Habitat preferences of sympatric red-necked (*Thylogale thetis*) and red-legged (*Thylogale stigmatica*) pademelons in temperate eastern Australia

Lucy E. V. Smith [1], **Nigel R. Andrew** [2, 3], **Karl Vernes** [Corresp. 1, 2]

[1] Ecosystem Management, University of New England, Armidale, New South Wales, Australia

[2] Natural History Museum, University of New England, Armidale, New South Wales, Australia

[3] Faculty of Science and Engineering, Southern Cross University, Lismore, New South Wales, Australia

Corresponding Author: Karl Vernes
Email address: kvernes@une.edu.au

Background. We studied habitat preferences of two co-occurring rainforest wallabies, the red-legged pademelon (*Thylogale stigmatica*) and the red-necked pademelon (*T. thetis*) in northeastern New South Wales, Australia. At our study site, both species inhabit closed forest environments and have overlapping distributions, but *T. stigmatica* remains within the forest and browses forest vegetation, while *T. thetis* spends daylight hours in forest but grazes at grassy forest edges at night. The objectives of the study were to investigate how structural attributes of two forest types, wet sclerophyll forest and rainforest, relate to the fine-scale occurrence of these two wallaby species within the forested environment. **Methods.** We gathered occurrence data from 48 camera trap stations divided equally between rainforest and wet sclerophyll forest. At each camera point, we also measured a range of structural habitat variables to determine habitat affiliations for the two *Thylogale* species. **Results.** There was no significant difference in detections of *Thylogale thetis* between vegetation types, but for *T. stigmatica*, significantly more animals were detected in rainforest. Multivariate analysis of fine-scale habitat attributes revealed that *T. thetis* occurrence increased with closeness to roads and grassy edges, and at sites that were less rocky and less steep. *T. stigmatica* occurrence was correlated with the presence of rainforest elements like vines, palms and ferns, more ground-level cover and tree-fall gaps, and at sites with few emergent eucalypts. Our findings have implications for managing these pademelons and their habitats. *T. thetis* is a common species that was encountered more often than *T. stigmatica*, and it responded positively to human disturbance like roadsides and grassy edges, presumably because these areas provided good grazing opportunities. By comparison, *T. stigmatica* is a threatened species, and it responded to natural disturbance like tree-fall gaps where lateral cover was greater, and where rainforest food plants may be more abundant. Our results suggest, therefore, that

conservation of the threatened *T. stigmatica* requires the preservation of tracts of rainforest some distance from anthropogenic edges like clearings and roads.

Habitat preferences of sympatric red-necked (*Thylogale thetis*) and red-legged (*Thylogale stigmatica*) pademelons in temperate eastern Australia.

Lucy E.V. Smith[1]
Nigel R. Andrew[2,3]
Karl Vernes[1,3]

[1]Ecosystem Management, University of New England, Armidale, NSW 2350, Australia
[2] Faculty of Science and Engineering, Southern Cross University, Lismore, NSW 2480, Australia
[3]Natural History Museum, University of New England, Armidale, NSW 2350, Australia

Karl Vernes[1]
[1]Ecosystem Management, University of New England, Armidale, NSW 2350, Australia
Email address: kvernes@une.edu.au

Abstract

Background. We studied habitat preferences of two co-occurring rainforest wallabies, the red-legged pademelon (*Thylogale stigmatica*) and the red-necked pademelon (*T. thetis*) in northeastern New South Wales, Australia. At our study site, both species inhabit closed forest environments and have overlapping distributions, but *T. stigmatica* remains within the forest and browses forest vegetation, while *T. thetis* spends daylight hours in forest but grazes at grassy forest edges at night. The objectives of the study were to investigate how structural attributes of two forest types, wet sclerophyll forest and rainforest, relate to the fine-scale occurrence of these two wallaby species within the forested environment.

Methods. We gathered occurrence data from 48 camera trap stations divided equally between rainforest and wet sclerophyll forest. At each camera point, we also measured a range of structural habitat variables to determine habitat affiliations for the two *Thylogale* species.

Results. There was no significant difference in detections of *Thylogale thetis* between vegetation types, but for *T. stigmatica*, significantly more animals were detected in rainforest. Multivariate analysis of fine-scale habitat attributes revealed that *T. thetis* occurrence increased with closeness to roads and grassy edges, and at sites that were less rocky and less steep. *T. stigmatica* occurrence was correlated with the presence of rainforest elements like vines, palms and ferns, more ground-level cover and tree-fall gaps, and at sites with few emergent eucalypts. Our findings have implications for managing these pademelons and their habitats. *T. thetis* is a common species that was encountered more often than *T. stigmatica*, and it responded positively to human disturbance like roadsides and grassy edges, presumably because these areas provided good grazing opportunities. By comparison, *T. stigmatica* is a threatened species, and it responded to natural disturbance like tree-fall gaps where lateral cover was greater, and where rainforest food plants may be more abundant. Our results suggest, therefore, that conservation of the threatened *T. stigmatica* requires the preservation of tracts of rainforest some distance from anthropogenic edges like clearings and roads.

Introduction

Ecological differences in species that allow for niche partitioning, and therefore coexistence, are manifest in three main ways. Different species may differ in the resources on which they specialise (resource partitioning). They may partition their activity in time (temporal partitioning), and/or they may differ their activity in space (spatial partitioning) (Amarasekare 2003). Habitat heterogeneity plays a key role in species richness and the ability of species with similar resource needs to co-occur, because an increase in the variety and structural complexity of available habitat types and the resources they support increases available niche space and allows more species to coexist (Stein et al. 2014; Tews et al. 2004). Anthropogenic fragmentation can also play a role in shaping competitive interactions because fragmentation can alter habitat structure through edge effects and reduction of the overall amount of original habitat, but it can also create new opportunities for species that are pre-adapted to exploit the

matrix of modified habitats in a fragmented landscape. Habitat fragmentation can therefore change the way closely-related species interact (Valiente-Banuet et al. 2015).

In forested ecosystems, plant communities largely determine the physical structure of the environment, and therefore wield important influence over the structure of animal communities, species richness and the coexistence of species. Vegetation may drive the fine-scale spatial distribution of sympatric species by dictating the availability of resources at multiple scales (Kubiak et al. 2015), both spatial and temporal. For example, Le Mar (2005) showed that sympatric wallabies in Tasmania had similar food requirements and foraged in the same habitats by night, but that their selection of daytime refuges differed markedly, probably due to their contrasting predator avoidance strategies.

Competitive interactions between species can also play an important role in shaping mammalian community assemblages. Competition may manifest in a number of ways, including behavioural changes, shifts in diet, or differential use of preferred habitat in space and time in order to avoid competition and other unfavourable encounters (Karanth et al. 2017). Historical competition between sympatric species may shape their current spatial distribution, resource use, and even phenotypic traits. For example, competitive interactions between sympatric species may lead to character displacement, where species exhibit phenotypic changes that reduce competition along one of more resource axes (Shi et al. 2018). Equally plausible, however, is that differences in resource use relate to evolution pressures developed in isolation before the two species were brought together. Regardless, populations of closely-related species are considered to be sympatric even if they are ecologically distinct, provided a high proportion of each population encounters individuals of the other along adjacent or shared ecotones (Mallet et al. 2009).

The red-legged pademelon (*T. stigmatica*) occurs from Cape York in northern Queensland to the mid north coast of New South Wales, Australia (Johnson & Vernes 2008). In the southernmost part of its range, *T. stigmatica* occurs in sympatry with the red-necked pademelon (*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, spending diurnal hours resting and browsing within the forest interior and nocturnal hours grazing at 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 & Phillips 1989) where it grazes at night on pasture edge close to the forest. When sympatric with *T. thetis, T. stigmatica* consumes only forest browse (Calaby 1966; Jarman & Phillips 1989; Vernes et al. 2006) and in northeastern New South Wales, our recent work has shown that they avoid open grassy areas at the forest edge, remaining in the forest interior (Smith et al. 2022). When sympatric, relative population densities can vary; Johnson (1977) reported *T. stigmatica* to be less abundant than *T. thetis* at an upland site at Dorrigo NSW, but McHugh et al. (2019) found the opposite to be the case in the North Coast Bioregion in far north-eastern New

South Wales. *T. stigmatica* also appears to be less abundant in the south of its range (when in sympatry with *T. thetis*), compared to when it occurs as the sole pademelon species in the north of its range (Vernes et al. 2022). Diet and habitat usage by the different species and sub-species of pademelons in eastern Australia is also borne out in studies of dental morphology; while both *T. thetis* and *T. stigmatica* have a dental morphology suited to browsing (Sanson 1989), differences in cranial morphology point towards *T. thetis* incorporating more grass in the diet than *T. stigmatica* generally, but for the northern sub-species of *T. stigmatica* to graze more than the southern sub-species (Mitchell et al. 2018).

In a recent study, we showed that small changes in temporal activity during daylight hours between the two pademelon species in the forest, and more pronounced habitat partitioning at night when *T. thetis* was grazing outside the forest and *T. stigmatica* was browsing inside the forest meant that these two closely-related species demonstrate strong spatiotemporal niche partitioning (Smith et al. 2022). The objectives of the current study were to investigate how structural attributes of two forest types, wet sclerophyll forest and rainforest, relate to the fine-scale occurrence of *T. stigmatica* and *T. thetis*. The specific aims were to determine what forest types are favoured by each species, which habitat variables affect their spatial distribution, and whether there is evidence of fine-scale habitat partitioning.

Materials & Methods

Description of Study Animals and Study Site

Two forest-dwelling wallabies (*T. stigmatica* and *T. thetis*) were the focal species for this study. Both are medium-sized macropods (*T. stigmatica*: males 3.7 – 6.8kg, females 2.5 – 4.2kg; *T. thetis*: males 2.5 – 9.1kg, females 1.8 – 4.3kg), have a similar overall appearance, and both require rainforest or other closed forest vegetation for shelter and diurnal browsing (Eldridge & Coulson 2015; Johnson & Vernes 2008).

The study took place in the Mount Hyland region of northeastern NSW, Australia, on the eastern slopes of the Great Dividing Range (study site centre: -30.165403°, 152.470407°; elevation range: 900 – 1040m). The mean maximum and minimum temperatures for the area are 20°C and 10°C, respectively (Bureau of Meteorology, 2018). The study area of approximately 400 ha encompasses three major vegetation types: Northern Warm Temperate Rainforest (hereafter 'rainforest'), Northern Hinterland Wet Sclerophyll Forest (hereafter 'wet sclerophyll forest') and an anthropogenic grassy area clear of trees or shrubs, spanning state forest and nature reserve (Figure 1). At the centre of the study area, a private parcel of land, called 'Motherland' (currently in transition to become part of Hyland Nature Reserve), consisted of forest vegetation situated around a large grassy clearing; the southern side of the clearing is predominantly surrounded by wet sclerophyll forest with a rainforest understorey. Rainforest dominates the northern side of the

property and extends into state forests and nature reserve with patches of forest dominated by emergent eucalypts (Figure 1).

Ethics approval for this research was obtained from the University of New England Animal Ethics Committee (Approval No. AEC-1708), and scientific licences for this research were issued by the New South Wales (NSW) Office of Environment and Heritage (Permit Nos. SL101721 and SL101837). While ethical approval specific to human subjects being caught incidentally on camera is not required in NSW, our standard procedure is to immediately delete any images of human subjects. However, as we set camera traps off-trail within a study site accessed via locked gates, no human subjects other than those directly associated with the project were captured.

Camera Trap Placement

We set forty-eight Scoutguard and UOVision white flash cameras in total: 24 were in wet sclerophyll with a rainforest understorey and 24 were in rainforest (Figure 1). Local fire trails allowed access to the forest habitat; these tracks were narrow and maintained an overstorey that limited the growth of non-forest vegetation. To ensure random distribution of cameras throughout the study area, we partitioned access trails into 100m segments, and at the terminus of each segment, we generated a random compass bearing and a random distance between 0 and 300m that dictated where each camera would be placed. Cameras were positioned approximately 0.5m above ground level and were positioned to face south. Small shrubs or leafy branches in the detection zone were pruned to avoid false triggers. Baits were used to prolong investigation of any passing animals and consisted of a porous PVC canister containing a bait of cotton wool soaked with truffle oil which was inaccessible to animals. A bait canister was placed 2m in front of each camera and approximately 80% of the LED flash bulbs on each camera were covered to prevent night photos being 'washed out' by excessive illumination of subjects at close (<2m) range. Camera batteries, memory cards and baits were replaced every 8–12 weeks during deployment that spanned 20 January 2017 to 21 March 2018. A record of an animal at a camera trap was termed an 'independent event' if photos of the same species at a camera were separated temporally by a gap of more than 30 minutes.

Habitat Variables

Habitat variables were assessed at each camera point within a 5m x 5m plot centred on the camera trap (Table 1). The slope of each site was measured using a clinometer. Overstorey was measured using a 'Model C' concave spherical crown densitometer (Forest Densiometers, Rapid City, South Dakota) that estimated cover based on how many of the 24 cells on the densiometer were obscured by vegetation. Four readings were taken (one in each cardinal direction from the plot centre) and a mean value calculated. Sub-canopy foliage cover was measured using an ocular tube at random points around the perimeter of the 5m x 5m plot, with random whole numbers between 1 and 10 used to determine the number of steps between each of the 10

measurement points. At each point, the sub-canopy was viewed through the tube's cross-hairs, and scored as either '1' (cross-hairs intersecting vegetation) or '0' (cross-hairs intersecting open sky). Lateral density was estimated using a 1 x 1-m white sheet positioned on the perimeter of the plot at each of the four cardinal directions. For each measurement, an observer would stand with their back to the centre reference tree while the white grid sheet was held vertically with one edge in contact with the ground. Percentage cover was calculated by counting the number of squares obscured by vegetation. Leaf litter was measured on a 0-3 ranked scoring system according to depth. Vines, palms and ferns were measured on a 0-3 ranked scoring system according to density per square metre. The number of woody stems in two size classes were estimated according to 0-3 ranked scoring system. Trees were classed according to their diameter at breast height then scored according to density. Rockiness of soil was also measured using a 0-3 ranked scoring system. Number of eucalypt emergents and any tree-fall gaps were counted within each plot. Distance to nearest road, forest edge and major water source (permanent creek) were also measured using a map and estimated to the nearest metre. The degree of decay of large logs and other fallen timber was scored according to a 5-point scale outlined by Maser et al. (1979) that used bark characteristics, presence or absence of twigs, wood texture, log shape, wood colour, and portion of log on the ground to estimate the degree of decomposition.

Statistical Analysis

All analyses were undertaken using R (R Core Team, 2020). Principle component analysis (PCA) was undertaken using the package ‘stats’ and visualized using the package ‘ggbiplot’. PCA examines quantitative associations between a group of variables, summarizing them parsimoniously into fewer variables, or ‘components’. We summarised the 17 habitat variables into components that described major trends in habitat. PCA loading scores, determined for each camera location, were used to establish the impact of individual variables on each principle component. Generalised linear modelling was then used to determine the efficacy of each component in predicting the fine-scale habitat preferences of each *Thylogale* species, the latter expressed as the total number of independent detections made of *T. stigmatica* and *T. thetis* at each camera trap.

Results

Structural variation of habitat types

PCA on pooled data between wet sclerophyll forest and rainforest reduced habitat variables into two main principle components that explained 32% of the total variation in vegetation structure (Figure 2). PC1, which explained 17% of the total variance, was correlated negatively with vines, palms, ferns, lateral cover and tree fall gaps, and positively with eucalypt emergents (Table 2). PC2, which explained 15.2% of the total variance, was positively correlated with increasing distance to the nearest road, distance to the grassy forest edge, the number of treefall gaps, increasing slope and increasing rockiness (Table 2). PC3, which explained 10% of total variance,

was positively correlated with decay class of fallen timber, sub-canopy cover, and medium stem density, and negatively correlated with number of emergent eucalypts and density of ground cover (Table 2). Ecologically, PC1 therefore described a transition from rainforest (more palms, vines, ferns and lateral cover) to more sclerophyll dominated forest (e.g., more emergent eucalypts), PC2 described a trend from human disturbance (increasing distance to roads and grassy edges) to more natural disturbance (treefall gaps), and PC3 appeared to describe a trend in historical rainforest disturbance (perhaps from logging), where fallen timber in the plot was heavily decayed, medium stems density was high, and there was dense sub-canopy cover.

Habitat Correlates of T. thetis *Occurrence*

Most cameras returned between 1–10 independent events for *T. thetis*, however, more than 80 independent events were recorded at seven cameras, with three of those returning more than 121 independent events. *T. thetis* occurred in both forest types, with no significant different between the number of independent events at cameras located in rainforest or wet sclerophyll forest (Figure 3). At a finer scale, the occurrence of *T thetis* was significantly negatively correlated with PC2 ($t = -2.454$; $P = 0.02$) suggesting that *T. thetis* favoured forest near roads and grassy edges, with few treefall gaps.

Habitat Correlates of T. stigmatica *Occurrence*

Cameras at a majority of the 48 sites detected between 1–10 independent events of *T. stigmatica*, with only three sites recording more than 60 independent detection events. Fifteen sites returned zero *T. stigmatica* detections. The number of independent detections of *T. stigmatica* was significantly higher at cameras located in rainforest compared with wet sclerophyll forest (Figure 3). At a finer scale, independent detections of *T. stigmatica* were negatively correlated with PC1 ($t = -2.599$; $P = 0.01$), suggesting that deep rainforest far from roads and edges, but with natural treefall gaps and dense lateral cover was preferred by *T. stigmatica*.

Discussion

Sympatric *T. thetis* and *T. stigmatica* at our study site showed specific preferences for certain combinations of habitat variables that indicated a degree of habitat partitioning. *T. thetis* showed no detectable preference for rainforest or wet sclerophyll forest but did prefer locations close to grassy forest edges and forest tracks. This result is easily interpretable in light of the preference of *T. thetis* for the abundant grassy resources found at forest edges (Johnson 1980); by contrast, *T. stigmatica* at our study site stayed within the forest and previous work showed that it did not venture onto pasture (Smith et al. 2022). *T. stigmatica* showed a clear preference for rainforest habitat, with specific affiliation for vines, palms and ferns, and for sites with treefall gaps where vegetation at ground level was dense.

Pademelons and many other small mammals rely on crypsis in dense vegetation for cover from predator attack, particularly during the daylight hours (Le Mar & Mcarthur 2005). Unlike other small macropods, *T. stigmatica* are active throughout much of the day and can move extensively throughout the forested parts of their range in daylight hours (Vernes et al. 1995) in search of favoured rainforest browse (Vernes 1995). Multilayered dense ground-layer rainforest vegetation would help to obscure *T. stigmatica* from predators, but would also offer them feeding opportunities for known food plants that include vines and ferns (Vernes 1994). Treefall gaps would similarly offer browsing pademelons a diversity of pioneer species that thrive in high light conditions created by a treefall.

Small terrestrial mammals tend have lower mobility and therefore restricted home ranges. They will perceive their environments at a fine 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 upper 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 location via known escape routes. *T. stigmatica* may frequent sites with these qualities more often due to the fitness benefits provided at a fine scale, such as cover from predators like wild dogs (*Canis familairis*) that are known to hunt pademelons (Vernes 2000).

Thylogale thetis were detected in greater numbers than *T. stigmatica*, however, they showed no preference for one forest type over another. Rather, detections of *T. thetis* were associated with disturbance attributes like edges and roads, where grasses grow in the greatest abundance. This is consistent with previous findings that *T. thetis* exploit forest-pasture boundaries (Jarman 1989; Johnson 1980; Wahungu et al. 1999) and our related study (Smith et al. 2022) that showed *T. thetis* was strongly crepuscular, with periods of heightened activity corresponding with foraging excursions to and from the forest 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). Our findings are consistent with earlier research that showed *T. stigmatica* does not venture past the forest edge when in sympatry with *T. thetis* (Jarman 1989); by comparison, *T. thetis* makes regular foraging excursions beyond the edges into the adjacent pasture (Smith et al. 2022). Fragmentation increases the amount of edge to interior forest and significantly alters habitat at fragment edges (Laurance et al. 2002). It stands to reason, therefore, that *T. thetis* should occur at greater density than *T. stigmatica* at our study site because the site had a large grassy clearing at its centre, and roads and tracks that bisected the site, some of which offered grassy edges. Rather than associating with ubiquitous anthropogenic edges like roads and clearings, *T. stigmatica* may

instead associate with tree-fall gaps that offer browsing opportunities for rainforest pioneer species away from grassy clearings.

When considering the conservation of species, understanding of habitat preference and niche utilisation is of obvious and paramount importance (Vernes 2003). Competition avoidance in the form of altered use of space and temporal activity are likely employed by pademelons at our study site to facilitate co-occurrence. For example, *T. stigmatica* were detected on some cameras that were deployed very close to the forest edge, indicating that despite an apparent lesser association with disturbance and edge effects, *T. stigmatica* still utilized forest habitat all the way to the forest edge. However, cameras in the adjacent grassy clearing (see Smith et al. 2022) did not detect a single *T. stigmatica* event, suggesting that *T. stigmatica* do not venture past the forest edge to graze pasture. Increased light penetration at forest edges can encourage an enriched understorey and a higher abundance of ground cover, which may at times attract *T. stigmatica* to edge-affected forest, however, competition with *T. thetis* probably excludes them from the 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). Research on temporal activity of pademelons at our study site (Smith et al. 2022) also indicated some temporal partitioning between the species, suggesting that the two species are ecologically similar and subject to competitive interactions.

Prior to anthropogenic fragmentation of their habitat, pademelons (*Thylogale* spp.) are thought to have been edge-dwelling generalist species that exploited both rainforest browse and grasses in forested ecotones (Vernes 1995; Vernes et al. 1995). However, when sympatric with other forest-dwelling macropods, competition may force some species to narrow their niche breadth. In northern Australia, *T. stigmatica* occurs as the sole pademelon species, and there, habitat use and diet is very differently from that seen in southern populations where *T. stigmatica* occurs in sympatry with *T. thetis.* These differences are also reflected in their cranial morphology; Mitchell et al. (2018) found that the southern subspecies of *T. stigmatica* (*Thylogale stigmatica wilcoxi*) had a broader cranium and a shorter and more robust muzzle – typical of browsing species, while the northern subspecies (*Thylogale stigmatica stigmatica*) possessed a more slender skull with a longer muzzle, a characteristic shared with *T. thetis* and that is commonly seen in grazing macropods. Direct competition for edge resources may have forced sympatric populations of *T. stigmatica* into a narrower niche and also driven their population density below what might be achieved in the absence of competition; our related work (Smith et al. 2022; Vernes et al. 2022) indicated that *T. stigmatica* occur at lower population densities when in sympatry with *T. thetis* than when they occur in isolation from them. Thus, when constrained within a narrower, more specialised niche, population density of *T. stigmatica* may be reduced.

Species that have adapted to forest edges benefit from 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). Continued disturbance of rainforest may not therefore negatively affect *T. thetis* into the future, however numbers of *T. stigmatica* may decline in those populations sympatric with *T. thetis* if fragmentation and other anthropogenic disturbances were to increase. Further research into the habitat selection, diet and niche specialisation in southern populations of *T. stigmatica* is therefore important for understanding their ecology and to help ensure their continued persistence. Protection of large tracts of rainforest where edge effects are minimized would clearly be advantageous for the conservation of *T. stigmatica* in the southern temperate parts of their range.

Conclusions

The objectives of the current study were to investigate how structural attributes of two forest types, wet sclerophyll forest and rainforest, relate to the fine-scale occurrence of *T. thetis* and *T. stigmatica*. We found that *T. thetis* showed no preference for broad forest type, but at a finer scale, preferred locations close to grassy forest edges and forest tracks where grasses were abundant. By comparison, *T. stigmatica* showed a preference for rainforest habitat, with fine-scale affiliation for sites where vegetation at ground level was dense, including sites near tree-fall gaps. Our results suggest that the threatened *T. stigmatica* requires tracts of undisturbed and unfragmented rainforest with fewer anthropogenic edges or incursions like roads. However, more research at a landscape scale in a range of landscape settings is needed to expand on these results.

Acknowledgements

We are grateful to Rosemary Yates for her hospitality and access to her property ‘Motherland’ to enable this research to take place. We extend our thanks to Andrew Robertson, Peter Smith and Tim Henderson for their assistance in fieldwork and data collection. Thanks also to Rose Andrew who gave advice on some statistical analyses.

References

Amarasekare P. 2003. Competitive coexistence in spatially structured environments: a synthesis. *Ecology Letters* 6:1109-1122. 10.1046/j.1461-0248.2003.00530.x

Calaby JH. 1966. Mammals of the upper Richmond and Clarence Rivers, New South Wales. Division of Wildlife Research Technical Paper No 10. Melbourne.

Eldridge MDB, and Coulson GM. 2015. Family Macropodidae (Kangaroos and Wallabies). In: Wilson DE, and Mittermeier RA, eds. *Handbook of The Mammals of the World*: Lynx Edicions, 630-735.

Harrington GN, Freeman AND, and Crome FHJ. 2001. The Effects of Fragmentation of an Australian Tropical Rain Forest on Populations and Assemblages of Small Mammals. *Journal of Tropical Ecology* 17:225-240.

Jarman PJ. 1991. Social behavior and organization in the Macropodoidea. *Advances in the Study of Behavior* 20:1-50.

Jarman PJ, and Phillips CM. 1989. Diets in a community of macropod species. In: Grigg G, Jarman P, and Hume ID, eds. *Kangaroos, Wallabies and Rat Kangaroos*. Sydney: Surrey Beatty and Sons, 143–[illegible].

Jarman PJP, C.M. 1989. Diets in a community of macropod species. In: Grigg G, Jarman, P., Hume, I, ed. *Kangaroos, Wallabies and Rat Kangaroos*. Surrey: Beatty and Sons, 14[illegible]9.

Johnson K. 1977. Ecology and management of the red-necked pademelon PhD. [illegible]versity of New England.

Johnson K. 1980. Spatial and Temporal Use of Habitat by the Red-necked Pademelon, *Thylogale thetis* (Marsupialia : Macropodidae). *Wildlife Research* 7:157-166. https://doi.org/10.1071/WR9800157

Johnson P, and Vernes K. 2008. Red-legged pademelon *Thylogale stigmatica*. In: Van Dyck SM, ed. *The Mammals of Australia*. Sydney: New Holland, 397–400

Kanowski J, Hopkins MS, Marsh H, and Winter JW. 2001. Ecological correlates of folivore abundance in north Queensland rainforests. *Wildlife Research* 28:1-8. https://doi.org/10.1071/WR99098

Karanth KU, Srivathsa A, Vasudev D, Puri M, Parameshwaran R, and Kumar NS. 2017. Spatio-temporal interactions facilitate large carnivore sympatry across a resource gradient. *Proceedings of the Royal Society B: Biological Sciences* 284. 10.1098/rspb.2016.1860

Kubiak BB, Galiano D, and de Freitas TRO. 2015. Sharing the space: distribution, habitat segregation and delimitation of a new sympatric area of subterranean rodents. *PLoS ONE* 10:e0123220.

Laurance WF, Lovejoy TE, Vasconcelos HL, Bruna EM, Didham RK, Stouffer PC, Gascon C, Bierregaard RO, Laurance SG, and Sampaio E. 2002. Ecosystem Decay of Amazonian Forest Fragments: a 22-Year Investigation. *Conservation Biology* 16:605-618. doi:10.1046/j.1523-1739.2002.01025.x

Le Mar K, and Mcarthur C. 2005. Comparison of habitat selection by two sympatric macropods, *Thylogale billardierii* and *Macropus rufogriseus rufogriseus*, in a patchy eucalypt-forestry environment. *Austral Ecology* 30:674-683.

Mallet J, Meyer A, Nosil P, and Feder JL. 2009. Space, sympatry and speciation. *Journal of Evolutionary Biology* 22:2332-2341. doi:10.1111/j.1420-9101.2009.01816.x

Maser CR, Anderson K, Cromack JR, Williams JT, and Martin RE. 1979. Dead and down woody material. . In: Thomas JW, ed. *Wildlife Habitats in Managed Forests, the Blue Mountains of Oregon and Washington*. Washington, D.C.: United States Department of Agriculture.

McHugh D, Goldingay RL, Link J, and Letnic M. 2019. Habitat and introduced predators influence the occupancy of small threatened macropods in subtropical Australia. *Ecology and Evolution* 9:6300-6317. 10.1002/ece3.5203

Mitchell DR, Sherratt E, Sansalone G, Ledogar JA, Flavel RJ, and Wroe S. 2018. Feeding biomechanics Influences craniofacial morphology at the subspecies scale am[illegible] Australian pademelons (Macropodidae: *Thylogale*). *Journal of Mammalian Evolution*.1-11.

Sanson GD. 1989. Morphological adaptations of teeth to diets and feeding in the Macropodoidea. In: Grigg G, Jarman P, and Hume ID, eds. *Kangaroos, Wallabies and Rat Kangaroos*. Sydney: Surrey Beatty and Sons, 151-168.

Shi JJ, Westeen EP, Katlein NT, Dumont ER, and Rabosky DL. 2018. Ecomorphological and phylogenetic controls on sympatry across extant bats. *Journal of Biogeography* 45:1560-1570. doi:10.1111/jbi.13353

Smith LEV, Andrew NR, and Vernes K. 2022. Activity patterns and temporal niche partitioning in sympatric red-legged and red-necked pademelons. *Austral Ecology* 47:557-566. 10.1111/aec.13135

Stein A, Gerstner K, and Kreft H. 2014. Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. *Ecology Letters* 17:866-880. 10.1111/ele.12277

Stirnemann I, Mortelliti A, Gibbons P, and Lindenmayer DB. 2015. Fine-scale habitat heterogeneity influences occupancy in terrestrial mammals in a temperate region of Australia. *PLoS ONE* 10:e0138681.

Strahan R. 1980. Kangaroos and wallabies. In: Strahan R, ed. *The Australian Museum Complete Book of Australian Mammals*. Sydney: Angus and Robertson, 225.

Tews J, Brose U, Grimm V, Tielbörger K, Wichmann M, Schwager M, and Jeltsch F. 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of biogeography* 31:79-92.

Turton S. 1997. Edge and aspect effects on the microclimate of a small tropical forest remnant on the Atherton Tableland, Northeastern Australia. *Tropical forest remnants Ecology, management, and conservation of fragmented communities*.

Valiente-Banuet A, Aizen MA, Alcántara JM, Arroyo J, Cocucci A, Galetti M, García MB, García D, Gómez JM, and Jordano P. 2015. Beyond species loss: the extinction of ecological interactions in a changing world. *Functional Ecology* 29:299-307.

Vernes K. 1994. Life on the edge: the ecology of the red-legged pademelon *Thylogale stigmatica* (Gould) (Marsupialia : Macropodidae) in fragmented rainforest in the north Queensland wet tropics. Master of Scienc[illegible]mes Cook University.

Vernes K. 1995. The diet of the red-legged pademelon *Thylogale stigmatica* (Gould) (Marsupialia: Macropodidae) in fragmented tropical rainforest, north Queensland, Australia. *Mammalia* 59:517-525. 10.1515/mamm.1995.59.4.517

Vernes K. 2000. Immediate effects of fire on survivorship of the northern bettong (*Bettongia tropica*): an endangered Australian marsupial. *Biological Conservation* 96:305-309. 10.1016/S0006-3207(00)00086-0

Vernes K. 2003. Fine-scale habitat preferences and habitat partitioning by three mycophagous mammals in tropical wet sclerophyll forest, north-eastern Australia. *Austral Ecology* 28:471-479. doi:10.1046/j.1442-9993.2003.01303.x

Vernes K, Elliott TF, and Elliott K. 2022. Activity patterns and detection rates of red-legged pademelons (*Thylogale stigmatica*) in tropical north Queensland and temperate north-eastern New South Wales. *Australian Mammalogy* 44:295-298. 10.1071/Am21021

Vernes K, Green S, Howes A, and Dunn L. 2006. Species richness and habitat associations of non-flying mammals in Gibraltar Range National Park. *Proceedings of the Linnean Society of New South Wales* 127:93-105.

Vernes K, Marsh H, and Winter J. 1995. Home-range characteristics and movement patterns of the red-legged pademelon (*Thylogale stigmatica*) in a fragmented tropical rainforest. *Wildlife Research* 22:699–707. https://doi.org/10.1071/WR9950699

Wahungu GM, Catterall CP, and Olsen MF. 1999. Selective herbivory by red-necked pademelon *Thylogale thetis* at rainforest margins: factors affecting predation rates. *Australian Journal of Ecology* 24:577-586. doi:10.1046/j.1442-9993.1999.01005.x

464

Figure Legends

Figure 1. The study area in northeastern NSW, showing patterns in vegetation types across different land tenures (Mount Hyland Nature Reserve, Chaelundi State Forest, Ellis State Forest and 'Motherland'; NSW Office of Environment and Heritage, 2013). Dark green = rainforest, light green = wet sclerophyll forest, white = grassy clearing. White triangles show position of the 48 cameras that were deployed in rainforest and wet sclerophyll forest.

Figure 2: Box and whisker plot of mean encounter rate (independent events/camera) of (a) red-necked pademelons (*Thylogale thetis*) and (b) red-legged pademelons (*T. stigmatica*) at cameras located in rainforest or wet sclerophyll forest. Boxes show the first to the third quartile, whiskers show the range, black horizontal lines show the median, and closed circles show the mean.

Figure 3: Principal component analysis (PCA) of habitat data based upon variables assessed at each camera trap location. The components (PC1 and PC2) were extracted from an original dataset comprising 17 biotic and landform variables that were chosen to reflect fine-scale habitat differences across the study area. Ellipses represent 95% confidence level for a multivariate t-distribution.

Figure 1

The study area in northeastern NSW, showing patterns in vegetation types across different land tenures (Mount Hyland Nature Reserve, Chaelundi State Forest, Ellis State Forest and ‘Motherland’; NSW Office of Environment and Heritage, 2013).

Dark green = rainforest, light green = wet sclerophyll forest, white = grassy clearing. White triangles show position of the 48 cameras that were deployed in rainforest and wet sclerophyll forest.

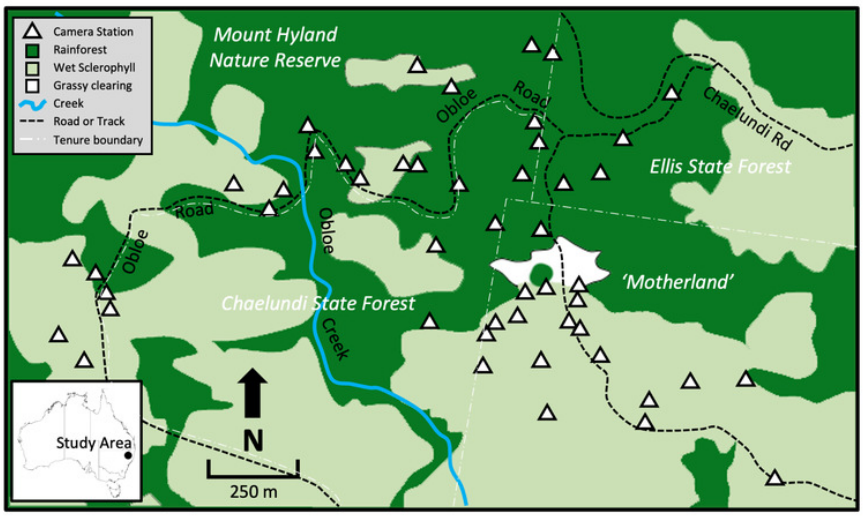
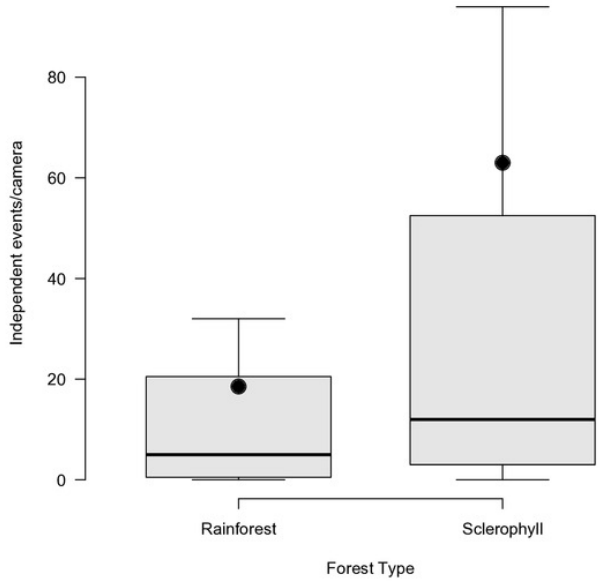

Camera Station
Rainforest
Wet Sclerophyll
Grassy clearing
Creek
Road or Track
Tenure boundary
Mount Hyland
Nature Reserve
Oblee
Road
Chaelundi Rd
Ellis State Forest
Road
Oblee
Oblee
'Motherland'
Chaelundi State Forest
Creek
Study Area
N
250 m

Figure 2

Box and whisker plot of mean encounter rate (independent events/camera) of (a) red-necked pademelons (*Thylogale thetis*) and (b) red-legged pademelons (*T. stigmatica*) at cameras located in rainforest or wet sclerophyll forest.

Boxes show the first to the third quartile, whiskers show the range, black horizontal lines show the median, and closed circles show the mean.

(a)


Independent events/camera
0
20
40
60
80
Rainforest
Sclerophyll
Forest Type

(b)

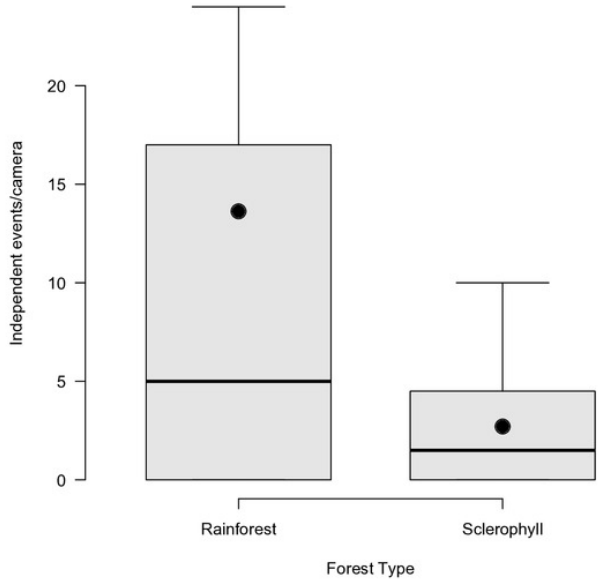

Independent events/camera
0
5
10
15
20
Rainforest
Sclerophyll
Forest Type

Figure 3

Principal component analysis (PCA) of habitat data from 17 biotic and landform variables assessed at each camera trap location that were chosen to reflect fine-scale habitat differences across the study area.

Ellipses represent 95% confidence level for a multivariate t-distribution.

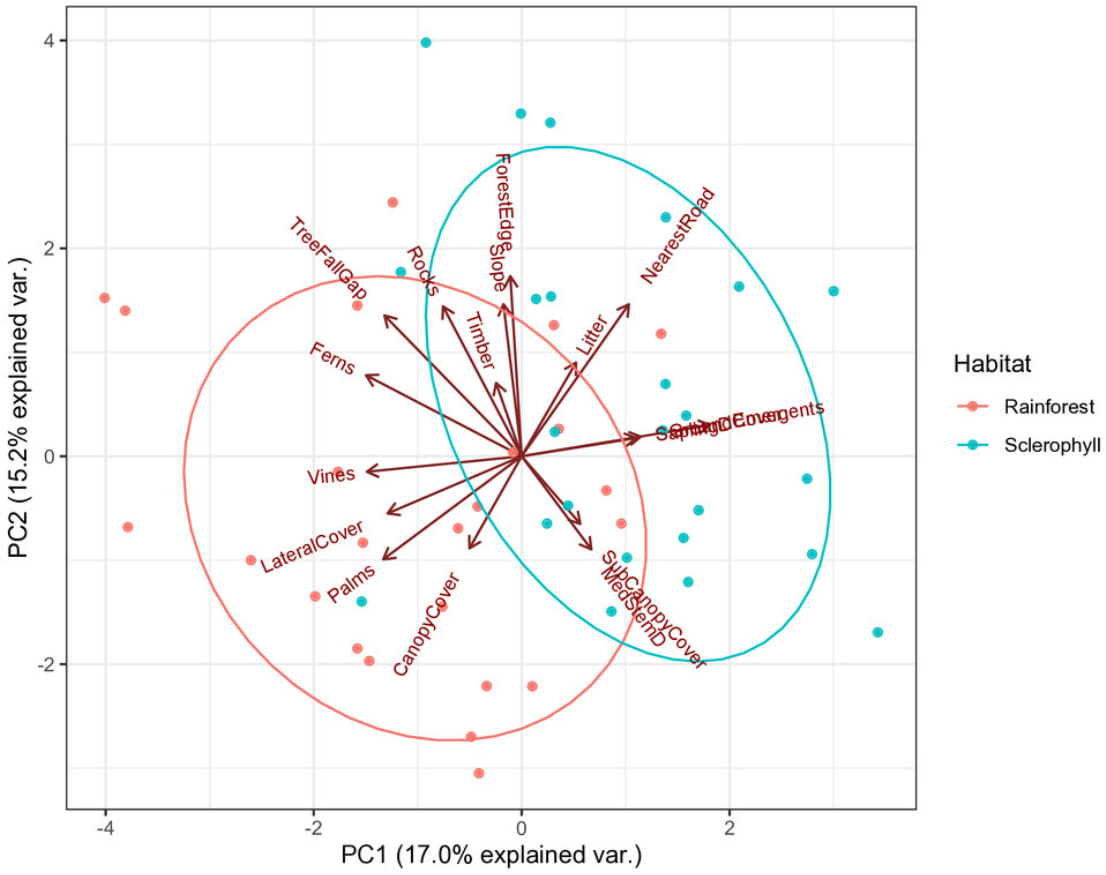

PC2 (15.2% explained var.)
PC1 (17.0% explained var.)
4
2
0
-2
-4
-2
0
2
TreeFallGap
Rocks
ForestEdge
Slope
NearestRoad
Timber
Litter
Ferns
Vines
LateralCover
Palms
CanopyCover
SubCanopyCover
MedStemD
Habitat
Rainforest
Sclerophyll

Table 1(on next page)

Vegetation and landform attributes assessed at each camera site in rainforest and wet sclerophyll forest at Mt Hyland, NSW.

1 Table 1: Vegetation and landform attributes assessed at each camera site in rainforest and wet
2 sclerophyll forest at Mt Hyland, NSW.

Measurement	Unit or Score	Description
Leaf litter depth	0 – 3	0: absent, 1: < 5cm, 2: 5–10cm; 3: >10cm
Vines, Palms, Ferns	0 – 3	0: absent, 1: <3 per m^2, 2: 3-5 per m^2; 3: >5 per m^2 (for each)
Rockiness of soil	0 – 3	0: absent, 1: <3 per m^2, 2: 3-5 per m^2, 3: >5 per m^2
Fallen Timber	0 – 4	see Maser et al. (1979)
Ground Cover	0 – 4	0: absent, 1: 1–25%, 2: 26–50%, 3: 51–75%; 4: > 75%
Lateral cover	%	% of 1x1m white grid obscured by 0-1m high vegetation at a distance of 5 m
Canopy cover	%	Estimated using convex spherical densiometer
Sub-canopy cover	%	calculated from 10 presence/absence random measurements using ocular tube
Small stem density (>10cm dbh)	0 – 3	0: absent, 1: <3, 2: 3-5; 3: >5
Medium stem density (10-30cm dbh)	0 – 3	As for small stem density
Slope		Evaluated using clinometer
Tree fall gaps	No. of gaps	in entire plot
Eucalypt emergent	No. of emergent	in entire plot
Distance to Nearest Road	m	Linear distance
Distance to edge	m	Linear distance

3

4

Table 2(on next page)

Spearman rank correlation coefficients indicating the relationship of each of the 17 trap location attributes to the first three principal components (PC) analysis axes.

Negative (–) and positive (+) relationships are indicated for each, with asterixes (*) indicating level of significance.

Table 2: Spearman rank correlation coefficients indicating the relationship of each of the 17 trap location attributes to the first three principal components (PC) analysis axes. Negative (–) and positive (+) relationships are indicated for each, with asterixis (*) indicating level of significance.

Measurement	PC1	PC2	PC3
Leaf litter depth			
Vines	* (–)		
Palms	* (–)		
Ferns	* (–)		
Rockiness of soil		* (+)	
Fallen Timber			** (+)
Ground Cover			* (–)
Lateral cover	* (–)		
Canopy cover			
Sub-canopy cover			* (+)
Small stem density			
Medium stem density			** (+)
Slope		* (+)	
Tree fall gaps	* (–)	* (+)	
Eucalypt emergent	** (+)		* (–)
Distance to Nearest Road		* (+)	
Distance to edge		** (+)	

* $P < 0.05$; ** $P < 0.01$