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Environmental variables driving habitat differentiation in two sympatric pademelon (*Thylogale*) species in northeast NSW

A Dissertation submitted by

Lucy Smith, BZool

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Abstract

A pivotal question for community ecologists is whether assemblages are structured as a result of general rules that can be applied to any ecosystem. Trade-offs in species performance of ecological functions are a common theory behind the structure of communities and the co-occurrence of species. The phenomenon of sympatry was originally described as the co-occurrence of two or more forms in the same geographical region. Intraguild sympatry between ecologically similar species is fundamental in shaping the dynamics of community assembly. Temporal and spatial partitioning between comparable sympatric species can facilitate biodiversity and contribute to the structural complexity of mammalian community assemblies. My research aimed to describe the ecology of two sympatric forest wallabies, the red-legged pademelon, *Thylogale stigmatica,* and the red-necked pademelon, *Thylogale thetis,* in a rainforest-wet-sclerophyll forest in northeastern New South Wales. The diel activity pattern of both species was mapped using camera traps over a 16-month period. Structural vegetation components measured at each camera site were used to determine the variation in usage by the two pademelon species between two forest types in the study area, and which structural habitat variables correlated with their occurrence. Camera trap data revealed that both *Thylogale* species were strongly crepuscular, however, *T. stigmatica* was more active before dawn than during the evening, indicating some evidence of temporal partitioning. *T. thetis* spatio-temporally partitioned their habitat remaining under forest cover diurnally and travelling beyond the forest-pasture edge overnight. Detection data revealed that *T. thetis* were positively correlated with the density of multi-layered detection cover as well as disturbance variables, indicating an affiliation for fine-scale habitat attributes rather than a particular vegetation type. *T. stigmatica* was correlated negatively with disturbance related factors, indicating a preference for closed forest and multi-layered cover. *T. stigmatica* showed some plasticity in their activity budgets when sympatric with the ecologically similar species *T. thetis*, and likely exhibited temporal partitioning in response as a form of niche partitioning. *T. stigmatica* appear to narrow their preferred niche and become more specialised in the presence of *T. thetis,* consequently occurring in lower densities. The composition of the entire mammal community detected by camera traps was significantly affected by both habitat type

and individual structural variables, indicating that fine-scale heterogeneity is important on an individual species scale as well as at a community level. In summary, this work shows that temporal and spatial niche partitioning allowed the ecologically similar *T. stigmatica* and *T. thetis* to co-occur in the same forest and contributed to the facilitation of high biodiversity in the wider mammal community.

Certification of Dissertation

I certify that the ideas, experimental work, results, analyses, software and conclusions reported in this dissertation are entirely my own effort, except where otherwise acknowledged. I also certify that the work is original and has not been previously submitted for any other award, except where otherwise acknowledged.

[redacted]

30/07/2019

Signature of Candidate

Date

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Chapter 1 – A review of mammalian community assembly theory, with a focus on rainforest pademelons (*Thylogale*)

1.1 Introduction

A fundamental question in ecology is whether ecological communities are structured as a result of general rules that may be applied to any combination of coexisting species across numerous habitat types. Understanding how local species assembly aligns with regional biogeographic and environmental context is an ongoing challenge. Intact ecosystems contain large numbers of competing yet coexisting species (Harpole & Tilman, 2007). Community ecologists are generally interested in species functional traits, which will ultimately enhance a species' overall fitness and their ability to establish and persist in a given habitat. Communities can converge in terms of their functional parameters yet may fail to do so in regards to species composition (Fukami, et al. 2005). Different subsets of community composition may be selected according to functional trait in larger, regional terms, however, dispersal and historical drift are more likely to determine actual species composition (Weiher, et al. 2011). Numerous species may be physically able to fulfill a certain role within an environment or habitat type, whether they are ecologically similar or dissimilar, however it is their historical dispersal and the pressures of other species already established in a given area that will ultimately determine the ability to persist. Composite subsets may be selected from the regional pool according to their potential to fill certain community niches, however it is the biotic pressures from other species that will determine the actual species composition of a community. It is for this reason many ecologists may be skeptical about the predictability of the species composition of an ecosystem. Processes determining niche availabilities may be more likely to affect the likelihood of species composition, rather than actually determining it.

Ecological approaches to community assembly have highlighted the interconnectedness of neutral processes as well as niche-based environmental filtering and species sorting (Weiher, et al. 2011). It has long been recognised that nonrandom processes such as competition and abiotic environmental filtering interact with demographic stochasticity to jointly determine community assembly (Shipley, et al. 2012). Trade-off based theories on both interspecific competition and neutral theory have been proposed as possible explanations for the assembly, structure and dynamics of ecological communities. Two main areas of inquiry have thus resulted, which rely on null models of community assembly. The first involves the development of models which test for patterns of species co-occurrence and differ from the null hypothesis that all species are independent of one another (Connor and Simberloff, 1979). The second avenue of inquiry involves ecomorphological analyses and considers the role of competition, limiting similarity and the resulting patterns consistent with these ideas (Weiher et al., 1998). For example, comparison of body size in desert rodents found uniform distribution within guilds (Brown and Bowers, 1982). In the granivore guild, similarly sized species with body mass ratios <1.5 coexist less frequently in localised communities and experience less overlap in geographic distributions than is expected by chance, suggesting that co-occurrence is impeded by interspecific competition (Brown and Bowers, 1982). Despite the fact that many different and independent factors can theoretically lead to similar patterns of species associations (Connor and Simberloff, 1979), theories based on null models look for evidence of competition. While a lack of competition suggests independence amongst species, other methods demonstrating the cause of patterns will need to be derived.

The classical niche theory states that differences between species can lead to either competitive exclusion or resource partitioning, depending whether the advantages of one trait are balanced by the trade-off of another trait (Courbaud, et al. 2012). Niche selection predicts that species' abilities to establish in a locality are determined by their traits, regardless of stochastic colonisation and extinction dynamics (Chase, 2007). When similar species coexist, variation among traits will also determine species relative abundance and overall community stability. The distribution of a species is set by limiting environmental factors such as temperature, and the conception of niche is often regarded as pre-interactive, being the potential area in which a species can live as opposed to the actual area in which it is found (Vandermeer, 1972). According to niche theory, it is the interaction between species that devises the difference between a species fundamental niche, being the possible area it can occupy, and its realised area being the actual area it occupies. The concept of niche theory is based on competitive exclusion, whereby if two species share the same niche, the inferior species will be outcompeted into extinction (Allesina & Levine, 2011). Theoretically speaking, niche differences cause species to limit their own populations more than they limit others, which promotes coexistence among species in a given locality (Chesson, 2000). Despite overwhelming evidence for niche variations, few studies have successfully appraised the importance for maintaining diversity in ecological communities (Adler, et al. 2007). The gap in empirical evidence for niche determined coexistence only highlights the need for further research into niche partitioning and its effect on species distribution and diversity.

Trade-offs in species performance of different ecological functions is one of the most common theories behind species co-existence in ecological communities (Kneitel and Chase, 2004). Trade-off based theories of resource competition predict patterns of species traits and separation based on a nutritional gradient (Tilman, 2004). The benefits reaped by performing one ecological function well, often come at the cost of another. Such trade-offs in a community context represent niche differentiation among species that imposes individual constraints at a localised level. Studies by Jones and Barmuta (2000), found niche differentiation occurred on three different dimensions in a size-structured guild of carnivorous marsupials, the eastern quoll *(Dasyurus viverrinus),* the spotted-tail quoll *(Dasyurus maculatus)* and the Tasmanian devil *(Sarcophilus harrisi).* Food resources were partitioned on a body size to prey size ratio but substantial overlap still occurred between species. Eastern quolls displayed habitat differentiation by utilising grasslands more extensively than the other two species. Spotted-tail quolls were found to have an increased level of arboreal activity that subsequently reflected a higher level of arboreal prey species in their diet. A strong relationship was also found between arboreal activity and morphological adaptation for climbing between both predator and prey species. Niche differentiation such as this allows for similar species to coexist on a local level however interspecific interactions dictate ecological function and utilisation of resources. Community assembly that is dependent on resource availability imposes stochastic limits on the similarity of competing species that can coexist in an ecosystem (Harpole & Tilman, 2007). Adding resources would reduce the number of limiting resources, allowing fewer trade-off opportunities and hence fewer coexistence opportunities.

Contrary to the niche paradigm, neutral theory assumes that species are ecologically equivalent and their regional abundance is randomly determined by demographic stochasticity (Hubbell, 1997; Fargione, et al. 2003; Tilman, 2004). Therefore, such an assembly model creates communities in which species occupy equal areas of spatial heterogeneity. This generates realistic distributions of relative species abundances for which there are strong correlations between species traits, abundances and environmental conditions (Tilman, 2004). In a neutral model, local community assembly is a random process driven by regional propagule abundances, therefore the only driver of population dynamics is random variations in births, deaths and dispersal (Adler, et al. 2007). Once a propagule arrives at a given site, the probability of successful integration and establishment in the community is independent of its traits relative to those of established species in the existing community (Fargione, et al. 2003). Unlike tradeoff models that predict resident species will inhibit the establishment of 'invader' species, neutral theory predicts random assembly independent of species traits. The theory proposes a simple way to relate the taxonomic composition of a local community to that of the regional taxa, creating a connection between community ecology and biogeography. Criticism for neutral theory focuses on the assumption that traits adjudicating competitive interactions on a local scale are unimportant, which conflicts with a large body of research related to species coexistence (Lowe & McPeek, 2014). Dispersal is a process that evolves by means of natural selection and varies between species (Clark, 2009) however Lowe & McPeek (2014) point out that a lack of empirical challenge to the theory implies an underlying level of acceptance that should be studied in order to advance our understanding of both community assembly, as well as the evolutionary and ecological forces that shape dispersal.

It is possible, however, for a combination of these components to occur simultaneously and thus obscure any evident patterns, or they may occur sequentially along environmental gradients (Mouchet et al., 2010). If so, the relative influence of assembly rules depends on the scale of observation. Patterns of traits and trade-offs at the species level may be different from those at the community level and may not accurately predict community structure (Lebrija-Trejos et al., 2010). Environmental filtering is assumed to be stronger at the regional scale whilst species interactions such as competition or limiting similarity drive community structural patterns at a local scale. Further study needs to be done to ascertain not which mechanism is ecologically valid, but which has the strongest influence on communities.

1.2 Scale

Attributes of assemblages are highly dependent on the scale at which they are examined (Williams, et al. 2002), so it is important to acknowledge issues regarding the scale at which assembly rules are expected to occur and how they are measured. Spatial scale particularly, should be precisely defined keeping in mind the principal components of the size of individual units of observation and the overall area in which the units of observation are located (Götzenberger et al., 2012). Local communities are established as the result of species interactions, most of which are negative interactions that limit similarity through competitive exclusion. At a larger scale however, the effect of habitat availability and climatic conditions become more relevant (Villalobos & Arita, 2014). In turn this affects processes operating at a smaller scale such as food and habitat fragment availability so that the same global processes can have different effects in different areas (Pastro, et al. 2013). Environmental filters can also act on a minute scale, affecting the assemblage of communities that sensitive to microclimates. Vegetation cover may be an integral factor determining microclimatic conditions and therefore the spatial distribution of affected species (Shibuya et al., 2011). The adaption of co-occurring species to similar abiotic environmental conditions can cause phenotypic attraction, which is the development of similar ecological preferences and functional traits (Bino, et al. 2013). On the contrary, increased competition for resources among co-occurring species can influence phenotypic revulsion by competitive exclusion, which places constraints on the coexistence of species. Therefore regional processes are not always an extrapolation of local factors. This is one of the potential effects of regional or global processes affecting community structure at a local scale. Comprehension of the effect of scale is vital to the research of community assembly as the variables between local and regional effects depend on the spatial scale at which the community is defined and the scale at which the actual processes occur (Weiher, et al. 2011).

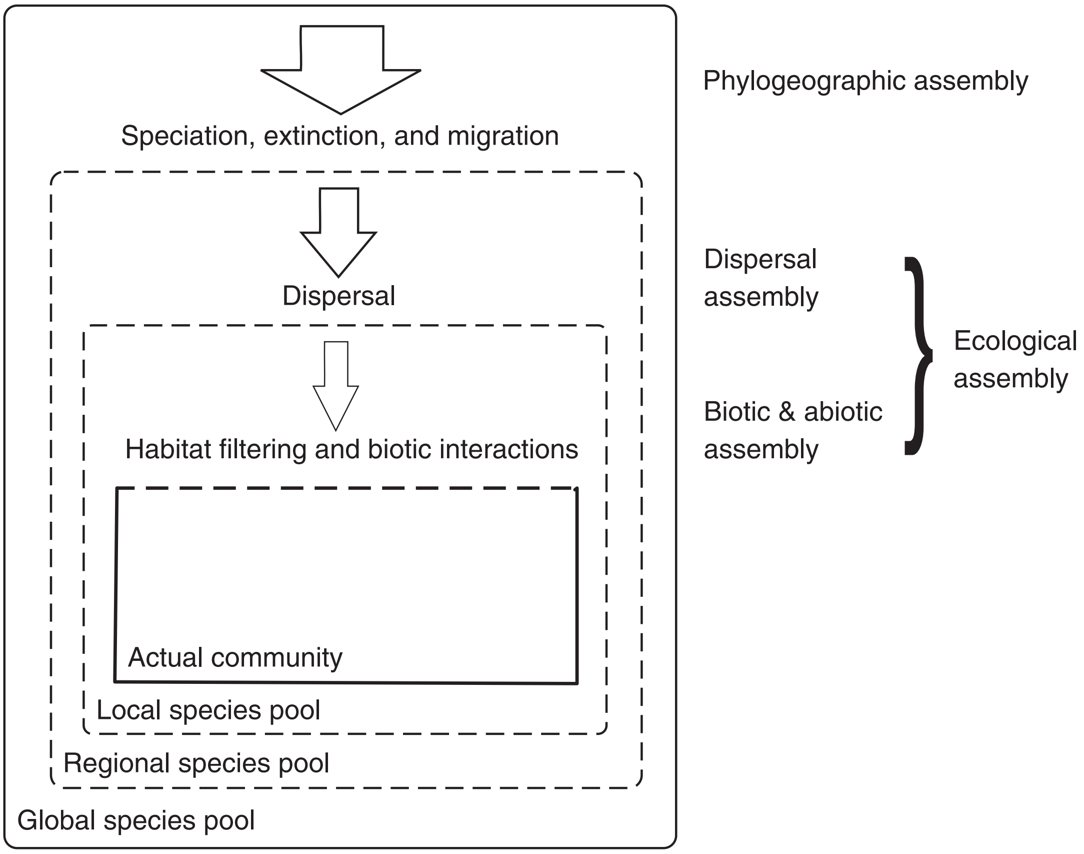


Figure 1.1: Processes potentially producing assembly rules and the influences of various scales on community structure (Götzenberger et al., 2012).

In niche-based theories, control of assembly structure is a bottom-up process, occurring at a local scale that has flow on affects at different spatial and temporal scales. Abiotic conditions, resource availability gradients, dispersal limitations and biotic interactions affect species distributions and community assemblages from continental to local scales (Pearson & Dawson, 2003). Biotic interactions between species at the same trophic level cause a certain niche to be filled resulting in further interactions either directly or indirectly (Götzenberger et al., 2012). Habitat fragmentation and matrix permeability driven by anthropogenic land use can limit species coexistence at a landscape level by altering population persistence, affecting exchanges within metapopulations, preventing dispersal and settlement (Barnagaud et al. 2014) and thus altering direct or indirect interactions. Habitat or environmental filtering describes the set of biotic and abiotic factors required by a species for its' survival (Emerson & Gillespie, 2008) and density dependent interactions among similar species such as competition may reduce the co-occurrence of ecologically similar or closely related species at a local spatial scale. Clustering of phylogenetically similar species should increase adjacent to spatial scale, thus encompassing the suite of habitat types and biogeographic pattern of a given area. Munoz et al. (2014) point out that habitat filtering can function over an environmental gradient, while the assembly of local guilds is neutral. For example, Stirnemann et al. (2015) found that small-scale heterogeneity was more important in the assembly of small mammals than broad scale heterogeneity. Their research found that the occurrence of bush rats (*Rattus fuscipes)* and long-nosed bandicoots (*Perameles nasuta)* was positively affected by fine-scale heterogeneity, while the occurrence of swamp wallabies (*Wallabia bicolor*) was positively affected by proximity to ecotones. Small mammals will utilise their habitat on a smaller scale, hence fine-scale heterogeneity is important in local guild associations for these animals. Bottom up environmental factors such as vegetation cover can strongly affect communities at a small scale and habitat heterogeneity can promote diversity (Rich et al., 2016). Species richness is most affected at fine spatial scales (González-Maya et al., 2015) and factors at this scale such as vegetation cover, food and water availability are paramount in determining how often density dependent interactions are likely to occur. The vagility of a species may depend on the permeability of surrounding habitat therefore it is more likely that the stronger species are able to persist at this scale. In other studies, Nupp & Swihart (2000) found granivorous rodent species responded to fragmentation effects individually with both positive and negative reactions. The definition of scale may therefore be a matter of semantics in regards to the size of a habitual area for a local population. There is little available research investigating the boundaries of scale and what rules might be used to effectively describe scale, other than guild according to body size (Nupp and Swihart, 2000). This is not necessarily a determinant of the density of the regional metapopulation. Habitat filters can also act at a local scale as generalist species with flexible adaptations can replace the less tolerant, specialist species along a gradient of human altered habitat. Ceradini and Chalfoun (2017), found that habitat altered by invasive cheatgrass did not affect overall species richness but increased the occupancy of the pocket mouse *(Perognathus* spp) and decreased that of the harvest mouse *(Reithrodontomys* spp), indicating a modification of community structure.

Other models propose that local assemblages are a subset of regional assemblage, implying a top-down control of community structure (Griffiths, 1997). However, assembly structure is most likely to be the result of different processes acting at different scales (Hughes, et al. 1999). In Australia, biogeographical history has had an important impact on regional patterns of terrestrial mammal assemblages, particularly in tropical habitats (Williams, et al. 2002). Studies carried out by Williams, et al (2002) found that local assemblage structure is a balance between local ecological interactions and the available regional species pool. Particularly for small mammals, local assembly and species diversity is determined by habitat capacity, within the limitations of the regional species pool. Research conducted thus far has found limited success in linking habitat structure and faunal diversity at appropriate scales (Caley and Schluter, 1997; Westoby, 1998) highlighting the need for future studies to address ecological interactions at a local scale as well as relationships between processes at a broader scale.

Local assemblages are constructed by a set of species with co-adjusted niches that partition limited resources. Competing species should occur less than expected by chance and within assemblages, species can differ in body size to reduce the potential overlap in resource use and make way for interspecific coexistence (Sanders et al., 2007). Local assemblages may exist at an inconsequential scale because each assemblage of individuals makes up part of a metapopulation, which is on par with regional scale. The metacommunity is composed of local communities linked by the dispersal of potentially interacting species (Shipley, et al. 2012). Nesting local communities within a larger metacommunity will likely result in a range of spatial dynamics, which can both directly and indirectly influence biodiversity by affecting local community processes that in turn alter features of the regional biota (Leibold, et al. 2004). Patterns in species co-occurrence and body size distributions can depend on the spatial scale analysed. As previously discussed, density dependent interactions can reduce the co-occurrence of similar species at a local scale. At regional spatial scales, body size distribution and co-occurrence patterns may accumulate if climate acts as a filter to limit potential colonising species. At a local scale, behavioural adjustments and micro-scale resource partitioning may promote co-occurrence (Sanders et al., 2007), particularly in phenotypically similar species. Gotelli and Ellison (2002) found species co-occurrence was non-random in forest ant communities. Species co-occurred less than expected and is likely due to competitive interactions. While some traits are closely linked with tolerance to climatic conditions, which affects a species' distribution, others are driven by local competitive regimes and resource exploitation and have little or no effect on habitat filtering (Ingram, 2011).

The importance of scale and its link to pattern-processes is well recognised however multi-scale spatial perspectives have not been widely incorporated into state-and – transition models, and the significance of spatial patterns is not always appreciated in the application of land management theories (Bestelmeyer, et al. 2011). Most studies, regardless of scale, have analysed communities with an assumed equilibrial state. There has been little consideration of whether co-occurrence patterns or an overlap in body size amongst species are temporally stable or spatially variable (Sanders et al., 2007). Meta-analysis of presence-absence matrices found species segregation is congruent with the hypothesis that competition and niche partitioning structure species assemblage (Gotelli and McCabe, 2002). Rosenzweig and Winakur (1969) found that relative densities of granivorous desert rodents were correlated with structural habitat variables and used the information to construct a model of habitat complexity. Their study is an example of using assembly models on a small scale to build a picture of regional or larger scale assembly. There is little consistency in the modification of assembly rules due to disturbance history or habitat type as such that the operation of assembly rules depends on spatial scale. It is also worth noting that different physical and biological processes prevail at various scales and as such, small-scale studies may only provide narrow view into the broader picture. Incorporating spatial scale specifically into the experimental design of field studies may provide a broader, landscape view of ecological systems and any applicable assembly rules (Hughes et al., 1999).

1.3 Assembly rules

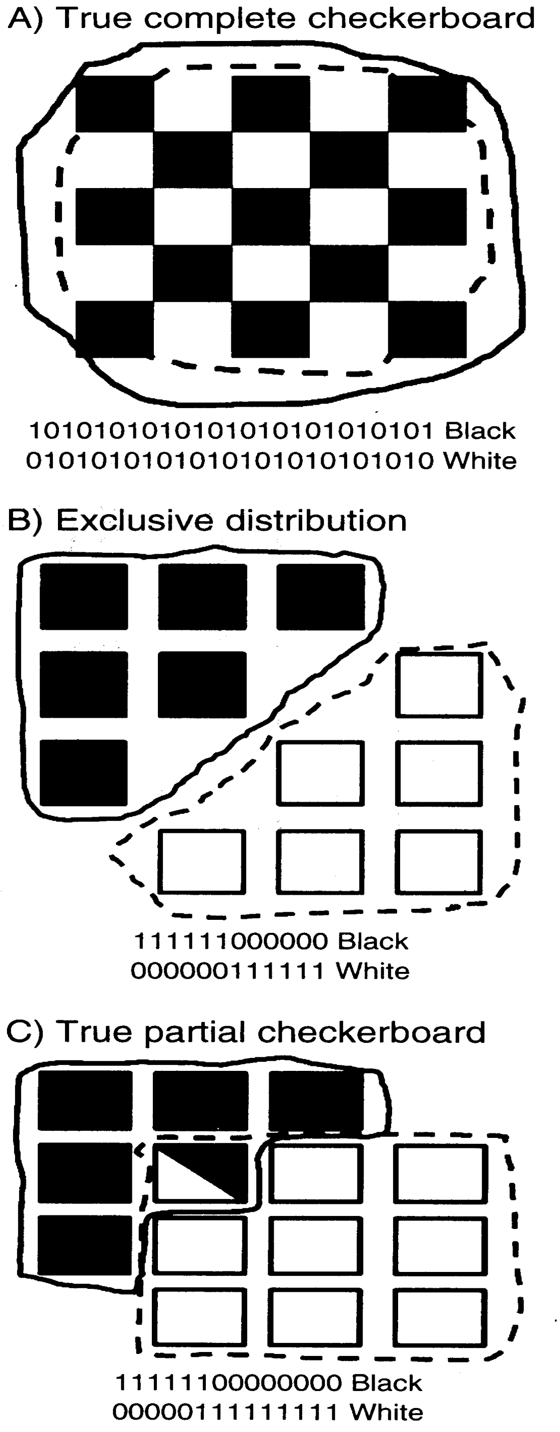
Assembly rules can be considered as specifically outlined constraints that predict a community's structure and in turn, its function. The objective of assembly rules is to predict which subset of the total species pool in a given region will occur in a localised habitat (Keddy, 1992). The concept of assembly rules is applicable to any community where species can move and where competition limits a species' ability to survive. If the latter effects are dependent on species involved, then assembly rules are in operation rather than simply the presence of other species (Wilson and Whittaker, 1995). An early attempt at evaluating assembly rules was carried out by Diamond (1975) who used a descriptive dataset of bird species present on an island archipelago to generate rules about species composition on islands of varying size. He proposed that within a guild of fruit-eating birds, the combination of species present in a community at any time will maximise resource utilisation yet allow each species to persist and reproduce. Diamond did however fail to show whether the bird assemblages were structured rather than random (Weiher and Keddy, 1995), prompting questions as to whether non-random patterns exist. Two authors have since attempted to recognise distinct types of assembly rules that shape community structure. Brown (1981) differentiated external physical factors from internal species interactions however did not separate factors that determine potential colonists from species that successfully colonise a site. In contrast, Keddy (1992) differentiated the availability of potential colonists from the ability of those species to survive in a potential habitat. His dissimilation of assembly and response rules contributed to the idea that patterns of community change may differ according to the direction of community change (Belyea and Lancaster, 1999). Both Brown (1981) and Keddy (1992) overlooked dispersal constraints but classified environmental constraints within their rules set. Belyea and Lancaster (1999) proposed that external constraints restricting the membership of a species from a community are essentially different from assembly rules that emerge from internal dynamics and interactions.

Diamond claimed to have produced a collection of principal rules determining co-occurrence patterns based on inter-specific competition within communities (Ulrich, 2004). Diamond explored the origin of variables in structure between different communities such as different islands of the same archipelago, different localities on the same island, differing adjacent habitats and different biogeographical regions. It was hypothesised that through diffuse competition, the component species of a community are selected, and then subsequently adjusted both in niche and abundance, in order to fit with each other and resist invaders (Diamond, 1975). This structural formation would optimise the carrying capacity of the local environment and increase the fitness of both the ecosystem as a whole, and the individual species components. Diamond's seven assemblage rules surmise that competitive interactions between species result in nonrandom co-occurrence patterns (Gotelli & McCabe, 2002). Diamond's argument was that interspecific interaction among bird species in the Bismark Archipelago produced a number of community assembly rules including forbidden species combinations, checkerboard distributions, and incidence functions. Meta-analysis conducted by Gotelli & McCabe (2002), yielded results consistent with Diamond's theory, however important alternative hypotheses can also produce nonrandom distributions. For example, some species may exhibit 'habitat checkerboards' and segregate due to affinities with different habitat types rather than direct competition. Some species may only co-occur infrequently due to previous allopatric speciation that has resulted in 'historical checkerboards' that reflect biogeographic and evolutionary history. Such checkerboards may not represent mutually exclusive hypotheses if evolutionary change reflects species interactions (the ghost of competition past (Connell, 1980)).

Researchers have also argued not only for the existence of randomness or non-randomness in communities but for more strategic, specific questions. Weiher & Keddy (1995) tactically posed explicit questions such as (1) what types of patterns exist in communities and what traits are expressed? (2) how do patterns change both spatially and temporally? and (3) what knowledge is needed in order to predict how communities are assembled from a common pool? By considering assembly rules as functional entities, rather than list of species names, patterns can be sought out and applied to predict structure. Rules based on species name and local species pool are specific to one area and applying to numerous sites or habitat types is difficult. Devising rules based on functional traits or trait-based functional groups will permit generalisation and hence comparison across habitat types and communities (Keddy, 1992). The identification of feeding guilds or trait-based functional entities enables a comparison between habitat types using rules as a type of control. Such trait-based rules would also enable impact assessment of the level of disturbance in a habitat due to the expected precedent of how that guild would function or operate. Rather than searching for the existence of randomness, to put forward explicit questions based on functionality gives definitive answers as to the structure of a community and enables a more accurate comparison between site and habitat types. In this way for example, community assembly theory can be applied as a framework for biological invasions and used to evaluate how native species interact with environmental filters on a community level (Pearson et al., 2018). The combination of a null model approach and trait functionality can reliably detect environmental filtering and limiting similarity when appropriate models are applied (Götzenberger et al., 2016). Establishing which traits have a close link with persistence in the abiotic environment and which represent the ability of a species to compete for resources will strengthen the methodology. Assembly theory provides a conceptual structure against which data can be compared to predict invasion outcomes. Understanding how the functional traits of native species affect their fitness response to community filters imposed by exotics can provide a measurable comparison of influential exotic traits on a community and key drivers that shift community structure.

A major issue in the assembly rules debate is the assignment of species to guilds. In theory, such guilds would represent sets of species that utilise resources in a similar fashion (Gotelli et al., 1997), thus overcoming the need for large amounts of information and determining the identity of each species (Fox and Fox, 2000). Connor & Simberloff (1979) criticised Diamond's designated guilds for not constituting an avifaunal systematic evaluation, which would be essential to establish a set of general assembly rules. Their own analyses however, of both congenial and confamiliaral groups have been criticised for including comparisons of species pairs that may never interact, hence the dilution effect (Diamond and Gilpin, 1982). Graves & Gotelli (1993) established guilds as subsets of ecologically similar congeneric species and their analysis provided empirical support for the dilution effect. Co-occurrence patterns at the level of ecological guilds were random and inconsistent, and analyses only detected significant checkerboard distributions for congeneric species in the same feeding guild (Gotelli et al., 1997). Wilson and Whittaker (1995) also outlined three approaches to seeking assembly; variance in richness may occur if the number of available niches is limited. An assembly rule may operate under these circumstances to limit the number of species that can potentially coexist. *A priori* guilds are groups of species that compete more with each other than species of other guilds and species dispersing to an area may have a lower chance of establishing if a major portion of the existing residents belong to the same guild, hence guild proportionality can limit the number of ecologically similar species. Intrinsic guilds are groups of species that generally exclude each other in the real community and even if species coexistence if restricted by guild membership. It is difficult to predict what guild classification the membership is based on. Use of this method guards against the possibility that the *a priori* guilds may be different from those actually operating. A likely explanation of co-exclusion in guilds is similarity in phenology however this could be investigated further. Assemblages with a high probability of coexistence are considered to be in 'favoured state', whereby the differences between number of species for each guild are never more than one (Fox and Fox, 2000). 'Unfavoured states' have a lower probability of existence and have a difference of more than one between the number of species in the guild or functional group.

The essence of checkerboard distribution is that species pairs occur on geographically dispersed islands and are likely to maintain their distribution by interspecific competition, but have an island-by-island distribution. While attempting his evaluation of assembly rules, Diamond (1975) proposed a metaphor of the 'checkerboard' whereby islands represent the alternating black and white squares of the game board and contain only one member of a pair of species. Diamond's (1975) idea was that the observation of a checkerboard distribution was evidence that the dispersal of species pairs is duly affected by interspecific competition. The idea that geographical distribution alone would provide a strong enough foundation to infer interspecific competition was criticised strongly by Connor and Simberloff (1979) and they argued the impact of its role in forming ecological communities. In doing so, they proposed the idea of the binary matrix for the distribution of species among islands. In their work, they likened the columns of a matrix to islands, the rows to species and the 1's and 0's in the matrix to represent either the presence or absence of a species (*Figure 1.2*). The presence-absence matrix is the fundamental unit of analysis in community ecology. Binary matrices measuring the presence or absence of species have been used in both biogeography and ecology for a number of years to compare similar sites, and the similarity of sets of sites occupied by pairs or larger groups of species (Collins et al. 2011), not exclusively islands or groups of islands.



A) True complete checkerboard

B) Exclusive distribution

C) True partial checkerboard

Figure 1.2: Representation of checkerboard distribution and the binary matrix. (A) A true checkerboard depicting the exclusive distribution of two species with geographic range represented by the solid and broken overlapping lines. (B) And exclusive distribution with geographic ranges not overlapping. (C) A partial checkerboard in which a pair shares a single island (Conner, et al. 2013).

That two species never co-occur is a necessary but not finite condition to establish a true checkerboard distribution. A fundamental condition for a true checkerboard is that two species never co-occur on any island yet the islands they occupy are interspersed, hence their geographical ranges overlap more than expected had they distributed independently of one another (Connor et al., 2013). The minimum criteria for defining a true checkerboard is that species pairs are exclusive, share a minimum of one island group and they are more interspersed than expected (Connor et al., 2013). Habitat patches become islands and animals use them according to a true checkerboard or more likely, a partial checkerboard. More research needs to be done to understand the checkerboard as a model for resource partitioning, particularly for marsupials. In a landscape highly modified by infrastructure and agriculture, habitat remnants may be utilised by ecologically similar species that in turn may utilise the same patches. Resource use and temporal activity patterns may be partitioned in such a manner to suit a checkerboard model. A structurally sound habitat matrix within a modified landscape can provide supplementary resources and increase the likelihood of movement throughout the landscape, thereby increasing overall species richness.

1.4 Ecology of Rainforest Pademelons

The original macropodids were likely to have been small, omnivorous forest-dwellers that were mostly nocturnal and relatively solitary (Kaufmann, 1974). *Thylogale* consists of six of the smallest macropodid species including the red-necked pademelon *(Thylogale thetis)* and the red-legged pademelon *(Thylogale stigmatica)* that occur in closed forest in northern Australia and New Guinea. Four subspecies of *T. stigmatica* are currently recognised: *T. s. stigmatica*, occurring in the wet tropics of northern Queensland, *T. s. coxenii,* occurring in the Cape York region, *T. s. wilcoxi*, from northern New South Wales and southern Queensland and *T. s. oriomo* from New Guinea (Johnson & Vernes, 1994). The distribution range of *T. s. stigmatica* and *T. s. wilcoxi* are separated by a dry habitat barrier, the Burdekin Gap (Macqueen et al., 2012). By comparison, the closely related *T. thetis* is distributed along the east coast of Australia from Nundaberg (Qld) to Jervis Bay (NSW) and is sympatric with *T. s. wilcoxi* throughout much of its northern range (Johnson, 1995)

Macropods evolved alongside numerous predators including the marsupial lion (*Thylacoleo carnifex*), and thylacine *(Thylacinus cynocephalus)* (Jarman, 2000). Modern predators of *Thylogale* include dingo (C*anis familiaris dingo*), which chases rather than stalks its prey, and large avian raptor species that prey on juvenile pademelons (Wahungu, et al. 2001). Smaller, solitary macropods are generally nocturnal, using crypsis in closed habitat or a nest to avoid predator detection (Jarman, 2000) which is typical of *Thylogale* behaviour. Due to the cryptic nature of *T. stigmatica* very little is known about the ecology of the species in the southern expanse of its range, or its ecological relationship with *T. thetis*.

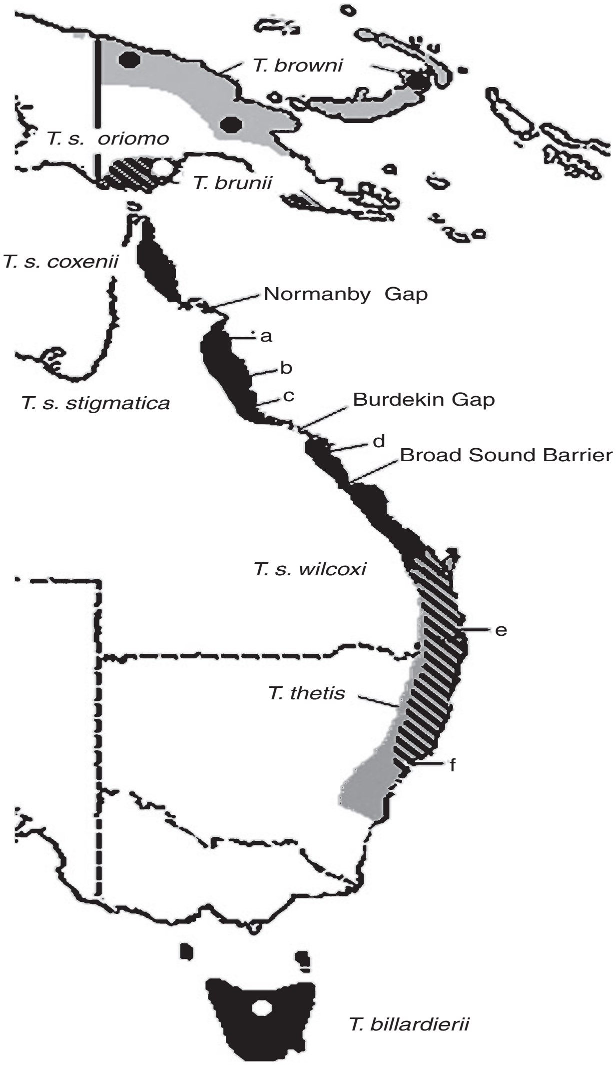


Figure 1.3: The distribution of *Thylogale* genus throughout Australia and New Guinea showing areas of sympatry (hatched) (Eldridge et al., 2011).

Mammalian social structure is only apparent if physical or behavioural adaptations allow the formation of social groups or environmental pressure encourages such behaviour (Kaufmann, 1974). Many mammal species limit the number of conspecifics regularly encountered, as frequent meetings with strange individuals is stressful for the individual and an expensive use of energy. Pademelon groups show very little social structure, and behavioural observations of the genus have not confirmed the existence of stable social hierarchy or predictable group constitution (Wahungu, et al. 2001). Aggregation in pademelons most likely occurs due to typical group fitness benefits such as increased feeding opportunity and reduced individual vigilance. The life-history traits of *T. stigmatica* are most likely similar to those displayed by the red-necked pademelon, *T. thetis*, and the Tasmanian pademelon, *T. billardierii*. Physical development of pouch young and major developmental events occur at similar times between the three species, which is to be expected given their similar maternal body mass, a key influence on variations of macropodid life-history traits (Johnson & Vernes, 1994).

The habitat preferences of *T. stigmatica* are primarily dense rainforest vegetation as well as wet sclerophyll forest and dry vine-thickets (Johnson, 1995). In northern Queensland populations, *T. stigmatica* spatio-temporally partitions its home range distinctly into rainforest and forest-pasture boundary (Vernes et al., 1995). The diurnal range is restricted to forest cover, while the forest-pasture boundary is utilised nocturnally, presumably to exploit readily available, nutrient rich grasses rather than the patchily distributed preferred forest browse. *T. stigmatica* is unusually active during the day compared with other macropods (Croft, 1989) and makes extensive movements during the diurnal part of a diel cycle (Vernes et al., 1995). In the southern parts of its range when in sympatry with *T. thetis*, anecdotal evidence suggests that *T. stigmatica* does not appear to venture from the forest edge, although this has not been explicitly tested. It is assumed to exist primarily on non-grassy vegetation (Jarman, 1989) and in such circumstances, population densities are reported to be lower than the sympatric *T. thetis* (Calaby, 1971) . It is known that *T. thetis* behave similarly to northern populations of *T. stigmatica,* and exploit forest-pasture boundary through the night, while remaining in forest cover by day (Johnson, 1980; Jarman, 1989; Wahungu et al., 1999).

The diet of *T. s. stigmatica* in northern populations consists of mostly grassy monocotyledons (43%) and dicotyledons (34%), which is consistent with the nocturnal excursions to forest-pasture boundaries (Vernes, 1995). The only study completed on NSW populations of *T. stigmatica* showed that mostly dicot leaves and fruit were consumed (Jarman, 1989) which is consistent with observations that they do not leave forest cover. Mitchell et al. (2018) found that *T. s. wilcoxi* has a broader cranium with a shorter and more robust muzzle, typical of browsing species while *T. s. stigmatica* possesses a gracile skull with a longer muzzle, similar to *T. thetis* and common amongst grazing macropods. It appears that northern populations of *T. stigmatica* use their habitat very differently from southern populations, particularly when occurring in sympatry with *T. thetis.* This is reflected in both their diet and cranial morphology and is indicative of competitive pressures through feeding regimes.

When food resources are limited, competition within guilds is expected particularly when other overriding factors may be absent. Such competition can come from interspecific partitioning of available resources. For sympatric species such as *T. thetis* and *T. stigmatica,* resource partitioning may be evidenced by habitat selection or choice of diet within a habitat. Research by Le Mar and McArthur (2005) on sympatric macropods *T. billardierii* and *Notamacropus rufogriseus* found that both species selected for closed habitats diurnally, but contrasted in specific fine-scale habitat preferences. *Thylogale billardierii* selected native forest whilst *N. rufogriseus* selected older plantation which may reflect differentiation in predator avoidance strategy and habitat partitioning. Both species strongly selected for young plantation nocturnally, which is indicative of selection relating to food resources. Nocturnal habitat was selected across two spatial scales, both within the home range and as a nocturnal foraging area. This indicates spatial partitioning of resources between two sympatric macropod species, similar to northern NSW populations of *T. thetis* and *T. stigmatica.* From a management perspective, understanding where animals forage and how they utilise their habitat will potentially lessen the impact of herbivorous species on agricultural productivity and enable efficient conservation efforts.

Foraging behaviour is also often determined by distance from protective cover, which may be an important factor in habitat selection and resource partitioning in sympatric species. Closed habitats offer protection from abiotic conditions such as extreme weather and, as previously discussed, predation risk. Studies of several macropod species including the eastern grey kangaroo *(Macropus giganteus)* (Banks, 2001), the red-bellied pademelon *(Thylogale billiardierii)* (While and Mcarthur, 2005) and red-necked pademelon *(Thylogale thetis)* (Wahungu et al., 2001) have determined that distance from cover is a highly decisive factor in foraging behaviour among macropods. Results from research conducted by While and McArthur (2006) on *M. rufogriseus* and *T. billardierii* found that there was a significant negative relationship between the distance of a food patch from cover and the amount of food consumed. This demonstrates a distinctive trade-off between foraging effort and predation risk. Individuals were prepared to further deplete resources closer to protective cover and, presumably, a lower risk of predation. Similarly, habitat selection is restricted in the quokka *(Setonix brachyurus)* when compared to the amount of overall available habitat (Hayward et al., 2004). The requirement for dense, swampy vegetation as diurnal habitat selection provides refuge from weather and provides a microhabitat preference necessitating close proximity to available fresh water bodies (Hayward et al., 2004). Predation is likely to inhibit inter-patch movement between areas of available habitat and indeed further impinge metapopulation structure. While there are no current studies of this kind for *T. stigmatica* and *T. thetis*, given the effect of predation risk and the importance of available closed habitat for other species of small macropod, it is likely that the same factors will affect *T. thetis* and *T. stigmatica*. Regular association with forest edges and ecotones increase the likelihood that distance from cover and predation risk are highly influential in the habitat selection of *T. stigmatica*. It is currently unknown what ecological associations occur between *T. stigmatica* and *T. thetis* in sympatric populations and further research may reveal more about their foraging behaviour and utilisation of habitat. This information would prove vital to understanding metapopulation structure and the preservation of the vulnerable *T. stigmatica.*

The home range size of *T. stigmatica* is small in relation to mean body weight (Vernes et al., 1995). Vernes et al. (1995) found that *T. stigmatica* spatially divided its home range into distinct diurnal and nocturnal components, moving slowly within and quickly between ranges. Home range size can also be affected by the reproductive strategies of species. In solitary, promiscuous species, searching for a mate becomes prominent in the male mating strategy. Male home ranges tend to increase in an attempt to overlap with as many receptive females as possible (Fisher and Lara, 1999). In bridled nailtail wallabies (*Onychogalea fraenata*) males with larger home ranges came into contact with more oestrus females most likely due to their wide ranging behaviour (Fisher and Lara, 1999). In high rainfall habitats, female macropods had the smallest home range size while males increased their home ranges beyond that of females by the greatest amount (Fisher and Owens, 2000). Studies on the Tasmanian pademelon *(Thylogale billardierii)* found that captive populations breed continuously compared to wild populations that experience a restricted breeding season, indicating that nutrition may impact female fertility and reproductive cycles in the wild (Rose and McCatney, 1982a). The reproductive cycle of *T. billardierii* is similar to patterns found in other species of macropod and pouch life of young is also similar to comparable species such as the parma wallaby *(Notamacropus parma)* (Rose and McCatney, 1982b). There are no previously published reports on the ovarian and uterine changes during pregnancy, nor any previous research on embryonic development in any members of the *Thylogale* genus (Rose et al., 1999). Possibly due to the impermeability of dense rainforest, there has been little research done on the mating habits of wild populations of *Thylogale.*

1.5 Thesis Aims and Structure

This study aims to shed light on the ecology of sympatric *T. thetis* and *T. stigmatica* populations in northern NSW and how habitat variables affect spatial distribution and habitat use. *Thylogale* will be the primary focus of the study, nested within a wider focus of the mammalian community. Camera traps will be used to map mammal occurrence and abundance, as well as track diel activity patterns. Measurements of structural habitat variables will give an overview of forest complexity and the depth of variation in habitat type. Together with camera trap data, the habitat affiliation and responses to habitat variation are assessed. In doing so, the ecological profile of a northeastern NSW population of *T. stigmatica* will be described in detail for the first time, thereby highlighting key differences between southern populations and north Queensland populations of *T. stigmatica,* as well as understanding how *T. stigmatica* responds to the competitive pressures of co-occurrence with *T. thetis.*

Chapter 2 will investigate the overlap in diel activities of both *T. stigmatica* and *T. thetis.* Sympatry shapes the dynamics of mammalian community and a suite of behavioural mechanisms such as dietary partitioning or differential use of space are used by ecologically similar species in order to avoid competition (Karanth et al., 2017). Sympatric species may use several niche axes to decrease overlap in resource use, either spatially, temporally or through dietary partitioning to avoid competition and enhance coexistence, which by default increases community diversity (Jones et al., 2001). Temporal partitioning decreases the chances of interspecific contact and reduces the number of interactions an individual can have in a diel cycle (Kamler et al., 2013). Ecologically similar, co-occurring species may therefore display some flexibility in their diel activity patterns in order to avoid agonistic interactions with one another. Investigating the overlap in the diel activity of *T. stigmatica* and *T. thetis* will allow a glimpse into the extent of competition, if any, that exists between the two ecologically similar species.

In Chapter 3, spatial partitioning and habitat affiliation of *T. stigmatica* and *T. thetis* are investigated. Habitat related factors may drive spatial distribution in sympatry due to the availability of suitable resources and microhabitats (Kubiak et al., 2015). Ecologically similar species may be forced into sympatry if disturbance effects limit habitat or resource availability, or if the distance between fragments hinders dispersal. Anecdotal evidence suggests that *T. thetis* behaves in a similar manner to northern populations of *T. stigmatica* whereby habitat is divided spatio-temporally into interior forest diurnally and forest-pasture boundaries nocturnally (Johnson, 1980; Jarman, 1989). This chapter aims to investigate the spatial use of habitat between *T. stigmatica* and *T. thetis* in a sympatric population and whether spatial niche partitioning occurs between the two species. Measurements of structural habitat components will reveal the structural complexity and variation in the habitat which, coupled with camera detection data, will reveal abundances of both species throughout the area and whether spatial partitioning is significant.

Finally, in Chapter 4, the complexity of the mammal community and impact of habitat on species composition is assessed. The diversity of a community and the individual characteristics of species may result from the variation and range of resources available (M'Closkey, 1976). The ability of a species to persist in a given area is often dependent on abiotic conditions, the resources available and what niches have already been filled by ecologically similar species. The environment is recognised as a selective pressure that filters out species unable to tolerate abiotic conditions.

Remaining species may share phenotypic similarities reflective of the tolerance to conditions (Kraft et al., 2015). A combination of structural habitat measurements and camera trap detection data will confirm species presence or absence throughout the habitat and allow a snapshot of the assembly composition within the area. Measurement of habitat variables provides an understanding of disturbance effects in the environment and the impact on mammalian community composition.

Chapter 5 provides a synthesis of research findings on both pademelon species, as well as the wider mammal community. Proposed priorities for further research on rainforest pademelons is discussed.

1.6 Conclusion

Ecologists have been debating the validity of assembly rules for decades and much research has been done on their potency and comparability between communities. Modern research now needs to formulate specific hypotheses that further the idea of assembly rules and deepen understanding of community assembly. As large expanses of habitat become smaller and more fragmented, scale and connectivity come to the forefront of community ecology in an effort to understand how species adjust to a changing landscape. The impact of habitat attributes on both an individual species and the community is paramount to ensuring effective conservation strategies in the future.

The significance of spatial patterns is not always considered in real world application and as such, mammalian communities may not be managed effectively. Checkerboard patterns and the idea of binary matrices are evident in assemblages but more research needs to be done to further understand the role of spatial patterns in regards to habitat use in a fragmented landscape. This in turn will broaden understanding of community assembly and sympatric species. Marsupials are particularly under-represented in such studies and cryptic or shy species even more so due to their inaccessibility. The advent of camera trapping allows new research to take place in previously inaccessible areas, broadening the research scope for both Australian researchers, as well as researchers around the world. Understanding what habitat affiliations sympatric populations of *T. thetis* and *T. stigmatica* have and how this affects their population distribution is an important first step towards understanding modern community assembly in a fragmented Australian landscape.

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Chapter 2 - Activity patterns and temporal niche partitioning in sympatric populations of red-legged *(Thylogale stigmatica)* and red-necked *(Thylogale thetis)* pademelons in northeastern NSW.

2.1 Abstract

Temporal partitioning between ecologically similar species facilitates biodiversity and can affect the dynamics of mammalian assembly structure both positively and negatively. The diel activity patterns of a sympatric population of red-legged (*Thylogale stigmatica*) and red-necked (*Thylogale thetis*) pademelons were monitored over an 18-month period from 2017 through to 2018. Both species displayed strongly crepuscular patterns typical of many macropod species, however *T. stigmatica* was less active during evening twilight than the morning, indicating evidence of temporal partitioning. Findings were consistent with earlier studies that *T. stigmatica* utilises covered habitat whilst *T. thetis* spatio-temporally divided their habitat, spending the diurnal period under cover and the nocturnal period at the forest-pasture edge. *T. stigmatica* showed some plasticity in their activity budgets when sympatric with the ecologically similar species *T. thetis*, and likely exhibited temporal partitioning in response as a form of niche partitioning.

2.2 Introduction

Many mammalian species regulate time budgets over a 24-hour diel period. Activity levels often coincide with varying light levels to optimise fitness according to appropriate hours of daylight and darkness (Bennie et al., 2014). Animals divide their time between activity and rest, and whilst activity is essential to fitness enhancement, it is more energetically expensive than resting (Rowcliffe et al., 2014). Activity increases risk by heightening exposure to predation and increasing physiological stress. Individuals must ensure an optimal amount of activity to meet basic needs, yet minimise energetic costs (Suselbeek et al., 2014). Activity involving the procurement of resources and mates increases exposure to predation, and activity patterns are likely to conform accordingly to minimise this risk (Bridges et al., 2004). Patterns of diel behaviour directly influence individual fitness, and therefore behavioural responses to time of day are important in defining niche dimensions within a community (Kronfeld-Schor and Dayan, 2003). Light levels and temperature ranges combine to create available niches that animals can tolerate and these abiotic factors in turn constrain community structure by limiting the number of available niches (Bennie et al., 2014).

Generally, two species cannot co-habit in the same environment as ultimately one would have greater fitness and suitability to the abiotic conditions and outcompete the other. The underlying principal of competitive exclusion states that two ecologically identical species cannot coexist indefinitely (Schwilk and Ackerly, 2005) because eventually one species will compete the other into local extinction. However, niche theory provided the first solution to the coexistence problem and consequently, niche overlap refers to expenditure of the same resource by two or more species (Abrams, 1983). Sympatric species may use several niche axes to decrease overlap in resource use, including space, food, and time, which can reduce competition and enhance co-existence which by default, increases diversity (Jones et al., 2001).

Several factors can influence the availability of niches in a community and how community members segregate access to resources. Ecological niches within a community are shaped by intraguild competition as it affects a species' ability to access limited resources (Bu et al., 2016). The temporal niche can be considered a species' distribution through the diel cycle and reflects a range of responses to perceived risk and opportunity, which fluctuates over that cycle (Shamoon et al., 2018). The flexibility of the temporal niche facilitates resource utilisation and is crucial for species persistence in sub-optimal conditions. Temporal partitioning decreases the likelihood of interspecies contact, thus reducing the number of interactions an individual can have within a diel cycle (Kamler et al., 2013) and minimising stress load induced by excessive interactions. Additionally, temporal partitioning reduces competition or aggressive interactions for ecologically similar species allowing coexistence in keeping with the carrying capacity of the environment.

Habitat loss (Norris et al., 2010) and anthropogenic disturbance (Shamoon et al., 2018) also affect species spatio-temporal activity patterns and modify their interactions. Competing species can co-exist if there is the capacity for flexibility in activity patterns, despite the consequence of ecological trade-off. The ability of some species to maintain their diel patterns and some to change it, highlights the role of interference competition and induced behavioural adjustments in herbivore population dynamics and community structure (Valeix et al., 2007). This suggests that the strength of interactions between competing species is linked to the availability of a shared resource. According to Monterroso et al. (2014) in a study of mesocarnivores on the Iberian Peninsula, competing species could locally adapt their strategies in response to environmental cues such as light levels associated with time of day to maximise foraging efficiency and reduce the opportunity of agonistic encounters with intraguild competitors. Studies of herbivorous guilds in Victoria, Australia (Davis et al., 2018) found evidence of high overlap in habitat use between native species such as the eastern grey kangaroo (*Macropus giganteus*) and swamp wallaby (*Wallabia bicolor*), and introduced species such as the European rabbit (*Oryctolagus cuniculus*) and hog deer (*Axis porcinus*) at a broad scale. Despite this evidence however, coexistence was likely facilitated by niche complementarity, including temporal and fine-scale spatial resource partitioning. The dynamics of community assembly are complex, and driven by several determining factors. The potential for plasticity in the activity patterns of species as well as niche complementarity encourages sympatry among ecologically similar species and contributes to community structure.

Understanding community structure is often determined by observational research. While some larger species of macropods have been studied extensively, few studies have been undertaken on smaller macropod species. Part of the problem in undertaking this type of research includes habitat accessibility (Cooper et al., 1999) or the cryptic nature of many smaller species. One possibility to improve the expansion of this research is the utilisation of camera traps. Camera traps enable researchers to study population dynamics, undertake inventories and gain insight into the day-to-day activities of wildlife through behavioural studies (O'Connell et al., 2010). Cameras are operational 24 hours a day and can be left unattended for several weeks at a time. Camera traps remove the need for an observer in situ and reduce potential bias on animal behaviour, allowing researchers to investigate questions that otherwise may have been too resource intensive (Meek et al., 2015a). As such, camera trapping provides a useful and non-invasive method for investigating patterns on spatial and temporal scales and their link with habitat use (Silveira et al., 2003), all of which are key elements in wildlife conservation research.

The genus *Thylogale* consists of six of the smallest macropodid species, including the red-necked pademelon *(Thylogale thetis)* and the red-legged pademelon *(Thylogale stigmatica)* that occur in closed forest in northern Australia and New Guinea. The habitat requirements of *T. stigmatica* is typically dense rainforest vegetation, and in some areas wet sclerophyll forest and dry-vine thickets (Johnson and Vernes, 1995). In northeastern Queensland, *T. stigmatica* is most prevalent in rainforest edges adjacent to pasture or open grassland. It browses various structural parts of forest plants during the day and ventures into open areas after sunset to consume grasses (Vernes, 1995). In the southern expanse of its range, *T. stigmatica* rarely leaves the forest and exists solely on non-grassy vegetation and in such circumstances, population densities appear to be lower than the sympatric *T. thetis* (Johnson, 1977). *T. stigmatica* is a species that regularly associates with forest ecotones and edges between rainforest and open grassland or agricultural land in northern Queensland. Due to the cryptic nature of *T. stigmatica* however, very little is known about the ecology of the species in the southern expanse of its range or its ecological relationship with *T. thetis*. *T. thetis* inhabits rainforest and vegetation with dense understorey in subtropical areas of eastern Australia (Strahan, 1980) and alos commonly occurs at forest adges adjacent to pasture (Jarman, 1989). The natural range of *T. stigmatica* and *T. thetis* coincides with habitat that has been highly impacted by anthropogenic land clearing and modification for agriculture and forestry. Many remaining tracts of habitat are reasonably well protected but threats remain in some parts of the range in the form of land clearing and through predation by introduced foxes and cats (Vernes and Johnson, 2008).

Very little research has been undertaken on sympatry in herbivorous guilds in Australia, however numerous studies of co-existence have been conducted on carnivorous intra-guild competition and niche overlap both internationally (Harrington et al., 2009) and in Australia (Glen and Dickman, 2008). The overlap of activity throughout the diel cycle was investigated between *T. stigmatica* and *T. thetis* using data collected from camera traps in a forest fragment in northeastern NSW. In doing so, it was hypothesised that temporal partitioning occurs between the two sympatric species and the activity of one species influences that of the other in respect to how habitat resources are utilised.

2.3 Methods

2.3.1 Location

Mount Hyland Nature reserve is situated in northern NSW on the Dorrigo plateau on the eastern slopes of the Great Dividing Range. Both Mount Hyland Nature Reserve and the adjoining Mount Hyland State Conservation Area are located approximately 30 kilometres north-west of Dorrigo (30°20.4'S, 152°42.6'E and approximately 35 kilometres south-west of Nymboida (29°56.4'S, 152°43.8'E) (Department of Environment and Climate Change, 2009). The mean maximum and minimum temperatures for the area are 20°C and 10°C respectively (Bureau of Meteorology, 2018). A section of Mount Hyland Nature Reserve was included on the World Heritage List as part of the Gondwana Rainforests of Australia property in 1986. The area satisfies three natural criteria for universal significance for containing examples of earth's major evolutionary history, including representation of significant ongoing geological processes, the biological evolution of human relationship with the natural environment, as well as significant habitat where threatened species still survive, and was extended in 1994 (Department of Environment and Climate Change, 2009).

2.3.2 Site Description

The research site spans a privately owned, 398-ha forest property, Motherland, adjoining Marengo State Forest and world heritage listed Mount Hyland Nature Reserve and includes the Mount Hyland Wilderness Retreat. The area contains five broad vegetation types of rainforest, wet sclerophyll forest, dry sclerophyll forest, dry sclerophyll woodland and semi-mesic grassy forest which can be sub-divided into 21 plant communities (Department of Environment and Climate Change, 2009). The cameras are specifically located in rainforest and wet sclerophyll forest.

The forest at Motherland is situated around a large grassy clearing with several clustered buildings. The southern side of the clearing is predominantly surrounded by wet sclerophyll forest with a eucalypt overstorey. Rainforest dominates the northern side of the property and into Marengo State Forest with patches of eucalypt dominants.

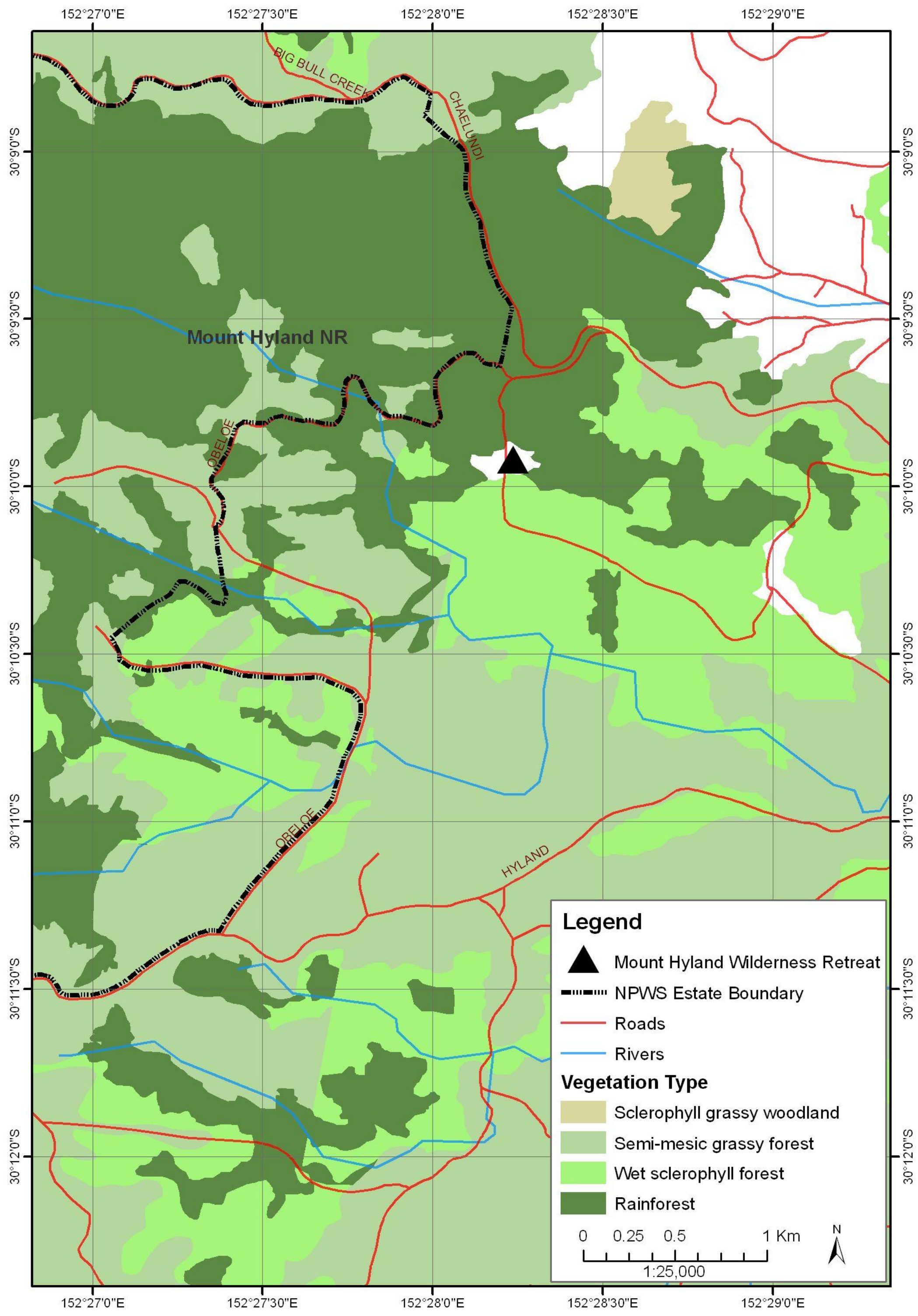

Figure 2.1: Vegetation types of Mount Hyland Nature Reserve (NSW Office of Environment and Heritage, 2013) including study site labeled ‘Mount Hyland Wilderness Retreat.

2.3.3 Camera Placement

2.3.3.1 Forest Deployment

Forty-eight Scoutguard and UOVision white flash cameras were deployed between the two forest types in the study site (*Figure 2.2*). To ensure random distribution throughout the area, a random distance and bearing were assigned to each camera using Microsoft Excel. The local fire trails enabled access to the site, and at every 100m, a camera was deployed according to its assigned distance and bearing. Nine cameras were deployed in rainforest along the Motherland entrance road, and another fourteen were deployed along Obloe Road. After 1500m along Obloe Road, the forest on either side of the trail was largely inaccessible due to a sharp incline on either side of the trail. The forest opened into wet sclerophyll, and another five cameras were deployed in that area. On the southern side of the house clearing, fire trails were again used for vehicle access and a further 19 cameras were deployed.

Camera positions were tracked using the iPhone GPS software, MotionX. Each track was recorded using MotionX and a waypoint was created at each camera site. Entry points into the forest were flagged at the appropriate trail for each camera. Where possible, cameras were positioned approximately 50cm above ground level facing south to minimise light and shade movement. Small shrubs or leafy branches in the detection zone were pruned to avoid 'empty' images. Each camera was then set to photo mode on deployment. Baits were used to prolong investigation of any passing individuals and consisted of a porous PVC canister containing cotton wool soaked with truffle oil, which was inaccessible to animals. It was expected that animals would be detected at the bait canister 2 metres from the camera, so approximately 80% of the LED flash bulbs on each camera were covered before deployment to prevent night photos being 'washed out' by excessive illumination of subjects at close (<2m) range. Camera batteries and memory cards were replaced every 8-12 weeks and baits refreshed.

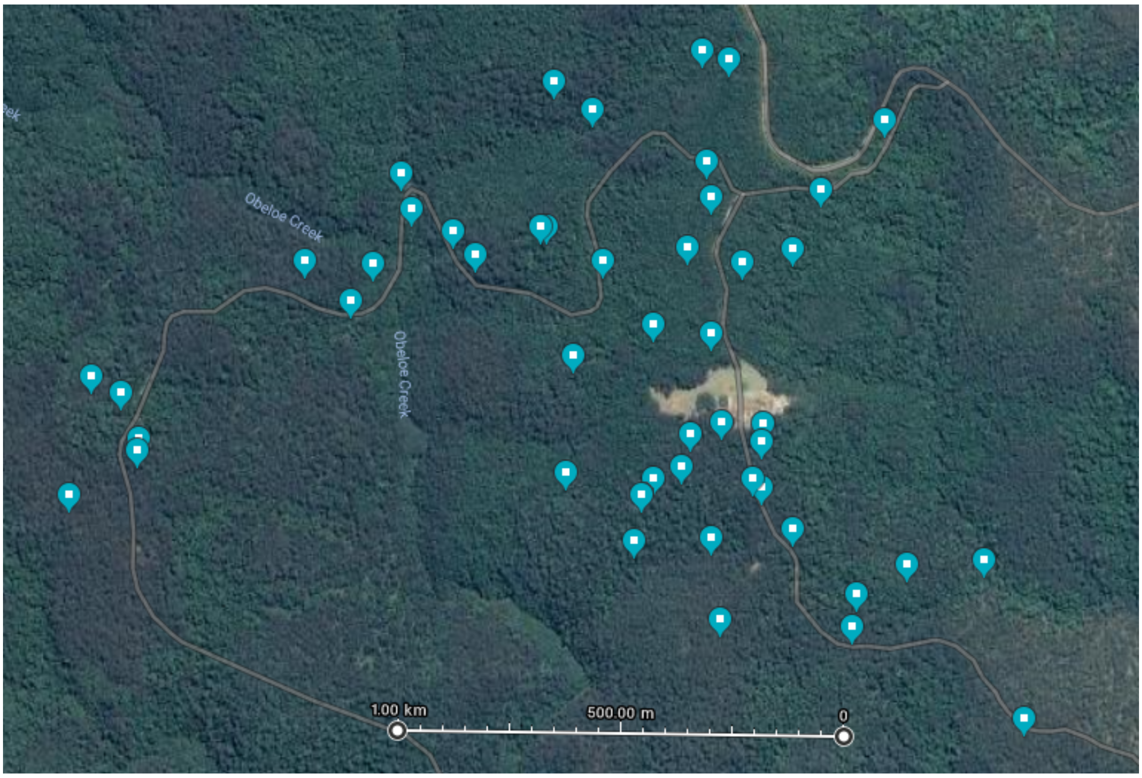

Figure 2.2: Forty-eight cameras were deployed through rainforest and wet sclerophyll forest.

2.3.3.2 Grassy Clearing Deployment

Prior to beginning the main study, a smaller deployment of cameras was also undertaken in this area in 2014 to determine which species of pademelon left the forest to graze the adjacent grassy habitat. In this study, 19 Scoutguard white flash cameras were deployed within a grassy clearing at the centre of the study site (*Figure 2.3*), with each camera approximately 10-30cm from the forest edge at random points around the perimeter of the clearing. This location is the only such clearing available to *Thylogale* within the study area (*Figure 2.2*) and scats present in the clearing at the time of the study suggested heavy, regular usage by pademelons.

Figure 2.3: Nineteen cameras were deployed around the main clearing at 'Motherland'.

2.3.4 Statistical Analysis

Raw camera images within each camera's folder were sorted according to the method outlined by Harris et al. (2010). The 'CameraSweet' software developed by Sanderson and Harris (2013) was then used to analyse camera data to generate a spreadsheet of independent records. Independent events were considered to be any detection 30 minutes or more apart to avoid any lingering individuals skewing results. Initial analysis for the two species was carried out using the 'Overlap' package in R (Meredith and Ridout, 2016). This package fits kernel density functions to temporal activity data, estimates coefficients of density overlap between two species and calculates bootstrap estimates of confidence intervals.

To investigate the potential influence of the two species on one another, generalised additive models (GAM) with a negative binomial distribution were used and carried out using the 'mgcv' package in R. The number of detections was set as the response variable, with species and hour as the explanatory variables. New data was reproduced to predict to and confidence intervals were generated. To determine effects of month and hour as well as interaction of the two variables, GAM with a negative binomial distribution were used again and performed independently for each species.

2.4 Results

The study site was surveyed for a total of 18,336 trap days and nights. During that time a total of 383 and 1,924 independent detections for *T. stigmatica* and *T. thetis* were recorded respectively.

2.4.1 Diel activity patterns within forest

Both species were strongly crepuscular with activity peaks occurring at approximately 0600 and 1800 hours (*Figure 2.4*). However, *T. stigmatica* tended more towards diurnal activity that *T. thetis*, with larger numbers of *T. stigmatica* detected around the dawn period than at dusk. *T. thetis* had a higher detection rate than *T. stigmatica* and displayed a bimodal activity pattern with more similar peaks of activity at both dawn and dusk. Bootstrapping routines simulated 1000 random observations generating a mean overlap between the two species of 76.6% (upper and lower 95% CI = 80.1% and 72.6%). The main difference in overlap stems from *T. stigmatica* restricting its activity to the early and mid-morning period, and having reduced activity in the late afternoon and early evening.

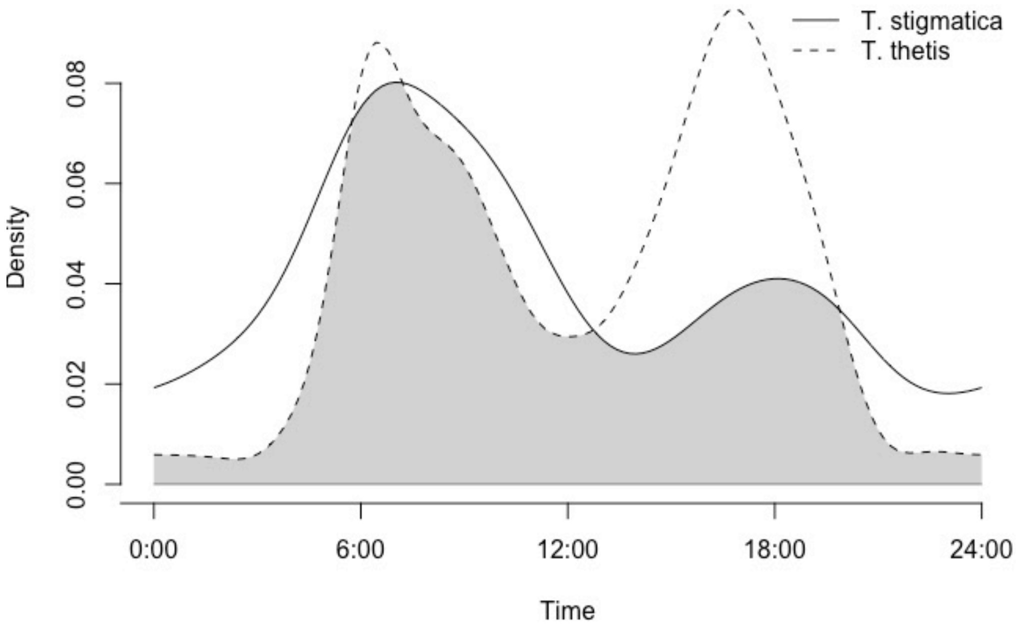

Figure 2.4: Kernel density of *T. stigmatica* and *T. thetis* over the diel cycle. The shaded area indicates proportion of overlap of diel activity patterns between the two species.

GAM also revealed significant results for the effect of interaction on the individual activity patterns of *T. stigmatica* and *T. thetis* during the diel period (*Figure 2.5).* Peaks in activity for *T. thetis* reached almost 15 individuals while overall detections for *T. stigmatica* remained at less than five. GAM revealed the detection rate per hour was significantly different for each species independently ($p < 0.001$), and the interaction of species and hour explained over half the rate of detection ($R^2 = 52.5$). For *T. thetis*, the detection rate was significantly different per hour ($p < 0.001$) and month ($p < 0.001$) however the interaction of these two effects did not significantly affect overall detection rate ($p = 0.19$), indicating that the diel pattern of activity doesn't change according to season. The diel crepuscular pattern of *T. thetis* remains relatively unchanged throughout the year (*Figure 2.6*).

Similarly to *T. thetis, T. stigmatica* follows a crepuscular pattern however activity is much higher in the morning than in the evening. GAM revealed a significant difference in the hourly detection of *T. stigmatica* ($P < 0.001$) but there was no significant effect on the number of detections per month ($P = 0.16$) or in the interaction of month and hour ($P = 0.33$), indicating no change in the diel cycle throughout the year (*Figure 2.7*). Cameras were not deployed during the month of April which has negatively affected results for that month, however, detection rates were highest during November through to January (*Figures 2.6 & 2.7*).

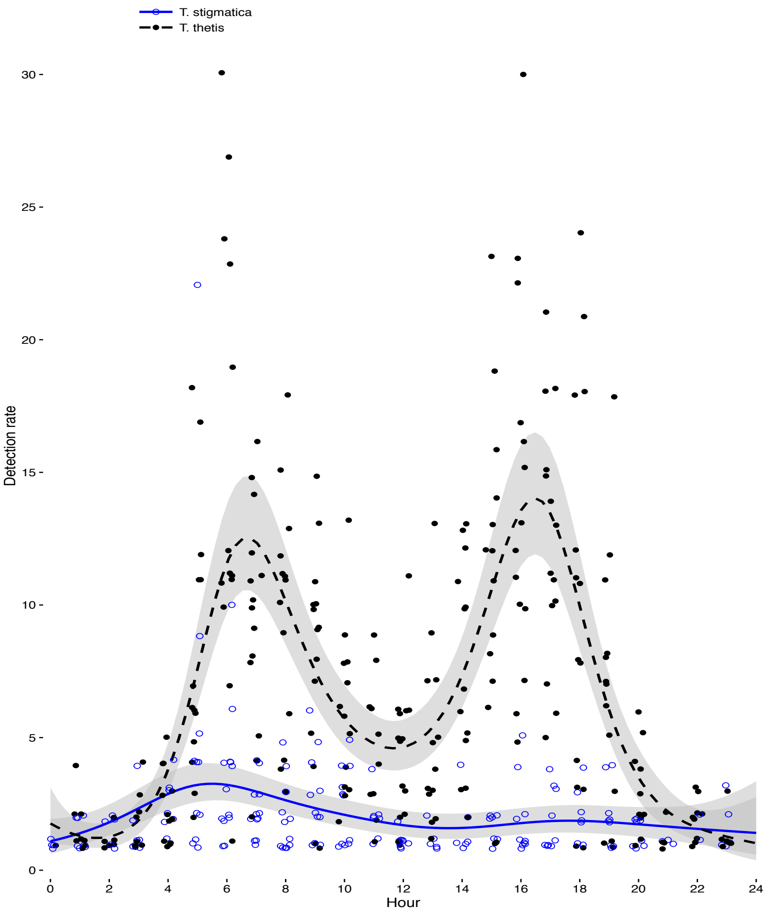

Figure 2.5: Generalised additive model of *T. stigmatica* and *T. thetis* detections.

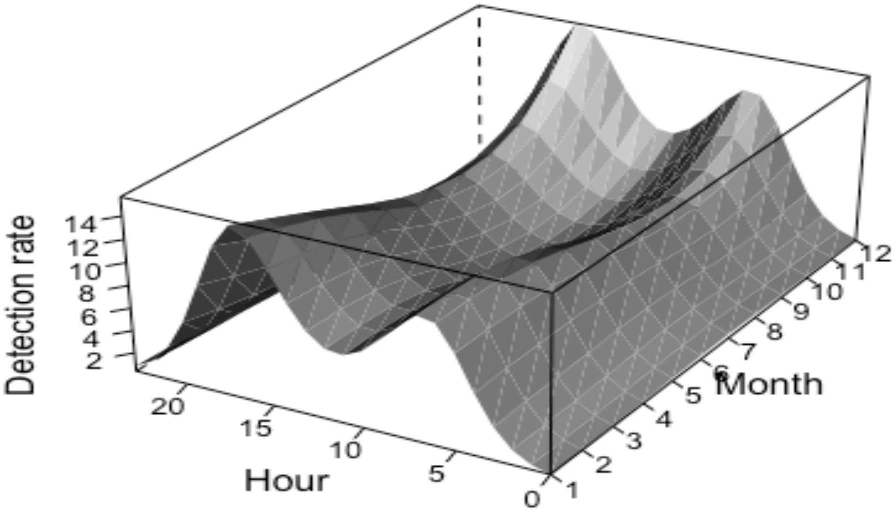

Figure 2.6: *T. thetis* diel activity over a 12-month period.

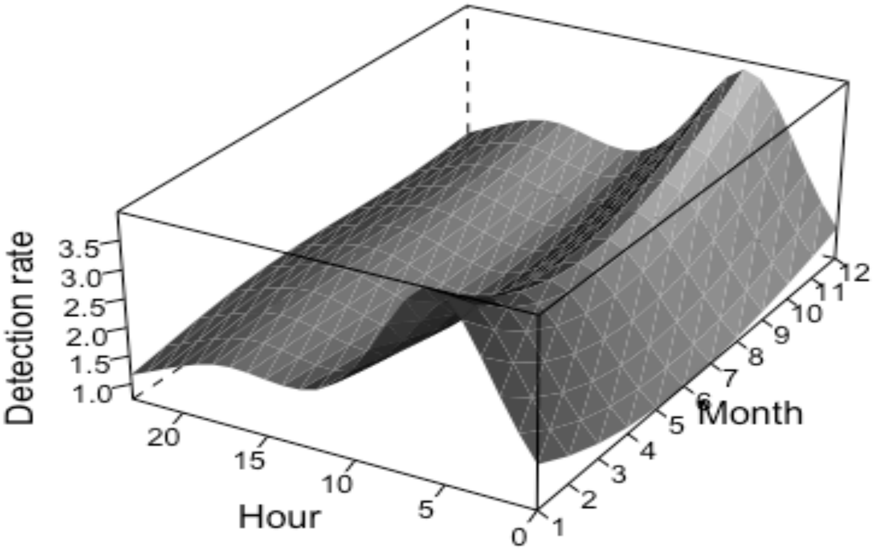

Figure 2.7: *T. stigmatica* diel activity pattern over a 12-month period.

2.4.2 Diel activity patterns on pasture

While both species were strongly crepuscular, *T. thetis* was nocturnally active on the grassy clearing and the forest-pasture boundary (*Figure 2.8*). Some cameras situated within the forest but only a few metres from the forest-pasture edge recorded *T. stigmatica* events, however, no *T. stigmatica* detection events were recorded by cameras located on pasture (over 418 camera nights where 957 independent events of *T. thetis* were recorded). While activity levels still decreased after approximately 6pm (*Figure 2.4*), kernel densities remained at approximately 0.06 throughout most of the nocturnal period (*Figure 2.8*), indicating that *T. thetis* spends this time out from the cover of the forest and in the pasture clearing. GAM yielded significant results for the interaction of hour and detection ($p < 0.001$), indicating that *T. thetis* engages in a significantly different level of activity from hour to hour on the grassy clearing.

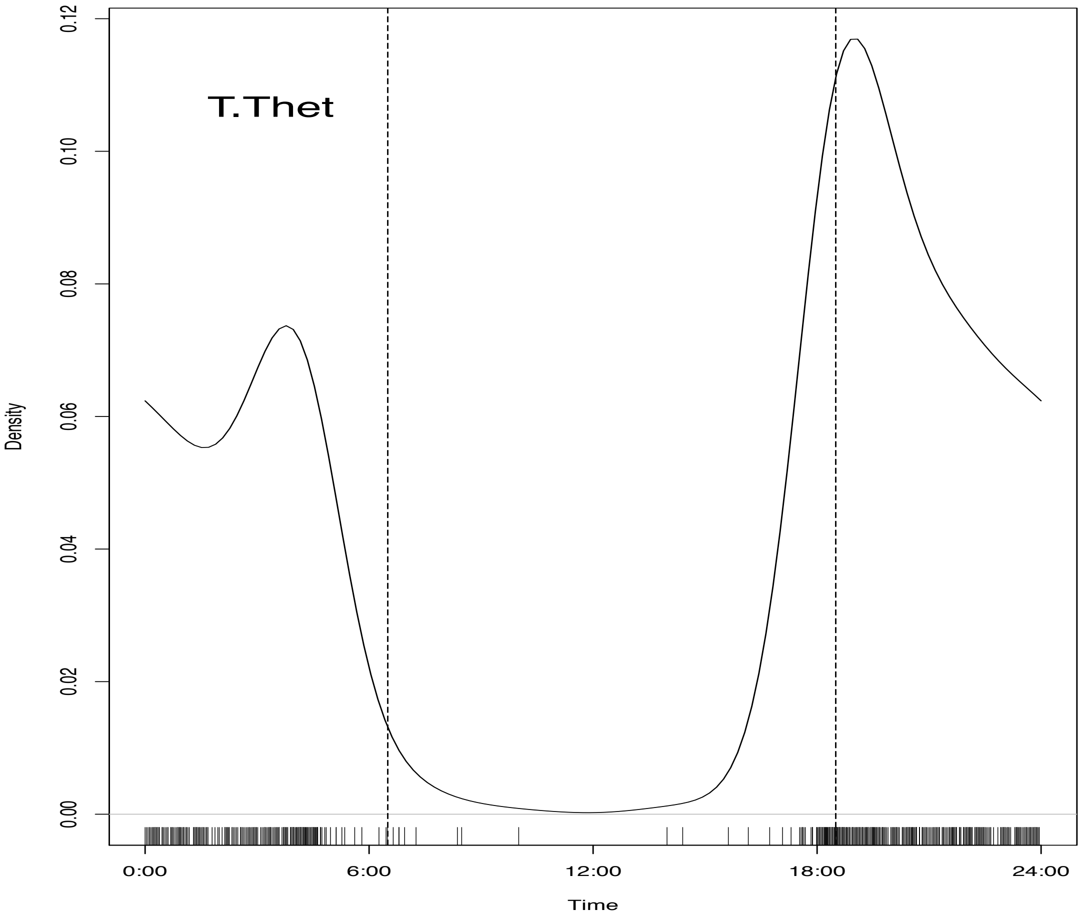

Figure 2.8: Kernel density of *T. thetis* over the diel cycle beyond the forest edge in the grassy clearing.

2.5 Discussion

Both *T. thetis* and *T. stigmatica* showed strongly crepuscular diel activity patterns. This is similar to the activity patterns of many large species of macropods (Priddel, 1986) as well as the several smaller wallaby species. *T. thetis* exhibited similarly high levels of activity during both morning and evening twilight which is most likely reflective of their nocturnal excursions to pastures for foraging and typical of a crepuscular diel cycle. This type of activity is also exhibited in the swamp wallaby (*Wallabia bicolor*), which remains in dense cover during the day and ventures to more open grassy areas at night (Hollis, et al. 1986; Johnson, 1977) as well as the black-striped wallaby, *Notamacropus dorsalis* (Jarman et al., 1991). This is indicative of a resting period and shade seeking behaviour during the day, which is a strategy used to avoid heat loading and subsequent water loss that occurs due to thermoregulation

(Blackshaw and Blackshaw, 1994; Roberts et al., 2016). A marked decrease in activity between 20:00 and 03:00 indicates a decrease in nocturnal activity (*Figure 2.4*), however data collected from a subset of the data from cameras situated in the grassy clearing, shows that while activity decreases somewhat after dusk, *T. thetis* remained active during the nocturnal period (*Figure 2.8*). Other macropod species are nocturnally active (Biebouw and Blumstein, 2003) and it is known that *T. thetis* exploit available grassed areas in their range (Johnson, 1980). The peaks in activity found in this study were consistent with earlier observations of movement to and from pastured areas to feed, and data from cameras in the grassy clearing show that *T. thetis* do indeed exploit pastured areas during the nocturnal period while *T. stigmatica* likely remain under forest cover as they were not detected on cameras in the clearing.

Diurnal activity patterns for both species remained the same throughout the entirety of the study period. Behavioural strategies are influenced by a combination of intrinsic and extrinsic factors, including ambient temperature (Zalewski, 2000). Given the relatively small difference between the two temperature extremes in the area, it is likely that the animals do not change their patterns throughout the year as a response mechanism to temperature variation. There was an apparent reduction in activity from March through to August, which is potentially influenced by a lack of camera deployment during April 2017 (*Figures 2.6* and *2.7*). Overall, there were lower detection rates during winter months, indicating that pademelon activity may be affected by cooler weather or shorter periods of daylight. The time of sunrise and sunset did not influence the activity of the pademelons throughout the year, however, this was not tested explicitly and could be explored further.

Unlike *T. thetis*, *T. stigmatica* showed high levels of activity during the morning and much lower levels of activity during the evening. While activity was lower overall nocturnally, it was higher than *T. thetis* under the forest canopy cover. No detections of *T. stigmatica* were recorded on pasture during the grassy clearing component of the study, underpinning Johnson's (1989) observation that *T. stigmatica* do not venture from forest cover. Many species have a crepuscular pattern however only a few are particularly active at dawn (Cooper et al., 1999). Similarly to our findings on *T. stigmatica*, Cooper et al. (1999) also reported a pre-dawn peak in parma wallabies, *Notamacropus parma,* whom also decreased their activity shortly after sunrise. Pademelons have a high metabolic rate and require year-round access to highly nutritious foods to maintain their basal metabolic rate (Wiggins and Bowman, 2011). Concentrated bursts of activity allow the animals to concentrate their efforts to a particular activity and a consistent pattern of resource selection would increase foraging efficiency (Le Mar and Mcarthur, 2005) and meet nutrition demands while minimising unnecessary energy expenditure.

T. stigmatica were not as active in the evening as they were in the morning, unlike *T. thetis* who were similarly active during both morning and evening twilight periods. In the northern expanse of their range, Vernes et al. (1995) reported *T. stigmatica* spatio-temporally partitioned their home-range, using rainforest diurnally and forest-pasture boundary during twilight and nocturnally. Findings for *T. thetis* were consistent with the those of Johnson (1980), and both species exhibited unusual macropodid behaviour in that they were exceptionally active during the diurnal part of the diel cycle (Croft, 1989), despite a midday lull in activity. Changes to conditions force interfering species to alter their behaviour in order to avoid competition costs and ensure their survival. This includes plasticity in strategies such as the choice and exploitation of resources, an increase or decrease in risk taking behaviour and temporal adjustments (Liesenjohann et al., 2011). Unlike the patterns of other small macropods (Stirrat, 2004; Wang and Fisher, 2012), in this study the presence of *T. thetis* influenced *T. stigmatica* to alter their diel pattern and exhibit temporal partitioning.

Potential food for pademelons is more abundant on pasture than in rainforest (Johnson, 1980) and selected habitats tend to be used on a discrete temporal basis. Hume (1977) found that red-necked pademelons required higher levels of nitrogen than other similar sized macropods. Incomplete fermentation in the stomach of pademelons is possibly correlated with relatively low fibre content of food available in their preferred rainforest habitat. Vernes (1995) reported that the diurnal activity of *T. stigmatica* was mostly associated with searching for preferred forest food items while nocturnal behaviour involved more intense grazing at the forest edge. The morning peak in activity is likely to be associated with more intense foraging around the interior forest and edge in search of food items. Typical of smaller species, pademelons have a high basal metabolic rate and their habitat use reflects their need for year round access to highly nutritious food sources to meet physiological requirements (Wiggins and Bowman, 2011). While there was significant overlap in the activity patterns of the two species, the interaction of species with time explained over half the detection rate. It is likely that while *T. stigmatica* still followed a crepuscular pattern, the presence of *T. thetis* encouraged them to concentrate their foraging efforts around sunrise. Some spatial partitioning may also occur alongside the temporal niche as *T. stigmatica* do not exploit available pasture when sympatric with *T. thetis,* they may spend a longer period of time foraging in the morning in order to be properly satiated prior to resting midday. Significantly more individuals were detected during pre-dawn twilight than evening, suggesting that foraging activity was concentrated most intensively during this time to either avoid competition or as a predator avoidance technique. The absence of *T. thetis* in the forest nocturnally may encourage *T. stigmatica* to forage overnight before intensifying their efforts pre-dawn. Alternatively, remaining under cover may be a trade-off to avoid competition with *T. thetis* while foraging sub-optimal food resources as increased illumination overnight can increase perceived predation risk (Prugh and Golden, 2014).

The findings of this study were consistent with those of Jarman and Phillips (1989) that *T. stigmatica* does not appear to leave the forest in the southern expanse of it's range, while *T. thetis* makes regular crepuscular excursions to forest edges throughout it's range (Johnson, 1980). Cameras also recorded fewer overall detections of *T. stigmatica* compared with *T. thetis*. The range of habitat suitable for pademelon occupation is somewhat fragmented throughout NSW, indicating that access to pasture resources may be indicative of larger population sizes. Fragmentation has extensively affected other small macropod species such as the tammar wallaby (*Notamacropus eugenii*) (Blumstein et al., 2002) and may cause similar negative effects on pademelons, particularly when in sympatry. Le Mar and Mcarthur (2005) reported that the red-bellied pademelon (*Thylogale billardierii*) also selects for open habitats in the evening, even when in sympatry with other macropod species (*Notamacropus rufogriseus*). This indicates that *Thylogale* may be an edge-dwelling species throughout its range. The plasticity in *T. stigmatica's* activity pattern may also be a trade off in response to predator avoidance. Pademelons rely on crypsis in dense, interior vegetation in order to avoid predators (Le Mar and Mcarthur, 2005). Unlike other macropodids, such as the tammar wallaby, *T. thetis* do not modify their vigilance behaviour with increasing group size, suggesting that each individual independently assesses and manages their predation risk, rather than relying on conspecifics. In an effort to avoid spatial competition and stress from interactions with *T. thetis* conspecifics, *T. stigmatica* may choose to utilise forest habitat throughout the diel not only for foraging resources but also for predator avoidance. Reduction of activity in the evening may reduce the chances of detection by nocturnal predators and use of forest cover nocturnally allows the animals to move freely about their range to forage, allowing a slightly more consistent level of activity. The peak of activity in the morning may be indicative of intense foraging prior to resting during the day. It appears that heightened activity around dawn and dusk is a 'hard-wired' pattern for *Thylogale* and while some flexibility can be shown within that activity pattern, a bimodal crepuscular pattern is innate.

2.6 Conclusion

There have been extensive studies into the diel activity and temporal partitioning of sympatric carnivores (Cozzi et al., 2012; Mugerwa et al., 2017) however much less research has been conducted on herbivorous guilds. These findings indicate the potential for plasticity in the diel activity of *T. stigmatica* when sympatric with *T. thetis*. It appears that while day length is less important to both species for daily activity, ambient temperature may affect their detectability in cooler months. The effect of forage availability on selection has been under researched for mammalian herbivores (Di Stefano and Newell, 2008) and the next step to further understanding the ecology of *T. stigmatica* in sympatry with *T. thetis* is understanding their feeding ecology and the effect of habitat fragmentation on the species. Further research with a different experimental design, such as deploying cameras in a grid formation so as to include any open grassed areas may provide further insight into the nocturnal time budgets of *T. thetis* and confirm target study findings that *T. stigmatica* do not venture onto forest-pasture boundaries in the presence of *T. thetis*. Understanding the impact of edge effects on both species will help management of forest fragments in a landscape matrix with agricultural land where pademelons may be considered pests. Understanding how their commonness and activity fits into the wider mammal assemblage will ensure appropriate management for continued biodiversity in forest fragments in Australia and prevent a further decline of the status of *T. stigmatica* in NSW.

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Chapter 3 - Spatial partitioning of sympatric populations of red-necked (*Thylogale thetis*) and red-legged (*Thylogale stigmatica*) pademelons in northeastern NSW

3.1 Abstract

Early observations of *T. stigmatica* have suggested differential habitat use between northern and southern populations. Southern populations often co-occur with *T. thetis* and sympatry appears to alter their spatial habitat use. Detailed habitat requirements of *T. stigmatica* and *T. thetis* are largely observational and there is virtually no ecological information available on NSW populations of *T. stigmatica*. Forty-eight camera trap sites were established alongside a sampling regime of structural habitat variables in two vegetation types. *Thylogale thetis* showed no particular affiliation with either forest type while *T. stigmatica* was most often detected in wet sclerophyll forest. Fine-scale multivariate analysis revealed that *T. thetis* were positively correlated with variables related to multilayered cover, as well as disturbance and edge attributes. *T. stigmatica,* however, were negatively correlated with disturbance variables, indicating they prefer not to associate with the forest edge or disturbed habitat. *T. stigmatica* appear to narrow their preferred niche and become more specialised in the presence of *T. thetis,* consequently occurring in lower densities. This may have implications for habitat management and their ongoing persistence in NSW.

3.2 Introduction

The phenomenon of intraguild sympatry shapes the dynamics of mammalian community assembly. The original definition of sympatry was the occurrence of two or more forms co-existing in the same geographical region (Mallet et al., 2009). Two populations are deemed sympatric if individuals from each are physically capable of encountering one another with moderate to high frequency (Mayr, 1963). Most new species arise in geographical isolation (Rice and Hostert, 1993), and therefore a key step in community assembly is the geographical expansion and overlap of previously isolated species. Dispersal is highly deterministic in driving predictable patterns of sympatry in vertebrates. The role of dispersal in both regulating population expansion and the transition to sympatry of similar species is still unclear, particularly over long macroevolutionary scales (Pigot and Tobias, 2015). A variety of behavioural mechanisms such as dietary partitioning or differential use of space and time can be used by sympatric species in order to avoid competition and other unfavourable encounters (Karanth et al., 2017). Subordinate species may also avoid activity centres or locations highly populated by dominant species to avoid excessive interaction. Broad scale sympatry could be dependent on competitive interactions that lead to character displacement or local extinction as a result of character displacement (Shi et al., 2018). Populations are therefore also considered to be sympatric even if they are ecologically segregated as long as a high proportion of each population encounters individuals of the other along adjacent or shared ecotones (Mallet et al., 2009).

Interactions among species are variable and affect the dynamics of community assembly in a variety of ways. Anthropogenic intervention can increase intra-guild competition by affecting species densities through modification of resource availability and distribution (Karanth et al., 2017). Defaunation due to anthropogenic influences also results in a loss of species interactions which affects species functionality and the ecosystem services they provide (Valiente‐Banuet et al., 2015). In a study of functional redundancy in large frugivores, Bueno et al. (2013) found that tapirs (*Tapiris terrestris*) and muriqui (*Brachyteles arachnoides*) were complementary in their roles as seed dispersers. Selective extinction of these animals would alter the spatial dispersal of seeds and cause negative recruitment effects for several plant species. Plants dispersed by these frugivore species may become clumped, causing resource hotspots through modification of the natural landscape and can encourage ecologically similar species to an area, increasing the likelihood of negative interactions. Habitat fragmentation may also isolate populations or reduce the natural home range of species that would otherwise move more freely through their environment to avoid interaction. The prevention of co-existence in ecologically similar species can similarly shape the community assembly as competition generates nonrandom patterns in community structure including the regular spacing of functional traits (Chase and Leibold, 2003). For example, if two potentially interacting species change their diel patterns in separate ways, the role of temporal partitioning may be inferred; one species changing its patterns may be due to factors such as temperature constraints or a diet shift suggesting temporal habitat use (Ikeda et al., 2016). Changes in activity patterns can be used to avoid direct competition of sympatric interspecifics (Ferreguetti et al., 2015) or for dual use of increasing opportunity for resources whilst avoiding negative interspecific interactions (Bischof et al., 2014).

Habitat filtering describes the set of biotic and abiotic conditions required by a species for survival. It is assumed that the co-occurrence of species is dictated by a set of non-random evolutionary and ecological processes driven in part by species interactions over an evolutionary timescale (Ricklefs, 2004). Adaption of co-occurring species to similar abiotic environmental conditions can pressure a species into phenotypic attraction whereby similar ecological preferences and functional traits are developed (Weiher and Keddy, 1995). Conversely, increased competition for the same resources amongst co-occurring species can drive phenotypic repulsion, or competitive exclusion, and restrict co-existence among similar species (Mayfield and Levine, 2010). Phylogenetic relatedness can also influence assembly structure and occurs when closely related species are more ecologically similar than expected through random diversification processes (Kraft et al., 2007). The effects of phylogenetic clustering and mobility by comparing sympatry and phylogenetic relatedness between species was assessed by Bino et al. (2013). The study found that across NSW, phylogenetic over-dispersion was observed as a significant negative correlation occurring between phylogenetic relatedness and sympatry. Phylogenetically similar species are likely to be ecologically similar and may interact competitively when occurring in sympatry.

Animals perceive their surroundings differently, and in turn their populations respond to habitat in two ways. Fine-grained species use a mosaic of habitat fragments in proportion to the abundance of those fragments, while in contrast, coarse-grained species select habitats preferentially (Morris, 1987). Vegetation related environmental factors may drive spatial distribution in sympatry due to the availability of resources and knock on effects to microhabitats (Kubiak et al., 2015). Smaller species have less mobility and smaller home ranges and will respond to fine scale resource abundance whilst larger species, even specialised ones, have the ability to select from preferred habitat patches in the matrix. Therefore the diversity of a community and the niche characteristics of individual species may be the result of resource range and variation (M'Closkey, 1976). Ecologically similar species may be forced into sympatry if resource availability is limited by altered microhabitats, disturbance effects or if distance between forest fragments hinders dispersal.

Camera trapping offers the opportunity to address unanswered questions in regards to interspecies ecology and community interactions such as spatial or temporal niche partitioning. Temporal dynamics are integral to niche theory, including individual species ecology and community assembly, as well as diel activity patterns and niche partitioning between sympatric heterospecifics (Frey et al., 2017). Technology for camera traps has improved significantly in recent years, providing enhanced usability that facilitates researchers with the means to investigate research areas that previously may have been too resource intensive (Vernes et al., 2014; Meek et al., 2015b). Various models allow researchers to use detection rate as a function of density and its relationship with population density (Rowcliffe et al., 2008; Nakashima et al., 2018) which allows researchers to monitor and gain information about wildlife populations with minimal labour intensity and the least possible disturbance to the subjects. While an animal's detectability can depend on the techniques used in camera trap data collection (Burton et al., 2015), using camera collected data can provide valuable information on spatial habitat use of the focal species as it minimises disturbance biases and the potential for human identification errors in the field. Although the white flash can cause disturbance, cameras with the ability to produce colour images allow a more accurate identification of individual species when phenotypically similar species co-occur (Meek et al., 2013). It is therefore ideal to consider the camera's features as well as its suitability to the size, locomotion and behaviour of the focal species (Green-Barber and Old, 2018).

Sympatric populations of red-legged pademelons (*Thylogale stigmatica*) and red-necked pademelons (*Thylogale thetis*) have received only minimal research focus in the past. The geographical range in Australia of *T. stigmatica* occurs from the Cape York region in northern Queensland through to Newcastle in NSW (Johnson and Vernes, 1995). In the southernmost part of its range it occurs in sympatry with *T. thetis*. In the northern part of its range where it occurs in the absence of *T. thetis*, *T. stigmatica* spatio-temporally partitions its range diurnally to the forest interior and nocturnally to the forest-pasture boundaries (Vernes et al., 1995). *T. thetis* inhabits rainforest as well as other forest vegetation types with a dense understorey in eastern Australia's subtropics (Strahan, 1980) and is most common at forest edges adjacent to pasture (Jarman, 1989), where it feeds nocturnally on pasture edge close to the forest. When sympatric with *T. thetis, T. stigmatica* appears to only consume forest browse (Jarman, 1989) and is anecdotally observed to avoid edge pastures, but rather remains in interior forest (Calaby, 1971). Large scale clearing of rainforest and eucalypt forest for agricultural grazing pastures has caused significant landscape alterations in eastern Australia (Pavlacky et al., 2015) and remaining forest fragments have been selectively logged, adjusting the vegetation structure of individual patches and the overall matrix. The continued existence of suitable habitat is uncertain for both species of pademelon given that they both associate closely with habitat that is routinely altered by human interference (Johnson, 1980).

The objectives of this study were to investigate the structural habitat variables of the two forest types, wet sclerophyll and dry rainforest, and their effects on the habitat utilisation for *T. stigmatica* and *T. thetis*. The specific aims were to determine what habitat variables affect spatial distribution between *T. thetis* and *T. stigmatica*, whether spatial habitat partitioning occurs and whether the two species are using different resources to avoid spatial competition. It is hypothesised that neither pademelon species would spatially partition vegetation types, but rather respond to certain variables in a combination of spatio-temporal partitioning to avoid competition.

3.3 Methods

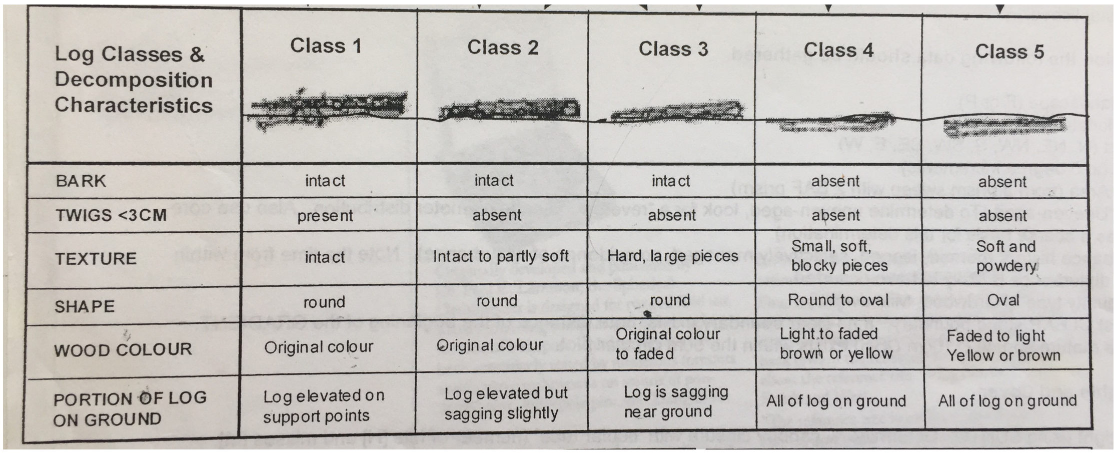
3.3.1 Camera Placement

Forty-eight Scoutguard and UOVision white flash cameras were deployed between dry rainforest and wet sclerophyll forest across the study site. Fire trails were used to access the forest and cameras were deployed at 100 metre intervals according to an assigned random distance and bearing. Cameras were secured to a tree and positioned approximately 50cm above ground level in a southerly direction to minimise ‘empty’ images caused by shadows. Cameras were set to high sensitivity with a 10 second delay between pictures. Each camera was set with a lure to attract any animals in the immediate vicinity to linger in front of the camera long enough for detection. Lures consisted of a small porous plastic canister containing cotton wool soaked in truffle oil that was inaccessible to the animal. A full description of camera trapping methods is provided in *section 2.3.3*

3.3.2 Vegetation Variables

To measure vegetation variables, 5m x 5m plots were marked around each camera. Vegetation variables were measured within the plots using a scoring system as denoted in *Table 1.*

Characteristics used to determine level of decay in fallen timber were defined according to a decomposition summary sheet used in the Fundy Forest bird research (Hunter Jr., 2011) and are detailed in *Figure 3.1.* Five classes were used with descriptions detailing the bark, twig presence, texture, shape, wood colour and portion of log on the ground.



Log Classes & Decomposition Characteristics	Class 1	Class 2	Class 3	Class 4	Class 5
BARK	intact	intact	intact	absent	absent
TWIGS <3CM	present	absent	absent	absent	absent
TEXTURE	intact	Intact to partly soft	Hard, large pieces	Small, soft, blocky pieces	Soft and powdery
SHAPE	round	round	round	Round to oval	Oval
WOOD COLOUR	Original colour	Original colour	Original colour to faded	Light to faded brown or yellow	Faded to light Yellow or brown
PORTION OF LOG ON GROUND	Log elevated on support points	Log elevated but sagging slightly	Log is sagging near ground	All of log on ground	All of log on ground

Figure 3.1: Log classes and decomposition characteristics for assessment of fallen timber (Hunter Jr., 2011).

Overstorey was measured using a forest densitometer. Four readings were taken and the mean calculated. Using the centre camera tree as the reference tree, readings were taken moving around the tree facing each of the cardinal directions. Sub-canopy foliage cover was measured using an ocular tube at random points around the perimeter of the 5m x 5m plot. Random whole numbers were generated between 1 and 10 and these readings were used to determine the number of steps between each of the 10 measurement points. Lateral density was measured similarly to overstorey using a 1m x 1m white sheet. At each cardinal direction, the observer would stand with their back to the centre reference tree while the white grid sheet was held on the perimeter of the plot. Percentage of cover was calculated by number of squares obscured by vegetation.

Vegetation was high in places making measurement of individual woody stems impractical. Similarly to other vegetation variables, stems were measured according to a scoring system. Trees were classed according to their diameter at breast height then scored according to density.

Number of eucalypt emergents and any tree fall gaps were counted within each plot. Distance to nearest road, forest edge and major water source were also measured using a map.

Table 3.1: Vegetation and landform attributes assessed at each camera site.

Measurement	**Unit or Score**	**Description**
Slope		Evaluated using clinometer
Overstorey cover	%	Densitometer see *www.forestry-suppliers.com*
Sub-canopy cover	%	Random measurements using ocular tube
Lateral cover	%	% of 1x1m white grid obscured by 0-1m high vegetation at a distance of 5 m
Leaf litter depth	0	absent
	1	<5cm
	2	5-10cm
	3	>10cm
Vines/Palms/Ferns	0	absent
	1	<3 per m^2
	2	3-5 per m^2
	3	>5 per m^2
Small stem density (>10cm dbh)	0	absent
	1	<3
	2	3-5

	3	>5
Medium stem density (10-30cm dbh)	Estimate by score	As for small stem density
Rockiness of soil	0	absent
	1	<3 per m^2
	2	3-5 per m^2
	3	>5 per m^2
Fallen Timber	0	Absent
	1	Class 1-2
	2	Class 3
	3	Class 4
	4	Class 5
Tree fall gaps	No. of gaps	in entire plot
Eucalypt emergent	No. of emergent	In entire plot
Distance to edge	m	Nearest edge

3.3.3 Statistical Analysis

Principle component analysis (PCA) was used to determine variation between the 17 vegetation factors measured. PCA loading scores were used to establish the impact of individual variables on each principle component. The individual principle component score was determined for each camera location, as well as the number of individual *T. stigmatica* and *T. thetis* detections. Generalised linear models (GLM) with a negative binomial distribution were then utilised to identify which principal components had a significant impact on distribution for each *Thylogale* species. New data predictions were generated that represented associated standard errors and back transformed as necessary for negative binomial models.

3.4 Results

3.4.1 Principal Components Analysis

PCA on pooled data between wet sclerophyll forest and dry rainforest narrowed habitat variables into two main principle components that explained 32% of the total variation in vegetation structure (*Figure 3.2*). PC1 explained 17% of the total variation, which was attributed to disturbance factors that increased along the axis. PC1 correlates negatively with vines, palms, ferns, rocks, lateral cover, canopy cover and tree fall gaps. Positive correlates for that axis were ground litter, ground cover, sub canopy cover, eucalypt emergents, distance to nearest road, sapling density and medium stem density. PC2 explained 15.2% of the total variance and was attributed to multilayered vegetation cover. PC2 was negatively correlated with ground litter, ferns, rocks, fallen timber, slope, tree fall gaps, nearest road and forest edge, and positively correlated with palms, lateral cover, canopy cover, sub canopy cover and medium stem density. The increasing attributes along PC1 largely described the wet sclerophyll forest, which was logged extensively in earlier years. The positive attributes of PC2 described the dry rainforest, which was more closed than the wet sclerophyll and had higher levels of canopy and lateral cover.

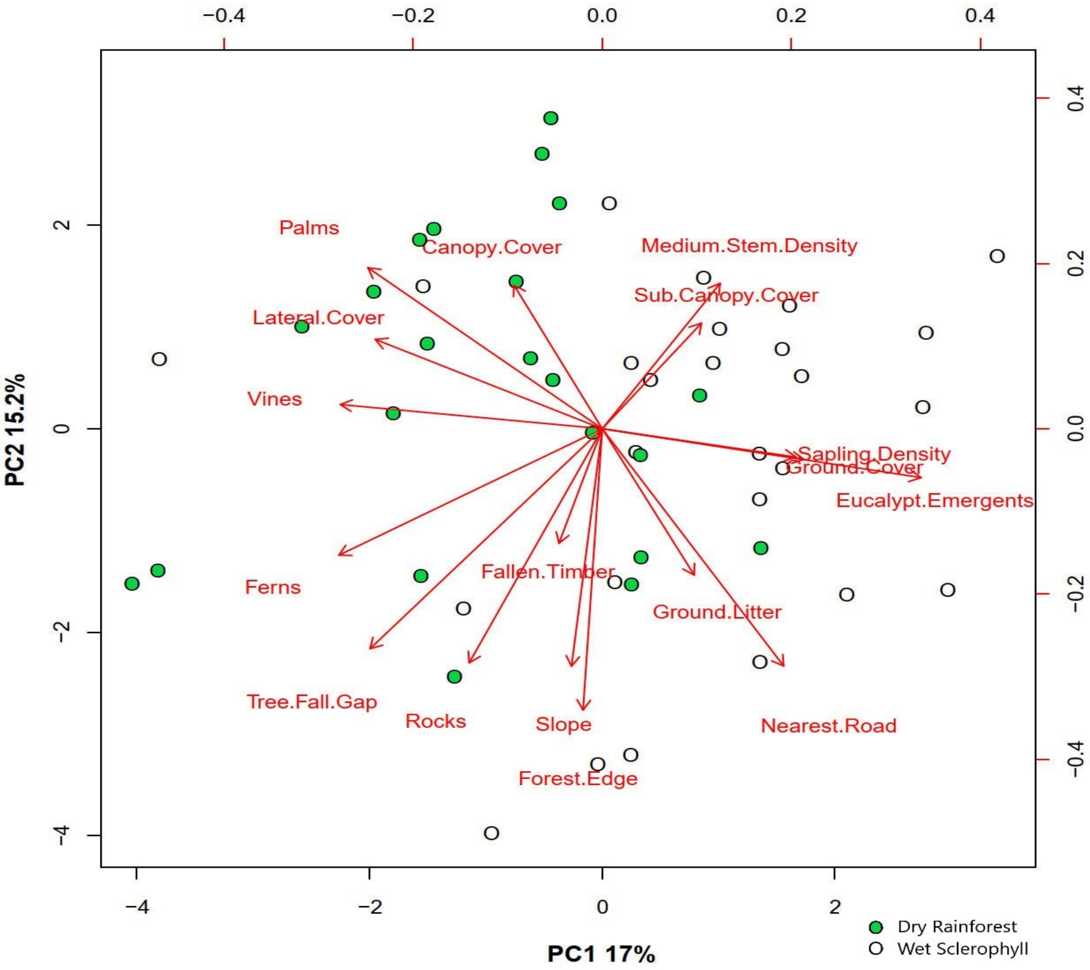


Figure 3.2: Principle component analysis of structural vegetation variables.

Eucalypt emergents, vines and ferns had the highest loading scores and hence had the largest impact on PC1 *(Table 2)*. Distance to forest edge, distance to nearest road and slope were the largest contributing factors to PC2. Factors with the highest loading scores for PC1 are largely associated with wet sclerophyll sample sites and positively impacted vegetation cover. Factors with the highest impact according to loading score on PC2 were correlated positively with disturbance effects and described both vegetation types.

Table 3.2: Loading scores of structural vegetation variables for PC1 and PC2.

Variable	**PC1**	**PC2**
Ground Litter	0.122	-0.221
Vines	-0.346	0
Palms	-0.31	0.244
Ferns	-0.348	-0.191
Rocks	-0.176	-0.354
Fallen Timber	0	-0.173
Ground Cover	0.267	0
Lateral Cover	-0.3	0.135
Canopy Cover	-0.117	0.218
Sub Canopy Cover	0.131	0.16
Slope	0	-0.359
Tree Fall Gaps	-0.307	-0.333
Eucalypt Emergents	0.422	0
Nearest Road	0.24	-0.359
Forest Edge	0	-0.426
Sapling Density	0.256	0
Medium Stem Density	0.156	0.22

3.4.2 Habitat Correlates of T. stigmatica *Occurrence*

Cameras at a majority of the 48 sites detected between 1-10 *T. stigmatica* as independent events. Only three sites recorded over 61 independent detection events and no *T. stigmatica* detections were recorded at 15 sites. A majority of sites where *T. stigmatica* detections were recorded were positively correlated with PC1 and located in wet sclerophyll forest (*Figure 3.3*). Generalised linear models however showed a negative correlation between an increase in variables associated with PC1 and *T. stigmatica* detections *(Figure 3.4)*. There was a positive correlation of *T. stigmatica* detections with an increase in variables contributing to PC2. There was a significant relationship between variables contributing to PC1 and the detection rate of *T. stigmatica* (P = 0.004) however there was no significant correlation between PC2 and *T. stigmatica* detections (P = 0.15).

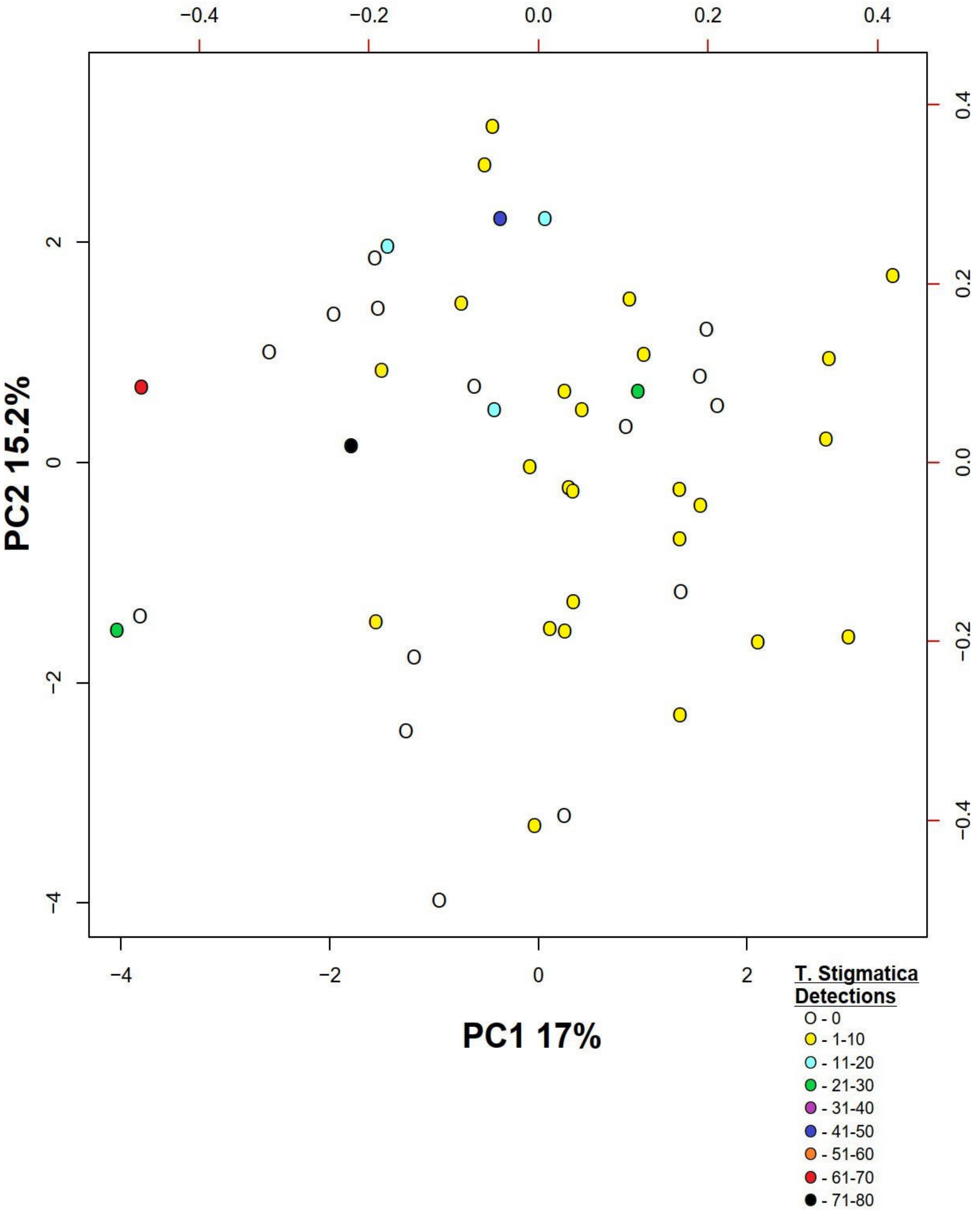


Figure 3.3: *T. stigmatica* detections by site along PC1 and PC2 axes.

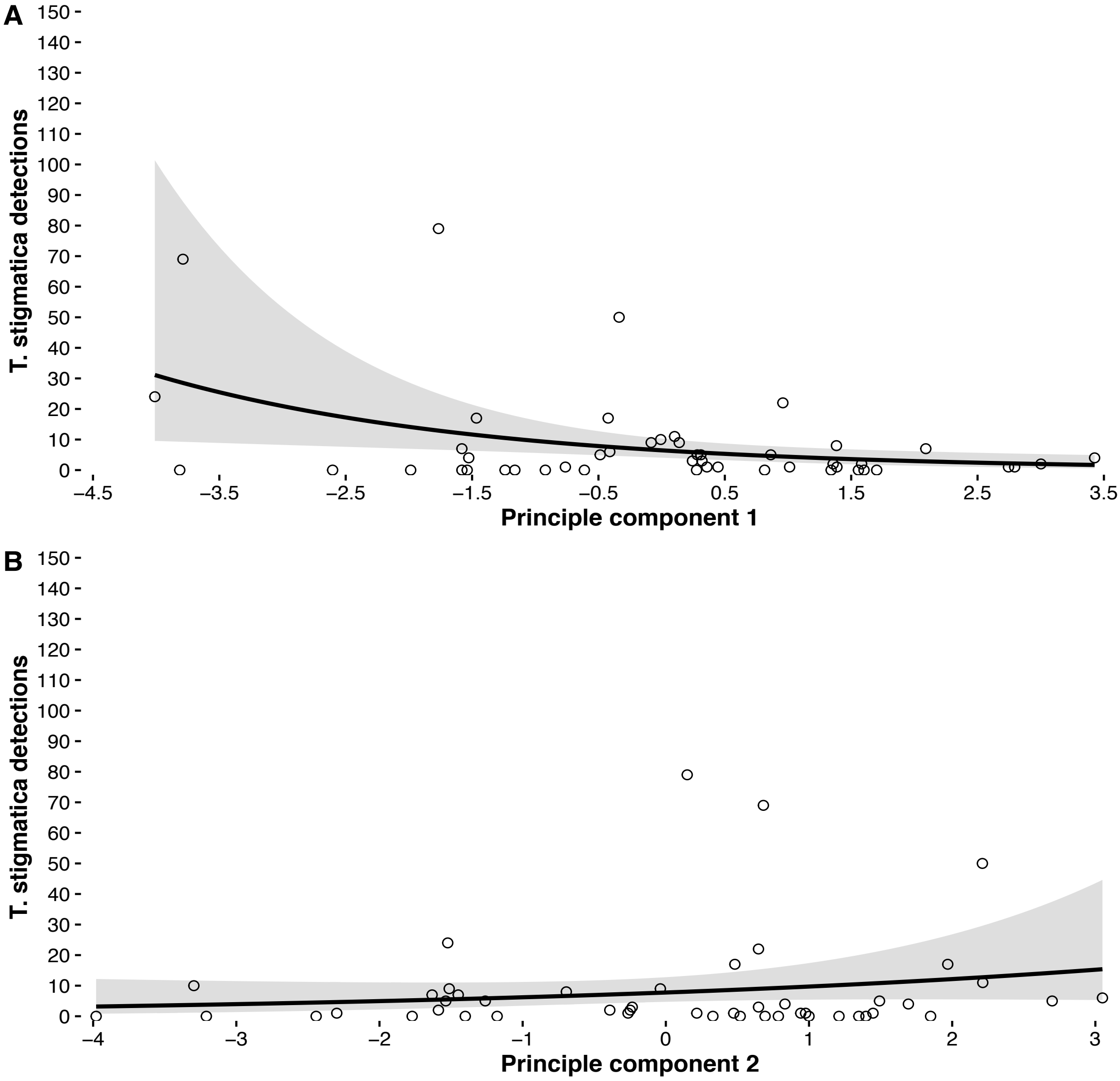


Figure 3.4: Generalised linear model of *T. stigmatica* detections along PC1 axis (A) and PC2 axis (B).

3.4.3 Habitat Correlates of T. thetis *Occurrence*

Most sites returned detections between 1-10 independent events for *T. thetis*. Over 80 individual events were recorded at seven different sites, with three of those sites detecting over 121 individuals. Most sites at which *T. thetis* were detected were positively correlated with PC1 and PC2 and distributed across both vegetation types (*Figure 3.5*). Generalised linear models revealed the detection rate of *T. thetis* was positively correlated with all principle component axes *(Figure 3.6)*. An increase in variables that contributed positively to PC1 significantly contributed to an increase in *T. thetis* detections (P = 0.02) and similar results occurred for PC2 (P <0.3).

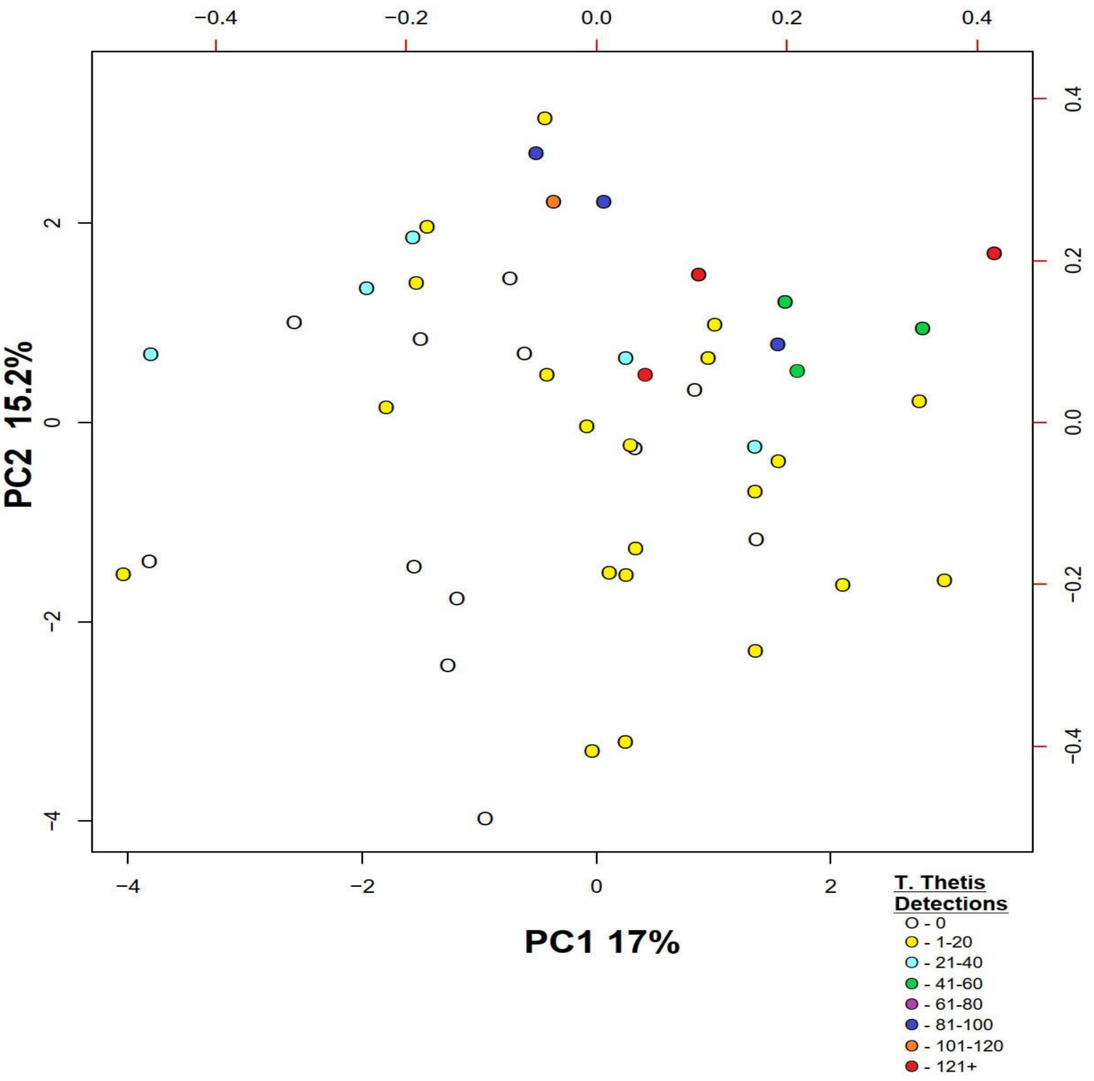


Figure 3.5: *T. thetis* detections by site along PC1 and PC2 axes.

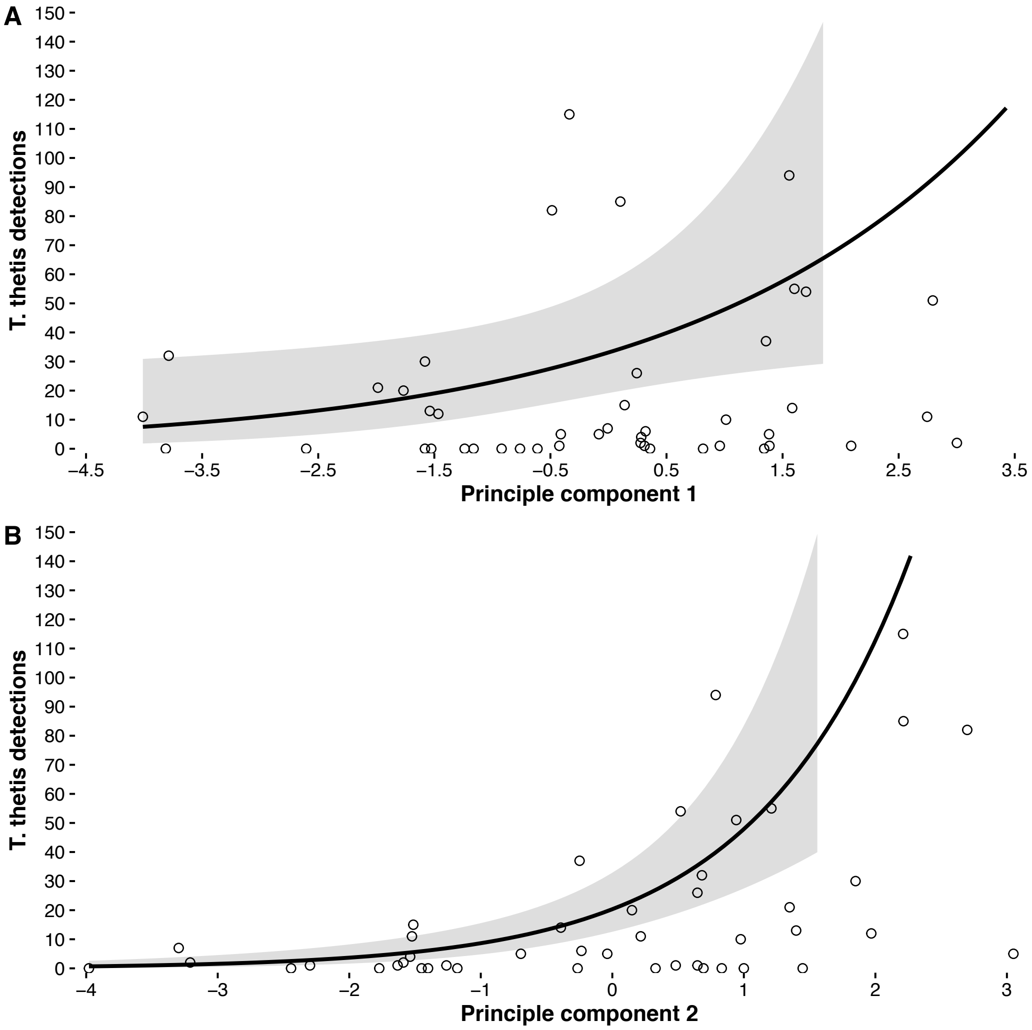


Figure 3.6: Generalised linear model of *T. thetis* detections along PC1 axis (A) and PC2 axis (B).

3.5 Discussion

Over half of *T. stigmatica* detections between one and ten individual events were recorded at cameras deployed in the wet sclerophyll forest while *T. thetis* detections occurred relatively evenly between both forest types. Despite this, the overall number of *T. stigmatica* detections decreased significantly with an increase in ground litter and cover, sub canopy cover, eucalypt emergents, distance to nearest road, sapling density and medium stem density. This indicates that the factors impacting negatively on PC1 such as vines, palms, ferns, rocks, lateral cover, canopy cover and tree fall gap were more important structural habitat variables to *T. stigmatica,* suggesting that *T. stigmatica* aligns themselves with rainforest attributes. Pademelons and many other small mammals rely on crypsis in dense vegetation for cover from predator attack, particularly during the diurnal periods (Le Mar and Mcarthur, 2005) and all variables that declined along PC1 are likely to provide cover for *T. stigmatica*. Factors increasing along the PC1 axis are all attributes of forest disturbance, indicating that at this location, *T. stigmatica* prefers not to associate with edges or disturbances. This is contrary to the findings of Vernes et al. (1995) where, in the northern part of its range, *T stigmatica* is regularly found along forest edges and pasture boundaries. Unlike other small macropods, *T. stigmatica* are unusually active in certain parts of the day and can move extensively throughout their range (Vernes et al., 1995). This diurnal activity is most likely associated with searching for favoured food resources. Ecotones and the edges of vegetation blocks tend to have greater diversity and density of food resources (Fisher, 2000). It is likely that *T stigmatica* may spend longer searching for food, or make more concentrated foraging efforts if they have reduced access to the abundant resources at accessible edge habitats and at this site prefers a more closed, multilayered habitat.

Given however, that analysis yielded only 32% of variance by the first two principal components, this may indicate that fine scale habitat heterogeneity may be of higher importance to *T. stigmatica* than habitat type. Habitat heterogeneity describes variability in habitat structure and can influence the distribution of fauna. The habitat heterogeneity theory states that highly heterogenous habitats provide greater benefits and resources, and therefore are more likely to be host to high levels of faunal diversity (Tews et al., 2004). Small terrestrial mammals tend have lower mobility and therefore restricted home ranges. They will perceive their environments at a small scale and are therefore more sensitive to fine-scale vegetation structure and immediate landscape heterogeneity (Stirnemann et al., 2015). Sapling density, sub-canopy cover and medium stem density all provide cover at a lower height than the top canopy and are an example of a fine-scale measure (10s of metres) of vegetation heterogeneity. Small-medium macropods shelter repeatedly at the same sites (Jarman, 1991) which suggests predator avoidance depends on the ability to flee to a familiar site. *T. stigmatica* may frequent sites with these qualities more often due to the fitness benefits provided at a fine scale, such as cover from potential avian predators and wild dogs.

Thylogale thetis were detected in larger numbers than *T. stigmatica* (*see Section 3.4*) and did not appear to be more closely associated with one forest type over another.

Detections of *T. thetis* were positively correlated with increasing variables along each principle component axis. This indicates that *T. thetis* did not favour one forest type over the other, but also prefers fine scale heterogeneity within their habitat. The increase of *T. thetis* detections was significant along each principle component axis, indicating they are associated with both disturbance attributes and interior forest attributes. This is consistent with previous findings that *T. thetis* exploit forest-pasture boundaries (Johnson, 1980; Jarman, 1989; Wahungu et al., 1999). Previous findings in *Chapter 2* found that *T. thetis* was strongly crepuscular and periods of heightened activity were most likely due to foraging excursions to and from the edge and adjacent pasture.

Effects of fragmentation include both declines and increases in the abundance of some species due to alterations to the microclimate within the fragment (Turton, 1997). The findings in this study are consistent with earlier research that *T. stigmatica* does not venture past the forest edge when in sympatry with *T. thetis* (Jarman, 1989) while *T. thetis* makes regular foraging jaunts beyond the edges to adjacent pasture. Fragmentation increases the amount of edge to interior forest and significantly alters habitat at fragment edges (Laurance et al., 2002). At fragment edges, penetration of sun and wind increases, which in turn alters the microclimatic regime of the forest understorey (Turton, 1997; Newmark, 2001). Anthropogenic disturbance significantly influences ecosystem properties such as vegetation structure and microclimate, which in turn affects niches available for faunal species. When considering the conservation of species, understanding of habitat preference and niche specialisation is of obvious and paramount importance (Vernes, 2003). Competition avoidance techniques such as the alteration of spatial movement and temporal activity have likely been employed by *T. stigmatica* at this study site in order to enable co-occurrence of both *Thylogale* species. Some cameras that were deployed very close to the forest edge detected *T. stigmatica*, indicating that despite a lower association with disturbance and edge effects, they still utilise habitat all the way to the forest edge. Cameras in the grassy clearing did not detect any independent *T. stigmatica* events (*Chapter 2*), confirming that *T. stigmatica* do not venture past the forest edge to graze pasture at this location. Increased light penetration at forest edges can encourage an enriched understorey and a higher abundance in ground cover, which likely attracts *T. stigmatica* towards the more abundant edge resources, however competition with *T. thetis* prevents exploitation of adjacent pasture.

In Australian vegetation communities, structural variation can govern the distribution of marsupials at various spatial scales (Kanowski et al., 2001). *T. thetis* appears to be spatio-temporally partitioning its habitat similarly to the way *T. stigmatica* does in the northern expanse of its distribution (Vernes et al., 1995). *T. thetis* showed strong crepuscular activity as well as a positive correlation with disturbance and edge-related variables. *T. thetis* was also positively correlated with variables that increasingly contributed to cover. This indicates that *T. thetis* spatio-temporally partitioned resources into forest interior diurnally, and pasture nocturnally. Previous chapters (*Chapter 2*) also indicated some temporal partitioning between the species, indicating that the two species are ecologically similar and subject to competitive interactions. A generalist is typically any phenotype whose fitness is equal in any given habitat patch, while a specialist typically experiences improved fitness in one patch over another (Rosenzweig, 1981). A comparison of findings between Vernes (1995) and Vernes et al. (1995) indicates that *Thylogale* is a generalist within their range and will readily exploit all available resources, except when in sympatry with other *Thylogale* species. Under sympatric circumstances one species shifts their niche into a narrow, more specialised range. This research revealed five sympatric macropod species (*Thylogale thetis, Thylogale stigmatica, Wallabia bicolor, Potorous tridactylus* and *Notamacropus parma*) within the study area. The presence of other ecologically similar macropods, such as *W. bicolor* who is also known to generalise between edge and interior (Johnson, 1977; Hollis et al., 1986) did not affect the habitat partitioning of *T. thetis*. Similarly the Tasmanian pademelon, *T. billardierii,* also partitions their habitat spatio-temporally into interior and adjacent pasture when sympatric with *Notamacropus rufogriseus* (Le Mar and Mcarthur, 2005). *T. billardierii* is geographically isolated from *T. thetis* and *T. stigmatica* so it is unknown whether they exhibit plasticity in their ecology when sympatric with other *Thylogale* species.

Thylogale is thought of as an edge dwelling species prior to anthropogenic fragmentation (Vernes et al., 1995) and current findings are consistent with this. Species that have adapted to forest edge are advantaged by the fragmentation process whereas forest specialists have a higher tendency towards extinction, particularly where the home range of the species is not significantly smaller than the available fragment (Harrington et al., 2001). Previous studies of *T. stigmatica* indicate they occur in lower population densities when in sympatry with *T. thetis* (Johnson and Vernes, 1995). This suggests that when constrained in a narrower, more specialised niche, population numbers are negatively affected. Diet selection frequently drives habitat selection, and thus small herbivores are more likely to be associated with habitats rich in high-quality food resources (Garnick et al., 2014). Potential food resources for pademelons are more abundant in pasture than rainforest (Johnson, 1980) and Hume (1977) reported that *T. thetis* required higher levels of nitrogen than other similarly sized macropod species. Mitchell et al. (2018) found that southern dwelling subspecies of *T. stigmatica* (*Thylogale stigmatica wilcoxi*) has a broader cranium presenting a shorter and more robust muzzle, typical of browsing species while northern dwelling subspecies (*Thylogale stigmatica stigmatica*) possesses a more slender shaped skull with a longer muzzle. The slim skull shape of *T. s. stigmatica* is similar to *T. thetis* and common amongst grazing macropods. It appears that northern populations of *T. stigmatica* use their habitat very differently from southern populations, particularly when occurring in sympatry with *T. thetis.* This is reflected in both their diet and cranial morphology and is indicative of competitive pressures through feeding regimes. Direct competition for edge resources has likely forced sympatric populations of *T. stigmatica* into a narrower niche and driven their population density below what might be achieved in the absence of competition.

Further dietary studies of *Thylogale* have investigated their role in fungal spore dispersal. *Thylogale stigmatica* may be important dispersers of hypogeous fungi between rainforest and open forest (Vernes and Trappe, 2007). This study found neutral or negative affiliation with habitat variables associated with fungal growth such as ground litter and fallen timber. One photograph from forest cameras depicted a *T. thetis* individual consuming what appears to be a mushroom or truffle however there were no such photographs of *T. stigmatica*, despite their narrower range inside the closed forest. Earlier studies have shown that the diet of *T. stigmatica* varies between northern and southern populations (Jarman, 1989; Vernes, 1995) and study of cranial morphology also reflects this (Mitchell et al., 2018). This is an unexplored area for future research to gain greater knowledge about the ecology of *T. stigmatica* when in sympatry with *T. thetis.*

3.6 Conclusion

T. thetis and *T. stigmatica* spatially partition their habitat when occurring in sympatry, even when both habitat types have similar attributes. This study supports earlier observations that *T. stigmatica* do not use their habitat in the same way as their northern counterparts when in co-occurring with *T. thetis*. In terms of their broad habitat use, *T. thetis* behaves in a similar manner to northern populations of *T. stigmatica*, suggesting that *Thylogale* spp. are primarily edge-associated species but have the ability to exhibit some plasticity in order to avoid competition. It would appear however, that the trade off to this plasticity is a narrower, more specialised niche and lower population numbers. Continued disturbance may not negatively affect *T. thetis* going forward, however numbers of *T. stigmatica* may further decline in NSW with increased fragmentation when co-habiting with *T. thetis*. Further research into the habitat selection, diet and niche specialisation in NSW is important for understanding the ecology of both species as well as national park management to ensure continued persistence in their current range.

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Chapter 4 – Habitat variables relating to the structure of a rainforest-wet sclerophyll mammal community in northeastern NSW

4.1 Abstract

The dynamics of the mammal community rely heavily on the structural integrity of available habitat. Habitat disturbance can alter microclimate and available niches, as well as affect community assemblage processes that influence overall composition. To understand the influence of habitat features on mammal occurrence in a closed forest community on the Dorrigo Plateau in northeastern NSW, mammal presence and absence was surveyed with camera traps and mammal occurrence was examined against a range of forest structural attributes. Twenty-two species of ground-dwelling mammals were detected, including 5 macropodids. Species composition was significantly different between the two major habitat types (rainforest and wet sclerophyll), although individual species did not align strongly with habitat type. Assembly composition was also affected by particular structural vegetation attributes, indicating the significance of fine scale habitat heterogeneity to mammal community assemblages, particularly those attributes related to cover and disturbance. The importance of this work in understanding the community ecology of northeastern NSW forests, and their conservation and management, is discussed.

4.2 Introduction

A fundamental inquiry of ecology is whether a set of general rules can be applied to explain community structure in any type of assembly. According to Diamond (1975), community assembly is characterised by a set of assembly rules that can be predicted by key variables such as the size of a species pool, interspecific interactions and the abiotic environment. Diamond (1975) observed, however, that in some cases community structure varied among sites with similarities in these key variables, which suggests that the timing of species invasions could lead to multiple stable equilibria. Assembly rules can be applied to any assemblage where individuals can move in or out of a community, or where competition limits the ability of a species to persist and survive. The diversity of a community and the individual characteristics of a species may be a result of resource range and variation (M'Closkey, 1976). Functioning ecosystems contain large numbers of competing yet coexisting species (Harpole and Tilman, 2007). Identifying and investigating the driving factors behind competition and sympatry are still relevant inquiries in modern ecology.

Several theories have attempted to explain the structure of community since the assembly rules theory was first suggested by Diamond (1975). Stochastic niche theory suggests that invading species only become established if individuals can avoid mortality whilst reaching maturity, consuming the resources left over by already established species (Tilman, 2004). After arriving at a site, propagules either fail to become established or they grow in numbers throughout the site, impacting resource levels and species abundance. Nonrandom processes such as competition for resources as well as abiotic environmental filtering interact with demographic stochasticity to collectively determine community assembly (Shipley et al., 2012). Furthermore, theories of resource competition based on trade-offs predict patterns of species traits and separation of nutrient gradients. These theories provide possible explanations for the high diversity in nature, predicting that habitat heterogeneity can potentially allow an unlimited number of species to coexist depending on their fitness under environmental constraints (Chesson, 2000). Ecologists therefore broadly recognise the relationship between neutral processes and niche-based environmental filtering in understanding community assembly (Weiher et al., 2011).

Habitat or environmental filtering describes the biotic and abiotic conditions required for a species to persist in any given area. Environmental filtering recognises the relationship between an organism and the environment, identifying that not all individuals or species will be able to successfully establish and persist in all possible abiotic conditions (Kraft et al., 2015). The environment is therefore a selective pressure, sifting out species unable to tolerate conditions at a particular location. If surviving species at a location share common phenotypic traits that allow appropriate tolerance of the abiotic conditions, phenotypic similarities reflective of that tolerance may be seen among community members (Kraft et al., 2015).

Deterministic processes inherent in niche-based theories of community assembly are more likely in low-productivity environments whereas stochastic processes are more predominant in higher-productivity systems (Chase, 2010). There are numerous species that may be physically able to fulfill a particular role in certain abiotic conditions, however a combination of historical dispersal and pressures of established species will ultimately determine the ability to persist. Species that can potentially tolerate harsher conditions are likely to be nested within a larger pool of species that can tolerate more benign habitats. Therefore regions with higher productivity or more tolerable abiotic conditions are more likely to have higher biodiversity. Evidence for stochastic processes shaping community assembly comes from research conducted in high-productivity environments such as tropical rainforest (Volkov et al., 2007).

Biodiversity loss is a global issue and community dynamics can be affected by the loss or decline of keystone species. Since European settlement in 1788, there has been a significant decline in Australian mammal fauna as well as the extinction of approximately thirty endemic species (Woinarski et al., 2015). Extinctions and population declines have not occurred equally throughout Australia, with medium-sized, ground-dwelling mammals most strongly affected (Short and Smith, 1994). Biodiversity is declining rapidly in tropical areas worldwide, affected mostly by exponential human population growth, habitat loss and degradation, hunting, introduction of invasive species and inadequate conservation reserves (Bradshaw et al., 2009). In contrast to this, mammal biodiversity loss in Australia is mostly driven by predation from introduced species and changed fire regimes (Lawes et al., 2015; Woinarski et al., 2015). The intensity of biodiversity monitoring in Australia remains low due to lack of design and implementation standards, and poorly developed arguments for long term and sustained monitoring (Lindenmayer et al., 2012). Conservation reserves may be failing to maintain some of the elements of biodiversity they were established to protect (Wayne et al., 2017). Continued fragmentation will confine forest tropical species to isolated fragment remnants that make up a small fraction of their natural ranges (Laurance, 1994). Complex habitats are multilayered with well-developed vertical strata while simple habitats have fewer strata and are less developed (August, 1983). Disturbance of these layers cannot only affect the overall structural integrity of the habitat, but also alter microclimates and in turn, available niches. The rate of extinction is far greater than previously recognised and many extant species are experiencing a steady decline, despite the low level of threats that affect mammal populations globally (Woinarski et al., 2015). Regular assessment of mammal communities affected by disturbance will assist in evaluating the effectiveness of protection measures, if taken, to preserve and restore connectivity (Meyer et al., 2015).

Mammal surveys can provide a range of useful information for researchers and conservation management plans. Information such as an evaluation of the diversity of a given site, comparison of diversity among multiple sites, refining distribution maps for individual species and evaluation of the impact of human activities on mammal communities (Tobler et al., 2008) provides an insight into community dynamics at both a local and landscape level that is paramount for effective conservation. A variety of sampling techniques have been developed to survey terrestrial mammals (Catling et al., 1997) and many techniques allow monitoring over large spatial and temporal scales. While live trapping can provide reliable information on species richness for terrestrial populations, particularly for population dynamics that rely on individual characteristics, it also presents several drawbacks. Some animals may become 'trap shy' or require specialised techniques in order to be captured successfully. There is also the negative impact of stress on individuals that are detained for a period of time in the trap. De Bondi et al. (2010), found that sampling methods for live trapping and camera trapping were comparable and that camera traps were able to detect rare and more elusive small- and medium-sized mammals. Camera trapping removes the need for an in situ observer and reduces disturbance to the animals, minimising potential behavioural bias. Technology for camera traps has improved significantly in recent years, becoming more user friendly and reducing the intensity of resources required, thereby allowing researchers to broaden their investigative scope (Meek et al., 2015b). With technological improvements have also come advances to analytical methods, using detection rate to model population density (Rowcliffe et al., 2008; Nakashima et al., 2018) and determine activity patterns (Rowcliffe et al., 2014). Camera trapping provides a low resource intensive option for investigating mammalian patterns and habitat use on both spatial and temporal scales (Silveira et al., 2003).

The objectives of this study were to identify the impact of habitat type on mammal species composition and evaluate the occurrence of both *Thylogale stigmatica* and *Thylogale thetis* within the mammal assembly. The hypothesis is that some species are likely to be more abundant than others, and that those species with higher density are more likely to be generalists and occur across both habitat types. Individual habitat variables were tested against species composition to determine the effects of structural variability on community assembly. Rodent populations were predicted to be more likely associated with attributes providing low level cover, whilst larger mammals and ground birds were likely to be associated with canopy cover and edge effects.

4.3 Methods

4.3.1 Camera Placement

48 Scoutguard and UOVision cameras were deployed at random locations within wet sclerophyll and warm temperate rainforest. Entry points were flagged at 100m intervals along fire trails and cameras were deployed according to randomly assigned distances and bearings. Each camera was secured approximately 50cm above ground level facing in a southerly direction to avoid 'empty' images caused by wind and shadow. Cameras were set to high sensitivity with a 10 second delay between photographs. Lures, consisting of truffle oil soaked cotton wool in a porous PVC canister, were placed approximately 2 metres in front of the camera to encourage any animals moving through the area to investigate long enough to enable detection by the camera. The lure canister was inaccessible to animals and attached to the top tent peg driven into the ground. For a full description of camera placement see *section 2.3.3.*

4.3.2 Vegetation Variables

To measure vegetation variables, 5m x 5m plots were marked around each camera. Vegetation variables were measured within the plots using a scoring system as denoted in *Table 1* (*see section 2.3.4*). Seventeen structural vegetation variables were measured in total to include a broad description of vegetation class, ground cover, lateral cover and canopy cover. A full description of data collection methods used is provided in *section 2.3.4.*

4.3.3 Statistical Analysis

A multivariate analysis was conducted to determine species composition according to habitat type using the 'mvabund' package (Wang et al., 2012) in the R statistical program (R Core Team, 2013). The combined species detection data were used as response variables in multivariate generalised linear mixed models (GLMM) to fit species composition to broad habitat type. Initially models were constructed using a Poisson distribution however checking model assumptions revealed that the variance exceeded the mean showing overdispersion in the data. Data was remodeled using negative binomial distribution in model parameterisation to account for overdispersion. The multivariate hypothesis of whether species composition varied across habitat type was tested using the ANOVA function. Likelihood ration tests and resampled *P*-values were used to look for a significant effect of habitat on species composition.

Univariate tests were run to look for significance of habitat type on individual species, using the ‘adjusted’ argument to take into account the correlation between response variables. Finally, individual habitat variables were fitted to species composition data using multivariate GLM to look for significance on individual habitat variables. The multivariate hypothesis was again tested using the ANOVA function.

4.4 Results

The study site was surveyed for a total of 18, 336 trap days and nights and 13, 284 independent events were recorded. Overall, 24 species were detected, including two large ground-dwelling bird species (*Table 3)*. A category for unidentified mammals (mostly rodents) was also included. Antechinus and rodent species made up approximately 5.7% of detection rates. Two species of bandicoot and three species of possums were detected, comprising 3.5% and 9.7% of the mammal community respectively. Five species of macropods, including the long-nosed potoroo (*Potorous tridactylus*), comprised 17% of the overall assembly of which *Thylogale thetis* was the most commonly detected. Only three species of medium-sized carnivores were detected, spotted-tailed quoll, wild dog and cat, which made up 1.3% of overall assembly. Bush turkey and lyrebird were the most often detected vertebrates and made up for 29% and 27% of detections respectively.

Table 4.1: List of mammal species and large ground dwelling birds detected at ‘Motherland’.

Family Name	**Species Name**	**Common Name**
Dasyuridae	*Antechinus flavipes*	Yellow-footed antechinus
	Antechinus stuartii	Brown Antechinus
	Antechinus swainsonii	Dusky Antechinus
	Sminthopsis murina	Common Dunnart
	Dasyurus maculatus	Spotted-tailed Quoll
Peramelidae	*Isoodon macrourus*	Northern Brown Bandicoot

	Perameles nasuta	Long-nosed Bandicoot
Muridae	*Melomys cervinipes*	Fawn-footed Melomys
	Pseudomys oralis	Hastings River Mouse
	Rattus fuscipes	Bush Rat
Macropodidae	*Notamacropus parma*	Parma Wallaby
	Thylogale stigmatica	Red-legged Pademelon
	Thylogale thetis	Red-necked Pademelon
	Wallabia bicolor	Swamp Wallaby
Potoroidae	*Potorous tridactylus*	Long-nosed Potoroo
Pseudocheiridae	*Pseudocheirus peregrinus*	Common Ringtail Possum
Phalangeridae	*Trichosurus caninus*	Short-eared Brushtail Possum
	Trichosurus vulpecula	Common Brushtail Possum
Phascolarctidae	*Phascolarctos cinereus*	Koala
Tachyglossidae	*Tachyglossus aculeatus*	Short-beaked Echidna
Menuridae	*Menura novaehollandiae*	Superb Lyrebird
Megapodiidae	*Alectura lathami*	Australian Brush-turkey
Felidae	*Felis catus*	House Cat
Canidae	*Canis familiaris*	Wild Dog

The 12 most frequently detected species were detected in both rainforest and wet sclerophyll vegetation (*Figure 4.1*). Of those 12 species, *M. novaehollandiae, T. thetis* and *T. vulpecula* were most abundant in wet sclerophyll vegetation. The three species most abundant in rainforest vegetation were *R. fuscipes, T. stigmatica* and *P. nasuta*. *F. catus* and *D. maculatus* were detected at wet sclerophyll sites but overall were more abundant in rainforest vegetation.

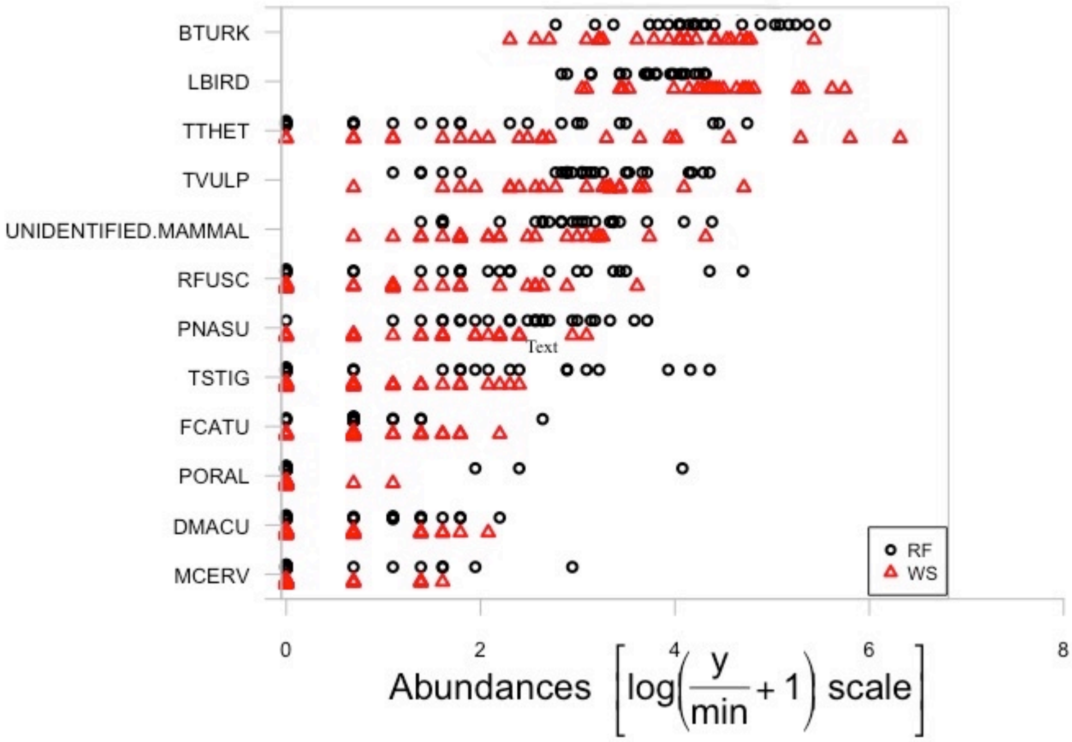

Figure 4.1: Top twelve most detected mammal and large ground dwelling bird species detected at 'Motherland' and Mount Hyland. Black circles represent rainforest habitat and red triangles represent wet sclerophyll forest.

Multivariate analysis yielded a significant difference in species composition between rainforest and wet sclerophyll ($P = 0.004$), however the habitat did not have a significant effect on the detection of individual species (*Table 4.2*), other than *M. novaehollandiae* which was more abundant in wet sclerophyll forest (*Figure 4.1*). Analysis of individual vegetation variables yielded significant results for vines, palms, ferns, rocks, canopy cover, eucalypt emergents, distance to nearest road and distance to forest edge (*Table 4.3*). Earlier PCA of vegetation (*Chapter 3*) yielded results that linked vines, palms, ferns and canopy cover to dry rainforest, which showed fewer signs of disturbance. Variables such as distance to nearest road and forest edge are signs of forest disturbance and are more closely associated with the wet sclerophyll forest, which was heavily logged in previous years.

Table 4.2: *P*-value pertaining to the significance of habitat type on individual species.

Species	***P*-value**
Antechinus flavipes	0.93
Antechinus stuartii	0.64
Antechinus swainsonii	0.80
Alectura lathami	0.77
Dasyurus maculatus	0.93
Felis catus	0.93
Isoodon macrourus	0.93
Menura novaehollandiae	**0.002***
Melomys cervinipes	0.93
Macropus parma	0.93
Phascolarctos cinereus	0.77
Perameles nasuta	0.07
Pseudomys oralis	0.80
Pseudocheirus peregrinus	0.93
Potorous tridactylus	0.93
Rattus fuscipes	0.37
Sminthopsis murina	0.93
Tachyglossus aculeatus	0.71
Trichosurus caninus	0.93
Thylogale stigmatica	0.70
Thylogale thetis	0.37
Trichosurus vulpecula	0.96
Unidentified Mammal	0.85
Wallabia bicolor	0.71
Canis familiaris	0.98

Table 4.3: *P*-values of the effect of individual habitat variables on overall mammal species composition.

Variable	***P*-value**
Ground Litter	0.07
Vines	**0.03***
Palms	**0.003***
Ferns	**0.05***
Rocks	**0.02***
Fallen Timber	0.85
Ground Cover	0.12
Lateral	0.76
Canopy Cover	**0.03***
Sub Canopy Cover	0.12
Slope	0.22
Tree Fall Gap	0.06
Eucalypt Emergents	**0.008***
Nearest Road	**0.009***
Forest Edge	**0.001***
Sapling Density	0.08
Medium Stem Density	0.33

On an individual level, most species were significantly affected by habitat variables correlated with PC1 or PC2 (*Table 4.4*). Species that increased significantly along PC1 were more likely to be positively correlated with the occurrence of ground litter, ground cover, sub canopy cover, eucalypt emergents, distance to nearest road, sapling density and medium stem density (i.e. wet sclerophyll and disturbance attributes). There was a decline of *A. lathami, P. oralis, P. tridactylus, R. fuscipes* and *T. stigmatica* with an increase in variables correlated with PC1 (*Appendix A*). Species significantly aligned with PC2 were more likely to be positively correlated with palms, lateral cover, canopy cover, sub canopy and sapling density (i.e. rainforest attributes). *T. thetis, T. vulpecula* were significantly affected by factors contributing to PC2 and there was a positive correlation with an increase along the PC2 axis (*Appendix A)*. Unidentified mammals were also positively correlated with an increase in PC2

(*Appendix A*). No correlation was considered if the detection rate was less than 5 individuals.

Table 4.4: *P*-values pertaining to the significance of effect of habitat variables pertaining to PC1 and PC2 on individual species detection and resultant habitat affiliations.

Species	**PC1**	**PC2**	**Habitat Type**
Antechinus flavipes	0.60	0.67	Indeterminate
Antechinus stuartii	0.10	**0.08***	Indeterminate
Antechinus swainsonii	0.41	0.32	Indeterminate
Alectura lathami	**0.05***	0.65	Rainforest
Dasyurus maculatus	**0.04***	0.73	Indeterminate
Felis catus	0.33	0.90	Indeterminate
Isoodon macrourus	0.97	0.42	Indeterminate
Menura novaehollandiae	**<0.001***	0.16	Wet sclerophyll
Melomys cervinipes	0.19	0.20	Indeterminate
Notamacropus parma	**0.01***	0.06	Indeterminate
Phascolarctos cinereus	0.08	0.30	Indeterminate
Perameles nasuta	0.37	**0.002***	Indeterminate
Pseudomys oralis	**0.007***	0.24	Rainforest
Pseudocheirus peregrinus	0.52	0.67	Indeterminate
Potorous tridactylus	**<0.001***	**<0.001***	Indeterminate
Rattus fuscipes	**<0.001***	0.86	Rainforest
Sminthopsis murina	0.50	0.31	Indeterminate
Tachyglossus aculeatus	**0.08***	0.70	Indeterminate
Trichosurus caninus	0.27	0.41	Indeterminate
Thylogale stigmatica	**0.005***	0.16	Rainforest
Thylogale thetis	**0.02***	**<0.001***	Wet Sclerophyll
Trichosurus vulpecula	0.66	**<0.001***	Rainforest
Unidentified Mammal	0.66	**<0.001***	Rainforest

Wallabia bicolor	0.30	**0.02***	Indeterminate
Canis familiaris	0.80	**0.008***	Indeterminate

4.5 Discussion

All species recorded in the survey were detected in both wet sclerophyll and dry rainforest habitat. The two most highly detected species were brush turkeys (*A. lathami*) and lyrebirds (*M. novaehollandiae*). Five macropod species were also detected, of which the most abundant was *T. thetis*. The three medium carnivorous species detected were the spotted-tail quoll (*Dasyurus maculatus*), feral cat (*Felis catus*) and wild dog (*Canis familiaris*), all of which were detected in very low numbers, likely resulting in low levels of predation. Analysis of quoll and wild dog diets in the Chaelundi and Marengo areas found that while medium-sized mammals were a staple in both species diets, canids typically preyed on larger animals (Glen and Dickman, 2008). The abundance of large ground-dwelling birds may be a response to low carnivore presence combined with the availability of suitable habitat. Low levels of predation may also be a contributing factor to the high numbers of macropods, particularly *T. thetis,* in the area. Optimal abiotic conditions and habitat carrying capacity allow herbivore populations to occur in healthy numbers in the presence of a carnivore guild.

Although all species were detected in both habitat types, the species composition of each habitat type was significantly different. A PCA of vegetation variables (*Chapter 3*) described 32% of variation in habitat types with disturbance attributes increasing along the PC1 axis, which mostly described the wet sclerophyll vegetation community. PC2 described factors pertaining to rainforest and multilayered cover. Almost all species significantly affected by PC1 (*A. lathami, D. maculatus, P. oralis, R fuscipes, T. stigmatica*) decreased significantly in detection rate with an increase in factors along the PC1 axis, indicating a closer affiliation with rainforest. Only *T. thetis* and *M. novaehollandiae* increased in number with an increase in PC1 factors, indicating preference for disturbance factors associated with the wet sclerophyll forest. Species significantly affected by PC2 (*T. thetis, T. vulpecula* and unidentified mammals) increased in detection along the PC axis, indicating an affiliation with multilayered cover associated with the rainforest habitat type. *T. thetis* was the only species that increased in detection along both PC axes, indicating their spatio-temporal partitioning of habitat while *T. stigmatica* preferred rainforest (*Chapter 3*). Anecdotal observation confirms that the study site has remained relatively undisturbed by major human activity for several decades however past logging activity caused some structural changes to the vegetation community.

Disturbance may be segregated into three classifications: those caused by direct anthropogenic impacts, biotic pressure and environmental changes such as abrupt alterations to abiotic conditions and the degradation of habitat quality (Mouillot et al., 2013). In general, disturbance causes an increase in mortality rates and decline in the reproduction rates of established species, causing the influence of density-dependent competition to weaken. Ecological disturbance can alter community assembly processes that influence variations in community composition. Disturbance can increase niche selection of tolerant species, causing convergence in community structure or alternatively, cause divergence by increasing habitat filtering across environmental gradients (Myers et al., 2015). Some disturbance factors did not affect *T. thetis* as detections increased along both PC axes, indicating an affiliation with both habitat disturbance variables and multi layered cover, while *T. stigmatica* did not associate with disturbed vegetation. The manipulation of habitat can have flow on effects for fauna due to direct and indirect changes to key habitat features (Eyre et al., 2015) which will continue to affect the mammal community. Logging causes long-term impacts such as a reduction in older trees that provide nesting hollows and less coarse debris and litter which provides essential habitat for small ground-dwelling mammals (Eyre et al., 2010). Logged environments are likely to have fewer foraging, shelter and nesting resources provided by large trees and shrubs, but alternative habitat resources may be increased in the form of coarse woody debris and higher leaf litter depth. This can alter community structure by opening up available resources for smaller ground-dwelling mammals, while excluding those species that rely on larger trees and shrubs. Spaces in canopy cover, or thinning of cover can promote higher levels of ground cover and sub canopy plant species, providing cover for very small mammals but potentially affecting medium and larger-sized mammals that rely on vegetation for crypsis. The wet sclerophyll forest had less canopy cover and lacked the mid canopy that *T. stigmatica* rely on for crypsis, thus altering community structure via habitat disturbance of key features required for this species.

None of the species detected were significantly affected by vegetation type on an individual level, other than *M. novaehollandiae*. However, species whose occurrence correlated with particular principal components can be interpreted as showing a greater preference for either rainforest or wet sclerophyll habitat. Habitats with high heterogeneity often provide more abundant resources and thus greater fitness to a range of faunal species (Tews et al., 2004). Given their size, smaller mammals in particular will be more sensitive to fine scale habitat attributes and respond to immediate landscape heterogeneity (Stirnemann et al., 2015). *Rattus fuscipes, P. oralis* and *M. cervinipes* all occurred more abundantly in rainforest habitat, which was positively correlated with vines, palms, lateral cover and medium stem density. Each of these variables contributes to fine scale heterogeneity, offering immediate variation in the landscape. Landscapes that appear largely homogeneous may provide microclimatic variation at fine scale resolutions that are meaningful to small animals (Milling et al., 2018). This provides variation in microclimate and available niches, unlike disturbed habitat which has decreased fine-scale heterogeneity. Vegetation cover may be a governing factor of available microclimates and affect the spatial distribution of species (Shibuya et al., 2011), as such providing microhabitats and microclimatic variation for smaller animals. Vines, palms, ferns and canopy cover all significantly contributed to a variance in species composition and it is likely that fine-scale heterogeneity in the presence of multi-layered cover provided a more ideal habitat for these species. Stirnemann et al. (2015) found that the occurrence and abundance of *R. fuscipe* and *P. nasuta* was positively affected by fine-scale heterogeneity indicating that immediate landscape heterogeneity is an important habitat factor for small and medium-sized mammals. Factors at this scale, such as ground level vegetation and food availability, determine available niches and density dependent interactions, all of which contribute to overall species diversity.

Variables related to disturbance, such as distance to nearest road and distance to forest edge, also contributed significantly to variation in species composition. Fragmentation increases the edge to interior ratio and can significantly alter microhabitats at forest edges (Laurance et al., 2002). Previous chapters found that *T. thetis* regularly associates with the forest edge, exploiting adjacent pasture resources on crepuscular visits. Research by Stirnemann et al. (2015) also found that as well as *R. fuscipes* and *P. nasuta* responding to fine-scale habitat heterogeneity, the larger, generalist swamp wallaby (*Wallabia bicolor*) responded positively to ecotones, indicating an affinity with fine-scale vegetation attributes. Although each species was not individually affected by habitat type, the significance of singular variables shows that species composition is affected by fine-scale heterogeneity. Habitat partitioning occurs on a fine scale between *T. thetis* and *T. stigmatica* however it would appear that for *Thylogale* genus, sympatry with other macropod species does not affect it's ability to maximise resources at and beyond the forest edge (*Chapter 3*). *T. thetis* appears to be the most abundant of the four macropods detected and is able to utilise its preferred spatial niche by exploiting both interior forest vegetation and edge-adjacent pasture. The wet sclerophyll vegetation community is characterised by eucalypt emergents, closer distances to edge and canopy gaps. While emergents are indicative of high level canopy cover, canopy gaps and proximity to edge allow higher levels of sun penetration and promotion of grasses and ground cover. For generalist species such as *T. thetis* and *W. bicolor* this provides the optimal niche to access food resources higher in nutrition whilst utilising canopy cover for avoiding predation. *T. stigmatica* and *M. parma* were more abundant in rainforest vegetation, which typically provided higher levels of multi-layered cover. Habitat heterogeneity has provided a variety of niches to allow sympatry and coexistence for a diverse macropod community.

Particularly for small mammals, local assembly and species diversity is determined by habitat capacity, within the limitations of the regional species pool. The habitat matrix can act as a selective filter as species that have a higher tolerance towards the matrix were more successful at persisting in the matrix (Laurance, 1994). Broad habitat types can affect the composition of species assembly and on a fine scale, habitat heterogeneity is even more important in determining species composition. Variation in the composition of mammalian community structure is affected by several influencing factors including habitat selectivity of the component species and significant variation in local components of principal landscape structure (Lomolino and Perault, 2000). Further studies should incorporate similar survey counts at a landscape level and incorporate both habitat size and the distance between patches into structural vegetation measurements. Habitat fragments with high heterogeneity may not support a diverse mammal assemblage due to size-related carrying capacity or lack of connectivity throughout the matrix.

Future researchers should also consider that detectability doesn't necessarily dictate abundance and not all species are equally detectable. Like alternative trapping techniques, camera trapping requires different approaches depending on the focal species. Camera traps are strongly dependent on animal body mass and tend to perform in favour of large species (Lyra-Jorge et al., 2008) however the sensitivity of camera traps would need to be very different for surveys in Australia where many species are small- to medium-sized (Meek and Pittet, 2012). For the purpose of this study, *Thylogale* were the primary focal genus and given the medium-size of pademelons, the height of the camera above ground and the adjustment of flash were most likely appropriate to capture small mammals as well as any potentially larger species. Setting the cameras to take a burst of three photos would have increased the probability of detecting fast moving animals but battery life would have been negatively affected by this setting.

4.6 Conclusion

This study confirms that habitat type does affect the species composition of mammal assembly in the Mount Hyland area. As well as broad habitat type, individual structural habitat variables also affected overall species contribution and fine scale habitat heterogeneity is important in the habitat requirements of small- and medium-sized mammals. Camera traps are an effective way to survey mammal diversity however technique plays an important role in the detectability of the species. Regular surveys such as this will contribute significantly the knowledge of mammalian biodiversity in Australia and contribute to the improvement and effectiveness of conservation work through understanding movement patterns, habitat use and community dynamics. Monitoring mammal community assembly on both small and large scales will broaden understandings of how fine scale structural vegetation variables contribute to biodiversity, and which attributes within the environmental matrix impact or enhance animal populations. Coupled with technological advancements in statistical software pertaining to camera trap data, researchers can predict community dynamics under a range of future climate change scenarios to assist in slowing the rapid decline of Australian fauna.

4.7 References

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4.8 Appendix A – Generalised linear models of species significantly affected by principal component variables

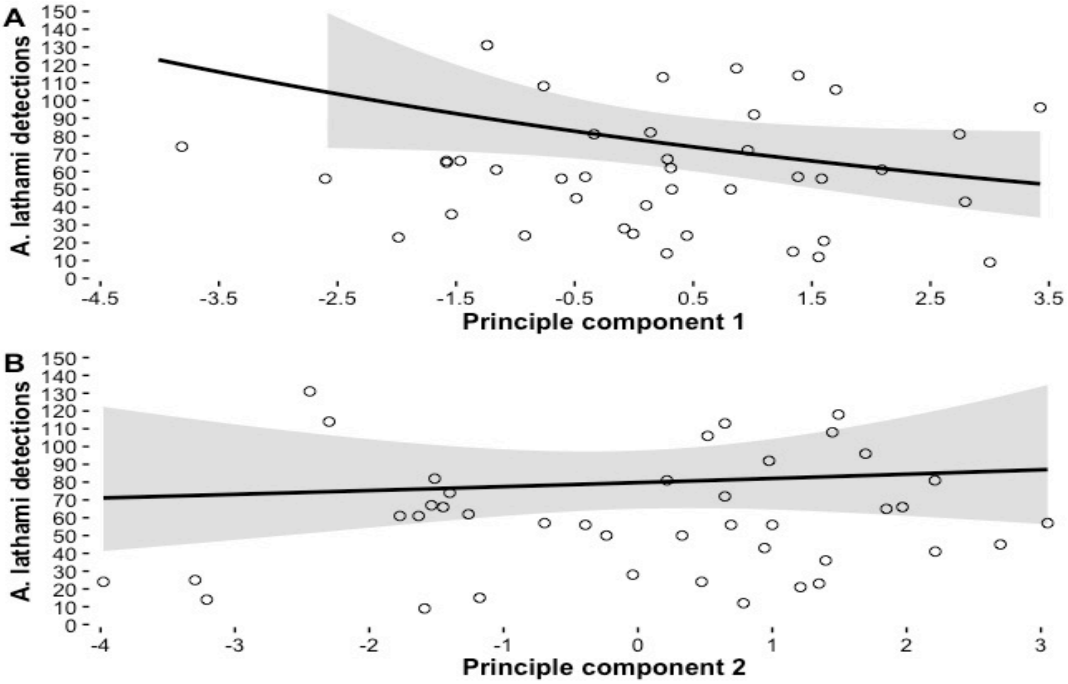

Figure 4.2: Generalised linear model of *A. lathami* detections along PC1 axis (A) and PC2 axis (B).

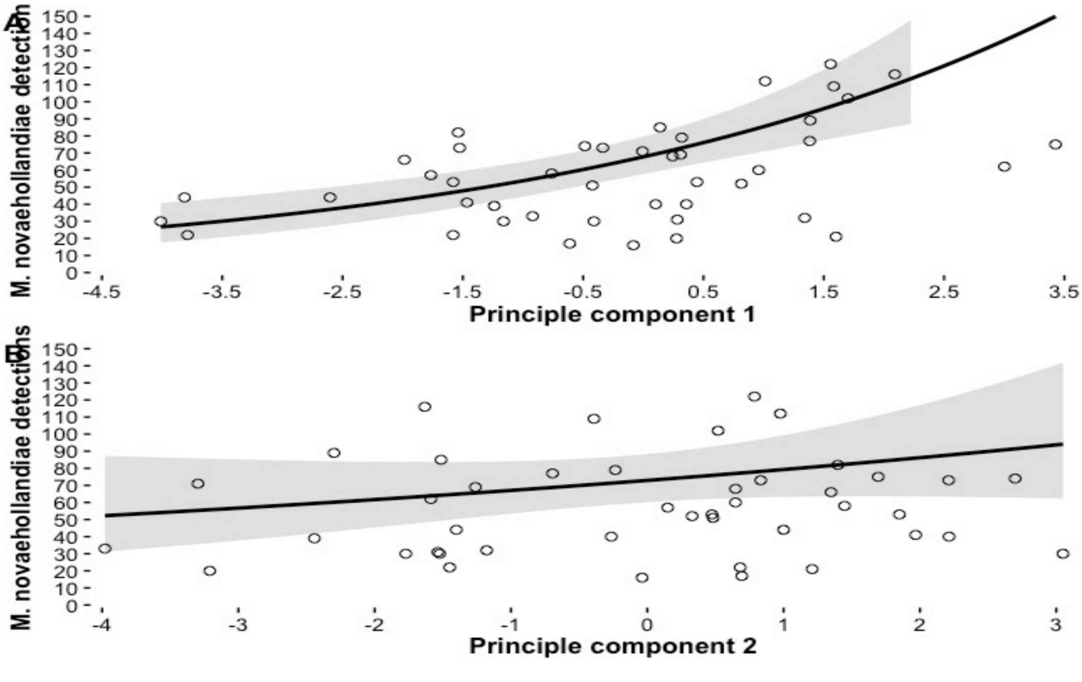

Figure 4.3: Generalised linear model of *M. novaehollandiae* detections along PC1 axis (A) and PC2 axis (B).

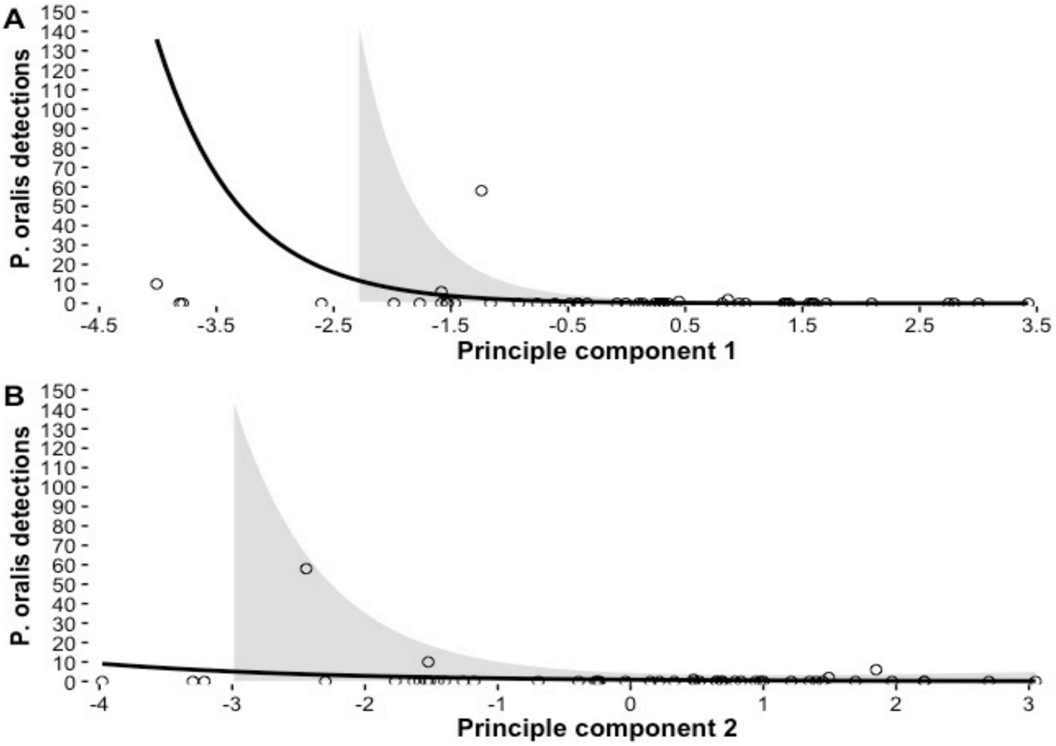

Figure 4.4: Generalised linear model of *P. oralis* detections along PC1 axis (A) and PC2 axis (B).

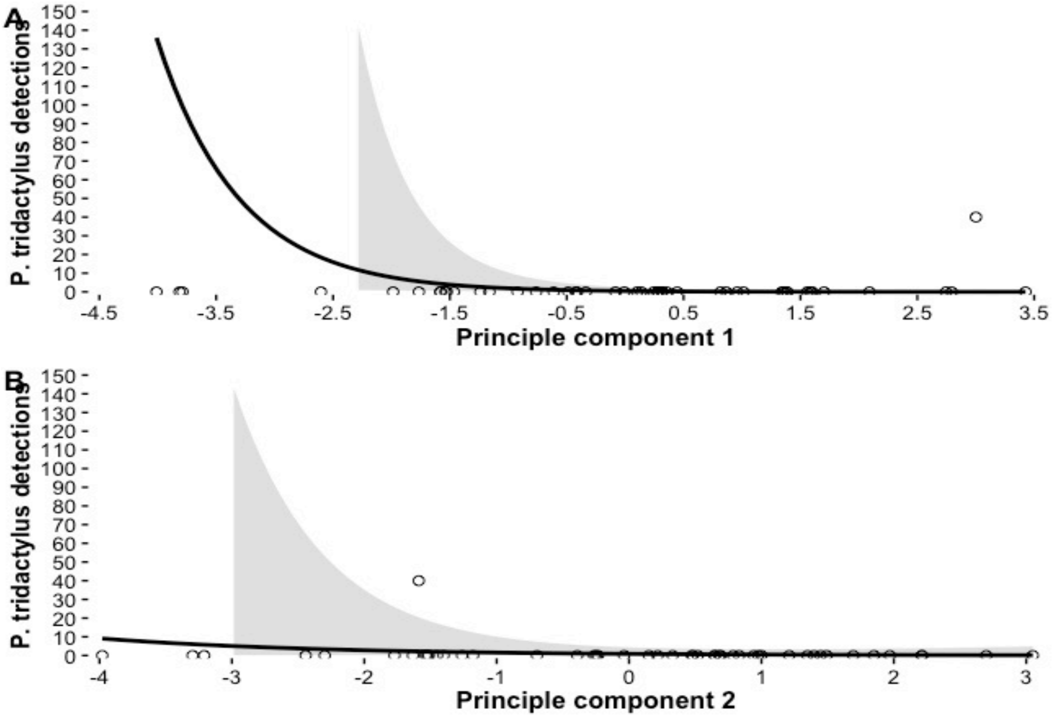

Figure 4.5: Generalised linear model of *P. tridactylus* detections along PC1 axis (A) and PC2 axis (B).

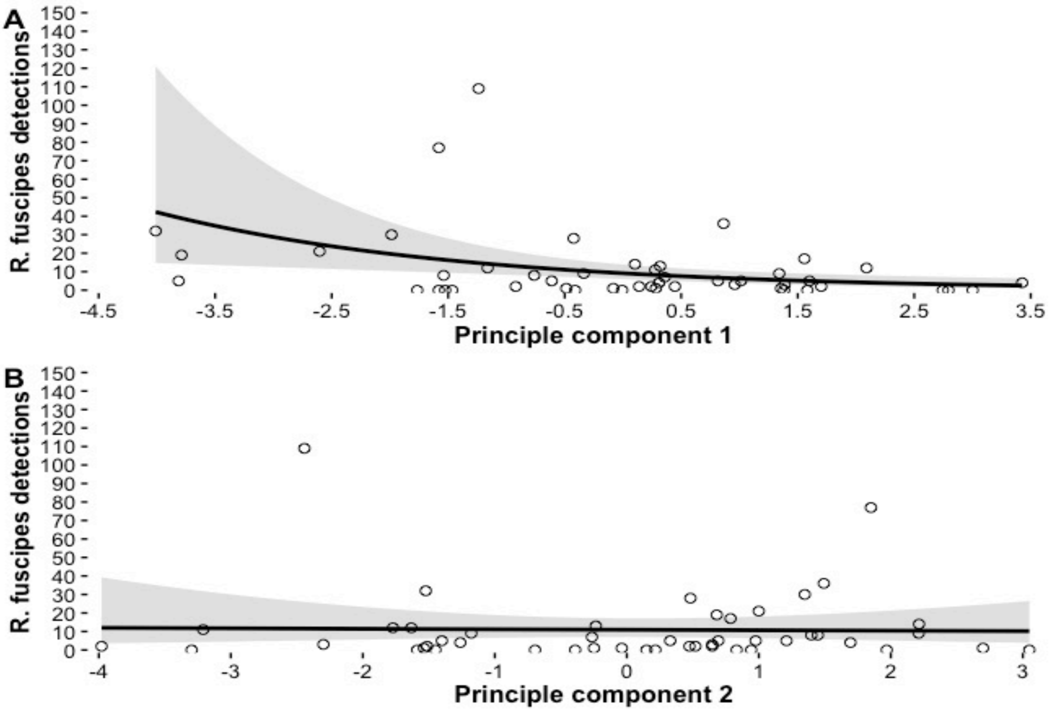

Figure 4.6: Generalised linear model of *R. fuscipes* detections along PC1 axis (A) and PC2 axis (B).

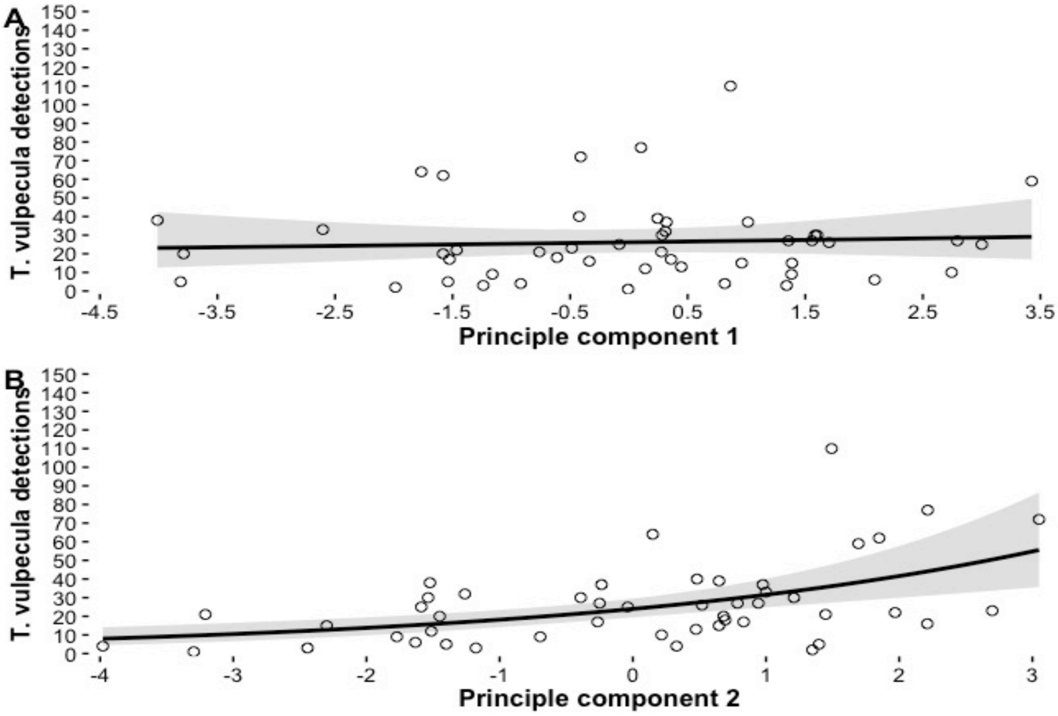

Figure 4.7: Generalised linear model of *T. vulpecula* detections along PC1 axis (A) and PC2 axis (B).

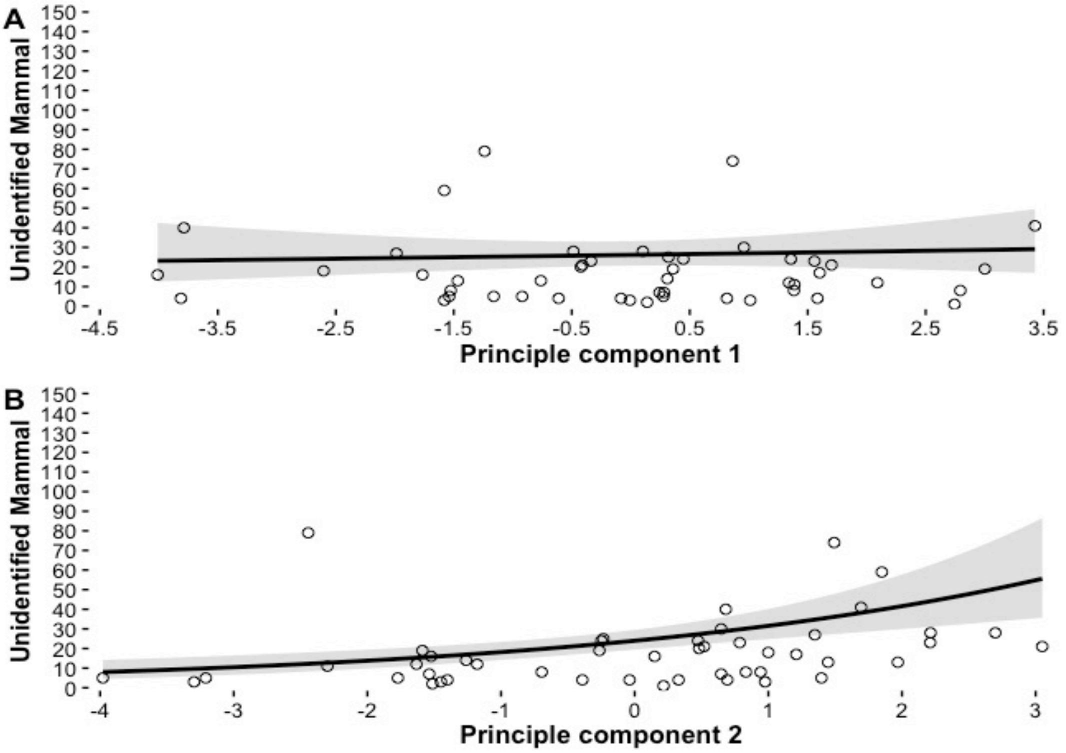

Figure 4.8: Generalised linear model of *Unidentified mammal* detections along PC1 axis (A) and PC2 axis (B).

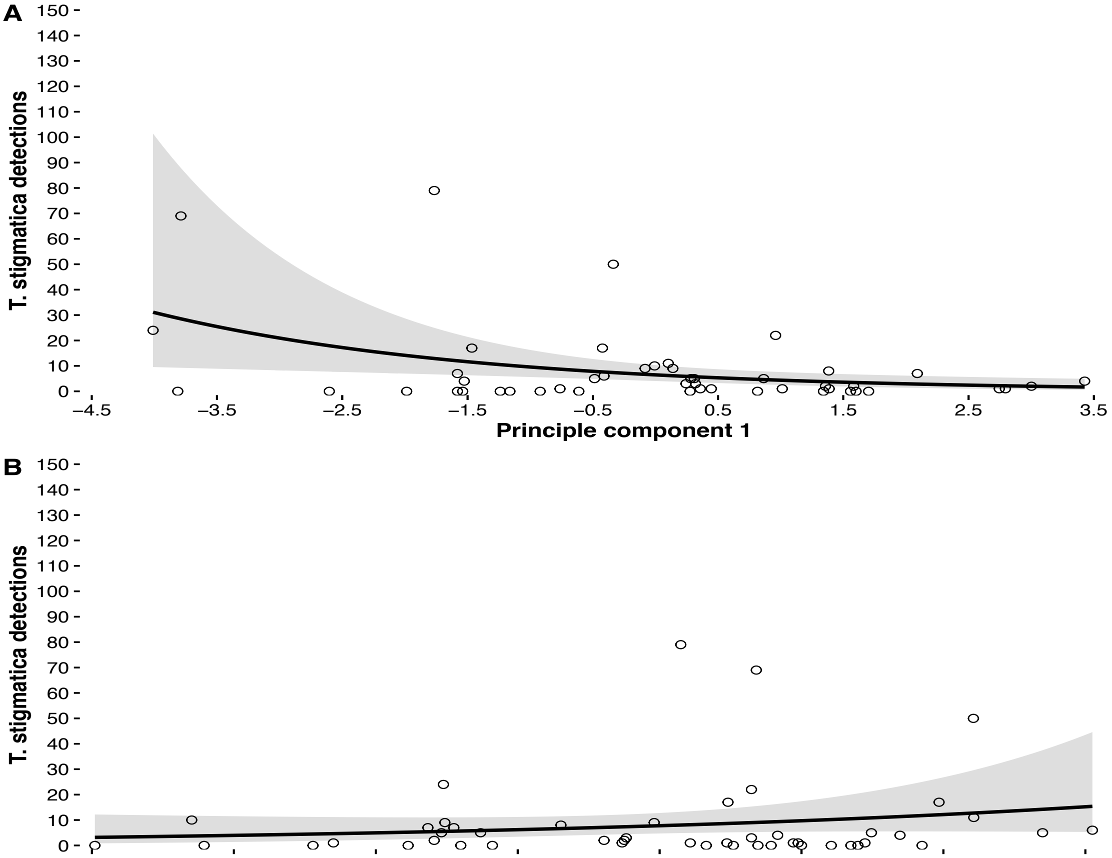

Figure 4.9: Generalised linear model of *T. stigmatica* detections along PC1 axis (A) and PC2 axis (B).

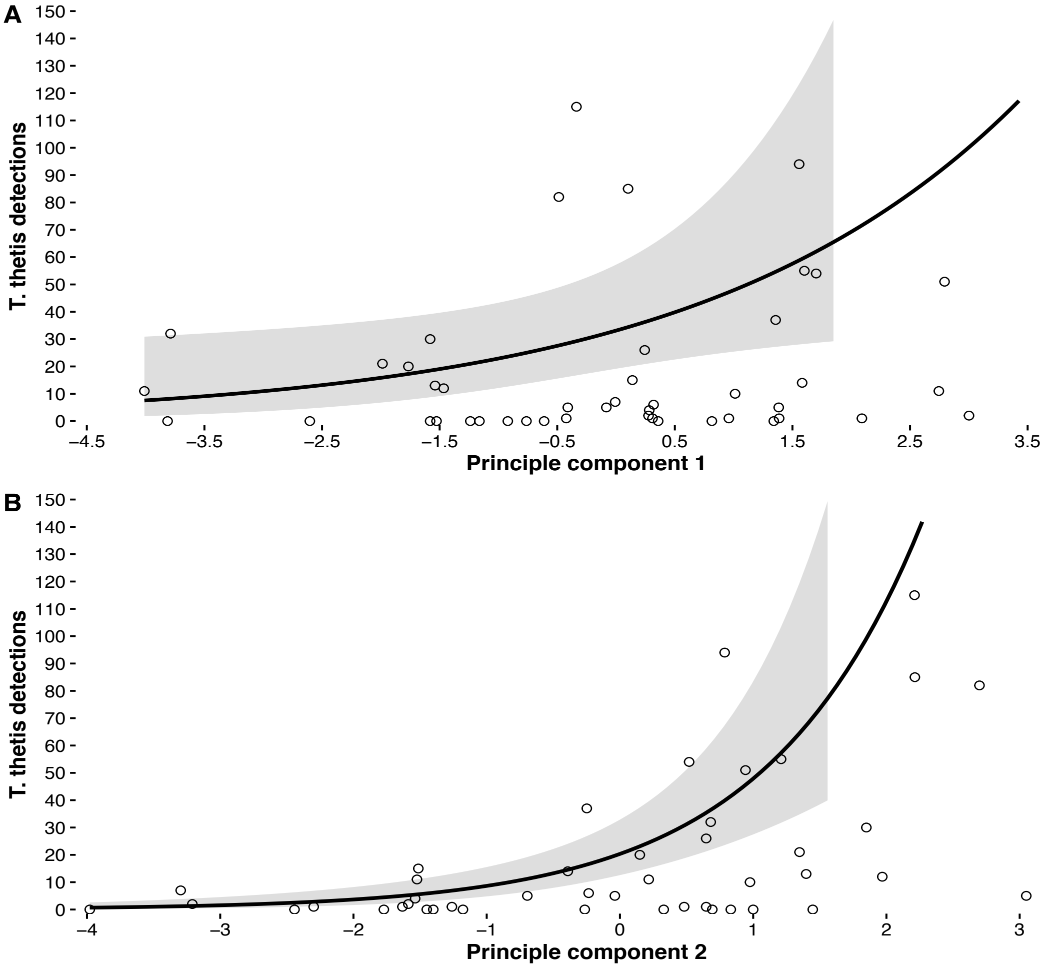

Figure 4.10: Generalised linear model of *T. thetis* detections along PC1 axis (A) and PC2 axis (B).

Chapter 5 – Synopsis: Temporal and spatial ecology of two sympatric pademelon species in northeastern NSW

The concept of community assembly continues to be at the forefront of ecological inquiry. Since Diamond's (1975) original premise of assembly rules, community ecologists continue to hypothesise about the factors that structure community assembly and whether all communities are structured by the same or similar sets of rules (Gotelli, 2016). The development of neutral theory (Hubbell, 2001) has shifted focus from random assemblages to neutrally or stochastically assembled communities structured by dispersal, ecological drift or low historical mobility (Weiher et al., 2011). This theory assumes a model in which all species occupy equal areas of spatial heterogeneity. Under such a model, species abundance is strongly correlated to its functional traits and environmental conditions (Tilman, 2004). Niche theory suggests that the differences between any given species will result in either competitive exclusion or niche partitioning depending on whether one particular trait is advantageous and thus balanced by the trade off of another trait (Courbaud et al., 2012). Contemporary niche theory originates in mechanistic consumer-resource models (MacArthur, 1970; Tilman, 1982) and was later described as a synthesis of historically incompatible niche definitions (Chase and Leibold, 2003). Modern coexistence theory introduces two types of mechanism that allow coexistence: equalising mechanisms that reduce the average fitness between species and stabilising mechanisms that facilitate a reduction in niche overlap (Letten et al., 2017).

Suggestions have been made that a synthesis of the two views will be more productive moving forward than a debate of neutral versus niche (Tilman, 2004; Leibold and McPeek, 2006). Experiments focused on community assembly have primarily involved either altering environmental factors and/or dispersal history and assessing the influence of diversity or their role in the assembly process (Weiher et al., 2011). Godsoe et al. (2017) suggests that answers to the question of biotic interactions and range limits will require a contrast between the effects of both biotic interactions and the abiotic environment on the expansion of local populations of a focal species, and appropriated to large scales. In mammal communities, the advancement of camera trap technologies introduces a novel method of observing species interactions. A time and date stamp on each photograph collected during a recorded camera trap event, along with improved and highly developed analytical programs allow for a detailed glimpse into the diel activity patterns of wildlife populations. Building comparative analytical models enables researchers to detect temporal patterns between individual species and trophic guilds. Predator-prey relationships can be determined by temporal activities and intra-guild associations can be examined by means of temporal avoidance or an overlap in activity patterns.

Camera traps can also be effective tools for investigating mammalian assembly relationships from a spatial perspective, however they are only as effective as the underlying experimental design (Meek et al., 2014; Burton et al., 2015; Meek et al., 2015a). Careful planning must be done to ensure the focal species are not misrepresented as a result of ineffective deployment techniques. Homogenisation of detection probability would improve the use of camera trap data by reducing potential bias and allowing a robust inter-site and inter-species data comparison (Franck et al., 2014). This can be done at a camera scale by selecting camera models with similar features that are appropriate for the data needed such as quick trigger speed for fast moving animals and adequate picture resolution to correctly identify individuals. At an ecosystem scale, implementing a standardised sampling scheme ensures an appropriate number of cameras, placement and spacing to achieve optimal results. A standard sampling protocol will also increase the power and reliability of statistical models as well as the interpretation of results (Franck et al., 2014). The novel use of camera traps will become ever more important to community ecologists as the landscape and climate continue to change rapidly. Species presence and functional role in a community is often influenced by inter-species interactions and the properties that emerge from such interactions (Drake, 1990). Camera trap data can give unique insight into the spatial and temporal relationships in a community as well as how individual species interact with their environment and identify global biodiversity trends (Steenweg et al., 2017). This data can be combined with predictive modeling to give insight into community structure under varying climate scenarios. This can assist land managers and national parks in preserving not only the current distribution of species but also predicting the future presence or absence of species in appropriate habitat, regardless of whether the abiotic conditions are appropriate. Fragmentation of landscape can prevent the future dispersal of species and predictive modeling will allow researchers to forecast future distribution range by understanding the current relationship of a species with its environment. How a species interacts with its surroundings will give greater insight into the mammal assemblage across a matrix.

Diverse, functioning and intact assemblages are vital to the continuity of healthy ecosystems and the provision of ecosystem services. Species richness is strongly related to functional diversity when species traits are equally interdependent (Petchey and Gaston, 2002) and there is a link between biodiversity and ecosystem services using functional diversity (Flynn et al., 2009) such as resource use complementarity. Biodiversity is an underlying factor that impacts ecosystem services via its functionality in ecosystem processes (Mace et al., 2012). If each species has a role to play in the process of ecosystem functionality, then ultimately highly diverse ecosystems are more likely to function healthily. Ecosystem processes typically depend on the combination of particular biotic and abiotic components being present and functioning. Functionally diverse ecosystems create a higher possibility of creating the optimal combination of biotic interactions, as well as biotic interactions with the abiotic components of the ecosystem to enable functional processes that result in ecosystem services. For future research, functional diversity must be correlated with ecosystem function to be a meaningful measurement and should provide information above what species richness or diversity can explain (Cadotte et al., 2011). Understanding the functional traits of individual species and how they interact with other species to embody functional diversity assists in more focused conservation efforts, particularly in unique environments or those that are especially sensitive to a change in global processes such as climate change.

Australia has lost many of its mammalian species since European settlement and mammal surveys can be difficult to undertake on a large scale. Biodiversity loss in Australia occurs mostly due to predation via introduced species and changed fire regimes (Lawes et al., 2015; Woinarski et al., 2015). This is unlike global trends in biodiversity decline, which are mostly affected by an increasing rate of human population growth, habitat loss, hunting, impacts from the introduction of invasive species and inadequate conservation reserves (Bradshaw et al., 2009). Understanding functional diversity of ecosystems in Australia will assist conservation efforts in preserving flora and fauna against threats unique to Australia. For *T. thetis* and *T. stigmatica* however, the continued existence of suitable habitat is uncertain due to continued human interference (Johnson, 1980). Since the 1970s, southeastern

Queensland and northern NSW have undergone the highest rates of forest clearance and a significant amount of endemic biodiversity stands to be negatively impacted (Bradshaw, 2012). Anthropogenic disturbance can significantly impact ecosystem properties such as vegetation structure and microclimate, which in turn alters available niches for fauna. *Thylogale* species appear to be primarily edge dwelling (Vernes et al., 1995) and spatio-temporally partition their habitat to maximise nutrient abundant edge habitats nocturnally, while utilising the cover of forest diurnally. When *T. thetis* and *T. stigmatica* are in sympatry, it appears that *T. thetis* may out compete *T. stigmatica* forcing it to utilise a smaller, less optimal niche, which in turn has affected overall population density. This study has unequivocally demonstrated that when co-occurring with *T. thetis*, *T. stigmatica* occupies interior forest, and does not emerge to graze on adjacent pasture. It is likely that this has also led to a concomitant contraction in individual home range size to avoid moving beyond forest edges, but that remains to be tested.

Fragmentation can affect the abundance of some species either positively or negatively due to alterations to microclimates both within and surrounding the fragment (Turton, 1997; Tuff et al., 2016). Fragmentation increases the amount of edge to interior ratio (Laurance et al., 2002) and edges experience increased wind and light penetration, altering the understorey regime (Debinski and Holt, 2000; Newmark, 2001) and enabling increase in ground cover plant species. An increase in fragmentation may positively affect *T. thetis* and *T. stigmatica* as an increase in available edge habitat will potentially provide additional access to highly nutritional pasture habitat and can, in turn, stimulate population growth, provided the remaining remnant forest is of suitable quality. In northeastern NSW however, where *T. thetis* and *T. stigmatica* occur in sympatry, population numbers of *T. stigmatica* may decline and in time there is a potential for a severe contraction of its range. If fragmentation continues, increased edge to interior ratio would be likely to encourage population growth of both *Thylogale* species individually, however in sympatry given the current circumstances, it is likely that over time *T. stigmatica* may no longer co-occur with *T. thetis* and hence it's range may contract to only northern parts of eastern Australia where *T. thetis* does not occur.

In sympatry, *T. stigmatica* appears to segregate itself from *T. thetis* through temporal partitioning. This research showed that whilst it followed a crepuscular activity pattern, it was more active in pre-dawn twilight and less so in the evening. *T. thetis,* on the other hand, was equally active in both the morning and evening twilight. Habitat loss or human interference can affect species spatial and temporal activity patterns (Norris et al., 2010; Shamoon et al., 2018) and modify interactions with other species. Plasticity in activity can form part of an ecological trade-off and permit co-existence amongst competing species. This research suggests that *T. stigmatica* has the potential to alter its spatial and temporal activity in response to competition from a functionally similar species. This potential for ecological plasticity may allow continued coexistence with *T. thetis* under a future scenario of increasing fragmentation, however abundance may diminish sufficiently to negatively affect population persistence.

Further research of pademelon spatial ecology should involve a landscape level survey whereby fragments of differing sizes are included. Several potential hypotheses could be tested such as whether *T. stigmatica* alters its behaviour in the southern expanse of its range in the absence of *T. thetis,* and whether other generalist edge dwelling species such as the swamp wallaby (*Wallabia bicolor*) affect its spatio-temporal partitioning. Le Mar and Mcarthur (2005) found that *Thylogale billardierii* did not alter their edge-dwelling behaviour in the presence of the red-necked wallaby (*Notamacropus rufogriseus*) and equivalent studies of sympatric *Thylogale* populations on the mainland is warranted. A suitable extension of this research would involve collection of detection data in fragments along the range of sympatric populations of *T. thetis* and *T. stigmatica* to determine whether fragment size contributes to plasticity in the activity of *T. stigmatica* and whether, given an appropriate fragment size, both species of *Thylogale* utilise forest edges. Given that the current research indicated neither species was attracted to a particular forest type *per se*, but rather fine scale structural vegetation attributes, deployment of cameras in a grid formation to include the forest edge and adjacent habitat would be appropriate experimental design in determining the spatial ranges and habitat partitioning of each species.

Alterations or plasticity in the ecology of one species can have knock on effects and implications for the dynamics of the community structure. The competition between *T. thetis* and *T. stigmatica* has stimulated a change in *T. stigmatica* activity and habitat use that may occur throughout the entire southern expanse of their range where populations are in sympatry with *T. thetis.* The ability to change or sustain their diel patterns highlights the role of interference competition between species and subsequent behavioural adjustments in population dynamics and mammalian community structure (Valeix et al., 2007). The reduced population numbers of *T. stigmatica* when in sympatry with *T. thetis* may open up available niches for species that prefer forest edge habitat but are more generalised. *Wallabia bicolor* regularly associate with ecotones (Stirnemann et al., 2015) and open forest or woodlands, and are more generalised in their diet (Di Stefano and Newell, 2008). The contraction of *T. stigmatica* in northern NSW may allow populations of *W. bicolor* to flourish which may cause further stress to *T. thetis* at forest edges and affect nutrient availability through plant predation. While larger macropods are unlikely to compete with small rainforest macropods such as *Thylogale*, smaller, more generalised species such as *W. bicolor* or *N. rufogriseus* may make use of available niches by a reduction in the number of *Thylogale.* Habitat matrices tend to be more permeable by generalist species that have a greater ability to move between fragments. Despite an increase in fragments potentially benefitting *Thylogale* species, the distance between fragments may render the matrix impermeable, affecting source and sink populations and reducing metapopulation dynamics.

In community ecology, abiotic niche filters determine whether a species is able to occupy and persist in a suitable habitat, biotic niche filters are then imposed by interactions with competitors, mutualists and consumers (Weiher, et al. 2011). Closely related species cannot coexist until they have diverged sufficiently in ecological traits. Ecologically similar species often have adjacent distributions, which suggests that competitive exclusion is a contributing factor of some natural communities (Esselstyn, et al. 2011). If competition for habitat results in exclusion and is the cause of an overlap in home range, then the competing species must occupy a similar ecological space. In this way, a checkerboard distribution may become apparent on a landscape level. Habitat fragments represent islands in the matrix of the landscape however, unlike islands, individuals may have the option to move between 'islands' depending on distance between patches and quality of the landscape between habitat fragments. Animal movement patterns and spatial use of the environment depends not only on food and nonfood resources but also conspecific and interspecific interactions. Studies of habitat use often neglect multiple factors and seldom include marsupials (Ellis et al., 2009).

A structurally sound habitat matrix within a modified landscape can provide supplementary resources and increase the likelihood of movement throughout the landscape, thereby increasing overall species richness. As landscapes are modified and altered more intensely by humans, factors influencing how wildlife use their environment can change significantly. Habitat patches become islands and animals use them according to a true checkerboard or more likely, a partial checkerboard. Conservation strategies often are focused on maintaining habitat quality within patches or providing appropriate habitat corridors to aid dispersal throughout the landscape. The landscape context of remnant patch habitat, the intensity at which land is used or the habitat attributes of the matrix may have an effect on wildlife in either a positive or negative way and are often overlooked (Brady et al., 2011). More research needs to be done to understand the checkerboard as a model for resource partitioning, particularly for marsupials. In a landscape highly modified by infrastructure and agriculture, habitat remnants may be utilised by ecologically similar species that in turn may utilise the same patches. Resource use and temporal activity patterns may be partitioned in such a manner to suit a checkerboard model. This research model has the potential for expansion into the landscape to identify whether checkerboards exist in the occurrence of *T. stigmatica* and *T. thetis*, and if so whether the behaviour of NSW populations of *T. stigmatica* without the competitive pressure of *T. thetis* is similar to that of northern Queensland *T. stigmatica* populations.

The increase of macropods at forest edges may also impact negatively on agricultural industries. Many herbivores become ‘pests’ in landscape mosaics because of the optimal combination of high quality available food and water resources in cleared land, accessible forest cover and low levels of predation in surrounding uncleared vegetation (While and McArthur, 2006). As primarily an edge dwelling species, the increase of adjacent forest and agricultural land is attractive habitat for *Thylogale* species however an increase in populations utilising cleared land can result in ‘pest’ status for the genus. Agricultural systems are typically managed to optimise the provisioning of ecosystem services such as food, fuel and fiber, however in the process they also receive a suite of disservices such as herbivory (Zhang et al., 2007). Agricultural systems embedded in a matrix of natural ecosystems present a challenge to manage both the services provided by the agricultural system whilst minimising the disservices caused by wildlife, while simultaneously preserving the natural ecosystems and the services they provide. There is a unique opportunity to manage the landscape as a whole, providing there is sufficient information on the functional diversity of the animals within the natural landscape and how they relate to their surroundings. Further research into the ecology of *T. thetis* and *T. stigmatica* in the landscape are important for their ongoing conservation and management. Camera data collected from both interior and edges of forest fragment will provide insight into habitat use on a landscape level, as well as how extensively edge resources are exploited. Species response to their environment can impact greatly both their ability to distribute in a fragmented landscape and the way they interact with other species in an assembly. Understanding how both species move about the landscape and what size fragments they respond most positively to will enable effective conservation management in conjunction with agricultural management. Conservation efforts must be focused on a specific outcome in order to achieve optimal results.

This, and other related research (Jarman, 1989; Vernes, 1995; Le Mar and Mcarthur, 2005) indicate that *Thylogale* is a generalist within their range, except when co-occurring with other members of *Thylogale* whereby they shift their range to a narrower, more specialised niche. Heterogeneous habitats provide greater fitness benefits and more abundant resources, hence they attract a larger number of species (Tews et al., 2004). Fine scale heterogeneity provides multilayered structure in the vegetation community, providing a higher number of available niches than simpler ecosystems. Rich and complex habitats provide more niche opportunities for a suite of functionally diverse species. This enables highly productive ecosystems to successfully provide effective ecosystem services. Camera data, alongside structural vegetation data, can provide important insights into the needs of not only the focal species, but also the entire mammal community. Measuring structural vegetation allows researchers to look to a small scale and decipher what features are important to various guilds within the mammal community, as well as individual species. Management can then be better focused and directed as it is understood to what disturbance factors animals are most likely to respond. Disturbance can increase the niche selection of tolerant species and cause convergence in community structure, or alternatively, create habitat filtering across the landscape and cause divergence

(Myers et al., 2015). Understanding what fine scale attributes are important to individual species, as well as trophic guilds and entire assemblages helps to implement effect conservation management strategies with specific goals.

Motherland and the adjacent Mount Hyland National Park hold a diverse and well-functioning ecosystem, and preservation is vital. Past logging, grazing and associated burning practices have affected the vegetation and habitat values of some areas (Department of Environment & Climate Change, 2009). According to the Department of Environment, nature reserves are appropriately managed so as to conserve biodiversity and maintain ecosystem functions, conserve features of cultural value, promote public appreciation and understanding of the reserve's natural and cultural values, and provide for appropriate research and monitoring. The area has also been identified as prime habitat for the endangered Hastings River Mouse (*Pseudomys oralis)* and has been proposed as one of ten management sites for species recovery (Department of Environment & Climate Change, 2009). It has also been recognised that several species of threatened macropod live there, three of which were recorded in this study (*T. stigmatica, M. parma* and *P. tridactylus*). When considering the conservation of a species, understanding their habitat preference and niche specialisation is of paramount importance (Vernes, 2003). The interactions of both biotic and abiotic components of a community form a complex web that determines the quality of services output. The complexity of these interactions remain poorly understood, even in simple communities, and it is not yet possible to predict how theses processes and interactions will change under complex and global stressors such as climate change (Mace et al., 2012). This study has highlighted the need for landscape scale studies with fine scale focal points to understand the complexities of these interactions and the influence of fine scale heterogeneity on both individual species as well as whole communities. This enables efficient management of ecosystems with a specific outcome or goal in mind to both preserve existing species and prevent future decline.

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