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Impacts of habitat fragmentation on microbats across an urban-rural landscape

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Abstract

It is well known that deforestation and habitat fragmentation, due to agriculture and urbanisation, modifies bat assemblages. Specifically, it has been found that bat diversity, abundance and foraging activity decrease as urban density increases and cover of remnant vegetation diminishes, although such effects are dependent upon functional identity of bat species. In many cases, remnant patches of vegetation are dispersed across complex, heterogeneous landscapes, whereby the landscape matrix is comprised of a complex suite of urban and agricultural habitats. Studies on other taxa, such as birds and invertebrates, have found that the configuration of the matrix often has a similar or greater influence on diversity within vegetation remnants than patch-scale attributes. However, the relative importance of patch and matrix characteristics on the diversity and activity of mammalian species in vegetation remnants is unknown. The objective of this study was to investigate the influence of habitat fragmentation on microbat diversity - specifically, 1) the variation in microbat assemblages across a modified woodland landscape and 2) the effects of landscape matrix on diversity and activity of microbats within woodlands remnants. A total of 47 sites were chosen for sampling between January and April of 2015, including woodlands of varying sizes, urban areas and agricultural land. Anabat II detectors were used to record foraging and non-foraging microbat activity. Microbat activity was not influenced by habitat fragmentation, yet the number of species was greatest in larger woodlands and agricultural areas. Small woodlands were found to house the least amount of species. It is likely that roosting and foraging resources were minimal in these woodlands. Urban density exceeding 55 % in the matrix surrounding a woodland patch adversely affected microbat diversity. Clutter-adapted species may have been deterred from visiting woodlands surrounded by high urban density due to light and noise pollution, or limited foraging resources. This arguably is the first study to examine the impact matrix condition has on microbat activity and diversity within fragmented woodland patches.

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Impacts of habitat fragmentation on microbats across an urban-rural landscape

By

Gemma L. Hopkins

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The information in this thesis is entirely the result of investigations conducted by the author, unless otherwise acknowledged, and has not been submitted in part, or otherwise, for any other degree or qualification.

Signed:

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Title page image

Chalinolobus morio, or Chocolate wattled bat, obtained from cavesaustralia.com.

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Abstract

It is well known that deforestation and habitat fragmentation, due to agriculture and urbanisation, modifies bat assemblages. Specifically, it has been found that bat diversity, abundance and foraging activity decrease as urban density increases and cover of remnant vegetation diminishes, although such effects are dependent upon functional identity of bat species. In many cases, remnant patches of vegetation are dispersed across complex, heterogeneous landscapes, whereby the landscape matrix is comprised of a complex suite of urban and agricultural habitats. Studies on other taxa, such as birds and invertebrates, have found that the configuration of the matrix often has a similar or greater influence on diversity within vegetation remnants than patch-scale attributes. However, the relative importance of patch and matrix characteristics on the diversity and activity of mammalian species in vegetation remnants is unknown. The objective of this study was to investigate the influence of habitat fragmentation on microbat diversity - specifically, 1) the variation in microbat assemblages across a modified woodland landscape and 2) the effects of landscape matrix on diversity and activity of microbats within woodlands remnants. A total of 47 sites were chosen for sampling between January and April of 2015, including woodlands of varying sizes, urban areas and agricultural land. Anabat II detectors were used to record foraging and non-foraging microbat activity. Microbat activity was not influenced by habitat fragmentation, yet the number of species was greatest in larger woodlands and agricultural areas. Small woodlands were found to house the least amount of species. It is likely that roosting and foraging resources were minimal in these woodlands. Urban density exceeding 55 % in the matrix surrounding a woodland patch adversely affected microbat diversity. Clutter-adapted species may

have been deterred from visiting woodlands surrounded by high urban density due to light and noise pollution, or limited foraging resources. This arguably is the first study to examine the impact matrix condition has on microbat activity and diversity within fragmented woodland patches.

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1.1.1. An overview of effects of habitat fragmentation on biodiversity

Habitat fragmentation is a form of anthropogenic landscape disturbance, whereby extensive, intact, continuous swathes of native vegetation are gradually broken up into small, isolated, discontinuous patches of vegetation (Fahrig, 2003). This process typically occurs as a result of expanding human activities, such as urbanisation and agriculture (Andren, 1994, Fahrig, 2003). This process frequently results in landscapes dominated by homogeneous human habitats that are depleted of native vegetation and fauna; for example, expansive swathes of cattle-grazed pasture, often dominated by one of very few non-native grasses, throughout which very small, degraded and disconnected remnant patches of native forest are distributed (Heinken and Weber, 2013, Ramalho *et al.*, 2014). Habitat fragmentation differs from habitat loss, in that, additionally to the loss of a habitat, the shrinking and isolation of patches can manipulate the composition of the remaining habitat (Fahrig, 2003). Recent reviews have found that as the level of fragmentation of a landscape increases, the following factors are reduced: spatial extent and level of connectivity of native vegetation (Heinken and Weber, 2013); increase in level of human disturbances, such as fire, logging and predation, within the remnant patches of vegetation (Porensky and Young, 2013); functionality of vital ecosystem processes, such as pollination and nutrient cycling (Brudvig *et al.*, 2015, Cho *et al.*, 2013, Van der Walt *et al.*, 2015).
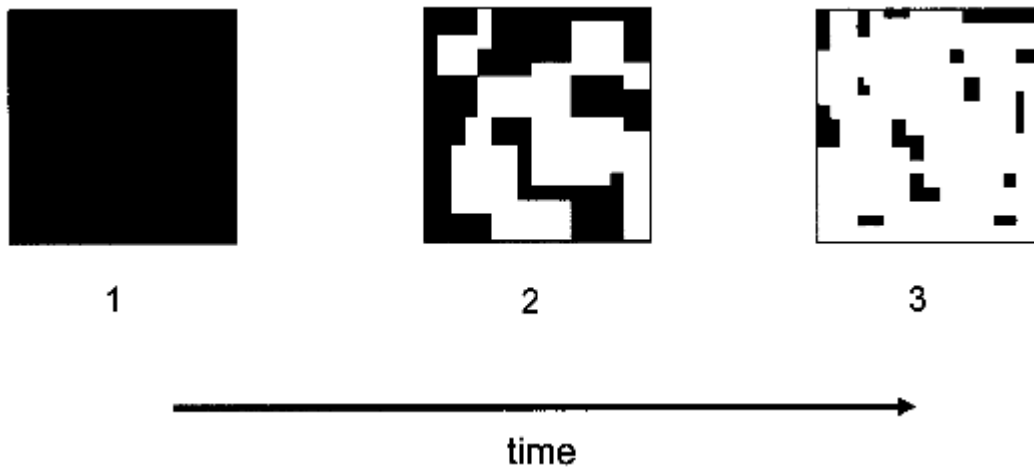
Figure 1: Habitat fragmentation transition from a large habitat (1), to the separation into smaller patches (2) and finally the isolation of small patches and dominance of matrix. Black regions represent habitat, while white areas denote matrix (Fahrig, 2003).

It is well-recognised that habitat fragmentation and landscape modification are the leading causes of biodiversity decline globally (Krauss *et al.*, 2010, Mantyka-pringle *et al.*, 2012, Ramalho *et al.*, 2014). Leigh and Briggs (1992) found that fragmentation in south eastern Australia due to grazing and agriculture, as well as industry and urban development, has resulted in the decline in biodiversity within a large number of flora communities. In 1992, a total of 81 species had become extinct due to human modification, while 131 species were presently endangered or on the brink of becoming endangered in the future (Groves and Willis, 1999, Leigh and Briggs, 1992). Drinnan (2005) discovered that fragmentation in Sydney suburbs had detrimental effects on biodiversity. Frog and bird species diversity declined by approximately 70 %, while plant richness decreased by 50 %, in response to decreasing size of remnant patches of vegetation (Drinnan, 2005).

Fragmentation also results in a disruption of interactions amongst native species, many of which are vital for the healthy functioning of the ecosystem (Magrach *et al.*, 2014). For example, fragmentation has been shown to have the greatest adverse effects on plant species that require interactions with other members of the ecosystem for their persistence; these include epiphytes, parasitic plants and those which require pollinators for successful reproduction (Sodhi *et al.*, 2010). Further studies have shown that fragmentation reduces the strength of mutualistic exchanges between plants and soil fungi, which results in a decline in plant populations (Johnson *et al.*, 2013, Magrach *et al.*, 2014, Sodhi *et al.*, 2010). Additionally, due to dependence on lower trophic levels and generally slower rates of reproduction an growth, species from higher trophic levels, including birds and large carnivores, are more susceptible to habitat fragmentation than fast-growing species from lower trophic levels (Komonen *et al.*, 2000, Krauss *et al.*, 2010).

1.1.2. Mechanisms by which fragmentation impacts native biodiversity: role of patch size, connectivity and edge effects.

The effects of remnant vegetation patch size on biodiversity of resident species have received considerable research attention over the past few decades (Burkey, 1989, Cagnolo *et al.*, 2009, Collingham and Huntley, 2000). It has been widely shown for a variety of biomes, ecosystems and taxa that the number of species that reside within remnant patches of vegetation decreases significantly as habitat patch size declines (Cagnolo *et al.*, 2009, Debinski and Holt, 2000, Devictor *et al.*, 2008). Decreasing habitat size has been found to dramatically reduce the abundance of rare species, which frequently decline at a much faster rate than common species (Cagnolo *et al.*, 2009). Rare species are usually specialists, in that they are restricted

to a certain habitat and are unable to branch out into heterogeneous landscapes (Devictor *et al.*, 2008). The decline of some species is due to their inability to switch to alternative resources, such as prey or shelter, when these resources are reduced within small fragments (Cagnolo *et al.*, 2009, Debinski and Holt, 2000).

The most intensive forms of fragmentation create isolated patches of remnant habitats. This limits the connectivity of native species across the landscape, as movement between patches may be limited in situations where the matrix is hostile territory for migrating species (Tigas *et al.*, 2002). Highly mobile taxa, such as birds, which often need to move across large distances to find mates, forage for food or form territories, may suffer declines if they are unable to adapt to moving across the disturbed matrix (Uezu *et al.*, 2005). Habitat isolation can ultimately result in fragmented populations that are poorly connected and have reduced genetic diversity. Indeed, it has been shown that with increasing isolation of patches there is an increase in genetic drift, inbreeding depression and, ultimately, localised population extinction (Dixo *et al.*, 2009). Since adaptive capacity is related to genetic diversity in many species, a decline in a species' genetic connectivity across isolated populations can make it vulnerable to new predators, parasites, diseases and long-term environmental changes (Lacy, 1987, Eszterbauer *et al.*, 2015, Serieys *et al.*, 2015).

In some cases, poor connectivity between remnant patches of vegetation can be mitigated through construction of wildlife corridors. Corridors commonly promote movement between disturbed patches, allowing individuals to seek more food and shelter resources, as well as enhance genetic diversity (Claridge and Lindenmayer, 1994, Croteau, 2010). However, these corridors are not effective for sessile or more sedentary species (Claridge and Lindenmayer, 1994, Croteau, 2010). These species

commonly rely on patches being within close proximity to each other, due to limited capacities for dispersal. Migration rates of organisms are highly dependent on distance between patches of suitable habitat availability, thus smaller patches reduce the rate at which an individual or populations are able to spread through heterogeneous, fragmented landscapes (Collingham and Huntley, 2000). While it is clear that ecological corridors assist migration across landscapes, species most benefitting from such corridors are highly mobile. For species that are sessile or more sedentary, size of habitat fragments is the leading determinant of migration success. Corridors may not provide the required amount of resources necessary for species unable to commute long distances for foraging or shelter purposes (Burkey, 1989, Collingham and Huntley, 2000). Large patches of fragmented habitats with minimal isolation can act as 'stepping stones' for migration, which reduces the risk of local extinctions in disturbed landscapes (Burkey, 1989, Collingham and Huntley, 2000).

Patches of remnant vegetation do not exist in isolation from the surrounding matrix, because many disturbances that occur in the matrix may intrude across habitat boundaries and into the remnant native vegetation. This is known as the 'edge effect', where the composition of the matrix ecosystem can modify the condition of a remnant habitat (Gascon *et al.*, 1999, Murcia, 1995). Some classic examples include the diffusion of nutrients, such as nitrogen and phosphorous, from intensively-managed farmland into remnant vegetation, or the spread of invasive plats or predatory vertebrates from urban areas into remnant habitats (Alston and Richardson, 2006, Treseder, 2004). Invasive species readily colonise human-disturbed landscapes (Gascon *et al.*, 1999), and have been shown to readily move from the matrix into edges of isolated remnants of native vegetation (Alston and Richardson, 2006). In

many instances, the new species arrivals also invade the interior parts of remnant patches, changing the composition of resident community (Alverson *et al.*, 1988, Gascon *et al.*, 1999, M Bartuszevige *et al.*, 2006). Species residing in small remnant patches are more prone to edge effects, due to the patch area: edge perimeter ratio being small. Thus, highly fragmented habitats will be susceptible to invasion of new species from edge environments (Anderson *et al.*, 2003, Woodroffe and Ginsberg, 1998).

Fragmentation can also result in an increase in negative trophic effects on native species across edges. This includes an increase in parasitism and predation of resident native species, particular by non-native predators (e.g. cats and foxes in Australia), that will actively move from the human-modified matrix (e.g. farmland) into the edges of remnant native habitat to hunt for native prey (Doherty *et al.*, 2015, McGregor *et al.*, 2015). This is particularly the case for migratory birds nesting in forests (Bayne and Hobson, 1997, Donovan *et al.*, 1997). Certain predators are able to rapidly adapt to a modified landscape, which gives them an advantage when hunting for prey across edges (Santos and Tellería, 1992). Such alterations to predation rates, due to disturbance, can expose vulnerable species inhabiting the remnant patch to risks of population extinction (Doherty *et al.*, 2015).

These patterns correspond to the theory of island biogeography (Farkas *et al.*, 2015), in which small, isolated 'islands' (in this case islands of remnant patches of vegetation throughout a 'sea' of human-modified landscape) can adversely influence an array of ecological processes (Farkas *et al.*, 2015).

1.2. Effects of matrix configuration on biodiversity of habitat remnants.

As described above, the size, shape and degree of isolation of habitat remnants significantly influence the diversity and types of native organisms that are able to persist in them. However, the configuration of the surrounding human-modified matrix can also significantly affect the diversity of organisms inhabiting remnant patches. In this section I introduce the two most common forms of human-modified landscapes – agricultural and urban land uses – and how these might differentially influence the diversity of remnant native habitats.

1.2.1. Agriculture

Agricultural land clearing is one of the key contributors to the global deforestation and habitat fragmentation. Grazing activity alone has affected more than 60 % of the landscape in New South Wales, Australia, and land used for cropping and irrigation purposes covers more than 20 % of New South Wales (Benson, 1991). The two leading disturbances associated with agriculture are livestock grazing and weed invasions (Hobbs, 2001, Yates and Hobbs, 1997). Farmlands that are regularly grazed or mown house the lowest biodiversity, due to the limited provision of food and shelter for native animals (Scougall *et al.*, 1993, Windsor *et al.*, 2000, Yates and Hobbs, 1997). Generally, grazing activity can significantly reduce the number of trees and shrubs in a vegetation patch, limit the number of native plant species present, increase soil compaction and thus inhibit plant growth for many dispersed seeds (Scougall *et al.*, 1993, Windsor *et al.*, 2000, Yates and Hobbs, 1997). Pettit et al (1995) investigated how native plant species responded to grazing by domestic livestock within habitat remnants. It was found that native shrub and perennial herb species richness significantly declined in areas subjected to high grazing activity

(Pettit *et al.*, 1995). Research conducted by Spooner et al (2002) found similar results using exclusion experiments: the erection of fences around remnant patches of woodland in southern New South Wales, in order to exclude livestock, significantly increased shrub and tree recruitment and diversity, indicating that grazing causes a decline in species richness of these habitats (Spooner *et al.*, 2002).

Clearing of vegetation, in order to create farmlands, commonly encourages a wide array of invasive plant species to colonise the landscape. Weed growth is controlled in managed agricultural landscapes, yet nearby remnant patches have become increasingly susceptible to changes in vegetation composition due to invasion (Reichard and White, 2001). Plant invasion is often linked to livestock grazing. Quite often, highly grazed remnant patches are more prone to weed invasions (Hobbs, 2001). Abensperg-Traun et al (1998) investigated the impacts of exotic weed invasion, due to agricultural activity, on native plant species occupying remnant woodland habitats. It was found that number of native species within a habitat greatly declined with increasing exotic invasion. The invasive species prevailed in these habitats, as they were able to out-compete natives for sunlight, moisture and nutrient resources (Abensperg-Traun *et al.*, 1998). Hobbs and Atkins (1991) examined the effects that native vegetation density had on invasive species distribution. It was found that invasion was highest in areas with open landscapes, such as agricultural fields. Thus, fragmented remnants with high grazing pressures are more subjected to modification of vegetation composition (Hobbs and Atkins, 1991).

1.2.2. Urbanisation

In recent decades, there has been a massive shift from dominantly rural landscapes to urban environments (Sharpe *et al.*, 1986). Many cities contain a wide

array of plant and animal species, but these are largely composed of alien species that replace the native species that become locally extinct (McKinney, 2002, Sukopp, 2004).

Bagnall (1979) investigated the effects human activity had on a forest in New Zealand, specifically, the impact of increasing recreational use near the forest, due to expansion of residential development along the forest margins. As expected, it was found that trampling caused significant damage to remnant trees within the forest, yet the most destructive result of human activity was from children playing amongst the vegetation. This caused significant modification to native species composition and structure, consequently leading to decline in population size of dominant species (Bagnall, 1979). Another study was conducted in forest of central Japan, which was also disturbed by urban development (Bhuju and Ohsawa, 1998). It was found that intensive recreational uses within this forest led to the increase in trampling on ground vegetation. This had indirect effects on native vegetation composition, as compaction of soil, due to trampling, inhibited woody plant growth. Thus, biodiversity of native vegetation significantly reduces with increasing modification of soil, as a result of human activity (Bhuju and Ohsawa, 1998). Hedblom and Soderstrom (2008) investigated how expansion of larger Swedish cities influenced remnant vegetation patches in surrounding areas. It was discovered that woodlands within close proximity to urban development were more subjected to clearing of understorey vegetation. Saplings and small trees were regularly removed, in order to enhance the appearance of woodland patches (as people often prefer open woodlands, opposed to cluttered patches). This reduced the biodiversity of remnant vegetation communities (Hedblom and Söderström, 2008).

Generally, as the extent of urban development in an area increases, the quality of remnant vegetation communities decline (Sukopp, 2004). In often cases, residential development leads to high dispersal of alien flora species. These species are commonly introduced to an area for ornamental and low-scale horticultural purposes (Kühn and Klotz, 2006, McKinney, 2008). With increasing introduction and dispersal of alien species, native species within remnant communities are likely to decline (Kühn and Klotz, 2006). An Australian study conducted by Morgan (1998) investigated the invasion patterns by non-native plant species into a remnant grassland patch, which is surrounded by an urban landscape. It was found that abundance and species richness of native plant species were most negatively affected by abundance of alien species invading the remnant patch (Morgan, 1998). Furthermore, when surveying native plant traits and susceptibility to local extinctions across an urban-rural gradient, Williams et al (2005) discovered that the probability of population extinction was highest in urban landscapes. This was due to an abundance of competitive, tall-growing alien species in urban areas, which were able to out-compete rare, native species for light and moisture resources (Williams *et al.*, 2005).

1.3. Effects of fragmentation on bat species

It is internationally known that deforestation and habitat fragmentation, as a result of agriculture and urbanisation, modifies bat assemblages (Stebbings, 1995, Walsh and Harris, 1996). In general, bat species respond negatively to increasing urban development and agricultural clearing. Diversity and abundance of many species decline with increasing land-clearing and consequent decrease in abundance of forest (Coleman and Barclay, 2012, Duchamp and Swihart, 2008, Gehrt and Chelsvig, 2003, Loeb *et al.*, 2009). However, some generalist species are able to persist in modified habitats, due to the ability to access additional resources outside of remnant patches, such as artificial shelters and food resources (Coleman and Barclay, 2012, Duchamp and Swihart, 2008, Gehrt and Chelsvig, 2003, Loeb *et al.*, 2009).

When researching insectivorous bat response to forest fragmentation in Paraguay, Gorresen and Willig (2004) revealed that bat communities were greatly influenced by landscape configuration. Specifically, community diversity was highest in relatively undisturbed forests. Furthermore, an increase in canopy cover, patch size and connectivity between patches were commonly associated with a high abundance of certain bat species. This demonstrates that patch attributes in fragmented landscapes significantly influence the assemblage of bats (Gorresen and Willig, 2004). A similar result was found by Cosson et al (1999), who investigated how the extent of forest fragmentation influence bat assemblages, in French Guiana, over a period of four years. Community diversity and abundance was found to rapidly decline in smaller fragments (Cosson *et al.*, 1999). In contrast, Estrada and Coastes-Estrada (2001) concluded from their research that bats within continuous forest and forest fragments in Mexico shared similar species richness. The dominant species in

these habitats possessed flexible commuting traits, which enabled them to fly efficiently through open spaces, as well as complex, dense vegetation. This suggests that some bat species are able to cope with or take advantage of landscape disturbances, in order to seek resources inaccessible to species with more specialist habitat requirements (Estrada and Coates-Estrada, 2002).

Only a handful of studies have found that bat assemblage, abundance and species richness were more influenced by patch size than degree of patch isolation (Struebig *et al.*, 2008, Montiel *et al.*, 2006, Watling and Donnelly, 2006). Quite the contrary, Jones et al (2003) found that some species were at great risk of extinction due to patch isolation. This was due to these species having low wing aspect ratios and small dispersal ranges. Thus, with increasing isolation, these bats are likely to decline in population size in situations where resources are limited (Jones *et al.*, 2003). Similarly, research conducted by Safi and Kerth (2004) investigated the effects of specialisation of bat species on extinction risks. It was found that species with short, broad wings (aka low wing aspect ratio) were more inclined to be at risk of extinction, possibly due to restricted migratory and dispersal capabilities (Safi and Kerth, 2004). Estrada et al (1993) agreed with the findings in their research, which examined the species richness and abundance of bats in Mexican forest fragments. It was found that species richness did not differ with increasing patch size, yet degree of isolation played a key role in determining the number of bat species present within a habitat (Estrada *et al.*, 1993).

Certain species respond negatively to the abrupt transition from a remnant habitat patch to a cleared vegetation matrix (Estrada and Coates-Estrada, 2001, Verboom, 1998). This was the case for bats investigated by Meyer et al (2008). When

researching Neotropical bat species and their sensitivity to fragmentation, it was concluded that species with low tolerances to edge effects were predisposed to decline in disturbed habitats (Meyer *et al.*, 2008). Likewise, Meyer and Kalko (2008) found that bat species richness was significantly higher in the centre of habitat patches, as opposed to the edges. However, no differences in abundance between the two locations were evident. This implied that certain traits possessed by some species allow occupancy and foraging along forest edges. Furthermore, it was suggested that the condition of the remnant habitat, as opposed to degree of fragmentation, influences bat assemblage (Meyer and Kalko, 2008). Morris et al (2010) too found a difference in bat assemblage between edges and centres of fragmented habitat, yet contrastingly, it was found that abundance and diversity was higher along the edges. This was due to the dominance of aerial-hunting species, which were able to forage in these margins. Some species were absent entirely in edge habitats, which further illustrates that bat response to edge effects varies with species (Morris *et al.*, 2010).

Many bat species are not responsive to fragmentation effects on patch size or isolation, yet rather the modification of remnant vegetation communities and structure (Jung *et al.*, 1999, Peters *et al.*, 2006). Zielinski and Gellman (1999) found that, as long as remnant canopy species are present in a disturbed habitat, regardless of patch size, bat activity did not vary across a continuous-fragmented habitat gradient (Zielinski and Gellman, 1999). Past research has frequently discovered that bat species respond differently to vegetation composition modifications (Jung *et al.*, 1999, Peters *et al.*, 2006). A study conducted by Ethier and Fahrig (2011) examined how vegetation density and fragmentation independently influenced bat abundance. It was found that some species responded positively to the decline in density and

diversity of vegetation, while others reacted negatively. This study suggested that habitat modification may increase accessibility to more foraging and roosting habitats for bat species that are adapted to commuting through open spaces (Ethier and Fahrig, 2011). Ober and Hayes (2008) found similar results when investigating the influence remnant condition had on habitat use by bats. Response to forest cover varied with species, yet it was clear that habitat use, whether commuting or foraging, by some species were constrained by certain vegetation architecture. This was surprising, as it was hypothesized that vegetation would indirectly affect bat assemblage, through affecting invertebrate diversity (Ober and Hayes, 2008). Likewise, Bobrowiec and Gribel (2010) found that while bat species richness between three types of secondary vegetation was similar, the assemblage of bat species significantly differed. This showed evidence for the variation in disturbance sensitivity amongst bat species, in relation to the condition of vegetation communities (Bobrowiec and Gribel, 2010).

It is clear that remnant size, edge effects and isolation, due to habitat fragmentation, have both positive and negative effects on certain species. It is poorly understood, however, how the configuration of the matrix itself influences bat composition within habitat patches. The condition of the matrix surrounding a habitat and its influence on a species composition has been studied for invertebrate and avian taxa. Wethered and Lawes (2003) investigated the response of avian species to matrix type in South Africa. It was found that more bird species visited forest fragments surrounded by grasslands than plantation forestry, indicating that the condition of a landscape surrounding forests adversely affected avian diversity (Wethered and Lawes, 2003). Hodgson et al (2007) analysed the response of insectivorous and nectarivorous bird species to urban density in the matrix of woodland patches. It was

found that nectarivores residing in the woodland were not affected by urban density in the matrix, yet species richness significantly declined with increasing urban density for insectivores, indicating that as a result of matrix configuration, the composition of avian communities can be altered due to resource requirements (Hodgson *et al.*, 2007). Sweaney et al (2014) conducted a systematic review of 24 research papers, which studied the effects that matrix configuration has on butterfly populations. It was found that 80 % of papers found that butterfly diversity declined with an increase in human-modified matrix (Sweaney *et al.*, 2014). Similarly, Sweaney et al (2015) researched the effects increasing plantation development had on ground-active beetles in south-eastern Australia. It was found that remnant patches, which the beetles resides in, surrounded by plantations housed less species than patches with a matrix dominated by agricultural land (Sweaney *et al.*, 2015). Very little research has been done on mammalian responses to matrix configuration (Lizée *et al.*, 2012, Driscoll *et al.*, 2013, Severns *et al.*, 2013, Sisk *et al.*, 1997, Vergnes *et al.*, 2012). Here lies a knowledge gap in bat responses to fragmentation; the relative importance of patch and matrix characteristics on the diversity and activity of bats in vegetation remnants is unknown.

1.4. Microbats

1.4.1. Biodiversity

The Australian wildlife is enriched with a vast range of ecologically important native species. Amongst these species are the insectivorous *Microchiroptera*, otherwise referred to as the microbat. Australian rodents and bats, including both sub-orders *Microchiroptera* and *Megachiroptera* (mega bats and flying foxes), are the only terrestrial placental mammals native to Australia (Geiser, 2006, Law, 1996). There are approximately 65 microbat species in Australia, accounting for roughly 20 % of all native mammals (Geiser, 2006, Law, 1996).

1.4.2. Biology and ecology

Microbats are distinct from all other bat species, including fellow insectivores, as they vary in lifespan and mobility (Law, 1996). In fact, these species can live up to an impressive 35 years, whereas megabat species have longevity of roughly 20 years (Kunz and Fenton, 2006). Many small bats possess relatively broad wingspan with a low aspect ratio, suitable for low-speed flight, which allows adaptation in highly vegetated habitats. This significantly increases mobility, as small wings enable swift movement through areas with numerous obstacles, a feature that megabats lack (Wimsatt, 1970). The wing shape for various microbat species determines their foraging and commuting habitat. Species with low-aspect wing ratio are more inclined to occupy and forage in highly cluttered areas, such as undisturbed native habitats, due to their slow-flight and high manoeuvrability through dense, vegetation strata. Quite the contrary, species with high-aspect wing ratio are often found in open areas, including urban and agricultural habitats, due to their inflexibility when it comes to flight (McKenzie *et al.*, 1995, Norberg and Rayner, 1987).

The most notable difference between the two sub-orders is that microbats have the ability to produce echolocation calls, in order to navigate and detect prey. This characteristic is considered a true marvel of nature, certainly a function beneficial when commuting or foraging in complete darkness (Troughton, 1951, Pettigrew *et al.*, 1989). Frequency of echolocation calls vary between species, which aids in determining where certain populations will be found. Species that forage or reside in highly cluttered areas are associated with having low frequency calls. This is due to the dense vegetation interfering with an echolocation call. Low frequency echolocation allows detection of large insects at long distances. Furthermore, high frequency calls are emitted by microbats that are adapted to open areas. The detection range is so large for open-adapted species, that it is not necessary to produce low-frequency calls (Arlettaz *et al.*, 2001, Schnitzler and Kalko, 2001)

As nocturnal insectivores, microbats primarily seek after moths, beetles, cicadas and mosquitoes (Churchill, 2009). Consumption of insects reaches such high volumes that occasionally, in most extreme cases, microbats ingest close to 100 % of their body mass per night (Jones, 2009). Pastures, revegetated areas and remnant tree patches benefit greatly from this foraging activity, as a variety of the prey species are considered 'pests' to flora communities (Lumsden and Bennett, 2010). Invertebrate herbivores can significantly reduce rates of plant reproduction, as they feed on flowers, seeds and other floral reproductive organs. Furthermore, the quality of crop produce is extremely poor in situations where high numbers of herbivorous invertebrates are present (Kalka *et al.*, 2008). Insect populations are kept under control in areas with high microbat abundance, improving the health of woodlands and crops, making them a valuable asset to Australian ecosystems (Lumsden and

Bennett, 2010). In fact, it is predicted that microbats have a stronger positive ecological impact on vegetation health than birds (Kalka *et al.*, 2008).

On a global scale, microbats are considered highly diverse in an ecological, taxonomic and trophic sense. Furthermore, species are geographically distributed worldwide (Medellin *et al.*, 2000). Given their ecological important to humans, and their sensitivity to a variety of human disturbances, they are considered to be useful biodiversity indicators, enabling research on the state of an ecosystem's health, by comparing species assemblages across a range of habitats (Jones, 2009, Medellin *et al.*, 2000). Truly insectivorous Australian *Chiroptera* (microbats) is significantly smaller in size than fruit bats (megabats) and can be distinguished from other sub orders through facial features (Troughton, 1951, Pettigrew *et al.*, 1989). A broad and short face, as well as wide, open ears and small, beady eyes are all unique characteristics of the microbat. Moreover, insectivorous bats possess W-shaped molar crowns for grinding and consuming invertebrates, a feature fruit bats lack. Rather, megabats have smooth molar crowns for pulping vegetable matter (Troughton, 1951, Pettigrew *et al.*, 1989). Unlike the fruit bat which contains two digits with claws, the thumb is the only clawed digit and the tail is always present, which dissimilar from fruit bats, is enclosed by the inner thigh membrane (Troughton, 1951, Pettigrew *et al.*, 1989).

1.4.3. Response to human modification

There has been extensive Australian research investigating the response of microbats to disturbed environments and how they're able to utilise human-modified landscapes (Basham *et al.*, 2011, Hanspach *et al.*, 2012, Caryl *et al.*, 2015, Law *et al.*,

1999, Law *et al.*, 2000, Threlfall *et al.*, 2011, Threlfall *et al.*, 2012a, Threlfall *et al.*, 2012b).

Distribution of microbat species across a fragmented landscape varies with possessed traits. Some species, including *Miniopterus schreibersii oceanensis* and *Chalinolobus gouldii*, have high wing loading and low echolocation frequency (as mentioned previously), which allows adaptation to cleared environments, including agricultural areas and residential spaces. Thus, these open-adapted species are relatively insensitive to human modification, and in many cases, are able to forage and roost in man-made structures (Kirsten and Klomp, 1998, Threlfall *et al.*, 2012b). Species with low wing loading and high echolocation frequency, such as *Rhinolophus megaphyllus* and *Falsistrellus tasmaniensis,* are more vulnerable to population decline with increasing human modification. Cluttered habitats are preferable for foraging and commuting activities, indicating that land clearing for anthropogenic purposes can significantly reduce the resource availability for these species (Threlfall *et al.*, 2012b). Luck et al (2013) investigated the response various microbat species had on urban density in south-eastern Australia. It was found that while open-adapted species were unresponsive to increasing urbanisation, clutter-adapted species were adversely affected. Thus, due to this, the diversity of bat species significantly declined with increasing urban density (Luck *et al.*, 2013). This demonstrates that human modification can have significant effects on the composition of Australian microbat communities.

Furthermore, artificial light sources can significantly alter the microbat community abundance and diversity within a landscape. Streetlights in urban settings can attract potential predators (Threlfall *et al.*, 2013b). Threlfall et al (2013) found

that an Australian microbat species, *Nyctophilus gouldi*, was less likely to visit remnant woodland patches within close proximity to light sources. This species has a slow flight, thus commuting through patches close to urban areas can increase the risk of fatality form predation (Threlfall *et al.*, 2013a). Additionally, artificial lighting can attract insect species, which microbats prey on. This can indirectly alter the community abundance and composition (Adams *et al.*, 2005). Adams et al (2005) investigated the effects UV lights had on microbat foraging activity in Kioloa, New South Wales, and found that microbats were more actively foraging in areas with artificial lighting, likely due to the abundance of insects. *Nyctophilus spp.* was not detected in lit areas, illustrating their sensitivity to light sources, which supports results from Threlfall et al (2013) (Adams *et al.*, 2005). Thus, it is clear that human modification adversely affects certain Australian microbat species more than others.

1.5. Study objectives

The overarching aim of this thesis is to examine the effects of habitat fragmentation on microbat diversity. Specifically, I assessed the variation in microbat diversity, activity and composition across an extensively fragmented, complex landscape of suburban and rural habitats interspersed with small, isolated patches of an endangered woodland ecosystem. My research was divided into two explicit aims, which are detailed below, along with their hypothetical framework:

1.5.1. Variation in microbat assemblages across a modified woodland landscape

My first aim was to examine variation in microbat diversity and activity between three dominant habitats within this disturbed landscape: remnants of endangered Illawarra Lowlands Grassy Woodland, agricultural landscapes and urban areas. As part of this aim, I examined microbat diversity amongst three size classes of woodlands, in order to determine possible threshold of fragment size below which bat diversity begins to decline.

I hypothesised that microbat activity and diversity will be highest in remnant patches and lowest in modified landscapes. Furthermore, I predicted that large woodlands will contain more activity and species richness than small patches. It was predicted that highly mobile species will be found in both urban and rural landscapes (Basham *et al.*, 2011). Based on previous studies conducted by Caragh Threlfall (2011, 2012, 2013), it was expected that microbat species with a low frequency of echolocation calls and fast-flying abilities will be the only species detected in urban areas. This is due to urban sites being 'open' areas, which are considered unsuitable for microbat species that have slow flight and high frequency calls, as they have less

success at foraging in these areas (Threlfall *et al.*, 2012a). Insect biomass decreases with housing density in an area, which increases foraging competition amongst microbats and other fauna. Thus, slower microbats have a smaller chance of catching insects (Threlfall *et al.*, 2012a). 'Cluttered' areas, which are sites of high vegetation density, have been found to have minimal impact on insect biomass, and therefore bat foraging activity, which indicates that housing density has more effect on the distribution of microbat species (Threlfall *et al.*, 2012a). However, it has also been discovered that the species with fast flight and low frequency calls are mostly active in urban (or open) areas, whereas the species that are slower and produce lower frequency calls are frequently associated with highly cluttered sites (Threlfall *et al.*, 2011).

1.5.2. Effects of landscape matrix on diversity and composition of microbats within woodlands remnants

My second aim was to examine how the diversity, activity and composition of microbats within remnant woodland patches are influenced by the configuration of the surrounding landscape matrix.

Most extant research on bats and other faunal groups focuses on how intrinsic attributes of remnant patches of vegetation (e.g. patch size, connectivity, stand structure) influence diversity, with very little focus on how the condition of the matrix in which the remnants are embedded moderate or influence the diversity of resident fauna. Based on research conducted for avian species, it was expected that microbat diversity will be dependent upon matrix configuration. It was hypothesised that highly mobile species will be uniformly distributed through matrixes with high vegetation

cover, as well as open landscapes. Species will low mobility will be most affected by

matrix composition.

Chapter 2 - Study Site and Habitat

2.1. Study Site

2.1.1. Location

This study was conducted within the Illawarra region, which is located on the south coast of New South Wales, Australia, approximately 80km south of Sydney. The majority of sampling took place in four suburbs: Shellharbour (34º34'47" S, 150º52'03" E), Albion Park (34º34'14" S, 150º46'34" E), Dapto (34º29'44" S, 150º47'41" E) and Wollongong (34º 25'54" S, 150º53'31" E).

2.1.2. Climate

The Illawarra region is characterized by a temperate climate, with warm to hot summers and mild winters, with no dry season (Bureau of Meteorology, 2015). The average daily maximum and minimum temperature ranges from 18 to 24 degrees and 9 to 15 degrees respectively, and the region receives an average of 800mm or more of rainfall per year, which falls consistently throughout the year (Bureau of Meteorology, 2015). Humidity levels can reach between 70 % and 100 % per day. There is a low count of frost days per year, as humidity levels are too high for cooling of water particles (Bureau of Meteorology, 2015).

2.1.3. Geology

The region's geology, which lies in the southern region of the Sydney Basin, is comprised of marine and non-marine sedimentary units, as well as volcanic rock (Young and Nanson, 1982). The landscape consists of three primary layers: the Illawarra Coal Measures, the Narrabeen Group and the Hawkesbury Sandstone. The Illawarra Coal Measures, which is composed of sandstone, claystone and coal, forms

much of the low coastal plains, as well as the base of the Illawarra Escarpment. This is interbedded and overlain by sandstone and mudrock of the Narrabeen Group. The Illawarra Escarpment is capped by the cliff-forming Hawkesbury Sandstone (Flentje, 2012, Loughnan, 1966) (see Figure 2).
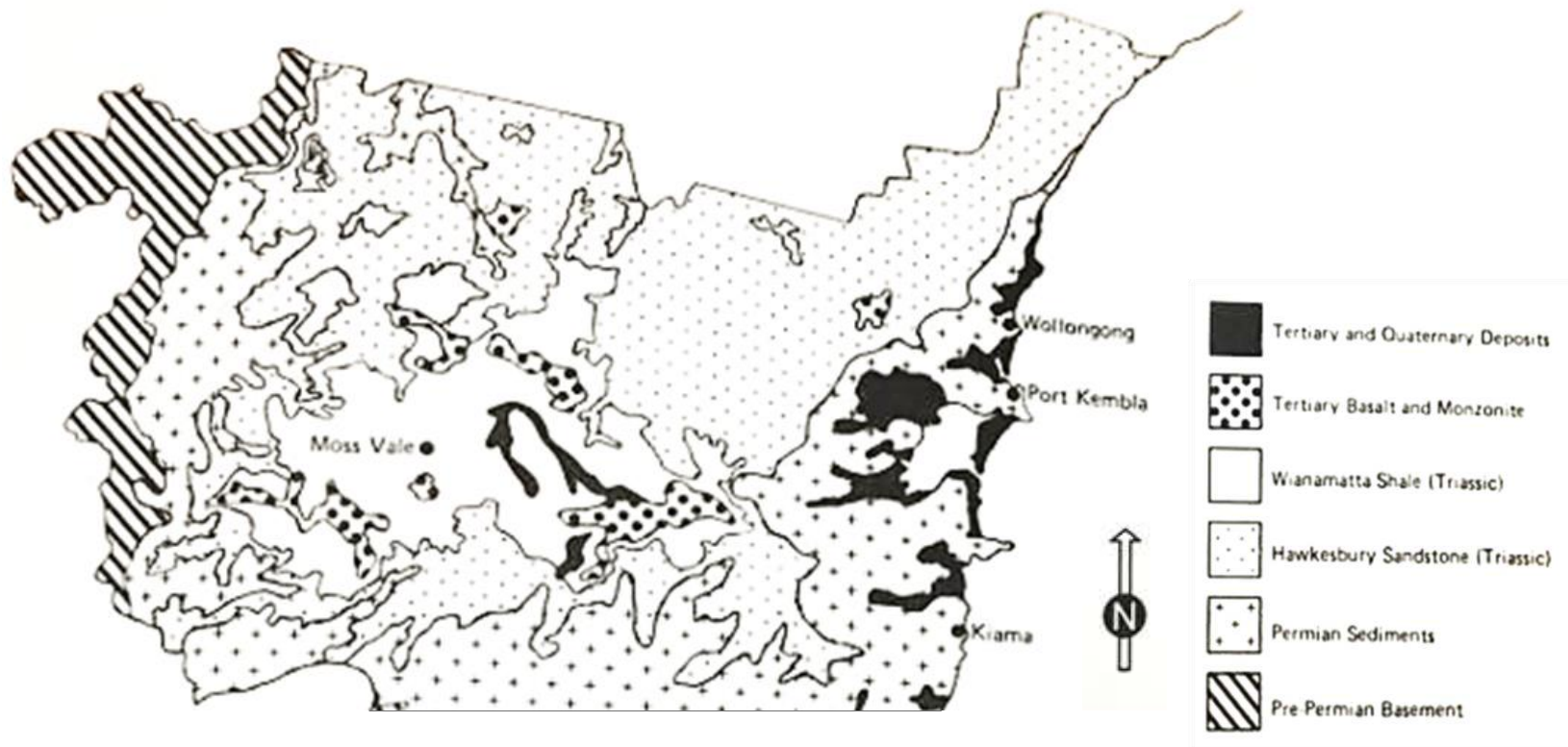
Figure 2: Geological map of the Illawarra, obtained from 'The Illawarra Region – Agricultural Land Classification Study' (Hindle *et al.*, 1987).

2.2. Habitat

2.2.1. Illawarra landscape modification

Prior to European settlement in the Illawarra region, that occurred approximately 200 years ago, the landscape was dominated by rainforest and woodland communities (Mills, 1988). In an effort to exploit cedar trees for timber, existing vegetation was subjected to substantial deforestation and fragmentation (Hindle *et al.*, 1987). After the rapid exhaustion of timber resources, land clearing for dairy and meat production further deteriorated the remnant communities (Hindle *et al.*, 1987). This vegetation was only able to recover when farmlands were abandoned (Mills, 1988).

The Illawarra region has progressively transitioned from a predominately agricultural landscape to a rapidly growing urban developmental zone over the last 65 years (Keys, 1978). In a five-year timeframe alone (from 1971 to 1976), the majority of the area between Albion Park and Wollongong experienced urban growth exceeding 15 %. Originally, the increasing urbanization was due to post-war migration of Australians from agricultural regions, as well as immigrants from Europe (Keys, 1978). With the success of Sydney as a major industrial city, many city residents desired to relocate to a more "environmentally attractive" area, yet still be within a reasonable distance from Sydney. The Illawarra region was considered perfect for this "out-migration" and thus residential development increased dramatically to meet these demands (Keys, 1978).

While agricultural fields and paddocks still exist in Dapto and Albion Park, the extent of these agricultural landscapes has diminished due to replacement with urban structures. Urban density now covers approximately 50 % of Illawarra landscape, while agricultural land and native vegetation covers the remaining area.

2.2.2. Illawarra Lowlands Grassy Woodlands

The Illawarra is comprised predominately of temperate native vegetation. There is a vast array of vegetation communities present within this region, which are subject to various levels of disturbance (see Appendix A for summary of communities).

My research was specifically conducted within the Illawarra Lowlands Grassy Woodland (ILGW), an Endangered Ecological Community, as listed under the Threatened Species Conservation Act (1995). The grassy woodland is a complex of two distinct woodland forms, the Coastal Grassy Red Gum Forest and the Lowlands Woollybutt-*Melaleuca* Forest, which cover areas of approximately 431.91 ha and 797.44 ha, respectively, across the Illawarra region (National Parks and Wildlife Services, 2002).

This woodland is of open-tree canopy, with infrequent presence of shrubs and small trees. The upper canopy layer mainly comprises of *Melaleuca decora* within the Lowlands Woollybutt-*Melaleuca* Forest community (Figure 3), and *Eucalyptus longifolia* and *Eucalyptus tereticornis* within the Coastal Grassy Red Gum Forest community (Figure 4) (National Parks and Wildlife Services, 2002). Shrubs include *Acacia mernsii*, *A. implexa* and *Exocarpos cupressiformis*. Herbs and grasses dominate the ground cover, with the most commonly abundant species being *Themeda australis*, *Microlaena stipoides* and *Echinopogon ovatus* (Department of Environment, 2010). In instances where woodlands have been subjected to intense disturbance, for grazing or clearing purposes, shrubs, saplings and grasses are more likely to dominate the ILGW community (Office of Environment and Heritage, 2011b).

Figure 3: Illawarra Lowlands Grassy Woodlands; Lowlands Woollybutt-Melaleuca Forest community

Figure 4: Illawarra Lowlands Grassy Woodlands; Coastal Grassy Red Gum Forest community

The ILGW occurs mostly on Berry Siltstone, Budgong Sandstone and Quaternary alluvium, on low-angle sloping lands which are less than 500m in elevation (Office of Environment and Heritage, 2011a). It is dispersed across the Illawarra region, with the majority of patches being clustered around areas in Dapto and Albion Park (Figure 5).
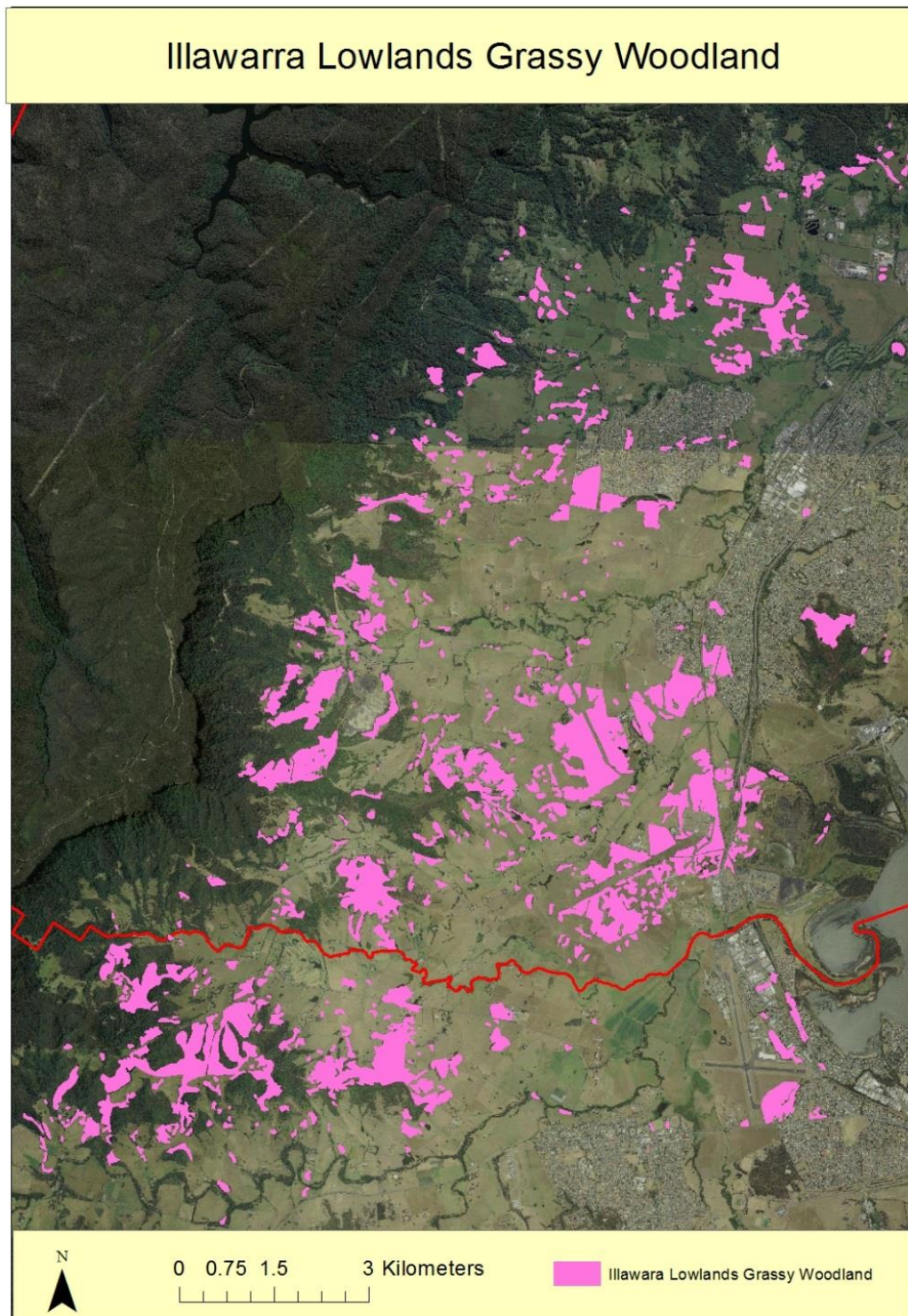
Figure 5: Map of the distribution of Illawarra Lowland Grassy Woodland patches across the Illawarra region in NSW, Australia. Obtained from the Office of Environment and Heritage.

Blackbutt Reserve, Purrungully Reserve and Croome Reserve are amongst the very few ILGW patches that are council reserves (Office of Environment and Heritage, 2011a). Both communities experience moderate to heavy disturbance, with approximately 65 % of total vegetation cover in the Illawarra being subjected to high disturbance, and consist mostly of highly scattered trees (see Appendix A). Most of this disturbance is external, resulting from land use and development occurring in surrounding areas, which are mainly for residential and agricultural purposes. This includes suburban development, dairy farming, sports grounds (specifically the case for Croome Reserve) and industrial processes. This level of disturbance has caused the ILGW patches to be severely fragmented and isolated (National Parks and Wildlife Services, 2002).

2.2.4. Woodland fragmentation

The ILGW patches are mainly surrounded by cleared landscapes, yet in some cases, are enclosed completely by urbanization (see Figure 6). This fragmentation impedes the value of this community as a resource for fauna (Department of Environment, 2013).

The remaining woodlands today are frequently intruded by lantana and other invasive species, as they have been highly altered with bare understories. These patches of ILGW have lost a large amount of remnant, hollow-bearing trees, with the remaining trees being isolated from one another. Based on the condition of these patches, it is evident that the ILGW community is rapidly deteriorating due to extensive fragmentation (Department of Environment, 2010).

A

B

C
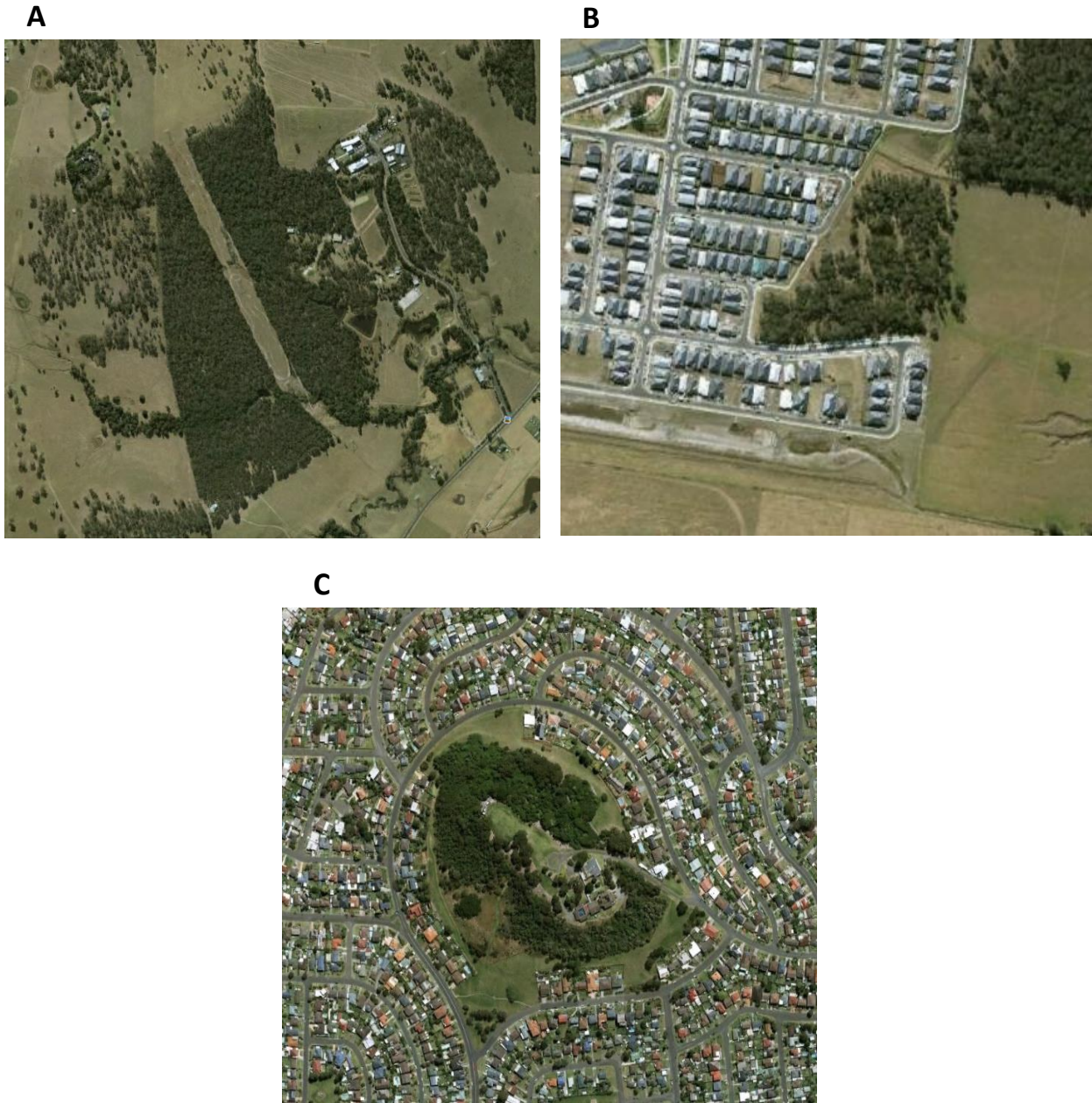
Figure 6: Illawarra Lowlands Grassy Woodland patches with a varying degree of urbanization in matrix. A) Completely agricultural, no urban; B) 50 % urban and 50 % agricultural and C) completely enclosed by urbanization.

Grassy woodlands are considered to be one of the most susceptible communities to intense grazing effects (Tozer *et al.*, 2010). Patches are frequently subjected to high grazing activity by livestock, which often seek shelter under the canopy. If the frequency of grazing is not managed correctly, this can encourages intrusive weeds to colonize the ground cover of these woodlands, which in turn increases resource competition between co-existing vegetation species (Department of Environment, 2010). Furthermore, excessive grazing can lead to substantial erosion of topsoil, which limits the growing ability of native seedlings (Tozer *et al.*, 2010).

Frequent occurrences of fires can disrupt the existing ecosystem functioning within the woodland patches, including life cycles in plants and animals, as well as damage to vegetation composition and structure (Department of Environment, 2010). Therefore, in order to avoid such consequences, the Threatened Species Hazard Reduction List states that no fire can occur "*more than once every 5 years for grassy woodland sub-community, and no more than once every 25 years for the moist forest sub-community*" (Department of Environment, 2011). However, at present, ILGW patches are not exposed to inappropriate fire regimes, thus fire is not considered a major contributor to disturbance (Department of Environment, 2013).

Selective logging can play a huge role in determining the value of an ILGW patch, in regards to viability as a habitat for fauna (Department of Environment, 2011). The removal of hollow-bearing trees significantly impact birds and bats, as they frequently rely on hollows as roosting sites. Additionally, logging can cause patches to reduce in size, thus diminishing corridor linkages. While this may not affect highly mobile faunal species, populations of animals that are less capable of commuting between woodland patches are limited by the distance between habitats(Department of Environment, 2011). While selective logging is

infrequent in the Illawarra region, it is still considered a potential threat to long term viability of ILGW patches (Department of Environment, 2010).

The most deteriorated woodlands are characterized as having lost the majority of canopy trees, have grazed or cleared understories and have minimal connectivity to adjacent patches (Department of Environment, 2013).

2.3. Microbat species in New South Wales

A total of 29 *Microchiroptera* species have been detected in New South Wales (see Table 1 for microbat species details). Additionally, 5 taxa of *Chiroptera* have been identified, yet these have not been formally described as microbat species (Pennay *et al.*, 2004).

Table 1: Biology and ecology of the 29 microbat species found in New South Wales, Australia. Information obtained from Churchill (2009) and Department of Environment Blank sections are 'unknown'.

Microbat species	Distribution	Habitat preference	Roosting preference	Diet	Mating period	Average size of wingspan (mm)	Type of flight	Population trend	Endemic to Australia?
Chalinolobus dwyeri	South East QLD down to coastal regions of NSW and Southern Highlands	Woodlands, sclerophyll forests and rainforests	Caves and crevices in cliffs and mines			277.5	Slow-flying with moderate mobility	Decreasing	Yes
Chalinolobus gouldii	Majority of Australia, except Cape York Peninsula and Nullarbor Plain	All habitats, including remnant vegetation, deserts, rural and urban areas	Tree hollows and buildings	Bugs and moths	End of Winter	295	Fast-flying with low mobility	Stable	No
Chalinolobus morio	Mainly south Australia, including TAS, VIC and south of WA. Also includes Eastern NSW	Woodlands, sclerophyll forests, treeless regions, shrublands and rainforests	Tree hollows, urban structures, caves and fairy martin nests	Predominately on moths and beetles, yet have preyed on a variety of aerial insects	Autumn and Winter	271.3	Fast-flying with low mobility	Stable	Yes
Chalinolobus nigrogriseus	Mostly northern Australia, including Kimberly WA, Cape York and Coffs Harbour	Forest, woodland, sclerophyll patches, rainforest, coastal scrub and grasslands	Tree hollows and rock crevices	Mostly beetles, ants and moths	Autumn and Winter	253	Fast-flying with low mobility	Stable	No

Species	Distribution	Habitat	Roost	Diet	Breeding		Flight	Population	Threatened
Chalinolobus picatus	Semi-arid regions of QLD and NSW	Mallee, open forests and woodlands	Trees, caves, mines and urban structures	Mainly moths	Late Winter – early Spring	249	Fast-flying with high mobility	Decreasing	Yes
Falsistrellus tasmaniensis	Coastal QLD, NSW and southern VIC. Also found in TAS	Wet sclerophyll and coastal mallee	Hollow trunks	Large insects, including beetles, ants and flies	Late Spring		Fast-flying with high mobility	Decreasing	Yes
Kerivoula papuensis	Along east coast of Australia, from north QLD to south NSW	Rainforests and sclerophyll forests	Abandoned nests of yellow-throated scrubwren and tree hollows	Orb-weaving spiders	Late Autumn	250	Slow-flying with high mobility		No
Miniopterus australis	East coast of QLD and NSW	Rainforests, sclerophyll forests and swamps	Caves and mines	Beetles, moths and flies	Middle of Winter	288	Fast-flying with moderate mobility	Stable	No
Miniopterus schreibersii oceanensis	East coast of Australia, from QLD to VIC	Rainforests, forests, woodlands and grasslands	Caves, mines and urban structures	Moths, cockroaches and beetles	Late Winter	341	Fast-flying with high mobility		No
Mormopterus beccarii	Mostly across north Australia, from WA to QLD, extending to the north-east corner of NSW	Rainforests, river flood plains, woodlands, shrublands and grasslands	Tree hollows and caves	Moths and beetles	Late Winter	285	Fast-flying with low mobility	Stable	No
Mormopterus norfolkensis	South coast of QLD to coastal areas of NSW	Forests and woodlands	Tree hollows		Middle of Autumn		Low mobility	Decreasing	Yes

Myotis macropus	Primarily coastal regions of Australia, including WA, NSW, QLD and VIC	Found near waterways, including streams	In caves, hollows and urban structures near waterways	Small fish, prawns and aquatic insects	Late Winter to early Spring	281			No
Nyctophilus bifax	Eastern Australia from Cape York in QLD to north NSW	Rainforests, monsoon forests and riverine forests	Under peeling bark, in tree hollows or in trunks	Moths, ants and beetles	Start of Winter	293	Slow-flying with moderate mobility	Stable	No
Nyctophilus geoffroyi	Majority of Australia, except north-east coast of QLD	All habitats, including remnant vegetation, deserts, rural and urban areas	Rock crevices, under peeling bark, urban structures and tree hollows	Moths, crickets and grasshoppers	Middle of Autumn	245	Slow-flying with high mobility	Stable	Yes
Nyctophilus gouldi	Eastern QLD and NSW, as well as most of VIC	Rainforests, sclerophyll forests and woodlands	Tree hollows, in fissures and under peeling bark	Moths and beetles	Middle of Autumn	276	Slow-flying with low mobility	Decreasing	Yes
Nyctophilus timoriensis	Largely restricted to Murray Darling Basin from south QLD to inland NSW	A wide variety of vegetation types, given that there is a dense, cluttered understorey layer	Tree hollows	Moths and beetles	End of Winter	236	Slow-flying with high mobility	Decreasing	No
Rhinolophus megaphyllus	East coast of Australia, from QLD to VIC	Rainforests, forests, woodlands, scrublands and grasslands	Caves and urban structures	Moths, beetles and flies	Early Winter	293	Slow-flying with high mobility		No
Saccolaimus	Most of Australia,	Almost all habitats,	Tree hollows	Beetles,	Late Winter		Fast-flying	Decreasing	No

Species	Distribution	Habitat	Roost	Diet	Season	Number	Flight	Trend	
flaviventris	except south-west WA and SA, as well as the whole of TAS	including remnant vegetation, deserts, rural and urban areas		grasshoppers and crickets			with low mobility		
Scoteanax rueppellii	Restricted areas of north QLD, mostly along coastal areas of south QLD and NSW	Coastal forests, cleared paddocks and tree-lined creeks	Tree hollows, cracks and fissures, as well as under dead branches	Beetles and spiders		395	Moderate-flying with low mobility	Decreasing	Yes
Scotorepens balstoni	Widespread through arid and semi-arid regions of Australia	Over waterways, open woodlands, shrublands and grasslands	Tree hollows and urban structures	Most insects, including beetles, ants, moths, cicadas, termites and crickets	Middle of Autumn	278	Fast-flying with high mobility	Decreasing	Yes
Scotorepens greyii	North Australia, excluding Cape York Peninsula, and inland areas to south NSW	Forests, woodlands and shrublands	Tree hollows and urban structures	Beetles, bugs and ants	Middle of Autumn	234	Moderate-flying with high mobility	Stable	No
Scotorepens orion	Eastern Australia, from Melbourne to south QLD	Rainforests, open forests and woodlands	Tree hollows		Early Spring				Yes
Tadarida australis	All areas of Australia except north coasts and TAS	All habitats, including remnant vegetation, deserts, rural and urban areas	Tree hollows and dead trunks	Moths, beetles and grasshoppers	Late Winter		Fast-flying with low mobility	Decreasing	Yes
Vespadelus	Inland semi-arid	Woodlands, mallee,	Tree hollows		Middle of		Fast-flying	Stable	Yes

baverstocki	and arid regions of Australia	shrublands and grasslands	and urban structures		Autumn		with high mobility	
Vespadelus darlingtoni	South coast of QLD to coastal regions of south VIC	Rainforests, sclerophyll forests, swamps and woodlands	Tree hollows	Ants, flies, bugs and beetles	Middle of Winter		Fast-flying with low mobility	Stable	Yes
Vespadelus pumilus	Scattered east of Great Dividing Range – coastal QLD and NSW	Moist forests, sclerophyll forests and rainforest gullies	Tree hollows	Moths, beetles, flies, wasps and ants	Middle of Autumn		Slow-flying with high mobility	Decreasing	Yes
Vespadelus regulus	South of Australian, along coastal regions, and east coast of NSW	Rainforests, sclerophyll forests, shrublands, woodlands and mallee	Tree hollows	Moths and beetles	Middle of Autumn		Moderate-flying with high mobility	Stable	Yes
Vespadelus troughtoni	Eastern QLD and northern NSW	Close to sandstone or volcanic escarpments, as well as woodlands and sclerophyll forests	Caves, mines and urban structures	Mosquitoes	Middle of Autumn		Slow-flying with low mobility	Stable	Yes
Vespadelus vulturnus	South QLD, majority of NSW and VIC, as well as eastern SA	Sclerophyll forest, woodland and mallee	Tree hollows and under dead branches	Aerial insects, including moths, bugs and beetles	Middle of Autumn		Fast-flying with high mobility	Decreasing	Yes

2.4. Methodology

2.4.1. Site selection

My project consisted of two discrete questions: (1) what is the variation in assemblage of microbats between remnant woodland patches and agricultural and urban landscapes (aka *Modified Landscape*)? and (2) how are microbat assemblages within remnant woodlands influenced by the configuration of the landscape matrix surrounding the woodland patches (aka *Matrix Configuration*)? In order to answer these two questions I first selected a total of 31 remnant patches of Illawarra Lowland Grassy Woodland of various sizes, ranging from 0.11ha to 83ha, as well as eight agricultural and eight urban sites. The woodland sites were chosen 'haphazardly' from a subset of those present in the Illawarra region. Although my selection of sites was somewhat limited by accessibility (i.e. most remnant patches are located on private property), the sites that I was able to sample were distributed evenly across the Illawarra coastal plain and were representative of the full range of sizes and shapes (see Figure 7 below).

Additionally to the 31 remnant patches, 8 urban and 8 agricultural sites were chosen to sample for *Question 1* (see operational definitions for agricultural and urban landscapes below). These sites were interspersed haphazardly with the set of woodlands across the Illawarra coastal plain (Figure 7).
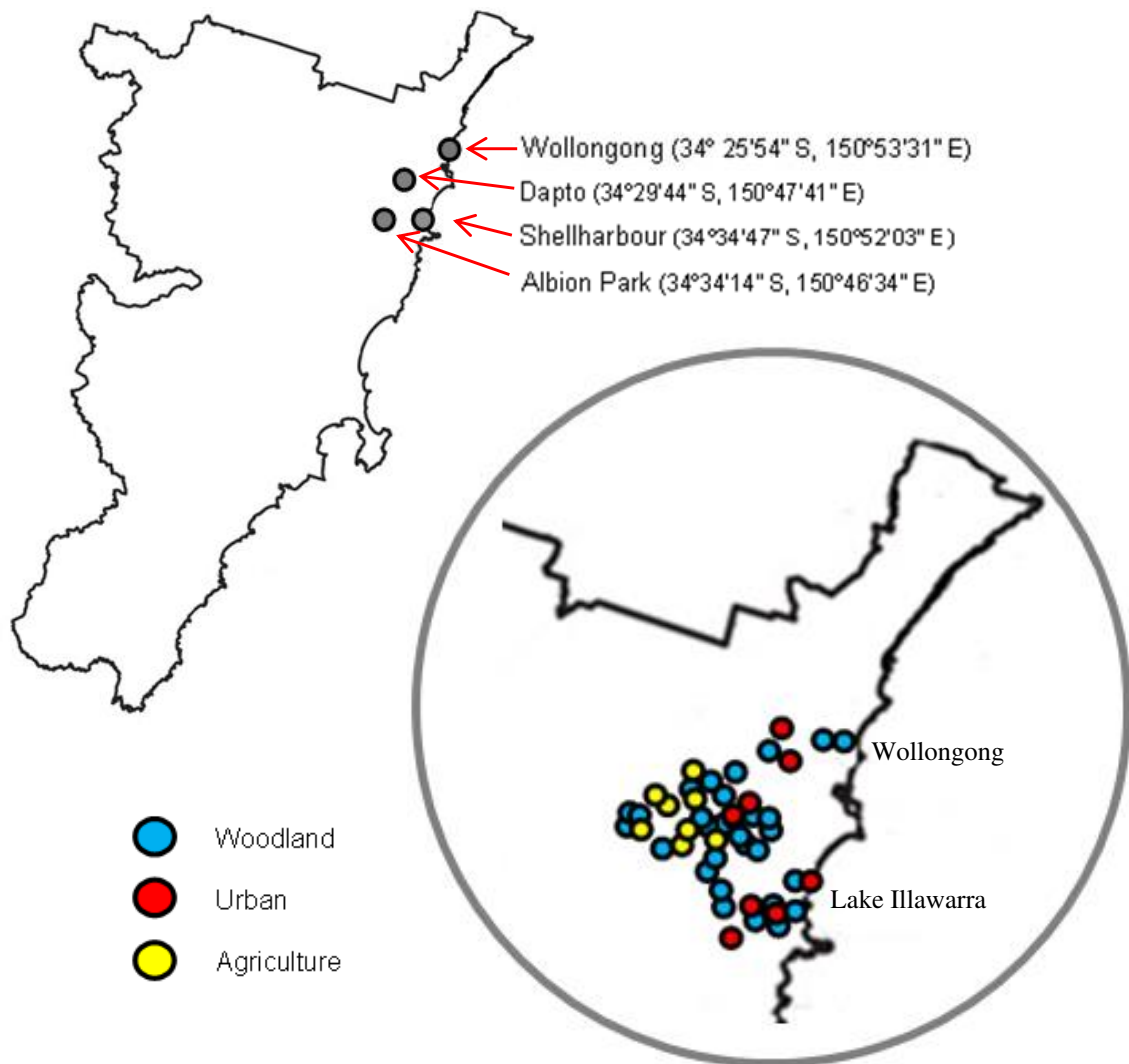
Figure 7: Distribution of woodland sites, urban sites and agricultural sites around the Illawarra region. Position of points is estimation and no location of sampling sites can be determined by this figure (to protect the rights of landowners).

Operational definitions of habitats

Urban habitats included residential dwellings, associated impermeable surfaces (for example; roads, paths and other structures), gardens, parks, golf courses and industrial and civic areas (Basham *et al.*, 2011). Based on these characteristic features, urban habitats were initially defined as areas within the matrix with more than 80 % cover of urban habitat within a 500m radius of the Anabat and < 10 % native vegetation (Threlfall *et al.*, 2012a) per 4ha. The definition of an urban area was considered to be a landscape containing artificial, impermeable surfaces and/ or man-made natural, permeable surfaces (including golf courses, parks and residential gardens).

Agricultural habitats included deforested land used actively for crop fields, livestock grazing or dairy farming (Gooden and French, 2014). They were characterized as having 0-5 dwellings (and other human surfaces) per ha and <10 % native remnant vegetation with 10 % canopy cover. The remaining >80 % landscape consisted of managed pastures (Rollinson and Jones, 2002, Threlfall *et al.*, 2012a).

Remnant vegetation included areas of high canopy cover and vegetation density, with no urban structures, artificial surfaces or impermeable surfaces. Remnant areas were characterized as having 0-5 dwellings per ha, presence of native trees characteristic of the Illawarra Lowland Grassy Woodland and no history of human management (Gooden and French, 2014, Threlfall *et al.*, 2012a).

2.4.2. Field surveying

As microbats may enter extended bouts of torpor during the cooler winter months, all 31 woodland, eight urban and 8 agricultural sites were sampled between January and April of 2015, when microbats were most active, as females were

lactating, and consequently resource requirements were greatest (Threlfall *et al.*, 2011, Threlfall *et al.*, 2012a).

Microbats are capable of flying more than 1km each night, and so sites within 500m of each other are likely to be highly connected and may share a similar bat assemblage (Basham *et al.*, 2011). Thus, in order to account for lack of independence due to distance between surveyed patches, adjacent sites were not surveyed on the same set of nights, which maximized spatial and temporal independence of samples. Each remnant woodland site varied in distance from nearby patches, extent of canopy cover, size and shape of patch, as well as condition of landscape matrix surrounding them.

Anabat detectors

An Anabat II recorder detects microbat activity by recording the echolocation calls of foraging and non-foraging bats (Luck *et al.*, 2013). Echolocation calls of microbats vary by species, allowing each call to be assigned to a particular species or species group (i.e. taxa). This enables the determination of relative levels of activity (number of passes per night) for individual species and all species combined in woodland, agricultural and urban landscapes (O'Farrell *et al.*, 1999).

Unless a site was considered significantly large, one Anabat was employed for each site. Larger patches, exceeding 50ha in size, had two Anabats in order to accurately represent the whole microbat activity within the patch. Detectors were set with microphones at a 45-degree angle from the horizontal plane, to optimize full detection of bats within the airspace. The microphone was threaded inside a simple two-segment pipe to protect it from moisture and detection by nearby humans or animals (see Figure 8). The top segment consisted of a small curved pipe, or 'snout',

which secured the microphone to the standard 45-degree position. A 1m straight pipe made up the bottom section, which supported the snout. This segmented pipe enabled the Anabat microphone to record microbat activity at a ~1m height, which is the recommended elevation for accurate detection of calls (O'Farrell *et al.*, 1999). Pipes were painted green to further prevent detection and potential damage. The snout of the pipe possessed a small hole on the bottom to drain any water that may enter. The bottom segment had a larger hole on the side, which allowed the microphone cord to be threaded out and connected to the Anabat detector. The pipes were secured by a tomato stake or the snout was secured to a tree or urban structure with duct tape in situations where interference might be common (e.g. actively grazing cows) (Luck *et al.*, 2013, Threlfall *et al.*, 2011, Threlfall *et al.*, 2012a, Tung and Francl, 2007). The Anabat detector itself was contained within a lunchbox container (to reduce risk of moisture damage and vandalism) and disguised with a plastic bag and loose vegetation to minimize the chance of the detector being identified. Detectors were calibrated so that they all had a sensitivity level of 6.5, AUDIO DIVISION of 16 and DATA DIVISION of 8 (see Figure 9).
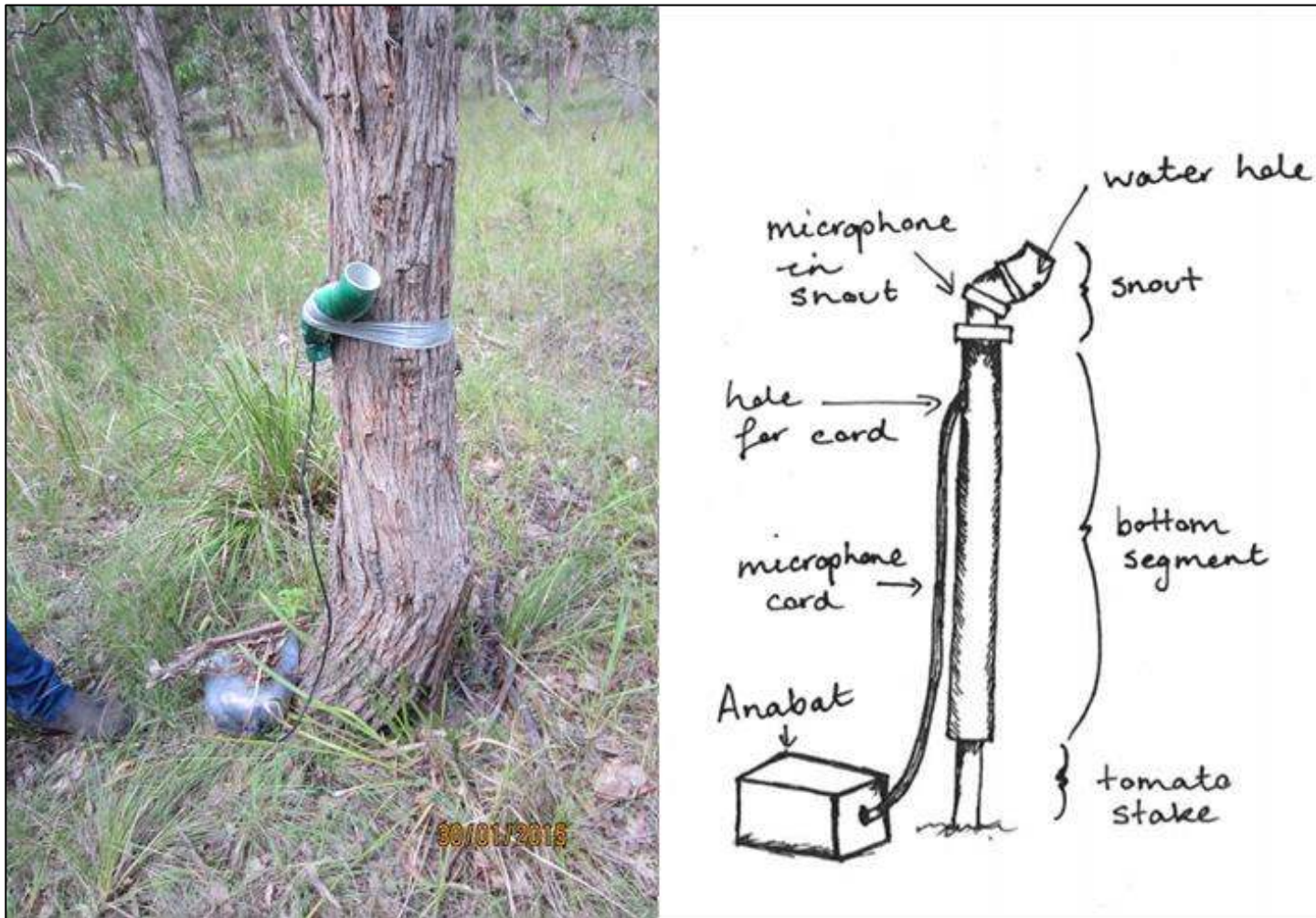
Figure 8: Anabat setup in the field: A) attached to a tree and B) secured by a tomato stake
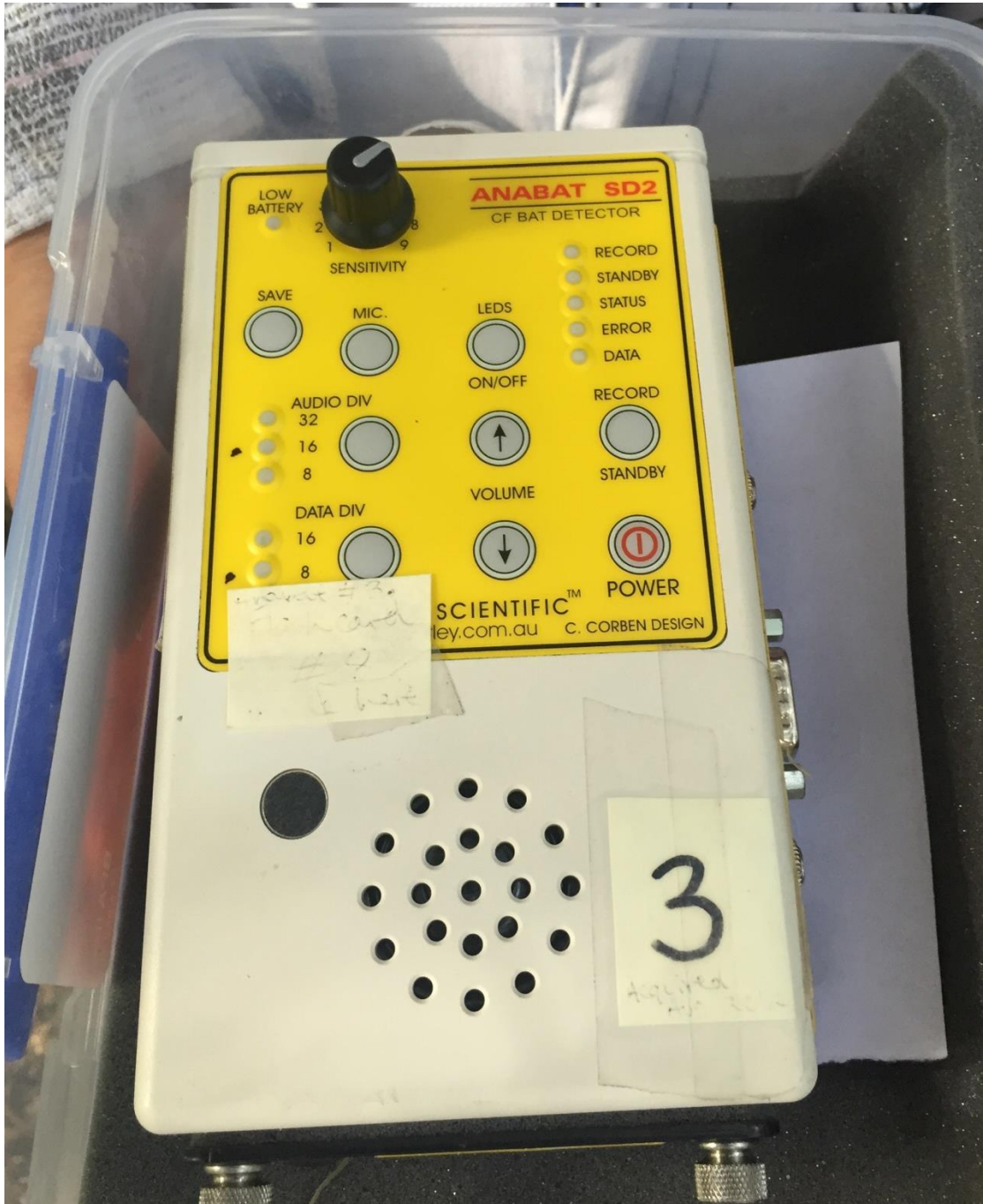
Figure 9: Anabat II detector

The standard detection range of the Anabat varies from 1m to 50m, depending on vegetation density and frequency/ amplitude of bat calls (Titley Scientific, 2015). Vegetation can significantly decrease the detection range, thus relatively open areas within each patch were preferred for placing Anabats (Threlfall *et al.*, 2012a). These areas are considered to have minimal tree canopy and low vegetation density. Furthermore, in instances where an Anabat was placed in a tree (to avoid consumption by cows), a branch with low canopy density was chosen. Anabats supported by a pipe were not placed in areas where the microphone would be facing a tree trunk, as trunks have the tendency to create echoes, thus reducing the ability to identify calls.

Furthermore, the placement of the Anabat was limited to 20m from the patch edge with the microphone facing adjacent to the border, in order to account for edge effects. This reduced "outside" influences, including traffic activity. 20m from the edge enabled inclusion of only microbat activity occurring *within* the patch, as the Anabat can only accurately detect echolocation calls, produced by both loud and soft calling species, within a 20m range (Threlfall *et al.*, 2011).

Levels of microbat activity obtained from the Anabat recorders were used to infer patterns of habitat use (O'Farrell *et al.*, 1999). In addition, species composition was compared between habitats (O'Farrell *et al.*, 1999). As Anabat detectors can measure the types of call produced by microbats, foraging and general activity could be distinguished which allowed us to infer the degree of habitat importance at each site. However, we could not investigate which habitats s by using abundance as a response variable.

2.3.3. AnaScheme analysis

The Anabat provides data for the shape, frequency and duration of a microbat call, from which we can identify the species making that call (O'Farrell *et al.*, 1999). Identification of microbat calls, as recorded by the Anabat recorder, was determined through the AnaScheme software. Each call was processed as individual files. AnaScheme is a program that uses regional identification keys in order to match potential calls to associated species, by comparing the shape and duration of call wavelengths. There is 98 % accuracy in correct classification of species, deeming this program to be exceptionally reliable (Threlfall *et al.*, 2011). Certain species share similar call wavelengths, making it near impossible to distinguish between species, thus were grouped into species complexes (Threlfall *et al.*, 2011). These included *Nyctophilus gouldii* and *Nyctophilus geoffroyi* (combined into *Nyctophilus spp.*) and all *Mormopterus* species except *Mormopterus norfolkensis*. Additionally, a selection of species that are considered either significantly threatened, or challenging to identify with AnaScheme, were manually double-checked using the Bat Calls of New South Wales guide (accessible from Department of Environment website). Such species included *Mormopterus norfolkensis, Chalinolobus dwyeri, Scoteanax rueppellii, Falsistrellus tasmaniensis, Saccolaimus flaviventris* and *Nyctophilus spp.*

The software produced outputs that indicated how many passes were made by a particular species, which was used as a measure of activity. Furthermore, as microbats produce noticeably distinct calls when detecting and hunting for prey, the AnaScheme was able to identify any feeding buzzes for species recorded (Threlfall *et al.*, 2011).

2.3.4. Response and predictor variables

Total microbat activity per site was averaged over the whole three-day sampling period. In cases where a site was sampled twice (due to the large area), total microbat activity was averaged for each Anabat separately over the three days, the mean activity for the two Anabats was found. Feeding buzzes were also averaged over the sampling period for each site, and the same method as total activity was followed for large sites. Feeding buzzes were used as a measure of foraging activity. Non-foraging activity was found through the total microbat activity that was NOT a feeding buzz (calculated by: total microbat activity – foraging activity). Species richness was measured as total number of microbat species detected over the three nights per sampling site (Table 2).

This diversity in the condition of woodland patches and their surrounding landscape enabled a determination of relative importance of intrinsic patch attributes, as well as matrix condition, on microbat diversity and activity within remnants, which was the focus of *Matrix Configuration*.

Site attribute sampling

For each patch of woodland surveyed, multiple variables were measured in order to test the assumption that patch condition determines microbat diversity and assemblage (Table 2). The distance from the patch edge to nearest edge of adjacent woodland patch, water body and bottom of escarpment were calculated through Google Earth satellite imagery, using the ruler tool set to metres. Type of water body was categorized based on visual estimations and only included natural water bodies (dams, creeks and ocean). The % canopy cover was also determined through Google Earth, by visual estimations of how much ground surface was observable from

satellite imagery. Canopy cover was divided into three categories: high (>20 % ground surface visible), medium (10-20 % ground surface visible) and low (<10 % ground surface visible).

Polygons of each Illawarra Lowland Grassy Woodland patch in the Illawarra were provided by the Office of Environment and Heritage, which contained a selection of information regarding each patch. This was imported into ArcGIS to retrieve data for predictor variables including size and perimeter of patch. These were then used to calculate the shape of patch, which was a simple patch perimeter (m): area (m^2) formula. The composition of vegetation, either categorized as dominantly Coastal Grassy Red Gum Forest or Lowland Woollybutt-Melaleuca Forest, was also acquired through spatial polygons.

Number of days until the next full moon data was determined through the U.S. Naval Observatory Astronomical Applications Department website (link: http://aa.usno.navy.mil). Dry bulb temperature (ºC), recorded every half hour, was requested from the Bureau of Meteorology. Only data between 7:30PM and 7AM per sampling night was selected for analysis. Each half hourly temperature per night was averaged to get one mean temperature per night. This was then averaged across the three sampling nights to determine the average nightly temperature per site.

Landscape attribute sampling

In order to measure the composition of the matrix surrounding each woodland patch, the percent cover of three dominant land types (urban, agricultural and natural) was estimated using ArcGIS and Google Earth. A 500m buffer was spatially created around each site polygon, in which 20m by 20m grid points were produced. Each site contained roughly 400 to 800 grid points, depending on patch size. The polygon,

buffer and grid points for each site were exported from ArcGIS as KMZ files and imported into Google Earth. At each grid point in Google Earth, the type of landscape under each point was identified and tallied. Any points occurring over the woodland patch polygon was removed from analysis. From the final tally, the abundance of each landscape type was calculated as a percentage. Natural vegetation and remnant woodland categories were pooled to form the 'total % vegetation' category.

Table 2: Description of patch condition and landscape predictor variables used to develop minimal best fit models for microbat species assemblage and diversity.

Type of variable	Variable definition	Type of variable	Units
Response variable			
Total microbat activity	Total number of microbat calls, including foraging and non-foraging, averaged across three sampling nights per site	Continuous	Mean number/site
Foraging activity	Feeding buzzes averaged across three sampling nights per site	Continuous	Mean number/site
Non-foraging activity	All microbat calls that were NOT feeding buzzes averaged across three sampling nights per site	Continuous	Mean number/site
Species richness	Total number of species identified per site, summed across three sampling nights	Continuous	Total number/site
Predictor variable			
Landscape type	Type of landscape in which sampling took place, as identified from 5 categories: large woodland (>50ha in size), medium woodland (20ha-50ha in	Categorical	

size), small woodland (<20ha in size), agricultural and urban.

Temperature	Average half-hourly dry bulb temperature per night between 7:30pm and 6:30am	Continuous	Degrees Celsius
Days from next new moon	Number of days from the FIRST of the three sampling nights until the NEXT new moon	Discrete	Number of days until new moon
Days from initial start date	Number of days from the initial field work start date to the FIRST of the three sampling nights	Discrete	Number of days since start date
Distance to nearest woodland patch (m)	The shortest distance in metres from the edge of a woodland patch to the edge of closest adjacent patch	Continuous	m
Distance from nearest water body (m)	The shortest distance in metres from the edge of a woodland patch to the edge of closest natural water body	Continuous	m
Type of water body nearest to patch	Type of natural water body nearest to patch; excludes pools but includes dams	Categorical	
Distance from edge of lower escarpment (m)	Distance in metres from the edge of the bottom of escarpment to the edge of patch nearest to escarpment	Continuous	m

% Agricultural landscape matrix	Total % of matrix surrounding a patch that is of an agricultural landscape	Continuous	% planar cover
% Urbanisation (total)	Total % of matrix surrounding a patch that is of an urban landscape; both permeable and impermeable surfaces	Continuous	% planar cover
% Remnant vegetation matrix (total)	Total % of matrix surrounding a patch that is of a remnant vegetation landscape; both woodlands and other vegetation communities	Continuous	% planar cover
Vegetation composition	Dominant vegetation community within patch	Categorical	
Shape of patch (perimeter: area ratio)	The shape of patch as calculated using a perimeter (m): area (m2) ratio	Continuous	
Size of patch (ha)	Size of patch in ha	Continuous	ha
Canopy cover	Canopy cover of patch, as determined using three categories: high = <10%, medium = 10-20 %, low = >20 %	Categorical	

2.3.5. Statistical analysis

Variation in microbat assemblages across a modified woodland landscape

The 31 remnant patches were separated into 3 categories based on size (m^2): Large Woodland (LW), Medium Woodland (MW) and Small Woodland (SW), where LW = >50ha in size, MW = 20-50ha and SM = <20ha. For *Modified Landscape*, this reduced the number of woodlands sampled within each category, which enabled a more balanced assessment when analysed alongside the agricultural and urban categories.

To determine whether the type of landscape contributed to changes in microbat assemblage and diversity, a one-factor ANOVA was conducted to compare landscapes (large woodland, medium woodland, small woodland, agricultural and urban) to microbat activity, species richness and diversity, using the statistical package JMP 11. All response variable data (for total activity, foraging activity, non-foraging activity, species richness and diversity) was transformed via square root. This enhanced the normality of residual distributions and homogenized variances. The Tukey Honest Significant Different (HSD) multiple comparison test was conducted in order to determine which landscape type/s contributed to significant changes in assemblage or diversity.

A PERMANOVA analysis was implemented to identify compositional differences in microbat assemblage across the five landscape types, using the statistical package PRIMER 7. Analyses were undertaken for both species abundance (measured as average activity per landscape type) and presence/ absence, to account for contributions made by rarer or less common species on changes in assemblage. Data was normalised for abundance prior to PERMANOVA analysis. In instances where there was significant variation in species assemblage, a pairwise test was performed to identify which species contributed most to these changes. In addition to PERMANOVA outputs, composition differences were also

represented visually through non-metric multidimensional scaling ordination plots (or nMDS). A SIMPER analysis was performed when difference in species composition was determined significant, which identified the species that caused the most variation in assemblages across landscape types.

Effects of landscape matrix on diversity and composition of microbats within woodlands remnants

In order to determine the predictor variables most responsible for changes in species assemblage across woodland sites, minimal best fit models were constructed. The predictors incorporated in analyses include all variables mentioned in Table 2 except landscape type (used solely for *Modified Landscape*). These models were implemented separately for all five response variables (total activity, foraging activity, non-foraging activity, species richness and diversity) using a backwards stepwise elimination process, which removed any variables that had a significance level of more than p=0.05. Each response variable underwent the same transformation procedure as *Modified Landscape* (mentioned previously). The Akaike's information criterion was acknowledged, in order to validate the precision of the model fit. Individual regression models were conducted for all response variables and their significant predictors, which further confirmed the accuracy in the stepwise elimination procedure.

In instances where outliers were clearly present in a dataset, the minimal best fit model and associated individual regression analyses were conducted again with outliers removed. This will determine whether any irregularity in data influences the results.

Chapter 3 - Results

3.1. Variation in microbat assemblages across a modified woodland landscape

3.1.1. Microbat activity

In total, 6362 calls representing 15 microbat species and one species group were detected across the 47 urban, agricultural and woodland sites, ranging from as few as one species in a small woodland habitat to as many as 15 in a large woodland habitat. Of these, 7 species were considered 'vulnerable' under the NSW Conservation Status. On average, across the five landscape categories, total microbat activity was approximately 43 ± 50.5 (mean ± SE) calls per site per night (Figure 10A). Approximately 94 % of these calls were likely associated with navigation through each habitat, and the remainder were associated with foraging activity (Figs. 8B & 1C). On average, large woodlands contained more than twice the rate of foraging activity than urban and agricultural landscapes and small woodland patches (Figure 10B), and 25 % more total and non-foraging activity than the other four categories (Figure 10A & 8C), although such apparent differences were not statistically significant (Table 3) .

Table 3: Output of results obtained through one-factor ANOVA models, which compared microbat activity, species richness and diversity across 5 landscape categories: Large Woodland, Medium Woodland, Small Woodland, Agriculture and Urban. Bold values denote significant effects. Tukeys Honestly Significant Difference (HSD) tests were conducted to identify which response variables differed amongst landscape types.

Response variable Predictor variable	*df*	*SS*	*F*	*P*	*r²*
Total activity per night					
Landscape Type	4	70104	1.267	0.2983	0.108
Error	42	581179			
Foraging activity per night					
Landscape Type	4	852.3	1.521	0.2134	0.127
Error	42	5882.3			
Non-foraging activity per night					
Landscape Type	4	57281.5	1.200	0.3249	0.103
Error	42	501063			
Total species richness					
Landscape Type	4	199.2	4.868	**0.0026**	0.317
Error	42	429.7			
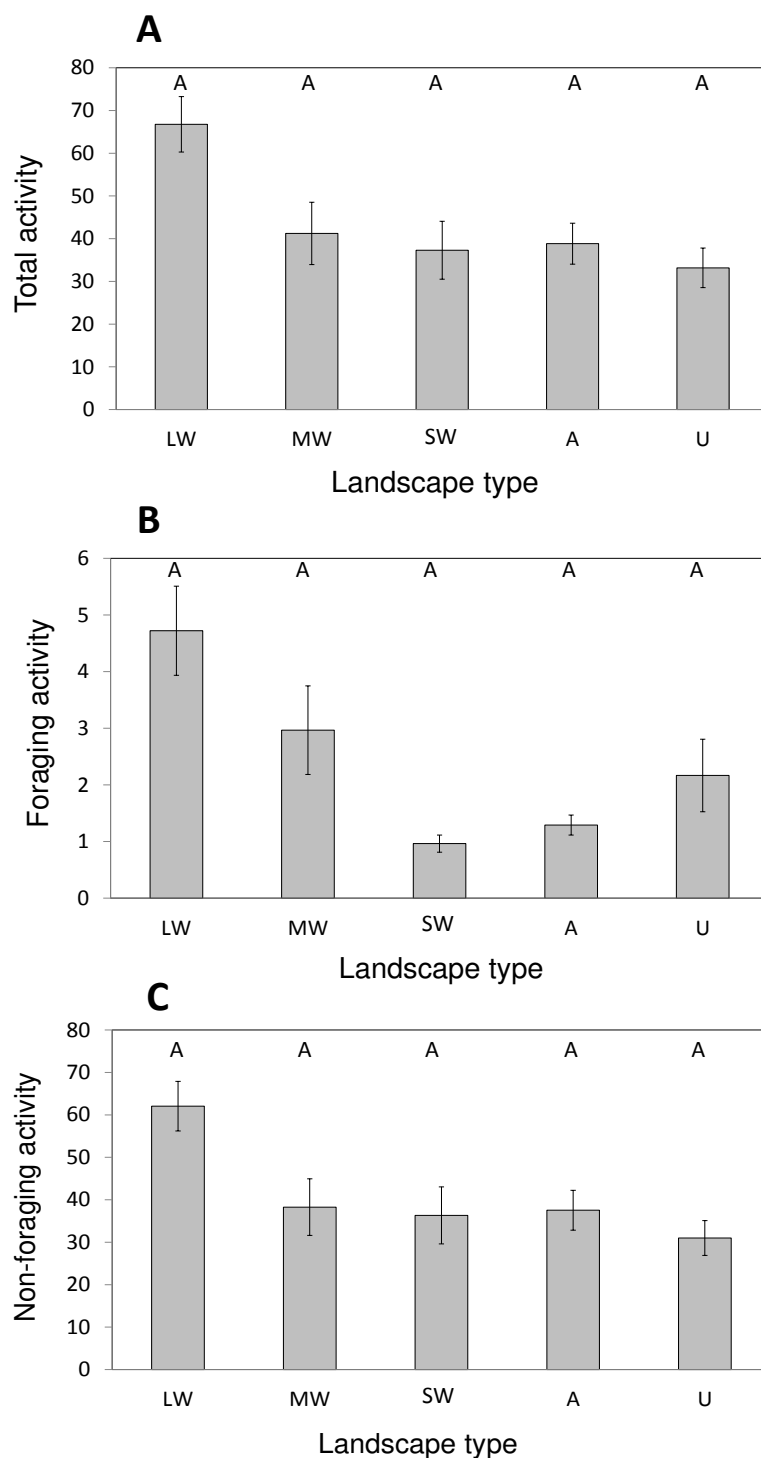
Figure 10: Variation in (a) total, (b) foraging and (c) non-foraging calls of microbats amongst five landscape categories (LW = Large Woodland, $n = 12$; MW = Medium Woodland, $n = 10$; SW = Small Woodland, $n = 9$; A = Agriculture, $n = 8$; U = Urban; $n = 8$). Values are averages ± one standard error. The letters signify significant differences in number of species between landscape types as determined by Tukeys HSD test.

3.1.2. Microbat diversity

Bat species richness varied significantly amongst the five landscape categories (Table 3, Figure 11). Small woodlands contained approximately three-times fewer microbat species than either large woodlands or agricultural landscapes, and the lowest species richness overall. Medium woodlands and urban landscapes had intermediate levels of species richness, which did not differ significantly from either large or small woodlands or agricultural areas. These results indicate a general pattern towards an increase in microbat species richness with increasing woodland patch size.
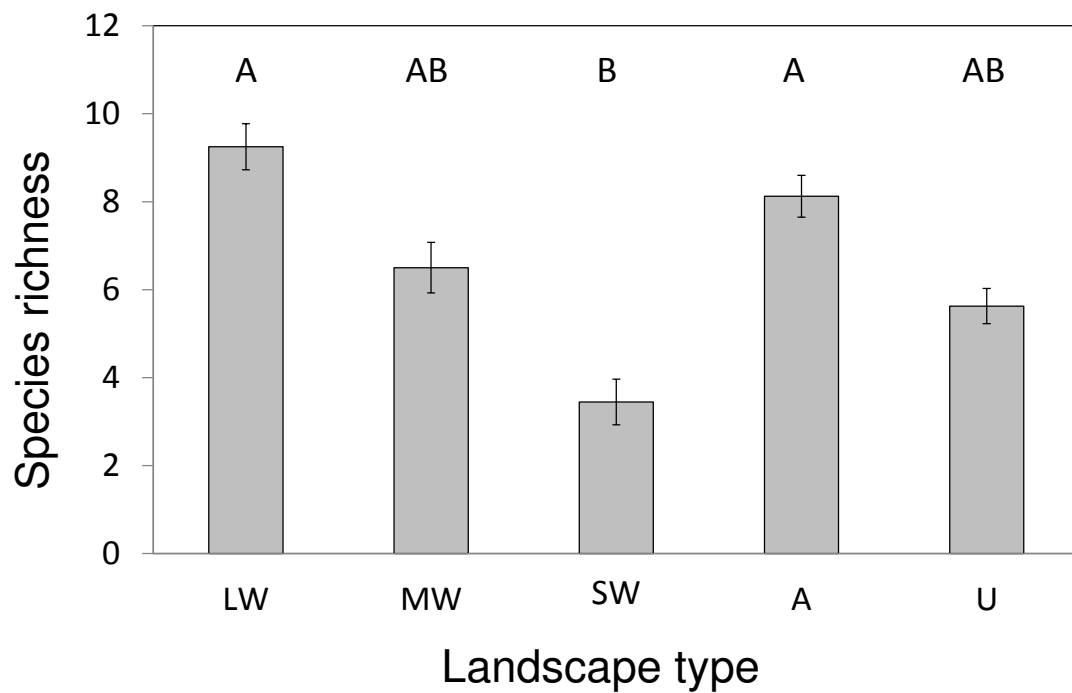
Figure 11: Variation in total species richness over 3 nights amongst five landscape categories (LW = Large Woodland, n = 12; MW = Medium Woodland, n = 10; SW = Small Woodland, n = 9; A = Agriculture, n = 8; U = Urban; n = 8). Values are averages ± one standard error. The letters signify significant differences in number of species between landscape types as determined by Tukeys HSD test.

3.1.3. Microbat community composition

The composition of the microbat community, based on each species' presence or absence at each site, varied significantly across the five landscape categories (Table 4, Figure 12A). Overall, remnant woodlands contained the full set of 15 species and one species group, and no taxa were unique to either urban or agricultural habitats. Large-eared pied bat, *Chalinolobus dwyeri*, was not present in agricultural sites, yet was detected on numerous occasions in urban and woodland landscapes (Table 5). Many taxa were not recorded in urban habitat, yet were frequently identified in woodland and agricultural habitats. These included the East-coast freetail Bat, *Mormopterus norfolkensis*, Yellow-bellied sheathtail bat, *Saccolaimus flaviventris*, Eastern broad-nosed bat, *Scotorepens orion,* and Eastern false pipistrelle, *Falsistrellus tasmaniensis* (Table 5)*.*

There was variation in species presence amongst the three woodland size categories. Medium woodlands contained the full set of 15 species and one species group, while large woodlands had 14 species and one species group (Eastern horseshoe bat, *Rhinolophus megaphyllus*, was absent in large woodlands). Only 11 species and one species group were detected in small woodlands: *S. flaviventris*, *Sc. orion*, Chocolate wattled bat, *C. morio* and Large forest bat, *Vespadelus darlingtoni*, were not present during sampling periods (Table 5). The suite of taxa that visited large woodlands differed significantly from those that visited both small woodlands and urban landscapes, whilst a similar suite of taxa was detected across large and medium woodlands and agricultural landscapes (Table 4). These patterns of variation in species presence were evident in nMDS plots, in which large woodland and agricultural sites were relatively tightly clustered and overlapped upon one another, indicating relatively homogenous compositions. In contrast, sites from each of the other three

landscape categories were widely separated from one another in the ordination space, which indicates that the suites of species were highly heterogeneous (Figure 12A).

Similarly, when the relative activity (i.e. total number of calls) of each species was considered in the compositional analyses, rather than simply whether or not each species was detected at a site, significant differences in microbat community composition across the five landscape categories were detected (Table 4). This result indicates that the difference in community composition amongst the five habitat types was likely driven by variation in the identities of species at each site, rather than their relative activity (as both responses were significant). These patterns were visually evident within nMDS plots, in which there was very strong clustering in the spread of sites between the five landscape categories (Figure 12B).

Table 4: Results acquired through PERMANOVA models, which compared the dissimilarity in microbat species assemblages across 5 landscape categories: Large Woodland, Medium Woodland, Small Woodland, Agriculture and Urban. Bold values denote significant effects. Pairwise tests were conducted in instances where significant effects were found.

Response variable **Source of variation**	*df*	*SS*	*Pseudo-F*	*p*
Assemblage of species in varying landscapes (presence/absence)				
Landscape Type	4	28.57	2.5853	**0.001**
Resemblance	42	116.03		
Pairwise test 'Landscape Type'			t	*p*
Large Woodland v. Medium Woodland			1.2703	0.126
Large Woodland v. Small Woodland			2.4924	**0.002**
Large Woodland v. Agricultural			1.3045	0.085
Large Woodland v. Urban			1.7352	**0.011**
Medium Woodland v. Small Woodland			1.4187	0.059
Medium Woodland v. Agricultural			1.274	0.11
Medium Woodland v. Urban			1.0658	0.333
Small Woodland v. Agricultural			1.8747	**0.005**
Small Woodland v. Urban			1.5658	**0.03**
Agricultural v. Urban			1.6376	**0.008**

Assemblage of species in varying landscapes (activity)

Landscape Type	4	105.76	1.6421	**0.001**
Resemblance	42	676.24		
Pairwise test 'Landscape Type'			t	*p*
Large Woodland v. Medium Woodland			1.1814	0.199
Large Woodland v. Small Woodland			1.765	**0.002**
Large Woodland v. Agricultural			1.3177	0.059
Large Woodland v. Urban			1.4554	**0.023**
Medium Woodland v. Small Woodland			1.1044	0.22
Medium Woodland v. Agricultural			1.0313	0.364
Medium Woodland v. Urban			0.98054	0.479
Small Woodland v. Agricultural			1.3994	**0.015**
Small Woodland v. Urban			1.165	0.188
Agricultural v. Urban			1.1273	0.216

Table 5: Summary of the 16 microbat taxa detected and their distribution. Each value represents the proportion (as a percentage) of the 5 landscape categories that is occupied by each species (where LW = Large Woodland, *n* = 12; MW = Medium Woodland, *n* = 10; SM = Small Woodland, *n* = 9; A = Agriculture, *n* = 8; U = Urban; *n* = 8). When a taxon was present at all sites surveyed for a particular category, value=100%. If a taxon was not detected at all for any sites of a specific category, value=0 %). Conservation status and foraging habitat obtained from the Department of Environment website and Threlfall et al (2011) respectively.

Microbat species	NSW conservation status	Preferred foraging habitat	LW	MW	SW	A	U
Chalinolobus dwyeri	Vulnerable	Clutter	17%	20%	22%	0	25%
Chalinolobus gouldii	Least Concern	Edge	92%	100%	78%	100%	75%
Chalinolobus morio	Least Concern	Edge	83%	50%	0	50%	38%
Falsistrellus tasmaniensis	Vulnerable	Edge	42%	10%	33%	13%	13%
Miniopterus australis	Vulnerable	Edge	75%	70%	33%	38%	25%
Miniopterus schreibersii oceanensis	Vulnerable	Edge	67%	50%	33%	63%	88%
Mormopterus norfolkensis	Vulnerable	Open	67%	40%	33%	88%	0
Mormopterus ridei	Least Concern	Open	92%	80%	33%	88%	75%
Nyctophilus spp.	Variant	Clutter	92%	60%	11%	50%	63%
Rhinolophus megaphyllus	Least Concern	Clutter	0	10%	11%	13%	0
Saccolaimus flaviventris	Vulnerable	Open	33%	10%	0	38%	0
Scoteanax rueppellii	Vulnerable	Edge	42%	10%	11%	63%	13%
Scotorepens orion	Least Concern	Edge	17%	10%	0	63%	0
Tadarida australis	Least Concern	Open	83%	60%	22%	50%	63%
Vespadelus darlingtoni	Least Concern	Edge	33%	20%	0	25%	13%
Vespadelus vulturnus	Least Concern	Edge	92%	50%	33%	75%	75%

A

B
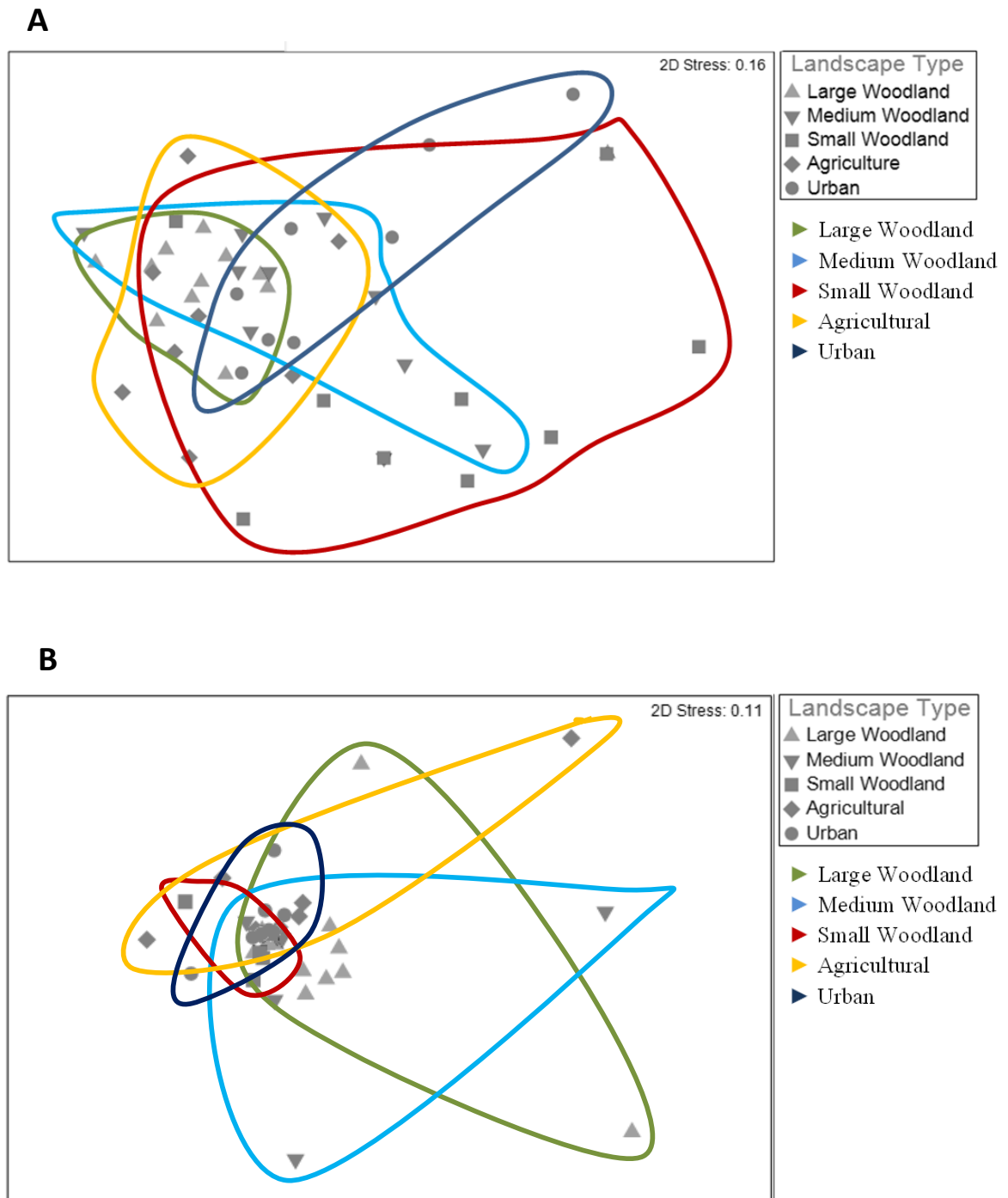
Figure 12: Output of non-metric multidimensional scaling ordination (nMDS) of microbat assemblage across 5 landscape types; (LW = Large Woodland, n = 12; MW = Medium Woodland, n = 10; SM = Small Woodland, n = 9; A = Agriculture, n = 8; U = Urban; n = 8). Figure depicts two-dimensional graphs for A: microbat presence/ absence and B: microbat activity. Symbols more closely clustered together show greater similarity in species assemblage (as determined by the Bray-Curtis indices of dissimilarity).

3.1.4. Species contributing to compositional change

Approximately half of the 15 species and one species group contributed up to 75 % to compositional differences between large and small patches of woodland. Each of these species occurred substantially more frequently throughout large woodland sites. For example, *Nyctophilus* spp. was found in only about 10 % of small woodland sites but occurred in > 90 % of large woodland sites (Table 6). Likewise, *C. morio* was not detected in small woodland sites, yet was more than 80 % likely to occur in large woodland sites. Thus, these results suggest that the likelihood of detecting any one microbat species diminishes significantly with decreasing size of remnant woodland patches, leading to an overall reduction in species richness and diversity.

Similar results were found when comparing small woodlands with agricultural landscapes. The leading contributor to compositional differences was *Mo. norfolkensis,* which had an 88 % likelihood of occurrence across agricultural sites, whilst only 33 % across small woodland sites (Table 6). Two species, *C. morio* and *Sc. orion*, were not recorded in small woodland sites, yet were likely to occur in greater than 50 % of agricultural sites (Table 6).

Urban sites differed from large woodland and agricultural sites in very similar ways, with the majority of species occurring in very few urban sites. For example, *M. norfolkensis* was the key contributor to variation in microbat composition between urban and large woodland sites, as well as urban and agricultural sites. This species was 67 % and 88 % likely to occur in large woodlands and agricultural landscapes, respectively, but was not detected across urban landscapes (Table 6). Likewise, the probability of recording *S. orion* in agricultural sites was 63 %, while the species was not detected in urban sites. However, one

species, Eastern bentwing bat, *Miniopterus schreibersii oceanensis*, was noticeably more common in urban areas (88 %), as opposed to agricultural landscapes (63 %).

Overall, species were more likely to be recorded in urban landscapes than small woodland sites (Table 6). In many cases, the probability of a species occurring was at least double in urban sites than in small woodland sites. *Mi. schreibersii oceanensis* was the highest contributor to this variation, with an 88 % chance of this species being detected in urban areas but only a 33 % chance of being detected in small woodlands.

In summary, for almost all species, there was a general trend towards a reduction in likelihood of occurrence with decreasing size of remnant woodland patches. Most of these species were equally likely to occur in large woodland patches and agricultural landscapes, but the chance of detecting these species was generally lower across urban landscapes. There was no difference in the relative activity of each species between each of the five landscape categories.

Table 6: Summary of *significant* results obtained through SIMPER analyses, which presents microbat species contributions to the variation between the presence/ absence of species (an indicator of assemblage) across 5 landscape types; Large Woodland, Medium Woodland, Small Woodland, Agriculture and Urban. The probability of a species occurring in a landscape ranges from 0-1; with 0 = not present and 1 = present in all sites.

Species	Presence/ absence of calls per night*		Average Dissimilarity	Dissimilarity/ SD	Contribution (%)	Cumulative contribution (%)
	Large Woodland (*n*=12)	**Small Woodland (*n*=9)**				
Nyctophilus spp.	0.92	0.11	6.02	1.86	10.46	10.46
Chalinolobus morio	0.83	0.00	5.81	1.87	10.10	20.56
Tadarida australis	0.83	0.22	5.61	1.04	9.75	30.31
Vespadelus vulturnus	0.92	0.33	5.01	1.21	8.70	39.01
Mormopterus sp. 2	0.92	0.33	4.96	1.18	8.62	47.63
Miniopterus australis	0.75	0.33	4.33	1.09	7.53	55.16
Mormopterus norfolkensis	0.67	0.33	4.14	1.00	7.20	62.36
Miniopterus schreibersii oceanensis	0.67	0.33	4.08	1.06	7.10	69.46
Falsistrellus tasmaniensis	0.42	0.22	2.95	0.87	5.13	74.59
	Large Woodland (*n*=12)	**Urban (*n*=8)**				
Mormopterus norfolkensis	0.67	0.00	3.86	1.32	9.69	9.69
Miniopterus australis	0.75	0.25	3.80	1.21	9.52	19.21
Chalinolobus morio	0.83	0.38	3.76	1.11	9.43	28.64
Nyctophilus spp.	0.92	0.63	2.88	0.77	7.23	35.87
Miniopterus schreibersii oceanensis	0.67	0.88	2.81	0.71	7.05	42.92
Tadarida australis	0.83	0.63	2.59	0.79	6.50	49.42
Scoteanax rueppellii	0.42	0.13	2.47	0.85	6.20	55.61
Chalinolobus gouldii	0.92	0.75	2.31	0.61	5.80	61.42
Mormopterus sp. 2	0.92	0.75	2.31	0.61	5.80	67.22
Vespadelus vulturnus	0.92	0.75	2.26	0.60	5.66	72.88
	Small Woodland (*n*=9)	**Agricultural (*n*=8)**				
Mormopterus norfolkensis	0.33	0.88	5.14	1.20	9.31	9.31

Species						
Mormopterus sp. 2	0.33	0.88	5.14	1.20	9.31	18.63
Vespadelus vulturnus	0.33	0.75	4.96	1.08	8.98	27.61
Scotorepens orion	0.00	0.63	4.57	1.19	8.28	35.89
Scoteanax rueppellii	0.11	0.63	4.52	1.14	8.19	44.08
Miniopterus schreibersii oceanensis	0.33	0.63	4.51	0.99	8.17	52.25
Tadarida australis	0.22	0.50	3.94	0.92	7.14	59.39
Nyctophilus spp.	0.11	0.50	3.85	0.91	6.97	66.36
Chalinolobus morio	0.00	0.50	3.51	0.94	6.36	72.72
	Small Woodland (*n*=9)	**Urban (*n*=8)**				
Miniopterus schreibersii oceanensis	0.33	0.88	6.73	1.19	12.46	12.46
Tadarida australis	0.22	0.63	6.16	0.97	11.40	23.85
Vespadelus vulturnus	0.33	0.75	5.96	1.07	11.03	34.88
Mormopterus sp. 2	0.33	0.75	5.70	1.10	10.55	45.43
Nyctophilus spp.	0.11	0.63	5.26	1.15	9.74	55.17
Chalinolobus gouldii	0.78	0.75	4.33	0.71	8.01	63.18
Chalinolobus dwyeri	0.22	0.25	3.91	0.64	7.24	70.41
	Agricultural (*n*=8)	**Urban (*n*=8)**				
Mormopterus norfolkensis	0.88	0.00	5.61	2.29	12.87	12.87
Scotorepens orion	0.63	0.00	3.86	1.22	8.84	21.70
Scoteanax rueppellii	0.63	0.13	3.78	1.15	8.66	30.36
Tadarida australis	0.50	0.63	3.34	0.95	7.66	38.03
Nyctophilus spp.	0.50	0.63	3.32	0.96	7.62	45.65
Chalinolobus morio	0.50	0.38	3.18	0.97	7.28	52.93
Miniopterus schreibersii oceanensis	0.63	0.88	2.77	0.79	6.35	59.28
Miniopterus australis	0.38	0.25	2.76	0.84	6.34	65.62
Vespadelus vulturnus	0.75	0.75	2.61	0.74	5.98	71.60

3.2. Effects of landscape matrix on diversity and composition of microbats within woodlands remnants

Total microbat activity was not influenced by either of the suite of patch or matrix attributes, but significantly declined with increasing number of days since the initial sampling event (Table 7, Figure 13A). There was also a significant reduction in feeding activity through time (Table 7, Figure 13B). It was apparent that non-foraging activity was not influenced by any predictor variables tested, yet the number of days since commencement of fieldwork was near significant (Table 7).

Table 7: Summary of general linear results for total microbat activity, total feeding activity and species richness. All response variable values were transformed prior to analysis. Bold values denote significant effects. Highest contributing predictor variables were determined using a stepwise elimination process. The elimination of insignificant predictor variables were verified using the Akaike's information criterion (AIC).

Response variable Predictor variable	DF	SS	F	p	r^2	AIC	Direction of response
Total microbat activity							
Model	1	68.21	7.6745	**0.0097**	0.209	160.5214	
Start Date	1	68.21	7.6745	**0.0097**			Negative association between total microbat activity and days since initial start date
Error	29	257.75					
Foraging activity							
Model	1	11.042641	11.9946	**0.0017**	0.29259	90.23213	
Start Date	1	11.042641	11.9946	**0.0017**			Negative association between feeding activity and days since initial start date
Error	29	14.302287					
Non - foraging activity							
Model	1	24.363440	4.1801	0.0501	0.125983	147.4406	
Start Date	1	24.363440	4.1801	0.0501			Negative association between feeding activity and days since initial start date
Error	29						
Species richness							
Model	4	11.772733	10.5306	**<0.0001**	0.618334	58.50297	
Urbanisation %	1	2.981762	10.6686	**0.0031**			Negative association between species richness and total urban

					matrix cover within a 500m buffer
Size (ha)	1	1.4881428	5.3245	**0.0292**	Positive association between species richness and size of patch (ha)
Start Date	1	2.3996057	8.5857	**0.0070**	Negative association between species richness and days since initial start date
Error	26	7.26703			
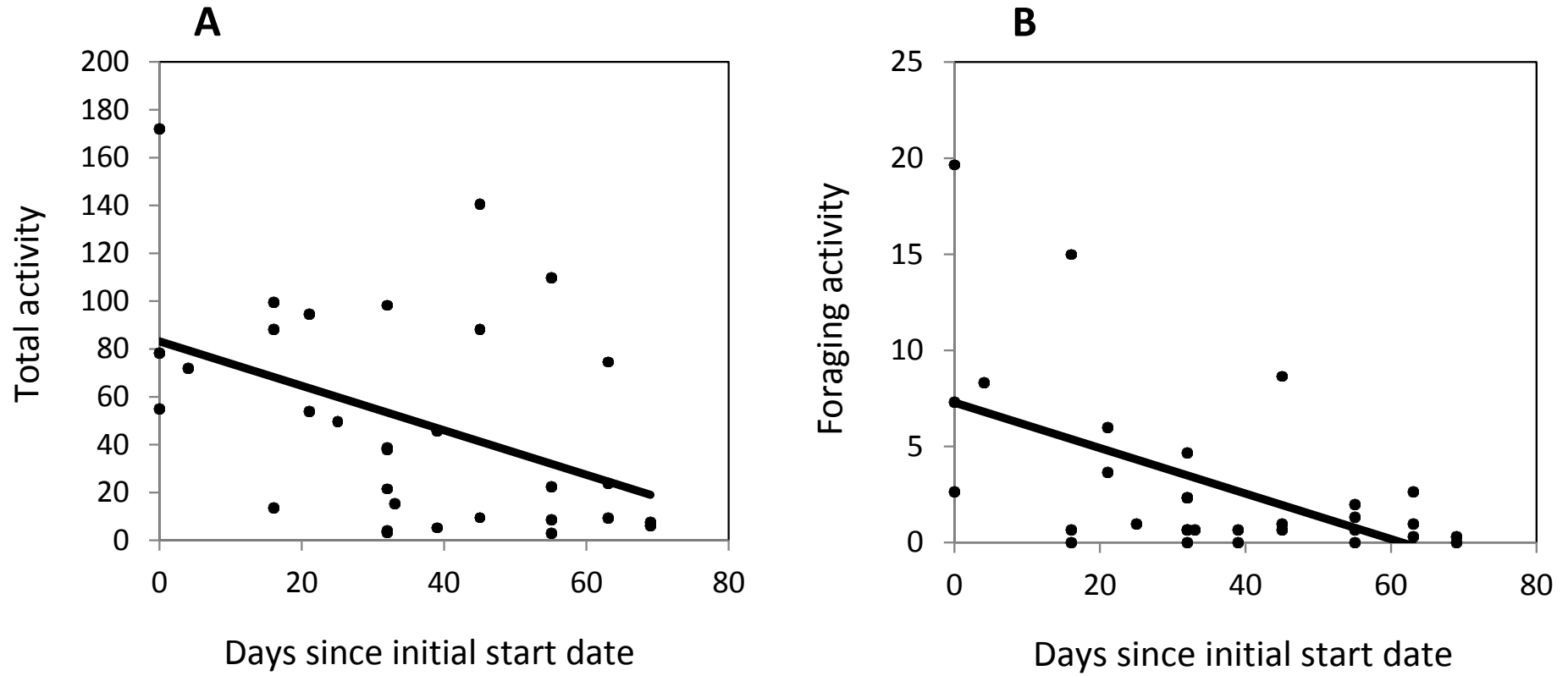
Figure 13: A: relationship between total microbat activity per night and number of days since initial start date and B: relationship between microbat feeding activity per night and number of days since initial start date (*n*=31).

Microbat species richness declined significantly with increasing percentage cover of urbanisation within the matrix surrounding the woodland patches (Table 7, Figure 14A). It was apparent that this negative relationship was non-linear, such that the decline in species richness did not occur until a minimum threshold of urbanisation of the landscape matrix was exceeded (Figure 14A). In order to determine whether or not this apparent threshold existed, I separated the data into two sets of samples: the first representing species richness of woodland sites surrounded by less than 30 % urbanisation and the second representing species richness of sites surrounded by greater than 55 % urbanisation (there were no woodland sites with levels of matrix urbanisation between 30 and 55 %). For each of these two sets of data I then ran individual regression analyses to determine the relationship between species richness and matrix urbanisation. As expected, there was no significant relationship between species richness and urbanisation at levels of less than 30 % within the surrounding matrix ($F = 0.0386$, $R^2 = 0.0030$, P = 0.8472, $n = 15$), yet there was a significant negative association between species richness and urbanisation at levels exceeding 55 % ($F = 7.3911$, $R^2 = 0.3455$, P = 0.0166, $n = 16$).

Woodland patch size was significantly and positively related to species richness (Table 7, Figure 14B). However, this positive relationship seemed to be overly influenced by one very large woodland site, Blackbutt Reserve, which was about three times larger than the second largest site. However, when I removed this site and ran a regression analysis, I found that the positive relationship between species richness and woodland patch size was retained and strongly significant ($F = 10.4394$, $R^2 = 0.271581$, P = 0.0031, $n = 30$). The number of days since the commencement of fieldwork also had a negative effect on the number of species present within woodland patches (Table 7, Figure 14C).
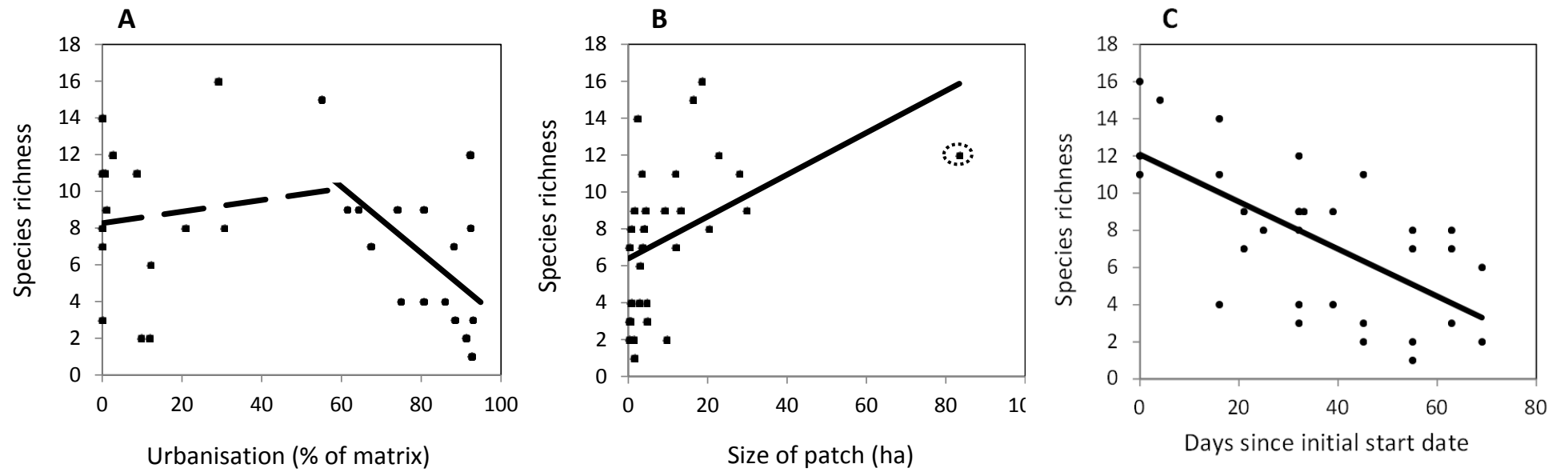
Figure 14: Relationship between total species richness per site and A: % urbanisation, B: size of patch (ha) and C: number of days since initial start date across woodland sites (*n*=31). Black line indicates a significant linear relationship, while the dotted line represents a non-significant relationship. Dotted circles denote outliers.

Chapter 4 – Discussion

4.1. Variation in microbat assemblages across a modified woodland landscape

Fragmentation is known to cause reductions in levels of microbat activity across many different ecosystems across the globe, such as forest and woodland habitats (Estrada and Coates-Estrada, 2001, Stebbings, 1995, Verboom, 1998, Walsh and Harris, 1996). In contrast, to this, however, I found that there was no association between microbat activity, including both foraging and non-foraging activity, and landscape type. Indeed, activity level remained fairly constant between each landscape category, regardless of woodland patch size, or extent or type of human modification of the surrounding landscape.

The total microbat activity (on average, 47 passes per night at each site combined across all landscapes) that I recorded was extremely low in comparison to other studies conducted in New South Wales, Australia. Lumsden and Bennett (2005) determined that the average microbat activity per site across an agricultural landscape of varying tree density in south eastern Australia was roughly 247 calls per night (Lumsden and Bennett, 2005). Law and Chidel (2002) detected 144 passes per night in riparian habitats in Chichester State Forest (Law and Chidel, 2002). Furthermore, Law and Chidel (2006) found an average of 302 passes per night in small remnant native vegetation, yet also found a mere 50 passes in agricultural paddocks (Law and Chidel, 2006). Similarly, Law et al (2011) detected a mean of 650 passes in remnant habitats and only 40 passes in paddocks (Law *et al.*, 2011b). However, in a study of bat activity across an intensely urbanised landscape by Threlfall et al (2011) in Sydney, bat activity was found to be about 35 passes per night. Given that the Illawarra region has been extensively cleared for agricultural and urban purposes, it is likely that the

entire region has suffered a dramatic reduction in bat activity, even in locations where patches of remnant woodland persist.

In contrast to my research, several other studies have found that microbat activity varies across different landscape types, with a general trend towards a reduction in activity in areas disturbed by human processes. For example, Threlfall et al (2011) found that activity in a highly urbanised region of Sydney, Australia, was significantly lower than activity in agricultural landscapes (Threlfall *et al.*, 2011). Similar results were found in international research. Walters et al (2007) studied the foraging preferences for *Lasiurus borealis*, a species of microbat distributed in the U.S.A, along an urban-rural gradient. It was found that this species was more active in grazed pastures than urban spaces, in fact they almost avoided visiting these areas entirely, possibly due to a reduced abundance of insects in urban settings (Walters *et al.*, 2007).

I found that microbat diversity was generally higher in remnant woodland patches than in the surrounding modified landscapes. However, there was a dramatic reduction on microbat diversity as the size of the woodland remnants decreased. Furthermore, bat diversity was 40 % lower in urban areas than large woodland patches. This supports the initial prediction that there would be significant variation in the diversity of microbat communities across the urban-rural-remnant gradient.

Similarly, Hourigan et al (2006) found that there was a wider array of microbat species that commuted and foraged in native vegetation than in anthropogenic-altered habitats. In fact, only one species was able to exploit resources in highly urbanised landscapes (Hourigan *et al.*, 2006). Hourigan et al (2010) compared the microbat diversity in remnant bushland and urban landscapes in Brisbane, Australia. A total of 14 species were detected, of which 100 % of these species were found in bushland, while 78 % were found in

high-density urban spaces. This result was likely due to the decrease in vegetation in areas with high urbanisation (Hourigan *et al.*, 2010).When investigating the response of insectivorous bat communities to human-altered landscapes in Indiana, U.S.A, Duchamp and Swihart (2008) found that species diversity was greatest in large forest habitats and declined with increasing urbanisation. It was predicted that the negative response to urbanisation was due to limited roosting resources for hollow-dwelling species. Furthermore, increasing urban development often leads to a reduction in insect abundance and a greater risk in fatality caused by increased traffic levels (Duchamp and Swihart, 2008).

Surprisingly, however, I found that agricultural landscapes were occupied by a level of microbat diversity similar to that of large woodland patches, indicating that agricultural land can retain high levels of diversity. There were approximately 20 % more species found in agricultural areas than urban spaces. This supports other Australian studies, including an investigation on microbat response to habitat modification along an urban-rural-forest gradient performed by Kirsten and Klomp (1998). It was found that species diversity was significantly lower in urban areas than agricultural habitats, while forest patches contained the most species (Kirsten and Klomp, 1998). Law et al (1999) found that the number of species visiting open agricultural fields in New South Wales was on par with large remnant patches. A suggested reason for this is due to more resource opportunities for open-adapted species, which consume insect pests drawn to crop fields (Law *et al.*, 1999). However, some studies have found contrasting results. Gehrt and Chelsvig (2003) found that microbats in Chicago, U.S.A, preferred to visit woodland and urban habitats more than agricultural sites. This was possibly due to there being more exposure to woodland edge in urban landscapes in this area, as agricultural land is typically not directly connected to woodland fragments in

Illinois. Moreover, certain bat species restrict their foraging activity to areas near a light source, as many insects are commonly attracted to illumination (Gehrt and Chelsvig, 2003).

The most notable difference in microbat diversity was between woodland patches of varying size. Species richness was significantly lower in small woodlands. In fact, there was approximately 65 % and 33 % more species found in large and medium woodlands, respectively, than small patches. This indicates that degree of habitat fragmentation, in terms of patch size, adversely influences microbat diversity. Clutter adapted species prefer habitats with large areas of dense vegetation when foraging, thus small woodlands are deemed unsuitable for these species (Threlfall *et al.*, 2011). However, this is inconsistent with past research. Many other studies found that number of microbat species were not associated with woodland size. Law et al (1999) examined the bat community response to fragmentation along the Great Dividing Range in Australia. Species richness did not differ between forest habitats of varying size, demonstrating that even the smallest patches provided conservation resources for bats. However, it was found that foraging activity was significantly lower in small patches, as opposed to large forests, indicating that the high microbat diversity in small remnants is not due to prey availability. Quite possibly, the smallest patches still contain roosting sites for bat species (Law *et al.*, 1999). Similarly, Law and Chidel (2006) found that microbats in southern New South Wales were not affected by habitat size; rather they were successful in exploiting even the smallest remnant patches. Thus, it is likely that small fragments still contained an abundance of hollow-bearing trees or insects upon which the microbats forage (Law and Chidel, 2006).

As originally predicted, the composition of microbat species varied significantly between landscape categories, which indicate that certain species are better adapted to fragmented and modified landscapes than others.

Specifically, *Mormopterus norfolkensis* was found in 88 % of all agricultural sites and 67 % of all large woodlands, yet was never detected in urban. This was expected, given that this species has a low echolocation frequency suitable for foraging and commuting in open areas. The pulse of low frequency echolocation calls is long in comparison to higher frequencies, allowing a signal to reach greater distances when detecting prey in open areas (Law *et al.*, 2011a). While indeed most records of detection for this species have been within eucalypt forests and woodlands, they show a preference for open spaces in vegetated habitats, including flyways and creek lines (Churchill, 2009). Time spent in cluttered environment is primarily for roosting, as this species prefers to reside in tree hollows, while open landscapes are suitable for foraging (Churchill, 2009). However, this species was only detected in 33% of all small woodland sites. This suggests that either the smaller patches contained less flyways or the hollow-bearing tree availability for this species was minimal.

When comparing highly urbanised landscapes with small patches of woodland, it was evident that many species would rather forage and commute in urban spaces. *Miniopterus schreibersii oceanensis* and *Vespadelus vulturnus* had an impressive 88 % and 75 % respective likelihood of being identified in urban areas, which was more than twice the chance of detection in small woodlands. This is an unexpected result, as these species are adapted to foraging along the edges of woodlands. However, *M. schreibersii oceanensis* has a moderate wing loading, indicating that this species can manoeuvre through low-cluttered areas. Additionally, this species is able to roost in urban structures, indicating that it is relatively tolerant to urbanisation (Threlfall *et al.*, 2011). *V. vulturnus*, however, has a low wing loading, thus is expected to visit woodland sites over urban areas (Threlfall *et al.*, 2011). Similar to *M. norfolkensis*, this species roosts in tree hollows (Churchill, 2009). Therefore, it is highly likely that hollow abundance is minimal in small remnant patches.

Miniopterus australis was three-times more likely to occur in large woodlands than urban sites. This species has relatively small wing loading, which is an adaptation that allows foraging in cluttered sites. Furthermore, they have high echolocation frequencies (>48 kHz), which is unsuitable for detecting prey in urban environments (Threlfall *et al.*, 2011). High frequencies have a shorter range, appropriate for receiving signals in crowded environments (Law *et al.*, 2011a). Thus, it is evident that traits possessed by this species limited its tolerance to urbanisation.

Nyctophilus spp. was eight times more likely to visit large woodlands than small patches. This species is particularly intolerant of artificial lighting, such as street lights in urban settings, as this leads to higher predation risks (Threlfall *et al.*, 2013b). Thus, it is likely that this species was adversely affected by decreasing patch size, due to the increased edge effects. Certain small woodlands surveyed were completely enclosed by urban structures, which could explain this result.

Chalinolobus morio was never identified in small woodlands and *Tadarida australis* had only a 22 % chance of detection in small woodlands, yet both species were recorded at 83 % of large woodland sites. As *C. morio* is well adapted to flying through cluttered areas, due to the small wing loading, this finding comes to no surprise. However, as *T. australis* is adapted to open spaces, detecting this species more frequently in large woodlands was not expected (Threlfall *et al.*, 2011).

These findings agree with previous research, including a study conducted by Hanspach et al (2012) in south eastern Australia. It was found that fast-flying species were more frequently detected in open landscape, including human-modified areas, which wasn't surprising given their relatively inability to manoeuvre through cluttered habitats. Highly vegetated patches were dominated by slow-moving, highly manoeuvrable species (Hanspach

et al., 2012). Law and Chidel (2002) found that certain species, including *Vespadelus darlingtoni* and *Falsistrellus tasmaniensis,* were highly more active in open areas than in cluttered landscapes, when investigating the difference in species assemblage between logged and unlogged forest patches (Law and Chidel, 2002). Ethier and Fahrig (2011), who investigated the effects of forest fragment size on insectivorous bat abundance in rural Canada, also obtained similar results. It was found that the effects of forest size were mixed amongst species. Certain species were highly abundant in large forest patches, while absent in open areas, whereas larger populations of other species resided in these open landscapes, yet not detected in forest patches. However, it was suggested that this difference in composition was due to varying roost preferences between species, not trait characteristics (Ethier and Fahrig, 2011).

4.2. Effects of landscape matrix on diversity and composition of microbats within woodlands remnants

4.2.1. Woodland patch attributes

It was clear that patch attributes had minimal effect on microbat activity and diversity. It was evident that microbats did not significantly respond to canopy cover or shape of woodland patch. This is likely due to invertebrate prey residing in the lower vegetation strata layers, thus not responsive to the condition of the upper tree canopy (Fenton *et al.*, 1998). Microbat activity and diversity have also been found to be unresponsive to patch shape and distance to nearest patches, since they are able to fly between adjacent habitats over large distances (Bernard and Fenton, 2007).

4.2.2 Matrix attributes

Furthermore, matrix attributes, including proximity to adjacent woodland patch, distance to nearest water body and distance from escarpment, did not significantly influence microbat activity and diversity. Connectivity commonly has little influence on microbat activity and diversity, as many species are capable of flying great distances, and thus can migrate between fragmented woodlands. Additionally, due to high dispersal abilities, these bats can travel to water bodies and the escarpment, regardless of distance from woodland patches (Law and Chidel, 2002, Law *et al.*, 2000).

Unexpectedly, the extent of agriculture and native vegetation cover in the surrounding matrix had no effect on microbat activity or diversity within remnant woodlands. However, there was a significant negative association between microbat diversity within woodlands and the extent of urbanisation surrounding a remnant woodland patch. Furthermore, urbanisation had no adverse effects on microbat diversity until urbanisation exceeded about 50 % of the total matrix. Above this threshold, the number of microbat species visiting a patch

significantly declined. In fact, with every 10 % increase of urban density beyond this threshold, approximately two microbat species were lost. There are a number of plausible reasons for this result. With increasing urbanisation comes a higher risk of vegetation destruction due to littering, trampling and clearing for aesthetic or recreational purposes (Hedblom and Söderström, 2008, Sukopp, 2004, Ode and Fry, 2006). Thus, woodland fragments predominately enclosed by urban development are more likely to deteriorate in ecological value with human activity, due to the loss of hollow-bearing trees and flowering shrubs that attract aerial insects (Hedblom and Söderström, 2008, Sukopp, 2004, Ode and Fry, 2006). Litteral and Wu (2012) discovered that high density of urbanisation in the matrix had negative effects on avian diversity within a remnant habitat. A possible reason for this was owing to the intense noise, light and human activity associated with urbanisation (Litteral and Wu, 2012). Insectivorous bats have been found to respond similarly to noise and light pollution (Barber *et al.*, 2010, Gaston *et al.*, 2013). Stone et al (2009) investigated how bats were influenced by artificial light in Britain and discovered that microbat activity was adversely affected by increased artificial lighting. In fact, these species altered their commuting routes to avoid this pollution (Stone *et al.*, 2009). Schaub et al (2008) studied the effects of noise pollution on microbat foraging preference in Germany and found that noises with similar signals to prey sounds deterred bats from foraging. It was suggested that this noise masked the bats' ability to detect prey using echolocation, indicating that less species will forage in areas with high noise pollution (Schaub *et al.*, 2008). Thus, it is likely that microbats in the Illawarra responded similarly to artificial lighting in the matrix surrounding woodlands. Noise and light pollution may deter certain species sensitive to urbanisation from commuting between woodlands across an urban matrix.

The activity and composition of microbat communities are highly influenced by the distribution of insects. Insects inhabiting remnant habitats are frequently predated on by clutter-adapted microbat species, while open-adapted bats forage on insects in cleared landscapes, including agricultural areas and some urban spaces (Threlfall *et al.*, 2011, Threlfall *et al.*, 2012a). Insect composition and abundance within remnant habitats, however, can be altered by the configuration of a surrounding matrix. Brown Jr and Freitas (2002) found that butterfly population size declined with increasing urbanisation in the matrix, due to an increase in human activity and pollution near forest fragments (Brown Jr and Freitas, 2002).This implies that insects are adversely affected by urbanisation within the matrix. Furthermore, studies have shown that with increasing light source in a habitat, more invertebrates are drawn to urban spaces (Connor *et al.*, 2002, van Langevelde *et al.*, 2011). Lim and Sodhi (2004) found that with increasing light source from urban development in Malaysia, insects were drawn to urban landscapes. As insect populations, which are drawn to light, migrate from remnant patches to urban structures, or sensitive to matrix effects and are at risk of death, the foraging resources available for clutter-adapted species will decline. Thus, it is possible that the microbat species inhabiting the woodlands will migrate to other patches.

4.3. Implications and recommendations for conservation

My results indicate that bat activity is very low throughout the Illawarra across all landscape types, compared with nearby regions of NSW, although the region contains 15 of the 29 known species of the larger region. Furthermore, the species that are retained in this landscape are limited to large remnant woodlands and agricultural areas. I also found that the number of bats that are active within the remnant woodlands declines as the agricultural areas are replaced with urban structures within the surrounding matrix. Given that many agricultural areas are being abandoned and transformed into urban land, it is likely that bat diversity will continue to decline across the Illawarra region.

This raises concern regarding the future status of microbat species population in the Illawarra region. If fragmentation of woodlands continues, as a result of extensive land clearing for urban development, clutter-adapted species will be restricted from commuting and foraging in woodlands, possibly leading to local extinctions. Thus, it is essential to protect the existing woodlands, through setting up reserves, as well as improving habitat availability for clutter-adapted species. One recommendation for increasing the size of small woodland patches is through revegetation. Encouraging the public to plant trees and shrubs in these patches will enhance the vegetation density, which potentially improves the population size of local clutter-adapted microbats.

The composition of microbat species significantly varied between urban, agricultural and remnant landscapes. Highly manoeuvrable species with high echolocation frequency were found in woodland patches, while species with low manoeuvrability and echolocation frequency were found in urban and agricultural lands. If urbanisation continues to grow in the Illawarra region, then the possibility of microbat composition in the area will increase in homogeneity is high. This will consequently reduce the microbat diversity, as clutter adapted

species may be more prone to mortality, due to a loss of foraging and roosting habitats. Thus, it is recommended that vegetation density in urban and agricultural landscapes is improved, through the planting of flowing shrubs, to attract aerial insects, and hollow-bearing trees. This will increase the foraging and roosting resources for species adapted to cluttered environments.

However, simply improving the condition of remaining woodland patches and planting more trees in urban and agricultural land may not be an adequate conservation effort when protecting microbat diversity. The configuration of the landscape surrounding a woodland patch greatly influences the diversity of species visiting the remnant woodlands of the Illawarra. Urbanisation density is the leading contributor to microbat biodiversity decline. Thus, containing woodland patches in reserves will not eliminate risks of diversity decline and population extinctions in the Illawarra. Instead, the landscape surrounding healthy woodland patches must be well managed and protected from potential urban development. A suggested strategy to manage these landscapes is through limiting urban density, within a 500 metre radius of woodland patches, to less than 55 % total cover. This will potentially enable all microbat species to commute and forage across the modified landscape in the Illawarra.

In order to improve biodiversity protection in the Illawarra, the best method for conserving microbat populations in Illawarra Lowland Grassy Woodland patches is to limit any future landscape modifications, especially urban development, which will restrict diversity decline and minimise the deterioration of woodland patch value to mammal species. Furthermore, through the planting of hollow-bearing trees and flowering shrubs, woodland patches can grow in size and human-modified landscapes can provide more resources for fauna residing in the Illawarra.

4.4. Recommendations for future research

Hollow availability was not considered in this study, which limited our understanding of the importance of hollow-bearing trees for microbats visiting a particular type of habitat. Rhodes and Wardell-Johnson (2006) found that *Tadarida australis* resided in areas with high hollow-bearing tree availability, regardless of whether these trees were in an urban or forested landscape, while Lumsden et al (2002) discovered that *Nyctophilus geoffroyi* and *Chalinolobus gouldii* preferred to roost in forests with greater hollow abundance (Lumsden *et al.*, 2002, Rhodes and Wardell-Johnson, 2006). Therefore, future studies should aim to include abundance of hollow-bearing trees in fragmented woodlands. It is possible that patches of woodlands with high hollow availability can buffer loses of microbat diversity as result of urbanisation within the landscape matrix. Likewise, bat diversity could be enhanced in woodland patches that have a depleted set of hollow-bearing trees through supplemented nest boxes (Smith and Agnew, 2002).

Furthermore, the effects of small-scale patch attributes (e.g. vegetation structure, tree hollow density and composition) on microbats were not examined, since my focus was on medium (e.g. patch size) and large (e.g. matrix configuration) scale effects. Canopy cover was measured as a categorical variable by visual estimations using Google Earth. However, it is clear from previous research that vegetation in the other strata layers can also influence microbat behaviour by impeding manoeuvrability and prey detection (Basham *et al.*, 2011). Thus, it is recommended that vegetation density and height for canopy, shrub and ground layers are considered in future studies. Furthermore, in order to determine the suitability of flyways for bats, as they tend not to prefer woodlands with minimal gaps between vegetation storeys, the vertical distance between canopy, shrub and ground cover should be measured (Basham *et al.*, 2011). Canopy species can influence bat activity and species richness. This is

due to some species providing roosting and feeding resources, which supports higher species richness and population densities of bats and other taxa (including insects; which are prey of bats) (Threlfall *et al.*, 2011). Additionally, the diameter of hollow-bearing tree trunks influences species richness, as some species are found to be commonly roosting in trees with a diameter greater than 80cm (Basham *et al.*, 2011, Threlfall *et al.*, 2013b). Upcoming research should therefore take canopy composition into account.

Insects are known to influence microbat distribution (Gonsalves *et al.*, 2013). Insect biomass was not measured in this study, thus it is not known whether urbanisation or fragmentation directly influences microbat assemblage, or indirectly through insect response. A recommendation for future studies is to measure invertebrate abundance and diversity, in order to assess whether foraging requirements influence distribution of microbats in fragmented landscapes. Light traps are frequently used in Australian studies to sample flying nocturnal insects which are a dominant component of a microbat's diet (Adams *et al.*, 2005, Threlfall *et al.*, 2012a).

While the Anabat is effective in recording microbat calls in order to identify the species present in a site, it is impossible to differentiate individuals making the calls. Thus, it is possible that the Anabat recorded the same individual numerous times. My research was restricted to measuring microbat activity and not abundance. Future research should include trapping methods, in order to measure abundance in fragmented woodlands. A common trapping method is the use of harp traps, which Milne et al (2005), Law et al (1998) and Anderson et al (2006) have all adopted in past research. Measuring abundance can aid in identifying which habitats are most important to a certain species (Anderson *et al.*, 2006, Law *et al.*, 1998, Milne *et al.*, 2005).

Chapter 5 - Conclusion

The objective of this research was to identify whether habitat fragmentation and human-modification influenced the activity and diversity of microbats in the Illawarra. It was found that while woodland condition and landscape modification had no effect on microbat activity, the species richness and composition of bat communities were significantly altered. Diversity declined with reduction in woodland patch size and more species favoured large woodlands and agricultural land over urban areas. This is likely due to the limited availability of roosting and foraging resources in smaller woodlands. Community composition varied with landscape type, due to the traits possessed by individual species. Clutter adapted species were dominant in larger woodlands and open adapted species were primarily found in agricultural land. Similarly, composition differed with roosting preferences; species that roost in tree hollows were found in larger woodlands, while other species were adapted to roosting in urban structures. Microbat diversity was also influenced by the condition of the matrix surrounding woodland patches. Species richness in woodlands surrounded by more than 55 % urban density significantly declined. This may occur because light and noise pollution associated with high-density urbanisation deter microbat species from visiting a woodland site, or insect populations are adversely affected by such urban density, that foraging resources within these woodlands are limited. In order to enhance microbat diversity in the Illawarra, it is recommended that revegetation practices take place and urban development is restricted to 50 % total landscape cover within a 500 metres radius of a woodland patch.

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Appendices

Appendix A

Table 8: Summary of vegetation communities present in the Illawarra region, with focus on disturbance level. All information obtained from the Bioregional Assessment; Native Vegetation of the Illawarra Escarpment and Coastal Plain (2002), produced by the NSW National Parks and Wildlife Services.

Vegetation community	Composition of canopy	Proportion of community subject to high disturbance (%)	Condition assessment
Coastal Grassy Red Gum Forest	*Eucalyptus tereticornis, Eucalyptus eugenioides, Angophora floribunda* and *Eucalyptus bosistoana*	65.4	Moderate to heavy disturbance with areas of scattered trees. 1 threatened species (*Pterostylis gibbosa*)
Lowlands Woollybutt-*Melaleuca* Forest	*Eucalyptus longifolia, Melaleuca decora, Eucalyptus globoidea, Eucalyptus eugenioides* and *Eucalyptus tereticornis*	63.9	Moderate to heavy disturbance with areas of scattered trees. 1 threatened species (*Pterostylis gibbosa*)
Coastal Headland Grassland	*Allocasuarina verticillata* and *Banksia integrifolia subsp. integrifolia*	25	Moderate disturbance with no threatened species
Coastal Sand Bangalay-Blackbutt Forest	*Eucalyptus botryoides, Eucalyptus Pilularis* and *Corymbia gummifera*	29.4	Moderate disturbance with no threatened species
Coastal Sand Swamp Mahogany Forest	*Eucalyptus robusta, Eucalyptus pilularis* and *Eucalyptus botryoides*	70.9	Heavy disturbance and no threatened species
Bangalay-Banksia Complex	*Eucalyptus botryoides, Banksia integrifolia subsp. Integrifolia* and *Syncarpia*	48.3	Heavy disturbance with no threatened species

	glomulifera subsp.glomulifera		
Escarpment Blackbutt Forest	*Eucalyptus pilularis, Syncarpia glomulifera subsp. glomulifera, Eucalyptus botryoides* and *Eucalyptus paniculata subsp. paniculata*	36	Light disturbance with no threatened species
Tall Open Gully Gum Forest	*Eucalyptus smithii, Eucalyptus piperita, Eucalyptus cypellocarpa, Eucalyptus muellerian* and *Eucalyptus elata*	4.9	Lightly disturbed and contains no threatened species
Moist Shale Messmate Forest	*Eucalyptus obliqua, Eucalyptus piperita, Eucalyptus cypellocarpa* and *Eucalyptus globoidea*	18.4	Light to moderate disturbance with no threatened species
Moist Brown Barrel Forest	*Eucalyptus fastigata, Eucalyptus smithii, Eucalyptus muelleriana* and *Syncarpia glomulifera subsp. glomulifera*	0	Light disturbance with no threatened species
Saltmarsh Complex	*Casuarina glauca* and *Avicennia marina subsp. australasica*		No assessment on wetland communities
Coastal Swamp Oak Forest	*Casuarina glauca*	45.5	Moderate disturbance with no threatened species. Areas of scattered trees.
Alluvial Swamp Mahogany Forest	*Eucalyptus robusta, Eucalyptus botryoides* and *Casuarina glauca*	50	Moderate disturbance with no threatened species. Areas of scattered trees.
Coastal Sand Freshwater Wetland	*Casuarina glauca*		No assessment on wetland communities
Cliffline Coachwood Scrub	*Doryphora sassafras, Banksia serrata, Tristaniopsis collina, Epacris longiflora* and *Polyosma cunninghamii*	0	Light disturbance with no threatened species
Budawang Ash Mallee Scrub	*Eucalyptus dendromorpha, Eucalyptus sieberi* and *Syncarpia glomulifera subsp. glomulifera*	0	Light disturbance with no threatened species

Escarpment Edge Silvertop Ash Forest	*Eucalyptus sieberi, Eucalyptus piperita, Syncarpia glomulifera subsp. Glomulifera* and *Corymbia gummifera*	16.3	Light disturbance with 1 threatened species (*Lomandra brevis*)
Highlands Swamp Gum-Melaleuca Forest	*Eucalyptus ovata* and *Melaleuca linariifolia*	0	Light disturbance with no threatened species
Exposed Sandstone Scribbly Gum Woodland	*Eucalyptus sclerophylla, Eucalyptus racemosa, Eucalyptus haemastoma, Corymbia gummifera, Eucalyptus oblonga, Eucalyptus sieberi, Eucalyptus piperita* and *Angophora costata*	4.7	Light disturbance with 4 threatened species (*Pomaderris adnate, Pultenaea aristata, Darwinia grandiflora* and *Darwinia diminuta*)
Upland Swamps: Sedgeland-Heath Complex	*Banksia robur, Melaleuca squarrosa, Hakea teretifolia, Leptospermum juniperinum, Banksia ericifolia, Pultenaea divaricata, Baeckea linifolia, Banksia oblongifolia, Hakea teretifolia* and *Epacris obtusifolia*	2.2	Light disturbance with no threatened species
Lowlands Dry-Subtropical Rainforest	*Cassine australis var. australis, Alectryon subcinereus, Planchonella australis, Ficus rubiginosa, Geijera salicifolia var. latifolia, Alphitonia excelsa, Dendrocnide excels* and *Melia azedarach*	43.2	Moderate to heavy disturbance with 3 threatened species (*Cynanchum elegans, Daphnandra sp. "Illawarra", Haloragis exalata subsp. Exalata var. laevis*)
Moist Box-Red Gum Foothills Forest	*Eucalyptus tereticornis, Eucalyptus quadrangulata, Eucalyptus salignaXbotryoides* and *Melaleuca styphelioides*	57.6	Moderate to heavy disturbance with 3 endangered species (*Cynanchum elegans Daphnandra sp.* and *Irenepharsus trypherus*)
Moist Blue Gum-Blackbutt Forest	*Eucalyptus salignaXbotryoides, Eucalyptus smithii, Eucaly ptus pilularis, Eucalyptus cypellocarpa, Eucalyptus*	8.3	Light disturbance with no threatened species

	elata, Eucalyptus muelleriana, Eucalyptus sieberi and *Syncarpia glomulifera subsp. glomulifera*		
Moist Coastal White Box Forest	*Eucalyptus quadrangulata Cassine australis var. australis, Cryptocarya microneura, Acmena smithii, Livistona australis, Pittosporum undulatum, Toona ciliata, Doryphora sassafras, Diospyros australis, Streblus brunonianus, Guioa semiglauca, Acacia maidenii, Dendrocnide excelsa,* and *Diploglottis australis*	19.7	Moderately disturbed with 2 threatened species (*Cynanchum elegans* and *Daphnandra Sp*)
Moist Gully Gum Forest	*Eucalyptus smithii, Eucalyptus muelleriana, Eucalyptus quadrangulata, Eucalyptus piperita, Eucalyptus elata* and *Eucalyptus cypellocarpa*	4.1	Light disturbance and contains no threatened species
Illawarra Escarpment Subtropical Rainforest	*Dendrocnide excelsa, Doryphora sassafras, Diploglottis australis, Toona ciliata, Ficus obliqua var. obliqua* and *F. rubiginosa*	25.9	Moderately disturbed and contain 2 threatened species (*Arthropteris palisotii* and *Daphnandra sp.*)
Coachwood Warm Temperate Rainforest	*Ceratopetalum apetalum, Acmena smithii, Doryphora sassafras* and *Cryptocarya glaucescens*	14.3	Lightly disturbed with 2 threatened species *(Haloragis exalata and Sphaerocionium lyallii)*
Robertson Cool-Warm Temperate Rainforest	*Acmena smithii, Doryphora sassafras* and *Acacia melanoxylon*	0	Moderately disturbed with no threatened species