. Mean and median GPS linear error was 20.7m ± 29.3 SD and 13.6m respectively (locality range: 10.5-40.5m). Fifty-percent of fixes had a spatial error of <13.6m, 75% were <24m, 90% <41m and 95% had an error <58m (n=6933). Mean and median HDOP was 2.96 ± 2.09 SD and 2.3 respectively.

Analysis

Activity and seed shadow estimation

An animal's net displacement from a fixed (starting) point in space has been used in the calculation of seed dispersal distances by endozoochorous vertebrates (Murray 1988; Westcott *et al.* 2005). Truffle-like fungi have a very similar dispersal strategy by attracting animals to ingest spore-bearing tissues of their sporocarps which subsequently move to new locations distant from the parent source and egest spore-bearing scats, thereby dispersing spores. Dispersal distances for seeds via endozoochory have been estimated using mechanistic models that incorporate information on an animals' movement behaviour and the time taken for propagules (seeds or spores) to pass through an animals' digestive system ('gut-retention times'). Due to truffle-like fungi employing the same primary mechanisms for dispersal of their spores, these mechanistic models can also be applied to the estimation of spatial patterns of spore deposition (i.e. spore dispersal kernels) and spore dispersal distances (i.e. dispersal curves) generated by mycophagous mammals (see Glossary). A mechanistic model incorporating real movement pathways (net displacement through time) was preferred to re-sampling techniques (Higgins *et al.* 2003; Spiegel & Nathan 2007; Kays *et al.* 2011) as it also allowed spatially explicit, two-dimensional (2D) spore dispersal kernels generated by swamp wallabies to be estimated using the same data as 1D spore-dispersal curves.

Net displacement starting points are analogous to the time at which a fungal spore is ingested by an animal. As such, where different rates of movement are exhibited by animals across the course of a day, the choice of a constant start point in time (i.e. 9 a.m.) for all net displacement series could

severely bias calculations of spore dispersal distance (Westcott & Graham 2000). Consequently, daily activity (movement) patterns were investigated following rationale used in previous studies (Westcott *et al.* 2005; Kays *et al.* 2011) to account for the potential influence on spore dispersal curve estimations. Activity level was inferred from the total net displacement (m) in each hour interval over a 24 hr period.

Spore dispersal distances offered by mycophagous mammals are a combination of animal displacement and gut-retention of spores through time that can be estimated through simple mechanistic models (see (Murray 1988; Higgins *et al.* 2003; Westcott *et al.* 2005). To parameterise the latter function, several commonly used PDFs (weibull, gamma, gaussian, and lognormal; Will & Tackenberg 2008; Rawsthorne, Roshier, & Murphy 2009; Koike *et al.* 2011; D'hondt & Hoffmann 2011; Guttal *et al.* 2011) to characterise gut-passage curves were fitted to previously published gut-retention time data (using truffle-like fungal spores) reported for swamp wallabies (Danks 2012). Maximum likelihood estimation methods were used to fit gamma distributions to the data, while goodness-of-fit was assessed using the Kolmogorov-Smirnov (KS) test (Soons & Bullock 2008). A weibull distribution provided a good fit to published retention times of truffle-like fungal spores (Danks 2012) reported for both a 10 kg (mean= 41.2 ± 13.8 SD; α=3.24 β=46.04; KS: D=0.274, P>0.05) and a 21 kg male swamp wallaby (mean=26.9 (±13.9 SD); α=2.04, β=30.44; Kolmogorov-Smirnov D=0.233, P>0.05). The two reported retention-time series were combined and assessed for goodness-of-fit to the distributions above in order to attain a single continuous measure of retention to use in a spore dispersal model. All distributions provided a good fit to data although the gaussian and weibull were the highest ranked respectively (Gaussian: D=0.165, P=0.435; Weibull: D= 0.167, P=0.415). The latter was chosen as a final distribution to parameterise gut-retention of spores as it: i) provided a good fit to individual retention times, ii) gave an intermediate estimate for first-passage of spores, and iii) did not greatly overestimate maximum gut-passage time.

4970 unique displacement distances (events) were sampled from movement data and used to calculate the probability of spore dispersal within an estimated maximum gut-passage time period (70 hrs.) using simple mechanistic models. Net displacement to the first fix over a maximum gut passage period of 70 hours was calculated for each animal (Higgins *et al.* 2003). A 70 hr period was based on a maximum gut-passage of 69 hours reported by (Danks 2012) with an additional hour added to ensure the probability of deposition would be 0 at hour 70. Start points for net displacement series were stratified by quarter-day periods to account for potential variation in movement across a 24 hr period (Westcott *et al.* 2005; Kays *et al.* 2011), resulting in an even number of start points within each quarter period. Final start points were randomly selected within these time periods using a function in Geospatial Modelling Environment v0.6.2.0 (Beyer 2012).

Ten displacement series were calculated for each of seven animals and a single displacement series from one additional animal tracked (n=71). For each time series, net displacement from the start point were estimated for each subsequent fix using euclidean distance (straight-line) following Westcott *et al.* (2005). The maximum displacement within each hour interval was selected to ensure that infrequent longer-distance movements facilitating important LDD events would be detected (Higgins *et al.* 2003; Nathan *et al.* 2008). Frequency of displacement in each distance interval (50 m) from movement start points within each hour interval (1-70) was used to estimate the probability of displacement in each distance x hour category. These values were multiplied by the weibull PDF of gut-retention times following a method similar to other previous mechanistic models for estimating 1D seed dispersal kernels via animal endozoochory (see Murray 1988; Holbrook & Smith 2000; Westcott *et al.* 2005).

Four frequency distributions (weibull, gamma, gaussian, and lognormal) were fit to resulting histograms of spore dispersal distances (i.e. 1D spore dispersal curves) calculated for the entire 1D model and for each individual animal using a simple mechanistic model. Goodness-of-fit to each distribution was assessed using a Kolmogorov-Smirnov test to determine the best descriptor of the shape and scale of spore dispersal kernels generated by swamp wallabies. Maximum likelihood estimates were made using 1000 iterations, equal probability, and unknown lower and upper domain bounds. The KS test was also used to test for significant differences among seed dispersal curves generated by individual animals (Russo *et al.* 2006).

Two-dimensional (2D) mechanistic models of spore kernels generated by swamp wallabies were constructed from the same displacement series as used for estimating the spore dispersal curve. The estimated probability of spore gut-retention over a 70 hr period was assigned to displacement series resulting in each relocation having a probability of spore deposition. To match gut-retention times to movement series in the calculation of 2D models of spore dispersal it was necessary to estimate the location of missing GPS fixes in radio-telemetry movement data. Animal location was estimated as randomly placed points along a line based on the euclidean distance between bounding successful GPS fixes. Spatial autocorrelation was reduced by displacing points randomly within a 25m distance of this line. The probability of spore deposition in 2D space was calculated as the sum probability assigned to all relocations in each 25m x 25 m cell of a grid defined by the extent of all inputs (points) plus a 200m boundary buffer. For the 2D spore kernels produced by individual animals, resulting grids were converted to point data and a kernel density estimate (KDE) applied using the squared cross validation (SCV) smoothing function for illustration purposes. This process produced a smoothed density surface representing the probability of spore deposition and allowed the visual interpretation of general spatial trends.

Using the methods above, two different spatial patterns of spore deposition were estimated for

individual animals. The first was the summed probability of all individual dispersal events (i.e. displacement time series) that had start points (n=10) stratified evenly across four 6 hr. time intervals within a 24 hr. day and randomly positioned within each interval. This model was an attempt to simulate patterns in spore deposition generated by swamp wallabies if fungal spores were ingested at starting points, each representing a hypothetical fungal sporocarp and collectively a population of discrete fungal units producing sporocarps. The second model used the same spore kernels generated from individual (70hr) displacement series (Figure 5.7: column A) but shifted in space to a shared (common), arbitrarily assigned, starting (i.e. consumption) point and subsequently averaged.

A final 2D map of spore deposition by the swamp wallaby was also estimated as a spatially explicit equivalent of the 1D spore-dispersal curve estimated for the species. This was calculated by summing and then averaging across all individual spore kernels (n=71) that were first shifted to a common start point in space, to derive an average probability for spore deposition in each 25m x 25m cell. Note that the original probability grids were used, not the smoothed kernels generated for illustration purposes (i.e. Figure 5.7). For spatial analysis, spore kernels and KDE100 (100% kernel density estimate representing animal space use) rasters were aggregated (summed) to a 50m x 50m cell size grid to account for locational error, reduce autocorrelation, and to allow analysis in one software program (SADIEShell v1.22; Conrad 2001) which had computational limits. A detailed map of vegetation was compiled using aerial photos of the study site, previous remote sensing vegetation mapping for the study area (Ecological Australia 2005; DECCW 2010), a digital elevation model (e.g. to derive aspect, elevation contours, and slope), and ground-truthing.

Spatial analysis

Major trends in the spatial structure of estimated spore kernels and relationship to space utilisation by swamp wallabies were explored following methods similar to those employed by García *et al.* (2012). The degree of spatial aggregation in spore deposition was quantified using spatial analysis by distance indices (SADIE)(Perry *et al.* 2002). A global measure of aggregation (*Ia*) was calculated for each 2D spore kernel where a value of 1=random, <1=dispersed, and >1=aggregated. Clustering index (υ) vectors were used to quantify high and low density clusters in both spore kernels and estimated space use by individual swamp wallabies (unweighted 100% kernel density estimates aggregated to a 50 m x 50 m cell size). The relationship between these two variables was tested using simultaneous autoregressive models (SAR) to account for the spatial non-independence of data and high level of autocorrelation in most spatial data. The SAR model produces coefficients that account for each location being a function of both the i) explanatory variable and the ii) values in neighbouring locations (Tognelli & Kelt 2004). The spatial structure

of spore deposition by the swamp wallaby estimated by the 2D model was quantified using a spatial autocorrelation analysis (Moran's I coefficient) which describes the global level of correlation in the data with increasing distance between points. Coefficients vary from +1 suggesting positive correlation (clustering) to -1 reflecting negative correlation (dispersion), with values close to 0 equating to spatial independence (random).

Spore dispersal across habitat boundaries was estimated from daily incidence of boundary crossings by swamp wallabies in which the animal spent at least one hour in each of the pair of habitats in question prior and preceding a habitat crossing. An average daily probability of a habitat crossing occurring was calculated as the number of days in which a crossing occurred divided by the total number of tracking days used in calculations, with the subsequent values averaged across all individuals. This probability was also weighted according to relative availability of each habitat pair (habitat 1 x habitat 2) within each animals home range to estimate the daily likelihood of spore dispersal occurring across pairs of habitats unbiased by habitat availability. The area of available habitat was calculated as the total area of each habitat type within the MCP (minimum convex polygon) home range estimate calculated for each individual animal (Kenward 2001; Hayward *et al.* 2004). These calculations were made to investigate i) whether spore dispersal across habitat boundaries were likely to occur, ii) the potential direction of spore dispersal events and iii) whether directed dispersal to amenable habitats for establishment may be facilitated by swamp wallabies.

Spatially-explicit analysis was undertaken in the freeware software SAM v4.0 (Spatial Analysis in Macroecology; Rangel, Diniz-Filho, & Bini 2010) and SADIEShell v1.22 (Perry *et al.* 1996; Conrad *et al.* 2006) and all other statistical analysis in R v2.15.0 (R Development Core Team 2012). Generic spatial data analysis and mapping was undertaken using Quantum GIS v1.7.0 (http://www.qgis.org/), ESRI ArcGIS (ESRI 2011), Geospatial Modelling Environment (http://www.spatialecology.com/gme/; Beyer 2012), and LandSerf v2.3 (http://www.soi.city.ac.uk/≈jwo/landserf/; Wood 2009).

Results

Daily activity patterns

Mean hourly rate of movement across all animals over a 24 hr period was 65 m (±SD 93 m; n=2651). A frequency distribution of hourly movement distances was strongly leptokurtic with a long narrow tail. Movements of ≤21 m occurred in 25% of hourly intervals, ≤40 m in 50%, ≤76 m in 75%, ≤132 m in 90%, ≤193 m in 95%, and ≤1696 m in 100%. There was a significant difference among hours in average movement rate per hour (Kruskal-Wallis: χ_2=273.5211, df=23, P<0.0001; Figure 5.3A). With day divided into four 6 hour periods there was also a significant difference in average movement rate (Kruskal-Wallis: χ_2= 169.5053, df=3, p-value<0.0001; Figure 5.3B). Pair-wise comparisons showed all time periods to be significantly different (P<0.01) although the two morning quarter periods were most similar (P=0.006). Afternoon movement rates were significantly (P<0.0001) lower and evening rates significantly (P<0.001) higher than other time periods. These results justified the use of stratified start points in different day periods for estimating displacement series and in calculating spore-dispersal curves.

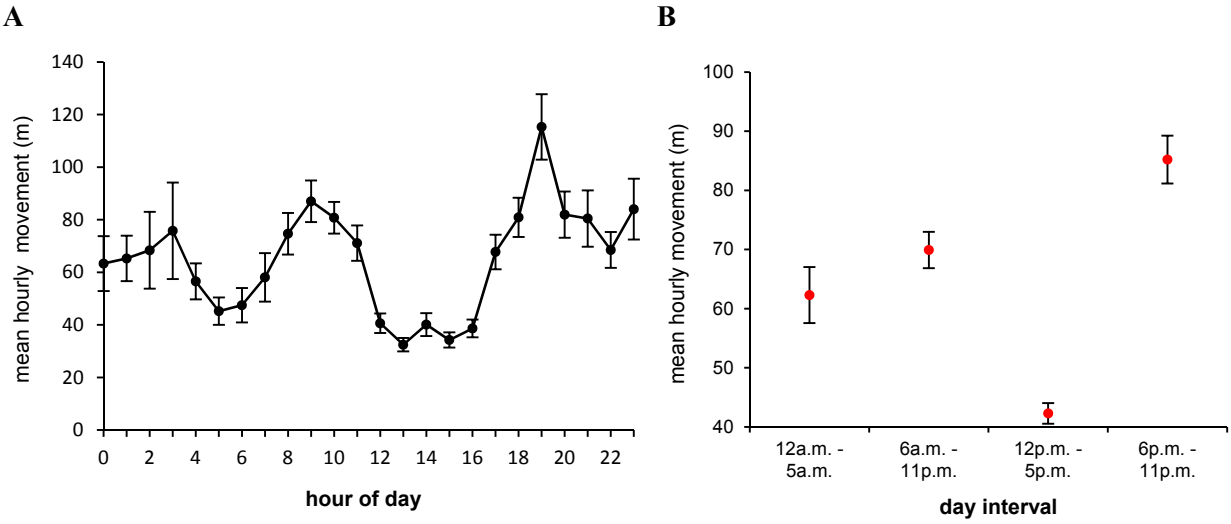


Figure 5.3 Average (±SE) hourly movement across all swamp wallaby *Wallabia bicolor* individuals at A) hourly and B) six-hour intervals over a 24-hour day period.

Home range

Home range estimates varied greatly among individual animals and appeared independent of the length of period tracked (33-383 ha; Table 5.1). Differences among individuals in home range size were considerably less when estimated using kernel density estimates (KDE95 and KDE75). Core use area (i.e. KDE50) did not correspond consistently with home range size or tracking period

length, and was more consistent across individuals than home range estimates. Home range size and core use area estimates showed animals ranged over very large areas within a relatively short period of time (9-21 days) but concentrated their activity in comparatively small areas that were a fraction of their entire foraging area (1.5-15.2%).

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).

				Home range and core use area (hectares)			
Animal	Sex	Days	# data points	MCP100	KDE95	KDE75	KDE50
00E1	F	9	1344	383	48	17	7
09E6	F	16	2316	95	31	16	8
25AD	M	21	3114	100	49	22	10
2771	F	14	2081	52	24	13	7
FC20	M	19	2765	128	39	19	9
SCTM	M	21	3121	33	18	10	5
Total	-	100	14741	-	-	-	-

Displacement

Peak average cumulative displacement over a 70 hr period occurred at approximately 20 hrs, followed by a decline and a plateau with a slight positive slope up to hour 70 (Figure 5.4). Displacements above a threshold of approximately 650 m were rare, indicative of home ranging behaviour and an upper threshold considering all animals. Rare, longer-distance displacements did occur and were of considerable magnitude (>1000 m), many times that of average displacement.

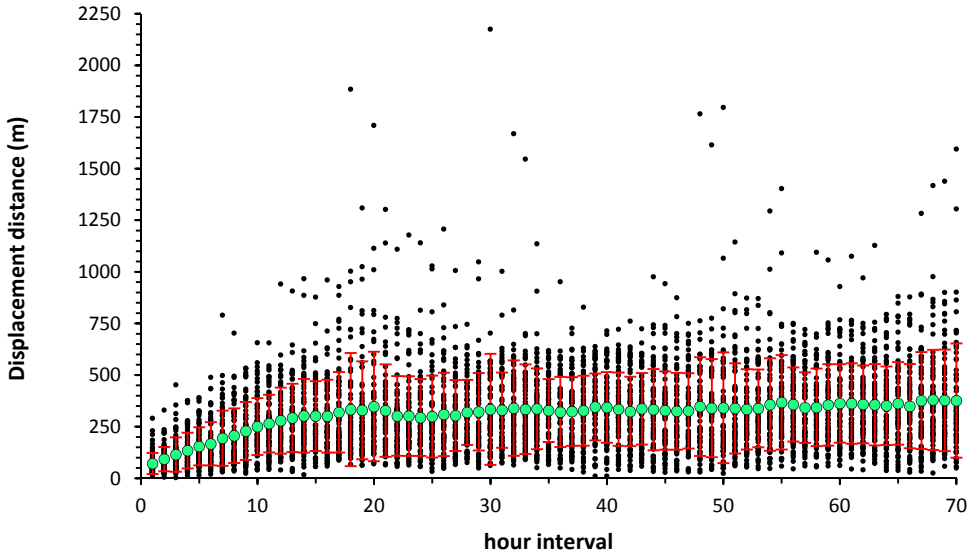


Figure 5.4 Observed cumulative displacement distances (m) for each hour interval over a 70 hr. period using all time series (n=71). Shown with average (green circles) cumulative displacement distance ± SD (red vertical bars) across time series for each hour interval up to a maximum gut-passage time (69 hrs) plus one hour (i.e. 70 hrs).

Maximum displacement distance over a 70 hr. period showed considerable variation among individuals (613-2175 m), and was higher in females (789-2175 m) than males (612-1179 m). Across all animals, mean and median displacement was 312m (± 203 SD) and 278 m respectively. Mean displacement differed significantly among individuals (χ^2=414.7, P<0.0001; range: 241-397 m) and by sex (χ^2=10.1, P=0.0015) with females having a greater average displacement (n=2840, 322 m ± 214 SD) than males (n=2130, 300 m ± 186). The greatest number (n=18) of outlier displacements in an individual - indicative of rare longer distance movement events - was for a female swamp wallaby ('00E1') which had movements ranging from 1000-2175 m and largely associated with three discrete periods of rapid movement outside the animal's home range (KDE95), each lasting between 1 and ≈8 hours interspersed with slower rates of movement. Of four discrete, long-distance, and rapid movement events exhibited by animal 09E6 outside its home range (KDE95), two followed similar routes within the landscape.

The median maximum displacement distance across all time series (n=71) was 622 m (range 308-2175 m). Within this 70 hr time period, 20% of displacement series recorded a maximum displacement of >1000 m. Longer-distance movement events were rare however, with only 0.8% (n=4970) of displacements used in the calculating the average displacement curve being >1000 m.

Spore Dispersal

The calculation of spore-dispersal curves and two-dimensional (2D) spore kernels used 4970

unique displacement distances (events) derived from high resolution GPS telemetry of seven animals. A one-dimensional spore dispersal curve estimated using a mechanistic model predicted spores to have a 0.92 cumulative probability of being dispersed >100 m, 0.59 of >250 m, 0.16 of >500 m, and >0.01 probability of being dispersed greater than 1000 m away from the parent fungi (Figure 5.5). The probability density function (PDF) of wallaby displacement tracked closely with the simulated spore-dispersal curve for the swamp wallaby (Figure 5.5). The best fit to the spore-dispersal curve was given by a gamma distribution (Table 5.2).

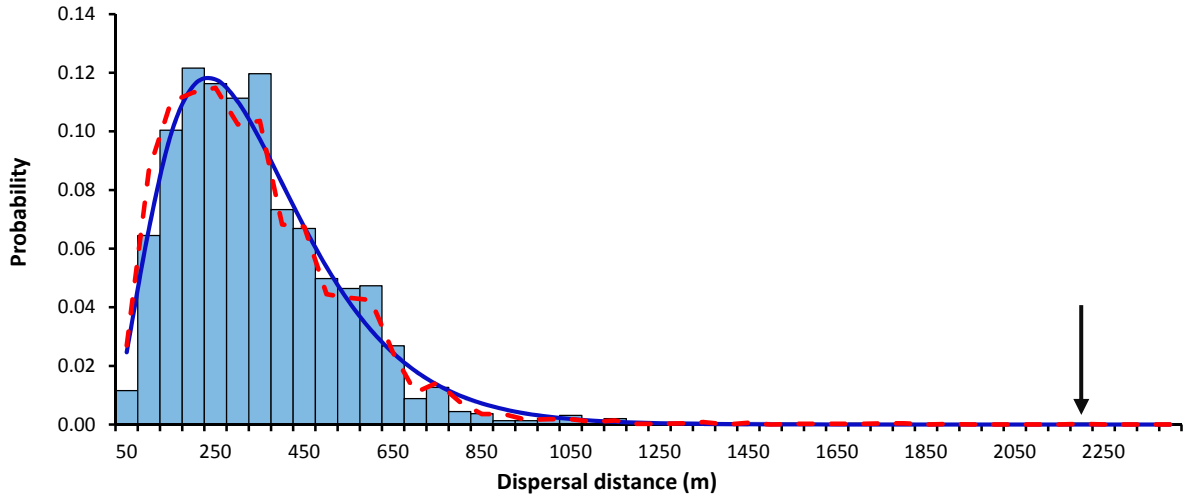


Figure 5.5 Estimated 1D spore-dispersal curve (distance distribution) generated by swamp wallaby *Wallabia bicolor* zoochory using all displacement series (n=71) and a 70 hr maximum gut-passage time. Shown with the PDF (probability density function) for net animal displacement (red dashed line) and the best-fit gamma distribution to the dispersal curve (blue line). Arrow denotes the greatest dispersal distance interval.

Similarly, a gamma distribution provided the best fit to individual animal spore-dispersal curves (Figure 5.6). Across animals, mean spore-dispersal ranged from 169-449 m and the median from 150-400 m. Individual-animal 1D dispersal curves had peaks ranging from 186-252 m. Average standard deviation, skewness, and excess kurtosis of fitted gamma curves were greatest in animal 00E1 and lowest in SCTM (Table 5.2). Dispersal curves estimated for males and females respectively, based on an average across animals, did not differ significantly (D=0.2, permutation test P=0.10). Similarly, there was no significant difference between averaged dispersal curves calculated for each sex (D=0.25, P=0.06). Incorporating gut passage had little influence on the model, as suggested by non-significant difference between PDFs estimated for displacement distance and spore-dispersal (D=0.229, permutation test P=0.094). However, dispersal curves generated by animals 09E6, 2771, and SCTM were significantly (P<0.01) different from those of 25AD, FC20, and 00E1 using Kolmogorov-Smirnov permutation tests. The latter animals

generated fatter-tailed kernels with greater excess kurtosis, suggesting a higher probability of longer-distance dispersal for fungal spores (Nathan *et al.* 2008; Guttal *et al.* 2011).

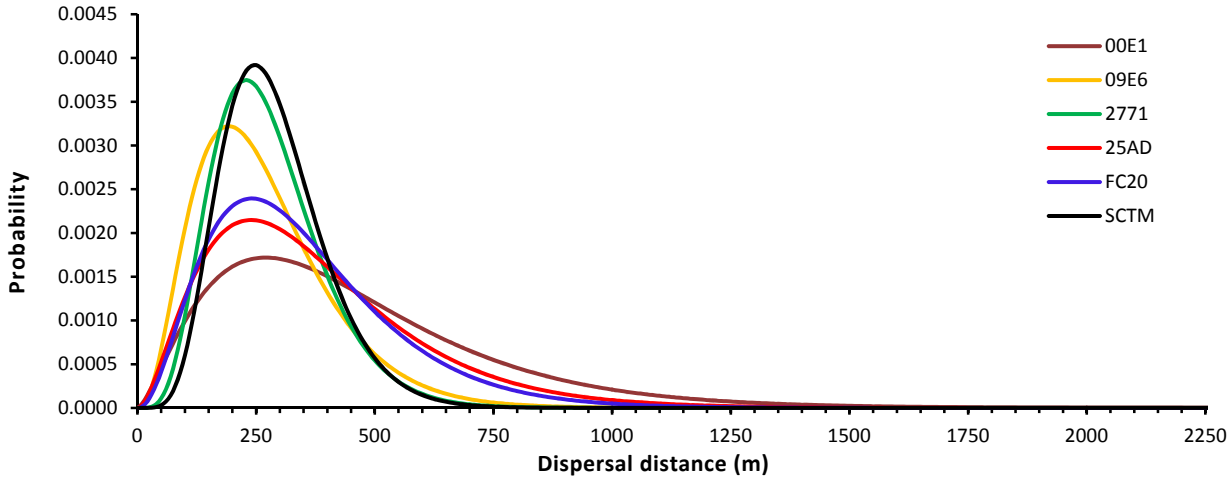


Figure 5.6 Best-fitting gamma distribution to spore-dispersal curves (distance distributions) calculated for each of six swamp wallaby *Wallabia bicolor* individuals using a simple mechanistic model. Line colour denote different animals (brown=00E1, yellow=09E6, green=2771, red=25AD, blue=FC20, black-SCTM).

Table 5.2 Statistics for spore-dispersal curves via swamp wallaby *Wallabia bicolor* zoochory and fitted gamma distributions. A lower Kolmogorov–Smirnov (KS) *D* statistic indicates less difference between the estimated kernel and the fitted gamma distribution. All *D* statistics were non-significant (*P*>0.05)

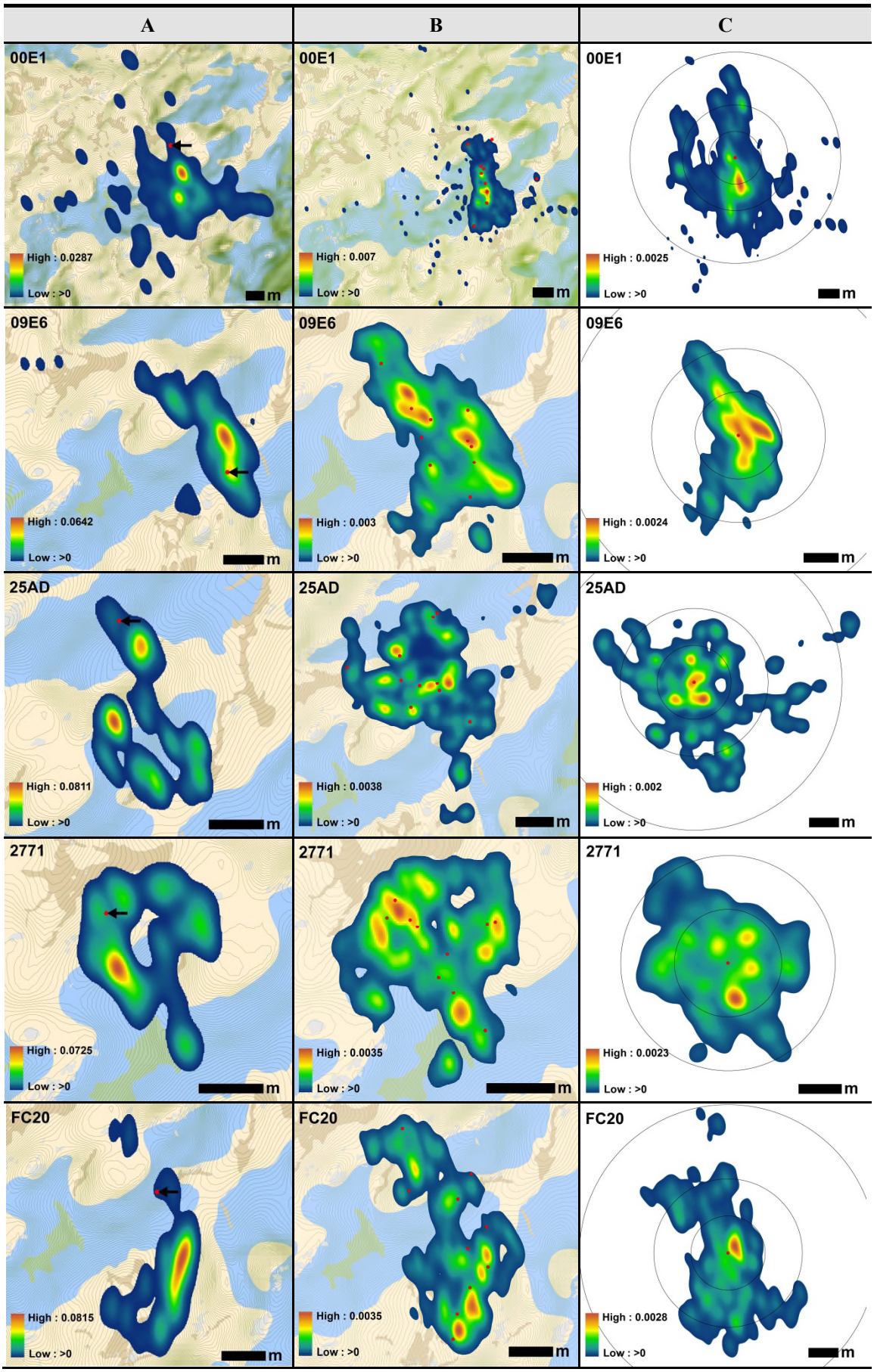
Model	Mean ± SD	Skewness	Excess Kurtosis	Shape α	Scale β	KS *D* statistic
Full 1D Model	346 (±197)	1.91	9.09	3.08	112.45	0.071
00E1	449 (±284)	2.35	8.99	2.51	178.97	0.103
09E6	267 (±141)	1.45	4.72	3.58	74.69	0.093
25AD	371 (±221)	1.12	1.33	2.82	131.58	0.083
2771	277 (±115)	0.78	1.02	5.78	47.83	0.110
FC20	348 (±193)	0.67	0.26	3.25	107.1	0.120
SCTM	288 (±108)	0.38	0.14	7.06	40.79	0.121

Visual inspection of simulated spore kernels generated from a single dispersal events (i.e. over a 70 hr. gut-passage time) estimated peak spore deposition to often occur at considerable distance (>100 m) from the parent source and be non-uniform in space (Figure 5.7: column A). Similarly, a simulated spore-dispersion pattern generated by wallabies for ten hypothetical truffle-like fungi 'parent' sporocarps (the 'starts' points in smoothed data version illustrated in Figure 5.7: column B)

was strongly spatially autocorrelated (global Moran I=0.912-0.948; Z=220.72, $P<0.001$) suggesting an overall clustered pattern in spore deposition. When probabilities were summed using a 50 m grid cell size (0.25 ha), spore density was found to be significantly aggregated in space (Table 5.3: '*la*' values) and also strongly correlated with each animals use of space (Table 5.3: SAR results). Spore deposition was also largely constrained within the animals home range (MCP100 and KDE95; not shown).

These patterns were largely maintained in a simulated 2D spore kernels for individual animals (Figure 5.7: column C) which were highly anisotropic and multi-modal. At least for half the animals, peak spore density was not centred on the parent source and consisted of multiple modes in two-dimensional space (i.e. an aggregated spatial pattern). Considerable differences among individual animals in the shape and scale of 2D spore kernels were also apparent, although largely conforming to expectations based on 1D spore-dispersal curves. In contrast to spore-dispersal curves, most animals generated nodes of high spore density well within 250 m of the hypothetical parent source.

There was considerable variation among individual animals in the scale of spore dispersal, notably for animal '00E1' where several long-distance movement events resulted in high dispersion of spore densities and considerably larger 95% isopleth estimates than other animals. Interestingly, single dispersal events were in some cases at a similar spatial scale as estimated 2D spore kernels. Spore deposition occurred across multiple vegetation communities, with many individual simulated dispersal events predicting dispersal of spores between discrete areas supporting the same vegetation type.


A
B
C
00E1
High : 0.0287
Low : >0
m
00E1
High : 0.007
Low : >0
m
00E1
High : 0.0025
Low : >0
m
09E6
High : 0.0642
Low : >0
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09E6
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09E6
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25AD
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2771
High : 0.0035
Low : >0
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2771
High : 0.0023
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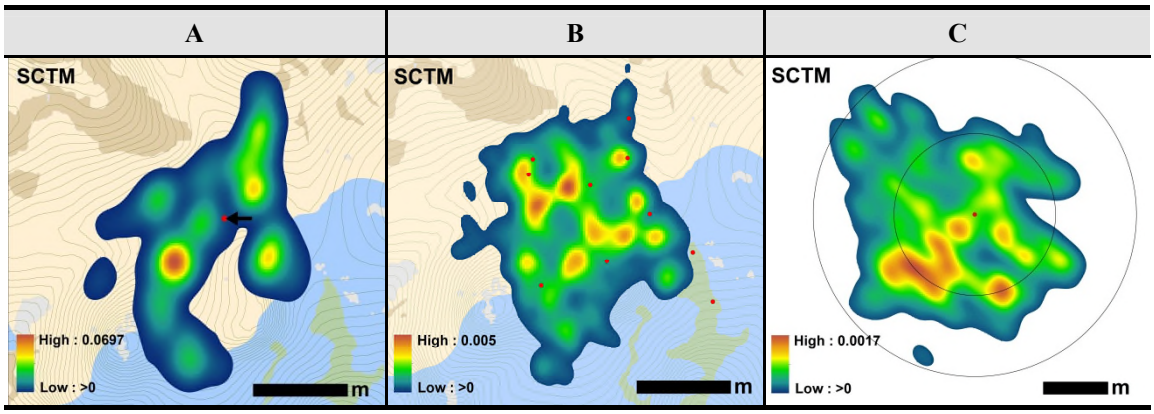

Figure 5.7 Spatial patterns in the probability of spore deposition by individual swamp wallabies *Wallabia bicolor* including examples of spore dispersal kernels generated by a single dispersal event (column A), average probability of deposition from 10 different hypothetical conspecific parent sources (column B), and simulated 2D spore density kernels (column C) calculated for each animal. Data was clipped to calculated 95% isopleths and was calculated from real 2D movement pathways of swamp wallabies recorded using GPS telemetry (10 min fix interval). Colour ramps represent the calculated probability of spore deposition after smoothing (SCV). Red dots indicate location(s) of start points (the proxy for parent source) for sampled movement series used to generate kernels. Maps in columns A and B are shown with vegetation type (blue=wet sclerophyll; beige=heathy woodland; green=rainforest; brown=montane bog; grey=granite outcrop). All maps shown with 200 m scale bar and column C figures with distance intervals of 250 m, 500 m, and 1000 m from the parent source.

Table 5.3 Spatial analysis results including SADIE aggregation index (Ia) 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*.

		SADIE	SAR (υ)			
Animal	n	*Ia*	r^2	*F*-value	SAR Coeff	t
00E1	360	3.22***	0.834***	1799.1	0.88 ± 0.03	33.68**
09E6	399	3.25***	0.864***	2518.0	0.87 ± 0.03	27.99**
25AD	475	4.15***	0.802***	1915.3	0.77 ± 0.03	25.71**
2771	224	2.89***	0.915***	2376.3	0.94 ± 0.04	25.72**
FC20	450	2.92***	0.882***	3364.1	0.84 ± 0.02	33.44**
SCTM	117	2.49***	0.846***	630.6	0.79 ± 0.06	13.11**

**P<0.001 ***P<0.0001

A simulated kernel of truffle-like fungal spores dispersed by swamp wallabies (Figure 5.8) exhibited a high level of anisotropy and spatial aggregation. Peaks in the probability of spore deposition occurred at considerable distance (>250 m) from the parent source. Rare dispersal events of considerable distance (>1000 m) were predicted, radiating outwards along a number of axis from the parent fungal source. The predicted spore kernel was elliptical in shape and there was a steep decline at ≈600 m corresponding to the 1D spore dispersal curve model. Similarly, peak spore deposition was not centred at the parent location (grey vertical bar in Figure 5.8) but rather at multiple modes within ≈250 m of the simulated fungal parent source. Nonetheless, the probability of deposition within close proximity (i.e. 50 m) of the parent source was predicted to be much higher than estimated by a 1D model (Figure 5.5). A correlogram (not shown) for the kernel exhibited a "single bump" pattern (Legendre and Fortin 1989) as has been reported for wind-dispersed seeds (Nathan *et al.* 2000), with a significant (P<0.05) positive autocorrelation in the nearest distance classes (0-450 m), significant (P<0.05) negative autocorrelation (dispersion) in intermediate distance classes (≈520-1400 m), and low positive autocorrelation at the furthest distance classes.

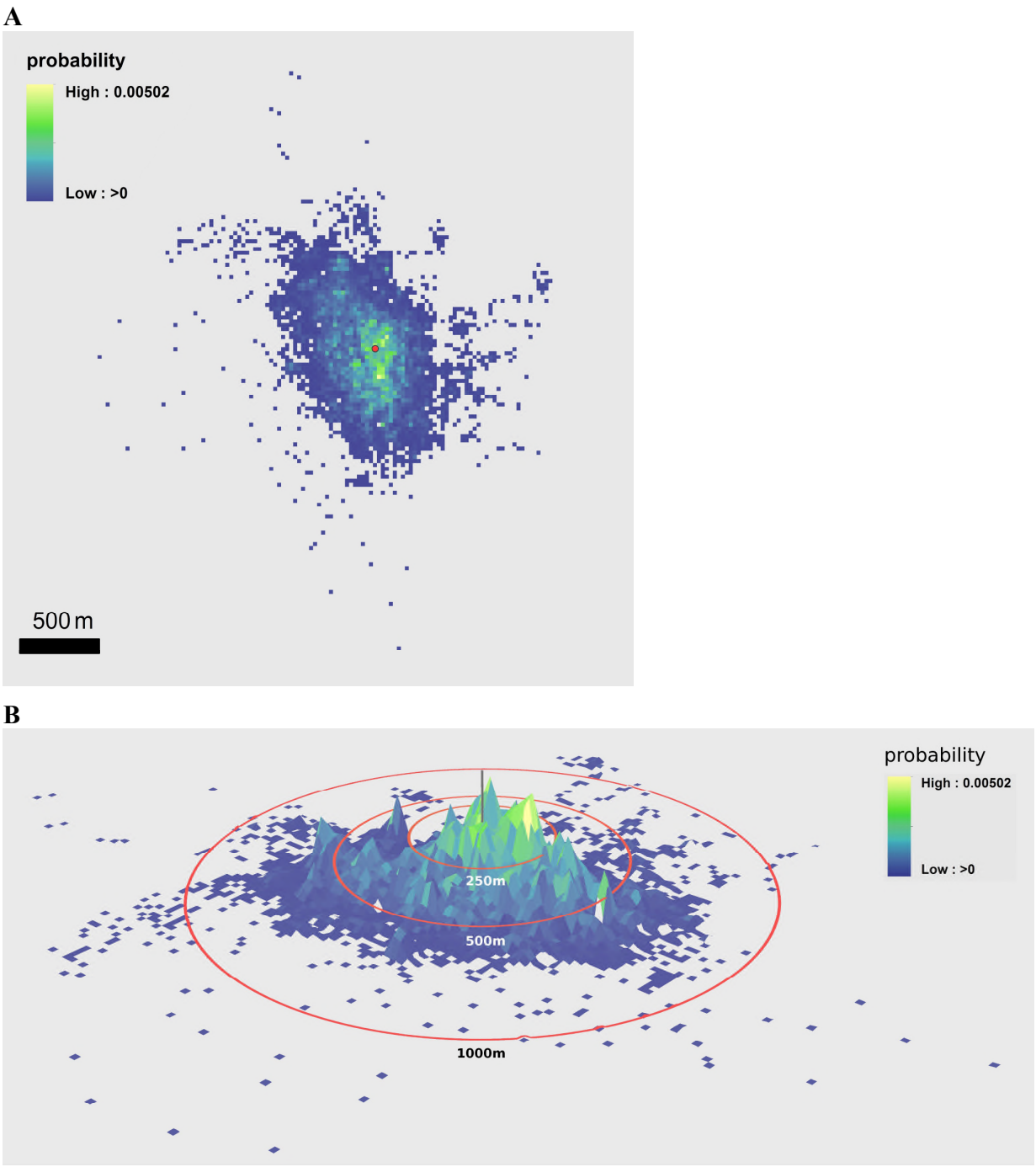

Figure 5.8 Estimated spatially explicit map of spore deposition (spore kernel) generated by the swamp wallaby *Wallabia bicolor* based on 2D high resolution GPS movement data (fix rate=10 minutes) and gut-passage rates reported in the literature (Danks 2012). Shown in 2D (top graphic) and 3D perspective (bottom graphic) using probability of spore deposition as a Z-value. The hypothetical truffle-like fungi 'parent' source is shown as a grey vertical bar (3D representation) or red dot (2D). The probability of spore deposition was calculated using a 25 m x 25 m grid cell size with all cell values summing to 1.

Movements across habitat boundaries

Movement across habitat boundaries by swamp wallabies was a relatively common occurrence over a 24-hour period for the two most abundant habitat types (wet sclerophyll and heathy woodland; Table 5.4). The average daily habitat crossings differed among habitat type pairs. When relative availability was considered, calculated values were more similar across pairings. However, movements from habitats supporting truffle-like fungi to those considered likely to be unamenable for establishment (i.e. non-habitats) were less frequent suggesting the potential for directed spore dispersal by swamp wallabies. There was no significant differences between sexes (Table 5.4) or individuals (Kruskal-Wallis: P=0.121-0.574) in the daily frequency of boundary crossings among habitat pairs suggesting similar movement behaviours among sexes and individuals.

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).

				Relative availability	
habitats	Female (n=50)	Male (n=63)	*P*-value	Female	Male
heathy woodland → wet sclerophyll	0.68 ± 0.11	0.51 ± 0.08	0.253	3.81	2.57
heathy woodland → rainforest	none	none	-	-	-
heathy woodland → non-habitat	0.16 ± 0.07	0.14 ± 0.05	0.952	4.06	4.23
wet sclerophyll → heathy woodland	0.84 ± 0.11	0.59 ± 0.08	0.077	4.71	2.97
wet sclerophyll → rainforest	0.04 ± 0.03	0.02 ± 0.02	0.430	3.70	1.87
wet sclerophyll → non-habitat	0.02 ± 0.02	0.03 ± 0.02	0.701	0.83	1.41
rainforest → heathy woodland	none	none	-	-	-
rainforest → wet sclerophyll	0.02 ± 0.02	none	0.262	1.85	-
rainforest → non-habitat	none	none	-	-	-

Discussion

The majority of truffle-like fungi are explicitly adapted to endozoochorous dispersal by mycophagous mammals, largely dependent on the consumption and subsequent dispersal of their spores to new locations removed from the parent fungi. Numerous mammals play a role in this process with at least 11 species contributing within the study area. Macropods are likely to play an important role for long-distance dispersal (LDD) which has been shown to be a major process in plant biogeography and population demographics (Clark *et al.* 1998; Nathan *et al.* 2008) and likely to be similarly important in truffle-like taxa due to the shared dispersal mechanisms involved.

In this chapter I estimated fungal spore dispersal curves (distance distribution) generated by swamp wallaby mycophagy using a simple mechanistic model. The spatial pattern of spore deposition was further explored through the estimation of 2D spore kernels for fungal spores dispersed by the swamp wallaby and individual animals, making these estimations spatially explicit. For individual animals, spatial patterns in spore deposition generated from mycophagous consumption of truffles at ten random locations was also estimated to depict a composite seed shadow of multiple parent fungi located within each animal's home range. At the time of writing, there were no equivalent published studies of spore dispersal kernels generated by a mycophagous mammal. To my knowledge, this is also the first study that applies methods developed in the field of seed ecology to describe endozoochorous spore dispersal for truffle-like fungi using mechanistic models. It is also among a small number of studies worldwide that have attempted to predict and describe two-dimensional kernels for either spores or seeds generated by endozoochory (Russo *et al.* 2006; Santamaría *et al.* 2007; Ward & Paton 2007; Kays *et al.* 2011).

Daily activity patterns

Activity levels in the swamp wallaby varied significantly throughout the course of a day. Animals exhibited a much lower rate of movement after midday which continued steadily until late afternoon (≈4 p.m.) when a higher rate of movement commenced, peaking between 6 p.m. and 8 p.m. and continuing until ≈3 a.m. Another peak in activity level occurred in the morning daylight hours (7 a.m. to 11 a.m.). Midday to late afternoon can be generally associated with higher temperatures and light levels over the diel cycle (i.e. 24 hr period). A trough in activity level was also observed between 3 a.m. and 8 a.m., generally corresponding with the coolest part of a diel cycle. Results suggest crepuscular behaviour and a bimodal activity pattern in the swamp wallaby, possibly as an anti-predator adaptation to their main predator (the native dingo *Canis lupus* subsp. *dingo*) which was well represented in the park (A.O. pers obs.). These patterns are in general agreement with previous studies that have observed different activity patterns over a diel cycle in

macropod species (Vernes *et al.* 1995; Stirrat 2004), including the swamp wallaby (Di Stefano 2007).

Patterns in daily activity have important implications for spore dispersal by the swamp wallaby and its estimation. Due to activity levels exhibiting an obvious temporal pattern within a 24 hr period, the time of day which the animal consumes a spore-bearing sporocarp could influence the distance and location spores may be dispersed to (Westcott *et al.* 2005; Russo *et al.* 2006; Kays *et al.* 2011; Hirsch *et al.* 2012). Therefore, the use of stratified start points for displacement series following Westcott *et al.* (2005) are justified in the current models. Also, temporal weighting of dispersal events should be applied in any future simulation or mechanistic models – that use resampling techniques to draw displacement distances and gut-retention times – for the species (Higgins *et al.* 2003; Spiegel & Nathan 2007).

Movement and home range

Hourly movement rates were generally low with 50% <40 m and the majority (95%) <200 m in scale. However, infrequent movements near an order of magnitude greater did occur in 5% of cases. This equates to a displacement curve with high leptokurtosis in low distance classes and a long narrow tail, suggestive of different classes of movement behaviour including rare and rapid longer-distance movements.

Home range estimates for swamp wallabies using fine-scale high resolution GPS telemetry illustrates the large areas animals range over within relatively short periods of time (9-21 days). General patterns of space use included relatively large amounts of time spent in small (core use) areas compared to their larger home range (MCP100). Each animal had several core use (KDE50) areas suggesting any ingested spores would have a higher probability of dispersal to these areas relative to the surrounding landscape. These results suggest spores could be dispersed over very large areas but are likely to be aggregated in space due to activity (time) being concentrated in comparatively much smaller areas.

Home ranging behaviour was suggested by average cumulative displacement reaching a plateau within only 20 hrs. Longer-distance movements were rare and were on average <650m in scale although further distances of >1000 m were recorded. The scale of movements varied greatly amongst animals and longer distance movement only rarely observed and characterised by rapid movement over relatively short periods of time (<2 hrs) before the animal returned to within its normal foraging range (KDE95). Estimates of home range were markedly greater than those predicted by Troy & Coulson (1993) but highly similar to those estimated by Di Stefano (2007) using conventional radio-telemetry techniques - average KDE95 of 34.8 ha in this study versus 31.1 ha in the latter.

Spore dispersal

This study shows that swamp wallabies may be important dispersers for truffle-like fungi. Most spores were predicted to be dispersed >100 m from the parent fungi and many >250 m from the source. There was a long thin tail to the dispersal curve resulting in scattered dispersal to distances greater than 250 m and rare long distance dispersal (LDD) to locations >1000 m. No comparative studies of endozoochorous spore dispersal have been undertaken but the similarity of underlying mechanisms allows comparisons to seed dispersal systems. Predicted dispersal distances are broadly similar to those produced for seed producing plants by frugivorous seed-dispersing mammals (Russo *et al.* 2006; Chapman & Russo 2007; McConkey & Chivers 2007) and some larger-ranging frugivorous bird species (Holbrook & Smith 2000; Westcott *et al.* 2005; Kays *et al.* 2011) but less than those predicted by some ruminant ungulates (Vellend *et al.* 2003; Will & Tackenberg 2008). Both the shape and scale of estimated 1D spore dispersal curves were similar to those estimated for larger-ranging frugivorous birds and mammals which exhibit high leptokurtosis, uni-modal distributions, and with most spores predicted to be dispersed >100 m away and potential LDD events of >1000m (Holbrook & Smith 2000; Wehncke *et al.* 2003; Westcott *et al.* 2005; McConkey & Chivers 2007; Spiegel & Nathan 2007). Thus the dispersal system for truffle-like fungal spores may be similar to that of many plants largely reliant on endozoochory for the dispersal of their propagules. The gamma distribution was a good descriptor of 1D spore dispersal curves following results for previous fitting of this distribution to seed dispersal curves generated by frugivorous birds (Carlo & Morales 2008), and supporting its further use in estimation methods for endozoochorous spore dispersal by swamp wallabies.

As found previously, two-dimensional (2D) anisotropic kernels produced more detailed and useful estimates of spore deposition than 1D isotropic counterparts (Santamaría *et al.* 2007; Savage *et al.* 2011). A 3D representation of the 2D simulated spore kernel (Figure 5.8) clearly illustrated that peak spore deposition was removed from the parent plant and exhibited distinct peaks within a 250 m distance class, reflecting a clustering pattern in high spore densities. 1D kernels suggested a unimodal distribution to spore deposition while 2D kernels suggested multimodal distributions in several directions radiating outwards from the parent source. The 2D kernel predicted a spore density mode closer (≈100 m) to the parent source than the 1D spore-dispersal curve (≈250 m). This may largely be attributed to a maximum hourly displacement distance being used in calculating the spore-dispersal curve, intended to capture LDD events but resulting in an underestimation of spore deposition closer to the parent source. The greater potential accuracy of the 2D dispersal kernel in estimating the probability of spore deposition in the nearest distance classes (i.e. 0-250 m) and also at further distance classes (including LDD events) suggests this method may better reflect dispersal distances facilitated by the swamp wallaby.

Spatial patterns in spore deposition by standard dispersal vectors may have important implications for subsequent life stages and recruitment in fungal taxa in addition to their plant hosts. Deposition of spores into spore banks can facilitate vegetation shifts of EcM plant hosts in response to fire or climate change (Vernes & Dunn 2009). Dispersal of spores across habitat boundaries may also be important for maintaining broad distributions of more common fungal taxa across multiple habitat types. The importance of the disperser is also influenced by the location it deposits spores with the more important vectors dispersing spores to habitat or microsites more amenable to establishment. In the case of EcM fungi, this would include being deposited within proximity of plant host species but also any association with broad habitat types (Chapter 2). Estimated spore dispersal kernels suggest swamp wallabies can disperse spores considerable distances (>100 m) from the parent source, between discrete patches of similar habitat, and across habitat boundaries. Densities of dispersed spores may be lower close to the parent fungi than at further distances (≥100 m) suggesting recruitment of new fungal units would be less likely close to a "parent" source.

Although the model system is one for truffle-like fungi, dispersal distances and deposition patterns for epigeous taxa consumed by swamp wallabies are likely to be highly similar. While species richness and abundance of epigeous spores observed in swamp wallaby and other macropod scats may be low, their spores may be as frequently encountered as those of truffle-like taxa (Vernes 2010; Chapter 4). Recently, a field and modeling-based study of several epigeous taxa revealed that 95% of basidiospores fell within 1 m of the cap. In comparison, swamp wallabies are predicted in this study to disperse the majority of spores >100 m away from the source location, suggesting endozoochorous dispersal may be a more important dispersal mode than previously considered in south-east Australia for some epigeous taxa (Galante *et al.* 2011). Consequently, animal-mediated dispersal may provide an alternative or superior mode of dispersal than wind-assisted dispersal in some macrofungi. Provided epigeous spores are capable of surviving gut-passage, endozoochorous dispersal in mammalian scats also has the potential to increase successful establishment through providing a nitrogen resource pool (i.e. faecal pellets), aggregating spores, and having lower spatio-temporal stochasticity than wind dispersal. However, dispersal via nitrogen-rich mammalian faecal pellets may benefit some EcM taxa more than others as nitrogen fertilisation may inhibit mycorrhiza formation in some EcM taxa (Wallander & Nylund 1992) and drive changes in fungal community composition (Cox *et al.* 2010; Weber *et al.* 2013).

Patterns of deposition and recruitment

Animal movement trajectories in 2D space were more similar to a simulated Levy walk than a random walk pattern (Jordano 2007), matching reported movement behaviours of frugivore seed dispersers (Westcott & Graham 2000; Holbrook & Smith 2000; Fragoso *et al.* 2003; Holbrook & Loiselle 2009; Holbrook 2011). Given a continuous probability of spore gut-retention, such

movement behaviour can result in a clumped pattern to spore deposition by concentrating spores in a relatively small area (concentration of spores in 2D space) followed by movement to a new area (longer distance movements), repeating this concentration of spores in another relatively small area far removed from the previous location (Jordano 2007). Corresponding to other studies of endozoochory, 2D kernels exhibited strong anisotropy (Santamaría *et al.* 2007) along with a heterogeneous pattern in spore deposition (Russo & Augspurger 2004; Russo *et al.* 2006). Significant aggregation of spores was predicted in 2D spore dispersal kernels generated by swamp wallabies. Aggregated seed deposition has similarly been reported for the rain forest tree *Virola calophylla* dispersed by spider monkeys *Ateles paniscus* (Russo & Augspurger 2004; Russo *et al.* 2006), for the palm *Maximiliana maripa* dispersed by lowland tapir *Tapirus terrestris* (Fragoso *et al.* 2003), and the fleshy-fruited shrub *Ephedra fragilis* dispersed by the frugivorous Balearic lizard *Podarcis lilfordi* (Rodríguez-Pérez *et al.* 2012a). Spore deposition can be heterogeneous (Russo *et al.* 2006) due to behaviour and movement patterns of animal vectors that aggregate seeds. For example, tapirs aggregated seeds at latrine sites (Fragoso *et al.* 2003) and spider-monkeys deposited more seeds at sleeping and parental sites (Russo & Augspurger 2004). Similarly, predicted box mistletoe *Amyema miquelii* seed rain generated by the mistletoebird *Dicaeum hirundinaceum* was also strongly aggregated. As in the truffle-swamp wallaby dispersal system, mistletoebirds had large home ranges but concentrated their activity in much smaller core use areas. Mistletoebird core-use areas were also strongly associated with higher plant densities (Ward & Paton 2007).

Aggregation of spore deposition in space may shape the spatial distribution of recruitment and reproductive mycorrhizal mats along with several other concurrent and post-dispersal processes. The hyphal bodies of truffle-like fungi are often thought to be patchily distributed in space as has been often observed of their sporocarps. EcM mats of truffle-like taxa within the genera *Gautieria* and *Hysterangium* have exhibited fine-scale spatial aggregation in young forest stands and higher dispersion in old-growth stands (Griffiths *et al.* 1996). Although no studies have directly linked spore dispersal dynamics to recruitment patterns in EcM fungi, Edman *et al.* (2004) implicated high spore deposition from local sources to account for observed colonisation of course woody debris by wood-decaying fungi. Similarly, Peay *et al.* (2007) found sporocarp production to be positively correlated with the number of tree 'islands' colonised by EcM fungi suggesting spore rain influenced recruitment and observed spatial patterns in species distributions. Spore concentration has been also observed to increase host colonisation rates in four *Rhizopogon* species (Bruns *et al.* 2009), suggesting that increased density of spores through spatial aggregation by mycophagous animals may result in a higher recruitment probability. Seed rain has been found to be strongly associated with recruitment patterns in a marsupial-mistletoe (García *et al.* 2009), a lizard-shrub (Santamaría *et al.* 2007; Rodríguez-Pérez *et al.* 2012b; a), and a primate-rain forest

tree system (Russo & Augspurger 2004). Vertebrate dispersal syndromes have also been strongly correlated with spatial aggregation of adult plants in a tropical system (Seidler & Plotkin 2006).

Increased colonisation rates with time since deposition suggest some truffle-like taxa have a dormancy period allowing viable spores to accumulate over time, potentially persisting for decades in some species (Bruns *et al.* 2009). Consequently, for some taxa the effect of dispersal may be cumulative through time as opposed to a single event where spore fate is greatly influenced by stochastic processes. At the local spatial scale, deposition into long-lived spore banks may also reduce aggregation through time as core-use areas of mycophagous animals change. These changes are likely to occur in response to spatio-temporal resource heterogeneity driven by seasonal, climactic, or successional cycles but also individual animal preferences. In this scenario, spatial variation in post-dispersal process such as microsite variation in spore bank decay may have a greater influence in recruitment patterns. However, as in the seeds of plants, truffle-like taxa may differ markedly in spore dormancy potential, reflecting different life strategies and having implications for dispersal and recruitment dynamics (Nara 2009).

Our knowledge of the fungal parent physical size, longevity, and reproductive output (spores) of most taxa is poor or entirely lacking. Consequently, 2D spore dispersal kernels estimated from a few (i.e. 10) dispersal events may be a more valid description of the true spore shadow where individual fungal parents (systems of hyphae) are short lived and reproductive output is low (i.e. only a few fruiting events within their life-time). Conversely, where individuals are long-lived and total life-time reproductive output is high, dispersal kernels estimated from many discrete dispersal events (e.g. Figure 5.8) may be a more valid representation of reality. Regardless of these differences, all estimated spore kernels exhibited a lower probability of dispersal close to the parent fungi (<50 m) than the next distance classes, highest probability of deposition and an aggregated 2D pattern within 500 m, and more dispersed pattern at further distances.

The considerable variation among predicted spore kernels produced by individual animals has been observed previously (Santamaría *et al.* 2007) and suggests localities will vary in spatial patterns of spore rain and inoculum potential based on the unique movement patterns of resident mycophagous dispersers. This study also suggests that spatial patterns in recruitment or genetic variation are unlikely to be detected unless undertaken at a large scale, defined by the home range of the most mobile standard dispersal vector and informed by calculations of dispersal distances such as undertaken here. The potential for non-uniform (e.g. aggregation) patterns of spore deposition and subsequent recruitment also suggests that spatial patterns in recruitment and genetic structuring may not be adequately described unless the spatial resolution of sampling is informed by predictive models of deposition, such as undertaken in this study.

Correlation with space use

Corresponding to models produced for white-tailed deer seed dispersal (Vellend *et al.* 2003), the estimated spore distance distribution was highly similar to the frequency distribution of net displacement. This similarity suggests movement behaviours were a strong determinant of the shape and scale of 1D spore dispersal kernels generated by the swamp wallaby. A long predicted gut-retention time (69 hrs) may allow movement behaviour to be a major determinant in shaping the shape and scale of dispersal kernels along with relative concordance between modes of displacement curves and gut-retention curves (hr 20 versus hr 30 respectively). Interestingly, the average cumulative net displacement (Figure 5.4) corresponded with the mode of 1D dispersal kernels at ≈250 m while an apparent common upper threshold of ≈600 m for net displacement also matched estimated dispersal distances for the majority of spores.

A strong influence of movement behaviour on predicted 2D spatial patterns of spore deposition was also observed. High and low clusters of spore density were strongly correlated with each animal's space use, further confirming the potential overriding importance of movement behaviours in determining spatial patterns of spore deposition in some endozoochore systems (Russo *et al.* 2006; McConkey & Chivers 2007) and the potential for influencing patterns of recruitment (Santamaría *et al.* 2007; Rodríguez-Pérez *et al.* 2012b).

Large differences in the shape and scale of dispersal kernels generated by animals and the rarity of longer-distance movement confirmed the need to sample numerous animals using high temporal resolution GPS telemetry to adequately describe both 1D and 2D dispersal kernels and capture rare dispersal events respectively. Lower temporal resolution movement data with only a few animals runs a serious risk of not capturing rare LDD events that are more important in the life histories of both plants fungi than their apparent frequency (Nathan *et al.* 2008).

Long-distance dispersal (LDD)

Long-distance dispersal of spores by the swamp wallaby was predicted to be a relatively rare event but large in magnitude (>2000 m), many times the mean dispersal distance. The wide geographic distribution of some truffle-like taxa would suggest dispersal vectors offering LDD events. Fatter-tailed distributions as exhibited by some animals can dramatically increase predicted spread rates for an organism (Nathan *et al.* 2008). Fatter-tailed spore-dispersal curves generated by some animals further suggest the importance of swamp wallabies as potential LDD vectors for truffle-like fungi due to the well-established relationship in driving more frequent LDD events. Considering the large dispersal distances conferred by swamp wallaby mycophagy, contribution to maintaining species distributions is possible through facilitating gene exchange among fungal populations separated by hostile habitat (i.e. discrete habitat patches), recolonisation of amenable

habitats post-fire, and dispersal between amenable unoccupied habitat and/or isolated hosts. LDD events have also been considered the likely process for maintaining fungal communities and diversity patterns associated with isolated host-plants in rainforest (Tedersoo *et al.* 2009b). LDD dispersal by large-ranging bison have been implicated in low genetic variation in AM fungi and potential absence of dispersal limitation at a landscape scale (Lekberg *et al.* 2011). Dominance of plant taxa can be reduced and diversity increased through differential dispersal and recruitment limitation where less competitive species are more often dispersed to suitable sites for establishment over more dominant taxa (Fragoso *et al.* 2003). Similarly, LDD dispersal agents such as swamp wallabies may maintain a diverse truffle-like fungal assemblage by dispersing the spores of such taxa to unoccupied microhabitats free of other competitively superior EcM fungal taxa.

An interesting result was the variation among individuals in estimated 1D dispersal curves which suggested some animals may facilitate LDD events more often than others. This should be accounted for by sampling enough animals to capture LDD events but also to capture a range of movement behaviours and habitat interactions through time. The use of fine-scale GPS telemetry was essential to capturing rare LDD events, which were an order of magnitude greater than an average dispersal distance provided by the swamp wallaby.

Directed dispersal

Spore dispersal distances combined with the wide range of habitats utilised confirm the swamp wallaby as an important dispersal agent for truffle-like fungi including after high intensity fires which have the potential to reduce the soil spore bank (Claridge 2002). Swamp wallabies may also disperse the seeds of plants (Auld *et al.* 2007) along with the truffle-like fungal spores of associated EcM fungi (Johnson 1996), although the role of vertebrates in dispersing plant seeds in Australia has only rarely been investigated (Dunn *et al.* 2006). Recent evidence for importance of LDD dispersal by large ranging vertebrates (emus) in shaping observed patterns of seed rain and recruitment has been found for a primarily ant-dispersed plant *Daviesia triflora* (He *et al.* 2009).

The direction of spore dispersal among habitats, as inferred from daily frequency of habitat crossings, was not always proportionate to availability. Movements from wet sclerophyll into 'non-habitats' (i.e. granite outcrops and montane bogs) and from heathy woodland into rainforest habitat were comparatively less common. Rainforest, montane bogs, and granite outcrops all had an open understorey structure (A.O. pers obs), shown to be an important factor in the species habitat selection (Di Stefano 2007; Di Stefano *et al.* 2009). The high cover of unsuitable substrates (i.e. bare rock and shallow soils) in granite outcrop habitat and the dominance of AM forming grass and sedge plant species in montane bogs suggests these may be less suitable habitats for the establishment of EcM fungal spores (Reddell *et al.* 1997; Keith 2004; Hunter & Bell 2007; Hunter

& Sheringham 2008). Similarly, rainforest habitat in the study area has been shown to be depauperate in EcM truffle-like fungi (Chapter 2). Consequently, spore dispersal by the swamp wallabies may be biased towards habitats more suitable for fungal growth and development i.e. a form of directed dispersal (see Glossary). Conversely, infrequent spore dispersal into less suitable habitats may facilitate vegetation shifts in mycorrhizal host-plants driven by natural fire regimes and climactic cycles (Vernes & Dunn 2009). Similarly, island EcM fungal communities associated with isolated eucalypts in rainforest may be maintained by mammalian spore dispersal across habitat boundaries (Vernes & Trappe 2007; Vernes & Dunn 2009). Spatial associations among habitats are also likely to influence the estimated dispersal of spores across habitat boundaries i.e. some spores were dispersed from wet sclerophyll to rainforest but none between heathy woodland and rainforest. This pattern is likely influenced by the later pair of habitat types never being adjacent to one another within the study site.

However, other mycophagous species may facilitate dispersal of truffle-like fungal spores into montane bogs and fens such as the mycophagous parma wallaby *Macropus parma* which has been positively associated with this habitat type (Vernes & Cooper 2007; Vernes 2010). In addition, the mycophagous pademelon (Vernes & Trappe 2007) and bush rat *Rattus fuscipes* may be more important for spore exchange across the wet sclerophyll-rainforest interface (Vernes & Dunn 2009).

Numerous truffle-like species are shared between the habitats of heathy woodland and wet sclerophyll (Chapter 2) and swamp wallabies are likely the more important vector for the exchange of spores and genetic material between these habitats, facilitating the maintenance of more widely distributed taxa with broad host-plant associations. In addition, swamp wallabies can facilitate spore dispersal among discrete patches of the same habitat types separated by considerable distance (i.e. wet sclerophyll), moving spores and genes among discrete populations (Johnson 1996). This process is likely more important for truffle-like taxa with greater host-specificity (Tedersoo *et al.* 2008, 2009b) or a more narrow habitat niche. It may also aid recolonisation and the functioning of metapopulation and metacommunities at the population and community level respectively.

Implications for gene flow and recruitment

Differences in primary mode of dispersal in fungi has been shown to influence the biogeography and invasive ecology of species, and also the genetic structuring of populations (Bonito *et al.* 2010; Douhan *et al.* 2011). Some truffle-forming fungi have exhibited low dispersion and associated high population structure over relatively small geographic scales (5-8.5 km) (Douhan *et al.* 2011). In contrast, wind-dispersed fungi have so far exhibited little genetic differentiation over much larger spatial scales (1-700 km) (Douhan *et al.* 2011). Spatial autocorrelation analysis has revealed that genetic clustering in two co-occurring truffle-like species (*Rhizopogon vinicolor* and *R.*

vesiculosus) was negligible at a within-plot scale (50 x 100 m), leading to the hypothesis that gene flow may be relatively unrestricted within the home range size of major mammalian dispersal vectors (Kretzer *et al.* 2005). Conversely, small home-range sizes of mammalian dispersal vectors has been implicated in a high level of genetic differentiation between populations of *Rhizopogon occidentalis* and *R. vulgaris* only a few kilometres distant from one another (Grubisha *et al.* 2007). Although dispersal distances by swamp wallabies are large compared to other co-occurring mammals, they are likely several times less than those conferred by larger-ranging ungulate mycophagous dispersers such as deer based on their large home ranges and long gut-passage (Launchbaugh & Urness 1992; Vellend *et al.* 2003; Myers *et al.* 2004; Will & Tackenberg 2008). The absence of equivalent larger-ranging mycophagous species in Australia could result in more fine-scale genetic differentiation among populations, a potential driver for higher species richness.

Using parentage analysis, Kretzer *et al.* (2005) also found recruitment was lower near the parent source, suggesting that animal-mediated spore dispersal may be important for dispersing spores beyond the competing parent. The predicted dispersal distribution in this study suggests that patterns of spore dispersal via mycophagous dispersers may also play some role in lowering recruitment near the parent source. Wind-dispersal of passively released spores has been described by a negative exponential distribution (Galante *et al.* 2011) suggesting that endozoochory, following a gamma distribution with peak deposition well-removed from the parent source, may provide a more effective mechanism for moving spores beyond the potential effects of intraspecific competition with the parent fungi. Recently, high spatial autocorrelation in species composition and density has been reported for EcM communities in neotropical rainforest, provide support for dispersal limitation in some EcM fungi-host plant systems (Tedersoo *et al.* 2009b). Similarly, distance distributions of recruitment in the wood decay fungus *Phlebia centrifuga* was recently predicted to be relatively short-range, counter to previous assumptions, with dispersal limitation beginning at tens of metres from the parent source and extending to only a few hundred metres further (Norros *et al.* 2012). Contrary to previous predictions, spore dispersal may be more important in spatio-temporal structuring of fungal populations and communities, emphasizing the potential importance of novel non-standard dispersal vectors for LDD events such as mycophagous animals for epigeous taxa.

Conclusion and future directions

The total dispersal kernel of any single fruiting fungal individual is a combination of all the spore kernels generated by each mycophagous animal (Nathan *et al.* 2008) and other dispersal vectors, such as wind, water, and ectozoochory (i.e. animal dispersal via attachment on external surfaces such as hair). Numerous other mammals are implicated in spore dispersal within the study area (Vernes & Dunn 2009; Chapters 3, 4, and 6). Considering the high frequency and diversity of

truffle-like taxa spores found in many small mammal diets, particularly bush rats (Chapter 3), the total dispersal kernel incorporating these additional dispersal agents would likely differ in shape with higher spore density close to the parent source than one predicted to be facilitated by swamp wallabies alone. This would be largely due to the smaller foraging range of small mammalian mycophagous species recorded within the study area. Home range size estimates for such species in Gibraltar Range (Chapter 3; Vernes & Dunn 2009; Vernes 2010) vary between 0.19 ha and 8.5 ha in size with the eastern pygmy-possum *Cercartetus nanu*s having the smallest home range of 0.19 ha (Harris *et al.* 2007) and the long-nosed potoroo *Potorous tridactylus* the largest, reaching up to 8.5 ha in size (range: 2.9 ha – 8.5 ha)(Lazenby-Cohen & Cockburn 1991; Scott *et al.* 1999; Fisher & Owens 2000; Rader & Krockenberger 2006; Sanecki *et al.* 2006). Consequently, a greater proportion of spores would likely be dispersed much shorter distances than predicted via swamp wallaby endozoochory alone.

Each truffle-like species may also be dispersed by a different combination of mycophagous mammals (a 'dispersal syndrome') due to disperser-specific preferences or ability to detect and excavate truffles. In turn, each of these species will produce unique spore dispersal kernels due to different movement capabilities and behaviours, gut-retention times, and habitat preferences. Through differences in consumption of spores, the quantity of dispersal by each mycophagous disperser will vary. Quality of dispersal through each vector will also differ based on the distances spores are dispersed and their deposition in space (Spiegel & Nathan 2007). Recruitment patterns may vary among truffle-like taxa depending on the combination of dispersal agents involved and the relative proportion of spores they disperse to habitats and microsites amenable to establishment, such as within the root zone of EcM plants. Spatial patterns of plant recruitment may be largely determined by the interplay between the dispersers use of space and local habitat features (Rodríguez-Pérez *et al.* 2012b). However, post-dispersal processes such as rates of spore predation and the potential role of dung beetles (Johnson 1996; Nichols *et al.* 2008) and other nonstandard vectors in secondary dispersal of spores into the rhizosphere await investigation. Pre-dispersal process and spatial trends, such as sporocarp production, also need concurrent quantification and may be incorporated into future mechanistic models. As for seeds of vascular plants, the final fate of spores will be determined by a complex web of interactions involving numerous biotic and abiotic processes. This study provides an additional step along the path to building a more detailed description of spore dispersal dynamics. As shown here, future studies of ecto- and endozoochorous spore dispersal by vertebrates can draw considerable insights from the methods and theory applied to the study of seed dispersal by vertebrate vectors.

Limitations

Spores may have varying gut-passage rates due to differing ornamentation and size. Danks *et al.*

(2011) used a truffle-like taxon *Austrogautieria* sp. that has ridged but relatively smooth walls. It is possible that taxa that produce spores with large spines or other ornamentation may have longer gut-passage rates. However, the plateau exhibited in cumulative displacement at only 20 hours suggests that a longer gut-passage would have little influence on maximum dispersal distances for spores. Gut-passage rates (mean retention time of spores: MRT) of swamp wallabies are similar to those of smaller macropodids (pademelon, bettong, potoroo; mean particulate markers MRT 29.2 hrs). MRTs were not greatly different among these species, suggesting more pronounced differences in movement behaviour and habitat use among these species may have a greater influence of the scale and shape of the spore kernels they would generate.

The correlation between animal space utilisation and probability of spore dispersal could be overestimated due to gut-passage of spores being parameterized as a continuous PDF in mechanistic models. In reality, spores are likely to be deposited in scats discrete in time and dispersal curves would be more irregular (cf Russo & Augspurger 2004; Westcott *et al.* 2005), as would the pattern of deposition in two-dimensional space (Russo *et al.* 2006). Investigation of scat deposition at a finer temporal scale than undertaken previously (Danks 2012) following the methods of Westcott *et al.* (2005) would provide further insights into patterns in deposition. Nonetheless, reported defecation rates from captive animals are relatively high, with an average of 73.2 (±13.5) pellets produced per day (Fancourt 2009), suggesting gut-passage could be well represented by a PDF if defecation is relatively continuous over a diel cycle.

Further investigation into the influence of daily activity patterns and the temporal distribution of feeding events on spore dispersal kernels is needed following methods similar to that undertaken for seed dispersal by vertebrates (Russo *et al.* 2006; Kays *et al.* 2011). The structure of habitat is also likely important to patterns of spore deposition and subsequent recruitment patterns (Kohlmann 2002). As has been illustrated for a endozoochorous dispersed plant species (Rodríguez-Pérez *et al.* 2012a), landscape habitat structure is likely to be an important potential determinant of spore rain along with spore deposition distances, movement behaviour and habitat preferences of the mycophagous dispersal vectors. Consequently, patterns of spore deposition may differ greatly in fragmented or modified landscapes (Herrera & García 2010). This should be considered when making inferences from models of spore dispersal estimated in relatively natural systems such as in the present study.

Chapter 6. Truffles in the Belfry and macrofungal spores in microbat diets

Introduction

Hypogeous or 'truffle-like' fungi are those fungi which produce subterranean or partially emergent sporocarps ('truffles') containing basidiospores that are not forcibly discharged or entirely enclosed (i.e. sequestrate) within the sporocarp. Truffle-like fungi do not form a monophyletic group; with the hypogeous sequestrate form having evolved independently several times among several fungal lineages (Peintner *et al.* 2001). Life cycles of fungi that produce 'truffle-like' or sequestrate sporocarps are poorly known although they are thought to be mostly ectomycorrhizal (EcM), forming an obligate mutualism with host plant species root systems (Luoma *et al.* 1991; Claridge 2002; Zeller & Maurice 2008). EcM fungi colonise the exterior of host root plant cells and are capable of transferring water and nutrients across to host plants via an hyphal mantle or Hartig net surrounding the root cells (Tagu *et al.* 2002). Associations with EcM fungi have been shown to increase water and nutrient uptake during plant development (Bougher & Lebel 2001; Turjaman *et al.* 2006) through increasing the effective surface areas of plant root systems and the uptake and transfer of mineral nutrients through excretion of organic acids and other mechanisms (Landeweert & Hoffland 2001; Gadd 2007). In exchange, the EcM fungi symbiont receives carbohydrates from their photosynthetic plant partners (Tagu *et al.* 2002). Through these beneficial processes, EcM fungi are thought to protect plant hosts from harsh environmental conditions, a relationship extending back at least 50 million years (LePage *et al.* 1997). Obligate EcM fungi are dependent on their plant hosts for completion of their life cycle (Bonito *et al.* 2010) and consequently their distribution is tied to that of their plant hosts. In contrast, saprobic or pathogenic fungi are not dependent on plant hosts and can inhabit and survive in a range of environments and conditions which obligate EcM fungi may not, such as post fire and other successional environments devoid of plant hosts (Claridge *et al.* 2009a).

Most macrofungi, particularly EcM, arbuscular mycorrhizal (AM), and endomycorrhizal species, are soil-borne filamentous fungi forming mycelia bodies close to the soil surface, most densely within the rhizosphere although sometimes extending above the soil horizon in litter or other organic material. Truffle-like taxa are thought to form mycelial bodies within the upper soil profile and associated with plant root systems. Macrofungi are capable of surviving in harsh environment such as deserts and tundra, and can be important pioneer organisms post disturbance such as after fire, volcanic eruptions, or glaciation. In the case of post fire fungi, recolonisation is thought to

occur via a soil spore bank (Claridge *et al.* 2009a) rather than through primary spore dispersal or mycelia regrowth. Bruns *et al.* (2009) found spore banks of truffle-like *Rhizopogon* taxa to remain viable for at least 4 years in field conditions. Although not dependent on plant roots for germination, spores of EcM fungi have been shown to have increased germination rates in their presence, thought to be result of exudates by plant roots (Ishida *et al.* 2008). Reproduction is not solely reliant on spores but can occur vegetatively through transfer of mycelia, although field evidence for this is sparse. The potentially greater importance of spores as a mode of reproduction and dispersal is suggested by the dominance of small and short-lived genets in a large number of EcM taxa (Dahlberg 2001; Ishida *et al.* 2008) and by the relative spatial location of parents and offspring in two truffle-like taxa (Kretzer *et al.* 2005). The dispersal of spores and maintenance of spore banks are likely to be important processes in shaping the distribution of truffle-like taxa across a landscape.

The dispersal of truffle-like fungal spores to new locations is largely dependent on animal vectors. In most taxa, spores are entirely encapsulated within the fungal fruit body (sporocarp) and cannot be dispersed via wind like spores of epigeous macrofungi (Bonito *et al.* 2010). Fungus consuming animals (mycophagous) consume the sporocarps and transport spores to a new location in their scats (faeces). Gut-passage may enhance spore germination rates in some species (Colgan and Claridge 2002); while animal dispersal is thought to increase plant root infection rates through depositing spores within the root zones of plants and concentrating the spores of several truffle-like taxa in their scats. Although insects (Fogel 1975) and birds (Simpson 2000) are reported to consume truffle-like fungi, terrestrial mammals are most strongly associated with this process (Claridge and May 1994). However, the extensive biogeographic range of some truffle-like genera (Bougher & Lebel 2001); occurrence on islands situated in deep seas and never connected to larger landmasses (Wedén *et al.* 2004); and ancient lineage of some families shared between land masses isolated from one another prior to the expansion of ground-dwelling mammals (Hosaka *et al.* 2008; Johnston 2010), suggests that long-distance dispersal events via other animal vectors with greater vagility may also be important in the current distribution of truffle-like taxa. Although rare in time, and infrequently observed, long-distance dispersal (LDD) events are thought to be a driving mechanism behind the expansion rates and distribution of many plant species (Cain *et al.* 1998; Nathan *et al.* 2003) and maintaining species genetic diversity during range expansion (Bialozyt *et al.* 2006).

The current investigation was initiated by the remarkable discovery of a truffle-like fungi colony within a cave system used by microchiropteran bats (microbats). This discovery is the first record of a truffle-like taxa growing within a cave environment and not associated with a plant root system within a field environment. Features of the truffle-like fungus discovered are described and

implications of the latter finding discussed in light of current understanding of life strategies, dispersal dynamics, and habitat requirements in truffle-like fungi.

A close association between fungal bodies and microbat faeces within the cave suggested microbats as one potential vector for the establishment of the fungal colony. Microbat diets were subsequently examined to examine whether microbats, including cave-roosting species (i.e. *Miniopterus schreibersii oceanensis*), could be potential spore dispersers for truffle-like taxa. Several species of microbats and localities were sampled to investigate how widespread among microbat species and landscapes this potential mutualistic interaction is. Currently, few LDD vectors are known for truffle-like fungi. In Chapter 5, the mycophagous swamp wallaby *Wallabia bicolor* was shown to be capable of dispersing spores considerable distances (92% spores dispersed >100 m) and across habitat boundaries. However, larger-scale LDD events of >1000 m were estimated to be relatively rare. Several traits of microbats suggest they could be a significant spore vectors including large movement distances, global and ubiquitous distribution across a wide variety of terrestrial habitats, and tolerance to habitat fragmentation. The potential contribution of microbats to dispersal dynamics in truffle-like fungi is explored via our current understanding of microbat biology and comparisons to other animal vectors including species discussed in previous Chapters (3-5).

Methods

Study area

The investigated cave system, the 'Belfry', was located at Timor, Upper Hunter Valley, central New South Wales, situated approximately 200 km north of Sydney and 80 km south of Tamworth and east of the township of Murrurundi (Figure 6.1). The cave is one of at least 80 caves within the Timor karst of New South Wales, formed through the weathering of limestone deposits (Rutledge 2008; DECCW 2011). The cave entrance was positioned above a valley floor and extended horizontally into a hillside. Land above the cave supported remnant grassy eucalypt woodland with extensive grass trees (*Xanthorrhoea glauca* subsp. *angustifolia*) in the understorey.

Sampling of microbat diets was undertaken on the New England Tablelands, New South Wales, at three localities (Little Mount Duval, Booroolong Nature Reserve, and Dumaresq Dam) immediately north of Armidale township and one locality, Gibraltar Range, encompassing both Gibraltar Range and Barool National Parks. Localities north of Armidale supported fragmented dry sclerophyll eucalypt forest within a largely pastoral landscape. Gibraltar Range variously supported eucalypt dominated tall sclerophyll forest or heathy woodland within an extensive area of wilderness.

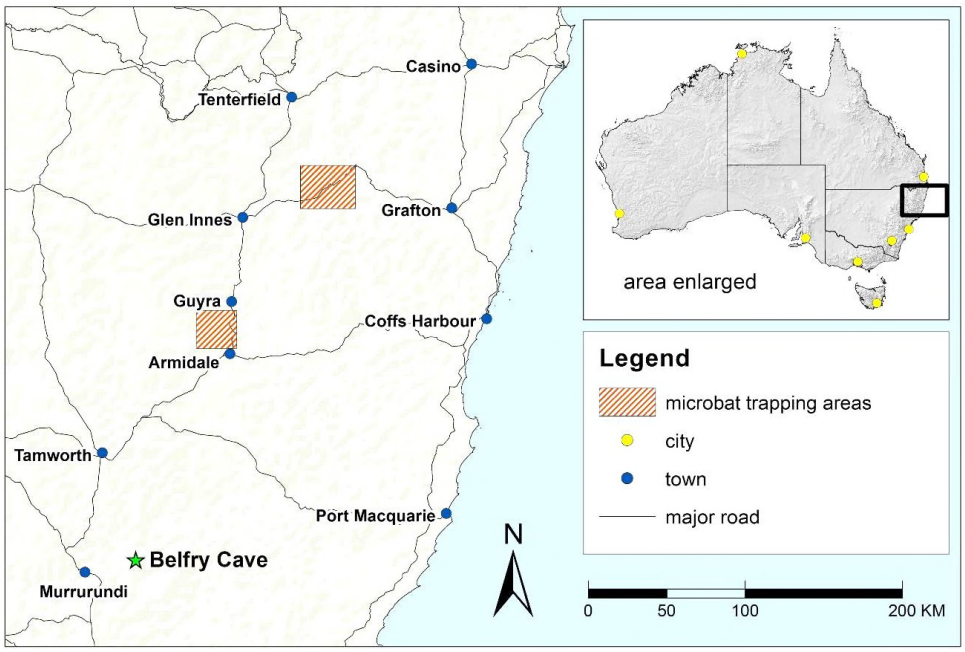

Figure 6.1 Location of microbat diet sampling areas and 'belfry cave' in north-eastern New South Wales, Australia.

Sampling

Faecal samples of microbat species were opportunistically obtained from individuals captured using harp traps in an unrelated study (K. Downs) undertaken in autumn between March (10/03/08) and May (11/05/08) 2008 at the aforementioned localities. Individual animals were removed from harp-traps at dawn, placed in individual calico handling bags and taken from the field. Faeces deposited in the handling bags were placed in seed envelopes and dried as for fungal sporocarps (Chapter 1). Microbats were described to species level and then released at night at the point of capture.

Individual microbats were the sampling unit as scats are likely to be strongly autocorrelated within individuals and not independent. Microbat species identity for samples taken within Gibraltar Range sites were not recorded but each sample represents a separate microbat individual. Species of microbat sampled within Gibraltar Range were *Chalinolobus gouldii*, *Chalinolobus morio*, *Falsistrellus tasmaniensis*, *Nyctophilus geoffroyi*, *Nyctophilus gouldi, Vespadelus darlingtoni*, *Vespadelus regulus*, and *Vespadelus vulturnus*. All microbat species captured are widespread throughout south-eastern Australia, inhabiting a large range of terrestrial habitats and landscapes. Dietary samples from the cave-roosting *Miniopterus schreibersii oceanensis* were also obtained from localities north of Armidale. All trapping was undertaken by K. Downs and A. O'Malley.

In total, 57 scats from 9 species of insectivorous bats were examined. A small amount of faeces was lightly crushed in a vial followed by the addition of 1ml of 70% ethanol. The contents were

vigorously stirred to loosen spores from binding mucus, fungal material, or insect remains then passed through a 100 µm sieve. The spore containing fine fraction that passed through the sieve was then decanted into a new vial, labelled appropriately, and left overnight for material to settle and concentrate at the bottom of the vial. This technique produces similar results to the labour intensive centrifuging. A single drop of this concentrate was placed one each of two glass slides. The ethanol was left to partially evaporate before the addition of a single drop of Meltzer's which produces an amyloid or dextrinoid reaction in the spores of some fungal genera and is an important diagnostic procedure. Processing of several samples from Gibraltar Range for initial inspection (i.e. not used in this analysis) followed similar methods with the exception that samples were more gently macerated and not vigorously shaken. This modified procedure allowed spores to be viewed in context to more intact insect remains and reduced the dispersion of clusters of spore types.

Slides were examined using standard light microscopy techniques at x400 and x1000 magnification. Fifteen fields of view for each slide were examined for fungal spores, which were counted and photographed where present. The study used photographs of truffle-like fungal spores collected from a previous survey of sporocarps on the New England Tablelands (Chapter 2) and observed in other mammal species diets to aid in identification (Chapters 3 and 4). Processing of sporocarps and examination in the laboratory followed methods detailed in Chapter 2.

Analysis

To investigate whether macrofungal spores are found in microbat diets consistently across a landscape, the nonparametric Kruskal-Wallace test was used to compare microbat diets among localities (n=4) in the mean number of spores and taxa detected. Samples from harp trapping sites were pooled by locality prior to analysis. Separate analyses were undertaken on datasets including i) all macrofungi and ii) truffle-like fungi. All statistical tests were performed in MYSTAT ver. 12 (SYSTAT Software Inc. 2011).

Species accumulation (rarefaction) curves and species estimation curves were calculated in EstimateS v8.2.0 (Colwell 2006) to assess the sampling completeness of the study and to estimate total species richness of fungi in microbat diets respectively. Sample-based accumulation (rarefaction) curves were calculated with 95% confidence intervals. The Jackknife2 and Chao2 incidence-based estimators were calculated by sampling plots randomly without replacement for 999 iterations. Presence-absence data was used for these calculations as numbers of spores carry little biologically meaningful information on taxon richness of fungi or relative abundance in animal diets.

Non-statistical comparisons were also made between microbats and other mammal species in the mean number of fungal morphospecies per scat sample and frequency of occurrence (% of samples

containing spores) of fungal taxa in dietary samples. Dietary data for other mammal species was obtained through a concurrent study of mycophagy in the Gibraltar Range locality (Chapters 3 and 4). Although dietary samples were not obtained at the same time as those for microbats and most in a different locality, all samples were from the same region and dramatic differences within species mycophagous habits are considered unlikely at this scale (Vernes 2010). Differences in sampling season may have biased comparisons and this is discussed below. The same sampling and microscopic examination techniques were applied to all samples.

Results

A truffle-like fungus in a cave environment

Sporocarps were collected from two distinctly separate fungal colonies within the rear chamber of a cave complex, approximately 80 m from the cave entrance. One fungal colony was located on the cave floor of a small chamber measuring 11 m x 4 m at greatest dimension. The colony was approximately fan-shaped and growing outwards from a single central point (Figure 6.2A). It covered an area approximately 1 m^2 and was comprised of a thin (<3 mm) mycelia mat over the compacted cave floor. The mycelium was not observed to penetrate the sediment horizon and was not associated with any plant roots Figure 6.2A-B). One large root system was observed to have penetrated the cave roof several metres distant from the fungal colonies but did not reach the cave floor. Sporocarps were produced along the growing front of the fungal colony (Figure 6.2A; red arrows denote the location of some sporocarps). Mycelia were generally most dense surrounding sporocarps. No obvious nutrient source was observed at the central point at which the mycelia appeared to arise from.

The second was a smaller colony, approximately 50 cm x 10 cm, growing amongst microbat faeces ('guano') accumulated on a horizontal ledge within a narrow vertical shaft being used for roosting by microbats. Considering the close spatial association between the microbat guano and fungal colony, this may have been a nutrient source exploited by the fungus. A dead microbat within the cave system was identified as *M. schreibersii oceanensis* suggesting this species may have been the source of guano. There was no obvious pattern in the arrangement of sporocarps in this colony. Some sporocarps were colonised by a microfungus which could not be identified but was likely to have been a saprobic or pathogenic species. Most sporocarps had numerous droplets of amber to clear liquid on their surfaces, appearing to be exuded by the sporocarp itself (Figure 6.2B).

The sporocarps were identified as *Scleroderma bougheri* Trappe, Castellano & Giachini, a species producing sequestrate hypogeous sporocarps and frequently collected in Australian eucalypt forest and also Brazilian eucalypt plantations (Giachini *et al.* 2000; Giachini *et al.* 2004). Mature sporocarps of this species have an internal section (gleba) composed of densely packed spores and hypha appearing black to the eye, and a peridium (outer layer) initially ivory to light greyish yellow (Figure 6.2B) bruising reddish-brown and when cut in cross-section (Figure 6.2C; Giachini *et al.* 2000). Specimen sporocarps were at a stage of development where the gleba had become disorganized and approaching a powdery state of dry spores. The peridium surface was tomentose (i.e. felty) and composed of abundant white to brown adpressed rhizomorphs which formed a distinctive basal clusters in most sporocarps. Specimen spores were brown, small (9.6 ±1.7 SD µm in diameter; range: 9-12 µm), and ornamented with crowded discrete pegs/spines (1.25 µm x 0.49

µm) occasionally coalescing into cone-like clusters, matching published descriptions for the species (Figure 6.2D; Giachini *et al.* 2000).

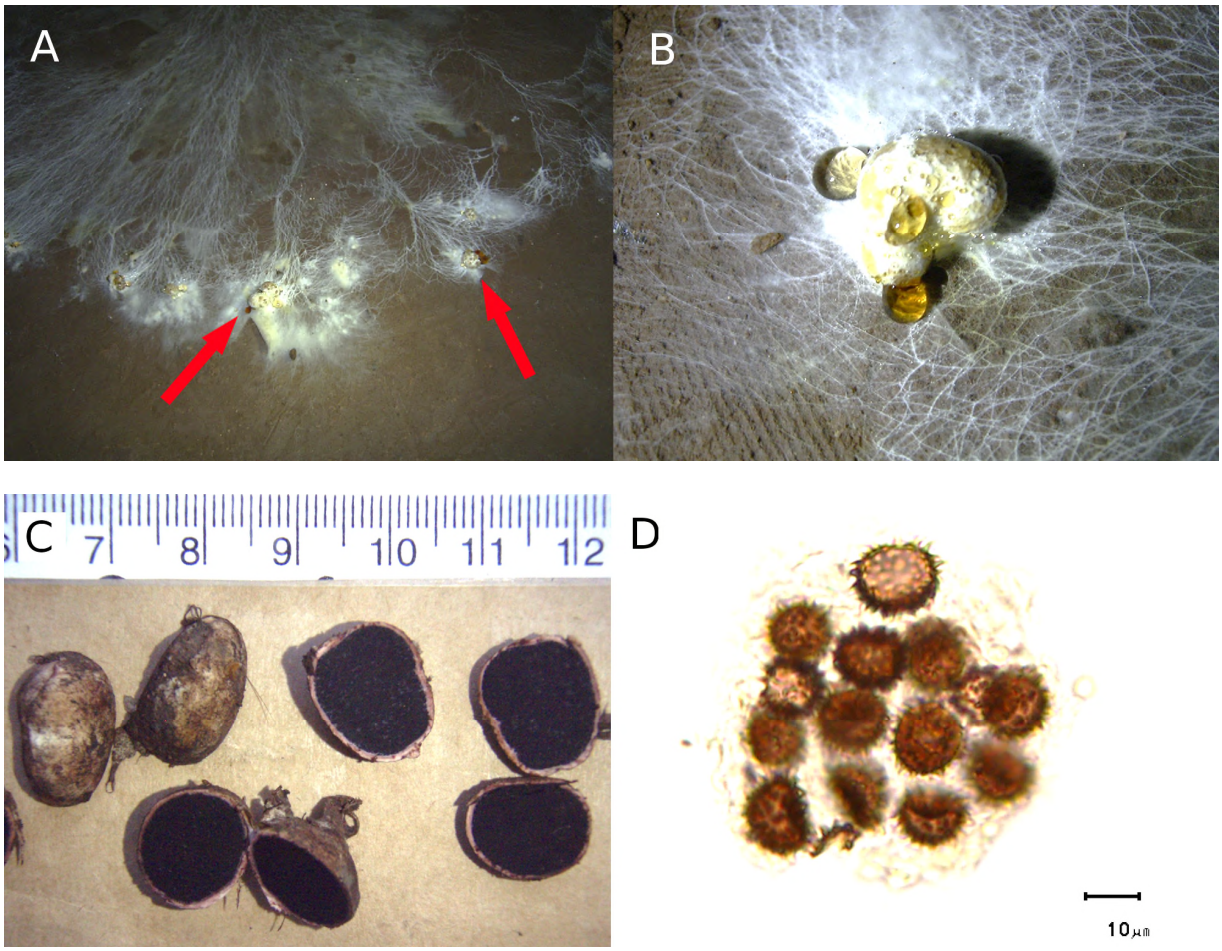

Figure 6.2 Photographs showing A) fungal colony of *Scleroderma bougheri* Trappe, Castellano and Giachini on the cave floor, growing outwards from a central point with sporocarps (arrows) arranged along the fan-shaped front; B) mature fruit-body of *S. bougheri* in-situ with mycelial mass; C) cross-section of fresh sporocarp specimens showing peridium and mature gleba contents; and D) *S. bougheri* spores at 1000 x magnification with scale bar (10 µm).

Fungal spores in microbat scats

Initial microscopic examination of microbat scats that were only gently macerated revealed fungal spores closely associated with insect body parts, particularly gut body parts (Figure 6.3A). Spores of truffle-like taxa were commonly observed clustered together; usually representing several taxa (Figure 6.3B). Subsequent samples processed using standardized techniques applied to other mammalian dietary samples resulted in mostly individual spores being observed in each field of view.

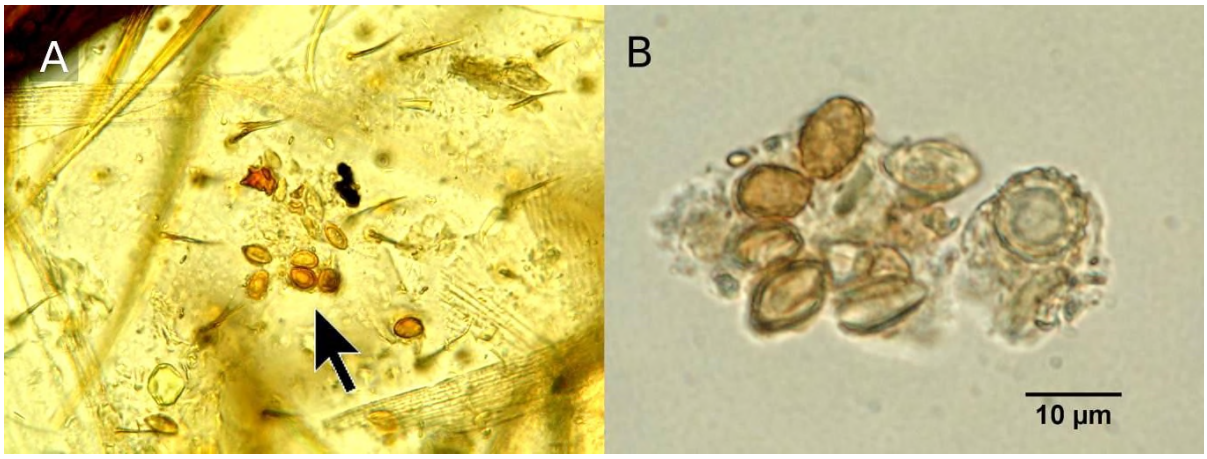

Figure 6.3 Photographs showing A) truffle-like fungal spores (arrow) of various taxa in a microbat dietary sample and associated insect dietary items, and B) cluster of truffle-like fungal spores belonging to *Rossbeevera*, *Cortinarius*, and Russulaceae with scale bar (10 µm).

Comparisons of microbat diets in the average number of spores and fungal taxa detected in diets showed no significant difference among localities (Kruskal-Wallis: χ^2_3=2.051-4.437; P>0.05). Dietary samples from Little Mount Duval contained the highest average number of spores (mean=22.3; n=13) and Gibraltar Range samples the lowest (mean=2.7; n=7). Localities supported similar average numbers of truffle-like taxa although Little Mount Duval (3.6 morphospecies) and Gibraltar Range (3.3 morphospecies) supported the highest.

In total, 49% of microbat dietary samples contained fungal spores and 47% contained fungal spores of truffle-like taxa. Twenty-three fungal morphospecies were identified in scats, 20 of which represented truffle-like taxa and three epigeous taxa. These morphospecies represented at least three epigeous and 17 truffle-like genera, showing that fungal spores in microbat scats were dominated by those of truffle-like taxa (Table 6.1). Most fungi morphospecies were encountered in a small proportion of samples (2-11%), with only one morphospecies, *Pogisperma* sp. 1, more frequently encountered (≈30%).

All microbat species diets, for which two or more samples were examined, contained spores representing at least one truffle-like genus although most contained several (Table 6.1). The microbat species, *F. tasmaniensis* had the greatest total number of fungal genera (8; n=2) despite only two samples being examined, followed by *M. schreibersii oceanensis* (7; n=13), a predominantly cave-roosting microbat species. Trends among microbat species in total number of morphospecies were similar, although the greatest total number were observed in *M. schreibersii oceanensis* scats (10), followed by *F. tasmaniensis* (8), *Nyctophilus* spp. (6-7), *Vespadelus* spp. (0-6) and *C. morio* (3) respectively. A pooled sample of microbat species diets from Gibraltar Range also exhibited a relatively high (9 genera; 13 morphospecies) fungal taxon richness.

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.

		Microbat species									
		Chalinolobus morio	*Falsistrellus tasmaniensis*	*Miniopterus schreibersii*	*Nyctophilus geoffroyi*	*Nyctophilus gouldi*	*Vespadelus darlingtoni*	*Vespadelus pumilus*	*Vespadelus regulus*	*Vespadelus vulturnus*	*Gibraltar Range species*
	samples (n)	3	2	13	5	14	4	1	4	3	7
Epigeous	*Agaricus*		1	1		1	1				
	Coprinacea										1
	Russulaceae										1
Truffle-like	*Arcangeliella*		1							1	
	Aroramyces			1							
	Chamonixia										2
	Chondrogaster		1		1						
	Cortinarius		1								1
	Cystangium										1
	Densospora				2	1				1	2
	Descomyces									1	
	Glomus			1							
	Hysterangium		1	1					1		
	Leucogaster		1								
	Mesophellia				1						
	Pogisperma	2	1	3	1	2	2		2	2	1
	Russulaceae		1	2		2				1	2
	Sclerogaster										1
	Scleroderma				1	1	1				
	unidentified Ascomycete			1							
	number of taxa	1	8	7	5	5	3	0	2	5	9

A species accumulation curve estimated using all samples did not reach an asymptote while 95% confidence intervals continuing to diverge from the mean until the last sample (Figure 6.4A). Similarly, the Jackknife2 species estimation curve did not reach an asymptote although Chao2 approached one, reaching a plateau at 50 samples (Figure 6.4B). Chao2 and Jackknife2 estimators predicted a total of 34 and 42 fungal species respectively, a figure much higher than observed (23 morphospecies; 55-68% of estimated total species richness). These results suggest that sampling completeness was low and that a greater diversity of fungal taxa is likely to be contained in diets than observed.

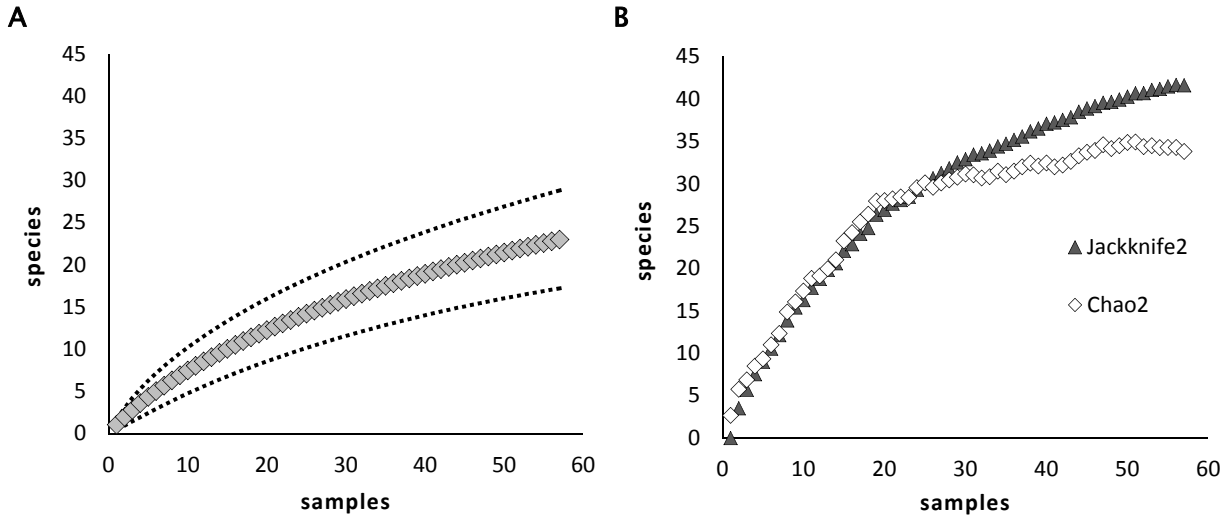

Figure 6.4 Mao Tau species accumulation (rarefaction) curve with 95% confidence intervals (A) and Chao2 and Jackknife2 species estimation (100 randomisations) (B) for fungal morphospecies from full dataset of microchiropteran species diets collected from four localities on the New England Tablelands, New South Wales, Australia.

Abundance of spores in scats was very low for all taxonomic groups of fungi with the exception of *Pogisperma* sp. 1. This species was found in comparatively high abundance in scats of all microchiropteran species examined, with the exception of *Vespadelus pumilus* where faeces from only one individual was available and no other spores were recorded. Frequency of occurrence of fungal taxa followed a similar trend, with most taxa occurring in a small number of samples and a small proportion of taxa occurring more frequently amongst samples. Nearly all spores observed had their spore walls intact - although some spores (particularly *Descomyces*) exhibited damage to their ornamentation - providing limited evidence for spore viability post gut-passage.

Comparisons to other mammalian species diets show that microbat diets contained a relatively low diversity of spore types both when considering all fungal taxa and also only truffle-like fungi (Figure 6.5A). The percentage of samples containing fungal taxa showed a similar trend among microbat species although was less pronounced, with just over half of microbat samples containing

fungal spores, compared to over 95% for the mycophagous swamp wallaby *Wallabia bicolor* and bush rat *Rattus fuscipes*. For both measures, microbat diets were most similar (although lower in both cases) to those of the insectivorous brown antechinus *Antechinus stuartii*. In contrast, the average number of fungal spores observed in samples was higher in microbat samples (13.0±4.0) than in brown antechinus samples (3.3±1.0) although fungal spore density in microbat and brown antechinus scats was dwarfed by that found in swamp wallaby (118.0±17.0) and bush rat (909.0±96.0) scats. Fungal spore density of truffle-like taxa showed the same trends among microbat species.

The origin of spores in microbat diets is likely to be through the consumption of mycophagous insects as opposed to direct consumption of fungal sporocarps. Insects, particularly larvae stage instars, were observed associated with truffles during a concurrent study within the Gibraltar Range locality. Beetle larvae were also encountered in several *Mesophellia* sporocarps, where all fungal tissue was observed to have been consumed (Figure 6.5B).

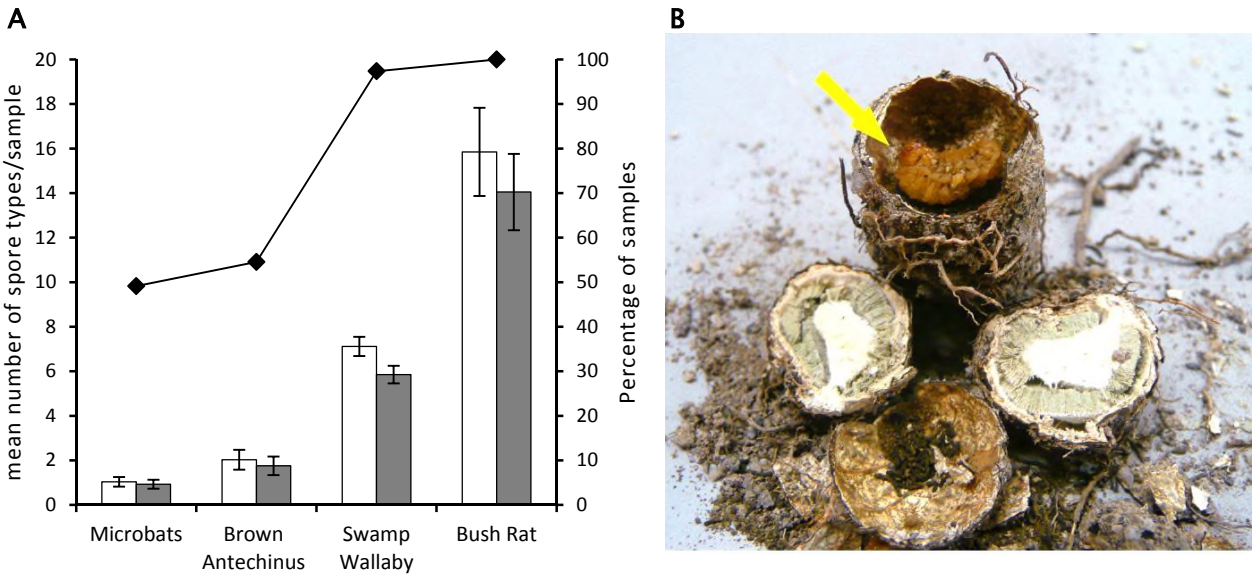

Figure 6.5 A) Comparison between microchiropteran and other mammal species diets (Chapters 3 and 4) in the mean number of spore types (bars) and frequency of occurrence (line; ◆ symbol) of fungal taxa observed in diets. The mean number of macrofungi (open bars) and truffle-like taxa (grey bars) detected in samples are shown with ± standard error. B) Photograph of *Mesophellia* glauca sporocarps broken open. Arrow denotes beetle larvae (Coleoptera, family Anobiidae) inside a sporocarp with no internal fungal tissue remaining.

Discussion

To my knowledge, this is the first account of a truffle-like fungus fruiting within a cave environment or exploiting animal derived organic matter for mineral nutrients. It is also the first reported observation of macrofungal spores in microbat faeces.

Growth and fruiting of a truffle-like fungus in a cave environment

Our general understanding of the diversity and function of fungi in cave systems is poorly documented (Engel 2010). Studies of fungi within karst cave environments have mostly focused on yeasts (Sugita *et al.* 2005; Mulec *et al.* 2012), pathogenic fungi (Lyon *et al.* 2004), or microfungi (Nováková 2009). Notable exceptions are recent surveys undertaken of fungal communities in the Kartchner Caverns in Arizona, USA (Vaughan *et al.* 2011) and in southwestern Puerto Rico (Nieves-Rivera *et al.* 2009). Nieves-Rivera *et al.* (2009) reported 19 Basidiomycota and three Ascomycota macrofungi species from three cave systems representing several genera including *Auricularia*, *Collybia*, *Geastrum*, *Lepiota*, *Mycena*, *Xylaria*, and *Ramaria*. Fungi were located below natural skylights or sinkholes and were not considered coprophilic or guanophilic by the authors, but rather saprotrophic (SAP) or edaphic and associated with decomposing plant matter buried in bat guano. The current observation of the truffle-like fungi *S. bougheri* provides a further novel account of a macrofungus fruiting in a cave environment and suggests future exploration and studies of cave environments should be aware that macrofungi may be present.

Little is known of the biology of *S. bougheri* apart from being associated with eucalypts in Australian forests and plantations in Brazil, native to the former and introduced to Brazil (Giachini *et al.* 2000). The gasteroid genus *Scleroderma* (family Sclerodermataceae) includes both epigeous and truffle-like taxa and has a pan global distribution comprising 35 described species (Chen 2006; Watling 2006; Nouhra *et al.* 2011a). Several species within the genus *Scleroderma* are confirmed to be EcM (Tedersoo *et al.* 2010), mycorrhizal symbionts of a broad range of host tree species, including eucalypts (Dell *et al.* 1994; Chilvers 2000; Chen 2006; Nara 2009; Sanon *et al.* 2009). These observations have led to assertions that species within the genus are EcM (Chen 2006; Phosri *et al.* 2009). It is unknown whether *Scleroderma* is a non-monophyletic genus and more likely to also include species with a divergent saprobic lifestyle such as *Endogone* that includes both EcM and SAP species (Tedersoo *et al.* 2010).

EcM fungi are generally reliant on their plant hosts for carbohydrates while SAP fungi can obtain sugars through the breakdown of non-living structures. Basidiomycete truffle-like fungi have been considered to have generally obligate EcM associations with plants, with the formation of ectomycorrhizae thought to be essential for fungal colony maturation and reproduction (i.e.

sporocarps) (Claridge *et al.* 2000b; Bougher & Lebel 2001). In a review of truffle-like taxa in the Pacific North-West region of the United States, only three species (<1%) out of 350 were considered likely to have a SAP life strategy, just one of which (*Agaricus inapertus*) belonged to the Basidiomycota (Trappe *et al.* 2009b). Only a single sequestrate species, *Guyanagaster necrorhiza* from South America, is confirmed to have an obligate SAP lifestyle. Although placed in its own genus, *Guyanagaster necrorhiza* was found to be most closely related to *Armillaria* which shares a wood-inhabiting life strategy but differs markedly in sporocarp morphology: having epigeous, stipitate, and gilled sporocarps.

Although one fungal colony was found in direct association with microbat guano and another had no observable hyphal connection to a plant-root system, it is doubtful that *Scleroderma bougheri* fungal thallus observed was living as a free-living saprophyte in association with bat guano or any other organic nutrient source. As all known truffle-like *Scleroderma* taxa are considered EcM, this would require a reversal from the ectomycorrhizal condition and recent evidence suggests this is highly unlikely (Martin *et al.* 2010; Tedersoo *et al.* 2010; Wolfe *et al.* 2012).

Reviews of EcM lineages and the trophic status of non-mycorrhizal sister taxa suggest that the majority of EcM lineages evolved from SAP ancestors (Hibbett *et al.* 2000; Tedersoo *et al.* 2010). This is supported by more recent molecular studies including evidence from a multi-gene phylogeny of the genus *Amanita*, which found a single SAP origin for EcM taxa within the genus (Wolfe *et al.* 2012). The EcM symbiosis has evolved independently across many fungal lineages, possibly at least 11 times in the Agaricales and without exception, from SAP ancestors (Matheny *et al.* 2006).

The potential for EcM lineages to exhibit reversals to a SAP condition and the related evolutionary stability of the EcM symbiosis has been a source of considerable debate in recent years. Transitions (i.e. reversals) from an EcM to SAP nutritional mode in several fungal lineages were initially suggested by the first large-scale phylogeny of EcM and SAP homobasidiomycetes (Hibbett *et al.* 2000). However, this finding was subsequently challenged based on the poorly resolved sampling and analytical techniques (Bruns & Shefferson 2004; Tedersoo *et al.* 2010; Wolfe *et al.* 2012). In a more recent phylogenetic analysis, Tedersoo *et al.* (2010) found no evidence for reversal to non-EcM lifestyles amongst a large number of lineages.

Additional evidence for the stability of the EcM mutualism and unlikely scenario of reversals to a free-living SAP state has come from a comprehensive multi-gene phylogeny for the genus *Amanita* (Wolfe *et al.* 2012) and genomic sequencing of the EcM truffle fungi *Laccaria bicolor* and *Tuber melanosporum* (Martin *et al.* 2010). Wolfe *et al.* (2012) found that decomposition pathways were irreversibly lost along EcM lineages in the genus *Amanita*, suggesting reversals from EcM to SAP are highly unlikely. Two cellulase genes critical in the extracellular decomposition of organic

matter were found to be lost in association with the EcM mutualism and marking the transition from saprotrophic decomposition of complex dead organic matter (SAP) to dependence on plant hosts for the supply of carbon (EcM). Similarly, genomic sequencing of the EcM fungi *Laccaria bicolor* and *Tuber melanosporum* found a reduced spectrum of enzymes involved in the breakdown of plant cell walls and the loss of critical exocellulase CBHI cellobiohydrolases in the genome sequences suggesting the inability to function independently as saprotrophs (Martin *et al.* 2010). Some potential for extracellular breakdown of simple organic matter was found in many *Amanita* species by the retention of a third gene involved in later stages of cellulose decomposition (Wolfe *et al.* 2012). Nonetheless, this recent evidence strongly suggests EcM fungi are unlikely to be able to acquire significant amounts of carbon from saprotrophy but rather are dependent on their plant hosts.

Based on this recent evidence, it is unlikely that organic matter was supplying significant carbohydrates to the observed *Scleroderma bougheri* colony. Although no hyphae were observed extending beyond the main colony, the hyphae and thallus of the fungus could be connected to plant roots by extraradical hyphae, which are difficult to discern on substrates due to loss of coloration and structure (M. Castellano pers. comm.). Consequently, *Scleroderma bougheri* should be considered trophically mycorrhizal and was in this case likely to be using plant-derived carbohydrates to "mine" organic material in the form of bat guano.

Microbat guano is a rich source of nutrients (Shahack-Gross *et al.* 2004; Ribeiro *et al.* 2012) and is important in sustaining populations of troglophiles and troglobites in cave environments including coprophilous fungi (Ferreira *et al.* 2000; Nieves-Rivera *et al.* 2009; Kunz *et al.* 2011). Fungal richness has been found to be greater on sediment and guano surfaces compared to mineral surfaces (Vaughan *et al.* 2011), with bat guano considered to be a rich media for fungal growth in cave environments (Nieves-Rivera *et al.* 2009). Fresh guano has an organic matter content of 53-56% by weight and is high in protein and iron. The most abundant elements in microbat guano are nitrogen (8-12%) and phosphorus (2-7%), associated with an insectivorous diet and abundance of chitin. The availability of aluminium (Al), potassium (K), and iron (Fe) increases with organic matter degradation while bacteria are likely important in the chemical diagenesis of sulphur (Kajihiro 1965; Shahack-Gross *et al.* 2004; Ribeiro *et al.* 2012).

EcM fungi play an important role in the mobilisation of nutrients to plant hosts including organic forms of nitrogen, phosphorus and potassium (Bending & Read 1995; Perez-Moreno & Read 2000; Read & Perez-Moreno 2003). High levels of nitrogen are required for EcM fungal metabolism and as a resource for host plants (Talbot & Treseder 2010). The EcM symbiosis has been shown to increase phosphate accumulation in eucalypts and increase growth where phosphorous availability is limited in the external environment (Malajczuk *et al.* 1975; Bougher *et al.* 1990; Pampolina *et al.*

2002), a characteristic feature of Australian soils (Wild 1958). Higher nitrogen availability has recently been associated with lower EcM hyphal foraging and nitrogen uptake (Nave *et al.* 2013). In nutrient poor soils, EcM mycelia may extend further to exploit patchily distributed pools of nitrogen, as may be case within the studied cave system. Microbat guano likely represented a rich pool of nitrogen, phosphorous, proteins and other trace mineral elements for the observed *Scleroderma bougheri* colony to exploit.

A broad range of extracellular enzymes can be produced by EcM fungi to extract nitrogen, phosphorous, and sulphur from organic sources (Talbot & Treseder 2010). Some cultural studies have shown that EcM fungi, including the sequestrate *Rhizopogon luteolus*, can utilise a wide range of carbon sources and have retained some ability to produce enzymes that can degrade plant cell walls (cellulose, pectin, and lignin) and may act saprotrophically in the soil (Lamb 1974; Hibbett *et al.* 2000; Talbot *et al.* 2008). Although the ecological importance of cellases secretion by some EcM fungi has been a source of contention among researchers (Baldrian 2009), it is being increasingly realised that mycorrhizal fungi play a role deeper in the soil in the breakdown of organic matter and acquisition and cycling of nitrogen, phosphorous and other organic substrates (Lindahl *et al.* 2007; Theuerl & Buscot 2010; Pritsch & Garbaye 2011).

Fungi also play important roles in the weathering of mineral substrates through the excretion of organic acids and secondary metabolites and physical breakdown of substrates through penetration of fissures and pores in mineral rocks. They are also important in mineral solubilisation, organic matter decomposition, transformation and cycling of organic matter (nitrogen, phosphorous, sulphur, carbon, oxygen, and hydrogen) and the transformation and incorporation of inorganic elements into macromolecules (Gadd 2007). These processes can facilitate the formation of suitable environments and nutrients for other organisms, including those within caves (Vaughan *et al.* 2011).

It is unknown whether the unique environmental conditions within the cave (e.g. high humidity, stable warm temperatures, low evaporation and mycophagous insect activity) were necessary for *Scleroderma bougheri* to exhibit mycelial growth and fruiting in an exposed situation above the cave-floor. These unique conditions combined with a rich nutrient source (bat guano) may in-part encourage fungal mycelial development and fruit-production (Nieves-Rivera *et al.* 2009). Germination and mycelial growth of several *Scleroderma* species has previously been achieved under similar conditions in the laboratory when provided a rich nutrient source, although colonies were small and were not reported to produce sporocarps (Chen 2006). Germination on artificial media is an uncharacteristic feature across EcM taxa (Tedersoo *et al.* 2010) although it is common in some groups. Such conditions are unlikely to be met in terrestrial environments and it is unknown whether *S. bougheri* can exploit organic substrates to the same degree under normal field

conditions.

The fruiting of *S. bougheri* in a cave environment on a flat sedimentary surface provided a unique observation of thallus structure and sporocarp production. Interestingly, sporocarps were arranged along the growing front of the fan-shaped thallus and at relatively even intervals, maximising the distance of fruit bodies from the point of initial growth and dispersal opportunities. Sporocarps were generally associated with more dense areas of mycelial growth, perhaps supporting sporocarp growth. Droplets of liquid observed on sporocarps may have been the result of condensation in the moist cave environment or possibly an exudate of the fungus itself, possibly an attractant for mycophagous animals, although this requires further investigation.

Microbat spore dispersal

Preceding growth of *S. bougheri* colonies within the cave, dispersal may have occurred through movement of water washing spores downwards into the cave from a soil spore bank above or via an animal vector. Clonal growth is also conceivable through the dispersal of mycelia into the cave from plant root systems penetrating the cave roof. Roots of eucalypt trees colonised by EcM fungi have been observed penetrating limestone caves in Western Australia (Lamont & Lange 1976). Alternatively, spores may have been dispersed by mycophagous insects such as beetles (Coleoptera) or springtails (Collembola), both of which have been recorded in the Timor Caves (Moore 1964; Bougher & Lebel 2001). However, the close association between bat guano and one *S. bougheri* colony suggests spores may have originated from microbat scats. Cave-roosting microbat species recorded within the Timor local area include *M. schreibersii oceanensis* and *Rhinolophus megaphyllus* (Atlas of NSW Wildlife; K. Downs pers. comm.). The discovery of both epigeous and truffle-like macrofungal spores in the scats of several microbat species, including the cave-roosting *M. schreibersii oceanensis*, allows for the possibility that spores of *S. bougheri* may have originated from microbat faeces and germinated and developed in-situ.

However, the viability of spores after passage through microbat guts is unknown and further research is required to establish whether spores remain viable post microbat gut-passage. Essential processes required for spore germination in truffle-like fungi are unknown although passage through animal guts has been observed to improve in some cases spore metabolic activity or mycorrhizal infection rates of plant-host roots (Colgan III & Claridge 2002; Caldwell *et al.* 2005). A dormancy period coupled with microbial activity has also been suggested as a prerequisite for germination, processes thought to facilitate a breakdown of the spore wall. Recently, a dormancy period was established for several truffle-like *Rhizopogon* species in which host-colonisation rates increased with time (Bruns *et al.* 2009). Microbial activity is likely to be high in bat guano due to high organic matter content (53-65%), and high nitrogen and phosphorous levels although the latter

may inhibit EcM formation; Shahack-Gross *et al.* 2004). Although these processes may not be explicitly required in *Scleroderma*, as several Australian species of *Scleroderma* have been shown to germinate and produce mycelia in artificial growth media in the absence of plant hosts, they may facilitate higher germination rates compared to that found in culture studies (Chen 2006: 0.1-0.8%; Nara 2009).

The discovery of fungal spores, particularly those of truffle-like fungi, in microbat diets was a surprising discovery to me. Most species contained at least some taxa suggesting the source of spores should be via a cosmopolitan dietary item shared amongst species. Direct consumption of fungal sporocarps is considered highly unlikely considering that no species are recorded as consuming macrofungi in Australia and only a small proportion of species (*Mormopterus* and *Nyctophilus* species) are recorded foraging on the ground in Australia. As the majority of Australian microbats are insectivorous, the main prey items being moths (Lepidoptera), bugs (Hymenoptera), and beetles (Fullard *et al.* 1991; Churchill 2008), the source of fungal spores is most likely through the consumption of mycophagous insects. Many invertebrate taxa are known to be mycophagous including springtails, crickets, millipedes, snails, aphids, and beetles (Bougher & Lebel 2001; Lilleskov & Bruns 2005). The mycophagous habitats of beetles are particularly well-documented (Epps & Arnold 2010) and have been observed consuming many species of truffle-like fungi in this study (AO pers. obs.) and elsewhere, including sporocarps of *Scleroderma* species (Fogel & Peck 1975; Claridge 2002; Houston & Bougher 2010). The dominance of truffle-like taxa compared to epigeous taxa suggests they are more frequently consumed by mycophagous insects preyed on by microbats. Lilleskov and Bruns (2005) have shown that numerous insects consume truffle-like fungal spores and that gut passage through some insect guilds does not damage the spore nuclei. Furthermore, gut passage through at least one taxa (a millipede) was found not to inhibit germination and subsequent EcM colonisation of a host plant. In contrast to Houston and Bougher (2010) observations of fungal spores in bolboceratine beetle faeces, only a small proportion of spores sampled from microbat diets in this study were observed to have damaged walls and loss of their cytoplasm. Although not conclusive evidence for spore viability, it suggests that viability should not be precluded and tested further to ascertain whether microbats are dispersers of viable spores.

Insectivorous microbats predominantly forage amongst the shrub and tree canopy strata with prey items caught in flight or through gleaning (Churchill 2008). Vertical partitioning of foraging microhabitat has been shown for one Australian community of microbats (O'Neill & Taylor 1989) suggesting that variation may exist among species in the likelihood of spore deposition directly at the soil-litter surface and hence in microhabitats favourable to spore germination and mycelia growth. However, even where vertical partitioning occurs, the majority of microbat species can be

caught in harp traps positioned at 1-3m above ground-level (Churchill 2008), suggesting that most do venture close to the ground and can deposit spores on the ground. In addition, microbat faeces are highly friable and likely to eventually fall on the forest floor.

It is interesting that two of the largest microbat species sampled, *F. tasmaniensis* (16.0-28.5g; Figure 6.6) and *M. schreibersii oceanensis* (8.6-19.5g[1]; Figure 6.6), had scats containing the largest number of fungal taxa. *M. schreibersii* is recorded as feeding mostly on moths (Milne *et al.* 2006) while *F. tasmaniensis* is recorded as a selective feeder in Tasmania (O'Neill & Taylor 1989), with Coleoptera (beetles) the main prey item (75%). Both *Nyctophilus* species are also recorded to have a high percentage occurrence (≈28-42%) of beetles (Family Scarabaeidae, Order Coleoptera) in their diets, as are three of the *Vespadelus* species sampled (>10% faecal volume; Lumsden & Bennett 2005) suggesting a higher likelihood of secondary spore dispersal through consuming these mycophagous insects. Geographic variation within many microbat species diets suggest they feed opportunistically, with relative consumption of insect prey reflecting insect availability (O'Neill & Taylor 1989). Both *N. gouldi and N. geoffroyi* are gleaners (twigs and barks and leaves) and ambush predators that are reported to occasionally forage on the ground for insects (Churchill 1998) suggesting they may more frequently encounter mycophagous insects. Both species are also known to forage low to the ground (2-5 m) amongst the shrub strata (O'Neill & Taylor 1989; Brigham *et al.* 1997) making them more likely to deposit spore-containing scats directly on the forest floor than higher flying species.

Figure 6.6 Photographs of the large-bodied eastern falsistrellus *Falsistrellus tasmaniensis* (left) and the migratory eastern bent-wing bat *Miniopterus schreibersii oceanensis* captured within the study area (right).

Secondary dispersal of plant seeds is recognized as an important process (Nathan & Muller-Landau

[1] range of weights recorded for Victorian and northern Australia *'Miniopterus schreibersii'* (Churchill 1998)

2000) but few cases of secondary dispersal have been reported for fungi. The northern spotted owl *Strix occidentalis caurina* is thought to disperse fungal spores through preying on the mycophagous northern flying squirrel *Glaucomys sabrinus*, a process also assumed to occur between other mycophagous mammals and their predators (Trappe & Claridge 2010). In Australia, secondary dispersal has been suggested for the sooty owl *Tyto tenebricosa* preying on the mycophagous smoky mouse *Pseudomys fumeus* (Luoma *et al.* 2003). Generally, top predators have much larger home range and daily movements than their mammalian prey, and therefore can facilitate longer range dispersal of spores than the latter alone can accomplish. Secondary dispersal can also alter the spatial arrangement of propagules (i.e. seeds or spores) to sites more amenable to establishment, such as the case of dung beetles processing the scats of mycophagous mammals and incidentally transporting spores down into the soil profile (Johnson 1996).

Based on the low spore density and taxon richness in microbat diets compared to major terrestrial mycophagous mammals encountered in this study (Figure 6.5 and Chapters 2-5), microbats are unlikely to play a significant role in short-distance spore dispersal and maintaining assemblages of truffle-like fungi at a small scale. In addition, low spore concentrations in faeces could influence dispersal success relative to other mammals as EcM colonization of plant roots has been shown to decrease with spore concentration in some truffle-like taxa (Bruns *et al.* 2009). Consequently, they would be considered 'non-standard' dispersal vectors for fungi (see Glossary). However, several ecological traits of microbats suggest they may play a significant role in long-distance dispersal (LDD) events for truffle-like taxa. Rare LDD events are thought to play a role in the biogeographic range of plant species through the dispersal of plant seeds via animal, wind, or water vectors, disproportionate to its frequency (Cain *et al.* 1998; Nathan *et al.* 2003). They are also important in gene exchange among populations, range expansion, and the distribution and range of sessile organisms. Although microbats may not disperse large numbers of spores, infrequent successful LDD dispersal and establishment events can have a large impact on these processes (Vellend *et al.* 2003), and dispersal distances through microbats are likely to be considerable. Dispersal distances are estimated by the time it takes a spore to pass through an animal's gut (i.e. 'passage time' or 'retention time') and the distance the animal has moved in the intervening time since ingestion ('displacement distance') (see Chapter 5).

Microbats are a highly mobile group of vertebrates compared to many other terrestrial mammals (Milne 2006) including other vertebrate mycophagous species. Microbat species move considerable distances between roost sites and foraging areas, among roost sites, during foraging, and via (in some species) migration events. Large movement distances between roost and foraging areas have been recorded for Australian *N. geoffroyi* (males: 1.9km; females: 6.7 km) and *Chalinolobus gouldii* (6.9 ± 1.6 km) with maximum distances of 10 km and 11 km respectively (Lumsden 2004).

Overseas, movements between roost and foraging areas of 200 m to >20000 m have been recorded for species of insectivorous microbats (Meyer *et al.* 2005b; Monadjem *et al.* 2009). Individual microbats also move considerable distances among numerous roost sites over short periods of time. For example, lactating female *N. geoffroyi* are recorded moving an average of 489 m ± 119 m (range: 28-2454 m) between consecutive roosts within a 15 day period (Lumsden 2004). Although few home range (HR) studies have been undertaken on microbats, they vary from 5.3 ha to 1589 ha, with the Australian *Chalinolobus gouldii* estimated to have a very large average HR of 698 ha (Kirsten & Klomp 1998). In New Zealand, *Chalinolobus tuberculatus* have impressive home range sizes of 1589 ha (males) to 1361 ha (females) with frequent movements over considerable distances, averaging 790 m per 15 minute interval (measured along a straight line trajectory), within their range (O'Donnell 2001). Although core activity areas were much smaller, these areas shifted on a nightly basis. Many microbat species have evolved physical traits enabling them to undertake long-distance migrations (maximum movement: 35-1900 km; Fleming & Eby 2003) to maternity roost sites, including the Australian *M. schreibersii* which moves hundreds of kilometres between wintering roost sites and maternity roosts (Dwyer 1966; Law *et al.* 1999). Flight speed can also be fast in Australian species, with *M. schreibersii* recorded flying at an estimated 50 km per hour (Churchill 1998). Considering the fast metabolic rates and high energetic costs of flight in microbat species (Morris *et al.* 1994), opportunistic predation is likely to occur during all forms of flight and hence the potential for spore dispersal via the consumption of spore-laden mycophagous insects.

Using marked pollen grains (20-75 μm in diameter) of native Australian plant species, Morris *et al.* (1994) reported a mean retention time (MRT; an estimation of the average time food particles take to pass through the digestive tract) of 5.38±0.57 hrs for *N. gouldi*, with first-passage at 1.34 hrs and the majority (70%) of pollen grains voided by 3.66 hrs. The decrease in spores concentration was negatively exponential, exhibiting a long tail, with spores (1-2%) continuing to be voided 10-25 hrs post ingestion. Compared to MRTs recorded in ground-dwelling mycophagous mammals (6.6-55.5 hrs) and those for the swamp wallaby (26.9-35.1 hrs; Danks 2012), microbat MRT is short. This is not surprising given that microbats are among the smallest-sized mammals and mean retention time scales positively with body size (White & Seymour 2005). Nonetheless, the reported microbat MRT is sufficient for spores to be transported considerable distances, perhaps several to tens of kilometres, from the fungal parent and many times that facilitated by swamp wallabies (Chapter 5).

Along with potential for dispersing spores long distances, several other ecological and biogeographic features of this group increase their potential as important spore dispersal vectors. Firstly, microbats have high habitat plasticity and a higher tolerance of fragmentation than many other faunal groups (Law 1996) suggesting they can disperse spores across vegetation boundaries

and among isolated patches in fragmented landscapes. Consequently, microbats may play some role in maintaining genetic exchange and recolonisation in landscapes where natural terrestrial mycophagous dispersers have declined or become locally extinct, much in same way that the exotic black rat *Rattus rattus* in Australia has been implicated in this process at a smaller spatial scale within fragmented landscapes (Vernes & McGrath 2009). In the Australian context, this is particularly important, as many 'critical-weight-range' (350g-5500g) terrestrial mammals have undergone severe declines since European settlement, a number of which are mycophagous mammals with large home ranges (e.g. *Bettongia* spp Johnson & Isaac 2009).

Considering the chronology of microchiropteran evolution, high mobility and insectivorous habit of most species in this group, and adaptation to long-distance migration in some, this fauna group may also be important in the biogeography of truffle-like fungi. Microbats have a global distribution with many genera represented across several continents, and are an ancient lineage with an origin potentially as far back as the early Palaeocene (65.5-55.8 Mya). The oldest fossil of an insectivorous bat is dated at 52.5 Mya during a period (52-50 Mya) of microbat diversification coinciding with an increase in plant diversity and insect diversity (Teeling *et al.* 2005; Miller-Butterworth *et al.* 2007; Conner & Corcoran 2012). Recent work on the phylogeny of the truffle-like order *Hysterangiales* suggest a requirement for transoceanic LDD vector to explain similarity among Australian and New Zealand taxa (Hosaka *et al.* 2008), a process also thought to be essential in explaining similarities in other fauna groups (McDowall 2008; Hand *et al.* 2009). Insects undoubtedly play a significant role in spore dispersal, although few other vertebrate fauna with the exception of birds could provide similar scale LDD events as microbats, particularly during microbat migration events. Consequently, microbats may have played some role in past biogeographic events shaping the current distribution of truffle-like fungi.

Limitations and further research

As microbat sampling was not designed to estimate diets, individuals were not retrieved immediately post-capture. Considering the estimated fast gut passage time for microbats (70% of pollen markers voided by the 5 hr mark; Morris *et al.* 1994) and that animals may have been in traps for several hours prior to placement in individual bags, the majority of spores may have passed prior to sampling - being deposited in the harp trap. In addition, if insects were the original source of fungal spores, the season in which sampling of microbats was undertaken may have further underestimated the general frequency of fungal spores in their diets. Insect activity was observed to be highest within the study area during late spring to late summer, declining towards the colder late summer to autumn months, during which sampling was undertaken. Ideally sampling of microbat diets would be undertaken during peak abundance of insects and particularly of Coleoptera species.

The potential for *Scleroderma bougheri* to exploit microbat guano as a source of nutrients requires confirmation through field sampling and experiments (Mayor *et al.* 2009). Further investigation on the frequency, extent, and success of microbat spore dispersal would provide useful insights into this novel relationship. Studies of spore viability post microbat gut-passage and subsequent host-plant infection rates would confirm these mammals as potential vectors. Sampling of microbat diets at a larger spatial scale, both at the regional and continental, and across varied habitat types would allow an assessment of how common this trophic interaction is. Finally, estimations of spore dispersal distances would allow comparisons to other animal vectors in the relative importance microbats play in LDD events in macrofungi.

Chapter 7. Synthesis

This study explored spatial patterns in species richness and assemblage structure of truffle-like fungi and dispersal dynamics involving mammal vectors. Patterns in species richness, composition and assemblage structure were explored among four broad habitat types. In three habitats confirmed to support diverse fungal assemblages, patterns in mycophagous habits and dispersal roles of mammals were explored. The results of sporocarp and dietary surveys were also compared to determine whether sampling mycophagous mammal diets could detect spatial trends in truffle-like taxon richness, abundance, and composition or reveal additional information on spatial trends or the efficacy of sporocarp sampling. Dispersal services provided by one major standard mammal dispersal vector, the swamp wallaby, was explored in detail by sampling diets and modelling movement behaviours and patterns of spore deposition facilitated by the species. Finally, the thesis reports on a novel discovery of a group of mammals (microbats) dispersing truffle-like fungal spores and their potential importance as non-standard dispersal vectors and facilitators of LDD events. The first account of a truffle-like fungus fruiting in a cave environment is also reported. Implications of these findings for the life history, ecosystem function, and biogeography of truffle-like fungi are discussed.

This chapter summarises the main findings of the study, a synthesis of the major themes, and resulting conservation management implications and ecological insights into mammal-fungi interactions.

Species richness was found to vary spatially by broad habitat type

In Chapter 2, a snapshot study of truffle-like fungi found observed and estimated local scale species richness was very high by global standards. Estimates of species richness from sporocarp surveys and the taxon richness observed in mammal diets were also high by global standards and confirm extraordinary diversity of this group on this continent. Comparisons to vascular plant diversity within the study area also illustrated the high diversity of fungal species estimated to occur within habitats. The many new species discovered coupled with the low sampling completeness suggested many more species yet remain undetected, highlighting our limited knowledge of truffle-like taxa in Australia. Most taxa belonged to the Basidiomycota and typical of EcM fungal communities, rare taxa dominated assemblages, a characteristic most pronounced in wet sclerophyll.

Sporocarp surveys revealed marked differences in total observed and estimated (Jackknife2) fungal richness among four contrasting habitat types following a gradient of wet sclerophyll>heathy woodland>dry forest>rainforest (Chapter 2). Wet sclerophyll was found to support a significantly

higher level of species richness than two other co-occurring eucalypt dominated habitats. In contrast, rainforest habitat sampled within the study area was found to be depauperate in EcM fungi, likely due to the monodominance of an AM forming tree species. Although the comparatively higher richness in wet sclerophyll was maintained by Jackknife2 estimates derived from mammal diets (Chapters 3 and 4), all mammal diets (pooled small mammal, bush rat, and swamp wallaby) indicated dry forest supported a much higher richness than heathy woodland, suggesting richness in the former habitat was under-estimated by sporocarp surveys. Both sporocarp surveys and diets corresponded in predicting a much higher richness in mesic wet sclerophyll compared to the most xeric habitat, heathy woodland. Consequently, local scale richness of truffle-like fungi may vary spatially according to marked changes in habitat structure, in turn reflecting contrasting biotic and abiotic conditions and characteristics. Results demonstrated that the natural landscapes studied are composed of discrete patches of habitat varying in their suitability for fungal establishment and proliferation.

Truffle-like fungi may form distinct assemblages by broad habitat type

Sporocarp surveys found some habitats to support distinct assemblages of truffle-like taxa (Chapter 2). Differences among habitats in species composition largely mirrored those exhibited in species richness. Assemblage differentiation was greatest at the genus-level, with wet sclerophyll and rainforest exhibiting the greatest within-habitat similarity and dissimilarity from other habitats. Both sporocarp surveys and analysis of individual swamp wallaby scats (Chapter 4) suggested high similarity between heathy woodland and dry forest despite marked differences in biotic and abiotic characteristics including plant composition and soil type. However, species-rich bush rat diets and grid-replicates of swamp wallaby diets suggested all three eucalypt-dominated habitats differed significantly in composition, including dry forest and heathy woodland, indicating each supports a distinct fungal assemblage. Previous recommendations for a habitat- or assemblage-based conservation management approach for truffle-like fungi are supported by these findings.

A large number of species and genera were identified as important in differentiating habitat types although this was most pronounced in wet sclerophyll and least in rainforest (Chapter 2). Mammal diets suggested differences between eucalypt-dominated habitats in assemblage structure were complex, driven by a greater number of taxa than suggested by sporocarp surveys. There was some correspondence between sporocarp surveys and mammalian diets in the important genera discriminating habitats and also dominant within habitats, particularly in wet sclerophyll. Some species and genera were strongly associated with specific habitat types while others were equally abundant across all habitats. In addition, the estimated number of species shared among habitats was low (Chapter 2) and the number observed in only a single habitat high (Chapters 2-4). These results suggest some species are habitat specialists (narrow niche range) while others may utilise a

range of habitats (broad niche range). Correspondence between species and genus-level patterns across habitats suggests that some related taxa may share habitat preferences.

Consequently, many truffle-like taxa are not uniformly distributed in the landscape and some may be restricted to certain habitats, having implications for their dispersal dynamics and conservation management. Dispersal by larger-ranging animal vectors, which can disperse spores between discrete patches of suitable habitat, may be more important than previously thought. However, differences in apparent habitat specificity suggest taxa likely differ in the relative importance of endozoochorous dispersal, particularly long distance dispersal (LDD), in maintaining their distributions and gene flow among populations. Composition differences among habitats and possible habitat-restricted occurrence of some taxa suggests habitat heterogeneity is important in the conservation of truffle-like fungi. Protecting and enhancing a broad range of habitats within a reserve network will likely facilitate the conservation of species and the maintenance of natural assemblages and dispersal processes.

Mammals differed in the quantity and quality of dispersal services provided to truffle-like fungi

Several mammal species were identified as possible spore dispersal vectors within the model system (Chapters 3-6). All mammals sampled contained some fungal spores in their diets. Truffle-like taxa dominated the macrofungal spores observed in all mammals sampled and across contrasting habitats in bush rat and swamp wallaby diets. Three of the four small mammals sampled and the swamp wallaby likely have mycophagous habits, ingesting spores directly through consumption of sporocarps.

Each mammal species contributed differently to the dispersal of individual truffle-like taxa and the assemblage as a whole by varying in the quantity, diversity, and composition of spores dispersed. Significant differences were found among small mammal species in the diversity and abundance of spores contained in their scats. They also differed in the composition of truffle-like taxa. Dissimilarities between bush rat and swamp wallaby diets in important taxa discriminating habitats suggested these two species also sampled different taxa or proportions of each within habitats. Although the diversity of spores in bush rat fungal diets was much greater than any other co-occurring species sampled, a greater number of truffle-like taxa were detected collectively across all small mammal diets sampled. For these reasons, naturally diverse mammal communities are likely important to the maintenance of dispersal dynamics in truffle-like fungal assemblages and for individual taxa. Each mammal species sampled also has different niche ranges and microhabitat preferences suggesting a greater diversity of mammalian vectors will facilitate spore dispersal to a greater range of habitats and cater for a greater array of truffle-like taxa with different habitat and

microsite preferences.

The bush rat and swamp wallaby are important standard dispersers for assemblages of truffle-like fungi among varying habitats within their ranges. A high percentage of both species scats contained truffle-like fungal spores, remaining relatively constant across habitats (bush rat: 100%; swamp wallaby: 83-100%). However, the bush rat provided the greatest quantity of spore dispersal services for fungal assemblages compared to all other mammals sampled. Bush rats dispersed a greater diversity and abundance of spores than co-occurring mammals sampled, including 96% of all morphospecies observed across small mammal diets. The average fungal richness in bush rat scats was also greater than that found in swamp wallaby scats in two of three habitats sampled. Spore abundance in swamp wallaby scats was also markedly lower (7 to 10 times) to that found in bush rat scats across all habitats. Based on the lower diversity, abundance, and frequency of spores observed in swamp wallaby scats, they are likely less heavily mycophagous than the bush rat and could be considered an 'opportunistic' consumer of truffles

Some mammals may be stable dispersers across multiple habitats while others may vary in their relative contribution due to changing mycophagous habits according to habitat type, subsequently altering the relative role of different dispersers. Results suggested bush rats broadened the diversity of truffles consumed according to availability. In heathy woodland the average number of taxa found in swamp wallaby scats was similar to that in bush rat scats but was markedly lower in wet sclerophyll and dry forest. At comparable sample size, the total number of observed truffle-like taxa in swamp wallaby diets was much lower than in bush rat diets in both dry forest and wet sclerophyll habitats, but was greater in heathy woodland. Mycophagy by the swamp wallaby appeared to follow an opposite trend to sporocarp availability among habitats, potentially reflecting a mixed feeding strategy. Lower consumption in wet sclerophyll may also have been a response to higher nitrogen availability in plant dietary items or a more dispersed pattern in truffle food resources. These results suggest bush rats are a stable primary dispersal vector across habitats while the contribution of swamp wallabies varies by habitat, being most important in heathy woodland and least in wet sclerophyll habitats.

Mechanistic models of swamp wallaby spore dispersal predicted most spores to be dispersed >100 m and many >250 m (Chapter 5). These large dispersal distances may be sufficient to remove spores away from any competitive or density dependent processes near the parent source that could inhibit recruitment success. Maximum dispersal distances facilitated by the swamp wallaby are several times greater than the linear width of small mammal home ranges within the model system. Estimated spore dispersal distances, spatially explicit models of spore deposition, and evidence for frequent movement between different habitats showed that wallabies are likely to facilitate movement of spores between discrete patches of similar habitat and also across habitat boundaries.

The swamp wallaby may also facilitate some level of directed dispersal of spores into habitats more suitable to establishment.

Consequently, the swamp wallaby likely plays a key role in the maintenance of fungal assemblages and successional dynamics at larger spatial scales than bush rats. This may be important in maintaining species distributions by aiding the (re)colonisation of areas after disturbance events (i.e. fire), successional dynamics, and gene flow among disjunct populations. In turn, swamp wallaby facilitated spore dispersal is an important process for maintaining the distribution and health of EcM plant hosts. The swamp wallaby may also disperse spores among dissimilar habitats, facilitating dispersal for taxa with broad habitat associations. The swamp wallaby also likely plays a pivotal role in maintaining the distribution of truffle-like taxa, particularly those with a narrow niche range. Mycophagous macropods such as the swamp wallaby play a greater role in determining dispersal limitation in truffle-like fungi, gene exchange among populations, and dispersal between habitats than smaller co-occurring ground-dwelling mammals. In comparison, bush rat spore dispersal may be more important for small-scale dispersal dynamics within habitats and dispersal of spores across ecotonal boundaries, facilitating expansion or contraction of EcM dominated plant communities (Vernes & Dunn 2009) but also contributing to maintaining the distribution of truffle-like taxa with broad niche ranges.

Swamp wallaby facilitated LDD of spores is a potentially important process in establishing and maintaining the biogeographic range of some truffle-like taxa. Both 1D and 2D mechanistic models predicted the swamp wallaby can facilitate rare LDD events of considerable scale (>1 km), far exceeding potential maximum dispersal distances facilitated by small mammal species within the model system. Fatter-tailed 1D kernels were also predicted for some animals suggesting potentially more frequent LDD events than predicted by the overall model. Rare LDD events could also play an important role in gene flow among disjunct populations of truffle-like taxa with narrow niche ranges and strongly associated with more spatially restricted habitats.

Microbat spore dispersal may also contribute to gene flow among disjunct populations but at a greater spatial and temporal scale, such as range expansion, landscape-scale gene flow, and larger-scale biogeographic patterns and events (Chapter 6). Examination of microbat diets revealed that several microbat species may disperse macrofungal spores, dominated by those of truffle-like taxa. A total of 34 to 42 fungal taxa were estimated to occur across microbat species diets. Spore abundance and diversity was very low compared to bush rats and wallabies diets although frequency and diversity was similar to the insectivorous brown antechinus *Antechinus stuartii*. Like the latter species, the origin of spores was likely through the consumption of mycophagous insects. Primary consumption by insects is an essential process for secondary dispersal of spores by microbats. Based on home range size estimates, flight speeds, nightly foraging movements, and

gut-retention times reported in the literature for microbat species, maximum spore dispersal distances for some microbat species are likely to greatly exceed those facilitated by the swamp wallaby, perhaps by an order of magnitude. In addition, several traits of microbats suggest they play an important role in LDD events for truffle-like fungi including high habitat plasticity, tolerance of habitat fragmentation, ancient lineage and in some species, migratory behaviour. Consequently, microbats may be important non-standard LDD vectors of truffle-like fungal spores at larger spatial scales than the swamp wallaby or similar-sized macropods, although the influence of small numbers of spores on dispersal success requires further investigation. This study also suggests there may be spatial nestedness in dispersal roles of mammalian groups such as small mammals, macropods, and microbats in Australian ecosystems. Further research is required to explore whether these species could be an important dispersal vector in shaping distribution patterns in fungi and past biogeographic events.

The dispersal distances facilitated by the swamp wallaby suggests dispersal limitation and spatial genetic structuring may be more pronounced in Australia compared to continents with larger-ranging or migratory ungulates. Consequently, genetic differentiation may occur at smaller spatial scales, a potential driver for high species richness and endemism through lower rates of gene exchange. However, dispersal limitation and genetic structuring could occur at much larger spatial scales if microbats are found to be significant dispersers of viable spores to microsites suitable for establishment.

In natural environments, truffle-like taxa with narrow niche ranges may benefit most from swamp wallaby and microbat spore dispersal. Spore dispersal services provided by mycophagous macropods and microbats may also be relatively more important in current times due to the absence or reduced abundance of several more heavily mycophagous mammals likely to confer considerable dispersal distances for a large proportion of truffle-like taxa. However, a number of shared traits of the swamp wallaby and microbats suggest they play an important role in the persistence of truffle-like fungi in modified landscapes characterised by habitat fragmentation. The considerable spore dispersal distances potentially facilitated by these animal vectors combined with their high habitat plasticity, wide distribution, and comparatively high tolerance to habitat fragmentation make them ideal candidates for the movement of truffle-like fungal spores and genes among otherwise isolated populations and assemblages. Consequently, the conservation of both the swamp wallaby and microbats may be crucial in fragmented landscapes for the long-term persistence of fungal and their symbiotic host-plants.

Models of swamp wallaby spore dispersal predicted an aggregated spatial pattern of spore deposition that was strongly correlated with animal space use

Results suggested swamp wallabies may generate an aggregated pattern of spore deposition, potentially influencing subsequent spatial patterns of recruitment. Both movement behaviour and 2D mechanistic models of swamp wallaby spore dispersal predicted spatial aggregation of dispersed spores. Movement trajectories were more similar to a Levy walk than a random walk which can result in non-random, clumped distributions in spore deposition. Such a pattern was suggested by 2D dispersal kernels generated by individual animals which exhibited strong anisotropy and predicted a clumped (i.e. aggregated) distribution of spores in space. A similar pattern was suggested by an overall 2D model of spore deposition from a single parent source. Deposition into a long-lived spore bank may increase the likelihood of spore dispersal being a strong deterministic process influencing patterns of recruitment. Spore concentration has been associated with increased colonisation of host-plant root systems in four related (*Rhizopogon*) truffle-like species (Bruns *et al.* 2009). Consequently, aggregation of spores could increase colonisation rates and result in a heterogeneous spatial pattern in recruitment. Such a pattern in spore deposition may be one explanation for observed spatial patchiness in truffle distributions.

Patterns of spore deposition were strongly correlated with movement behaviour and space use. The close correspondence between frequency distributions of spore dispersal and net displacement suggested movement behaviour may be a greater influence over swamp wallaby spore dispersal distances than gut-retention time. In addition, patterns in animal space use were strongly correlated with predicted patterns of spore deposition, providing further evidence for the potential importance of animal movement behaviour in determining spore dispersal patterns. Average cumulative net displacement corresponded with the mode of 1D dispersal kernels at ≈250 m. An upper threshold of ≈600m for net displacement also matched the spatial extent in which the majority of spores were predicted to be dispersed. Not surprisingly, spatially explicit mechanistic models predicted the majority of spores would be dispersed within each animal's core foraging range (KDE95) while the MCP home range estimate provided a good estimate of maximum spore dispersal distance. Considering these results, inferences on the relative scale and pattern of spore dispersal facilitated by different mammals could possibly be made based on the home range size, movement behaviour, and space use of individual mammalian vectors. However, further testing of this hypothesis is likely required as the relative importance of gut-retention to movement behaviour in determining dispersal patterns may vary by species.

Time-census surveys of sporocarps and sampling of mammal diets can provide ecological insights into the spatial distribution of truffle-like fungi and interactions with mammals.

Simultaneous sampling provided insights into the mycophagous habits of the bush rat and swamp wallaby across contrasting habitat types, their contribution to dispersal services for assemblages of truffle-like fungi, and spore dispersal dynamics for some truffle-like taxa. Numerous additional genera were also detected by sampling mammal diets. Sampling diets also provided complimentary data for assessing the validity of conclusions drawn from the results of the sporocarp time-census technique. The much higher representation of some truffle-like taxa in diets compared to sporocarp surveys suggested erosion of standing crops by mycophagous mammals. Consequently, simultaneous sampling of mammal diets allowed a reassessment of the relative abundance of some taxa subject to preferential consumption by animals. Comparisons of sporocarp surveys results to mammal diets revealed an underestimation of relative species richness in one habitat by sporocarp surveys but also provided additional evidence for marked differences between two other habitats (wet sclerophyll and heathy woodland). Diets suggested that different sampling intensities may be required for differing habitat types using the time-census technique. This may be particularly applicable to environments where turning over the uppermost soil-litter horizon is more challenging, such as grassy habitats with more compacted and heavy soils. Diets also indicated taxon composition differences among habitats are more complex than suggested by sporocarp surveys. Simultaneous sampling also allowed an assessment of whether mammal species' diets could detect spatial trends in truffle-like taxon richness and composition.

Both bush rat and swamp wallaby diets provided additional evidence for one eucalypt-dominated habitat (wet sclerophyll) supporting a distinct assemblage of truffle-like fungi. This technique also differentiated two habitats in taxon composition (wet sclerophyll and heathy woodland) which were indistinguishable based on the results of time-census sporocarp sampling technique. Consequently, it is possible diets may be more sensitive in detecting differences among habitats in assemblage composition. Diets provided a different picture of assemblage structure within habitats compared to sporocarp surveys although there was relatively high similarity in dominant genera within habitats estimated by the two different techniques. There was also some correspondence between small mammal diets and sporocarp surveys in estimates of relative species richness within some genera and also important taxa differentiating assemblage composition in wet sclerophyll from other habitats.

Results suggested sampling of bush rat diets, and swamp wallaby diets to a lesser degree, could possibly be used to detect spatial patterns in truffle-like fungal richness and composition. However, the choice of indicator species is an important consideration, as estimates derived from different

mammal species may suggest different trends in richness or composition. Overall, bush rat diets appeared to provide better estimates of species richness, composition, and assemblage structure than swamp wallaby diets even at a much low sample size. The technique was successful in detecting differences in truffle-like taxon composition and diversity among habitats. Bush rats broadened the diversity of taxa consumed according to availability and in one habitat (wet sclerophyll) consumed a number of taxa according to relative availability. Dietary results also corresponded to dominant genera detected in the soil through sporocarp surveys.

Although swamp wallaby diets may also detect differences in richness and composition among habitats they required a large number of samples and higher spatial replication than undertaken in the current study. Swamp wallaby diets may also provide incorrect estimates of taxon richness due to varying mycophagous habits across habitats. However, based on comparisons to results of a previous study (Vernes 2010), they may provide reliable and consistent estimates of genus richness and dominance in more xeric habitats such as heathy woodland. Lower sensitivity of individual scats in detecting composition differences was attributed to species-poor and variable samples, perhaps reflecting the opportunistic mycophagous habits of swamp wallabies and their larger foraging range compared to bush rats. Detection of composition differences among habitats was greatly improved when scat samples were pooled by grid. Greater spatial replication and pooling of swamp wallaby scats is recommended for any future use of swamp wallaby diets to indicate composition differences among habitats in truffle-like fungi.

Results suggest mammal diets could be used in the preliminary identification of potential hotspots of diversity for truffle-like fungi. Results could also guide broad assemblage- or habit-based conservation management actions. As assemblage composition differences among habitats were also reflected at the genus-level, use of diets and analysis at coarser taxonomic resolution could suggest more specific species-level patterns. Combined with molecular tools these techniques could provide significant insights into the spatial and dispersal ecology of truffle-like taxa.

Conservation Management Implications

Our incomplete knowledge of truffle-like fungi and the key ecological processes that enable their persistence poses a great challenge to the conservation management of this group and also the mycophagous mammals dependent on them as a food resource. Although there are significant knowledge gaps, general guidance on appropriate management approaches must be sought and implemented for truffle-like fungi and mycophagous mammals. Appropriate management will benefit not only these two groups but will also assist in the protection of important ecosystems services they provide which contribute to overall ecosystem health. Based on the results of this study and previous research, the following broad management recommendations can be made:

- Previous recommendations for a habitat- or assemblage-based (where broad assemblages are known) management approach for conserving truffle-like fungi should be used (Bougher & Lebel 2001).
- The complex nature of interactions between macrofungi and mammals and poor knowledge at the species-level supports a systems-based approach (Molina *et al.* 2011) in conserving member groups and associated ecosystem services.
- Sampling of mammal diets can provide an alternate or complimentary technique for detecting spatial trends in fungal richness and composition. Rapid surveys should be undertaken to identify species richness hotspots and broad assemblage types and to guide regional conservation management of truffle-like fungi.
- Management actions that conserve or promote a naturally diverse mammal community will assist in the maintenance of dispersal dynamics of fungal assemblages and individual truffle-like taxa.
- Conservation and promotion of healthy populations of swamp wallabies and microbats in fragmented landscapes of south-eastern Australian should be an important consideration in any plan seeking to ensure the long-term persistence of EcM fungal assemblages and their symbiotic host-plants.
- Protecting and enhancing a broad range of habitats within a reserve network with likely facilitate the conservation of truffle-like taxa and the maintenance of natural assemblages and dispersal processes. Provision of structural connectivity among similar broad habitat types is also required.
- Provision of habitat diversity in modified landscapes will ensure that the widest array of truffle-like taxa and mammalian dispersers will be conserved along with the retention of EcM spore inoculum for any future habitat restoration work.
- The conservation and restoration of vegetation mosaics with high habitat heterogeneity should be sought to increase the availability and diversity of truffle food resources for mycophagous mammals.

Future Research

Multi-season and year surveys are required to confirm if distinct assemblages of truffle-like fungi within habitats and trends in species richness are maintained across seasons and years. Whether the dispersal roles of animal vectors are similarly maintained through time and over larger spatial scales also require investigation.

A better understanding of non-standard secondary spore dispersal vectors for truffle-like fungi is required, particularly those conferring LDD of spores. Further research is required to establish whether microbats disperse viable spores in sufficient concentrations to colonise plant roots and also to determine the global extent of this trophic interaction. The role of mycophagous insects in fungal dispersal dynamics along with a quantification of ecological interactions with microbats requires investigation.

More realistic mechanistic models incorporating multiple dispersal vectors and the relative quantity and quality of dispersal services provided by each vector are required. Pre- and post-dispersal processes also await investigation and inclusion in models such as potential secondary dispersal by dung beetles, spore predation rates, spore bank longevity, colonisation rates, and spore production.

Linking predicted patterns of spore deposition to subsequent recruitment should be undertaken using modelling and field-based studies in order to determine the importance of dispersal as a process shaping the distribution of truffle-like fungi and their host-plants. Links between dispersal traits and distribution patterns in individual taxa also needs further exploration. For example, the wide distribution and broad niche range of some *Mesophellia* taxa is perhaps not surprising considering the powdery spore masses produced by these taxa which may enable wind or ectozoochorous dispersal, vectors which have the potential to confer LDD events of comparatively greater magnitude than endozoochory (Will & Tackenberg 2008; Peay *et al.* 2012). Links between traits and function allows extrapolation across taxa and generalisations on life history traits.

Glossary

Anisotropy/anisotropic: the spatial property of directional dependency. Refers to inequalities in directionality or orientation of a subject in space. The opposite of isotropy in which there is uniformity in all directions.

Diplochory: dispersal involving two or more vectors.

Dispersal kernel: A probability density function (PDF) describing the spatial pattern of spore/seed deposition with respect to the source. Used here in reference to the two-dimensional patterns of spore/seed deposition and represented by a probability per unit area.

Dispersal vector: an agent transporting spores or other dispersal units (e.g. seeds). Dispersal vectors may be biotic, such as mycophagous mammals, or abiotic, such as wind or water.

Distance distribution: a histogram or frequency distribution of distances travelled (i.e. dispersed) by a spore or seed usually in reference to its parent source. Used here interchangeably with 'dispersal curve'.

Dispersal restriction: in a specific sense, the failure of spores/seeds to colonise favourable sites for establishment. Also referring to the process of dispersal restricting the distribution of species or genes. Also referred to as 'dispersal limitation'.

Ectozoochory: the dispersal of spores or seeds through attachment to external surfaces on an animal.

Endozoochory: the dispersal of spores or seeds through the inside of an animal. Largely refers to spores or seeds being passed through the gut of an animal.

Fat-tailed dispersal kernel: any tail that declines more gradually than any negative exponential kernel. Referring to a dispersal kernel with high leptokurtosis and a high probability of LDD events occurring or high frequency of occurrence.

Gut-passage time/rate: The time taken for a spore/seed to pass through the gut of an animal but also a frequency distribution or PDF of spore/seed passage.

Nonstandard dispersal vector: a dispersal vector for which a species is not specifically adapted to exploit.

Polychory: the state of being dispersed by multiple standard dispersal vectors (i.e. multiple mycophagous mammals).

Spore density: The number of spores per unit area. Sometimes used in relation to spatial patterns in spore deposition.

Spore dispersal: the movement of spores away from the parent fungi by a dispersal vector. 'Primary dispersal' refers to movement directly from the sporocarp while 'secondary dispersal' refers to additional movement after primary dispersal by any particular vector.

Spore-dispersal curve: A frequency distribution of distances spores are moved from the parent sporocarp. Used here is relation to one-dimensional estimations of dispersal distance and the euclidean distance between the point of origin and the final deposition site.

Dispersal distance: The euclidean (i.e. straight-line) distance between the spore point of origin (i.e. the parent fungal sporocarp) and its point of deposition.

Spore bank: a store of viable spores in the soil including those that remain dormant.

Spore rain: the pattern of spore deposition on the ground.

Spore shadow: the spatial distribution of spores dispersed from a single sporocarp. Can also apply to the summed spore shadow for a population or discrete group of individual sporocarps.

Spore predation: consumption or destruction of spores or viability and often referring to fungivory by insects.

Standard dispersal vector: a dispersal vector for which the fungi species is adapted to be dispersed by and the one dispersing the majority of spores.

Total dispersal kernel: the entire dispersal kernel generated by all vectors of a single fungal species or a single individual sporocarp.

Zoochory: the dispersal of spores or seeds by animals.

Sources: Allaby 1998; Nathan & Muller-Landau 2000; Wang & Smith 2002; Levin *et al.* 2003; Chapman & Russo 2007; Nathan *et al.* 2008.

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Appendix A Supplementary details on methodology used in sporocarp surveys

Deriving estimates of sporocarp biomass (dry weight) for selected truffle-like taxa

Estimates of sporocarp dry weight for some species of truffle-like fungi required non-standard methods to reduce the bias these species could introduce into estimates of sporocarp production among habitats and differences in sporocarp availability to mycophagous mammals. The following methods for estimating dry weight were applied to sporocarp samples of *Mesophellia* spp., *Hysterangium aggregatum*, and *Gummiglobus joyceae*. In explanation, these species commonly encrust soil, plant rootlets, sand, and other external material around the sporocarp or within the peridium structure (*Mesophellia*) that can bias honest comparisons in estimates of biomass. This was a particularly concern with the higher frequency of *Mesophellia* in two of the habitat types sampled.

To resolve the potential bias these species could introduce, sporocarps (n=44) of *Mesophellia* collected outside of this survey (but within the study area) had gleba and spore contents removed from the encrusting peridium and weighed to provide a mean percentage of these components relative to total weight with encrusting peridium in each taxa, and to provide a minimum weight range for these sporocarps. The carbonaceous-like peridium of *Mesophellia* sporocarps are assumed to weigh little in comparison to the soil and plant rootlets incorporated into the peridium. Therefore, it was considered likely that there would be little loss in the true weight of fungal material from this calculation. For example, the mean percentage of gleba and spore:total weight ratio (31.5±7.6 SD) from 44 *Mesophellia* sporocarps measured was used to multiply the total weight for each collection, providing a lower weight representing the dry weight of gleba and spore mass. No *Gummiglobus* collections were available to replicate this process However, as this genus has a similar sporocarp structure it was considered warranted to apply the same calculated ratio as for *Mesophellia* sporocarps. Individual *Hysterangium aggregatum* sporocarps were separated from embedding material and weighed to provide a likewise ratio estimation.

Appendix B Species accumulation curves for different habitat types based on sporocarp collections

The upwards slope of Jackknife2 species accumulation curves for all habitat types suggested species richness may be substantially greater than that observed and that sample completeness may be low, with the possible exception of rainforest habitat (Figure 7.1: A-D). Further evidence for insufficient sampling was the lack of convergence and decline of 'uniques' and 'duplicates' curves in any habitat, although they approached a plateau in dry forest and rainforest habitats. These results indicate a need for greater sampling effort to provide an accurate estimate of total species richness within each habitat.

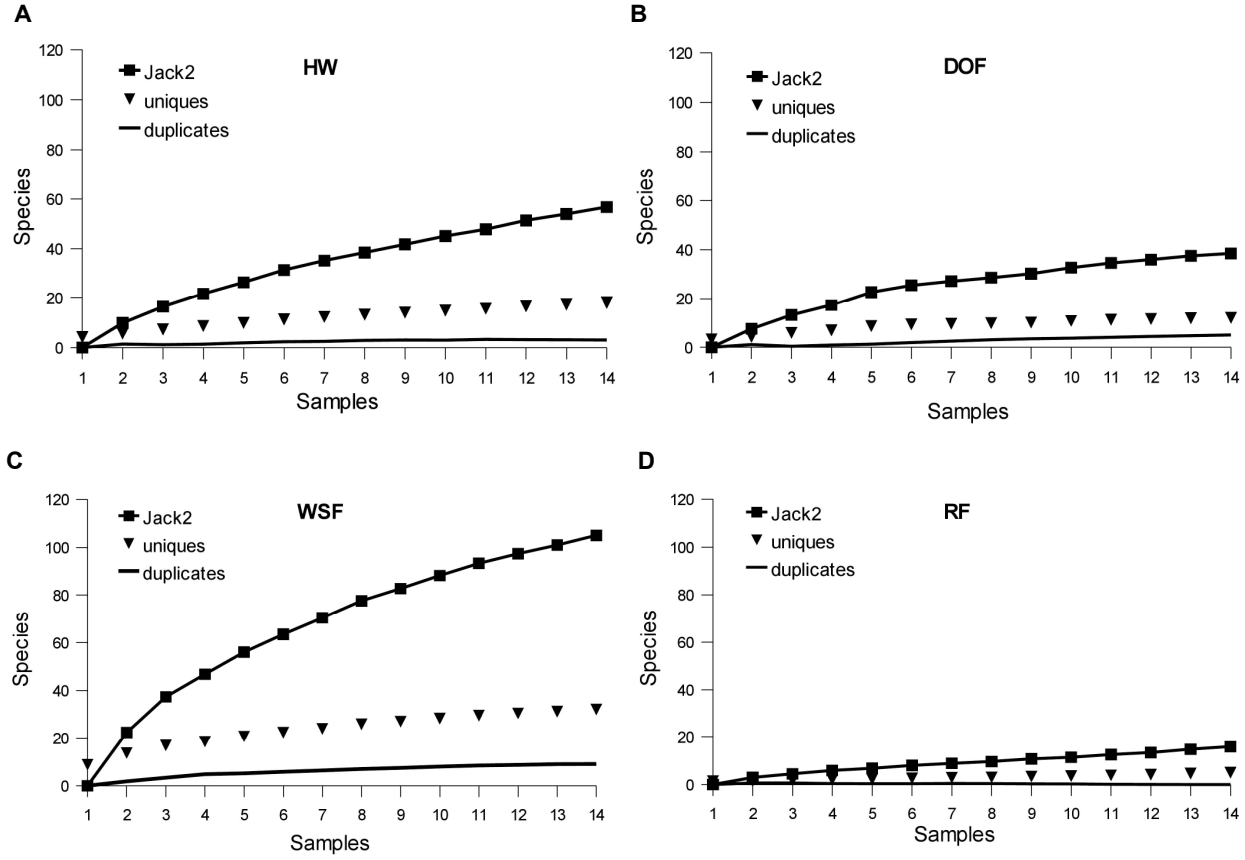

Figure 7.1 Species richness accumulation curves for truffle-like fungi using the Jackknife2 estimator (100 randomisations) based on truffle collections. Shown with unique and duplicate mean values for truffle-like species among four habitat types (A-D): A. heathy woodland, B. dry forest, WSF. wet sclerophyll, RF. rainforest.

Appendix C Spatial variation in the composition of fungal spores observed in swamp wallaby scats within habitats

NMDS ordinations of scat samples suggested no segregation of samples by grid in heathy woodland and wet sclerophyll habitats (Figure 7.2: A and C) but some differences between grids in dry forest (Figure 7.2: B). However, all ordinations had high stress levels (>0.1) and subsequent ANOSIM tests revealed a significant global differences (P<0.05) among grids within each habitat (Table 7.1). Qualitative evaluations of R-values (Dethier & Schoch 2006; Vernes 2010) suggest that absolute differences in taxon composition may not be large, particularly in wet sclerophyll and heathy woodland (Global R-values: 0.112-0.158), although comparatively greater in dry forest (Global R-value: 0.328; P=0.001; Table 7.1). Also, as grids were spatially arranged according to number (i.e. grid 9 was closest to grid 10), greater differences among more distant grids were not apparent (Table 7.1).

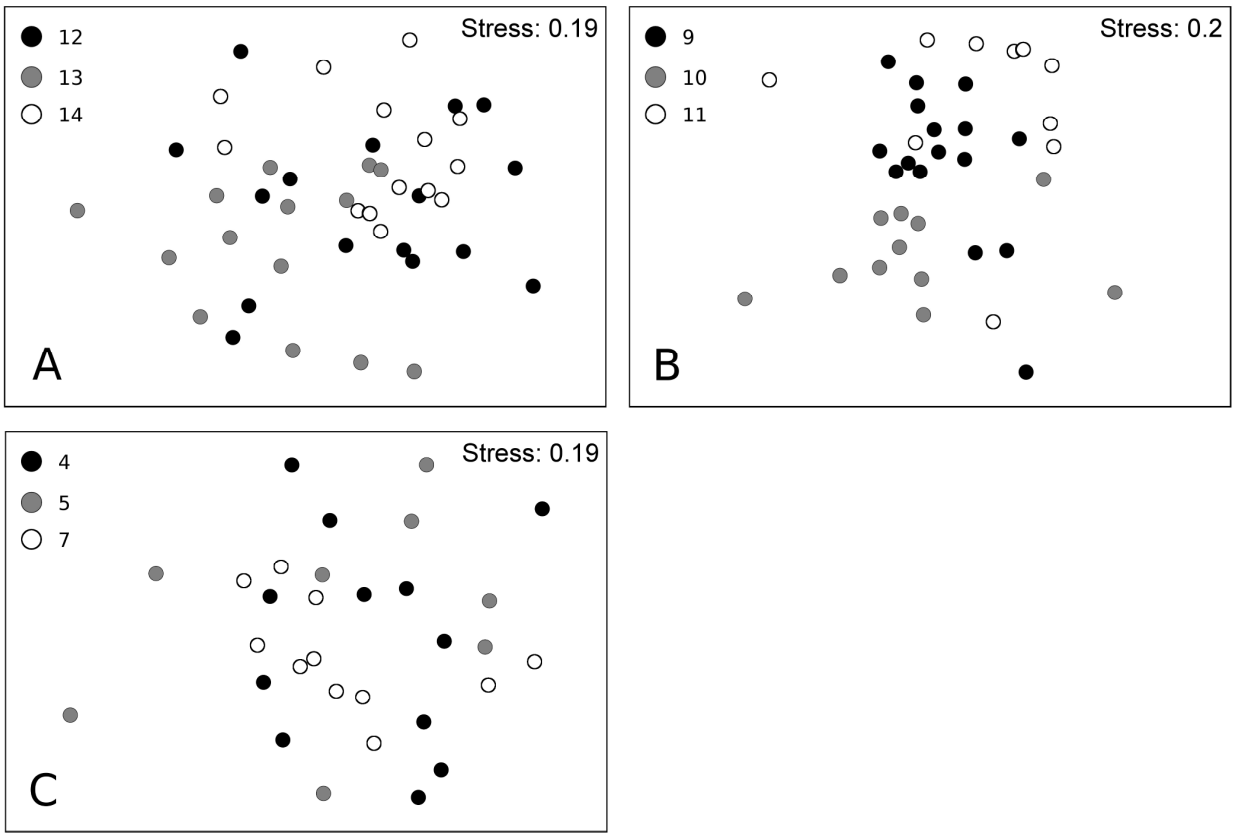

Figure 7.2 NMDS ordinations comparing truffle-like morphospecies (spore type) composition (presence/absence) in swamp wallaby *Wallabia bicolor* diets (scats) among grids within the habitats A) heathy woodland, B) dry forest, and C) wet sclerophyll. Symbols represent the respective grid from which each swamp wallaby scat was sampled.

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.

Habitat		Grid	*R-value*	*P*
heathy woodland	Global	-	0.112	0.005
	Pair-wise	12, 13	0.047	n.s.
		12, 14	0.038	n.s.
		13, 14	0.300	0.001
dry forest	Global	-	0.328	0.001
	Pair-wise	9, 10	0.336	0.001
		9, 11	0.199	0.015
		10, 11	0.502	0.001
wet sclerophyll	Global	-	0.158	0.005
	Pair-wise	4, 5	0.250	0.011
		4, 7	0.074	n.s.
		5, 7	0.233	0.007

Appendix D Purpose-designed field equipment

Soft-walled wallaby traps

In mid-2006 I designed soft-walled traps that were highly successful in safely trapping and handling swamp wallabies *Wallabia bicolor* - both for the researcher and animals. The basic trap design was based on a soft-walled trap design previously reported in the literature (Di Stefano *et al.* 2005) and broadly consisted of a modified wool-pack bag suspended from a metal frame (Figure 7.3). The wool-pack was sewn so that the bag tapered towards the back, allowing the bag to be tightly suspended from the frame and increasing the distance between the soft bag wall and the metal trap frame. This modified 'bag' was suspended from the metal frame using nylon cords and winged rope fasteners. The door panel was composed of a sewn bag made of high-density shade cloth that could be tightly slid over the metal frame to form a taught double layered soft-walled panel. In addition, thick pipe insulation foam was attached to all hard surfaces of the trap which an animal could possibly make contact with. Overall, these design elements reduce the potential for injury due to contact with the hard metal surfaces of the frame.

Once the animal is trapped in the bag, the top back of the bag can be released from the cage and a draw string encircling the bag's mid-section can be tightened to restrain the animal in the back half of the bag. The rest of the bag is then released from the cage frame allowing the animal to be weighed in the same bag and then anaesthetised in a short period of time. Traps were stabilized by anchoring the top back corners of the frame to adjacent trees. The trigger mechanism is a thin wood board positioned underneath the bag, attached at its end by a nylon cord that is looped over the back top bar of the trap frame by a pulley and then to a metal pin which holds the trap door open (Figure 7.3). Diver weights were used as a partial counter-weight for the trap door to reduce pressure on the metal pin so that free release would occur when the wooden treadle was pushed downwards by an animal entering the back half of the trap. Petroleum jelly was also used to reduce friction at key friction points. Once the pin is released, the trap door closes with high speed and is locked in place by a sliding metal bar. The whole trap frame was covered by a thick sheet of plastic concrete underlay to protect the animal from rain and keep the trap dry for extended periods of trapping.

Figure 7.3 Soft-walled wallaby trap used to capture swamp wallabies set for pre-baiting (left) and door release/trigger mechanism (right).

There were no deaths of animals in traps or any evidence for post-capture myopathy. Several animals were re-trapped on repeat occasions and there was no observed weight loss or other signs of stress or injury observed. Recaptured female wallabies exhibited continued growth of pouch young during the course of trapping. Only one young-at-foot was captured with an adult in a trap and this was unharmed during the process. The trap design allowed the rapid restraint of animals, reducing the likelihood of the adult injuring the young animal. In the single event detailed, I anaesthetised the adult and transferred the young-at-foot to a hessian bag which was then suspended. Once I had processed the adult, the young-at-foot was positioned beside the mother under a covering blanket. The juvenile remained in this position until the parent recovered, as evidenced by a large pile of small scats. The only non-target captures were of Mountain Brushtail Possums *Trichosurus cunninghami*.

Most animals exhibited little movement in the trap until researchers approached within ≈25m of the trap, after which rigorous movement followed. One male exhibited contrary behaviour, being relatively calm from the first capture onwards with the exception instance where the animal did not achieve full recovery from sedation before dawn. This animal was the most frequently captured and was notable for making nests of hay within traps. Animals exhibited much lower stress when they were captured and able to recovery in the dark. Covering of animals with blankets was found to be insufficient. Consequently, it is strongly recommended that trapping and all processing of swamp wallabies be undertaken only during the night and finished well before dawn. Traps should be closed during daylight hours for this reason as animals move extensively during the day (Chapter 5).

Animal GPS data loggers

In 2006, extensive research was undertaken (A.O. and Brad Dawson) to facilitate the development of inexpensive in-house built GPS animal data-loggers for collecting short-period swamp wallaby movement data. Major components of the unit consisted of an inexpensive off-the-shelf GPS receiver (Fastrax Ltd) and microchip board with data logging capabilities, a GPS patch antenna, a rechargeable lithium (Li-Ion) battery, and a VHF radio-transmitter (Figure 7.4). The unit was built by Brad Dawson (UNE) along with software for downloading GSP location data and communicating with the GPS receiver. A 'backpack' design was used so that a unit could be temporarily attached to an animal's back (by fixing onto a shortened patch of fur using adhesive veterinary surgical glue) before being groomed off and retrieved by the researcher. In most cases the unit was removed by animals within a few days with no skin breakage or any other adverse effect, as observed when animals were re-captured in traps and also through surveillance using infra-red camera traps. Two of these units were used in collecting some short periods of swamp wallaby movement data.

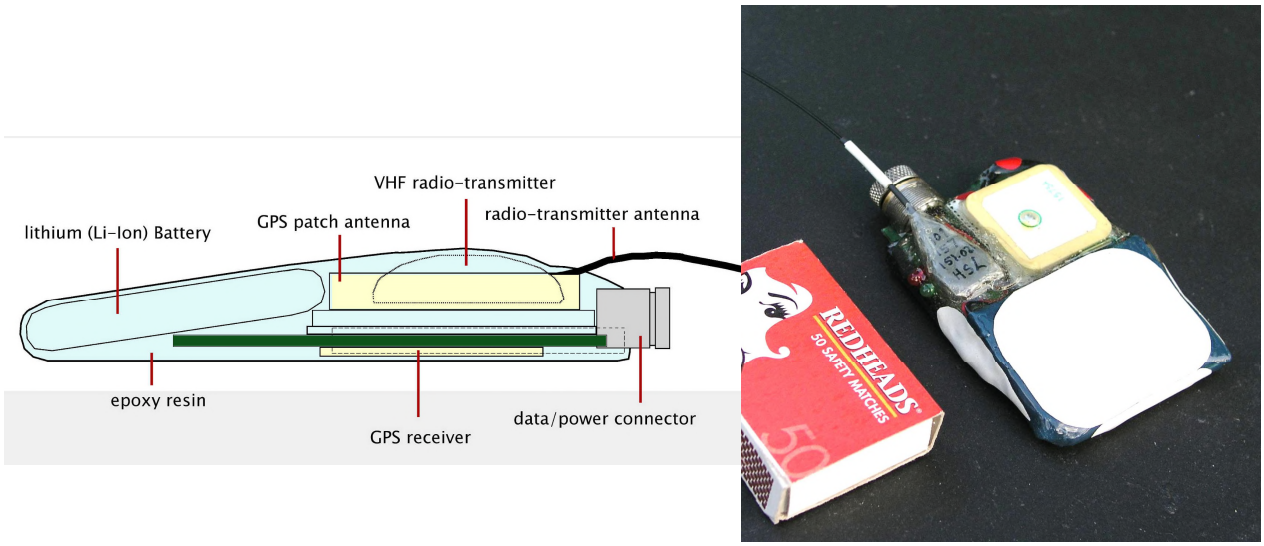

Figure 7.4 Prototype diagram of GPS animal data-logger (left) and photo of the final unit (right) used for recording animal movement over short periods of time (right). Black ink was used over the epoxy resin at certain locations to obstruct light for LEDs during deployment on animals.