Contrasting the effects of vegetation clearance on two insectivore communities and their prey at perennial streams in temperate Australia

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ABSTRACT

The movement of organisms and material between adjacent ecosystems is a ubiquitous process. Over the last three decades, many works have uncovered factors that influence the flux of spatial subsidies. The emergence of new ecosystems via riparian vegetation clearance, for instance, can impact the quantity and quality of the spatial subsidies that move between perennial streams and riparian zones, and this likely incurs complex responses from riparian consumers. This thesis asks two main questions: 1) how does environmental variables in both the donor (streams) and recipient (riparian zones) systems as a result of riparian vegetation clearance impact the relative quantity of active subsidies? 2) Do insectivores with different mobilities and foraging behaviours respond differently to the flux of spatial subsidies and does this interact with environmental variables?

I answered these questions across four empirical chapters. This thesis focused on a biome identified as both impacted by agricultural intensification and comprising important perennially flowing freshwater (on the world's driest inhabited continent): Australia's temperate zone. In chapter two, I demonstrate longitudinal trends in riparian vegetation clearance at our study streams and tested models relating to spatial subsidies and riparian spider responses. I conducted vegetation surveys and monitored in-stream temperature at six perennial streams that run through a riparian vegetation clearance gradient, and related these to abundances, biomass and community composition of riparian spiders and their prey (including emergent aquatic invertebrates). In chapter three, I focused on the orb-weaving spider species, *Tetragnatha valida* and compared the relative contributions of low flux, high quality aquatic prey and terrestrial prey to its diet at perennial streams using stable isotope analysis.

In chapter four, I investigated the role of riparian vegetation structure and the abundance and biomass of emergent aquatic prey in explaining variation in the foraging activity and community composition of insectivorous bats that occupy perennial stream habitats. Finally, in chapter five I continuously monitored the activity of insectivorous bats at a survey reach to investigate potential concordance between foraging activity, moon illumination and heat accumulation by the stream. This thesis represents 'another string in the bow' of spatial subsidy research that focuses on biomes and taxa that are seldom studied. The literature identifies that active subsidies, including emergent aquatic invertebrates, must be studied in the context of donor and recipient ecosystem dynamics. Despite this, few studies thoroughly measure these dynamics. The present study bucks this trend and extensively surveys relevant ecosystem characteristics including in-stream temperature and vegetation structure, and in-so-doing provides valuable context which underpins diverse riparian insectivore responses to the flux of spatial subsidies. By contrasting different modes of insectivory, this thesis provides new insight into the trophic dynamics of stream-riparian systems. Studies like these are important in a rapidly changing world.

DECLARATION

This is to certify that:

1. The thesis comprises only my original work towards the PhD except where indicated.
2. Due acknowledgement has been made in the text to all other material used.
3. The thesis is fewer than 100 000 words in length, exclusive of tables, maps, bibliographies and appendices.

Signed________________________

Bradley Kendall Clarke-Wood

ACKNOWLEDGEMENT OF COUNTRY

I would like to acknowledge the Wurundjeri people who are the Traditional Custodians of the Lands and Waters upon which this thesis was written. I would also like to extend this to the Taungurung people, from whose Lands and Waters I extracted data. I acknowledge and pay respects to their respective Elders past, present and emerging.

The territory of the Wurundjeri lies within the inner city of Melbourne and extends north of the Great Dividing Ranges, east to Mt Baw Baw, south to Mordialloc Creek and west to the Werribee River. The Taungurung people occupy the lands north of the Great Dividing Range to south-east of Mansfield, northwards past Benalla, across to Wangaratta in the west. The western boundary is provided by the Great Dividing Range then proceeds south to Kyneton, embracing the catchment areas for the Campaspe and Goulburn Rivers, as well as Broken River and Broken Creek.

Sovereignty was never ceded.

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“It’s such a wonderful thing to love” he reminded me.

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Earlier this year, two women passed away. Aunty Enid and Aunty Joanie looked after us kids while mum had to work. They helped mum and myself pay for my education. They were there for me from dot and I am who I am in no small part because of these two women. So finally, I would like to thank Aunty Enid and Aunty Joanie for their love.

I slowly reclaimed an aspect of them that was also myself — a natural determination.

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Words in italics are adapted from Patti Smith’s ‘M Train’.

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1.1 INTRODUCTION

Resources, which move across ecosystem boundaries, often significantly influence the ecosystem dynamics (Lindeman, 1942; Vannote et al., 1980) and trophic interactions (Loreau and Leroux, 2008; Polis et al., 1997a) of recipient systems (Marcarelli et al., 2011; Subalusky and Post, 2019). While cross-boundary resources have featured prominently in the literature over the last century (Cole et al., 2006; Marcarelli et al., 2011; Summerhayes and Elton, 1923), Polis et al. (1997) provided the first explicit definition of such spatial subsidies. According to this definition, a spatial subsidy is "a donor-controlled resource (prey, detritus, nutrients) from one habitat to a recipient (plant or consumer) from a second habitat which increases population productivity of the recipient, potentially altering consumer-resource dynamics in the recipient system". This was a seminal step forward, which to date has been used broadly across the field (Massol et al., 2011; Subalusky and Post, 2019) including within stream (Allan and Castillo, 2007), marine (Estes et al., 1998) and desert (Ward, 2016) ecology. Through these different explorations, researchers have highlighted the significant influence of spatial subsidies within most systems. Spatial subsidies have been shown to augment (Polis and Strong, 1996; Vadeboncoeur et al., 2005) and diminish trophic interaction intensity (Nakano and Murakami, 2001), hasten nutrient cycling (Wallace et al., 2015; Young et al., 2010) and disrupt ecosystem processes (Menninger et al., 2008; Subalusky et al., 2015). Increasingly, the interdependent reciprocity of spatial subsidies has also been recognised (Baxter et al., 2005; Muehlbauer et al., 2014; Nakano and Murakami, 2001). This inevitably complicates the approach needed for understanding drivers of spatial subsidy flux and the processes that mediate them (Leroux and Loreau, 2012; Subalusky and Post, 2019).

Flux in spatial subsidies can occur either passively as a result of abiotic factors (Polis et al., 1997b; Watkins et al., 2010) or actively in terms of dispersing organisms (McKie et al., 2018; Wesner, 2010). The shedding of leaves and bark from riparian trees, for instance, represents a passive spatial subsidy (Brett et al., 2017; Wallace et al., 2015). Wind conditions and flooding regimes transport materials otherwise suspended in terrestrial systems, into adjacent lakes and streams (Roberts et al., 2007; Wallace et al., 2015). Conversely, the seasonal emergence of mayflies (order Ephemeroptera) represents an active spatial subsidy (Watanabe et al., 1999). A recent review by Subalusky and Post (2019) summarised the wide-ranging significance of active subsidies including their role in diffusing allochthonous resources beyond the interface of adjacent ecosystems (Fig. 1.1; Bauer and Hoye, 2014; Naiman and Helfield, 2006). Links between ecosystems through dispersing organisms (Carlson et al., 2016; Conrad et al., 1999), migration (Bauer and Hoye, 2014) and egestion/excretion (Lundberg and Moberg, 2003; Wolf et al., 2013), for example, transports nutrients across boundaries and natural gradients (Lindeman, 1942; Loreau and Leroux, 2008).

Recent studies have identified that adult caddisfly, for example, can move laterally within catchments but can also overcome major catchment boundaries during dispersal (Collier and Smith, 1997; Petersen et al., 2004; Yaegashi et al., 2014). This can reasonably be considered an expression of Lindeman's Differential Subsidisation Model (1942), which postulates that geomorphic characteristics influence the deposition of subsidies within ecosystems (Marcarelli et al., 2011). Mountain peaks, for example, are described as 'functionally convex' as few subsidies are deposited on them, while waterbodies receive high amounts of subsidies from a range of adjacent ecosystems and are therefore, on the high end of a depositional continuum (Loreau and Leroux, 2008). Active subsidies, while able to circumvent these natural gradients, are likely to favour the path of least resistance (Li et al., 2010; Tonkin et al., 2018). Razeng et al. (2016), for example, demonstrated that community composition of aquatic invertebrates was influenced primarily by landscape concavity during lateral dispersal with strong-flying dispersers showing no spatial aggregation, while weak dispersers were restricted to concave landforms (e.g. valleys). Our understanding of what drives the flux of spatial subsidies, however, has developed beyond these natural gradients to accommodate the advent of new ecosystems (Gravel et al., 2010; Tolkkinen et al., 2016). The transformation of stream-riparian ecosystems by agricultural land-use, for example, alters subsidy deposition (Watkins et al., 2010), in particular the emergence of aquatic invertebrates (Stenroth et al., 2015).

Additionally, active subsidies like insects may aggregate in time and space (Capps and Flecker, 2013; Paetzold et al., 2005; Subalusky and Post, 2019), which in turn, can aggregate consumers, thus leading to foraging hubs (Fukui et al., 2006; Murakami and Nakano, 2002; Young et al., 2010). Paetzold et al. (2005), for instance, demonstrated that the degree of spatial and seasonal aggregation of consumers at the interface of streams and riparian zones coincided with the proportional contribution of aquatic insects to their diets. In addition, active subsidies often link the distinct ecologies of consumers, such as foraging modes and life histories, to the wider functioning of ecosystems (Atkinson et al., 2017; Vanni et al., 2002). Vanni et al. (2002), for instance, demonstrated that concentrations of phosphorous varied significantly between the excretions of fish and amphibians from different families. This suggests that the composition of consumers is a strong determinant of nutrient cycling within recipient ecosystems (Atkinson et al., 2017; Vanni et al., 2002).

The redistribution of allochthonous resources through the movement of organisms has been widely documented (Landry and Parrott, 2016; Wolf et al., 2013), but probably most extensively in freshwater ecosystems (Bultman et al., 2014; Gratton and Vander Zanden, 2009; Marcarelli et al., 2011). Mobile aquatic organisms such as emergent aquatic invertebrates can subsidise land with aquatic nutrients, creating a link between terrestrial and aquatic ecosystems (Burdon and Harding, 2008; Kautza et al., 2016). Emergence events (Yuen and Dudgeon, 2016) and dispersal characteristics (Lancaster and Downes, 2017a; McKie et al., 2018) can drive the redistribution of allochthonous resources in these instances. This pulse of high-quality resources can both influence ecosystem processes (Massol et al., 2017; Raitif et al., 2018) and trophic structure (Malison and Baxter, 2010) in terrestrial systems. Evidence suggests that riparian consumers specialise in foraging on aquatically-derived subsidies (Kato et al., 2003), for example, and can select for these resources during times of high energetic demand (Clare et al., 2011). This highlights that spatial subsidies can drive significant consumer community responses, which mediate the redistribution of spatial subsidies in recipient ecosystems (Richardson et al., 2010). In this thesis, I focus on the community responses of two distinct insectivores: spiders (Kato et al., 2004) and bats (Fukui et al., 2006), and compared modes of insectivory. Multiple studies have confirmed that emergent aquatic invertebrates contribute significantly to the diets of riparian insectivores (Krell et al., 2015; Lam et al., 2013; Law and Urquhart, 2000; Zapata and Sullivan, 2019). The degree to which these subsidies vary in importance to riparian consumers and what underpins their use is still poorly understood (Salvarina, 2016). Researchers have struggled to isolate the direct effects of subsidies on consumers due to the significant range of environmental variables that may be both directly influencing consumers and tightly correlated with the magnitude of subsidies. Additionally, few studies have investigated these relationships with respect to the inherent interactions between space and time (Atkinson et al., 2017; Vanni et al., 2002).

Again, in their review, Subalusky and Post (2019) developed a framework for understanding and predicting the effects of active subsidies, such as emergent aquatic invertebrates, on ecosystem dynamics (Fig. 1.1). This framework considers the quantity, quality, timing and duration of spatial subsidies, the distinct consumer ecologies that mediate their assimilation into ecosystems but also how these vary over space and time. Subalusky and Post's (2019) framework first considers how the quantity, quality, timing and duration of spatial subsidy flux is determined by an interaction between donor system and active subsidy characteristics (Fig. 1.1). Martin-Creuzburg et al. (2017) highlights this interaction and demonstrates that lake depth strongly influenced the timing of emergence for aquatic invertebrates. This study suggests that a disparity in near-ground water temperature at different depths, to which larval invertebrates are exposed to during development, drives this interaction (Martin-Creuzburg et al., 2017; Ouimet, 2001). The emergence of 50% of total aquatic invertebrate biomass was delayed by more than two months from lake sections that were 8 – 13 m deep (and relatively cooler) compared to those with a depth of 0 – 2 m (which were warmer; Martin-Creuzburg et al., 2017). Next the framework identifies that active subsidies are then filtered by both physical boundary characteristics and consumers, which further define the quantity, quality, timing and duration of the subsidy (Fig. 1.1; Subalusky and Post, 2019). Harding et al. (2004) highlights this by demonstrating the assimilation of marine resources into stream food-web via petrels. Organisms were enriched with higher $\delta^{15}N$ signatures in small streams associated with petrel colonies than in nearby streams where petrels were absent (Harding et al., 2004). Soil processes (which are tightly linked to soil structure and composition), however, determine how much and the rate at which this subsidy percolated into the recipient system (Harding et al., 2004; Subalusky and Post, 2019).

From here Subalusky and Post's (2019) framework considers how the subsidy influences the trophic structure and ecosystem function of recipient systems. Sato et al. (2016) highlights this by demonstrating that the timing of subsidies affected community dynamics within stream food-webs. The addition of terrestrially-derived subsidies (invertebrates) at the start of spring, while directly increasing the population of stream trout, also indirectly slowed detrital decomposition by increasing predation pressure on benthic invertebrates (Sato et al., 2016). Another important aspect of this part of the framework is the mobility of consumers as this has implications for how quickly subsidies are assimilated into recipient systems (Levi et al., 2015). Levi et al. (2015), for instance, demonstrated different mobilities among consumers enabled more differential exploitation of salmon (returning from marine systems to spawn) in freshwater streams. Highly mobile avian predators were able to exploit stochastic salmon spawning events, while brown bears depended on "reliable" seasonal salmon spawning and foraged intensely prior to hibernation (Levi et al., 2015).Thus, consumer mobility may be a key determinant of the duration and spatial influence of a subsidy (Muehlbauer et al., 2014; Subalusky and Post, 2019). The framework then acknowledges that ecosystem effects may ripple forward (influencing future responses to subsidies) and may loop back (influencing donor systems; Fig 1.1). See Subalusky and Post (2019) for more details regarding this framework. Their review is a clarion call for action to gather certain types of data with regards to spatial subsidies and the present thesis addresses some of these knowledge gaps.

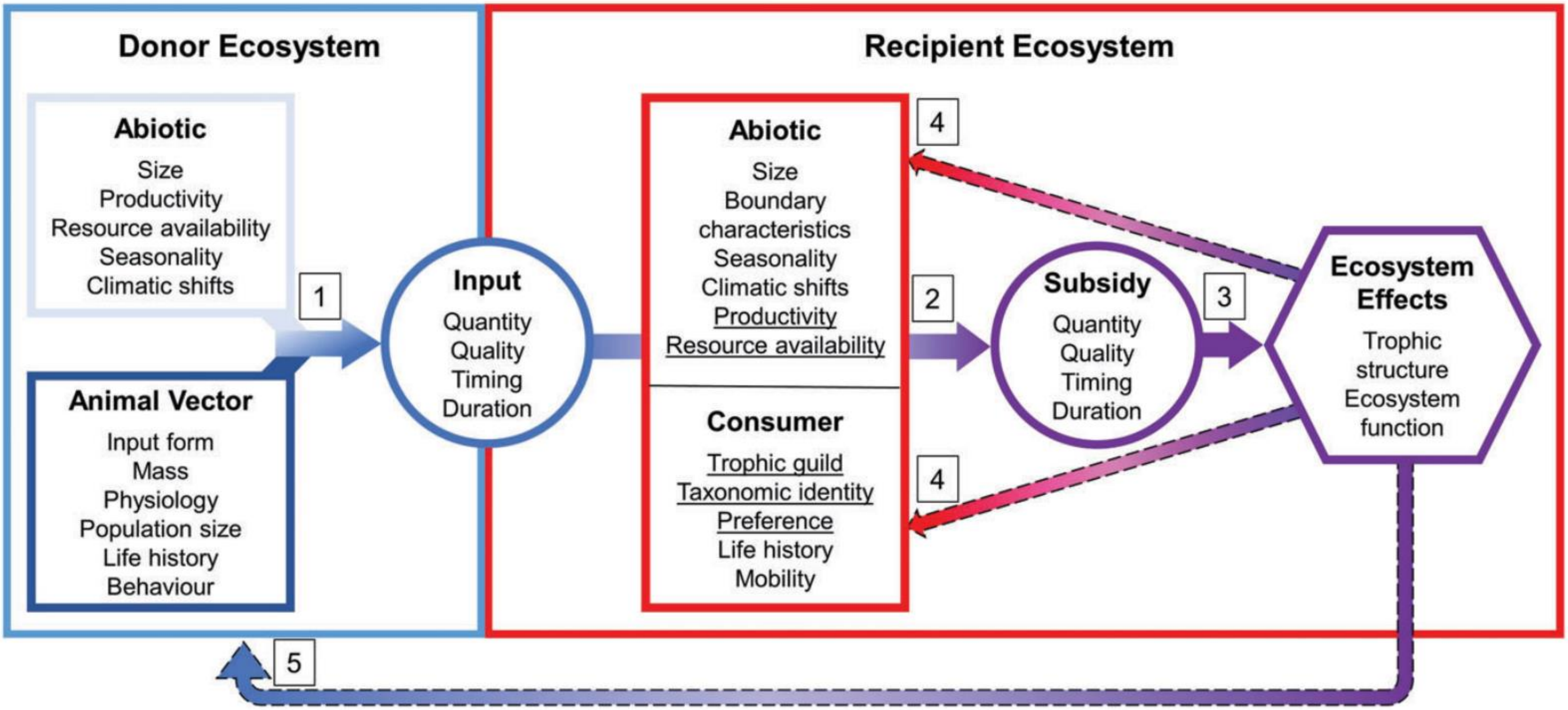

Figure 1.1. This framework has been extracted from Subalusky and Post (2019). It illustrates a conceptual framework on the influence of animal resource subsidies on ecosystem dynamics. 1) Abiotic characteristics of the donor ecosystem (light blue box/arrow) interact with characteristics of the animal vector (dark blue box/arrow) to influence the quantity, quality, timing and duration (QQTD) of a resource input (blue circle) to a recipient ecosystem. 2) Input QQTD are translated through the lens (blue-purple arrow) of both abiotic and consumer characteristics of the recipient ecosystem (red box) to yield the QQTD of the resource subsidy (purple circle). 3) Subsidy QQTD (purple circle/purple arrow) determine ecosystem effects (purple hexagon) in the recipient ecosystem. 4) Recipient ecosystem effects can alter the lens through which future inputs are translated (purple-red dashed arrows) through changes in certain abiotic and consumer characteristics (underlined characteristics are responsive to feedbacks). 5) Recipient ecosystem effects also can feed back into the donor ecosystem to influence future inputs (purple-blue dashed arrow).

1.1.1 Questions and objectives

This thesis was largely consistent with recommendations from Subalusky and Post (2019) and addresses fundamental questions within spatial subsidy ecology. In the first instance, I developed a study design that accounted for the inherent environmental variability associated with measuring active subsidy flux and community responses. I achieved this with a balanced sampling regime over three months of the field season, which coincided with the typical emergence period of aquatic invertebrates (Collier and Smith, 1997). This allowed me to measure and report the stochasticity of resource subsidies, which is an important factor for determining their relative quantity (Atkinson et al., 2017; Subalusky and Post, 2019). Further, such a sampling method was necessary because while the crux of our questions pertained to differences across space, temporal variability is important to document as this can drive consumer responses such as aggregation (Holt, 2008; Ober and Hayes, 2008a). This adds a layer of complexity but as Subalusky and Post (2019) states "[this] will be particularly important in a changing world".

Further, I considered the role of two diverse groups of insectivores in transporting spatial subsidies. For riparian spiders, this meant considering the expression of a web as a quantitative measure of foraging behaviour. Spiders mediate the redistribution of aquatically-derived subsidies (Kato et al., 2004) but also regulate an array of trophic interactions (Tagwireyi and Sullivan, 2016). This, however, is likely to be different between distinct ecosystems including those generated through human alteration (Stenroth et al., 2015). I predicted that low-mobility foraging strategies, such as web-building, would reduce in intensity as a result of riparian vegetation clearance. Such a relationship would be consistent with other studies that identify spiders play a significant role in ecosystem processes such as nutrient cycling and early ecosystem development (Hodkinson et al., 2001; Schmitz et al., 2010; Takada and Miyashita, 2014). Crucially, riparian spiders respond to ecosystem characteristics such as vegetation structure (Henschel et al., 2001; Laeser et al., 2005) but also respond to stream characteristics, including in-stream temperature, via nutritional links (Moyo et al., 2017). Similarly, insectivorous bats respond to both stream (Grindal et al., 1999) and riparian characteristics (Adams and Law, 2011) but do so through a starkly different foraging strategy. As highly mobile consumers, bats use echolocation to capture prey. Unlike web-building spiders, which are to some degree vegetation density-dependent (Diehl et al., 2013), insectivorous bats must manoeuvre vegetation during foraging (Norberg and Rayner, 1987; Reside and Lumsden, 2011). In this thesis, I contrast these two modes of insectivory with the objective of understanding how animal mobility and foraging behaviour can influence the use of spatial subsidies (Subalusky and Post, 2019).

This thesis asks two main questions: 1) how does environmental variables in both the donor (streams) and recipient (riparian zones) systems as a result of riparian vegetation clearance impact the relative quantity of active subsidies? 2) Do insectivores with different mobilities and foraging behaviours respond differently to the flux of spatial subsidies and does this interact with environmental variables?

I answered these questions across four empirical chapters. This thesis focused on a biome identified as both impacted by agricultural intensification and comprising important perennially flowing freshwater (on the world's driest inhabited continent): Australia's temperate zone. In chapter two, I demonstrate longitudinal trends in riparian vegetation clearance at our study streams and tested models relating to spatial subsidies and riparian spider responses. I conducted vegetation surveys and monitored in-stream temperature at six perennial streams that run through a riparian vegetation clearance gradient, and related these to abundances, biomass and community composition of riparian spiders and their prey (including emergent aquatic invertebrates). In chapter three, I focused on the orb-weaving spider species, *Tetragnatha valida* and compared the relative contributions of low flux, high quality aquatic prey and terrestrial prey to its diet at perennial streams using stable isotope analysis.

In chapter four, I investigated the role of riparian vegetation structure and the abundance and biomass of emergent aquatic prey in explaining variation in the foraging activity and community composition of insectivorous bats that occupy perennial stream habitats. Finally, in chapter five I continuously monitored the activity of insectivorous bats at a survey reach to investigate potential concordance between foraging activity, moon illumination and heat accumulation by the stream.

1.2 ECOSYSTEM BOUNDARIES

Whether it is the blood of marine mammals (Catenazzi and Donnelly, 2008) or West African dust (Bristow et al., 2010), the classification of a resource as 'allochthonous' is dependent on the assumption that boundaries between ecosystems are clear discontinuities across the landscape (Cadenasso et al., 2003; Post et al., 2007). It is likely the case, however, that boundaries are context specific (Muehlbauer et al., 2014; Subalusky and Post, 2019), depending on environmental gradients and fluctuating variables (Marín-Spiotta et al., 2014). In this section, I will briefly discuss this assumption and relate it to my sampling design and methods. Then, I will discuss the study area and agricultural land-use from a boundaries and spatial subsidy perspective.

In a review, Post et al. (2007) states that defining "ecosystem [boundaries] can be problematic when the processes of interest operate at potentially different scales". Muehlbauer et al. (2014), for example, demonstrated an inconsistency between physical structure-based boundaries (Post et al., 2007), and lateral biological boundaries of stream ecosystems. The "biological stream width", as determined by the proximity of aquatically-derived resources to stream systems, often extends into what is considered geomorphologically as terrestrial systems (Muehlbauer et al., 2014). The deposition of emergent aquatic invertebrates, including caddis-, may- and stoneflies into riparian zones, for instance, was greatest within 3 m of a stream and this steeply declined inland (Carlson et al., 2016; Muehlbauer et al., 2014). This suggests that while traditional ecosystem models assume that stream ecosystems "end" at the channel boundary, the effects of these donor systems do not and extend into adjacent, recipient ones. Failure to establish sampling regimes that acknowledge this inconsistency may cloak lateral changes in consumer community composition, particularly if consumers are tracking the availability of subsidies.

In this thesis, a range of sampling methods are outlined. In chapter two, for instance, I sampled riparian spiders from emergent in-stream vegetation, vegetation within 5 m of the stream and vegetation 50 m away from the stream, at each survey reach. This was an appropriate method as it accounted for ecologically meaningful discontinuities in the landscape for these taxa, where beyond 1.2 m away from the stream half the energy consumed is estimated to be aquatic in origin, and half is terrestrial according to Muehlbauer et al. (2014). Similarly, in chapter four, I adapted the methodology for insectivorous bats by monitoring within 5 m of the stream and well beyond the measurable effects of the stream on bat activity, 300 m away, at each survey reach (Muehlbauer et al., 2014). These decisions were consequential as I detected significant community composition shifts in spiders, bats and their prey between these survey points, respectively. Our results here are consistent with Subalusky and Post (2019)'s framework, which identifies that 1) taxonomic identity and consumer preference mediates the redistribution of spatial subsidies and drives how consumers relate to the boundaries, and 2) species characteristics including life history traits, determine how active subsidies will interact with boundaries and recipient system characteristics. Emergent aquatic invertebrates (including trichopterans and ephemeropterans), for instance, were highest in abundance immediately adjacent the stream (i.e. the donor system) and declined inland. This provides insight into how animal movement and behaviour can influence food-webs and ecosystems, which when coupled with detailed surveys of recipient and donor system characteristics will address knowledge gaps associated with the context dependency of spatial subsidies (Subalusky and Post, 2019).

1.2.1 Australia and land-use

As the world's driest inhabited continent (Lambers, 2018), Australia has proportionally few perennial aquatic systems (Finlayson et al., 2013). As freshwater is a limiting factor, ecosystem boundaries are significantly more dynamic, shifting over time (Larsen et al., 2016). The effects of spatial subsidies also appear to be more variable and generally stronger in water-limited ecosystems (Hagen and Sabo, 2011; Mccluney and Sabo, 2009), such as those in Australia. Due to this scarcity of freshwater, aquatic systems across the continent are hubs for productivity, driving a broad range of ecosystem processes (Power et al., 1995; Reich et al., 2009; Starrs et al., 2015). As a result, Australia's aquatic systems support a substantial biodiversity (Blakey et al., 2017a; Kingsford, 2000) with often international distributions (i.e. migratory species; Kingsford et al., 1999).

Despite this, significant knowledge gaps remain (Brinson and Malvárez, 2002; Kennard et al., 2010) with much of the research focused on 4th-6th order streams (Hughes and James, 1989; Kennard et al., 2010) in the northern hemisphere (Salvarina, 2016). As subsidy dynamics are likely controlled by ecosystem size (Subalusky and Post, 2019), this affinity for larger streams by researchers is likely to have implications for what we know about how spatial subsidies diffuse into terrestrial ecosystems (Muehlbauer et al., 2014; Wolf et al., 2013). It may be that larger streams, as physically larger ecosystems, supersaturate consumers by exporting relatively large amounts of subsidies (Henschel, 2004). More subsidies may then avoid immediate consumption by predators at the boundaries between these systems and riparian zones (Carlson et al., 2016; Muehlbauer et al., 2014). The totality of research presented in this thesis, however, was conducted along six, 2nd/3rd order perennial tributaries in regional Victoria, Australia (Taungurung Country, Goulburn-Broken Catchment; Fig 2.5.2), including Hollands, Hughes and Ryans creeks, and the Broken, Delatite and Howqua rivers. This order-of-magnitude size difference between large and small streams may result in different consumer distribution and quantity of subsidy patterns.

Widespread flow diversion and land clearing has hastened the decline of such aquatic systems in Australia (Kingsford et al., 2016) with intense anthropogenic alterations occurring in the urban and agricultural centres of Australia's south-east and south-west (Capon and Pettit, 2018; Finlayson et al., 2013). The present study investigates the effects of such land clearance by incorporating streams that exhibit longitudinal changes in vegetation density. Five out of the six streams were deliberately selected as examples of systems where vegetative cover was continuous in the upper reaches but run through agricultural systems in the lower reaches. In contrast, the segment of Delatite River surveyed comprised a riparian zone of continuous native vegetation for its length. Studies have demonstrated that changes in the density of riparian vegetation can impact the permeability of ecosystem boundaries (Greenwood, 2014; Subalusky and Post, 2019) and in-stream temperatures (Ebersole et al., 2003; Macdonald et al., 2003; Ouellet et al., 2017). Macdonald et al. (2003), for instance, demonstrated even five years after riparian vegetation removal, in-stream temperatures were approximately five degrees warmer and much more variable than those streams with an intact riparian buffer. Cold-water refugia within streams are important for prey production and life-history events of aquatic species (both consumers and subsidies) including migration and egg incubation (Ebersole et al., 2003). Temperature impacts as a result of riparian vegetation removal are likely associated with declines in available cold-water refugia (Macdonald et al., 2003), and in turn, the abundance of consumers (Ebersole et al., 2003). This link between riparian zones and in-stream temperature is then an important determinant of ecosystem boundaries, driving thermoclines and thermal heterogeneity that can exclude some biota (including those that would be active subsidies) and establish discontinuities across the landscape (Post et al., 2007; Schindler et al., 1996).

1.3 LIFE HISTORIES OF SPECIES THAT ARE SPATIAL SUBSIDIES

Species that deliver subsidies can incur strong community responses in recipient ecosystems (Hagen and Sabo, 2011; Loreau and Leroux, 2008). These subsidies can also contribute as much as 100% of energy to the diets of consumers (Baxter et al., 2005; Gonsalves et al., 2013), substantially supplementing their growth (Akamatsu et al., 2007; Wallace et al., 2015). Nevertheless, this process is significantly influenced by aspects of the life histories of species that deliver subsidies (Lancaster and Downes, 2013; Massol et al., 2011), which are constrained by the characteristics of the donor (Peckarsky et al., 2000; Subalusky and Post, 2019) and recipient systems (Greenwood, 2014). Seasonality is one such donor system constraint that determines the timing and quantity of subsidies (Correa and Winemiller, 2018; Subalusky and Post, 2019). Correa and Winemiller (2018), for instance, demonstrated that seasonal flooding of rivers enabled fish to access forest resources. During annual floods, forest plant matter and canopy-dwelling invertebrates made a greater proportional contribution to fish diets (Correa and Winemiller, 2018) and this has been documented in other systems (Baxter et al., 2005; Nakano and Murakami, 2001). Despite this, few spatial subsidy studies have considered how life history traits, including egg development and adult dispersal, inform patterns of subsidy quantity, quality and timing. For species with populations connected by dispersal, namely emergent aquatic invertebrates, variation in egg supply, can determine population sizes (Bovill et al., 2019; Reich, 2004) and in turn, the quantity of subsidies. Further, conditions experienced by individuals over their development (Arendt, 2010; Atkinson, 1994) can impact the quality of the subsidy they provide (Bartels et al., 2012; Gladyshev et al., 2009; Marczak et al., 2007; Twining et al., 2018). In this section, I will briefly summarise processes that pre-empt the flux of spatial subsidies across boundaries and underpin the quantity, quality and timing of those subsidies.

Maternal care via oviposition and resource allocation can have profound effects on the survival (Encalada and Peckarsky, 2006) and growth (Tigreros et al., 2019) of offspring during their early stages (Hendry et al., 2001; Reich, 2004). Large-scale manipulation experiments have shown that increases in preferred habitats correlated with increases in egg density and in turn, increases in larval densities of mayflies (Encalada and Peckarsky, 2012). At the antipodal point of this cycle, Peckarsky et al. (2000) demonstrated that the emergence of *Baetis* mayflies are driven by the distribution of preferred oviposition sites (i.e. boulders) with respect to fluctuating hydrological variables within streams. These findings are consistent with Subalusky and Post's (2019) framework, which identifies that donor system characteristics significantly influences the magnitude of spatial subsidy flux. Moreover, because the body size of these active subsidisers is generally responsive to environmental variables, donor system characteristics can influence their quality (Marcarelli et al., 2011; Subalusky and Post, 2019). Cooler in-stream temperatures, for example, slow rates of development, thereby allowing individual aquatic invertebrates more time to feed and grow prior to emergence (Arendt, 2010; Atkinson, 1994). Assuming there is no decoupling of biomass and nutritional content (Moyo et al., 2017), individuals that grow larger and emerge slower (low-flux, high-quality subsidies) may diffuse higher quality subsidies into riparian zones (Gladyshev et al., 2009) and extend their effects (Uno, 2016).

Once emerged, adult aquatic invertebrates often disperse (McKie et al., 2018; Petersen et al., 2004). While it is understood that aquatic invertebrate emergence is in part driven by environmental cues (Harper and Peckarsky, 2006; Jourdan et al., 2019), circumstances that facilitate greater lateral dispersal from streams, however, remains understudied (Lancaster and Downes, 2017a; Muehlbauer et al., 2014). Previous studies have suggested that recipient system characteristics including vegetation (Carlson et al., 2016; Delettre and Morvan, 2000; Greenwood, 2014) and geomorphology (Hagen and Sabo, 2011; Razeng et al., 2016) are important determinants of lateral dispersal for emergent aquatic invertebrates. Greenwood (2014), for instance, demonstrated that the lateral dispersal of caddis-, may- and stoneflies were reduced in areas with increased shrub density. While obstacles such as these can elevate the mortality rates of emerging adults and hasten the assimilation of subsidies into recipient systems (Harris et al., 2018; Jackson and Fisher, 1986), other studies suggest that denser vegetation facilitated the greater dispersal of adults by providing cover from consumers and moderating environmental conditions, such as desiccation (Carlson et al., 2016; Petersen et al., 1999), prolonging their availability. Carlson et al. (2016), for instance, demonstrated that emergent aquatic invertebrates are more likely to subsidise consumers further away from stream channels as a function of increased vegetation density. These studies highlight that recipient system characteristics interact with active subsidies and can influence their timing and availability. Timing and availability remain understudied, however, and my work addresses a significant gap by investigating temporal aspects of spatial subsidies across a land clearance gradient that spans the segment of the streams surveyed.

1.4 TWO MODES OF INSECTIVORY: COMPARING CONSUMER MOBILITY

The life-history, foraging strategy and mobility of consumers determines how quickly they can use in-coming subsidies (Subalusky and Post, 2019). Consumers that restrict their foraging to ecosystem boundaries (Kato et al., 2003) or switch diets readily (Hagen and Sabo, 2014), are strategically positioned to access temporally variable spatial subsidies. These foraging traits can lead to changes in community composition (Hagen and Sabo, 2011; Ober and Hayes, 2008b) and consumer diversity (Anderson et al., 2008), which in turn affects the intensity of trophic interactions in recipient systems (Murakami and Nakano, 2002; Nakano and Murakami, 2001). This thesis is centred on two highly diverse groups of riparian insectivores: web-building spiders and echolocating bats. While this offers a comparison between two distinct modes of insectivory, some challenges need to be considered when studying community responses to spatial subsidies within taxa-rich groups.

1.4.1 Spiders

The total number of Australian spider species is estimated at ~17, 500. So far, however, only 4,000 have been described (Whyte and Anderson, 2017). This diversity represents a broad range of predation strategies including (but not limited to) the ambush predator *Selenocosmia crassipes*, which regularly consumes small vertebrates (McCormick and Polis, 1982). Even within insectivory, spiders use an array of modes including (but not limited to) fossorial, sit-and-wait, wandering and web-building strategies (Pekár and Toft, 2015; Uetz, 1992). Members of the Zodariidae family mimic the behaviours and chemical traits of their prey to lure and ultimately consume them (Pekár and Křál, 2002; Woinarski et al., 2002), while others, namely from the sub-family Cyrtarachninae, swing an adhesive, pheromone-imbued droplet of silk targeting moths (Yeargan, 1994). These examples highlight the diverse predatory strategies present within the order Araneae and suggests that spatial subsidies are likely to be used differentially across spider communities.

Nevertheless, this thesis focuses significantly on those taxa in riparian zones that intercept prey, including active subsidies, using a web (Warmbold and Wesner, 2018). Despite their relative low mobility, web-building spiders are considered early responders to spatial subsidies, increasing in density with the flux of active subsidies (Hodkinson et al., 2001; Kato et al., 2003). Many studies have documented the aggregation of these spiders at the boundaries between terrestrial and aquatic ecosystems (Laeser et al., 2005; Malison and Baxter, 2010), which results in higher abundances and species richness of spiders (Greenwood et al., 1995; Paetzold et al., 2006; Williams et al., 1995). As a part of this mode of insectivory, web-building spiders are subject to a prospective trade-off between the relatively high availability of aquatically-derived subsidies and competition for habitat (Chan et al., 2009; Hambäck et al., 2016; Tagwireyi and Sullivan, 2016). In this regard, web-building insectivory is vegetation density-dependent (Fasola and Mogavero, 1995; Peres et al., 2007) with foraging success limited by the availability of web anchorage points. Chan et al. (2009), for example, demonstrated that the addition of artificial substrates resulted in an ~28% increase in the number of webs in riparian zones. This suggests that the availability of suitable web anchorage points is a significant driver of web-building spider distribution (Chan et al., 2009). Notwithstanding further predation, low-mobility insectivory, however, constrains the transport of subsidies within recipient systems by these consumers to the stream's edge (Muehlbauer et al., 2014).

1.4.2 Echolocating bats

Insectivorous bats are another diverse group of consumers (accounting for ~18% of terrestrial mammal diversity in Australia; ~70 species) that often depend on aquatic systems for drinking (Carter, 2017; Grindal et al., 1999), foraging (Fukui et al., 2006) and roosting (Adams and Hayes, 2008; Francl, 2008). For some bats, riparian corridors represent a break in otherwise dense vegetation, which is preferential for foraging (Law and Chidel, 2002; Ober and Hayes, 2008c). As hubs for productivity, aquatic systems support relatively higher abundances of flying invertebrates than adjacent terrestrial systems and as a result may be important centres for bat foraging (Hagen and Sabo, 2011; Seidman and Zabel, 2001). Several hydrological variables including pool depth and width (Jackrel and Matlack, 2010; Seibold et al., 2013), flow (Clare et al., 2011; Lloyd et al., 2006; Lumsden and Bennett, 1995) and flooding regime (Blakey et al., 2017a; Pereira et al., 2009) drive the occupancy of insectivorous bats over aquatic systems. This suggests that insectivorous bats are likely sensitive to habitat alteration within these systems (Lentini et al., 2012).

Furthermore, bats exhibit species-specific responses to habitat structure (Adams and Law, 2011; Brooks et al., 2017). The density of clutter in habitats can affect a bat's ability to forage on flying insects as it can impact manoeuvrability (Patriquin and Barclay, 2003; Schnitzler et al., 2003) and the quality of echolocation (Denzinger and Schnitzler, 2013). In terms of perennial streams, habitat complexity over water and in turn, ultrasound interference is relatively low (Mackey and Barclay, 1989). Despite this, the relative importance of vegetation structure over prey availability to insectivorous bat foraging is likely to shift across various spatial (Akasaka et al., 2010; Ober and Hayes, 2008b) and temporal (Doty et al., 2019; Milne et al., 2005) scales.

Prey availability is a key determinant of bat foraging within a habitat (Fukui et al., 2006). Spatial and temporal variation in emergent aquatic prey likely drives an aggregative response of insectivorous bats communities at perennial streams (de Jong and Aheln, 1991; Hagen and Sabo, 2012; Müller et al., 2012). Some bat species extract aquatic prey from these systems using trawling foraging methods (Almenar et al., 2009; Campbell, 2011), while others exploit aquatic invertebrate emergence events during pregnancy and lactation (Kurta et al., 1989; Kurta and Whitaker, 1998). Regardless, as highly mobile consumers, insectivorous bats can transport aquatic subsidies beyond the immediate banks of a stream (Muehlbauer et al., 2014; Subalusky and Post, 2019).

1.5 SUMMARY OF FINDINGS

Again, this thesis asks two main questions: 1) how does varying environmental variables in both the donor (perennial streams) and recipient (riparian zones) systems as a result of riparian vegetation clearance impact the relative quantity of active subsidies? 2) Do insectivores with different mobilities and foraging behaviours respond differently to the flux of spatial subsidies and does this interact with environmental variables? I answered these questions with a study design that accounted for the inherent environmental variability associated with measuring active subsidy flux and community responses, and with a balanced sampling regime over three months of the field season, which coincided with the typical emergence period of aquatic invertebrates.

Overall, I identified a negative relationship between the relative quantity of aquatically-derived subsidies and intensifying riparian vegetation clearance (chapters two and four). Further, these subsidies were detected in higher abundances at the stream's edge compared to upland habitats (chapter four). Trichopterans and ephemeropterans, for example, were rarely detected 300 m away from perennial streams, independent of the amount of riparian vegetation clearance (chapter four). Several key indicators of habitat alteration, including mature tree stem density and in-stream temperature, were identified as important explanatory variables for emergent aquatic invertebrate abundance and biomass (chapters two and four).

These patterns in emergent aquatic invertebrate abundance and biomass, as well as riparian vegetation structure informed the explanatory models for riparian spider abundance and web density (chapter two). Ultimately, spider responses were complex with prominent taxa, including those from the families Tetragnathidae and Linyphiidae, sensitive to the availability of subsidies. Further, I found evidence that aquatically-derived subsidies (i.e. ephemeropterans) contributed substantially to the diet of *Tetragnatha valida*, a prominent species across our field sites (chapter three). This was independent of riparian vegetation clearance with *T. valida* communities at agricultural survey reaches as supported by spatial subsidies as those at natural survey reaches (chapter three). In this chapter, I also report a significant and positive trophic position – body size relationship for this species, which may inform how aquatic resources are redistributed into riparian zones.

Vegetation structure and spatial subsidies were also key drivers for bat foraging activity (chapter four). Along perennial streams, upstream reaches with intact native vegetation had double the amount of foraging activity than downstream agricultural reaches. This relationship was due to underlying relationships between bats, prey and structure, notably a weak positive relationship with mature stem density and active subsidies (chapter four). In fact, aquatically-derived subsidies were identified as significant explanatory variables for five insectivorous bat taxa including *Chalinolobus gouldii, Miniopterus schreibersii oceanensis, Momopterus planiceps, Nyctophilus-Myotis complex* and *Vespadelus regulus.* Building on this, I assessed fluctuating insectivorous bat activity over 148 days as a response to temporal variation in environmental variables (e.g. moon illumination and temperature). By-in-large those lunar phases associated with greater moon illumination (i.e. full and gibbous moons) and hotter nights had higher bat activity. This information supports the need for monitoring programs to incorporate greater temporal scales and contextualise their sampling periods more explicitly.

This thesis represents ‘another string in the bow’ of spatial subsidy research that focuses on biomes and taxa that are seldom studied. Subalusky and Post (2019) identifies that active subsidies, including emergent aquatic invertebrates, must be studied in the context of donor and recipient ecosystem dynamics. This thesis extensively surveys relevant ecosystem characteristics including in-stream temperature and vegetation structure, and in-so-doing provides valuable context which underpins riparian insectivore responses to the flux of spatial subsidies. Studies like these are important in a rapidly changing world (Larsen et al., 2016; Subalusky and Post, 2019).

CHAPTER 2. FEWER STEMS, FEWER SUBSIDIES: CONTRASTING EFFECTS OF LONGITUDINAL PATTERNS IN RIPARIAN VEGETATION CLEARANCE ON RIPARIAN SPIDER COMMUNITIES AT PERENNIAL STREAMS IN TEMPERATE AUSTRALIA

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ABSTRACT

The movement of organisms and material between adjacent ecosystems is a ubiquitous process. Over the last three decades, many works have uncovered factors that influence the flux of spatial subsidies. The emergence of new ecosystems via riparian vegetation clearance, for instance, can impact the quantity and quality of the spatial subsidies that move between perennial streams and riparian zones, and this likely incurs complex responses from riparian consumers. In this study, we tested whether riparian spider community dynamics differed along six, 2nd/3rd order perennial streams that span a riparian vegetation clearance gradient in temperate Australia. We used an analysis of variance of environmental variables to validate assumptions of longitudinal local land-use changes and to confirm reductions in the abundance and biomass of riparian spiders and emergent aquatic invertebrates were statistically significant. We then characterised longitudinal changes in spider community composition using generalised linear models and finally assessed the relative importance of environmental variables to spider and prey communities. Our results suggest that mature tree stem density was highly influential on flying invertebrate abundance. While spider responses were complex, prominent taxa including those from the families Tetragnathidae and Linyphiidae were sensitive to the availability of subsidies. We further identified significant explanatory variables (including leaf area index and emergent aquatic invertebrate biomass) for riparian spider abundance and web densities. The results in this chapter also demonstrate the importance of considering temporal variation in both the consumer and the subsidy.

KEY WORDS: Spatial subsidies, Land clearing, Spiders, Emergent aquatic invertebrates, Australia.

2.1 INTRODUCTION

The movement of organisms and material between adjacent ecosystems is an ubiquitous process (Greenwood, 2014; Soininen et al., 2015). This flux has been documented at the interface of a wide range of ecosystems including woodlands and tundras (Hoset et al., 2017), farmlands and rainforests (Luskin et al., 2017), and forests and streams (Silva-Junior et al., 2014). Seminally, these spatial subsidies both contribute to the energy budgets of recipient systems (Silva-Junior et al., 2014) and influence trophic interactions within them (Richardson and Sato, 2015; Sato et al., 2016). For example, Sato et al. (2016) demonstrated that the timing of subsidies affected community dynamics within stream food-webs. The addition of terrestrially-derived subsidies (invertebrates) at the start of spring, while directly increasing the population of stream trout, also indirectly slowed detrital decomposition by increasing predation pressure on benthic invertebrates (Sato et al., 2016). Over the last three decades, many other works have similarly uncovered factors that influence such community responses to spatial subsidies (Murakami and Nakano, 2002; Polis and Hurd, 1995; Roach et al., 2015). Particularly in stream ecosystems, riparian vegetation structure is a significant determinant of subsidy flux (Kautza and Sullivan, 2015; Vannote et al., 1980). For example, O'Toole, Robson, & Chambers (2017) demonstrated significant shifts in aquatic invertebrate assemblages as riparian vegetation clearance reduced riparian subsidies and shading. Riparian vegetation provides both food and habitat for aquatic invertebrates via the deposition of organic matter (Lancaster and Downes, 2017b). The clearing of this vegetation can then alter the in-stream composition of aquatic invertebrate communities by limiting access to these resources (Greenwood, 2014; O'Toole et al., 2017).

Increasingly, spatial subsidy research has sought to untangle similar interactions within terrestrial ecosystems as a result of aquatically-derived subsidies (Richardson et al., 2010; Stenroth et al., 2015). Emergent aquatic invertebrates provide sustenance for an array of terrestrial insectivores (Murakami and

Nakano, 2002; Terui et al., 2017). These invertebrates also deliver physiologically important compounds (such as Omega-3 polyunsaturated fatty acids) to terrestrial ecosystems (Gladyshev et al., 2013; Kato et al., 2004). In light of extensive alterations to Earth's ice-free land via agricultural practices (Luskin et al., 2017; Ramankutty, Evan, Monfreda, & Foley, 2008; Xiang, Zhang, & Richardson, 2017), however, the flux of these organisms into riparian zones is affected in a range of complex ways (Langhans et al., 2013; Stenroth et al., 2015). For instance, Jonsson and Stenroth (2015) demonstrated that while measures of biomass did not reduce significantly along a forest-agricultural land-use gradient, community composition of emergent aquatic invertebrates shifted from comprising large-bodied plecopterans and trichopterans, and towards small-bodied chironomids. Key riparian insectivores were shown to be negatively associated with the loss of these high-quality prey, despite the prevalence of other aquatically-derived subsidies (i.e. adult chironomids; Stenroth et al., 2015).

The emergence of aquatic invertebrates are among the most influential factors determining the distribution of riparian spiders (Henschel et al., 2001; Kato et al., 2003; Shimazaki and Miyashita, 2016), especially Tetragnathids (Tagwireyi and Sullivan, 2016). Across biomes, riparian spiders aggregate at the interface of stream and riparian habitats, and have been shown to track the abundance of emergent aquatic invertebrates (Iwata, 2007; Muehlbauer et al., 2014; Tagwireyi and Sullivan, 2016). Furthermore, aquatically-derived subsidies can both disrupt and intensify trophic interactions (Henschel et al., 2001; Romero and Srivastava, 2010). Henschel et al. (2001), for instance, demonstrated that emergent aquatic invertebrates supported high densities of riparian spiders at the stream's edge. This, in turn, suppressed herbivory through heightened predation of leafhoppers (Henschel et al., 2001). Declines in riparian vegetation, however, can also limit the distribution of riparian spiders by reducing the amount of available web anchorage points (Laeser et al., 2005; Tagwireyi and Sullivan, 2016). Therefore, an understanding of the relative importance of spatial subsidies to quantitative and behavioural responses of riparian spiders is crucial for our understanding of food-webs in temperate Australia.

Hypotheses

In this study, we tested whether riparian spider community dynamics differ across local land clearing gradients. Our hypotheses were divided into two major themes: 1) those that are designed to demonstrate longitudinal land-use changes (Table 2.5.1A) and 2) those testing models relating to spatial subsidies and consumer responses (Table 2.5.1B). We compared spider abundances, biomass and community composition within and between the riparian zones of six perennial streams that run through a riparian vegetation clearance gradient. We predict strong differences in spider abundance, biomass and community composition between reaches with different riparian vegetation structures (H_A & H_I; Tables 2.5.1A & B). Greater abundances and biomass are expected at upper survey reaches where native vegetation is virtually unaltered and spatial subsidies are available. Further, we predict that upper survey reaches will be more taxa rich and if correct, this implies that changes in vegetation structure, longitudinally can impact the distribution and quantity of spiders. Alternatively, if spider abundance, biomass and community composition vary between streams (but not within streams) this suggests that discrete environmental differences (e.g. the arrangement of riparian vegetation) governs the responses of these consumers (H_3; Table 2.5.1B). These predictions also apply to the responses of flying invertebrates in these habitats. We predict also that spider abundance and web density will be concentrated within 5 m of perennial streams (H_2; Table 2.5.1B) as a product of the lateral differences in vegetation within reaches. This would also support a close association between perennial streams and the resources they provide. Further, we considered changes in responses over the survey period (H_D &H_4; Table 2.5.1A & B). Finally, we assessed the relative importance of environmental variables and spatial subsidies to spider abundance and web density (H_5; Table 2.5.1.B).

2.2 MATERIALS AND METHODS

2.2.1 Study area

This study was conducted along six, 2nd/3rd order perennial tributaries in regional Victoria, Australia (Taungurung Country, Goulburn-Broken Catchment; Fig 2.5.2). Hollands, Hughes and Ryans creeks were surveyed between November and February 2016-2017, while the Broken, Delatite and Howqua rivers were surveyed between November and March 2017-2018 (austral spring-summer, respectively; Fig. 2.6.2). Because the Broken River is impounded twice before joining the Goulburn River, we restricted our sampling to the segment (length: 50 km) upstream of Lake Nillahcootie (-36.883894, 145.999773; the utmost impoundment). Overall, this study area spans part of Australia's temperate zone and has a mean annual temperature of 13.5°C (Bureau of Meteorology, 2018a). While the catchment receives 400-500 mm of rainfall annually, the main source of water for these tributaries comes via an annual springtime snow melt (1600 mm; Murray-Darling Basin Authority, 2018). The mean daily temperature and mean monthly rainfall for the survey period was 18.6 °C and 58 mm, respectively (Bureau of Meteorology, 2018b, 2018c).

Five out of the six streams were deliberately selected as examples of systems where vegetative cover was continuous in the upper reaches. In contrast, the segment of the Delatite River surveyed comprised a riparian zone of continuous native vegetation for its length. The Delatite River was surveyed like this as to expand the range of values for inclusion in our stepwise regression analysis (see below) over which hypotheses can be tested. Vegetation communities in upstream areas predominately included tall *Eucalyptus* spp. such as *E. radiata*, *E. viminalis* and *E. globulus*. The understorey in these areas generally comprised medium and small herbs, ground ferns and shrubs (Department of Environment Land Water and Planning, 2004a, 2004b). This native riparian vegetation however, becomes patchily distributed as streams run through agricultural systems (Goulburn-Broken Catchment Management Authority, 2005). In contrast, downstream riparian zones are highly altered consisting of low complexity grasslands and willows (*Salix* spp.). Given this pattern of tree cover, three survey reaches (1 ha; 2-9 km apart) were randomly selected per stream included in this study (n = 18). These sites were used as replicates of the typical vegetation condition present along stream channels in upper, middle and lower reaches of streams, respectively. Within survey reaches, we sampled changes in vegetation and spider communities as a result of lateral zonation within sub-blocks hereafter referred to as "units". Below we outline the details of these units.

2.2.2 Establishing a local land clearing gradient

Riparian vegetation was surveyed at each reach in a two-step approach. Firstly, we determined Leaf Area Index (LAI; m^2 foliage area / m^2 ground area) using a digital canopy photography method derived from the TERN vegetation monitoring protocol (Terrestrial Ecosystem Research Network, 2013). Five x 100 m transects (20 m spacing, perpendicular to the stream) were established on flat or gentle sloping terrain (slope ≤15°). An image of canopy cover (one stop under auto-exposure) was taken every 10 m along each transect (50 photos per study site in total, approximately 3936 x 2624 pixels) using a DSLR camera (Nikon D600; > 10 Megapixel sensor of 24 mm size) with a 50 mm prime lens (24 mm CCD/CMOS with 1.5/1.6 multiplication factor), ISO 400 and an aperture of f8.0. DCP software (v3.14; MacFarlene, 2017) was used to analyse these images. This program classifies pixels as either sky or canopy and then determines the fraction of crown cover and the fraction of cover porosity within each image. LAI is derived using the following formula (Terrestrial Ecosystem Research Network, 2013):

LAI = -(the fraction of crown cover) x ln(the fraction of cover porosity)/ light extinction coefficient at the zenith of 0.5

(see *Macfarlane, Griggs, & Evangelsita, 2007).*

This LAI data was collected exclusively for Chapter Two.

Secondly, vegetation height (m) and width/diameter at breast height (DBH; m) were measured at 1 m intervals (with a 2 m buffer either side) along 2 x 100 m transects (400 m^2) oriented parallel to the stream. The first transect was on the edge of the stream (≤5 m) and the second, 150 m away from the stream (hereafter referred to as "units"). These units were designed to account for changes in structure due to lateral zonation in riparian vegetation. For vegetation, greater than 2 m, a clinometer was used to estimate heights (to the nearest whole number) from a reference point of 2 m away. The density of mature trees was determined by taking the sum of the cross-sectional area of all trees (with a DBH > 0.65 m) along our transects. Mature tree stem density is expressed as m^2 ha^{-1}. We also determined the crude density of ferns, graminoids and shrubs within each transect (no. stems ha^{-1}). The density of sprawling vegetation (e.g. blackberries) was not determined. Vegetation transect data collected from ≤5 m of the stream was shared with Chapter Four.

Finally, we deployed a temperature logger (OneTemp Pty Ltd, Adelaide, South Australia, Australia) at each survey reach. These loggers recorded the in-stream temperature, hourly for seven months (November – May 2018-2019; austral Spring-Autumn). This data was shared with chapters four and five.

2.2.3 Invertebrate sampling

At each survey reach, emergent aquatic and terrestrial aerial insects were sampled three times over the period outlined above. One light trap was deployed for two nights (~8 hours/night) at each survey reach approximately 10 m away from the stream's edge. Light traps comprised a plastic tray (28 x 22 x 5 cm) filled with water and ethanol (to a concentration of 70%), with the tray placed within a circular tub (top diameter = 39 cm; height of tub = 32 cm; Downes, Lancaster, Glaister, & Bovill, 2017). A fluorescent, ultraviolet blacklight (12 DC V, 8 watts) was laid across the top of the tray (Downes et al., 2017). This arrangement ensured that only invertebrates flying directly overhead or nearby were attracted and trapped (Collier and Smith, 1997). It should be noted that light traps systematically under sample flying insects that are diurnal (i.e. dragonflies) or not positively phototactic (i.e. mayflies and stoneflies). This may have implications for the abundances of these taxa observed here. Samples were preserved in 70% ethanol then identified to taxonomic order (lower where necessary), which was used to describe taxa as either terrestrial, aquatic or an indeterminant in origin (Table 2.5.2). Specimens were then counted and measured (cm) before being dried for ~48 hours in an oven at 80 °C. Next, we weighed the specimens to determine their dry weight (g). This invertebrate data was collected exclusively for Chapter Two.

Spider communities were sampled concurrently at all survey reaches to correspond with known adult aquatic invertebrate emergence periods of prey (November-April; Ballinger, McNally, & Lake, 2005; Lancaster & Downes, 2017b). A sweep-net was used on all vegetation within 3 randomly selected quadrats (30 x 2x 2 m; located at 50 m, ≤5 m and 0 m from the stream margin) to sample all vegetation-dwelling spiders from each ecological unit (hereafter referred to as "units"). These units were designed to account for changes in spider community as a result of lateral zonation in riparian vegetation. These specimens were preserved in 70% ethanol then counted, measured and identified to family, in the first instance, and genus where possible (keys: Davies, 1986; Okuma, 1987; Whyte & Anderson, 2017) prior to being dried in an oven for ~48 h at 80 °C and weighed. Additionally, web-building spiders were surveyed at night. Two separate randomly selected quadrats (units; 30 x 2 x 2 m) were established at each reach (≤5 m and

50 m distance from the bank). All intact webs present had their distance from the ground/water (cm) measured and recorded. Details of the spider and web anchorage points (i.e. to what webs were connected to) were also recorded, including size and genus of spider (where possible).

2.2.4 Statistical framework

Our approach for data analysis had three broad components: 1) analysis of variance with repeat measures for singular environmental and taxa responses, 2) analysis of deviance using multiple generalise linear models for community-level responses and 3) a canonical correspondence analysis and a forward stepwise regression were used to identify the single "best" explanatory model for invertebrate abundance and biomass using environmental factors. Analyses were completed in R (R Core Team, 2013). All figures are presented with standard error bars unless where otherwise specified.

2.2.5.1 Randomised block factorial with repeat measures (RBF)

Our study design is a randomised block factorial with repeat measures (RBF), which considers the distinct effects of each individual block ("stream"), sub-blocks ("survey reach" and "unit"), survey month and their interactions, on responses (Kirk, 1995). This design has two error terms: 1) between blocks and 2) between months. Each error term (where applicable) contains an interaction that cannot be estimated, and we assume that these interaction terms explain a negligible amount of variation. While specific models are outlined below (Table 2.5.3), the general structure of our RBF is:

$$X_{ijk} = \mu + \pi_i + \alpha_j + \beta_k + \tau + (\alpha\beta\pi\tau)_{jki} + \epsilon_{ijk}$$

Where X_{ijk} is any response for each block, μ is overall mean effect, π_i is the effect of each stream (block), α_j is the effect within each survey reach (sub-block), β_k is the effect within each unit (sub-block), $(\alpha\beta)_{jk}$ is the interaction between sub-blocks, τ is the effect of survey month and $(\alpha\beta\pi\tau)_{jki}$ is all interaction terms. Sub-blocks were fixed effects, while survey month was a random effect. We constructed mixed-effects models (MEM) using base R (v3.5.0; R Core Team, 2013) to analyse the effects of survey reach (upper, middle and lower), unit (50 m, ≤5 m and 0 m) and their interactions with stream effects and time of sampling. We completed these analyses with and without the Delatite River to identify whether it was a source of difference among streams or driver of interactions between terms. Further, a Tukey's Honest Significant Difference (Tukey's HSD) test to investigate whether levels within terms all significantly differed and to determine the nature of interactions. Response variables were transformed using log(x+1) for analysis.

2.2.5.2 Multiple generalise linear regression for community-level responses (GLM)

Next, spider community composition were examined using non-metric multidimensional scaling (nMDS) plots derived from Bray-Curtis similarity matrices using 'vegan' in R (v2.5-2; Oksanen et al., 2018). Ellipses were drawn based on a multivariate t-distribution, encompassing a 95% confidence interval of raw abundance data. Then, community-level responses (i.e. specific spider taxa abundance and web anchorage points) to our blocking and sub-blocking factors (i.e. stream, survey reach, unit and survey month) were assessed. This was done by fitting the raw abundance of 13 taxonomic groups to a generalised linear model (GLM; derived from Table 2.5.3). Negative binomial distributions were used for these GLM as this allowed us to meet two assumptions: 1) taxa were independent and 2) sites were independent (Wang et al., 2012). The significance of each variable was tested using the likelihood ratio test (LRT) statistic and P-values were estimated using a PERMANOVA-based resampling method and adjusted for multiple comparisons. The 'mvabund' package in R (Wang et al., 2012) was used to complete this analysis.

2.2.5.3 Environmental variable assessment and forward stepwise regression

Finally, we examined the relative importance of environmental variables to spider abundances and web density using a canonical correspondence analysis (CCA) and forward stepwise regression (with AIC adjusted for small samples sizes, as the selection criterion). All environmental variables (and elevation; mASL) were included in these analyses, initially (Table 2.5.3). In CCA, those variables that are more influential on spider abundances and web density are represented by longer vectors. The proximity of taxa to a vector indicates the strength of the relationship with that variable (e.g. further away or closer to the base of a vector indicates a weak relationship). Similarly, the position of a vector with respect to other vectors signifies their relationship (e.g. those pointed in the same direction suggest a colinear relationship). The package 'vegan' in R was used to construct our CCA (Oksanen et al., 2018).

Stepwise regression allowed us to construct a model comprising those variables that explained the most variation in in spider/web measures (Hammerson et al., 2017; Neter et al., 1996). This process can be useful in qualitatively identifying a subset of variables but has been criticized for underestimating P-values (Wilkinson and Dallal, 1981) and struggling with multicollinearity (De Veaux and Ungar, 1994). As a result, we interpreted the results cautiously (Hammerson et al., 2017). To limit the effects of multicollinearity, however, we considered the variance inflation factor (VIF) of each environmental variable in a full model (i.e. one containing all environmental variables; Fox and Monette, 1992). VIFs quantify the severity of multicollinearity and provides an index that measures how much the variance of an estimated regression coefficient is increased due to collinearity (Akinwande et al., 2015; Lindsey and Sheather, 2010). As a general rule, VIFs >5 represent high levels of multicollinearity among environmental variables, where regression coefficients are poorly estimated and resulting p-values are problematic (Lindsey and Sheather, 2010). Environmental variables with a VIF>5 were identified and systematically removed from this analysis. An intercept only model was run as our base model (Neter et al., 1996).

To scrutinise the model derived from the stepwise regression process (referred to hereafter as the "best" model), we generated a set of unique models comprising all available combinations of environmental variables before taking a subset of these models that represented <2AIC (Grueber et al., 2011). This subset of models and the best model were then ranked based on their AIC to identify the most parsimonious model. The package 'AICcmodavg' was used to complete this portion of the analysis (Mazerolle, 2019). A model averaging approach was then used to identify the relative importance of each variable (Grueber et al., 2011), using the 'MuMin' package (Barton, 2019). The relative importance of a variable is commonly estimated by summing the weights of models where the variable appears (Galipaud et al., 2014). Variables were deemed relatively important if they had a relative variable importance ≥ 0.73; equivalent to an ΔAIC of 2, a common 'rule-of-thumb' to indicate a significant effect (Richards, 2005).

2.3 RESULTS

2.3.1 Environmental variables

In-stream temperatures peaked in January with a mean daily temperature of 23.5 °C. All survey months were significantly different based on pairwise comparisons, except February and December. The warmest mean daily temperature was recorded at Ryans Creek's lower survey reach on January 25th (33.3 °C) and the coolest was at the Delatite River's lower survey reach on May 17th (6.1 °C). Despite this, once the Delatite River was removed from our analysis of variance, the remaining streams were not significantly different in terms of temperature (Table 2.5.5). Upper survey reaches were on average 2 °C cooler than their lower counterparts, with or without the Delatite River, and this difference was significant (Table 2.5.5, Fig. 2.6.3).

Leaf area index was significantly greater at upper survey reaches than middle and lower survey reaches (Table 2.5.6, Fig. 2.6.4) and this was supported by our pairwise comparisons. Broken River's and Ryans Creek's upper survey reaches had the highest LAI values, while Ryan Creek's lower survey reach had the lowest (Table 2.5.4). Similarly, average riparian vegetation height decreased longitudinally, however, this varied between survey reaches and units (Table 2.5.7; Fig. 2.6.5 & Fig. 2.6.6). Our Tukey's HSD revealed that this interaction was driven by average vegetation height being largely the same ≤5 m of the stream, regardless of survey reach. Further, average vegetation height did not significantly differ 150 m away from the stream between upper and middle survey reaches but were starkly (and significantly) different between upper and lower and middle and lower, respectively. Stem density of mature trees reduced longitudinally from 49.84 ± 6.51 m^2 stems ha^{-1} to 7.99 ± 3.89 m^2 stems ha^{-1} but while this was significant it did vary between stream and survey reach (Table 2.5.8). High stem densities recorded along the Delatite River drove this interaction, and once removed this interaction disappeared. Crude graminoid density did not significantly differ, longitudinally, however they were restricted to the stream's edge (Table 2.5.9). In contrast, shrubs were more densely situated 150 m away from the stream, although they did reduce significantly, longitudinally (Table 2.5.10). The Delatite River only influenced those analyses mentioned above.

2.3.2 Flying invertebrates (RBF)

Most flying invertebrates sampled were terrestrial (60.3%; predominantly, lepidopterans: 37.4% & coleopterans, families Scarabaeidae, Carabidae, Silphidae: 10.4%) while 29% had an aquatic larval stage (predominantly, trichopterans: 25.8% & ephemeropterans: 3.7%). The remaining 10.7% had an indeterminate larval habitat and comprised entirely of small-bodied nematocerans. Our analysis of variance demonstrated that emergent aquatic invertebrate abundance was significantly different between survey reaches (Fig. 2.6.7; Table 2.5.11). Our Tukey's HSD revealed, however, that while abundances at the upper and middle survey reaches were significantly greater than those downstream, these survey reaches did not significantly differ based on a pairwise comparison. Similarly, emergent aquatic biomass was significantly greater at upper survey reaches (Fig. 2.6.7; Table 2.5.11), however, Middle and lower survey reaches did not significantly differ based on a pairwise comparison. While emergent aquatic invertebrate abundances varied over time (Fig. 2.6.7; Table 2.5.11), only January and February-March, significantly differed as per our Tukey's HSD. Emergent aquatic biomass did not exhibit any relationship with survey month (Fig. 2.6.7; Table 2.5.11).

Flying terrestrial invertebrates did not reduce significantly in terms of abundance, longitudinally (Fig. 2.6.7; Table 2.5.12). In contrast, the biomass of flying terrestrial invertebrates was significantly greater at upper and middle survey reaches than downstream (Fig. 2.6.7; Table 2.5.12), however, these did not significant differ based on a pairwise comparison. Both flying terrestrial abundance and biomass did significantly differ between survey month (Fig. 2.6.7; Table 2.5.12), however, November and January did not significantly differ based on pairwise comparisons, respectively. The abundance and biomass of nematocerans were highly variable and only significantly differed between survey months (Table 2.5.12). These results were identical with and without the Delatite River.

2.3.3 Spider abundance, biomass and web density

Spider abundance varied between streams, survey reach and unit, however significant interactions were detected between survey reach and unit, survey reach and stream, survey month and stream, and survey month and unit (Fig. 2.6.8; Table 2.5.13). Without the Delatite River, the interactions between survey reach and stream, survey month and stream, and survey month and unit vanished. Furthermore, the Tukey's HSD revealed that abundances only reduced longitudinally ≤5 m of the stream. The only other significant differences detected were between the ≤5 m and the 50 m units at upper survey reaches and between 0 m units of upper and lower survey reaches. Similarly, spider biomass varied between streams, survey reach and unit, but significant interactions were only detected between survey reach and stream, and unit and stream (Fig. 2.6.9; Table 2.5.13). These interactions, however, did not disappear once the Delatite River was removed. Only Hughes Creek exhibited significant longitudinal trends in spider biomass as revealed by our Tukey's HSD. The spider biomass recorded at Hughes Creek's upper survey reach was also significantly greater than any other upper survey reach. With respect to unit and stream, only those units within Hughes Creek significantly differed in terms of spider biomass (as per our Tukey's HSD). In fact, spider biomass was significantly greater across Hughes Creek's 50 m units than any other comparable unit at any other stream surveyed.

As a part of our web surveys, 1358 web-building spiders were recorded. The families Tetragnathidae (genus *Tetragnatha*; 49.85%), Linyphiidae (28.27%) and Araneidae (14.51%) were the most surveyed webs with 6.78% of webs unable to be attributed to a family group. Of the araneids, *Phonognatha* was the most common genus surveyed (5.67%), followed by *Eriophora* (5.15%), *Austracantha* (2.06%), *Nephila* (1.47%) and *Agriope* (0.07%). No other families were identified to genus. The linyphiids were the dominant taxa within riparian units (50 m; 55.27%), while tetragnathids dominated at the stream's edge (≤5 m; 84.29%). The highest number of webs were recorded at most upper survey reaches (17.81 ± 1.49; Fig. 2.6.10 & 2.6.11) and this count significantly decreased, longitudinally (Middle reach: 12.47 ± 1.32; Lower reach: 7.44 ± 1.21; Table 2.5.13). Our Tukey's HSD confirmed this pattern. An inverse relationship was observed at the Delatite River and this drove a significant interaction between survey reach and stream (Table 2.5.13). This interaction vanished when the analysis was repeated without the Delatite River. While the number of webs recorded varied significantly between survey month (Table 2.5.13), our Tukey's HSD revealed that only November significantly differed from the other survey months. For Ryans and Hughes creeks, and Howqua River, significantly fewer webs were recorded in January than any other survey month. The remaining streams had peaks in web count during January.

2.3.4 Spider community responses (GLM)

Our nMDS analysis revealed distinct spider communities between units (Fig. 2.6.12). Subsequent analysis however indicates that community composition varied significantly across all treatment effects (Table 2.5.14). Additionally, significant interactions were detected at multiple levels (Table 2.5.14). Tetragnathids and dolomedids were significantly more abundant within 5 m of the stream and the only taxa groups to significantly differ between survey reaches (Table 2.5.14). Tetragnathid abundance did not significantly differ along the Delatite River, which drove a significant interaction term here (Table 2.5.14). Further, tetragnathids were significantly more abundant in January than other survey months (Table 2.5.14). Phonognathids, linyphiids, austracanthids and nephilids were all significantly more abundant 50 m away from the stream (Table 2.5.14). Phonognathids and linyphiids also varied between streams, although for linyphiids this variation between streams depended on survey month (Table 2.5.14).

The dominant anchorage points for webs were on native graminoids and shrubs (Table 2.5. 15; Fig. 2.6.13). The use of native graminoids for web anchorage did not differ significantly between survey reaches but did differ between units. Most webs attached to these graminoids were within 5 m of the stream. Similarly, the use of native shrubs as anchorage points differed between units with most found 50 m away from the stream. Although, this varied between survey months (Table 2.5.15). Use of these shrubs also significantly decreased, longitudinally (Table 2.5.15; Fig. 2.6.13).

2.3.4 Explanatory models for invertebrate abundance, biomass and web density

Our stepwise regression analyses resulted in the formation of a range of highly significant explanatory models (Table 2.5.16, 2.5.18 & 2.5.20). Prior to this analysis, however, mean vegetation height was removed due to high degrees of multicollinearity (i.e. VIFs > 5).

The explanatory models for flying invertebrate abundance and biomass all included mature tree stem density (Table 2.5.16). In fact, emergent aquatic invertebrate abundance and biomass were both parsimoniously explained by mature tree stem density alone. Flying terrestrial invertebrate biomass was best explained by mature stem density and crude shrub density (Table 2.5.16). For all prey responses, mature stem density was also identified as a significant explanatory variable with crude graminoid density also being significant for flying terrestrial abundance, despite not featuring in the explanatory model (Table 2.5.17). These models explained between 14 – 26% of flying invertebrate abundance and biomass variation (Table 2.5.16).

A visual assessment of the CCA biplot for spider abundance showed several strong associations between spider taxa abundance and environmental variables (Fig. 2.6.14). Variables such as crude graminoid and shrub density, elevation and mean in-stream temperature were relatively influential on the data given the length of their vectors. Linyphiid abundance was strongly associated with crude shrub density while tetragnathid abundance was associated with crude graminoid density and mean in-stream temperature (Fig. 2.6.14). Both araneid and phonognathid abundance showed a moderate positive association with mature tree stem density and elevation (Fig. 2.6.14). When considering the CCA biplot for spider web density, linyphiid web density remained closely associated with crude shrub density (Fig. 2.6.15). Similarly, tetragnathid web density remained closely associated with crude graminoid density and mean in-stream temperature (Fig. 2.6.15).

Our stepwise regression process supported many of these relationships (Table 2.5.18 & 2.5.20). The explanatory model for linyphiid abundance, for instance, included mean in-stream temperature and crude shrub density, and these were identified as a significant explanatory variable (Table 2.5.19). Tetragnathid abundance was best explained by mean in-stream temperature, emergent aquatic invertebrate biomass, mean LAI and elevation, which was consistent with the CCA (Fig. 2.6.14; Table 2.5.18). This model explained 74% variation in tetragnathid abundance (Table 2.5.18), where both mean in-stream temperature and emergent aquatic invertebrate biomass were identified as significant explanatory variables for this taxon (Table 2.5.19). Phonognathid abundance was best explained by mean in-stream temperature, crude shrub density, crude graminoid density and elevation (Table 2.5.18). Crude graminoid density, mean leaf area index, flying terrestrial invertebrate biomass, mature tree stem density and mean in-stream temperature were identified as significant explanatory variables of araneid abundance (Table 2.5.19).

Emergent aquatic invertebrate abundance, mature tree stem density, mean in-stream temperature and mean leaf area index explained 73% of tetragnathid web density (Table 2.5.20). The explanatory model for linyphiid web density included emergent aquatic invertebrate biomass, mature tree stem density and mean in-stream temperature and explained 61% of variation (Table 2.5.20). A full outline of explanatory models and significant explanatory variables can be found in Tables 2.5.16, 2.5.17, 2.5.18, 2.5.19, 2.5.20 & 2.5.21.

2.4 DISCUSSION

2.4.1 Longitudinal trends in environmental conditions

The riparian zones at lower survey reaches should have reduced structural complexity in that vegetation and canopies are less dense. Further, in-stream temperatures should be warmer at these reaches due to differences in elevation but also reduced shading from riparian vegetation. We tested these hypotheses by surveying vegetation structure and monitoring in-stream temperature at the upper, middle and lower survey reaches of perennial streams. In the first instance, these surveys were to confirm environmental differences at survey reaches that amounted to a local land clearing gradient. Upstream survey reaches comprised on average cooler waters, fuller canopies, taller vegetation and greater densities of mature trees and shrubs than reaches downstream. These longitudinal differences were consistent with our ‘within streams’ hypothesis (H_A; Table 2.5.1A), in which stream-riparian systems are structurally distinct (i.e. upstream vs. downstream) due to riparian vegetation clearance. Longitudinal patterns in vegetation (Palmquist et al., 2018; Tabacchi and Planty-Tabacchi, 1996) and in-stream temperature (Mckie, 2008; Ouellet et al., 2017) are widely recognised and so, our results here are uncontroversial. These comparisons of environmental variables were necessary to establish, however, given they formed the basis of our hypotheses for the flux of spatial subsidies and their consumers, in ecologically meaningful terms.

The effects of riparian vegetation clearance on vegetation structure and in turn, invertebrate communities are well-documented (Downie et al., 1999; Maskell et al., 2019; Tonkin et al., 2016; Wickramasinghe et al., 2004). Downie et al. (1999), for instance, demonstrated that the easing of grazing pressure on bracken and herbs is associated with increases in spider diversity. Further, Maskell et al. (2019) identified that uncleared heathlands comprising shrubs and bracken were positively associated with flying invertebrate species richness. Our results show reductions in vegetation across all strata at lower survey reaches where cattle and sheep grazing were prominent. These strong longitudinal declines, particularly in the shrub and ground layers of riparian zones are likely to have flow-on effects for the invertebrates in these habitats (Downie et al., 1999; McKie et al., 2018). Therefore, our results here confirm that our study design is appropriate for investigating the effects of riparian vegetation clearance on spatial subsidies.

Notwithstanding strong longitudinal trends, mean in-stream temperature and leaf area index did also vary between perennial streams, while a significant interaction was detected between survey reach and stream for mature tree stem density. This pattern is consistent with our ‘between streams’ hypothesis (H_c; Table 2.5.2A), in which the spatial separation of streams is the source of environmental differences. Unsurprisingly, this was not true of all environmental variables and was to be expected given the distribution of vegetation across out study area. Furthermore, mean in-stream temperature significantly varied between survey month. While this relationship varied across streams, this pattern supports our ‘between months’ hypothesis (H_D; Table 2.5.3A), where responses will vary over time. A significant strength of our study is its balanced replication, which enables us to ask whether patterns are consistent over time. This is critical for investigating the flux of spatial subsidies such as emergent aquatic invertebrates, as life history events often respond to discrete environmental changes over time and space (Bovill et al., 2019; Harper and Peckarsky, 2006; Lund et al., 2016). Few studies have considered spatiotemporal interactions however, and our understanding of how organisms respond to thermal cues for example, is limited (Turschwell et al., 2016).

2.4.2 Prey community responses to the local land clearing gradient

The abundance and biomass of flying invertebrates should be less at lower survey reaches (H_1; Table 2.5.4B). Further, these measures should vary between perennial stream (H_3; Table 2.5.5B) and survey month (H_4; Table 2.5.6B). Inputs of organic matter from riparian vegetation can represent an important food resource for some in-stream consumers (Nakano and Murakami, 2001; Wallace et al., 2015). Further, riparian vegetation moderates temperature extremes (Dohet et al., 2015). Both can significantly impact the development and emergence of aquatic invertebrates (Nelson et al., 2017; Watanabe et al., 1999). Reductions in terrestrial vegetation for instance, may result in species loss from aquatic invertebrate assemblages (Hering et al., 2013; Lorenz and Feld, 2013). In the present study, total invertebrate abundance and biomass significantly reduced, longitudinally but did not differ between perennial streams. This trend was replicated in emergent aquatic invertebrate abundance and biomass. Previous studies have demonstrated that small-bodied aquatic nematocerans have higher abundances in agricultural riparian zones, while large-bodied trichopterans and plecopterans were more abundant in forested zones (Jonsson and Stenroth, 2016; Stenroth et al., 2015). Although we found that nematoceran abundance was largely unaffected by increasing riparian vegetation clearance, our results were consistent with this literature as emergent aquatic invertebrates were more prevalent at survey reaches where native vegetation was intact and in-stream temperatures were cooler. While this may come (in part) due to their exclusion from agricultural streams, an alternative explanation may be that emergent aquatic invertebrates generally aggregate in headwater reaches before dispersing between catchments (Parkyn and Smith, 2011).

Interestingly, our stepwise regression for emergent aquatic invertebrate abundance and biomass identified mature tree stem density as the only influential environmental variable. These models provide evidence for our ‘between reaches’ hypothesis as reduced mature tree stem density is closely associated with agricultural riparian zones. Other studies however, have reported an inverse effect of land-use on emergent aquatic invertebrate abundances (Carlson et al., 2016; McKie et al., 2018). Carlson et al. (2016) for instance, documented peaks in trichopteran abundance at agricultural streams compared to those forested. Dispersal beyond the stream’s bank, however, was restricted for these invertebrates (Carlson et al., 2016). While these studies involved boreal systems and used different methodologies, abundance was significantly greater during northern hemispheric midsummer (July; Carlson et al., 2016) and this was consistent with our results.

Like emergent aquatic invertebrates, flying terrestrial invertebrate abundance and biomass peaked during midsummer (January; H_4). Flying terrestrial invertebrate biomass also varied between survey reach and tracked longitudinal declines in mature tree stem density, crude graminoid density and mean leaf area index. Larger invertebrates are more prone to decline when associated with open (often agricultural) grasslands (Kotze and O’Hara, 2003) and our results support this. Overall, our results here confirm that timing, and the degree of riparian vegetation clearance needs to be considered when investigating the flux of spatial subsidies and the standing stock of terrestrial prey.

2.4.3 Relative importance of vegetation structure and spatial subsidies to riparian spider communities

Measurements of total riparian spider abundance, biomass and web densities should be greatest at upper survey reaches. Community composition should be more taxa rich, upstream (H_1). Further, spider abundance and spiderweb density should be higher at the stream's edge (H_2). Although, these should be different between perennial streams (H_3) and survey month (H_4). Despite this, the only prevailing hypothesis was 'between streams' for total riparian spider abundance and biomass. While both abundance and biomass were significantly different between survey reaches, this varied between streams. Similar abundances along the Delatite River and at Howqua River's lower and middle survey reaches drove this interaction. Similarly, the biomass of riparian spiders at upper and middle survey reaches did not differ across most streams. Only Hughes and Hollands creeks demonstrated strong longitudinal trends (as hypothesised) likely due to the relatively high density of large-bodied nephilids at their upper reaches. As hypothesised (H_1) however, total web density did reduce, longitudinally. Previous studies have found similar relationships between web-building spiders and riparian vegetation clearance (Laeser et al., 2005). Laeser et al. (2005) for example, observed that the abundance of web-building spiders in several streams of northern Japan reduced by ~70% because of riparian vegetation removal.

Our analyses of spider community composition revealed that few taxonomic groups responded to riparian vegetation clearance, longitudinally. Consistent with our 'within streams' hypothesis (H_1), only tetragnathids were less abundant at lower survey reaches where riparian vegetation clearance was most intense. This represents a change in the community composition of riparian spiders (H_1). Our explanatory models identified that mean in-stream temperature, mean leaf area index and emergent aquatic invertebrate abundance were positively associated with tetragnathid abundance and web density. These variables also exhibited strong longitudinal trends. Further, emergent aquatic invertebrate abundance and biomass were identified as significant explanatory variables for tetragnathid abundance and web density, respectively (H_5). Our results here are consistent with previous studies that investigated the relative importance of vegetation structure and prey subsidies to tetragnathid abundance (Chan et al., 2009; Laeser et al., 2005). Likewise they support Tagwireyi & Sullivan (2016), who identified that canopy and emergent aquatic density were positively associated with tetragnathid distribution. Although, these studies ultimately identified that vegetation structure was more influential (Chan et al., 2009; Tagwireyi and Sullivan, 2016). Other studies, however, have revealed species-specific responses to changes in landscape structure driven by spider body size, dietary preference and foraging strategy (Duan et al., 2019; Mestre et al., 2018) and so, we recommend greater taxonomic resolution incorporated into future studies.

At upper and middle survey reaches, spider abundance was greatest in ecological units closer to the stream (i.e. ≤5 and 0 m), while at lower survey reaches, the highest abundances were recorded 50 m away. This relationship also varied over time with abundances 50 m away peaking at summer's end while spider abundance in the other units peaked during midsummer. As an explanation, Paetzold, Schubert, & Tockner, (2005) suggests that the degree of spatial and seasonal aggregation at the stream's edge coincides with the proportional contribution of aquatic invertebrates to a consumer's diet. The patterns detected in the present study may be a product of spider communities responding to peaks in seasonal aquatic invertebrate emergence (Paetzold et al., 2005; Sánchez-Montoya et al., 2016) in natural habitats. In highly altered habitats, however, emergent aquatic invertebrates may not contribute meaningfully to the diets of riparian spiders and so, few individuals aggregate at the stream's edge. Regardless, greater taxonomic resolution is required to investigate different predatory niches when considering where and when spiders aggregate (Opatovsky et al., 2016; Sensenig et al., 2011).

Interestingly, total web density did not differ between ecological units. While it is recognised that tetragnathids are an aquatic obligate (Tagwireyi and Sullivan, 2016), other web-building spiders such as phonognathids may only capture emergent aquatic prey, opportunistically (Michalko and Pekár, 2016; Schmidt and Rypstra, 2010). Instead, preferences for denser vegetation may drive the 'within reach' distribution of these spiders. Similarly, linyphiids responded positively to increased mature tree stem density and crude shrub density but also emergent aquatic biomass (H_5). It is important to note that such a response may also be an artefact of related variables including soil moisture and soil organic content (Barton et al., 2017; Lal, 2005), which also interact with available prey. Further, as webs for this taxon were more prevalent 50 m away from the stream, this positive association with emergent aquatic biomass may be facilitated by beyond bank dispersal (Carlson et al., 2016; Tonkin et al., 2016).

2.4.4 Limitations with stepwise regression

A key aim of stepwise regression is to isolate the relationship between each environmental variable and the response variable (Tabachnick and Fidell, 1996). Unfortunately, stepwise regressions are generally burdened by biases and encourage an inappropriate reliance on a single "best" model (Derksen and Keselman, 1992; Whittingham et al., 2006). Further, collinearity among environmental variables can be problematic for stepwise regression as it becomes difficult for models to separate the effects of individual independent variables on dependent variables, in isolation (Burnham and Anderson, 2003; Tabachnick and Fidell, 1996). This thesis encounters similar issues. To address these, we 1) considered the variance inflation factors (VIF) of the full model (i.e. one containing all environmental variables) and systematically removed those variables with a VIF > 5, and 2) compared the "best" model (as per the stepwise regression) to a subset of top models that represented <2AIC (Grueber et al., 2011). Ultimately, however, the caveats associated with stepwise regression may be insurmountable, statistically and we endorse Whittingham et al. (2006) statement that "ecologists and behavioural scientists should make use of alternative methods".

2.4.5 Conclusion

The emergence of new ecosystems via riparian vegetation clearance impacts the flux of spatial subsidies (Capon and Pettit, 2018; Morse et al., 2016; Stenroth et al., 2015). While riparian consumer responses are complex, tetragnathids responded to key environmental factors associated with a homogenising of riparian zones. Although tetragnathid abundance and web density were sensitive to the availability of subsidies, we recognise that responses may be additive and/or operate over greater scales in conjunction with vegetation structure (Davis et al., 2015; Laeser et al., 2005). Finally, we endorse further spatial subsidies studies at greater taxonomic resolutions as species-specific responses may highlight the intricacies of consumer-subsidy interactions (Terui et al., 2017).

2.5 TABLES

Table 2.5.1A Categories of formative hypotheses (H_{A-D}) that confirm different spatial and temporal patterns in environmental variables. These are designed to demonstrate that land-use changes were as expected. Possible underlying mechanisms, and the scale (within streams, between streams and between times) at which responses are likely to be most variable, are also outlined.

Hypothesis		Source of variation	Statistical approach
	General hypothesis The clearing of native vegetation fundamentally changes stream-riparian ecosystems. This is achieved directly through impacting the structure and density of vegetation and indirectly through in-stream temperature changes.		
H_A	Vegetation height and density, and canopy structure will decrease, longitudinally *Mechanism: At the local scale, riparian vegetation is frequently degraded by clearing or by activities such as livestock grazing and trampling* In-stream temperature will increase, longitudinally *Mechanism: Streams flow across natural thermal gradients from high (cold) to low (warm) elevations, unnatural gradients from dense (cold) to open (warm) vegetation.*	Within streams	See Section 2.2.5.1
H_B	Vegetation structure (canopy structure, height, density etc) within 5 m of perennial streams will be significantly different from 50 m away *Mechanism: Lateral zonation of vegetation*	Within reaches	
H_C	The above responses will vary with spatial separation of streams *Mechanism: Stream-level differences in vegetation communities and in-stream conditions due to landscape*	Between streams	
H_D	In-stream temperature will vary with temporal separation of sampling *Mechanism: Stream- and reach-level differences in in-stream are not constant and vary between days, weeks, months, seasons.*	Between times	

Table 2.5.1B Five categories of alternative hypotheses ($H_{1\text{-}4}$) that predict different spatial and temporal patterns in invertebrate abundance and biomass, and community composition. Possible underlying mechanisms, and the scale (within streams, between streams and between times) at which responses are likely to be most variable, are also outlined

	Hypothesis	Source of variation	Statistical approach
H_1	The abundance and biomass of large-bodied emergent aquatic invertebrates will decrease, longitudinally *Mechanism: Riparian vegetation clearance at the stream-level that can change the quantity and quality of spatial subsidies*	Within streams	See Section 2.2.5.1
	The abundance and biomass of other flying terrestrial invertebrates will decrease, longitudinally *Mechanism: Riparian vegetation clearance at the stream-level that can reduce the available habitat for other flying invertebrates and in turn their abundance and biomass*		
	The abundance, biomass and web density of riparian spiders will decrease, longitudinally *Mechanism: Land-use changes reduces available habitat and spatial subsidies*		
	Riparian spider community composition will be more taxa rich, upstream and distinct from those downstream *Mechanism: Riparian vegetation clearance reduces available habitat and spatial subsidies*		See Section 2.2.5.2
H_2	Spider abundance and web density will be concentrated within 5 m of perennial streams *Mechanism: Reach-level differences in vegetation communities that effects where spiders distributed*	Within reaches	See Section 2.2.5.1
H_3	The above responses will vary with spatial separation of streams *Mechanism: Stream-level differences in invertebrate diversity that effects distribution*	Between streams	
H_4	The above responses will vary with temporal separation of sampling *Mechanism: Stream- and reach-level differences in invertebrate diversity are not constant*	Between times	
H_5	Spider abundance and web density will respond strongly to the presence of spatial subsidies *Mechanism: The higher availability of spatial subsidies will support riparian consumers*	The relative importance of environmental variables	See Section 2.2.5.3

Table 2.5.2 Grouping guide for flying invertebrates captured in this study

	Order	Family/Sub-order	Specific key(s)
General			Gooderham & Tsyrlin, 2002; Taxonomic Research & Information Network/CSIRO, 2012
Aquatic	Coleoptera	Dytiscidae Hydrophilidae Noteridae	Moore, 1980; Slipinski & Lawrence, 2013; Watts, 2002
	Diptera	Tilupidae	
	Ephemeroptera		
	Hemiptera	Corixidae Notonectidae	
	Odonata		
	Plecoptera		
	Trichoptera		Holzenthal, Blahnik, Prather, & Kjer, 2007
Terrestrial	Blattodea		
	Coleoptera	(All others)	Moore, 1980; Slipinski & Lawrence, 2013; Watts, 2002
	Diptera	(All others not listed)	
	Hymenoptera		
	Isoptera		
	Lepidoptera		Nielsen, Edwards, & Rangsi, 1995
	Mantodea		
	Neuroptera		
	Orthoptera		
Indeterminate	Diptera	Nematocera	

Table 2.5.3 Mixed-effects models for response variables

Variable category	Response variable	Model structure
Environmental	In-stream temperature	$X_{ij} = \mu + \pi_i + \alpha_j + \tau + (\alpha\pi)_{ji} + (\alpha_j\tau) + (\pi_i\tau) + \epsilon_{ij}$
	Mean crude graminoid density	$X_{ijk} = \mu + \pi_i + \alpha_j + \beta_k + (\alpha\beta)_{jk} + (\alpha\pi)_{ji} + (\beta\pi)_{ki} + \epsilon_{ijk}$
	Mean crude shrub density	$X_{ijk} = \mu + \pi_i + \alpha_j + \beta_k + (\alpha\beta)_{jk} + (\alpha\pi)_{ji} + (\beta\pi)_{ki} + \epsilon_{ijk}$
	Mean LAI	$X_{ij} = \mu + \pi_i + \alpha_j + (\alpha\pi)_{ji} + \epsilon_{ij}$
	Mean mature tree stem density	$X_{ijk} = \mu + \pi_i + \alpha_j + \beta_k + (\alpha\beta)_{jk} + (\alpha\pi)_{ji} + (\beta\pi)_{ki} + \epsilon_{ijk}$
	Mean vegetation height	$X_{ijk} = \mu + \pi_i + \alpha_j + \beta_k + (\alpha\beta)_{jk} + (\alpha\pi)_{ji} + (\beta\pi)_{ki} + \epsilon_{ijk}$
Invertebrates	Spider abundance and biomass	$X_{ijk} = \mu + \pi_i + \alpha_j + \beta_k + \tau + (\alpha\beta)_{jk} + (\alpha\pi)_{ji} + (\beta\pi)_{ki} + (\alpha_j\tau) + (\beta_k\tau) + (\pi_i\tau) + (\alpha\pi\tau)_{ji} + (\beta\pi\tau)_{ki} + (\alpha\beta\tau)_{jk} + \epsilon_{ijk}$
	Spiderweb count	$X_{ijk} = \mu + \pi_i + \alpha_j + \beta_k + \tau + (\alpha\beta)_{jk} + (\alpha\pi)_{ji} + (\beta\pi)_{ki} + (\alpha_j\tau) + (\beta_k\tau) + (\pi_i\tau) + (\alpha\pi\tau)_{ji} + (\beta\pi\tau)_{ki} + (\alpha\beta\tau)_{jk} + \epsilon_{ijk}$
	Terrestrial aerial invertebrate abundance and biomass	$X_{ij} = \mu + \pi_i + \alpha_j + \tau + (\alpha\pi)_{ji} + (\alpha_j\tau) + (\pi_i\tau) + \epsilon_{ij}$
	Aquatic emergent invertebrate abundance and biomass	$X_{ij} = \mu + \pi_i + \alpha_j + \tau + (\alpha\pi)_{ji} + (\alpha_j\tau) + (\pi_i\tau) + \epsilon_{ij}$

Table 2.5.4 Measurements of canopy structure for riparian zones of survey reaches. Values presented are Leaf Area Index (LAI), crown cover (f_c; % ground covered by the vertical projection of solid crowns), foliage cover (f_f; % ground covered by the vertical projection of foliage and branches), cover porosity (Φ; % of space between foliage and branches) and gap fraction (GF; % of space unobstructed by foliage or branches; Macfarlane et al., 2007; Welles & Cohen, 1996)

	Survey reaches																	
	Broken River			Delatite River			Hollands Creek			Howqua River			Hughes Creek			Ryan Creek		
	Upper	Middle	Lower	Upper	Middle	Lower	Upper	Middle	Lower	Upper	Middle	Lower	Upper	Middle	Lower	Upper	Middle	Lower
LAI	1.78±0.09	1.58±0.12	0.45±0.08	1.59±0.16	1.72±0.1	1.35±0.11	1.71±0.14	0.38±0.08	0.32±0.07	1.58±0.12	1.4±0.1	0.36±0.12	1.78±0.12	1.63±0.14	0.51±0.09	1.78±0.16	1.55±0.11	0.28±0.11
f_c	0.72±0.03	0.64±0.04	0.23±0.04	0.62±0.03	0.74±0.03	0.56±0.05	0.62±0.04	0.18±0.04	0.2±0.04	0.63±0.04	0.62±0.05	0.1±0.03	0.7±0.04	0.65±0.04	0.24±0.04	0.67±0.04	0.69±0.04	0.12±0.03
f_f	0.5±0.02	0.44±0.03	0.14±0.03	0.43±0.03	0.5±0.02	0.38±0.03	0.45±0.03	0.11±0.03	0.12±0.02	0.44±0.03	0.41±0.03	0.07±0.02	0.49±0.03	0.45±0.03	0.15±0.02	0.47±0.03	0.48±0.03	0.09±0.02
Φ	0.32±0.02	0.34±0.03	0.58±0.05	0.32±0.02	0.36±0.03	0.34±0.03	0.33±0.03	0.69±0.05	0.65±0.05	0.35±0.03	0.4±0.03	0.56±0.06	0.33±0.03	0.35±0.03	0.57±0.05	0.4±0.04	0.36±0.03	0.68±0.06
GF	0.5±0.02	0.56±0.03	0.86±0.03	0.57±0.03	0.5±0.02	0.62±0.03	0.55±0.03	0.89±0.03	0.88±0.02	0.56±0.03	0.59±0.03	0.93±0.02	0.51±0.03	0.55±0.03	0.85±0.02	0.53±0.03	0.52±0.03	0.91±0.02

Table 2.5.5 Analysis of variance of in-stream temperature

Source	SS (Type 3)	df	MS	F	P
Between blocks					
Stream (block)	2.565	5	0.513	9.956	**<0.001**
Reach	0.214	2	0.107	4.456	**0.014**
Stream x Reach	0.055	10	0.006	0.107	0.998
Between times					
Month	6.221	7	0.887	36.949	**<0.001**
Month x Stream	0.204	35	0.006	1.657	**0.028**
Month x Reach	0.006	14	0.001	0.019	0.998
Residual error + Month x Stream x Reach	0.062	70	0.001	-	-
Total					

Table 2.5.6 Analysis of variance of leaf area index

Source	SS (Type 3)	df	MS	F	P
Between blocks					
Stream (block)	14.11	5	2.822	21	**<0.001**
Reach	62.06	2	31.031	230.92	**<0.001**
Stream x Reach	16.44	10	1.644	-	**-**
Total		17			

Table 2.5.7 Analysis of variance of vegetation height

Source	SS (Type 3)	df	MS	F	P
Between blocks					
Stream (block)	2.197	5	0.439	2.265	0.092
Reach	7.093	2	3.546	18.282	**<0.001**
Unit	0.32	1	0.32	0.647	0.429
Reach x Unit	1.419	2	0.709	3.515	**0.043**
Reach x Stream	2.106	10	0.211	1.085	0.421
Unit x Stream	0.503	5	0.101	0.204	0.958
Residual error + Stream x Reach x Unit	1.249	10	0.125	-	**-**
Total					

Table 2.5.8 Analysis of variance of mature tree stem density

Source	SS (Type 3)	df	MS	F	P
Between blocks					
Stream (block)	5.89	5	1.178	1.786	0.167
Reach	47.39	2	23.697	35.929	**<0.001**
Unit	2.18	1	2.181	0.746	0.396
Reach x Unit	0.53	2	0.267	0.255	0.776
Reach x Stream	16.33	10	1.633	2.476	**0.045**
Unit x Stream	3.22	5	0.644	0.22	0.95
Residual error + Stream x Reach x Unit	5.94	10	0.594	-	**-**
Total					

Table 2.5.9 Analysis of variance of crude graminoid density

Source	SS (Type 3)	df	MS	F	P
Between blocks					
Stream (block)	7.82	5	1.564	0.548	0.738
Reach	13.16	2	6.582	2.307	0.128
Unit	38.05	1	38.05	31.293	**<0.001**
Reach x Unit	1.93	2	0.96	1.116	0.341
Reach x Stream	6.73	10	0.673	0.236	0.988
Unit x Stream	4.02	5	0.8	0.661	0.656
Residual error + Stream x Reach x Unit	7.36	10	0.74	-	-
Total					

Table 2.5.10 Analysis of variance of crude shrub density

Source	SS (Type 3)	df	MS	F	P
Between blocks					
Stream (block)	17.02	5	3.405	2.189	0.101
Reach	12.36	2	6.182	3.974	**0.037**
Unit	7.46	1	7.456	4.61	**0.042**
Reach x Unit	8.02	2	4.009	2.912	0.07
Reach x Stream	11.75	10	1.175	0.756	0.667
Unit x Stream	5.85	5	1.169	0.723	0.613
Residual error + Stream x Reach x Unit	6.681	10	0.668	-	-
Total					

Table 2.5.11 Analysis of variance of total flying invertebrate and emergent aquatic invertebrate abundance and biomass. Sums of squares are type 3. Bolded P-values indicate significance.

		Aquatic invertebrate abundance				Aquatic invertebrate biomass			
Source	*df*	*SS*	*MS*	*F*	*P*	*SS*	*MS*	*F*	*P*
Between blocks									
Stream (block)	5	6.47	1.294	0.65	0.663	0.077	0.015	0.713	0.617
Reach	2	27.47	13.735	6.901	**0.002**	0.356	0.178	8.243	**0.001**
Residual error + Stream x Reach	10	11.37	1.137	-	-	0.068	0.007	-	-
Between times									
Month	2	15.75	7.876	5.43	**0.007**	0.087	0.044	2.428	0.099
Month x Stream	10	15.91	1.591	0.727	0.694	0.351	0.035	1.662	0.129
Month x Reach	4	63.94	2.448	1.723	0.162	0.024	0.006	0.329	0.857
Residual error + Month x Stream x Reach	20	30.192	1.51	-	-	0.314	0.016	-	-
Total	53								

Table 2.5.12 Analysis of variance of flying terrestrial invertebrate and indeterminate invertebrate abundance and biomass. Sums of squares are type 3. Bolded P-values indicate significance.

		Flying terrestrial invertebrate abundance				Flying terrestrial invertebrate biomass				Nematoceran abundance				Nematoceran biomass			
Source	*df*	*SS*	*MS*	*F*	*P*	*SS*	*MS*	*F*	*P*	*SS*	*MS*	*F*	*P*	*SS*	*MS*	*F*	*P*
Between blocks																	
Stream (block)	5	11.71	2.342	2.066	0.093	1.222	0.244	1.797	0.138	6.1	1.219	0.549	0.738	0.002	0.0003	0.381	0.858
Reach	2	6.88	3.44	3.034	0.061	3.797	1.899	13.963	**<0.001**	9.54	4.768	2.147	0.132	0.001	0.0005	0.614	0.547
Residual error + Stream x Reach	10	15.4	1.54	-	-	1.363	0.136	-	-	31.95	3.195	-	-	0.006	0.0006	-	-
Between times																	
Month	2	9.48	4.74	3.853	**0.029**	1.55	0.775	6.399	**0.004**	18.67	9.334	4.5	**0.02**	0.008	0.004	6.488	**0.003**
Month x Stream	10	10.34	1.034	0.86	0.577	1.09	0.109	0.529	0.858	8.16	0.816	0.311	0.974	0.005	0.0005	0.781	0.646
Month x Reach	4	3.1	0.775	0.63	0.643	0.479	0.119	0.988	0.424	6	1.499	0.723	0.58	0.001	0.0002	0.395	0.811
Residual error + Month x Stream x Reach	20	17.899	0.895	-	-	1.776	0.089	-	-	47.12	2.356	-	-	0.02	0.0008	-	-
Total	53																

Table 2.5.13 Analysis of variance of the spider abundance, biomass and web count including the Delatite River. Sums of squares are type 3. Bolded P-values indicate significance.

		Spider abundance (sweep net)				Spider biomass (sweep net)				Spiderwebs (survey)				
Source	*df*	*SS*	*MS*	*F*	*P*	*SS*	*MS*	*F*	*P*	*df*	*SS*	*MS*	*F*	*P*
Between blocks														
Stream (block)	5	22.96	4.593	10.89	**<0.001**	0.282	0.056	6.222	**<0.001**	5	372	74.4	1.076	0.381
Reach	2	27.9	13.702	32.49	**<0.001**	0.314	0.157	17.342	**<0.001**	2	2093	1046.4	15.136	**<0.001**
Unit	2	7.18	3.59	8.511	**<0.001**	0.096	0.048	5.283	**0.006**	1	98	98.2	1.421	0.237
Reach x Unit	4	6.17	1.542	3.657	**0.008**	0.025	0.006	0.692	0.599	2	61	30.3	0.438	0.647
Reach x Stream	10	14.83	1.483	3.515	**<0.001**	0.447	0.045	4.931	**<0.001**	10	1461	146.1	2.114	**0.034**
Unit x Stream	10	5.41	0.541	1.283	0.249	0.356	0.036	3.931	**<0.001**	5	197	39.4	0.57	0.723
Residual error + Stream x Reach x Unit	20	6.04	0.302	-	-	0.632	0.032	-	-	10	257	25.7	-	-
Between times														
Month	2	1.99	0.995	1.624	0.201	0.005	0.002	0.126	0.881	2	750	375.2	5.75	**0.004**
Month x Stream	10	10.00	1	2.082	**0.002**	0.125	0.012	0.776	0.652	10	1399.3	139.9	3.055	**0.004**
Month x Reach	4	0.05	0.013	0.021	0.999	0.046	0.012	0.613	0.654	4	227	56.80	0.871	0.484
Month x Unit	4	6.68	1.715	2.798	**0.03**	0.043	0.011	0.572	0.683	2	265	132.4	2.029	0.137
Month x Reach x Unit	8	3.12	0.39	0.637	0.746	0.064	0.008	0.408	0.914	4	148	37.1	0.568	0.686
Month x Stream x Reach	20	6.44	0.322	0.671	0.847	0.174	0.008	0.542	0.941	20	739	37	0.807	0.694
Month x Stream x Unit	20	8.97	0.449	0.672	0.846	0.17	0.008	0.446	0.98	10	673	67.3	0.842	0.591
Residual error + Month x Stream x Reach x Unit	40	8.108	0.203	-	-	0.354	0.009	-	-	20	774.4	38.7	-	-
Total	161									107				

Table 2.5.14 Analysis of deviance of spider community composition and spider taxa abundance response to treatment effects. Bolded P-values indicate significance. LRT = likelihood ratio test statistic.

		Spider community composition		Tetragnatha abundance		Phonognatha abundance		Linyphiidae abundance		Dolomedes abundance		Austracantha abundance		Nephila abundance	
Source	*df*	*LRT*	*P*	*LRT*	*P*	*LRT*	*P*	*LRT*	*P*	*LRT*	*P*	*LRT*	*P*	*LRT*	*P*
Between blocks															
Stream (block)	5	215.4	**0.001**	7.579	0.454	27.913	**0.001**	40.385	**0.001**	18.765	**0.022**	9.683	0.428	15.009	0.067
Reach	2	83.3	**0.001**	25.261	**0.001**	2.399	0.938	3.46	0.881	13.558	**0.018**	0.929	0.983	3.056	0.91
Unit	2	385.7	**0.001**	169.232	**0.001**	37.188	**0.001**	32.244	**0.001**	7.787	0.133	17.08	**0.004**	20.825	**0.002**
Reach x Unit	4	34.3	0.203	12.606	0.147	0.009	0.999	0.431	0.991	2.287	0.973	4.397	0.793	0.001	0.999
Reach x Stream	10	123.3	**0.007**	25.736	**0.026**	19.613	0.159	3.972	0.938	0.529	0.938	11.667	0.55	6.24	0.766
Unit x Stream	10	79.5	**0.005**	13.036	0.529	16.922	0.252	2.924	0.908	3.061	0.908	2.908	0.908	0.001	0.908
Residual error + Stream x Reach x Unit	20	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Between times															
Month	2	74.9	**0.005**	26.127	**0.002**	3.45	0.945	7.285	0.563	4.511	0.872	2.405	0.962	0.503	0.976
Month x Stream	10	234.5	**0.001**	28.806	0.069	28.048	0.069	35.266	**0.01**	13.105	0.211	15.587	0.179	5.982	0.423
Month x Reach	4	78.2	0.072	6.239	0.979	1.829	0.979	3.353	0.979	11.812	0.776	7.971	0.948	6.188	0.979
Month x Unit	4	82.6	**0.001**	18.944	0.061	2.948	0.677	3.685	0.677	12.118	0.119	0.002	0.711	0.001	0.711
Month x Reach x Unit	8	23.6	**0.001**	15.163	**0.001**	7.841	**0.037**	0.567	0.494	0.002	0.494	0.001	0.927	0.001	0.927
Month x Stream x Reach	20	130.4	**0.001**	63.437	**0.002**	13.811	**0.046**	23.189	**0.046**	0.002	0.618	0.001	0.656	5.546	**0.046**
Month x Stream x Unit	20	88.7	**0.001**	35.426	**0.001**	3.7	0.237	31.292	**0.001**	4.499	0.175	0.001	0.618	0.001	0.656
Residual error + Month x Stream x Reach x Unit	40	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Total	161														

Table 2.5.15 Analysis of deviance of web anchorage points response to treatment effects. Bolded P-values indicate significance. LRT = likelihood ratio test statistic.

		Blackberry		Ground fern		Other grasses		Native graminoids		Shrubs		Trees	
Source	*df*	*LRT*	*P*	*LRT*	*P*	*LRT*	*P*	*LRT*	*P*	*LRT*	*P*	*LRT*	*P*
Between blocks													
Stream (block)	5	11.189	0.192	15.649	0.055	6.55	0.567	0.568	0.956	5.51	0.567	1.79	0.934
Reach	2	3.9	0.461	6.587	0.184	8.388	0.095	2.405	0.647	18.034	**0.001**	5.683	0.222
Unit	2	0.925	0.705	15.098	**0.002**	29.437	**0.001**	160.877	**0.001**	10.012	**0.006**	50.119	**0.001**
Reach x Unit	4	10.929	0.094	1.099	0.973	0.965	0.973	0.001	0.973	0.747	0.973	0.663	0.973
Reach x Stream	10	0.406	0.826	6.724	0.826	30.588	0.114	27.865	0.114	18.617	0.362	10.517	0.826
Unit x Stream	10	0.925	0.784	3.337	0.784	3.193	0.784	0.001	0.784	10.357	0.37	8.349	0.411
Residual error + Stream x Reach x Unit	20	-	-	-	-	-	-	-	-	-	-	-	-
Between times													
Month	2	4.299	0.683	1.197	0.879	20.615	0.006	9.73	0.19	1.893	0.864	6.675	0.461
Month x Stream	10	2.707	0.64	11.928	0.64	6.028	0.64	37.375	0.135	17.861	0.64	23.003	0.64
Month x Reach	4	4.484	0.533	27.036	**0.035**	10.956	0.309	14.597	0.164	7.08	0.533	20.677	0.065
Month x Unit	4	0.001	0.68	16.229	**0.001**	0.107	0.68	0.001	0.855	39.785	**0.001**	1.71	0.649
Month x Reach x Unit	8	0.001	0.343	0.001	0.377	0.001	0.377	0.001	0.599	5.53	0.105	4.101	0.105
Month x Stream x Reach	20	0.001	0.593	8.789	**0.009**	23.48	**0.009**	44.222	**0.001**	66.495	**0.001**	29.816	**0.009**
Month x Stream x Unit	20	0.001	0.656	0.002	0.345	0.001	0.345	0.001	0.834	33.952	**0.001**	30.448	**0.001**
Residual error + Month x Stream x Reach x Unit	40	-	-	-	-	-	-	-	-	-	-	-	-
Total	161												

Table 2.5.16 Explanatory models for the flying invertebrate abundance and biomass using a forward step-wise regression process. ΔAIC represents the difference between the model's AIC (Akaike's Information Criterion); w_i is the Akaike weight (i.e. the weight of the model/relative support for the mode); R^2 is the statistical measure that represents the proportion of the variance explained by the most parsimonious model. Equations are provided for the "best" model as per the stepwise regression (indicated by an asterisk*) and the two top models that ranked the highest for each response. All models were significant.

Response	Model structure	ΔAIC_c	w_i	R^2
Emergent aquatic invertebrate abundance	Mature tree stem density*	0	0.26	0.14
	Crude graminoid density + mature tree stem density	1.04	0.15	
	Mean leaf area index + mature tree stem density	1.24	0.14	
Emergent aquatic invertebrate biomass	Mature tree stem density*	0	0.28	0.14
	Mature tree stem density + elevation	1.09	0.16	
	Crude graminoid density + mature tree stem density	1.35	0.14	
Flying terrestrial invertebrate abundance	Crude graminoid density + mature tree stem density*	0	0.27	0.11
	Crude graminoid density + mature tree stem density + mature shrub density	0.13	0.25	
	Crude graminoid density + mature tree stem density + mean in-stream temperature	0.8	0.18	
Flying terrestrial invertebrate biomass	Crude shrub density + mature tree stem density*	0	0.36	0.26
	Crude shrub density + mature tree stem density + mean leaf area index	0.24	0.32	
	Crude shrub density + mature tree stem density + crude graminoid density	1.77	0.15	

Table 2.5.17 Relative variable importance (RVI) on flying invertebrate abundance and biomass; calculated from Akaike weights. Variables with RVI ≥ 0.73 (indicated in bold) are considered significant explanatory variables.

RVI	Emergent aquatic invertebrate abundance	Emergent aquatic invertebrate biomass	Flying terrestrial invertebrate abundance	Flying terrestrial invertebrate biomass
Mean LAI	0.27	0.14	0.14	0.34
Crude graminoid density	0.27	0.13	**0.99**	0.17
Crude shrub density	0.24	0.15	0.45	**0.99**
Mature tree stem density	**0.99**	**0.99**	**0.98**	**0.99**
Mean in-stream temperature	0.12	0.15	0.46	0.02
Elevation	0.1	0.17	0.03	0.16

Table 2.5.18 Explanatory models for the total spider, tetragnathid, phonognathid and linyphiid abundance using a forward step-wise regression process. ΔAIC represents the difference between the model's AIC (Akaike's Information Criterion); w_i is the Akaike weight (i.e. the weight of the model/relative support for the mode); R^2 is the statistical measure that represents the proportion of the variance explained by the most parsimonious model. Equations are provided for the "best" model as per the stepwise regression (indicated by an asterisk*) and the two top models that ranked the highest for each response. All models were significant.

Response	Model structure	ΔAIC_c	w_i	R^2
Total spider abundance	Mature tree stem density + emergent aquatic invertebrate biomass + flying terrestrial invertebrate biomass*	0	0.36	0.22
	Mature tree stem density + emergent aquatic invertebrate biomass + mean in-stream temperature + elevation	0.93	0.23	
	Mature tree stem density + emergent aquatic invertebrate biomass + flying terrestrial invertebrate biomass + elevation + crude graminoid density	1.09	0.21	
Tetragnathid abundance	Mean in-stream temperature + emergent aquatic invertebrate biomass + mean leaf area index + elevation*	0	0.27	0.74
	Mean in-stream temperature + emergent aquatic invertebrate biomass	0.04	0.26	
	Mean in-stream temperature + emergent aquatic invertebrate biomass + mean leaf area index + elevation + crude graminoid density	0.22	0.24	
Phonognathid abundance	Crude graminoid density + crude shrub density + elevation + mean in-stream temperature*	0	0.36	0.21
	Crude graminoid density + crude shrub density + elevation + emergent aquatic invertebrate abundance	0.12	0.34	
	Crude graminoid density + crude shrub density + elevation + emergent aquatic invertebrate biomass + mean in-stream temperature	1.45	0.17	
Linyphiid abundance	Mean in-stream temperature + elevation + crude shrub density	0	0.37	0.24
	Mean in-stream temperature + elevation + crude shrub density + mature tree stem density	0.71	0.26	
	+ crude shrub density + elevation + emergent aquatic invertebrate abundance + mean in-stream temperature	0.94	0.23	
Araneid abundance	Crude graminoid density + mean leaf area density + flying terrestrial invertebrate biomass + mean in-stream temperature	0	0.3	0.38
	Crude graminoid density + mean leaf area density + flying terrestrial invertebrate abundance + mean in-stream temperature + flying terrestrial invertebrate biomass + mature tree stem density	0.48	0.23	
	Crude graminoid density + crude shrub density + mean leaf area index + mature tree stem density + mean in-stream temperature + flying terrestrial invertebrate biomass	1.43	0.14	

Table 2.5.19 Relative variable importance (RVI) on spider abundance; calculated from Akaike weights. Variables with RVI ≥ 0.73 (indicated in bold) are considered significant explanatory variables.

RVI	Total spider abundance	Tetragnathid abundance	Phonognathid abundance	Linyphiid abundance	Araneid abundance
Mean LAI	<0.01	**0.74**	<0.01	<0.01	**0.99**
Crude graminoid density	0.21	<0.01	**0.92**	<0.01	**0.98**
Crude shrub density	<0.01	0.24	**0.87**	**0.98**	0.17
Mature tree stem density	**0.98**	<0.01	<0.01	0.26	**0.99**
Mean in-stream temperature	**0.79**	**0.96**	**0.98**	**0.98**	**0.99**
Emergent aquatic invertebrate abundance	<0.01	<0.01	<0.01	0.14	0.02
Emergent aquatic invertebrate biomass	**0.95**	**0.97**	0.51	0.23	0.02
Flying terrestrial invertebrate abundance	<0.01	<0.01	0.34	<0.01	0.25
Flying terrestrial invertebrate biomass	**0.77**	<0.01	<0.01	<0.01	**0.99**
Elevation	**0.79**	0.27	**0.87**	**0.97**	<0.01

Table 2.5.20 Explanatory models for the total spider, tetragnathid, phonognathid, linyphiid and araneid web density using a forward step-wise regression process. ΔAIC represents the difference between the model's AIC (Akaike's Information Criterion); w_i is the Akaike weight (i.e. the weight of the model/relative support for the mode); R^2 is the statistical measure that represents the proportion of the variance explained by the most parsimonious model. Equations are provided for the "best" model as per the stepwise regression (indicated by an asterisk*) and the two top models that ranked the highest for each response. All models were significant.

Response	Model structure	ΔAIC_c	w_i	R^2
Total web density	Mature tree stem density + mean in-stream temperature + emergent aquatic invertebrate biomass*	0	0.46	0.29
	Mature tree stem density + emergent aquatic invertebrate abundance + emergent aquatic invertebrate biomass	0.12	0.43	
	Mature tree stem density	4.86	0.04	
Tetragnathid web density	Mean in-stream temperature + mean leaf area index + mature tree stem density + emergent aquatic invertebrate abundance*	0	0.5	0.73
	Mean in-stream temperature + mean leaf area index + mature tree stem density + crude graminoid density + emergent aquatic invertebrate abundance	0.59	0.38	
	Mean in-stream temperature + mature tree stem density + emergent aquatic invertebrate abundance	4.20	0.06	
Phonognathid web density	Mean in-stream temperature*	0	0.37	0.04
	Crude graminoid density + emergent aquatic invertebrate biomass + flying terrestrial invertebrate biomass + mean in-stream temperature	0.55	0.28	
	Emergent aquatic invertebrate biomass + flying terrestrial invertebrate biomass + mean in-stream temperature	0.67	0.27	
Linyphiid web density	Mean in-stream temperature + mature tree stem density +emergent aquatic invertebrate biomass*	0	0.36	0.61
	Mean in-stream temperature + mean leaf area index +emergent aquatic invertebrate biomass	0.05	0.35	
	Mean in-stream temperature + elevation +emergent aquatic invertebrate biomass	0.39	0.29	
Araneid web density	Crude graminoid density + crude shrub density + mature tree stem density + flying terrestrial invertebrate abundance + flying terrestrial invertebrate biomass*	0	0.53	0.20
	Crude graminoid density + crude shrub density + mean leaf area index + flying terrestrial invertebrate abundance + flying terrestrial invertebrate biomass	1.93	0.2	
	Crude graminoid density + crude shrub density + mature tree stem density + flying terrestrial invertebrate abundance + flying terrestrial invertebrate biomass + emergent aquatic invertebrate abundance	1.94	0.2	

Table 2.5.21 Relative variable importance (RVI) on spider web density; calculated from Akaike weights. Variables with RVI ≥ 0.73 (indicated in bold) are considered significant explanatory variables.

RVI	Total web density	Tetragnathid web density	Phonognathid web density	Linyphiid web density	Araneid web density
Mean LAI	<0.01	**0.9**	<0.01	0.35	0.23
Crude graminoid density	0.47	0.43	<0.01	<0.01	**0.95**
Crude shrub density	<0.01	0.02	0.28	<0.01	**0.97**
Mature tree stem density	**0.99**	**0.98**	<0.01	0.36	**0.97**
Mean in-stream temperature	**0.91**	**0.98**	**0.92**	**0.97**	**0.98**
Emergent aquatic invertebrate abundance	0.53	**0.97**	0.27	<0.01	0.23
Emergent aquatic invertebrate biomass	**0.96**	0.02	0.28	**0.98**	0.03
Flying terrestrial invertebrate abundance	0.47	0.98	<0.01	<0.01	**0.97**
Flying terrestrial invertebrate biomass	<0.01	0.02	0.55	<0.01	**0.97**
Elevation	0.28	**0.73**	<0.01	0.29	0.28

2.6 FIGURES

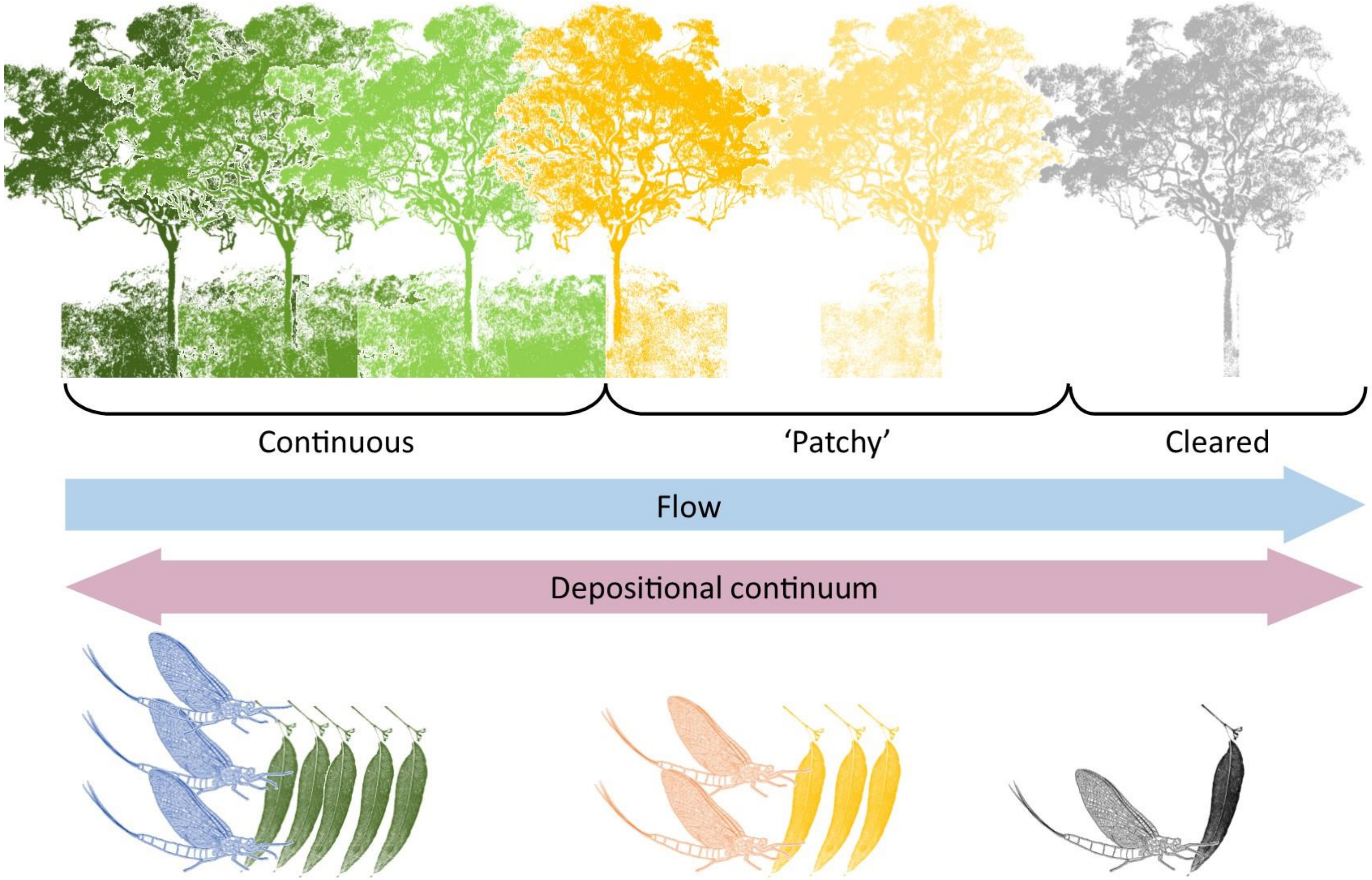

Figure 2.6.1 Deposition continuum of spatial subsidies along an agricultural land-use gradient. Previous studies have demonstrated that spatial subsidies such as leaflitter and aquatic emergent invertebrates reduce along rivers with increasing agricultural land-use intensity.

Figure 2.6.2 Study area within the Goulburn-Broken Catchment in regional Victoria, Australia. Green areas are crude approximation of forest boundaries, rather than an indication of forest density. These were derived from VicMap Lite (Department of Land Water and Planning, 2013).

Figure 2.6.3 Mean daily temperature across all perennial streams (n=6) over the survey period.

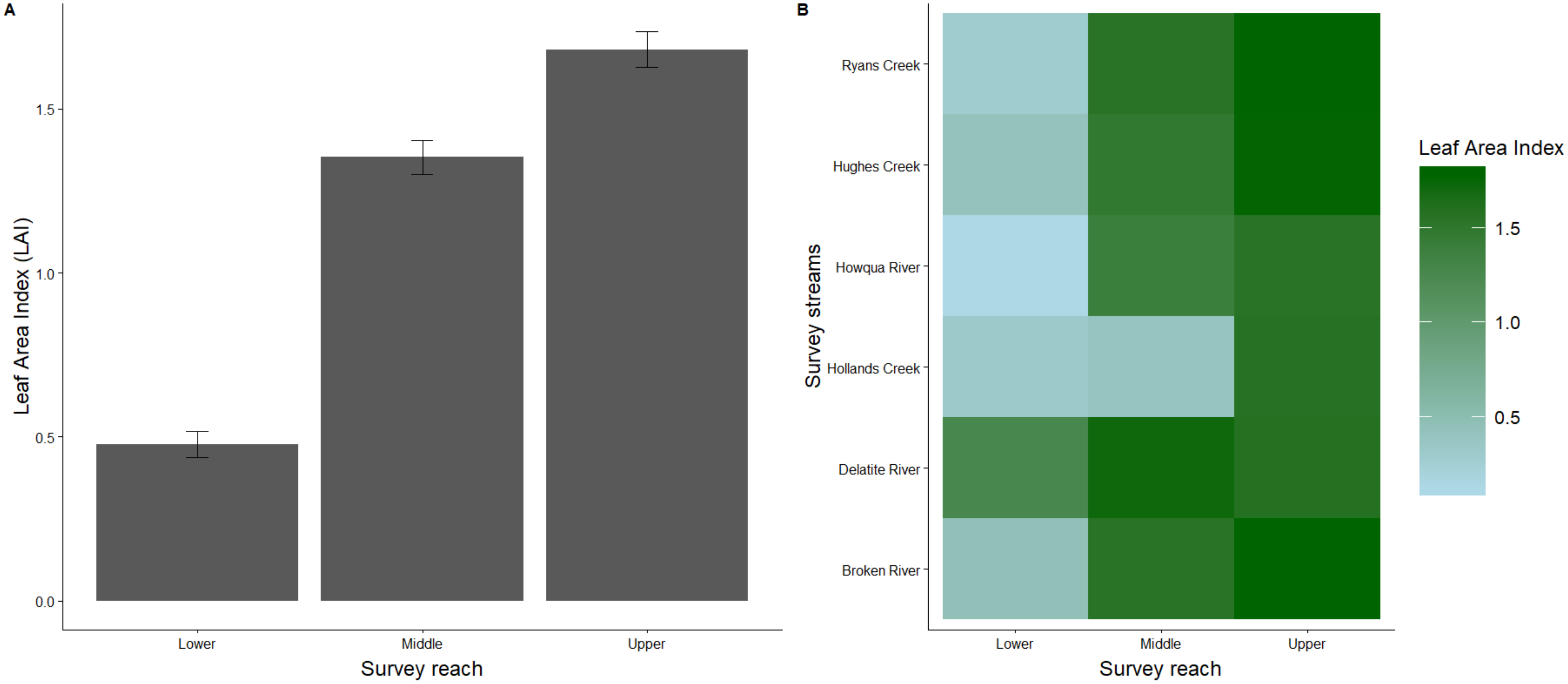

Figure 2.6.4 A) Average leaf area index (LAI) along survey reaches, and B) longitudinal changes in LAI per survey reach. Values are presented with standard error bars.

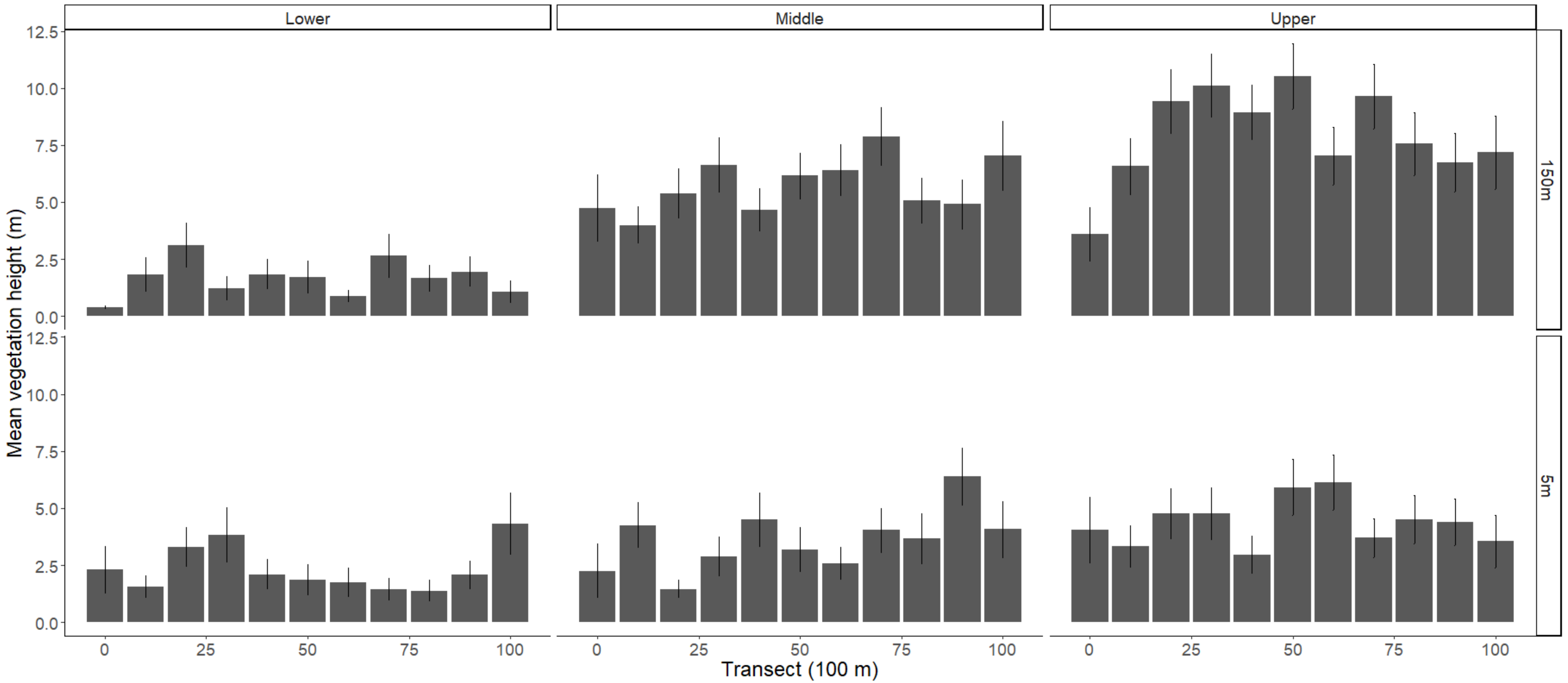

Figure 2.6.5 Mean height of riparian vegetation (m) along 100 m transects at 10 m intervals for survey reaches. Heights are presented with respect to survey reach (n = 6; upper, middle and lower) and transects (150 m and 5). Values are presented with standard error bars.

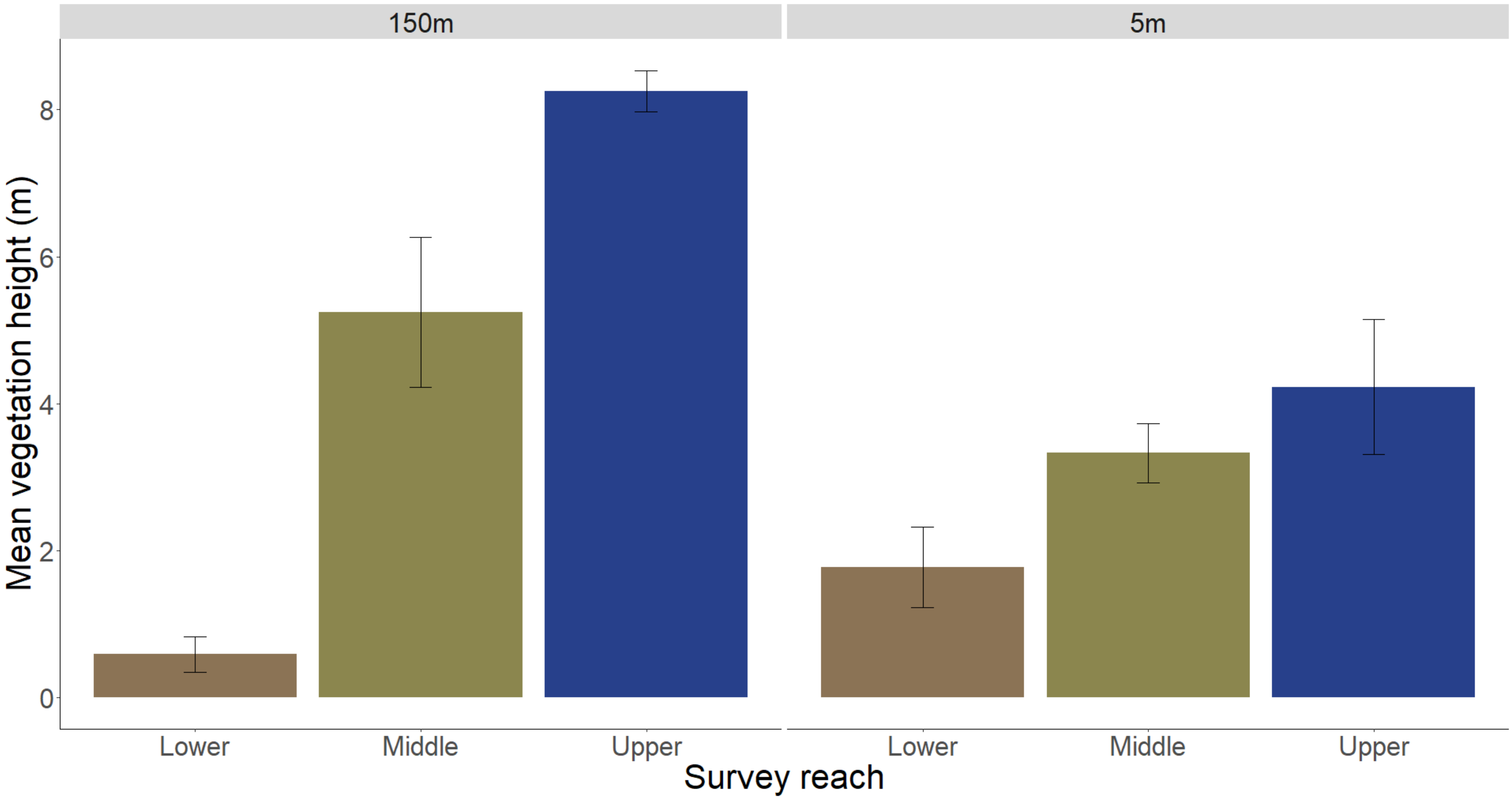

Figure 2.6.6. Mean height of riparian vegetation (m) between units (150 m and 5m). Values are presented with standard error bars.

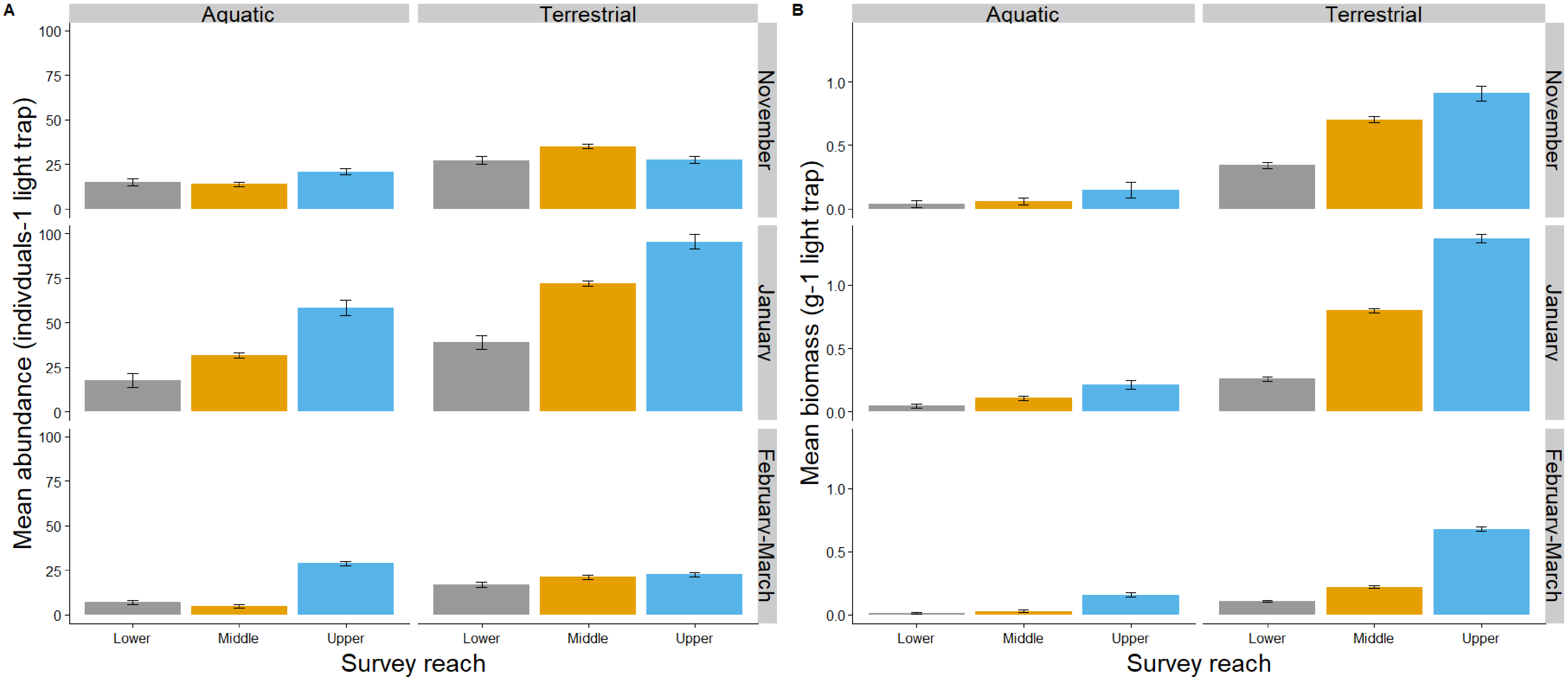

Figure 2.6.7 Mean (A) abundances and (B) biomasses of flying invertebrates across survey reaches and months. Values are presented with regards to broad grouping and standard error bars.

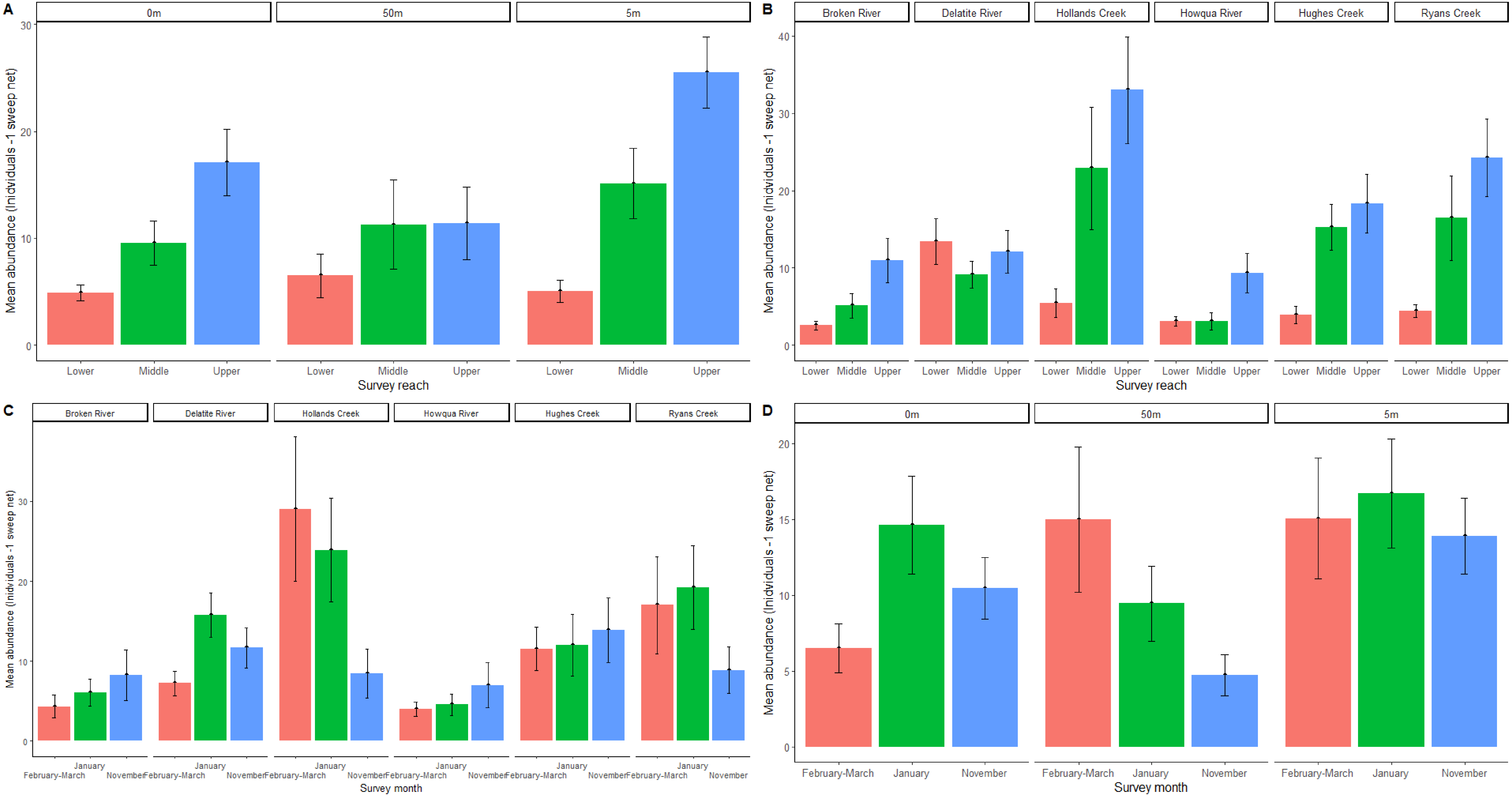

Figure 2.6.8 Mean spider abundances across A) unit and survey reach, B) stream and survey reach, C) stream and survey month and D) unit and survey month. Values are presented standard error bars.

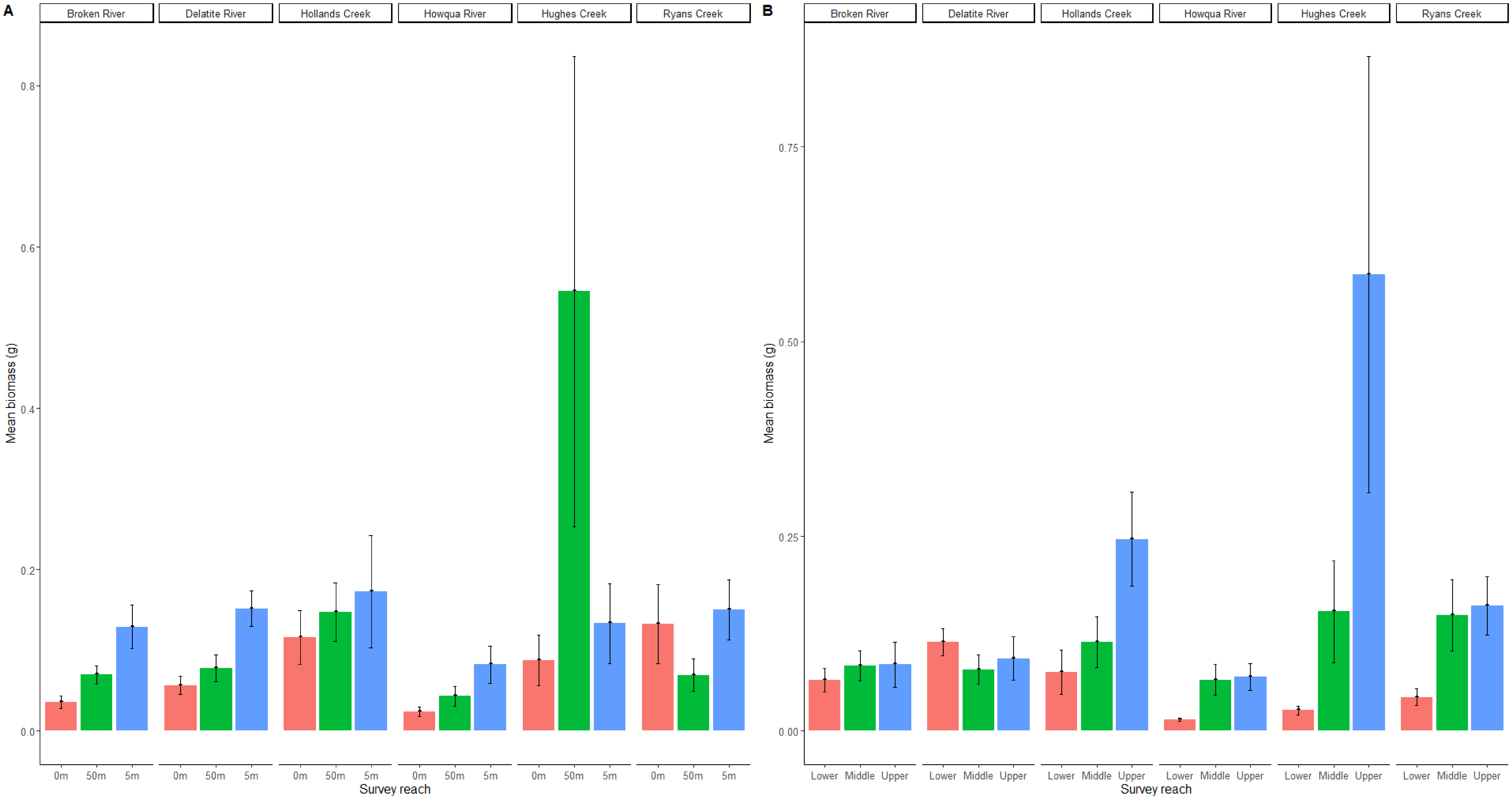

Figure 2.6.9 Mean spider biomasses across A) streams and unit, and B) stream and survey reach. Values are presented with regards to broad grouping and standard error bars.

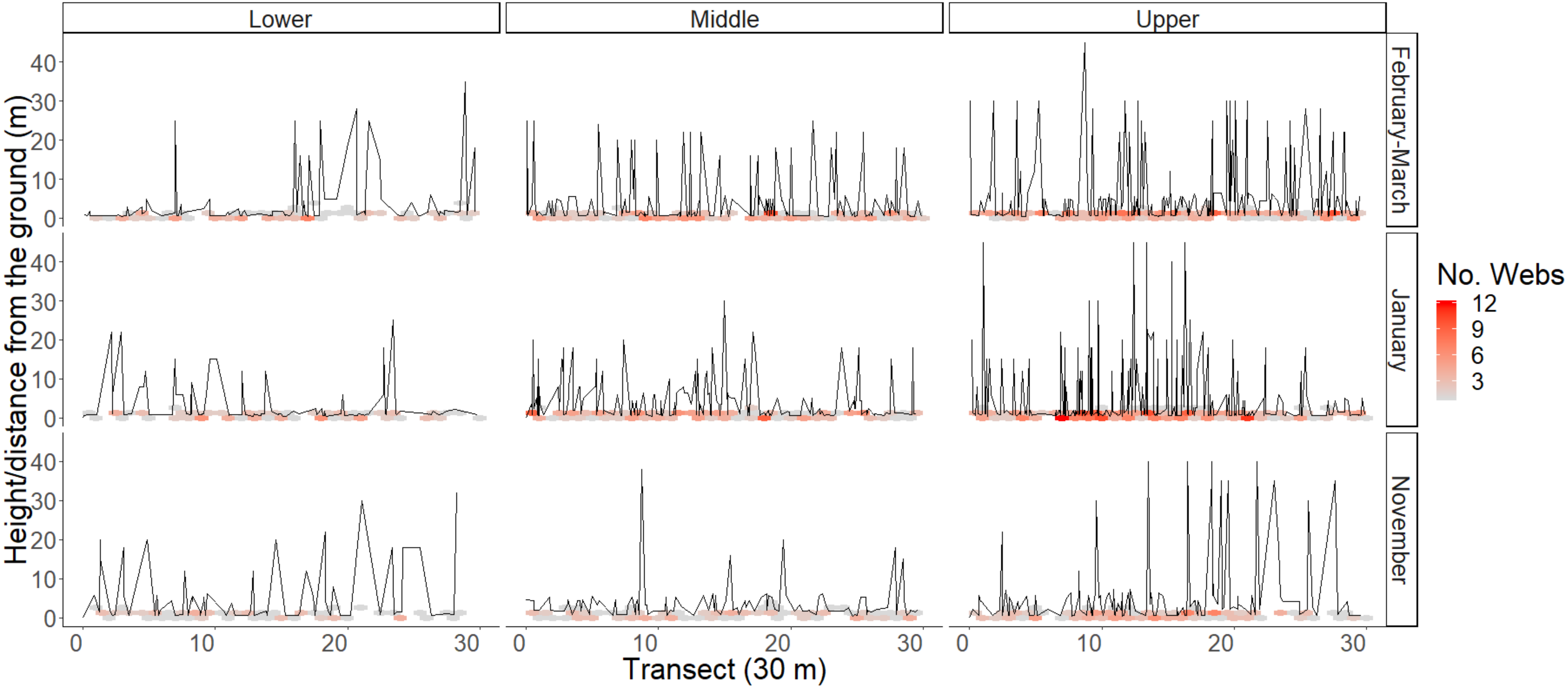

Figure 2.6.10 Composite of webs counted at all survey reaches (excluding the Delatite River). Tiles indicate the position of webs along transects, where darker tiles represent higher counts. Counts have been group by survey month (November 2016/17, January 2017/18 and February and March 2017/2018, respectively). The black lines represent the average height of the substrate each web was attached to.

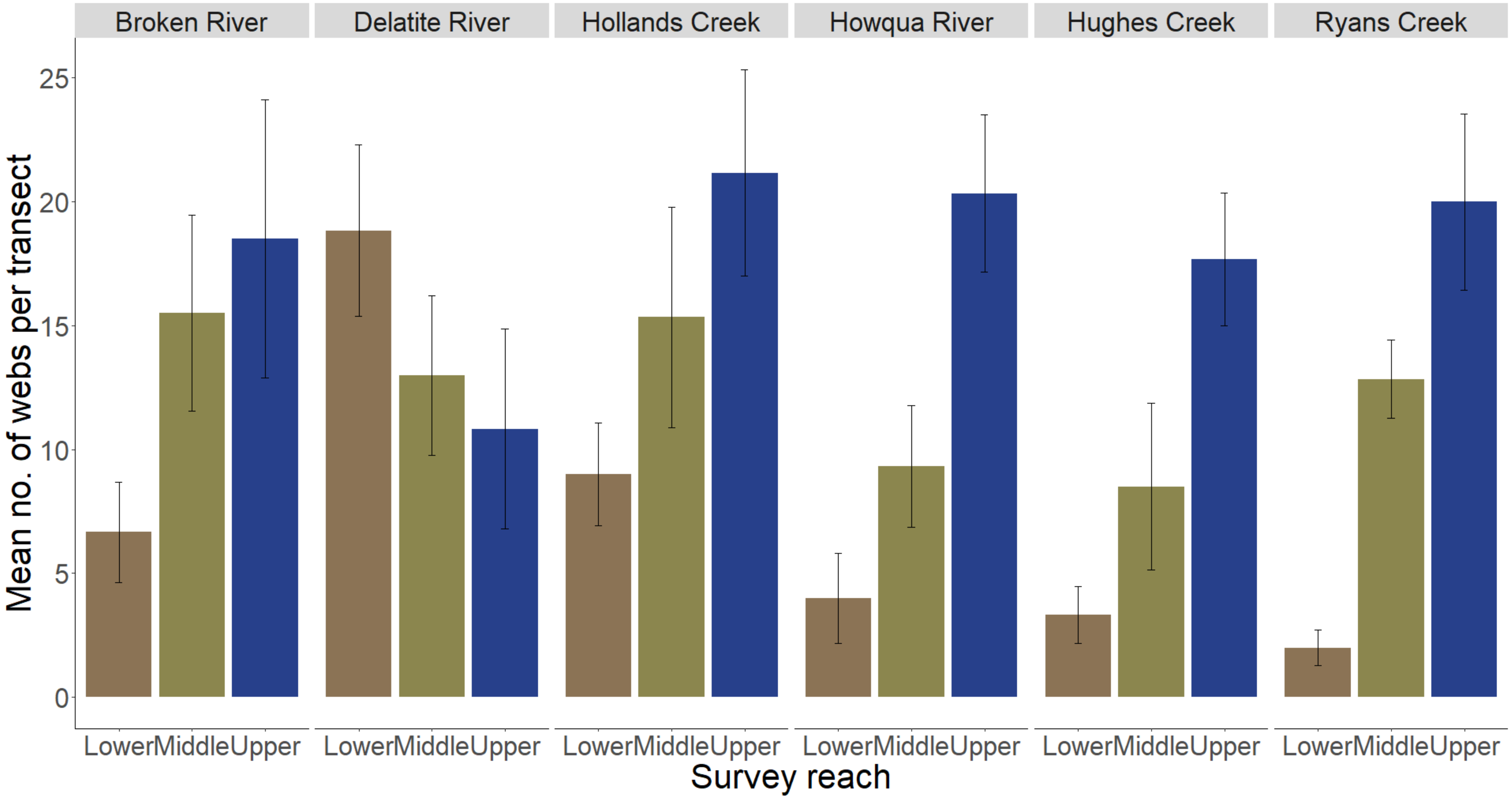

Figure 2.6.11 Mean number of spiderwebs with respect to stream and survey reach. Values are presented with regards to broad grouping and standard error bars.

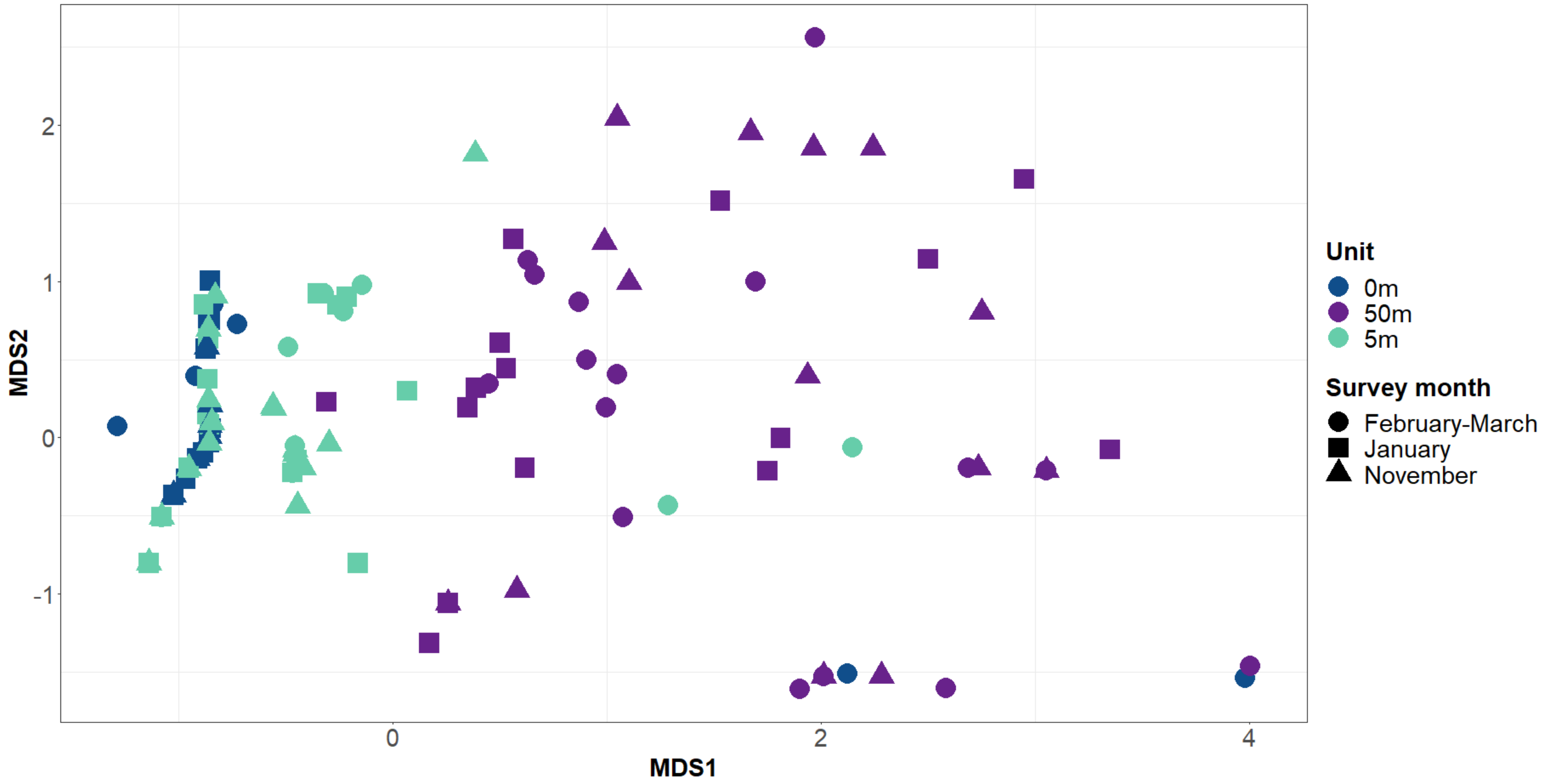

Figure 2.6.12 nMDS plot of spider community abundance for surveyed streams. Closed circles = February-March, closed squares = January and closed triangles = November. Stress = 0.07.

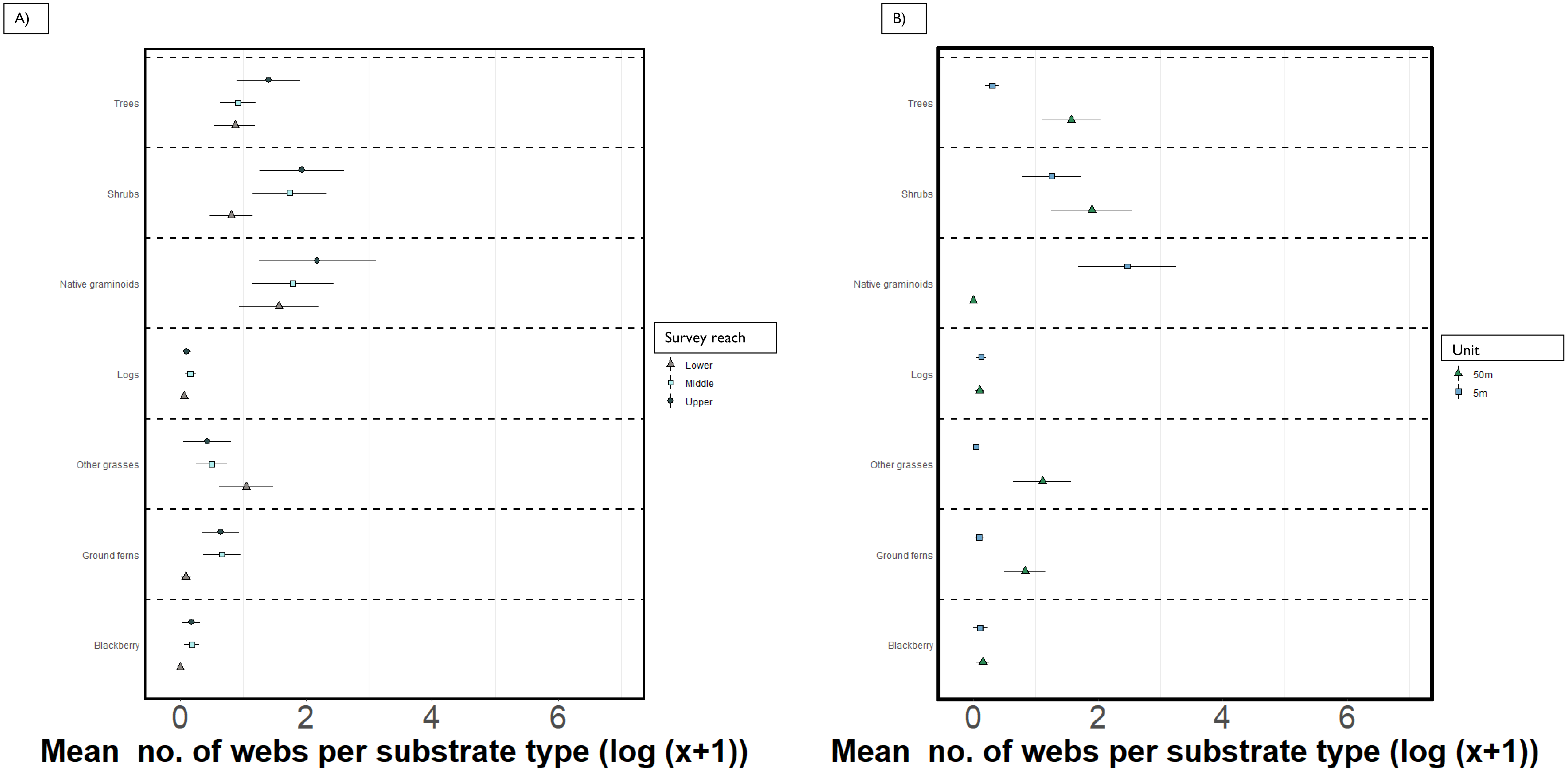

Figure 2.6.13 The mean number of webs per substrate type with respect to A) survey reaches (n=18) and B) units.

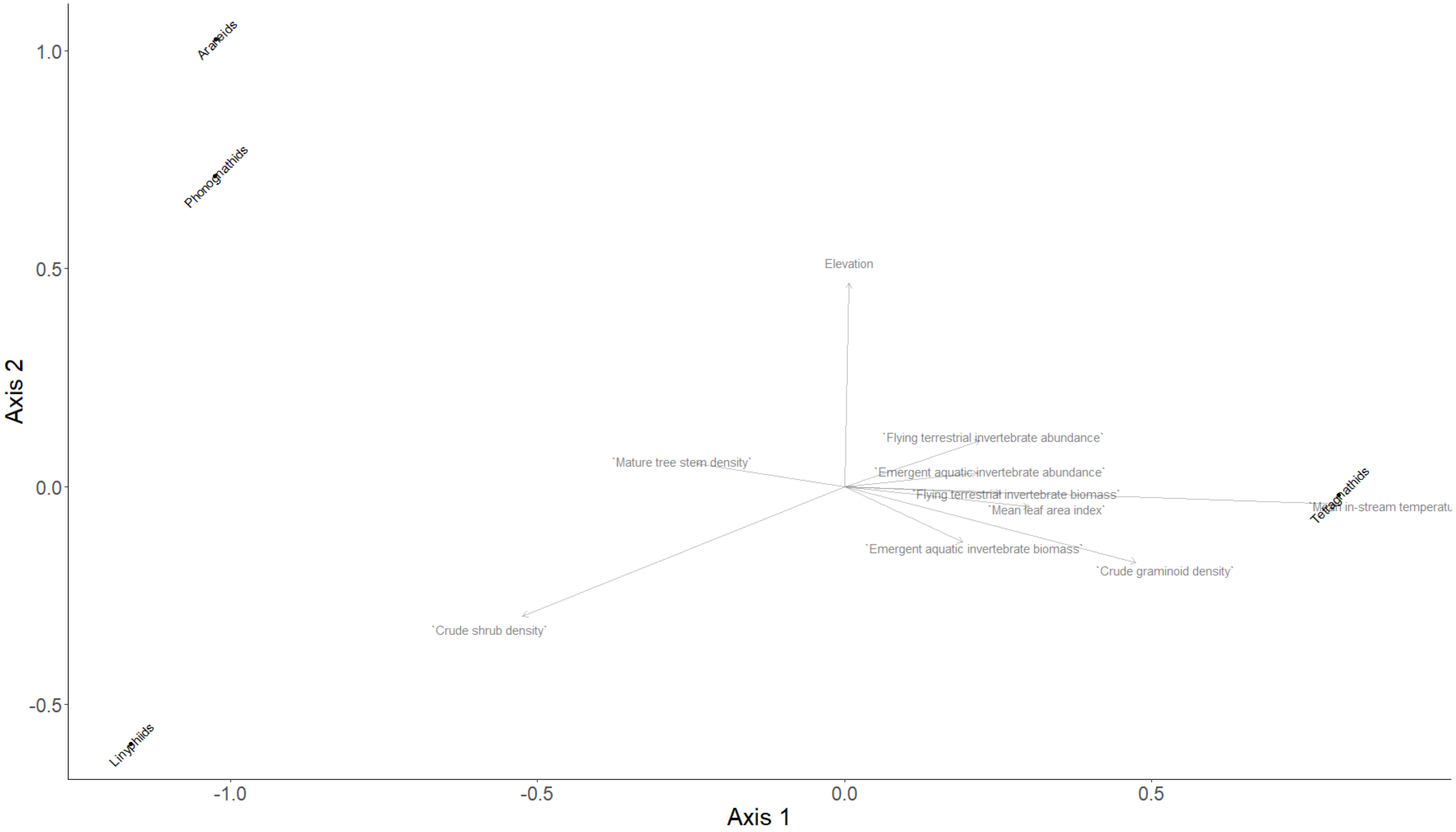

Figure 2.6.14 A Canonical Correspondence Analysis (CCA) ordination for the abundances of four spider family groups. Spiders are represented by bolded black text and environmental variables are represented by vectors. A spider's positioned closer to or further along an environmental variable vector indicates a stronger relationship with that variable.

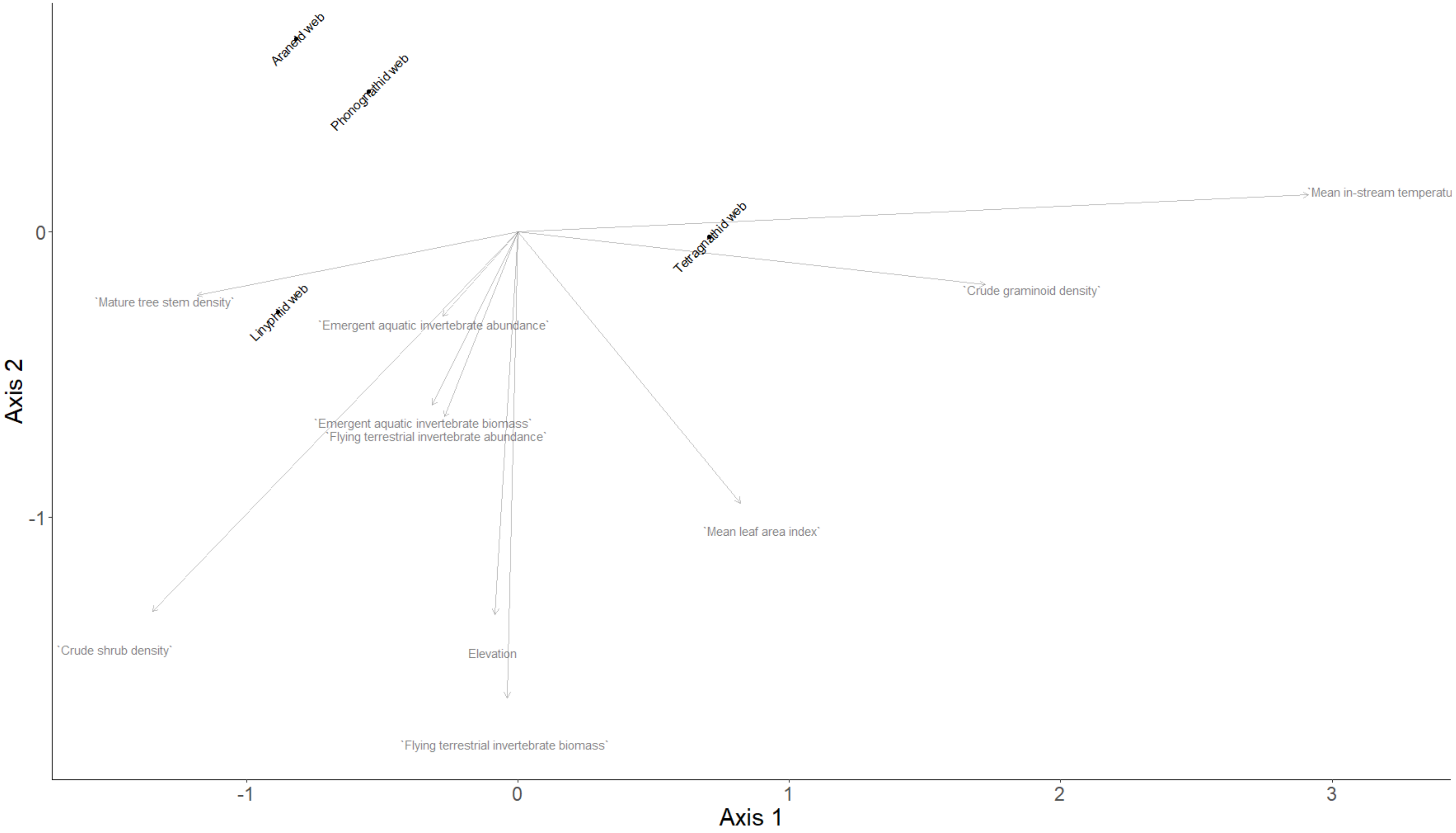

Figure 2.6.15 A Canonical Correspondence Analysis (CCA) ordination for the web densities of four spider family groups. Spiders are represented by bolded black text and environmental variables are represented by vectors. A spider's positioned closer to or further along an environmental variable vector indicates a stronger relationship with that variable.

CHAPTER 3. *TETRAGNATHA VALIDA*-MEDIATED REDISTRIBUTION OF PERENNIAL STREAM RESOURCES IN TEMPERATE AUSTRALIA

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ABSTRACT

A series of intricate processes redistribute resources from one ecosystem to another. Few stable isotope studies pertaining to predatory invertebrates, however, consider the redistribution of spatial subsidies at the species-level. In this study, we investigated the diets and relative trophic position of *Tetragnatha valida* at five perennial streams that run through a local land clearing gradient in regional Victoria, Australia. We predict that the diets of *T. valida* ($\delta^{13}C$) will comprise few emergent aquatic invertebrates as these resources are less available at survey reaches with intense riparian vegetation clearance. Next, we considered the effects of body length on the relative trophic position of individual *T. valida* ($\delta^{15}N$). We found that *T. valida* diets were similar across an agricultural gradient with all communities equally supported by aquatic subsidies. We also detected a significant and positive trophic position – body size relationship. We advise the distributions of prey proportion estimates be considered along with our results. Our results show that the importance of spatial subsidies at the interface of natural and anthropogenic ecosystems are species-specific, given the range of foraging strategies and trophic interactions adopted by and relevant to consumers.

KEY WORDS: genus Tetragnatha, Spatial subsidies, Stable isotope analysis, Land clearing, Australia

3.1 INTRODUCTION

A series of intricate processes redistribute resources from one ecosystem to another (Lindeman, 1942; Massol et al., 2011). The deposition of leaf litter into streams, for instance, is widely recognised as providing significant nutritional support to headwater communities (Vannote et al., 1980; Wallace et al., 2015). Similarly, dispersing emergent aquatic invertebrates introduce high-quality resources to terrestrial food-webs (Gladyshev et al., 2009; Moyo et al., 2017). Multiple studies have also revealed the cascading effects of spatial subsidy flux, which can both disrupt or intensify trophic interactions (Baxter et al., 2005; Nakano and Murakami, 2001). Baxter et al. (2004), for instance, showed that experimentally reducing terrestrial invertebrate inputs to streams both triggered a trophic cascade and reduced the reciprocal flux of emergent aquatic invertebrates into adjacent riparian zones. Clearly, an array of consumers and trophic interactions mediate the cycling and recycling of subsidies across ecotones (Iwata et al., 2003; Kato et al., 2004).

Stable isotope analyses (e.g. $\delta^{15}N$ and $\delta^{13}C$) of riparian consumer tissue can provide useful insights into the composition of respective diet (Ben-David and Flaherty, 2012; Jardine et al., 2005) by differentiating $\delta^{13}C$ between depleted sources (typical of aquatic prey) and more enriched sources (typical of terrestrial prey; Paetzold et al., 2005; Sanzone et al., 2003). Sanzone et al. (2003), for instance, found that orb-weaving spiders inhabiting riparian vegetation were obtaining ~100% of their carbon from aquatic prey as indicated by relatively depleted $\delta^{13}C$ levels (>-24 ‰). In contrast, ground spiders were most likely feeding on terrestrial prey as indicated by relatively enriched $\delta^{13}C$ levels (~-22 ‰; Sanzone et al., 2003). Further, as $\delta^{15}N$ increases with each trophic step of a food web, the relative trophic level of a consumer can be described (Akamatsu et al., 2007; Post, 2002). Significant trophic position-body size relationships can also be demonstrated using $\delta^{15}N$ (Hobson and Welch, 1995; Swanson et al., 2003), which may contribute to our understanding of how consumers mediate the flux of spatial subsidies.

Few stable isotope studies of predatory invertebrates consider the redistribution of spatial subsidies at the species-level (Mader et al., 2018; Paetzold et al., 2006). Instead, there is an assumption that related species within ecosystems exploit similar resources (Gerisch et al., 2012) and so they are grouped into broad taxonomic (Stenroth et al., 2015; Terui et al., 2018) and functional categories (Dreyer et al., 2012; Yan et al., 2019). While this is often justifiable given the complexity of trophic interactions, it potentially blurs distinct responses to spatial subsidies within diverse communities (Greenwood and Booker, 2016; Terui et al., 2017). Moreover, even within species, diets can shift between locations (Mader et al., 2018), life stages (Akamatsu et al., 2007), seasons (Paetzold et al., 2005; Terui et al., 2017) and sizes (Beaubien et al., 2019). Akamatsu et al. (2007), for instance, demonstrated that emergent aquatic invertebrates accounted for ~50% of the diet of juvenile *Nephila clavata* (Araneidae) but this reduced to ~19% for adults. So, grouping consumers too broadly can lead to a mischaracterising of the overall composition of their diet and dependency on spatial subsidies.

These considerations are especially important in dryland systems that follow a ‘boom-and-bust’ cycle (Bunn et al., 2006). Intense rainfall events (Razeng et al., 2016) and seasonal flooding (Boulton and Lloyd, 1992) can alter the amount and type of aquatically-derived subsidies, which in turn, can influence consumer responses (Hagen and Sabo, 2012; Williams et al., 1995). Species from the orb-weaver family Tetragnathidae, as one such consumer group, are prevalent in riparian habitats (Tagwireyi and Sullivan, 2016; Yoshida, 1981). Many tetragnathids construct horizontal webs that act to ensnare emergent aquatic invertebrates (Baba and Tanaka, 2016; Unzicker and June, 1978). Globally, tetragnathids are a staple of spatial subsidy research (Lafage et al., 2019; Walters et al., 2008). Kato et al. (2004), for instance, demonstrated that tetragnathid diets altered with peaks and troughs of emergent aquatic invertebrates. Tetragnathid $\delta^{13}C$ values became closer to those of terrestrial prey during times of reduced aquatic invertebrate emergence (Kato et al., 2004). In Australia, there are ~29 species of tetragnathids with the majority (20) within the genus *Tetragnatha* (Dimitrov and Hormiga, 2011). Given the diversity of biomes across Australia and the distinct ecologies of tetragnathids therein, questions remain regarding trophic position-body size relationships, the composition of diets and the extent to which spatial subsidies support these communities.

Local land clearance is intensifying within biomes across the globe (Ellis and Ramankutty, 2008; Ramankutty et al., 2008). In Australia, the temperate zone overlaps with the continent's agricultural centre (Bond et al., 2008; Kingsford et al., 2015). Freshwater ecosystems, such as perennial streams, within this zone support extensive agricultural activity (Kingsford et al., 2016). Previous research has demonstrated that land-use changes can fundamentally alter the diets of riparian consumers (Lafage et al., 2019; Larsen et al., 2016): first by impacting the quantity of aquatic prey (Carlson et al., 2016; Raitif et al., 2018) and then by altering the composition of prey communities (Stenroth et al., 2015). In chapter two, we provided evidence that vegetation structure and the quantity of aquatically-derived subsidies were important explanatory variables for *Tetragnatha* abundance and web density along a local land clearing gradient. One such species, *Tetragnatha valida* is a widely distributed riparian spider in temperate Australia (Okuma, 1987) and surveys presented in chapter two showed they were prominent across our study area. As a result, *T. valida* is ideal for investigating the trophic dynamics and spatial subsidy assimilation across a local land clearing gradient.

3.1.1 Hypotheses

In this study, we investigated the diets and relative trophic position of *T. valida* at five perennial streams that run through a local land clearing gradient in regional Victoria, Australia. We predict that the diets of *T. valida* ($\delta^{13}C$) will comprise relatively few emergent aquatic invertebrates because these resources are less available at survey reaches with intense riparian vegetation clearance (H_1; Table 3.5.1). Finally, we considered the effects of body size on the relative trophic position of individual *T. valida* ($\delta^{15}N$; H_2; Table 3.5.1).

3.2 MATERIALS AND METHODS

3.2.1 Study area

We conducted our investigation at three sites along five, 2nd/3rd order perennial streams (Hollands, Hughes and Ryans creeks and Broken and Howqua River) in regional Victoria, Australia (Taungurung Country) between January and February 2018 (austral summer). These streams were deliberately selected as examples of systems where vegetative cover was only continuous in the upper reaches (See Section 2.2.2). The mean daily ambient air temperature and the mean monthly rainfall for the study area, during the sampling period, was 31.4 °C and 22.8 mm, respectively (Bureau of Meteorology, 2018b, 2018c). The region on average received 460.6 mm of accumulative precipitation in 2018 (Bureau of Meteorology, 2018c). See chapters two and four for analysis of riparian and in-stream conditions.

3.2.2 Invertebrate sampling for stable isotope analysis

Invertebrates were sampled using a two-step approach. First, 12 V DC 8-watt insect light traps comprising a plastic tray (28 x 22 x 5 cm) filled with saline solution (100 g salt^{-1} L of water), within a circular tub (top diameter = 39 cm; height of tub = 32 cm; Downes, Lancaster, Glaister, & Bovill, 2017) were deployed within 10 m of the stream's edge, at each site (n = 15). This restricted sampling of flying nocturnal invertebrates to those individuals close to the stream, in the first instance. Light traps were deployed twice over the sampling period for three consecutive nights (n = 6). A previous study of *T. valida* within an adjacent catchment revealed that ephemeropterans and trichopterans were among the most captured prey items (Maiden, 1999). As a result, all individuals from the orders Trichoptera, Ephemeroptera, Lepidoptera and Coleoptera were extracted upon collection from the sample and frozen at -18 °C in a portable freezer (Engel MT45FP Digital Platinum Series Fridge/ Freezer). These taxa represent both aquatic and terrestrial sources (Table 3.5.2). Only the lepidopteran sub-family Crambinae (webworm moths) and the coleopteran genus *Phyllotocus* (nectar scarabs) were ultimately included in this study as they were the most consistently available, small-bodied, flying, terrestrial invertebrates sampled.

Next, we used a sweep-net to brush all emergent vegetation within 5 m of the stream (targeting the native graminoids, *Lepidosperma* and *Lomandra* spp) for *Tetragnatha valida* (Okuma 1987). We continued this until ~6 individuals with a body length >0.45 mm, were sampled at each site. While previous quantitative sampling of riparian spiders (outlined in chapter two) revealed that *Tetragnatha valida* were abundant at these sites, we sampled each site twice within the survey period. Once collected, individuals were also frozen at -18 °C in a portable freezer (Engel MT45FP Digital Platinum Series Fridge/ Freezer).

3.2.3 Stable isotope analysis

In total, 253 specimens (across five taxa groups; Table 3.5.2) were prepared for stable isotope analysis. These specimens had their identification confirmed (Table 3.5.2) prior to being dried at a constant 50 °C for ~48 h. We then measured the body length (exclusive of chelicerae; to the nearest 0.1 mm) and dry weight (to the nearest milligram) of each *T. valida* specimen. Whole-body tissues (excluding wings, legs and exoskeleton) for each sample were ground into a fine powder. Stable isotope analyses were performed on a Thermo Flash 2000 HT (elemental analyser) paired to a Thermo Delta V Advantage (mass spectrometer). Weight % (w/w%, regarding reference materials) data were calculated using a thermal conductivity detector and calibrated against acetanilide (Werner and Brand, 2001; Zimmermann and Keefe, 1997) sourced from ThermoFischer, Bremen, Germany. Reference values are as follows: $\delta15\mathrm{N}_{\mathrm{Air}}$ -0.32 ‰, $\delta^{13}\mathrm{C}_{\text{V-PDB}}$ -41.30 ‰, USGS41a; $\delta15_{\mathrm{NAir}}$ +47.55 ‰, $\delta^{13}\mathrm{C}_{\text{V-PDB}}$ +36.55 ‰. Results are reported in δ (‰) notation defined as:

Equation 1 where R is $^{13}\mathrm{C}/^{12}\mathrm{C}$ or $^{15}\mathrm{N}/^{14}\mathrm{N}$, respectively. Typical analytical precision was 0.08‰ for $\delta^{15}\mathrm{N}$ and 0.19‰ for $\delta^{13}C$.

$$\delta^{13}\mathrm{C} \text{ or } \delta^{15}\mathrm{N} = 100\left(\left[\frac{R_{\text{sample}}}{R_{\text{standard}}}\right]-1\right)$$

For information regarding the above notations, see Sharp (2005).

3.2.4 Statistical approach

Our approach for data analysis had two components: 1) a Bayesian approach to estimate the probability distribution of prey contributions to a consumer's diet (in our case *T. valida*) and 2) a simple linear regression to investigate the relationship between trophic level and body length. Statistical analyses were conducted using the software R (R Core Team, 2013).

3.2.4.1 Assessing *T. valida* diet composition along an agricultural gradient

In preparation for formal analyses, we first confirmed that stable isotopic signatures of prey (and prey groupings) were significantly different using an ANOVA (see here for results Table 3.5.3). This is a prerequisite for such analyses as it allows discrimination between prey in terms of their contribution to a consumer's diet. We also applied trophic enrichment factors (TEFs) to sources for *T. valida* isotopic signatures as recommended by Mccutchan *et al.* (2003; i.e. 0.5 ± 0.13 ‰ for $\delta^{13}\mathrm{C}$ and 2.2 ± 0.3 ‰ for $\delta^{15}\mathrm{N}$). These values represent the average TEFs for non-fluid-feeding consumers (Mccutchan et al., 2003; Vanderklift and Ponsard, 2003) and have been used widely in comparable aquatic food-wed research (Terui et al., 2017; Vander Zanden and Fetzer, 2007).

Next, we estimated the proportional contribution of each prey item for *T. valida* by running Bayesian mixing models (Parnell et al., 2013). These employ a Gaussian likelihood and are fitted to the data via a single Markov Chain Monte Carlo chain (MCMC; 500,000 iterations, 15 thinning, and 50,000 burn-in, storing 30,000 MCMC samples to obtain posterior probabilities). One of the benefits of these models is that they take into account uncertainty and variation in consumers, sources, and TEFs (Bond and Diamond, 2011; Parnell et al., 2013).

An assumption of the above models is that the variability in isotopic signature of consumers (after accounting for fractionation corrections) is contained within the variability of the assimilated food sources (Phillips et al., 2014). We tested this assumption by generating dietary mixing polygons with 10^4 Monte Carlo iterations (sufficient for the variance of the mixing polygon's area to stabilise) of convex hulls that could result from the proposed dietary sources and TEFs (Smith et al., 2013). This method is a quantitative way of determining the likelihood that *T. valida* diet can be explained by the nominated prey (Smith et al., 2013). We plotted the resulting consumer signatures against consumer mixing space, producing 10% probability contours (one 5% contour included) indicating the extent that signatures were explained by the nominated prey (Blakey, 2017; Smith et al., 2013). To avoid misrepresenting the uniqueness of our results, we also report the distribution of feasible solutions rather than focusing on a single value such as the mean (Phillips et al., 2014; Phillips and Gregg, 2003). The packages 'SIAR' (Parnell and Jackson, 2015), 'simmr (Parnell, 2019), 'sp' (Pebesma and Bivand, 2015) and 'splancs' (Bivand et al., 2017) were used to complete this analysis.

In addition, isotopic niche breadth space for $\delta^{13}C$ and $\delta^{15}N$ was then calculated by estimating 40% dietary ellipses for *T. valida* at upper, middle and lower survey reaches (hereafter referred to as 'communities'). We used the data's covariance matrix (Eq. 2) to define the ellipses' shape, size, and means of $\delta^{13}C$ and $\delta^{15}N$, which in turn defined the ellipses' location (Jackson et al., 2011). These ellipses represent a measure of the total amount of isotopic niche exploited by each community and is considered a surrogate for the trophic range within a community. In the present study, we examined niche overlap between these communities, noting that this overlap was comparative, rather than an absolute measure (Jackson et al., 2011).

Equation 2 Covariance matrix for ellipses that encompasses 40% dietary area. The sample variance (s^2) provides an unbiased estimate of the population variance (δ^2) for $\delta^{13}C$ and $\delta^{15}N$ data. *See Jackson et al. 2011 for more details.*

$$\left(\Sigma = \begin{bmatrix} \sigma_x^2 & \mathrm{cov}(x,y) \\ \mathrm{cov}(y,x) & \sigma_y^2 \end{bmatrix}\right)$$

The package 'SIBER'(Jackson and Parnell, 2019) was used to complete this analysis.

3.2.4.2 The relationship between trophic level and body length

We then assessed the relationship between *T. valida* body length and relative trophic level (TL) with a simple linear regression using only those individuals collected exclusively for stable isotope analysis. The TL was estimated assuming a ^{15}N trophic enrichment factor of 3.4‰ (Del Rio and Wolf, 2005; Hobson and Welch, 1992), according to the following formula:

$$TL = 2 + [(\delta^{15}N_{\text{trophic group}} - \delta^{15}N_{\text{primary consumers}})/3.4]$$

Where $\delta^{15}N_{\text{primary consumer}}$ was the mean $\delta^{15}N$ for ephemeropterans sampled.

3.3 RESULTS

3.3.1 *T. valida* diet compositions

The results of the Bayesian mixing models suggests that ephemeropterans made up the largest proportion of *T. valida* diet (~40-50%), however, webworm moths (~30-40%) and trichopterans (~10-30%) were also likely to be included in the diet (Fig. 3.6.1). Nectar scarabs likely contributed the least (<10%) to *T. valida* diet. The dietary mixing polygon indicated as much as 77% of possible *T. valida* diets are explained by the nominated prey (Fig. 3.6.1). Although, for ten individuals there was <5% chance that the nominated prey explained their diets (Fig. 3.6.3). Despite this, the dietary proportions of trichopterans is quite uncertain as indicated by broad credibility intervals and running for approximately 4-29% (Table 3.5.4; Fig. 3.6.2).

The niche breadth ellipse of *T. valida* for upper survey reaches covered the smallest area, while middle survey reaches occupied the largest. Despite this, diets (as shown by niche breadth ellipses; Fig. 3.6.4) of *T. valida* substantially overlapped across this local land clearing gradient. This indicates that these spiders were eating similar prey.

3.3.2 Body length and relative trophic position

T. valida body length ranged from 0.47 to 1.40 cm and averaged 0.88 ± 0.03 cm. The $\delta^{15}N$ values for *T. valida* ranged 1.46 and 11.63 and averaged 4.41 ± 0.17. Relative trophic level (TL) showed a positive and significant relationship with *T. valida* body length ($r^2 = 0.34$, df = 96, P = <0.001; Fig. 3.6.5), described by the following equation:

TL = 1.225 + 3.599(*T. valida* body length)

3.4 DISCUSSION

3.4.1 *T. valida* dietary composition

T. valida at lower, agricultural survey reaches are expected to assimilate fewer aquatic subsidies than those at upper survey reaches (H_1; Table 3.5.1). We tested this hypothesis using a Bayesian approach to estimate the probability distribution of prey contributions to the diet of *T. valida*. We found that *T. valida* diets were similar across an agricultural gradient with all communities equally supported by aquatic subsidies. These results were contrary to our 'within streams' hypothesis and suggest that while riparian vegetation clearance reduces the abundance and biomass of emergent aquatic invertebrates (see Chapter Two), these subsidies remain important to riparian consumers. Our results here are consistent with other studies that demonstrate the prominence of emergent aquatic invertebrates as a prey resource in agricultural riparian zones (Krell et al., 2015; Stenroth et al., 2015). Stenroth et al. (2015), for instance, identified that emergent aquatic invertebrates contributed as much as 60% to carabid beetle and linyphiid spider diets despite these consumer's affinity with agricultural streams. Similarly, Krell et al. (2015) demonstrated that the diets of tetragnathids, which inhabited vineyards near streams, comprise approximately 60% emergent aquatic invertebrates.

Most empirical studies of spatial subsidies lack high taxonomic resolution (Paetzold et al., 2006; Terui et al., 2017). In fact, species-level responses to the flux of spatial subsidies is often dismissed (Gottschalk et al., 2007; Nakano and Murakami, 2001), despite the broad range of foraging behaviours that exist even within taxonomic families (Downes et al., 2011; Giery et al., 2013). The present study represents one such species-specific investigation. While we did not find a significant difference between our treatments (i.e. riparian vegetation clearance), other studies have demonstrated significant difference in the assimilation of aquatic resources between closely related species, seasons (Terui et al., 2017) and life stages (Akamatsu et al., 2007).

3.4.2 *T. valida's* relative trophic position

Theoretically larger *T. valida* should have relatively higher trophic positions (H_2; Table 3.5.1). We tested this hypothesis with a simple linear regression comparing the body lengths and relative TL of individuals across five perennial streams. We found evidence ($R^2 = 0.34$) that higher TL were associated with large-bodied *T. valida.* Previous studies have demonstrated links between body-size and trophic position (Cohen et al., 1997; Thierry et al., 2011). In general, predators are larger than their prey (Jonsson et al., 2005; Woodward et al., 2005), and this demonstrates the relationship between a community's trophic structure and body-size (Brown et al., 2004). In particular, a larger body-size enables predators to use a broader range of food resources (Brose et al., 2006; Woodward et al., 2005). Woodward and Hildrew, 2002, for instance, demonstrated that a significant determinant of trophic structure within a stream macroinvertebrate community was body-size. In this study, the largest predator, *Cordulegaster boltonii* was only preyed upon by larger individuals of the same species, while the smallest predator, *Zavrelimyia barbatipes* was consumed by all other predators surveyed (Woodward and Hildrew, 2002). It might be the case that different sized spiders sample different size ranges of prey, due to the dimensions of the mesh size of the web, smaller prey can fly through the larger gaps of webs built by larger spiders (Blackledge and Zevenbergen, 2006; Herberstein et al., 2000). Further, the relationship between riparian spider body-size and trophic position is likely to be complicated due to intraguild predation (Rickers et al., 2006), conspicuous sexual dimorphism (Beaubien et al., 2019; Sanzone et al., 2003) and frequent cannibalism (Deventer et al., 2017; Wilder and Rypstra, 2008). Rickers *et al.* (2006), for instance, demonstrated that wolf spiders, which preyed upon their wolf spider competitors had pronounced $\delta^{15}N$ compared with those that ate herbivores. Very little is known of the extent these dynamics occur within the family Tetragnathidae (Elgar et al., 1990), however, Maiden (1999), did not document any cases of cannibalism by *T. valida*.

T. valida exhibit subtle sexual dimorphism (see Okuma 1987): Chelicerae in the males, for example, are equipped with long, intricate guide teeth compared to females, while body length (exclusive of chelicerae) is generally larger in females. In other species, these differences have not resulted in significantly different trophic levels (Beaubien et al., 2019; Binford et al., 2016). Beaubien et al. (2019) demonstrated, for instance, that despite female *Tetragnatha elongata* exhibiting a larger body-size, there was no significant difference in $\delta^{15}N$ values. Our study did not relate $\delta^{15}N$ values to the sex of individuals, but differences between sexes may ultimately be inconsequential as male and females may be consuming the same prey and at the same relative trophic position (Beaubien et al., 2019).

3.4.3 Assumptions and limitations

The results of isotopic studies can be influence by various assumptions (Ben-David and Flaherty, 2012; Post, 2002). Trophic enrichment factors and variable discrimination of different prey types, for instance, are often assigned based on broad functional groupings (Bond and Diamond, 2011; Mccutchan et al., 2003) and inferences from the isotope signals of functionally similar consumers (Paetzold et al., 2005; Post, 2002). While we attempted to make this study robust to these uncertainties by only providing comparative and descriptive analyses of *T. valida* diet and trophic position, the use of these values in a species-specific study may qualitatively change the results. Analyses conducted by Terui et al. (2017), however, suggests that an assumed 3.4 ‰ for nitrogen rather than 2.3 ‰ did not significantly impact their conclusions. Regardless, more laboratory experiments are needed to validate assumptions such as these (Gannes et al., 1997).

Moreover, there is no statistical test for missing prey (Parnell et al., 2013). Many Bayesian stable isotope mixing models rely on ecological observations to adequately describe food-webs to inform analyses (Phillips et al., 2014) and this may be pertinent for species-specific studies as a result of specialised foraging techniques (Kato et al., 2004; Maiden, 1999). Phillips et al. (2014) advocates for researchers to report the distributions of prey proportion estimates and not just summary statistics and we advise these distributions should be considered along with our results (Table 3.5.4; Fig. 3.6.2). Nevertheless, this study provides evidence that *T. valida* rely on emergent aquatic invertebrates at perennial streams in temperate Australia.

Another consideration is the sexual dimorphism in terms of behaviour for tetragnathids. Males are often vagrant, existing on the periphery of webs built by females (Danielson-Francois et al., 2002; Huber, 2005). Some tetragnathid males also forage in a limited capacity (or not at all) once they reach sexual maturity. Diet analyses that include males may be problematic if their signatures reflect either their foraging history as juveniles, or food stolen from females (Chaves-Ulloa et al., 2016; Sanzone et al., 2003). Again, our study did not relate isotopic signatures to the sex of individuals, however, previous studies have shown that tetragnathids may not differ in terms of isotopic signature due to sex (Beaubien et al., 2019).

3.4.5 Conclusion

Reliance on emergent aquatic invertebrates as a prey did not change for *T. valida*, even in highly altered environments like agricultural riparian zones. The importance of spatial subsidies at the interface of natural and anthropogenic ecosystems may be species-specific, given the range of foraging strategies and trophic interactions adopted by and relevant to consumers. Therefore, we suggest that future studies consider consumer responses at the species-level. Our understanding of how recipient food-webs respond to the flux of spatial subsidies can only improve with increased taxonomic resolution. Further, we endorse studies that incorporate times outside of mass emergence events by aquatic invertebrates as there may be a significant interaction between riparian vegetation clearance and season.

3.5 TABLES

Table 3.5.1 Two categories of complementary hypotheses (H_{1-2}) that predict the different trophic positions and diet composition of *T. valida*. Possible underlying mechanisms, and the scale (within taxa and within streams) at which responses are likely to be most variable, are also outlined

Hypothesis		Source of variation
H_1	*T. valida* diets are distinct between survey reaches with intensifying agricultural land-use, reflecting limited reliance on aquatic subsidies. *T. valida* will exploit isotopic niches at intact, upstream sites than agricultural, downstream sites. *Mechanism: agricultural land-use reduces the availability of emergent aquatic prey resulting in limited overlap in T. valida diets.*	Within reach
H_2	*T. valida* body length will positively correlate with relative trophic position (i.e. $\delta^{15}N$) *Mechanism: If differences in mass or physiology affects diet, larger individuals may be able to assimilate prey larger prey resulting in their higher trophic position*	Within taxa

Table 3.5.2 Grouping guide for taxa captured in this study including identification key, the number of specimens (No.) and streams they were sourced from (Br = Broken River, Hol = Hollands Creek, How = Howqua River, Hu = Hughes Creek and Ry = Ryans Creek)

Taxa	Grouping	Key	No.	Stream	Survey reach
Tetragnatha valida	Consumer	Okuma 1987	98	Br (21), Hol (17), How (24), Hu (18), Ry (18)	Lower (34), Middle (28), Upper (36)
Coleoptera (Scarabaeidae; Phyllotocus spp.)	Terrestrial prey	Moore 1980; Slipinski and Lawrence 2013; Britton 1978	20	Br (5), Hol (5), How (5), Hu (5),	Upper (20)
Ephemeroptera	Aquatic prey	Gooderham and Tsyrlin 2002	45	Br (9), Hol (9), How (9), Hu (9), Ry (9)	Lower (15), Middle (15), Upper (15)
Lepidoptera (Crambinae spp.)	Terrestrial prey	Nielsen et al. 1995	45	Br (9), Hol (9), How (9), Hu (9), Ry (9)	Lower (15), Middle (15), Upper (15)
Trichoptera	Aquatic prey	Holzenthal et al. 2007	45	Br (9), Hol (9), How (9), Hu (9), Ry (9)	Lower (15), Middle (15), Upper (15)

Table 3.5.3 Analysis of variance of $\delta^{15}N$ and $\delta^{13}C$ of taxa and prey groupings (see Table 3.5.3). Bolded P-values indicate significance.

		df	SS	MSS	F	P
Taxa	$\delta^{15}N$	3	2218.1	739.4	131.8	**<0.001**
	$\delta^{13}C$	3	368.0	122.66	24.37	**<0.001**
Prey grouping	$\delta^{15}N$	1	952.2	952.2	68.95	**<0.001**
	$\delta^{13}C$	1	97.4	97.43	14.46	**<0.001**

Table 3.5.4 Proportions of prey groups in the diet of T. valida, representing probability quantiles of dietary proportions in credibility intervals of 97.5, 75, 50, 25 and 2.5% for the ingested prey source across all sites."

	2.5%	25%	50%	75%	97.5%
Deviance	775.239	778.046	780.194	782.791	789.818
Coleoptera (scarabaeidae; phyllotocus spp)	0.006	0.015	0.023	0.034	0.069
Ephemeroptera	0.379	0.421	0.443	0.465	0.504
Lepidoptera (crambinae spp)	0.294	0.346	0.374	0.401	0.445
Trichoptera	0.041	0.111	0.156	0.201	0.285

3.6 FIGURES

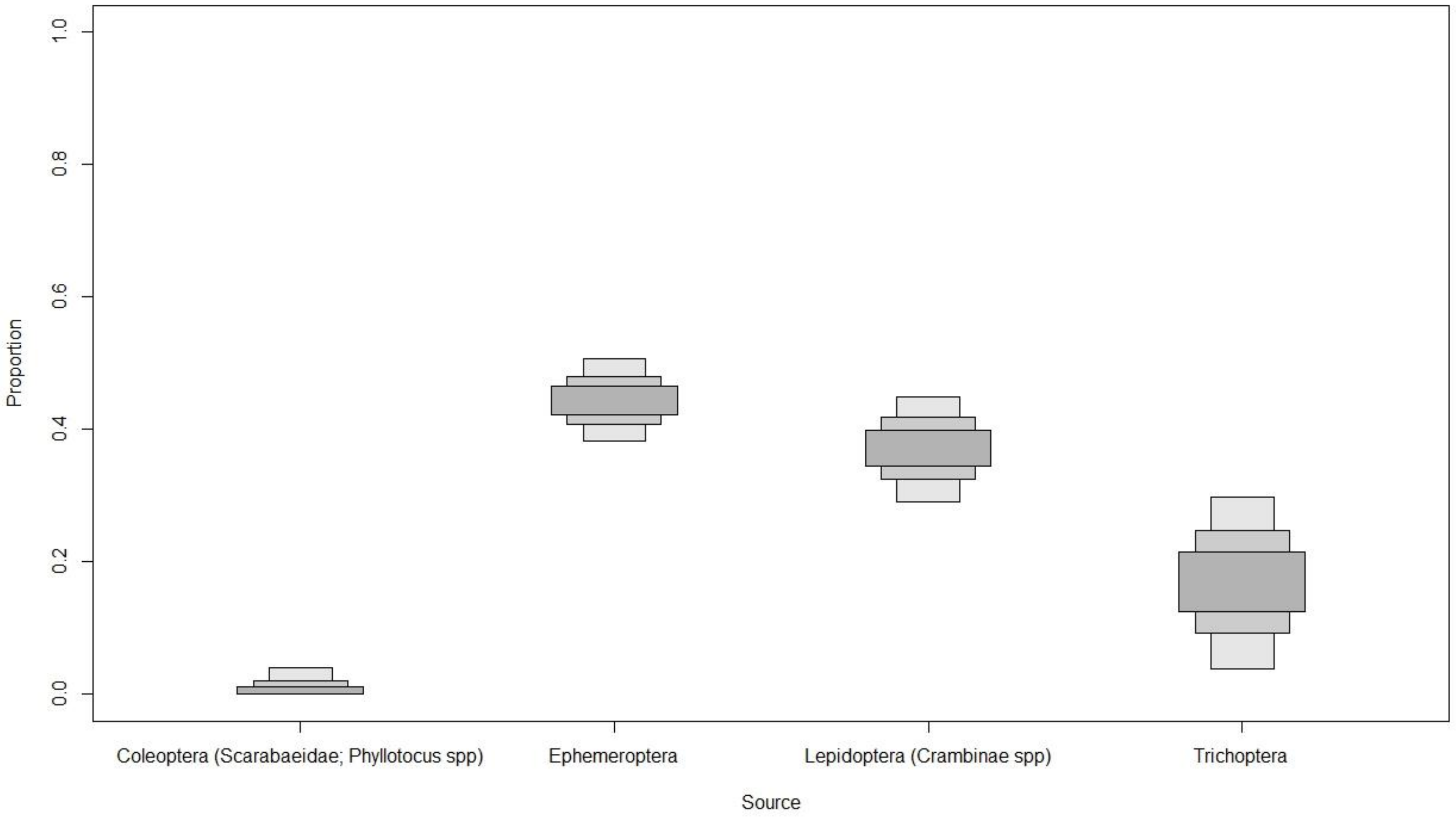

Figure 3.6.1 Proportions of prey groups in the diet of *T. valida*. The Boxplots represent the probability densities in credibility intervals of 95, 75 and 25% for the ingested prey source across all sites. The width of boxes corresponds with these credibility intervals.

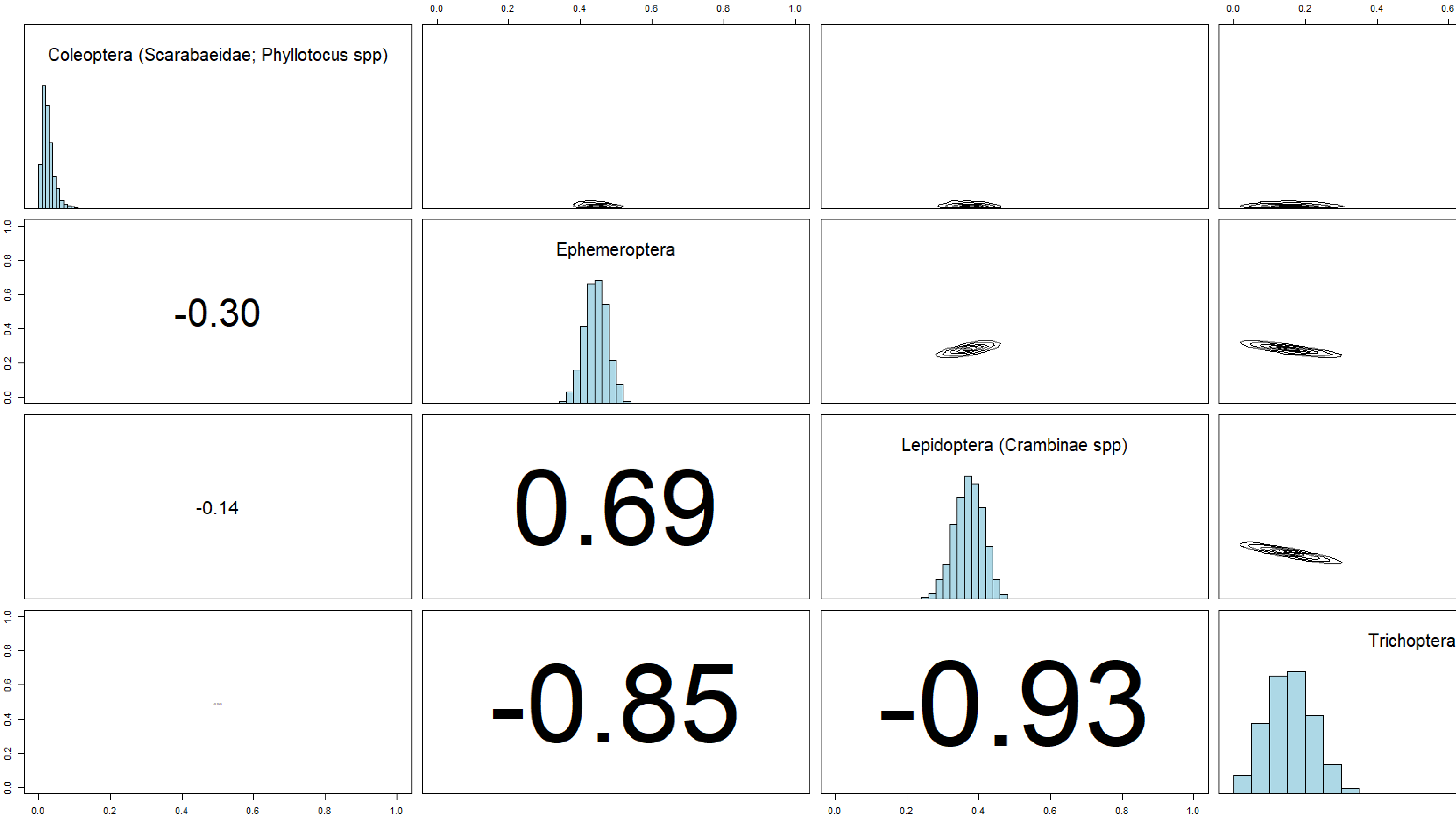

Figure 3.6.2 Matrix plot of food sources for *T. valida* at perennial streams along an agricultural gradient. The diagonal cells show the posterior probability distributions for each of the four prey. The cells below the diagonal show the correlations between contributions for pairs of prey. The cells above the diagonal show contours of the joint posterior probability distribution for contributions for pairs of prey.

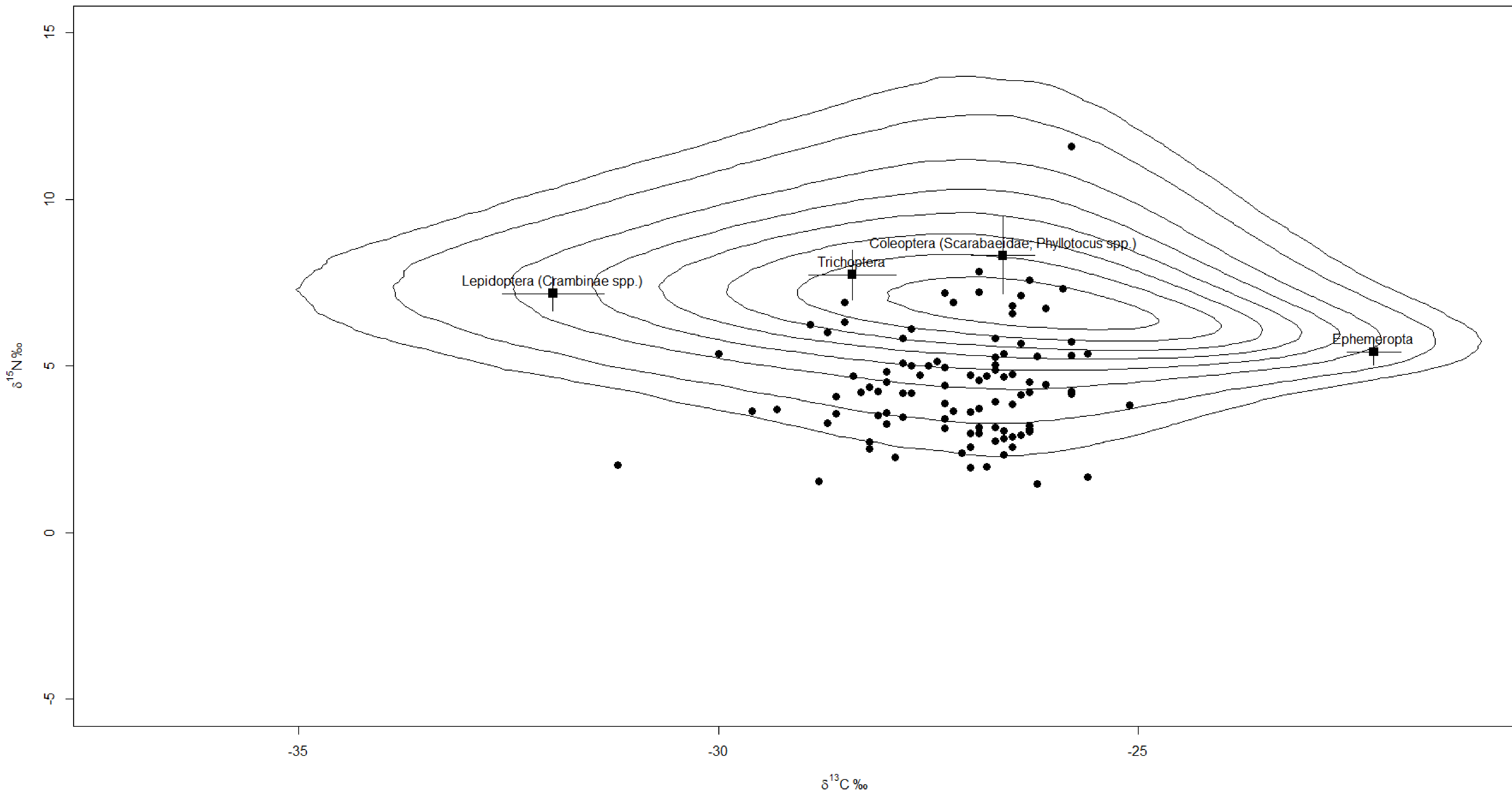

Figure 3.6.3 Simulated (mixing polygon) dietary signatures from whole-body *T. valida* samples. Dietary signatures of individuals shown with black points and mean dietary signatures of prey shown with squares (and standard error bars), transformed by their enrichment factors. Outside the outermost contour (solid line) only 5% of the 10,000 possible diets modelled could be explained. Each sequential contour was a 10% level of probability with the innermost contour indicating that 90% of modelled diets were explained by the sources displayed.

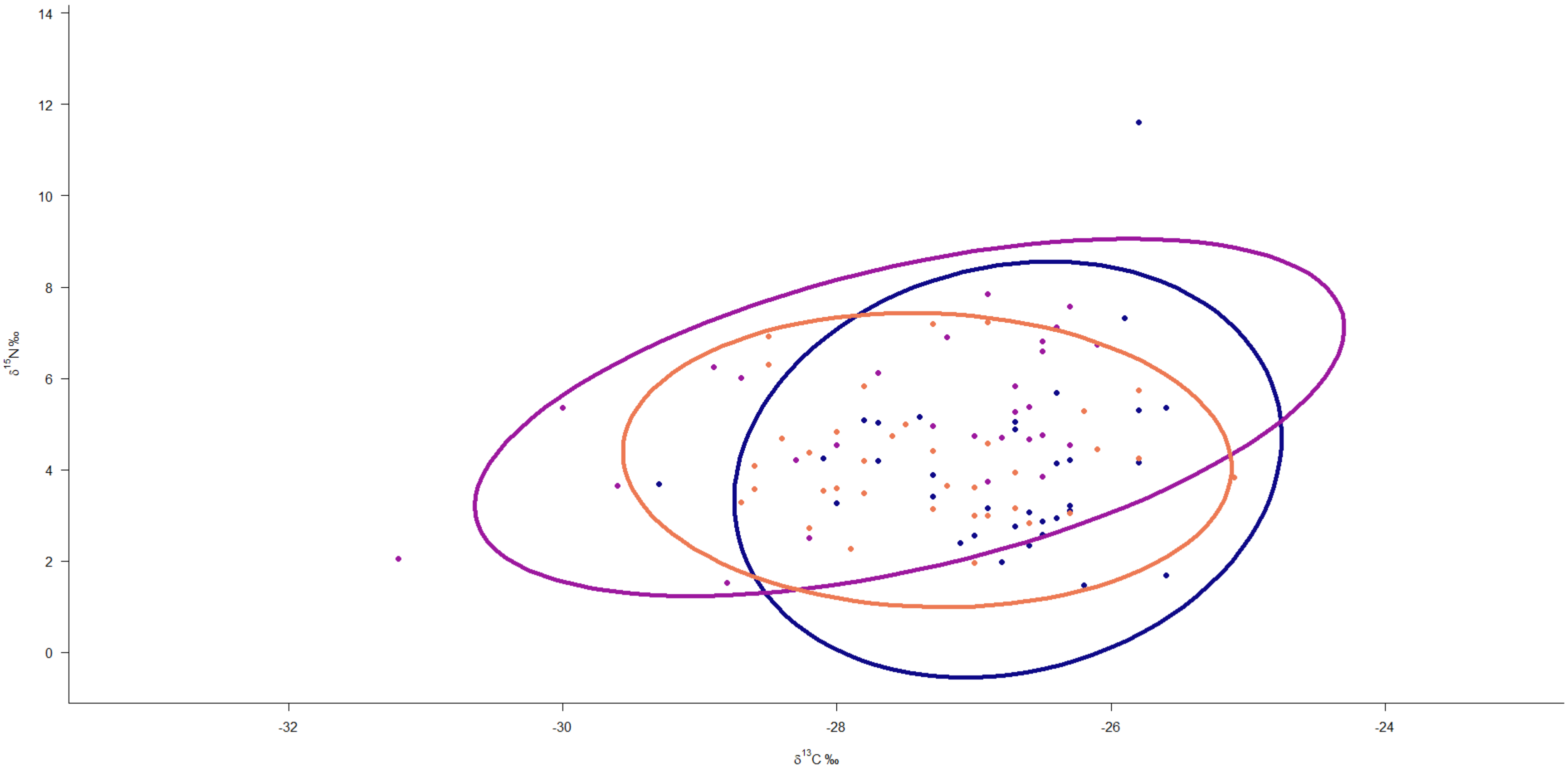

Figure 3.6.4 Isotopic niche size of T. valida across an agricultural land-use gradient. Ellipses encompass approximately 95% of the data (orange = Upper, purple = Middle and blue = Lower survey reaches). Posterior estimates of the Bayesian standard ellipse areas for each community are as follows: Upper: 3.24, Middle: 6.55, Lower: 3.88)

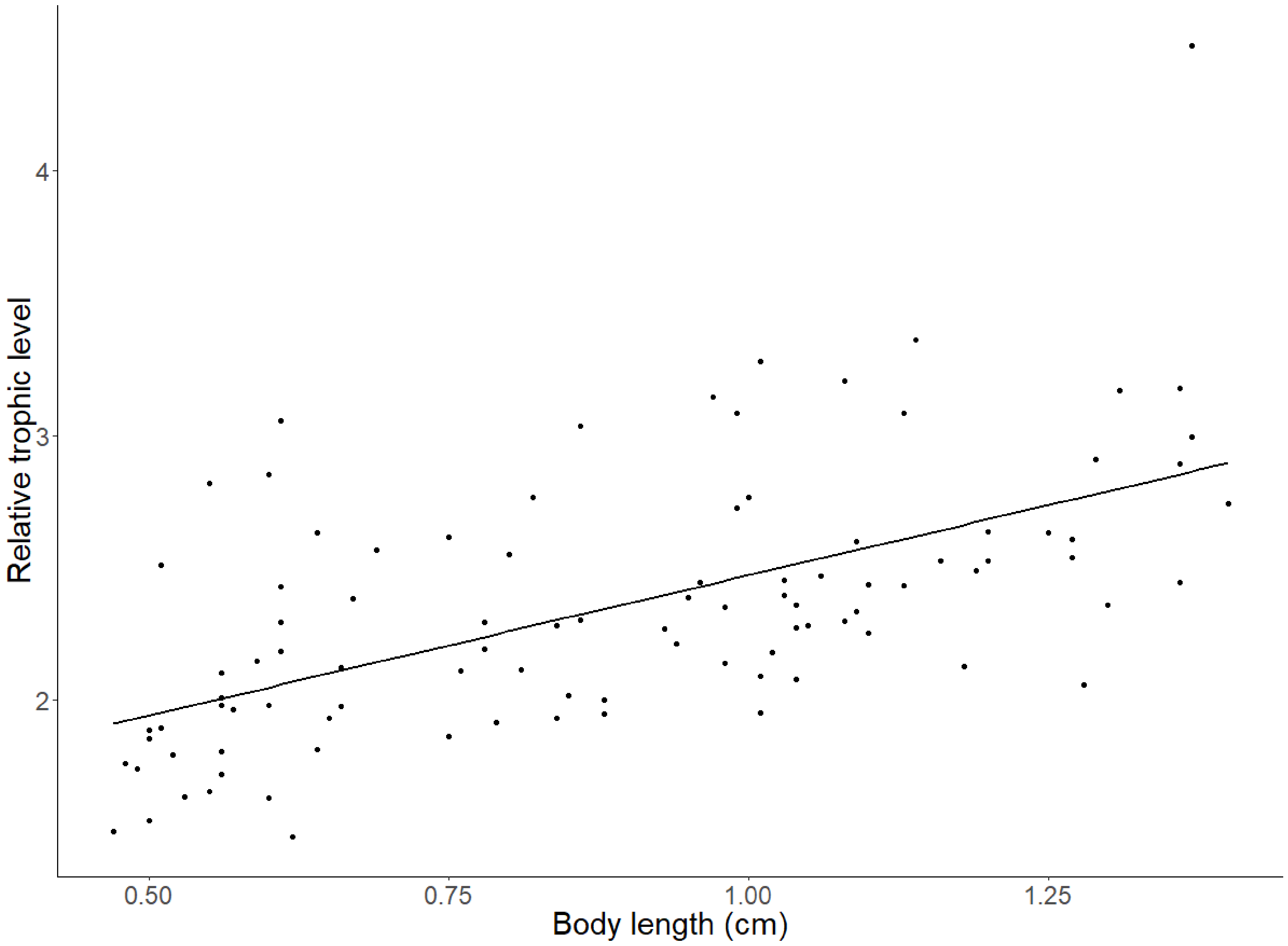

Figure 3.6.5 Relative trophic level of *T. valida* was positively associated with *T. valida* body length. This relationship was significant. The black line indicates the overall trend.

CHAPTER 4. RELATIVE IMPORTANCE OF SPATIAL SUBSIDIES AND RIPARIAN VEGETATION TO INSECTIVOROUS BAT FORAGING ACTIVITY ALONG PERENNIAL STREAMS IN TEMPERATE AUSTRALIA

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ABSTRACT

Food-web ecology identifies the movement of materials and organisms as a resource pulse across ecotones. To make strides in the field, however, researchers need to consider how these subsidies change the community structure of a diverse group of terrestrial consumers. This is particularly important for those biomes that are underrepresented in the literature. In this study, we tested whether insectivorous bat community dynamics differed along six, 2nd/3rd order perennial streams that span a local land clearing gradient in temperate Australia. We used an analysis of variance of environmental variables to validate assumptions of longitudinal land-use changes and to confirm reductions in the foraging activity of insectivorous bats and emergent aquatic invertebrate abundance and biomass were statistically significant. We then characterised longitudinal changes in bat community composition using generalised linear models and finally assessed the relative importance of environmental variables to bat and prey communities. Our results suggest that canopy structure was highly influential on flying invertebrate abundance and biomass. While bat responses were complex, total bat activity was sensitive to the availability of emergent aquatic invertebrates. Aquatically-derived subsidies were identified as significant explanatory variables for five insectivorous bat taxa including *C. gouldii, Mi. schreibersii oceanensis, Mo. planiceps, Nyctophilus-Myotis complex* and *V. regulus.*

KEY WORDS: Spatial subsidies, Land clearing, Insectivorous bats, Emergent aquatic invertebrates, Australia.

4.1 INTRODUCTION

Food-web ecology identifies the movement of materials and organisms as a resource pulse across ecotones (Free et al., 2013; Polis et al., 1997a). These subsidies elicit complex trophic responses by intensifying or disrupting 'top-down' and 'bottom-up' processes (Leroux and Loreau, 2012; Loreau and

Leroux, 2008). For the most part, research has been centred around the addition of terrestrially-derived subsidies to aquatic systems (Marcarelli et al., 2011; Sato et al., 2016). To make strides in the field, however, researchers need to consider how these subsidies change the community structure of a diverse group of terrestrial consumers (Ballinger and Lake, 2006; Graf et al., 2017). This is particularly important for those biomes (generally in Africa, Asia, Oceania and South America) that are underrepresented in the literature (Salvarina, 2016).

In terrestrial systems, including riparian zones, landscape characteristics such as geomorphology (e.g. elevation, land forms, etc; Hagen and Sabo, 2011; Laeser et al., 2005) and vegetation (Adams et al., 2009; Blakey et al., 2017b) have direct effects on the distribution of consumers. This is further complicated by the indirect effects of spatial subsidies on these consumers (Murakami and Nakano, 2002). As a result, it is difficult to independently investigate the effects of spatial subsidies on consumer communities without considering the effects of landscape (Denno et al., 2005; Greenstone, 1984). In fact, neither consumer nor available prey act in isolation of a range of environmental variables (Finke and Denno, 2002; Rypstra et al., 1999). Vegetation complexity, for instance, both modulates the foraging rates of consumers (Finke and Denno, 2002; Wright et al., 2019) and increases the abundance and biomass of prey (Ober and Hayes, 2008b). Demonstrating this, Finke & Denno (2002) found that while vegetation complexity reduces predation pressure on meso-predators (e.g. secondary consumers), it increases the overall predation pressure on herbivores. Insectivorous bats, as predominant riparian consumers (Fukui et al., 2006; Seidman and Zabel, 2001), similarly respond to both landscape characteristics and spatial subsidies, concurrently (Müller et al., 2012; Threlfall et al., 2012).

Research into the relationship between insectivorous bats and vegetation have largely focused on sub-canopy vegetation density ("clutter"; Adams & Law, 2011) and canopy permeability hypotheses (Ober and Hayes, 2008c). From these, the general consensus is that insectivorous bat communities exhibit strong species-specific responses to structural changes in vegetation, (McConville et al., 2014) informed by adaptive traits (Denzinger and Schnitzler, 2013; Dunlop and Bullen, 2011). As an overview, foraging and habitat selection by insectivorous bat species are driven by morphological adaptations that enable efficient flight and echolocation (Denzinger and Schnitzler, 2013; Schnitzler et al., 2003). Long duration-low frequency calls for instance, travel long distances and therefore are suited for homogenous, open habitats such as grasslands (Schnitzler et al., 2003; Siemers and Schnitzler, 2000). In contrast, short duration-high frequency calls, which travel a short distance, are suitable to navigating complex habitats such as cluttered understories (Melendez et al., 2013; Schnitzler et al., 2003). Manoeuvrability (as determined by wing shape) similarly indicates a species suitability to a habitat (Jung et al., 2012; Norberg and Rayner, 1987). Large bats with high wing loading and large aspect ratio are much more manoeuvrable in open habitats, while small bats with lower wing loading and low aspect ratio undertake more efficient flight in cluttered habitats (Norberg and Rayner, 1987). For bat communities, these traits exist along a continuum with many species selecting for moderately dense or open habitats ("edges"; Blakey, Law, et al., 2017; Norberg & Rayner, 1987). Despite this, only recently have researchers begun considering these traits in relation to anthropogenic changes to landscape and vegetation (Bader et al., 2015; Heim et al., 2018).

Wetlands are disproportionately important for insectivorous bats (Blakey et al., 2017a). In the Anthropocene, these habitats are under intense pressure (Zedler and Kercher, 2005). Globally, as much as 87% of these ecosystems have been degraded or destroyed since the 18th Century (Davidson, 2014; Kingsford et al., 2016), accompanied by unprecedented rates of decline in dependent biodiversity (Clarke-Wood et al., 2016; Ocock et al., 2017). Perennial and headwater streams, as a type of riverine wetland, experience unique pressures due to their predominance in river networks (Baattrup-Pedersen et al., 2018; Globevnik, 2007). The degradation of these systems can change the composition of food-webs (Downes et al., 2017; Stenroth et al., 2015). Downes et al. (2017) for instance, demonstrated that reductions in vegetation cover and available detritus, and increases in water temperature along a harsh agricultural gradient were associated with losses in emergent aquatic invertebrate species. Dispersing (flying) adults were most abundant in upstream reaches where riparian vegetation was continuous and fewer emergent aquatic species were recorded in downstream agricultural landscapes (Downes et al., 2017). This has implications for consumers of emergent aquatic invertebrates, especially insectivorous bats (Blakey et al., 2017a; Kurta et al., 1989).

Local land clearance influences insectivorous bat communities indirectly via their prey (Heim et al., 2017, 2016) and directly through changes to vegetation structure (Rodríguez-San Pedro et al., 2019). Heim et al. (2016) for instance, demonstrated that those species adapted to open-edge habitats foraged intensively in simplified agricultural ecosystems. Conversely, clutter-tolerant species were maladapted to these environments and in turn, were exposed to a greater risk of predation (Heim et al., 2016). Further, edge-dwelling species tracked increases in flying invertebrate abundance in agri-ecosystems where little surrounding woodland remained (Heim et al., 2017). Aquatically-derived subsidies, although impacted by land-use, still persist in agricultural systems (Stenroth et al., 2015), which suggest that the effects of perennial streams as productivity hubs, may further augment bat foraging activity (Kerbiriou et al., 2017; Salvarina, 2016). Kerbiriou et al. (2017), for example, detected a strong positive effect of streams on the relative abundance of many insectivorous bat species in highly protected nature reserves. Despite this, our understanding of the interactions between the positive effects of perennially available freshwater and the impact of riparian vegetation clearance on insectivorous bat community composition and foraging has yet to be realised.

Hypotheses

In this study, we tested whether insectivorous bat community dynamics differ across local land clearing gradients. We compared bat activity, species richness and community composition within and between the riparian zones of six perennial streams that run through a local land clearing gradient. We predict strong differences in bat activity, species richness and community composition between reaches with different riparian vegetation structures (H_1; Table 4.5.1). Higher foraging activity is expected at upper survey reaches where native vegetation is virtually unaltered and spatial subsidies are available. Further, we predict that upper survey reaches will be more taxa rich and if correct, this implies that changes in vegetation structure, longitudinally can impact the distribution of insectivorous bats. We predict also that bat activity and invertebrate abundance will be concentrated within 5 m of perennial streams (H_2; Table 4.5.1) as a product of the lateral differences in vegetation within reaches. Alternatively, if bat activity, species richness and community composition vary between streams (but not within streams) this suggests that discrete environmental differences (e.g. the arrangement of riparian vegetation) governs the responses of these consumers (H_3; Table 4.5.1). These predictions also apply to the responses of flying invertebrates in these habitats. This would also support a close association between perennial streams and the resources they provide. Finally, we considered changes in responses over the survey period (H_4; Table 4.5.1).

4.2 METHODS

4.2.1 Study Area

We monitored insectivorous bat activity along six 2nd/3rd order perennial streams in regional Victoria, Australia (Fig. 4.6.1; Taungurung country). As in Section 2.2.1, these streams included the Broken (segment length: 50 km), Delatite (length: 50 km) and Howqua (length: 65.6 km) rivers, as well as Holland (length: 41 km), Hughes (length: 70.4 km) and Ryans (length: 35 km) creeks. The segment of Delatite River surveyed comprised a riparian zone of continuous native vegetation for its length, while the remaining five streams were deliberately selected as examples of systems where vegetative cover was only continuous in the upper reaches. The Delatite River was surveyed like this as to expand the range of values for inclusion in our stepwise regression analysis (see below) over which hypotheses can be tested. As tributaries within the Goulburn-Broken Catchment, these streams assist in transporting 11% of the Murray-Darling Basin' water despite spanning less than 2% of the basin's overall area (Murray-Darling Basin Authority, 2018). Streams in this region are fed by both high annual rainfall and snow melt (approx. 1600 mm per annum) in headwater areas (Murray-Darling Basin Authority, 2018). These streams are in the epicentre of Australia's sheep and cattle production (Australian Bureau of Agricultural and Resource Economics, 2017) with downstream reaches (excluding the Delatite's) running through highly modified, irrigated pastures (Gray et al., 2014). Within survey reaches, we sampled changes in vegetation and bat communities as a result of lateral zonation within sub-blocks hereafter referred to as "units". Below we outline the details of these units.

4.2.2 Establishing a local land clearing gradient

Riparian vegetation was surveyed at each site in a two-step approach. Firstly, we determined Leaf Area Index (LAI; m^2 foliage area / m^2 ground area) using a digital canopy photography method derived from the TERN vegetation monitoring protocol (See section 2.2.2 for more details; Terrestrial Ecosystem Research Network, 2013). Two x 100 m transects (≤5 m and 300 m, parallel to the stream) were established on flat or gentle sloping terrain (slope ≤15°). An image of canopy cover (one stop under auto-exposure) was taken every 10 m along each transect (20 photos per study site in total, approximately 3936 x 2624 pixels) using a DSLR camera (Nikon D600; > 10 Megapixel sensor of 24 mm size) with a 50 mm prime lens (24 mm CCD/CMOS with 1.5/1.6 multiplication factor), ISO 400 and an aperture of f8.0. DCP software (v3.14; MacFarlene, 2017) was used to analyse these images. This LAI data was collected exclusively for Chapter Four.

Secondly, vegetation height (m) and width/diameter at breast height (DBH; m) were measured at 1 m intervals (with a 2 m buffer either side) along 2 x 100 m transects (400 m^2) oriented parallel to the stream. The first transect was on the edge of the stream (≤5 m) and the second, 300 m away from the stream (hereafter referred to as "units"). For vegetation, greater than 2 m, a clinometer was used to estimate heights (to the nearest whole number) from a reference point of 2 m away. The density of mature trees was determined by taking the sum of the cross-sectional area of all trees (with a DBH > 0.65 m) along our transects. Mature tree stem density is expressed as m^2 ha^{-1}. We also determined the crude density of ferns, graminoids and shrubs within each transect (no. stems ha^{-1}). Vegetation unit data collected from ≤5 m of the stream was shared with Chapter Two.

Finally, we deployed a temperature logger (OneTemp Pty Ltd, Adelaide, South Australia, Australia) at each survey reach. These loggers recorded the in-stream temperature, hourly for seven months (November – May 2018-2019; austral Spring-Autumn). This data was shared with chapters two and five.

4.2.3 Invertebrate sampling

At each survey reach, nocturnal aerial insects were sampled surveyed twice over January 22nd-27th and February 20th – 26th, 2018 (austral Summer). Light traps comprised a plastic tray (28 x 22 x 5 cm) filled with water and ethanol (to a concentration of 70%), with the tray placed within a circular tub (top diameter = 39 cm; height of tub = 32 cm; Downes, Lancaster, Glaister, & Bovill, 2017). A fluorescent, ultraviolet blacklight (12 DC V, 8 watts) was laid across the top of the tray (Downes et al., 2017). This arrangement ensured that only invertebrates flying directly overhead or nearby were attracted and trapped (Collier and Smith, 1997). It should be noted that light traps systematically under sample flying insects that are diurnal (i.e. dragonflies) or not positively phototactic (i.e. mayflies and stoneflies). This may have implications for the abundances of these taxa observed here. Samples were preserved in 70% ethanol then identified to taxonomic order (lower where necessary), which was used to describe taxa as either terrestrial, aquatic or an indeterminant in origin (Table 4.5.2). Specimens were then counted and measured (cm) before being dried for ~48 hours in an oven at 80 °C. Next, we weighed the specimens to determine their dry weight (g). This invertebrate data was collected exclusively for Chapter Four.

4.2.4 Insectivorous bat monitoring

Concurrently, insectivorous bat activity was monitored at each reach using Anabat SD1 ultrasonic call detectors (Titley Electronics, Ballina, New South Wales, Australia). Two Anabats were deployed at each survey reach (n = 18; (1) within 5 m of the stream and (2) 300 m from the stream; hereafter referred to as "units"). These units were calibrated to detect 40 kHz at 15 m, using a bat chirper (Nevada Bat Technology, Las Vegas, NV, USA) as to restrict calls recorded to the sub-canopy strata of the riparian zone (Blakey et al., 2016). Anabats were paired with light traps but were stationed ~100 m way while still maintaining their distance from the stream. They were also deployed for three consecutive nights (totally six nights per site; Law, Gonsalves, Tap, Penman, & Chidel, 2015). The microphones of the Anabats were pointed downstream, where those within 5 m of the stream were upstream of pools. Microphones were positioned 1 m off the ground and angled 45° upwards, away from vegetation clutter to reduce sound attenuation (Adams and Law, 2011; Patriquin and Barclay, 2003). Anabats were set to record between 20:00 and 07:00 (from approx. an hour before sunset until after sunrise). We sampled 9 survey reaches and 2 units each sampling night, with survey reaches along each stream sampled, concurrently.

Bat calls (each sound file recorded comprising of a sequence of pulses) were analysed using automated call identification software, ANASCHEME (Adams et al., 2010) and local identification keys (Lumsden and Bennett, 2005). These automated keys separated calls from ambient noise and identified each call to species/ taxa group where possible. ANASCHEME however, often misidentified ambient noise as *Austronomous australis* and as a result these calls were manually checked against a reference call for this species (Bhardwaj et al., 2017). Further, this key is unable to separate *Nyctophilus geoffroyi*, *Nyctophilus gouldi* and *Myotis macropus* calls due to their respective linear structure and as result, these calls were grouped in to a '*Nyctophilus-Myotis*- complex'. Once identified, species were grouped into six guilds (adapted from Bullen and McKenzie 2011, Blakey et al. 2016 and Threlfall, Law, Penman, & Banks, 2011; Table 4.5.12): closed-space (CS), edge-space high, medium and low frequencies (ESH, ESM and ESL, respectively), above- canopy (AC) and open-space (OS). These guilds describe the typical flight patterns, wing shape, call structures and vegetation niches of each taxa (Milne, 2006), where 'niches' are referred to as either 'closed', 'edge' or 'open' depending on the amount of vegetation "clutter" present (Bhardwaj et al., 2017; Gonçalves et al., 2017).

4.2.5 Statistical Approach

Our approach for data analysis had three broad components: 1) analysis of variance with repeat measures for singular environmental and taxa responses, 2) analysis of deviance using multiple generalise linear models for community-level responses and 3) a canonical correspondence analysis and a forward stepwise regression were used to identify the single "best" explanatory model for bat activity and invertebrate abundance and biomass using environmental factors. Analyses were completed in R (R Core Team, 2013). All figures are presented with standard error bars unless where otherwise specified.

4.2.5.1 Randomised block factorial with repeat measures (RBF)

Our study design is a randomised block factorial with repeat measures (RBF), which considers the distinct effects of each individual block ("stream"), sub-blocks ("survey reach" and "unit"), survey month and their interactions, on responses (Kirk, 1995). This design has two error terms: 1) between blocks and 2) between months. Each error term (where applicable) contains an interaction that cannot be estimated, and we assume that these interaction terms explain a negligible amount of variation. While specific models are outlined below (Table 4.5.3), the general structure of our RBF is:

$$X_{ijk} = \mu + \pi_i + \alpha_j + \beta_k + \tau + (\alpha\beta\pi\tau)_{jki} + \epsilon_{ijk}$$

Where X_{ijk} is any response for each block, μ is overall mean effect, π_i is the effect of each stream (block), α_j is the effect within each survey reach (sub-block), β_k is the effect within each unit (sub-block), $(\alpha\beta)_{jk}$ is the interaction between sub-blocks, τ is the effect of survey month and $(\alpha\beta\pi\tau)_{jki}$ is all interaction terms. Sub-blocks were fixed effects, while survey month was a random effect. We constructed mixed-effects models (MEM) using base R (v3.5.0; R Core Team, 2013) to analyse the effects of survey reach (upper, middle and lower), unit (≤5 m and 300 m) and their interactions with stream effects and time of sampling. We completed these analyses with and without the Delatite River to identify whether it was a source of difference among streams or driver interactions between terms. Further, a Tukey's Honest Significant Difference (Tukey's HSD) test to investigate whether levels within terms all significantly differed and to determine the nature of interactions. Response variables were transformed using log(x+1) for analysis.

4.2.5.2 Multiple generalise linear regression for community-level responses (GLM)

Next, insectivorous bat community composition was examined using non-metric multidimensional scaling (nMDS) plots derived from Bray-Curtis similarity matrices using 'vegan' in R (v2.5-2; Oksanen et al., 2018).

Ellipses were drawn based on a multivariate t-distribution, encompassing a 95% confidence interval of raw activity data. Then, community-level responses (i.e. specific bat taxa activity and invertebrate abundance) to our blocking and sub-blocking factors (i.e. stream, survey reach, unit and survey month) were assessed. This was done by fitting the raw activity of 15 bat taxa and 29 invertebrate abundances to a generalised linear model (GLM; derived from Table 4.5.3). Negative binomial distributions were used for these GLM as this allowed us to meet two assumptions: 1) taxa were independent and 2) sites were independent (Wang et al., 2012). Significance of each variable was tested using the likelihood ratio test (LRT) statistic and P-values were estimated using a PERMANOVA-based resampling method and adjusted for multiple comparisons. The 'mvabund' package in R (Wang et al., 2012) was used to complete this analysis.

4.2.5.3 Environmental variable assessment and forward stepwise regression

Finally, we examined the relative importance of environmental variables to bat activity and species richness using a canonical correspondence analysis (CCA) and forward stepwise regression (with AIC adjusted for small samples sizes, as the selection criterion; Burnham and Anderson 2003). All environmental variables (and elevation; mASL) were included in these analyses (Table 4.5.3). In CCA, those variables that are more influential on bat activity and species richness are represented by longer vectors. The proximity of taxa to a vector indicates the strength of the relationship with that variable (e.g. further away or closer to the base of a vector indicates a weak relationship). Similarly, the position of a vector with respect to other vectors signifies their relationship (e.g. those pointed in the same direction suggest a colinear relationship). The package 'vegan' in R was used to construct our CCA (Oksanen et al., 2018).

Stepwise regression allowed us to construct a model comprising those variables that explained the most variation in bat activity and species richness (Hammerson et al., 2017; Neter et al., 1996). This process can be useful in qualitatively identifying a subset of variables but has been criticized for underestimating P-values (Wilkinson and Dallal, 1981) and struggling with multicollinearity (De Veaux and Ungar, 1994). As a result, we interpreted the results cautiously (Hammerson et al., 2017). To limit the effects of multicollinearity, however, we considered the variance inflation factor (VIF) of each environmental variable in a full model (i.e. one containing all environmental variables; Fox and Monette, 1992). VIFs quantify the severity of multicollinearity and provides an index that measures how much the variance of an estimated regression coefficient is increased due to collinearity (Akinwande et al., 2015; Lindsey and Sheather, 2010). As a general rule, VIFs >5 represent high levels of multicollinearity among environmental variables, where regression coefficients are poorly estimated and resulting p-values are problematic (Lindsey and Sheather, 2010). Environmental variables with a VIF>5 were identified and systematically removed from the analysis. An intercept only model was run as our base model (Neter et al., 1996).

To scrutinise the model derived from the stepwise regression process (referred to hereafter as the "best" model), we generated a set of unique models comprising all available combinations of environmental variables before taking a subset of these models that represented <2AIC (Grueber et al., 2011). This subset of models and the best model were then ranked based on their AIC to identify the most parsimonious model. The package 'AICcmodavg' was used to complete this portion of the analysis (Mazerolle, 2019). A model averaging approach was then used to identify the relative importance of each variable (Grueber et al., 2011), using the 'MuMin' package (Barton, 2019). The relative importance of a variable is commonly estimated by summing the weights of models where the variable appears (Galipaud et al., 2014). Variables were deemed relatively important if they had a relative variable importance ≥ 0.73; equivalent to an ΔAIC of 2, a common 'rule-of-thumb' to indicate a significant effect (Richards, 2005).

4.3 RESULTS

4.3.1 Environmental variables (RBF)

Leaf area index was significantly greater at upper survey reaches than middle and lower survey reaches (Table 4.5.4 & 4.5.5, Fig. 4.6.2). Although this varied between streams with the Delatite River having similar canopy LAI values for the length of the segment surveyed. Overall, LAI was greater 300 m away from the stream than ≤5 m (Table 4.5.5, Fig. 4.6.2). Similarly, mean vegetation height reduced, longitudinally (Table 4.5.6, Fig. 4.6.3 & 4.6.4). Vegetation was on average taller 300 m away from the stream at upper and middle survey reaches, while at lower survey reaches mean vegetation height did not significantly differ between units (Table 4.5.6, Fig. 4.6.3 & 4.6.4). Stem density of mature trees reduced longitudinally from 39.84 ± 5.87 m^2 stems ha^{-1} to 5.41 ± 2.7 m^2 stems ha^{-1} (Table 4.5.7). Mature tree stem density did not differ significantly between units (Table 4.5.7). Crude graminoid density did not significantly differ between survey reaches, however, they were restricted to the stream's edge (Table 4.5.8). Crude shrub density at the stream's edge did not differ between survey reaches (Table 4.5.9). At upper survey reaches however, shrub density was highest 300 m away from the stream and this reduced, longitudinally (Table 4.5.9). These patterns remained consistent with and without the Delatite River. A full output of in-stream temperature results can be found in Chapter 2 (Section 2.3.1).

4.3.2 Flying invertebrate abundance and biomass (RBF)

Over thirty-six thousand flying invertebrates were sampled as a part of this study. Lepidopterans (50.6%), small-bodied nematocerans (29.68%) and trichopterans (8.35%) were the most common taxa sampled, while neuropterans (0.02%), plecopterans (0.02%) and odonates (0.01%) were the least. The largest abundance recorded in one night was 1239 at the Delatite River's upper survey reach while the lowest was 80 at Hughes Creek's lower survey reach. Emergent aquatic invertebrate abundance was significantly greater at all upper survey reaches except the Delatite River and Ryans Creek (Table 4.5.10; Fig. 4.6.5).

Emergent aquatic invertebrate abundance also did not significantly differ between middle and lower survey reaches at Howqua River (Table 4.5.10; Fig. 4.6.5). These drove an interaction between survey reach and stream in our RBF (as per our Tukey's HSD). Emergent aquatic invertebrates were overall more abundant within 5 m of the stream than 300 m away (Table 4.5.10; Fig. 4.6.6). Emergent aquatic invertebrate abundance did not significantly vary between survey month and no other significant interactions were detected (Table 4.5.10). Flying terrestrial invertebrate abundance only varied significantly between stream and survey reach (Table 4.5.11; Fig. 4.6.7) with the highest abundances recorded at the Delatite River and upper survey reaches, respectively. While nematoceran abundance did not differ significantly between treatment effects (Table 4.5.11). These patterns remained consistent with and without the Delatite River.

In terms of biomass, terrestrial flying invertebrates were the dominant taxa (90.71%). Overall, lepidopterans (50.21%), scarabs (12.71%), elaterids (11.06%), orthopterans (7.95%) and trichopterans (4.85%) contributed the most biomass to our samples. Similarly, emergent aquatic invertebrate biomass reduced longitudinally, however, significant interactions were detected between unit and stream (Table 4.5.10). As per the Tukey's HSD, the Delatite River showed an inverse relationship to the other streams, while for Hughes Creek the greatest biomass was recorded at the middle survey reach. Further, emergent aquatic invertebrate biomass recorded 300 m away did not vary significantly between survey reaches (Fig. 4.6.6). Again, flying terrestrial invertebrate biomass only varied significantly between stream and survey reach (Table 4.5.11; Fig. 4.6.7) with the greatest biomass recorded at the Broken River and upper survey reaches, respectively. While nematoceran biomass did not differ significantly between treatment effects (Table 4.5.11; Fig. 4.6.7).

4.3.3 Bat activity and species richness (RBF)

Our study area supported 17 species (15 taxa) of insectivorous bat at the time of sampling. In total, we recorded over twenty-two thousand identifiable calls (Table 4.5.12). Overall, bat activity varied between streams, survey reaches, units and months (Table 4.5.13; Fig. 4.6.8). There was significantly less activity at lower survey reaches compared with upstream reaches. Our Tukey's HSD revealed that middle and lower survey reaches did not significantly differ. Bats were also more active within 5 m of the stream compared to 300 m away. Further, bats were more active in February than January. These patterns in activity remained consistent with or without the Delatite River included. Bat species richness only varied between units with more species, on average, detected within 5 m of the stream (Table 4.5.13). Once the Delatite River was removed, however, species richness at upper and lower survey reaches significantly differed (as per the Tukey's HSD). All other patterns in species richness remained consistent with or without the Delatite River.

4.3.4 Community-level responses (GLM)

Nocturnal flying invertebrate communities significantly differed between stream, survey reach, unit and survey month (Table 4.5.14; Fig. 4.6.9). Only unit did not significantly interact with another factor in our analysis at the community-level (Table 4.5.14) with ephemeropterans and trichopterans more abundant within 5 m of the stream. Other taxa (including the blattodean Ectobiidae, the coleopterans Scarabaeidae, Elateridae and Silphidae, the dipteran Tipulidae, and the hymenopteran Ichneumonidae) were more abundant at upper survey reaches than downstream, without any interactions detected (Table 4.5.14 & 4.5.15). The 21 other taxa included in our GLMs (such as the lepidopterans) did not significantly differ base on the factors included here.

Similarly, Insectivorous bat community composition varied significantly between unit (Table 4.5.16; Fig. 4.6.9) with *C. gouldii*, *Mi. s. oceanensis*, *Nyctophilus-Myotis* complex *and R. megaphyllus* all being more active within 5 m of the stream (Table 4.5.16 & Table 4.5.17). No species was more active 300 m away from the stream, nor were significant interactions detected suggesting this pattern was uniform across all streams, survey months and survey reaches. Community composition also varied between stream, survey reach and month, however, significant interactions were detected between stream and survey reach, stream and survey month, and survey month and survey reach (Table 4.5.16). These interactions are best explained through the responses of individual taxa (Table 4.5.16, 4.5.17 & 4.5.18). *A. australis, F. tasmaniensis, Sa. flaviventris* and *Sc. orion*, for example, were significantly more active at lower survey reaches than upstream. In contrast, *V. vulturnus* was more active at upper survey reaches and this was consistent across streams, survey months and units. Comparatively high activity levels of *Mo. ridei* at Hughes Creek drove an interaction between stream and survey reach for this taxon. Otherwise, *Mo. ridei* activity was either significantly reduced at upper and middle survey reaches or exhibited no significant longitudinal trends at other streams. *Nyctophilus-Myotis* complex activity a long Hughes, Holland and Ryans creeks was significantly higher at the upper survey reaches but did not significantly differ between the lower and middle survey reaches. At the middle and upper survey reaches of Broken and Howqua rivers, *Nyctophilus-Myotis* complex activity did not significantly differ but were both significantly higher than lower survey reaches. The activity of this taxon did not significantly differ between the Delatite's survey reaches. In January, *C. gouldii* was significantly more active at upper survey reaches. This changed in February when *C. gouldii* activity was significantly higher at all middle survey reaches, except at Ryans Creek where activity was generally reduced. *V. darlingtoni* was more active at the upper survey reaches of four streams, while activity at Howqua River's upper and middle survey reaches, and for the length of the Delatite did not significantly differ.

4.3.5 Explanatory models for taxa responses (forward stepwise regression)

Our stepwise regression analyses resulted in the formation of a range of highly significant explanatory models (Tables 4.5.20, 4.5.22 & 4.5.24). Prior to this analysis, however, in-stream temperature and mean vegetation height were removed due to high degrees of multicollinearity (i.e. VIFs > 5).

Mean LAI featured in the explanatory models for emergent aquatic invertebrate abundance and biomass and flying terrestrial invertebrate abundance and was identified as a significant explanatory variable (Tables 4.5.20 & 4.5.21). Crude graminoid density also featured in these models and was identified as significant (Tables 4.5.20 & 4.5.21). Elevation featured in all flying invertebrate explanatory models but was only a significant explanatory variable for flying terrestrial invertebrate abundance and biomass and emergent aquatic invertebrate abundance (Tables 4.5.20 & 4.5.21). These models explained between 28 – 51% of flying invertebrate abundance and biomass variation.

A visual assessment of the CCA biplot for bat activity showed several strong associations with environmental variables (Fig. 4.6.10). Variables such as elevation, emergent aquatic abundance and biomass and crude graminoid density were relatively influential on the data given the length of their vectors. Elevation was positively associated with *Mi. schreibersii oceanensis, V. regulus, C. gouldii* and *Nyctophilus-Myotis* complex activity (Fig. 4.6.10). *Mo. ridei* activity was moderately and positively associated with mean LAI and mature tree stem density, while *V. vulturnus* was closely and positively associated with flying terrestrial invertebrate biomass (Fig. 4.6.10). Our stepwise regression process supported many of these relationships (Table 4.5.22 & 4.5.24). Total bat activity was best explained by flying terrestrial invertebrate abundance, emergent aquatic invertebrate biomass, mature tree stem density, elevation and crude graminoid density, for instance, and this model explained 36% of variation (Table 4.5.22). Similarly, the explanatory model for bat species richness included crude graminoid density, mature tree stem density and crude shrub density. Elevation was identified as a significant explanatory variable for *V. darlingtoni, V. vulturnus, Mo. planiceps, Mo. ridei, Mi. schreibersii oceanensis* and *V. regulus* activity (Table 4.5.23 & 4.5.25). While mature tree stem density was a significant explanatory variable for *Mo. ridei, V. darlingtoni* and *Nyctophilus-Myotis* complex activity. A full outline of explanatory models and significant explanatory variables can be found in Tables 4.5.22, 4.5.23, 4.5.24 & 4.5.25.

4.4 DISCUSSION

4.4.1 Trends in vegetation structure

The riparian zones at lower survey reaches should have reduced structural complexity in that vegetation and canopies are less dense. We tested this hypothesis by surveying vegetation structure at the upper, middle and lower survey reaches of perennial streams. In the first instance, these surveys were to confirm changes in vegetation at survey reaches that amounted to a local land clearing gradient. Our results here largely coincided with those in chapter two and were consistent with our 'within streams' hypothesis (H_A; Table 4.5.7A), in which riparian zones are structurally distinct (i.e. upstream vs. downstream) due to riparian vegetation clearance. Further, our analysis of variance of crude graminoid and shrub density, and leaf area index provided evidence for lateral changes in vegetation away from perennial streams (H_B; Table 4.5.8A). As noted in chapter two, these results are not controversial as longitudinal (Palmquist et al., 2018; Tabacchi and Planty-Tabacchi, 1996) and lateral (Reinecke et al., 2015; Sieben and Reinecke, 2008) changes in vegetation are widely recognised. It is important, however, to establish statistical support for these differences as they underpin many of our hypotheses for the flux of spatial subsidies and insectivorous bat activity.

Increasingly, the effects of riparian vegetation clearance on insectivorous bat activity and community composition are being investigated (Braun de Torrez et al., 2017; Lentini et al., 2012). Braun de Torrez et al. (2012), for instance, demonstrated that remnant forest patches were sites of increased nightly bat activity compared to a surrounding grassland matrix. Further, Lentini et al. (2012), identified that fields with scattered mature trees supported a higher bat species richness than those without. Nevertheless, the relationship between insectivorous bats and vegetation structure is complicated. While scarce vegetation limits the distribution of some species and creates a thresholds for foraging activity, the same is true for highly dense vegetation (Blakey et al., 2017b). As in chapter two, our results show reductions in vegetation across all strata at lower survey reaches where riparian vegetation clearance is most intense. These strong longitudinal and lateral differences, particularly in the shrub and ground layers of riparian zones are likely to influence habitat selection for insectivorous bat activity and availability of their prey (Law and Chidel, 2002; Ober and Hayes, 2008b). Therefore, our results here confirm that our study design is appropriate for investigating the effects of riparian vegetation clearance on insectivorous bat communities and their preference for emergent aquatic prey.

4.4.2 Prey community responses to the local land clearing gradient

The abundance and biomass of flying invertebrates should be less at lower survey reaches (H_1; Table 4.5.9B) and should be concentrated within 5 m of perennial streams (H_2; Table 4.5.10B). Further, these measures should vary between perennial stream (H_3; Table 4.5.11B) and survey month (H_4; Table 4.5.12B).Terrestrially-derived subsidies from riparian zones can provide important resources for some aquatic consumers (Nyström et al., 2003; O'Toole et al., 2017). Further, riparian vegetation and canopies regulate in-stream temperatures (Buczyńska et al., 2016; Van Looy and Piffady, 2017). The fragmentation of riparian vegetation, for instance, can cause water temperatures to increase, which as O'Toole et al. (2017) identified likely explains the loss of large-bodied aquatic emergent invertebrates such as stone- and mayflies. Reductions in terrestrial vegetation can significantly impact the development and emergence of aquatic invertebrates (Nelson et al., 2017; Watanabe et al., 1999). In the present study total flying invertebrate abundance only varied between stream and survey month, which was consistent with our 'between stream' and 'between month' hypotheses. Interactions between survey reach and stream meant that longitudinal reductions in total emergent aquatic invertebrate abundance and biomass were not consistent across all streams.

Consistent with our 'within reach' hypothesis, however (H_2; Table 4.5.13B), overall emergent aquatic invertebrate abundance was concentrated within 5 m of the perennial stream and no interactions were detected. Previous studies have found a complex relationship between lateral dispersal and vegetation structure (Carlson et al., 2016; Graham et al., 2017; Greenwood, 2014). Greenwood (2014), for instance, documented that shrub density at the stream-riparian zone interface impeded lateral dispersal by emergent aquatic invertebrates. Further, Graham et al. (2017) found that emergent aquatic invertebrates were likely to disperse farther in open habitats than in forested landscapes. In contrast, Carlson et al. (2016) documented that dispersal beyond the stream's bank, however, was restricted for these invertebrates at agricultural sites. Our results were consistent with the latter as trichopterans and ephemeropterans were most abundant at the stream's edge across the local land clearing gradient. With that said, very little is known about the dispersal patterns of emergent aquatic invertebrates and our study design does not provide details regarding the distance travelled by adults prior to being captured. Nevertheless, our results here do provide evidence for the distribution of foraging bats.

Crude graminoid density, leaf area index and elevation contributed to our explanatory models for emergent aquatic invertebrate abundance and biomass. Crude graminoid density was identified as influential for these taxa, and this was consistent with other studies (Carlson et al., 2016; Stenroth et al., 2015). Crude shrub density was also identified as a significant explanatory variable for emergent aquatic invertebrate biomass. Interestingly, the lowest crude shrub density was recorded 300 m away from the stream at agricultural reaches, while the highest was recorded 300 m away at upper survey reaches. Further, our CCA revealed that emergent aquatic invertebrate biomass had an inverse relationship with crude shrub density. This 1) provides support for our hypothesis that emergent aquatic invertebrate biomass will be concentrated within 5 m of perennial streams and 2) suggests that there may be an upper and lower limit to shrub density which impacts the flux of spatial subsidies. Further, these results broadly support our findings from Chapter Two, despite some spatial and temporal variation.

4.4.3 Relative importance of vegetation structure and spatial subsidies to insectivorous bat communities

Bat foraging activity should be greatest at upper survey reaches. Community composition should be more taxa rich, upstream (H_1). Further, bat foraging activity should be concentrated within 5 m of the stream (H_2). Although, these should be different between perennial streams (H_3) and survey month (H_4). Overall, insectivorous bat activity associated with perennial streams exhibited strong longitudinal trends across a local land clearing gradient (H_1). Upper survey reaches (overall tree density: ~642 stems ha^{-1}, mature tree density: ~107 stems ha^{-1}) were consistently important foraging habitats for insectivorous bat communities. Conversely, lower survey reaches, (overall tree density: ~50 stems ha^{-1}, mature tree density: ~5 stems ha^{-1}) hosted little foraging activity. Similarly, bat foraging activity and species richness was significantly greater at the stream's edge than 300 m away (H_2). This activity also varied significantly between streams (H_3) and between survey reaches (H_4).

In the present study, riparian vegetation structure was identified as an important driver of these community shifts at the reach scale. As hypothesised, declining vegetation attributes (namely mature tree stem density) were consistently the most important factor for foraging activity. Previous works have also found that vegetation characteristics at finer spatial scales are likely to be influential drivers of bat foraging in riparian zones (Akasaka et al., 2010; Lloyd et al., 2006). Akasaka et al (2010) for instance demonstrated that fine scale canopy and vegetation structure drove increases in insectivorous bat abundance more than broader landscape trends. Our results suggest that the distribution of insectivorous bat foraging along perennial streams is constrained by significant, longitudinal reductions in mature tree stem density at the reach scale.

We observed the exclusion of clutter-tolerant species, longitudinally as riparian zones became pastures. The (clutter-tolerant) *Nyctophilus-Myotis* complex for example, foraged less at lower survey reaches. An interaction between survey reach and stream for this group was driven by non-significantly different activity levels recorded at the middle and upper reaches of some streams. Further, this taxon's close association with mature tree stem and crude graminoid density suggests that intense riparian vegetation clearance limits their foraging distribution. This is consistent with other studies (Blakey et al., 2017b; Langton et al., 2010) including Campbell et al. (2009) who, demonstrated that despite the close proximity of two *My. macropus* populations along the Broken River, significant genetic differences remained between them. These authors suggests that the fragmentation of continuous, native riparian zones may restrict the movement of individuals (and in turn their foraging activity; Campbell et al., 2009) to habitats with specific vegetation qualities. For the present study, vegetation structure at the middle and upper survey reaches was identified as a highly important explanatory variable for *Nyctophilus-Myotis* complex foraging activity.

Consistent with other studies (Hanspach et al., 2012; Lumsden and Bennett, 2005), we detected reduced foraging activity for edge-dwelling species at survey reaches with stem densities below ~50 stems ha^{-1}. There was a slight positive association between *V. darlingtoni* activity with mature tree stem density, for example, signalling a preference for those survey reaches with tree stem densities greater than 600 stems ha^{-1}. Blakey et al. (2017b) noted, however, that in forests with comparable stem densities (>500 stems ha−1), there was considerable variability in bat activity, which may reflect differences in habitat use at the species and trait level. With this in mind however, the arrangement of vegetation (e.g. into distinct cluttered and open areas) may be more important to this species, rather than overall stem density (Blakey et al., 2017b). Regardless, *V. darlingtoni* activity demonstrated strong longitudinal trends and positive associations with increased canopy cover. Other studies have hypothesised that the likelihood of bat activity increases with decreased canopy cover (Ober and Hayes, 2008c). Ober & Hayes (2008), for instance, identified this to be the case for those species that foraged above the canopy (AC). Potentially due to the harsh environmental gradient we surveyed, however, no such relationship was observed.

As highly mobile consumers, insectivorous bats respond to a broad range of ecological processes during habitat selection. There is a plethora of literature outlining this habitat use and partitioning (Aldridge and Rautenbach, 1987; Milne, 2006; Reside and Lumsden, 2011). Generally, landscape characteristics (Hagen & Sabo, 2011; Johnson, 1980) and prey availability within landscapes (Fukui, Murakami, Nakano, & Aoi, 2006; Johnson, 1980) are postulated as the main determinants of resource and habitat preference. Our data, and evidence from other studies, suggest that total insectivorous bat activity along agricultural perennial streams in temperate Australia is shaped by a loss of mature trees (Blakey et al., 2017a; Hagen and Sabo, 2012). Due to the moderate-to-high importance of available prey in our analysis, however, flying insects (particularly emergent aquatic invertebrates) are likely to still drive bat foraging.

In the present study, total bat activity responded positively to emergent aquatic invertebrate abundance. This was consistent with our hypothesis that insectivorous bat foraging will track differential amounts of aquatically-derived subsidies along a local land clearing gradient. Such a positive response to aquatic abundance is an interesting one as it may reflect dietary requirements (Clare et al., 2011; Schalk and Brigham, 2008). Clare et al. (2011), for instance, demonstrated shifts in the diet of a generalist insectivorous bat species, away from small-bodied dipterans and towards ephemeropterans (an emergent aquatic invertebrate). This higher consumption of emergent aquatic invertebrates corresponded with maternity and therefore, a greater demand for high quality prey (Clare et al., 2011). Our study took place at the end of the maternity period for many species in our study region (Lumsden et al., 2002) but during a critical time for younger bats. Further, aquatically-derived subsidies have been shown to influence the distribution (Fukui et al., 2006) and community structure of insectivorous bats (Hagen and Sabo, 2011;

Ober and Hayes, 2008a), and the present study supports this. As a key emergent aquatic prey item, tipulids were less abundant at agricultural reaches. The loss of these aquatically-derived subsidies was important for *Nyctophilus-Myotis complex, C. gouldii, Mo. planiceps, Mi. schreibersii oceanensis* and *V. regulus*, taxa with distinct habitat and foraging requirements.

As there were few lateral differences in vegetation structure, the relative importance of aquatically-derived subsidies can potentially be isolated. The present study identified that emergent aquatic prey including ephemeropterans and trichopterans were significantly more abundant within 5 m of the stream rather than 300 m away. Overall bat activity in the upper survey reaches, where riparian vegetation was continuous, were starkly greater within 5 m of the stream than 300 m away. The magnitude of difference however, shrunk as riparian vegetation clearance increased. Further, the trend was consistent across a broad range of foraging guilds including *C. gouldii* (ESL), *Mi. s. oceanensis* (ESH), *Nyctophilus-Myotis* complex (CS) and *R. megaphyllus* (CS). On balance, *C. gouldii* and *Mi. s. oceanensis* forage at the edge of dense vegetation and likely aggregate along streams as they provide a break in the riparian vegetation (Adams and Law, 2011). For those clutter-tolerant taxa, however, the increased abundance of emergent aquatic invertebrates is likely to be a key driver of lateral differences (Blakey et al., 2016; De Oliveira et al., 2015). Blakey et al. (2016) for instance, identified that CS taxa (e.g. *Nyctophilus* spp.) responded positively to habitats with high amounts of vegetation clutter. This response was analogous to that of trichopterans, which also responded negatively to the removal of this clutter (Blakey et al., 2016). As terrestrial flying prey were not aggregated within 5 m of streams (in the present study) and have been found to respond positively to clutter removal (Blakey et al., 2016), the reduced availability of emergent aquatic invertebrates beyond perennial streams may be a critical determinant of foraging activity (Hagen and Sabo, 2011).

4.4.4 Limitations with stepwise regression

Again, a key aim of stepwise regression is to isolate the relationship between each environmental variable and the response variable (Tabachnick and Fidell, 1996). Unfortunately, stepwise regressions are generally burdened by biases and encourage an inappropriate reliance on a single "best" model (Derksen and Keselman, 1992; Whittingham et al., 2006). Further, collinearity among environmental variables can be problematic for stepwise regression as it becomes difficult for models to separate the effects of individual independent variables on dependent variables, in isolation (Burnham and Anderson, 2003; Tabachnick and Fidell, 1996). This thesis encounters similar issues. To address these, we 1) considered the variance inflation factors (VIF) of the full model (i.e. one containing all environmental variables) and systematically removed those variables with a VIF > 5, and 2) compared the "best" model (as per the stepwise regression) to a subset of top models that represented <2AIC (Grueber et al., 2011). Ultimately, however, the caveats associated with stepwise regression may be insurmountable, statistically, and we endorse Whittingham et al. (2006) statement that "ecologists and behavioural scientists should make use of alternative methods".

4.4.5 Conclusion

Our results suggest that longitudinal changes in riparian vegetation structure along perennial streams that run through a local land clearing gradient directly influence insectivorous bat community composition and foraging activity. In our study, decreasing crude graminoid and mature tree stem density were identified as important explanatory variables of flying invertebrate abundance and biomass, and bat activity along a stream's longitudinal axis. Overall bat activity decreased with increased riparian vegetation clearance. Furthermore, the congregation of emergent aquatic invertebrates in ecotones close to perennially flowing water was influential when considering the proximity of foraging activity to perennial streams. Although we found strong associations between some insectivorous bat species and the availability of aquatically-derived subsidies, this was not universal across all species. Little is known about the taxonomic resolution at which insectivorous bats select for prey. Likewise, more work is needed to understand when and under what circumstances these bats target aquatic prey over terrestrial ones. Our results indicate that increasing riparian vegetation clearance marks the loss of riparian complexity, the availability of key subsidies and their consumers.

4.5 TABLES

Table 4.5.1A Categories of formative hypotheses ($H_{A\text{-}D}$) that confirm different spatial and temporal patterns in environmental variables. These are designed to demonstrate that land-use changes were as expected. Possible underlying mechanisms, and the scale (within streams, between streams and between times) at which responses are likely to be most variable, are also outlined

Hypothesis			
General hypothesis The clearing of native vegetation fundamentally changes stream-riparian ecosystems. This is achieved directly through impacting the structure and density of vegetation and indirectly through in-stream temperature changes.			
		Source of variation	Statistical approach
H_A	Vegetation height and density, and canopy structure will decrease, longitudinally *<u>Mechanism:</u> At the local scale, riparian vegetation is frequently degraded by clearing or by activities such as livestock grazing and trampling* In-stream temperature will increase, longitudinally *<u>Mechanism:</u> Streams flow across natural thermal gradients from high (cold) to low (warm) elevations, unnatural gradients from dense (cold) to open (warm) vegetation.*	Within streams	See Section 4.2.5.1
H_B	Vegetation structure (canopy structure, height, density etc) within 5 m of perennial streams will be significantly different from 50 m away *<u>Mechanism:</u> Lateral zonation of vegetation*	Within reaches	
H_C	The above responses will vary with spatial separation of streams *<u>Mechanism:</u> Stream-level differences in vegetation communities and in-stream conditions due to landscape*	Between streams	
H_D	In-stream temperature will vary with temporal separation of sampling *<u>Mechanism:</u> Stream- and reach-level differences in in-stream are not constant and vary between days, weeks, months, seasons.*	Between times	

Table 4.5.1B Five categories of alternative hypotheses (H_{1-4}) that predict different spatial and temporal patterns in invertebrate abundance and biomass, and community composition. Possible underlying mechanisms, and the scale (within streams, between streams and between times) at which responses are likely to be most variable, are also outlined

	Hypothesis	Source of variation	Statistical approach
H_1	The abundance and biomass of large-bodied emergent aquatic invertebrates will decrease, longitudinally *<u>Mechanism:</u> Riparian vegetation clearance at the stream-level that can change the quantity and quality of spatial subsidies* The abundance and biomass of other flying terrestrial invertebrates will decrease, longitudinally *<u>Mechanism:</u> Riparian vegetation clearance at the stream-level that can reduce the available habitat for other flying invertebrates and in turn their abundance and biomass* The number of bat foraging calls will decrease, longitudinally *<u>Mechanism:</u> Riparian vegetation clearance reduces available habitat and spatial subsidies*	Within streams	See Section 4.2.5.1
	Bat community composition will be more taxa rich, upstream and distinct from those downstream *<u>Mechanism:</u> Riparian vegetation clearance reduces available habitat and spatial subsidies*		See Section 4.2.5.2
H_2	Insectivorous bat activity and flying invertebrate abundance/biomass will be concentrated within 5 m of perennial streams *<u>Mechanism:</u> Reach-level differences in vegetation communities that affects where bats forage and where invertebrates aggregate*	Within reaches	See Section 4.2.5.1
H_3	The above responses will vary with spatial separation of streams *<u>Mechanism:</u> Stream-level differences in invertebrate diversity that affects distribution*	Between streams	
H_4	The above responses will vary with temporal separation of sampling *<u>Mechanism:</u> Stream- and reach-level differences in invertebrate diversity are not constant*	Between times	
H_5	Insectivorous bat activity will respond strongly to the presence of spatial subsidies *<u>Mechanism:</u> The higher availability of spatial subsidies will support riparian consumers*	The relative importance of environmental variables	See Section 4.2.5.3

Table 4.5.2 Grouping guide for flying invertebrates captured in this study

	Order	Family/Sub-order	Specific key(s)
General			Gooderham & Tsyrlin, 2002; Taxonomic Research & Information Network/CSIRO, 2012
Aquatic	Coleoptera	Dytiscidae	Moore, 1980; Slipinski & Lawrence, 2013; Watts, 2002
		Hydrophilidae	
		Noteridae	
	Diptera	Tilupidae	
	Ephemeroptera		
	Hemiptera	Corixidae	
		Notonectidae	
	Odonata		
	Plecoptera		
	Megaloptera		
	Trichoptera		Holzenthal, Blahnik, Prather, & Kjer, 2007
Terrestrial	Blattodea		
	Coleoptera	(All others)	Moore, 1980; Slipinski & Lawrence, 2013; Watts, 2002
	Diptera	(All others not listed)	
	Hymenoptera		
	Isoptera		
	Lepidoptera		Nielsen, Edwards, & Rangsi, 1995
	Mantodea		
	Neuroptera		
	Orthoptera		
Indeterminate	Diptera	Nematocera	

Table 4.5.3 Mixed-effects models for response variables

Variable category	Response variable	Model structure
Environmental	In-stream temperature	$X_{ij} = \mu + \pi_i + \alpha_j + (\alpha\pi)_{ji} + \tau + (\alpha\pi\tau)_{ji}$
	Mean crude graminoid density	$X_{ijk} = \mu + \pi_i + \alpha_j + \beta_k + (\alpha\beta)_{jk} + (\alpha\beta\pi)_{jki} + \epsilon_{ijk}$
	Mean crude shrub density	$X_{ijk} = \mu + \pi_i + \alpha_j + \beta_k + (\alpha\beta)_{jk} + (\alpha\beta\pi)_{jki} + \epsilon_{ijk}$
	Mean LAI	$X_{ij} = \mu + \pi_i + \alpha_j + \beta_k + (\alpha\beta)_{jk} + (\alpha\beta\pi)_{jki} + \epsilon_{ijk}$
	Mean mature tree stem density	$X_{ijk} = \mu + \pi_i + \alpha_j + \beta_k + (\alpha\beta)_{jk} + (\alpha\beta\pi)_{jki} + \epsilon_{ijk}$
	Mean vegetation height	$X_{ijk} = \mu + \pi_i + \alpha_j + \beta_k + (\alpha\beta)_{jk} + (\alpha\beta\pi)_{jki} + \epsilon_{ijk}$
Taxa	Bat activity and species richness	$X_{ijk} = \mu + \pi_i + \alpha_j + \beta_k + \tau + (\alpha\beta)_{jk} + (\alpha\pi)_{ji} + (\beta\pi)_{ki} + (\alpha_j\tau) + (\beta_k\tau) + (\pi_i\tau) + (\alpha\pi\tau)_{ji} + (\beta\pi\tau)_{ki} + (\alpha\beta\tau)_{jk} + \epsilon_{ijk}$
	Terrestrial aerial invertebrate abundance and biomass	$X_{ijk} = \mu + \pi_i + \alpha_j + \beta_k + \tau + (\alpha\beta)_{jk} + (\alpha\pi)_{ji} + (\beta\pi)_{ki} + (\alpha_j\tau) + (\beta_k\tau) + (\pi_i\tau) + (\alpha\pi\tau)_{ji} + (\beta\pi\tau)_{ki} + (\alpha\beta\tau)_{jk} + \epsilon_{ijk}$
	Aquatic emergent invertebrate abundance and biomass	$X_{ijk} = \mu + \pi_i + \alpha_j + \beta_k + \tau + (\alpha\beta)_{jk} + (\alpha\pi)_{ji} + (\beta\pi)_{ki} + (\alpha_j\tau) + (\beta_k\tau) + (\pi_i\tau) + (\alpha\pi\tau)_{ji} + (\beta\pi\tau)_{ki} + (\alpha\beta\tau)_{jk} + \epsilon_{ijk}$

Table 4.5.4 Measurements of canopy structure for riparian zones of survey reaches and units. Values presented are Leaf Area Index (LAI), crown cover (f_c; % ground covered by the vertical projection of solid crowns), foliage cover (f_f; % ground covered by the vertical projection of foliage and branches), cover porosity (Φ; % of space between foliage and branches) and gap fraction (GF; % of space unobstructed by foliage or branches; Macfarlane et al., 2007; Welles & Cohen, 1996)

		Broken River			Delatite River			Hollands Creek			Howqua River			Hughes Creek			Ryan Creek		
		Upper	Middle	Lower	Upper	Middle	Lower	Upper	Middle	Lower	Upper	Middle	Lower	Upper	Middle	Lower	Upper	Middle	Lower
≤5 m	LAI	1.15±0.31	1.23±0.32	0±0	1.05±0.26	1.19±0.24	1.06±0.28	1.47±0.28	0.52±0.2	0.43±0.12	1.37±0.26	0.93±0.24	0.15±0.15	1.5±0.35	1.31±0.26	0.06±0.06	1.3±0.24	1.13±0.21	0.25±0.17
	f_c	0.33±0.09	0.36±0.09	0±0	0.29±0.07	0.37±0.07	0.32±0.09	0.44±0.08	0.19±0.06	0.14±0.04	0.4±0.07	0.28±0.07	0.06±0.05	0.4±0.08	0.4±0.08	0.03±0.02	0.4±0.08	0.32±0.06	0.08±0.06
	f_f	0.47±0.12	0.51±0.13	0±0	0.43±0.1	0.57±0.11	0.48±0.13	0.66±0.12	0.28±0.09	0.22±0.07	0.62±0.11	0.42±0.1	0.1±0.09	0.56±0.11	0.59±0.11	0.04±0.04	0.61±0.11	0.46±0.09	0.12±0.08
	Φ	0.52±0.11	0.43±0.1	1±0	0.44±0.1	0.49±0.09	0.47±0.1	0.47±0.1	0.57±0.13	0.55±0.11	0.48±0.1	0.46±0.1	0.76±0.13	0.43±0.11	0.47±0.09	0.87±0.1	0.48±0.09	0.44±0.1	0.81±0.1
	GF	0.68±0.09	0.65±0.09	1±0	0.72±0.07	0.64±0.07	0.69±0.09	0.57±0.08	0.82±0.06	0.87±0.04	0.61±0.07	0.73±0.07	0.95±0.05	0.61±0.08	0.61±0.08	0.98±0.02	0.61±0.08	0.69±0.06	0.93±0.06
300 m	LAI	1.83±0.11	1.67±0.19	0.24±0.21	1.01±0.16	1.34±0.15	0.91±0.13	1.39±0.15	0.29±0.16	0.55±0.22	1.73±0.31	1.46±0.28	0±0	1.89±0.21	1.43±0.14	0.71±0.21	1.61±0.36	1.35±0.26	0.45±0.21
	f_c	0.56±0.03	0.49±0.05	0.08±0.06	0.31±0.05	0.42±0.05	0.3±0.05	0.44±0.04	0.14±0.07	0.16±0.07	0.5±0.07	0.4±0.08	0.01±0.01	0.55±0.05	0.45±0.04	0.23±0.06	0.45±0.08	0.42±0.07	0.15±0.06
	f_f	0.85±0.05	0.72±0.06	0.1±0.08	0.48±0.08	0.67±0.07	0.49±0.07	0.71±0.06	0.19±0.09	0.23±0.09	0.73±0.09	0.58±0.11	0.01±0.01	0.8±0.05	0.72±0.05	0.34±0.09	0.65±0.11	0.65±0.1	0.21±0.09
	Φ	0.35±0.02	0.33±0.04	0.67±0.14	0.34±0.03	0.37±0.02	0.4±0.02	0.39±0.03	0.63±0.13	0.52±0.11	0.34±0.04	0.3±0.06	0.91±0.1	0.33±0.03	0.38±0.03	0.5±0.12	0.41±0.08	0.37±0.03	0.48±0.13
	GF	0.45±0.03	0.52±0.05	0.93±0.06	0.7±0.05	0.59±0.05	0.71±0.05	0.57±0.04	0.87±0.07	0.85±0.07	0.51±0.07	0.61±0.08	1±0.01	0.46±0.05	0.56±0.04	0.78±0.06	0.56±0.08	0.59±0.07	0.86±0.06

Table 4.5.5 Analysis of variance of leaf area index

Source	SS (Type 3)	df	MS	F	P
Between blocks					
Stream (block)	1.68	5	0.336	2.717	**0.02**
Reach	20.87	2	10.437	84.285	**<0.001**
Unit	1.41	1	1.411	11.393	**<0.001**
Stream x Reach	8.01	10	0.801	6.467	**<0.001**
Stream x Unit	0.95	5	0.191	1.539	0.18
Reach x Unit	0.04	2	0.019	0.152	0.86
Residual error + Stream x Reach x Ecotone	0.83	10	0.083	-	**-**
Total					

Table 4.5.6 Analysis of variance of vegetation height

Source	SS (Type 3)	df	MS	F	P
Between blocks					
Stream (block)	2.49	5	0.499	2.753	0.051
Reach	7.16	2	3.58	19.738	**<0.001**
Unit	0.255	1	0.255	0.52	0.478
Reach x Unit	1.458	2	0.729	3.597	**0.04**
Reach x Stream	2.035	10	0.204	1.123	0.39
Unit x Stream	0.405	5	0.081	0.165	0.973
Residual error + Stream x Reach x Unit	1.145	10	0.115	-	**-**
Total					

Table 4.5.7 Analysis of variance of mature tree stem density

Source	SS (Type 3)	df	MS	F	P
Between blocks					
Stream (block)	7.86	5	1.571	2.688	0.055
Reach	44.75	2	22.376	38.279	**<0.001**
Unit	0.41	1	0.408	0.160	0.692
Reach x Unit	0.35	2	0.173	0.193	0.826
Reach x Stream	9.23	10	0.923	1.579	0.19
Unit x Stream	2.94	5	0.588	0.231	0.95
Residual error + Stream x Reach x Unit	6.83	10	0.683	-	-
Total					

Table 4.5.8 Analysis of variance of crude graminoid density

Source	SS (Type 3)	df	MS	F	P
Between blocks					
Stream (block)	4.43	5	0.886	1.833	0.949
Reach	1.74	2	0.868	0.216	0.807
Unit	61.98	1	61.98	128.28	**<0.001**
Reach x Unit	1.74	2	0.87	1.53	0.232
Reach x Stream	4.06	10	0.406	0.101	0.999
Unit x Stream	4.43	5	0.89	1.833	0.144
Residual error + Stream x Reach x Unit	4.06	10	0.41	-	-
Total					

Table 4.5.9 Analysis of variance of crude shrub density

Source	SS (Type 3)	df	MS	F	P
Between blocks					
Stream (block)	17.739	5	3.548	2.109	0.11
Reach	12.778	2	6.389	3.798	**0.042**
Unit	9.69	1	9.687	6.329	**0.019**
Reach x Unit	9.36	2	4.678	3.88	**0.032**
Reach x Stream	7.194	10	0.719	0.428	0.914
Unit x Stream	3.83	5	0.766	0.5	0.772
Residual error + Stream x Reach x Unit		10		-	**-**
Total					

Table 4.5.10 Analysis of variance of total flying and emergent aquatic abundance and biomass. Sums of squares are type 3. Bolded P-values indicate significance.

		Emergent aquatic abundance				Emergent aquatic biomass			
Source	*df*	*SS*	*MS*	*F*	*P*	*SS*	*MS*	*F*	*P*
Between blocks									
Stream (block)	5	13.95	2.79	2.78	**0.032**	0.035	0.007	0.52	**<0.001**
Reach	2	18.09	9.05	9.02	**<0.001**	0.91	0.453	33.59	**<0.001**
Unit	1	112.66	112.66	112.36	**<0.001**	2.17	2.17	161.14	**<0.001**
Reach x Unit	2	0.24	0.12	0.12	0.89	0.52	0.26	19.1	**<0.001**
Reach x Stream	10	23.22	2.32	2.32	**0.032**	0.61	0.061	4.55	**<0.001**
Unit x Stream	5	6.69	1.34	1.33	0.27	0.07	0.014	1.006	0.428
Residual error + Stream x Reach x Unit	10			-	-			-	-
Between times									
Month	1	0.05	0.05	0.038	0.85	0.006	0.01	0.24	**<0.001**
Month x Stream	5	7.38	1.48	0.996	0.43	7.38	1.48	0.99	0.43
Month x Reach	2	1.63	0.82	0.6	0.55	0.015	0.01	0.28	0.76
Month x Unit	1	0.03	0.03	0.02	0.88	0.015	0.01	0.55	0.46
Month x Reach x Unit	2	3.52	1.76	1.29	0.28	0.032	0.02	0.61	0.55
Month x Stream x Reach	10	11.81	1.181	0.299	0.98	0.185	0.019	0.195	0.996
Month x Stream x Unit	5	6.39	1.28	0.86	0.51	0.05	0.01	0.176	0.97
Residual error + Month x Stream x Reach x Unit	10	5.29	0.53	-	-	0.12	0.012	-	-
Total	71								

Table 4.5.11 Analysis of variance of flying terrestrial and nematoceran abundance and biomass. Sums of squares are type 3. Bolded P-values indicate significance.

		Terrestrial invertebrate abundance				Terrestrial invertebrate biomass				Nematoceran abundance				Nematoceran biomass			
Source	df	SS	MS	F	P	SS	MS	F	P	SS	MS	F	P	SS	MS	F	P
Between blocks																	
Stream (block)	5	26.47	5.29	4.94	**0.002**	3.97	0.79	3.11	**0.02**	36.64	7.33	2.19	0.077	0.02	0.004	0.54	0.75
Reach	2	32.88	16.44	15.34	**<0.001**	11.35	5.68	22.21	**<0.001**	2.7	1.35	0.4	0.67	0.02	0.01	1.56	0.22
Unit	1	2.18	2.178	2.034	0.16	0.19	0.19	0.72	0.4	10.52	10.52	3.14	0.085	0.01	0.01	2.03	0.16
Reach x Unit	2	1.64	0.82	0.77	0.47	0.85	0.42	1.66	0.21	6.68	3.34	0.997	0.38	0.007	0.003	0.48	0.62
Reach x Stream	10	11.88	1.19	1.12	0.38	3.96	0.4	1.55	0.16	59.36	5.94	1.77	0.1	0.06	0.006	0.82	0.61
Unit x Stream	5	1.52	0.3	0.28	0.92	0.56	0.11	0.44	0.82	27.3	5.46	1.63	0.18	0.06	0.01	1.66	0.17
Residual error + Stream x Reach x Unit	10	6.14	0.614	-	-	3.03	0.3	-	-	44.5	4.45	-	-	0.08	0.008	-	-
Between times																	
Month	1	1.63	1.64	1.21	0.28	0.03	0.03	0.09	0.76	13.38	13.38	3.016	0.088	0.02	0.02	2.13	0.15
Month x Stream	5	6.6	1.32	1.318	0.56	2.1	0.42	1.51	0.22	23.64	4.73	1.18	0.33	0.09	0.02	2.99	**0.02**
Month x Reach	2	0.66	0.33	0.246	0.78	0.07	0.04	0.1	0.9	0.77	0.39	0.09	0.92	0.005	0.003	0.37	0.69
Month x Unit	1	0.55	0.55	0.41	0.53	0.003	0.003	0.008	0.93	0.07	0.07	0.02	0.9	0.001	0.001	0.09	0.77
Month x Reach x Unit	2	0.6	0.3	0.22	0.8	0.003	0.003	0.004	0.996	8.07	4.04	0.91	0.41	0.02	0.01	1.23	0.3
Month x Stream x Reach	10	5.1	0.51	0.51	0.87	1.63	0.16	1.51	0.21	23.63	3.36	0.88	0.56	0.05	0.005	0.77	0.66
Month x Stream x Unit	5	4.43	0.89	0.55	0.74	0.859	0.17	0.32	0.89	3.76	0.75	0.19	0.97	0.03	0.005	0.87	0.51
Residual error + Month x Stream x Reach x Unit	10	18.98	1.898	-	-	4.51	0.45	-	-	37.29	3.73	-	-	0.049	0.004	-	-
Total	71																

Table 4.5.12 Total number and percentage of calls identified of each species of insectivorous bat. Calls were identified using ANASCHEME (Bat call analysis system; Adams et al. 2010) using keys developed for relevant survey regions (Lumsden and Bennett, 2005). Br = Broken, De = Delatite, Hol = Hollands, Hu = Hughes, How = Howqua and Ry = Ryans

Species	Guild[a]	Total number of calls identified	Percentage of total identified calls	Streams detected at
Mormopterus ridei	AC	1072	4.85	Br, De, Hol, How, Hu, Ry
Mormopterus planiceps	AC	2073	9.37	Hol, Hu, Ry
Nyctophilus-Myotis complex[b]	CS	1011	4.57	Hol, Hu, Ry
Rhinolophus megaphyllus	CS	12	0.05	Br, De, Hol, How, Hu, Ry
Chalinolobus morio	ESH	3542	16.02	Br, De, Hol, How, Hu, Ry
Miniopterus schreibersii oceanensis	ESH	585	2.65	Br, De, How
Vespadelus regulus	ESH	412	1.86	Br, De, Hol, How, Hu, Ry
Vespadelus vulturnus	ESH	2592	11.72	Br, De, Hol, How, Hu, Ry
Chalinolobus gouldii	ESL	1170	5.29	Br, De, Hol, How, Hu, Ry
Scotorepens balstoni	ESL	40	0.18	Hol, Hu, Ry
Scotorepens orion	ESM	8	0.04	Br, De, How
Falsistrellus tasmaniensis	ESM	44	0.2	Br, De, How
Vespadelus darlingtoni	ESM	9257	41.86	Br, De, Hol, How, Hu, Ry
Austronomus australis	OS	264	1.19	Br, De, Hol, How, Hu, Ry
Saccolaimus flaviventris	OS	32	0.14	Br, De, Hol, How, Hu, Ry
	Total	22114		

[a] Adapted from Blakey et al. 2016, Bullen and McKenzie 2011 and Threlfall, Law, Penman, & Banks, 2011

[b] The *Nyctophilus-Myotis* complex comprises three species - *Nyctophilus geoffroyi*, *Nyctophilus gouldi* and *Myotis macropus*.

Table 4.5.13 Analysis of variance of total bat activity and species richness. Sums of squares are type 3. Bolded P-values indicate significance.

		Total bat activity				Total bat species richness			
Source	df	SS	MS	F	P	SS	MS	F	P
Between blocks									
Stream (block)	5	8.72	1.74	4.42	**0.003**	10.54	2.11	1.75	0.15
Reach	2	7.24	3.62	9.17	**<0.001**	4.37	2.19	1.81	0.18
Unit	1	3.017	3.017	7.64	**0.009**	12.22	12.22	10.12	**0.003**
Reach x Unit	2	4.35	0.435	1.1	0.39	2.28	1.14	0.94	0.4
Reach x Stream	10	0.77	0.15	0.39	0.85	25.31	2.53	2.1	0.051
Unit x Stream	5	0.59	0.29	0.75	0.48	11.21	2.24	1.86	0.13
Residual error + Stream x Reach x Unit	10	1.42	0.142	-	-	5.92	0.59	-	-
Between times									
Month	1	5.43	5.43	14.81	**<0.001**	0.45	0.45	0.29	0.59
Month x Stream	5	2.28	0.46	1.89	0.12	8.99	1.8	1.29	0.28
Month x Reach	2	1.09	0.55	1.49	0.23	2.19	1.09	0.72	0.49
Month x Unit	1	0.02	0.02	0.04	0.84	1.68	1.68	1.1	0.3
Month x Reach x Unit	2	0.93	0.47	1.27	0.29	0.53	0.26	0.17	0.84
Month x Stream x Reach	10	2.53	0.25	1.05	0.42	20.24	2.024	1.68	0.12
Month x Stream x Unit	5	0.56	0.11	0.27	0.92	3.38	0.68	0.49	0.79
Residual error + Month x Stream x Reach x Unit	10	1.38	0.14	-	-	6.05	0.61	-	-
Total	71								

Table 4.5.14 Analysis of deviance of Invertebrate community composition and taxa abundance response to treatment effects. Bolded P-values indicate significance. LRT = likelihood ratio test statistic.

		Invertebrate community composition (taxa)		Coleoptera (Scarabaeidae)		Ephemeroptera		Lepidoptera		Trichoptera		Diptera (Tipulidae)	
Source	*df*	*LRT*	*P*	*LRT*	*P*	*LRT*	*P*	*LRT*	*P*	*LRT*	*P*	*LRT*	*P*
Between blocks													
Stream (block)	5	254.1	**0.001**	10.392	0.794	8.404	0.946	13.475	0.433	3.313	0.971	11.089	0.733
Reach	2	164.2	**0.001**	16.022	**0.007**	7.526	0.259	7.203	0.271	4.709	0.676	12.178	**0.034**
Unit	1	74.6	**0.001**	0.768	**0.998**	12.443	**0.011**	0.042	**0.999**	16.776	**0.002**	1.991	0.98
Reach x Unit	2	53.4	0.243	0.347	0.973	1.762	0.972	0.566	0.973	0.933	0.973	1.007	0.973
Reach x Stream	10	308.7	**0.011**	20.084	0.386	14.186	0.784	9.563	0.784	6.925	0.902	21.57	0.326
Unit x Stream	5	132.7	0.081	10.142	0.855	8.135	0.944	3.006	0.971	6.332	0.952	8.428	0.944
Residual error + Stream x Reach x Unit	10	-	-	-	-	-	**-**	-	-	-	-	-	-
Between times													
Month	1	63.9	**0.004**	0.989	0.999	0.655	0.999	4.277	0.663	0.606	0.999	1.421	0.995
Month x Stream	5	0.001	**0.001**	21.541	**0.998**	3.502	**0.998**	3.926	**0.999**	2.144	**0.998**	7.935	0.942
Month x Reach	2	590	**0.005**	4.653	0.795	4.311	0.82	0.477	0.968	0.204	0.968	1.76	0.963
Month x Unit	1	157.2	0.101	0.367	**0.998**	0.132	**0.999**	0.06	**0.998**	0.012	**0.999**	0.023	**0.999**
Month x Reach x Unit	2	19.8	0.474	0.001	**0.998**	0.004	0.99	0.672	0.942	1.717	0.915		
Month x Stream x Reach	10	85	0.212	10.837	0.859	0.001	0.999	7.554	0.93	2.881	0.987	0.001	0.999
Month x Stream x Unit	5	20.9	0.745	0.598	0.99	0.001	0.999	0.765	0.99	3.355	0.988	0.001	0.999
Residual error + Month x Stream x Reach x Unit	10	-	-	-	-	-	-	-	-	-	-	-	-
Total	71												

Table 4.5.15 Analysis of deviance of Invertebrate community composition and taxa abundance response to treatment effects. Bolded P-values indicate significance. LRT = likelihood ratio test statistic.

		Blattodea (Ectobiidae)		Hymenoptera (Ichneumonidae)		Coleoptera (Elateridae)		Coleoptera (Silphidae)	
Source	*df*	*LRT*	*P*	*LRT*	*P*	*LRT*	*P*	*LRT*	*P*
Between blocks									
Stream (block)	5	11.465	0.697	7.603	0.946	5.882	0.964	7.23	0.946
Reach	2	14.325	**0.015**	14.576	**0.015**	17.634	**0.003**	20.837	**0.001**
Unit	1	0.445	0.999	0.379	0.999	0.003	0.999	1.563	0.992
Reach x Unit	2	3.329	0.96	0.366	0.973	0.984	0.973	1.862	0.972
Reach x Stream	10	13.483	0.784	7.556	0.902	22.897	0.25	17.816	0.574
Unit x Stream	5	7.762	0.944	8.455	0.944	5.001	0.969	10.753	0.816
Residual error + Stream x Reach x Unit	10	-	-	-	-	-	-	-	-
Between times									
Month	1	0.315	0.999	0.841	0.999	0.023	0.999	0.638	0.999
Month x Stream	5	5.643	0.996	0.771	0.998	12.855	0.507	8.228	0.999
Month x Reach	2	0.67	0.968	4.022	0.834	2.314	0.933	1.422	0.963
Month x Unit	1	3.888	0.796	0.031	0.998	2.693	0.89	0.533	0.999
Month x Reach x Unit	2	0.001	0.999	3.756	0.731	7.191	0.602	0.001	0.999
Month x Stream x Reach	10	0.001	0.999	10.258	0.859	15.21	0.655	0.001	0.999
Month x Stream x Unit	5	0.001	0.999	0.001	0.999	0.001	0.999	0.001	0.999
Residual error + Month x Stream x Reach x Unit	10	-	-	-	-	-	-	-	-
Total	71								

Table 4.5.16 Analysis of deviance of insectivorous bat community composition and taxa activity response to treatment effects. Bolded P-values indicate significance. LRT = likelihood ratio test statistic.

		Insectivorous bat community composition (taxa)		*V. darlingtoni* activity		*C. gouldii* activity		*Nyctophilus-Myotis* complex activity		*V. regulus* activity		*Mi. s. oceanensis* activity	
Source	*df*	*LRT*	*P*	*LRT*	*P*	*LRT*	*P*	*LRT*	*P*	*LRT*	*P*	*LRT*	*P*
Between blocks													
Stream (block)	5	711.1	**0.001**	31.968	**0.001**	5.433	0.449	8.022	0.449	21.996	**0.006**	237.701	**0.001**
Reach	2	249.1	**0.001**	22.177	**0.001**	22.717	**0.001**	34.396	**0.001**	1.421	0.717	4.812	0.197
Unit	1	79	**0.001**	3.206	0.418	11.403	**0.013**	19.372	**0.001**	3.438	0.405	11.537	**0.013**
Reach x Unit	2	26.1	0.273	1.07	0.992	4.187	0.714	5.762	0.529	2.466	0.934	0.293	0.999
Reach x Stream	10	209.7	**0.001**	40.924	**0.001**	27.7	**0.011**	40.773	**0.001**	5.507	0.96	5.02	0.96
Unit x Stream	5	63.1	0.145	4.242	0.932	14.974	0.13	15.284	0.126	5.66	0.906	2.628	0.979
Residual error + Stream x Reach x Unit	10	-	-	-	-	-	**-**	-	-	-	-	-	-
Between times													
Month	1	237.4	**0.001**	15.457	**0.003**	5.953	0.119	5.747	0.123	2.087	0.495	0.016	0.951
Month x Stream	5	339.7	**0.011**	28.003	**0.016**	21.603	**0.018**	9.557	0.343	28.564	**0.016**	5.366	0.721
Month x Reach	2	114.5	**0.004**	12.623	**0.032**	23.272	**0.008**	23.525	**0.008**	3.48	0.384	26.353	0.008
Month x Unit	1	34.6	0.125	4.252	0.573	0.35	0.988	0.018	0.988	0.223	0.988	21.769	0.124
Month x Reach x Unit	2	42.4	0.365	31.584	0.168	0.655	0.948	3.088	0.823	1.082	0.948	9.515	0.51
Month x Stream x Reach	10	224.2	**0.04**	27.988	0.142	28.011	0.142	47.132	0.099	47.972	0.099	25.027	0.142
Month x Stream x Unit	5	168.8	0.125	9.476	0.51	8.823	0.656	38.348	0.284	15.272	0.402	7.593	0.656
Residual error + Month x Stream x Reach x Unit	10	-	-	-	-	-	-	-	-	-	-	-	-
Total	71												

Table 4.5.17 Analysis of deviance of insectivorous bat community composition and taxa activity response to treatment effects. Bolded P-values indicate significance. LRT = likelihood ratio test statistic.

		R. megaphyllus activity		*C. morio* activity		*F. tasmaniensis* activity		*A. australis* activity		*Sa. flaviventris* activity		*Mo. ridei* activity	
Source	*df*	*LRT*	*P*	*LRT*	*P*	*LRT*	*P*	*LRT*	*P*	*LRT*	*P*	*LRT*	*P*
Between blocks													
Stream (block)	5	13.59	0.122	13.486	0.122	40.094	**0.001**	24.27	**0.005**	8.5	0.449	93.613	**0.001**
Reach	2	17.989	**0.002**	3.517	0.318	23.268	**0.001**	46.573	**0.001**	45.282	**0.001**	11.966	**0.015**
Unit	1	12.72	**0.008**	1.766	0.613	0.312	0.97	0.031	0.989	0.001	0.993	2.866	0.433
Reach x Unit	2	0.035	0.999	5.676	0.529	0.136	0.999	4.757	0.65	0.001	0.999	0.078	0.999
Reach x Stream	10	0.031	0.96	9.107	0.787	4.263	0.96	11.211	0.656	0.001	0.96	47.383	**0.001**
Unit x Stream	5	0.001	0.979	2.139	0.979	0.069	0.979	2.778	0.979	6.632	0.895	4.737	0.932
Residual error + Stream x Reach x Unit	10	-	-	-	-	-	-	-	-	-	-	-	-
Between times													
Month	1	14.789	**0.005**	11.345	**0.013**	18.215	**0.001**	65.69	**0.001**	0.516	0.879	0.073	0.951
Month x Stream	5	0.659	0.769	194.591	**0.011**	3.517	0.769	5.625	0.721	4.058	0.769	34.68	**0.016**
Month x Reach	2	0.001	0.946	0.34	0.899	0.422	0.899	1.61	0.557	0.001	0.899	4.788	0.32
Month x Unit	1	1.757	0.851	2.061	0.838	0.489	0.988	0.001	0.988	0.506	0.988	3.121	0.715
Month x Reach x Unit	2	1.689	0.895	16.984	0.404	0.001	0.999	0.001	0.998	0.001	0.993	0.001	0.999
Month x Stream x Reach	10	0.361	0.688	47.623	0.099	0.001	0.948	0.044	0.782	0.001	0.96	0.001	0.999
Month x Stream x Unit	5	0.001	0.969	21.178	0.353	0.001	0.999	0.001	0.999	8.83	0.656	68.249	0.189
Residual error + Month x Stream x Reach x Unit	10	-	-	-	-	-	-	-	-	-	-	-	-
Total	71												

Table 4.5.18 Analysis of deviance of insectivorous bat community composition and taxa activity response to treatment effects. Bolded P-values indicate significance. LRT = likelihood ratio test statistic.

		M. planiceps		*Sc. balstoni*		*Sc. orion*		*V. vulturnus*	
Source	*df*	*LRT*	*P*	*LRT*	*P*	*LRT*	*P*	*LRT*	*P*
Between blocks									
Stream (block)	5	167.304	**0.001**	35.803	**0.001**	9.364	0.368	60.87	**0.001**
Reach	2	5.878	0.1	0.083	0.958	8.97	**0.027**	14.565	**0.006**
Unit	1	5.619	0.161	0.17	0.97	6.517	0.113	2.602	0.447
Reach x Unit	2	1.2	0.992	0.392	0.999	0.013	0.999	2.53	0.946
Reach x Stream	10	14.761	0.331	3.051	0.96	0.014	0.96	10.973	0.706
Unit x Stream	5	1.413	0.979	2.523	0.979	0.016	0.985	16.85	0.08
Residual error + Stream x Reach x Unit	10	-	-	-	-	-	-	-	-
Between times									
Month	1	85.752	**0.001**	3.699	0.284	8.057	**0.05**	11.59	**0.008**
Month x Stream	5	0.001	0.996	3.471	0.769	0.015	0.996	74.74	**0.01**
Month x Reach	2	5.37	0.32	12.734	0.032	0.014	0.899	6.65	0.212
Month x Unit	1	0.004	0.988	0.001	0.988	0.022	0.988	2.86	0.74
Month x Reach x Unit	2	0.001	0.999	0.001	0.97	0.026	0.999	0.001	0.999
Month x Stream x Reach	10	0.001	0.999	0.001	0.999	0.013	0.782	39.32	0.093
Month x Stream x Unit	5	0.531	0.905	0.001	0.972	0.001	0.999	17.33	0.378
Residual error + Month x Stream x Reach x Unit	10	-	-	-	-	-	-	-	-
Total	71								

Table 4.5.19 Analysis of deviance of insectivorous bat guild composition and guild activity response to treatment effects. Bolded P-values indicate significance. LRT = likelihood ratio test statistic.

		Insectivorous bat community composition (guild)		OS		ESH		ESL		ESM		AC		CS	
Source	*df*	*LRT*	*P*	*LRT*	*P*	*LRT*	*P*	*LRT*	*P*	*LRT*	*P*	*LRT*	*P*	*LRT*	*P*
Between blocks															
Stream (block)	5	238.1	**0.001**	24.211	**0.002**	7.519	0.481	4.972	0.481	33.417	**0.001**	160.493	**0.001**	7.501	0.481
Reach	2	164.2	**0.001**	60.55	**0.001**	10.336	**0.008**	23.333	**0.001**	24.887	**0.001**	9.688	**0.008**	35.448	**0.001**
Unit	1	46	**0.001**	0.007	0.95	3.923	0.126	11.587	**0.005**	3.889	0.126	6.472	**0.047**	20.136	**0.001**
Reach x Unit	2	23.2	**0.041**	3.434	0.458	8.696	0.102	4.4	0.42	0.147	0.959	0.423	0.959	6.077	0.255
Reach x Stream	10	204.2	**0.001**	12.445	0.248	18.572	0.1	29.608	**0.003**	22.254	**0.044**	80.422	**0.001**	40.917	**0.001**
Unit x Stream	5	51.1	**0.024**	6.13	0.774	4.863	0.793	17.387	0.064	2.474	0.793	4.436	0.793	15.79	0.078
Residual error + Stream x Reach x Unit	10	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Between times															
Month	1	86.1	**0.001**	48.811	**0.001**	0.428	0.531	5.806	**0.046**	14.122	**0.001**	11.717	**0.004**	5.194	**0.046**
Month x Stream	5	325	**0.001**	6.081	0.385	173.282	**0.001**	20.856	**0.011**	28.554	**0.003**	86.43	**0.001**	9.763	0.228
Month x Reach	2	68.3	**0.001**	4.117	0.252	1.933	0.408	23.977	**0.001**	8.06	0.058	5.485	0.181	24.762	**0.001**
Month x Unit	1	14.2	0.091	1.131	0.709	5.594	0.183	0.051	0.972	5.002	0.213	2.426	0.496	0.001	0.976
Month x Reach x Unit	2	12	0.543	0.018	0.974	5.918	0.538	0.249	0.925	2.71	0.768	0.001	0.974	3.134	0.768
Month x Stream x Reach	10	158.6	**0.006**	0.006	0.15	50.182	**0.011**	32.757	**0.022**	27.216	**0.027**	4.43	0.06	43.972	**0.015**
Month x Stream x Unit	5	83	0.059	0.001	0.866	8.669	0.627	6.637	0.716	6.214	0.716	20.101	0.087	41.412	0.061
Residual error + Month x Stream x Reach x Unit	10	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Total	71														

Table 4.5.20 Explanatory models for invertebrate abundance and biomass using a forward step-wise regression process. ΔAIC represents the difference between the model's AIC (Akaike's Information Criterion); w_i is the Akaike weight (i.e. the weight of the model/relative support for the mode); R^2 is the statistical measure that represents the proportion of the variance explained by the most parsimonious model. Equations are provided for the "best" model as per the stepwise regression (indicated by an asterisk*) and the two top models that ranked the highest for each response. All models were significant.

Response	Model structure	ΔAIC_c	w_i	R^2
Emergent aquatic invertebrate abundance	Crude graminoid density + elevation + mean leaf area index	0	0.21	0.45
	Crude graminoid density + mature tree stem density*	0.28	0.19	
	Crude graminoid density + elevation + mature tree stem density	0.79	0.14	
Emergent aquatic invertebrate biomass	Crude graminoid density + mean leaf area index + crude shrub density + elevation*	0	0.77	0.51
	Crude graminoid density + mean leaf area index + crude shrub density	2.41	0.23	
	Crude graminoid density + mean leaf area index + crude shrub density + elevation + mature tree stem density	2.42	0.14	
Flying terrestrial invertebrate abundance	Mean leaf area index + elevation + crude graminoid density	0	0.59	0.36
	Crude shrub density + elevation + crude graminoid density	1.32	0.3	
	Mean leaf area index	3.78	0.09	
Flying terrestrial invertebrate biomass	Mature tree stem density + elevation*	0	0.37	0.28
	Mature tree stem density + elevation + crude shrub density	0.12	0.35	
	Mature tree stem density	0.62	0.27	

Table 4.5.21 Relative variable importance (RVI) on invertebrate abundance and biomass; calculated from Akaike weights. Variables with RVI ≥ 0.73 (indicated in bold) are considered significant explanatory variables.

RVI	Emergent aquatic invertebrate abundance	Emergent aquatic invertebrate biomass	Flying terrestrial invertebrate abundance	Flying terrestrial invertebrate biomass
Mean LAI	0.67	**0.92**	**0.96**	<0.01
Crude graminoid density	**0.99**	**0.98**	**0.98**	<0.01
Crude shrub density	0.18	**0.83**	0.39	<0.01
Mature tree stem density	0.56	0.23	0.09	**0.98**
Elevation	0.62	**0.76**	**0.98**	**0.73**

Table 4.5.22 Explanatory models for total, *V. darlingtoni*, *V. vulturnus* and Nyctophilus- Myotis complex activity, and species richness using a forward step-wise regression process. ΔAIC represents the difference between the model's AIC (Akaike's Information Criterion); w_i is the Akaike weight (i.e. the weight of the model/relative support for the mode); R^2 is the statistical measure that represents the proportion of the variance explained by the most parsimonious model. Equations are provided for the "best" model as per the stepwise regression (indicated by an asterisk*) and the two top models that ranked the highest for each response. All models were significant.

Response	Model structure	ΔAIC_c	w_i	R^2
Total bat activity	Flying terrestrial invertebrate abundance + emergent aquatic invertebrate biomass + mature tree stem density + crude graminoid density*	0	0.30	0.36
	Flying terrestrial invertebrate abundance + crude graminoid density + elevation + mature tree stem density	1.20	0.16	
	Flying terrestrial invertebrate abundance + emergent aquatic invertebrate biomass + elevation +mature tree stem density	1.47	0.14	
Bat species richness	Crude graminoid density + mature tree stem density + crude shrub density*	0	0.23	0.25
	Crude graminoid density + mature tree stem density + elevation + flying terrestrial invertebrate biomass	0.37	0.19	
	Crude graminoid density + crude shrub density + elevation + flying terrestrial invertebrate biomass	0.56	0.17	
V. darlingtoni activity	Crude graminoid density + elevation + mean leaf area index + mature tree stem density	0	0.23	0.4
	Mean leaf area index + crude graminoid density + elevation + mature tree stem density + flying terrestrial invertebrate abundance*	0.23	0.2	
	Crude shrub density + elevation +mature tree stem density + emergent aquatic invertebrate biomass	1.57	0.1	
V. vulturnus activity	Elevation + mature tree stem density	0	0.25	0.21
	Elevation + mature tree stem density + flying terrestrial invertebrate abundance	0.46	0.2	
	Elevation + mature tree stem density + flying terrestrial invertebrate biomass	0.53	0.19	
Nyctophilus-Myotis complex activity	Mature tree stem density + crude graminoid density + emergent aquatic invertebrate biomass	0	0.29	0.35
	Mature tree stem density + crude graminoid density + mean leaf area index + emergent aquatic invertebrate biomass*	0.22	0.26	
	Mature tree stem density + crude graminoid density + elevation+ emergent aquatic invertebrate biomass	1.42	0.14	

Table 4.5.23 Relative variable importance (RVI) on bat activity and species richness; calculated from Akaike weights. Variables with RVI ≥ 0.73 (indicated in bold) are considered significant explanatory variables.

RVI	Total bat activity	Bat species richness	*V. darlingtoni* activity	*V. vulturnus* activity	*Nyctophilus-Myotis* complex activity
Mean LAI	<0.01	<0.01	**0.61**	0.14	0.46
Crude graminoid density	**0.88**	**0.99**	**0.79**	0.11	**0.98**
Crude shrub density	0.16	**0.73**	0.2	0.1	<0.01
Mature tree stem density	**0.99**	**0.98**	**0.99**	**0.98**	**0.99**
Emergent aquatic invertebrate abundance	0.12	<0.01	<0.01	<0.01	<0.01
Emergent aquatic invertebrate biomass	**0.74**	0.14	0.3	<0.01	**0.83**
Flying terrestrial invertebrate abundance	**0.98**	0.5	0.49	0.2	<0.01
Flying terrestrial invertebrate biomass	0.13	<0.01	<0.01	0.19	0.21
Elevation	**0.98**	0.64	**0.99**	**0.99**	0.25

Table 4.5.24 Explanatory models for bat activity using a forward step-wise regression process. ΔAIC represents the difference between the model's AIC (Akaike's Information Criterion); w_i is the Akaike weight (i.e. the weight of the model/relative support for the mode); R^2 is the statistical measure that represents the proportion of the variance explained by the most parsimonious model. Equations are provided for the "best" model as per the stepwise regression (indicated by an asterisk*) and the two top models that ranked the highest for each response. All models were significant.

Response	Model structure	ΔAIC_c	w_i	R^2
C. gouldii activity	Mature tree stem density + crude graminoid density + elevation + crude shrub density*	0	0.42	0.18
	Mature tree stem density + crude graminoid density + emergent aquatic invertebrate abundance	1.09	0.24	
	Mature tree stem density + emergent aquatic invertebrate abundance	1.83	0.17	
C. morio activity	Flying terrestrial invertebrate abundance*	0	0.12	0.04
	Flying terrestrial invertebrate biomass	0.15	0.11	
	Crude shrub density + flying terrestrial invertebrate abundance	0.31	0.11	
Mo. planiceps activity	Crude shrub density + elevation + emergent aquatic invertebrate biomass + flying terrestrial invertebrate abundance	0	0.27	0.33
	Crude shrub density + elevation + flying terrestrial invertebrate abundance	1.21	0.15	
	Mature tree stem density + elevation + emergent aquatic invertebrate biomass + flying terrestrial invertebrate abundance	1.28	0.14	
Mo. ridei activity	Elevation + mature tree stem density*	0	0.37	0.34
	Elevation + mature tree stem density + flying terrestrial invertebrate abundance	0.43	0.3	
	Elevation + mature tree stem density + flying terrestrial invertebrate biomass	1.49	0.18	
Mi. schreibersii oceanensis activity	Elevation + crude shrub density	0	0.15	0.37
	Elevation + crude shrub density + crude graminoid density + emergent aquatic invertebrate abundance	0.21	0.14	
	Elevation + crude shrub density + emergent aquatic invertebrate abundance+ emergent aquatic invertebrate biomass	0.65	0.11	
V. regulus activity	Elevation + emergent aquatic invertebrate abundance	0	16	0.17
	Elevation + emergent aquatic invertebrate abundance + mature tree stem density	0.38	0.13	
	Elevation + emergent aquatic invertebrate abundance + crude shrub density	0.5	0.12	

Table 4.5.25 Relative variable importance (RVI) on bat activity calculated from Akaike weights. Variables with RVI ≥ 0.73 (indicated in bold) are considered significant explanatory variables.

RVI	*C. gouldii* activity	*C. morio* activity	*Mo. planiceps* activity	*Mo. ridei* activity	*Mi. schreibersii oceanensis* activity	*V. regulus* activity
Mean LAI	<0.01	<0.01	<0.01	<0.01	0.06	0.3
Crude graminoid density	0.42	0.11	0.11	0.15	0.49	<0.01
Crude shrub density	**0.83**	0.24	0.27	<0.01	**0.97**	0.4
Mature tree stem density	0.98	0.22	**0.75**	**0.99**	<0.01	0.28
Emergent aquatic invertebrate abundance	**0.73**	<0.01	0.14	<0.01	0.19	**0.98**
Emergent aquatic invertebrate biomass	<0.01	0.18	**0.74**	<0.01	**0.73**	0.06
Flying terrestrial invertebrate abundance	<0.01	0.52	**0.88**	0.3	0.12	0.28
Flying terrestrial invertebrate biomass	<0.01	0.38	0.11	0.18	0.19	<0.01
Elevation	0.66	<0.01	**0.99**	**0.98**	**0.99**	**0.99**

4.6 FIGURES

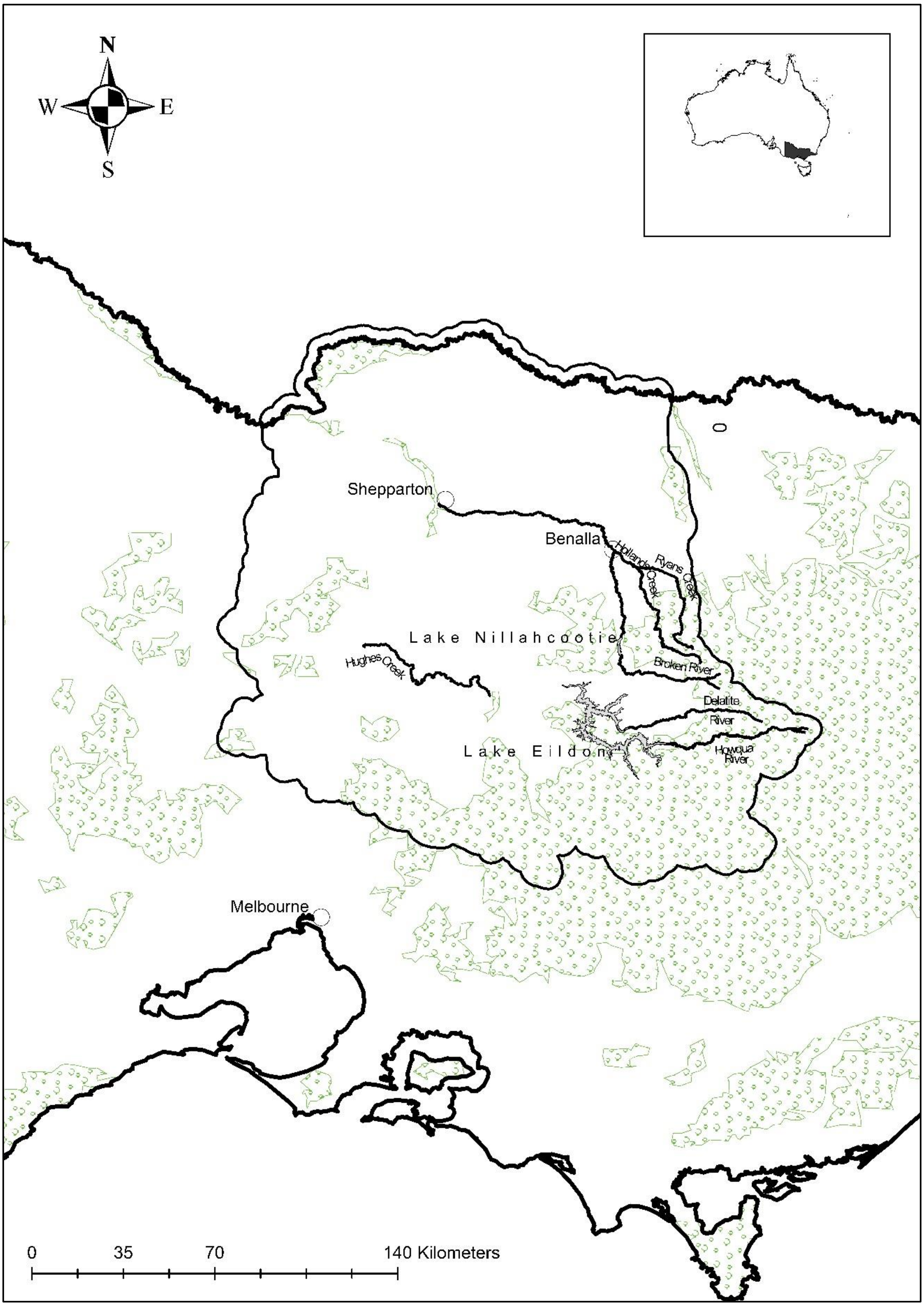

Figure 4.6.1 Study area within the Goulburn-Broken Catchment in regional Victoria, Australia. Green areas represent forest cover boundaries and were derived from VicMap Lite (Department of Land Water and Planning, 2013).

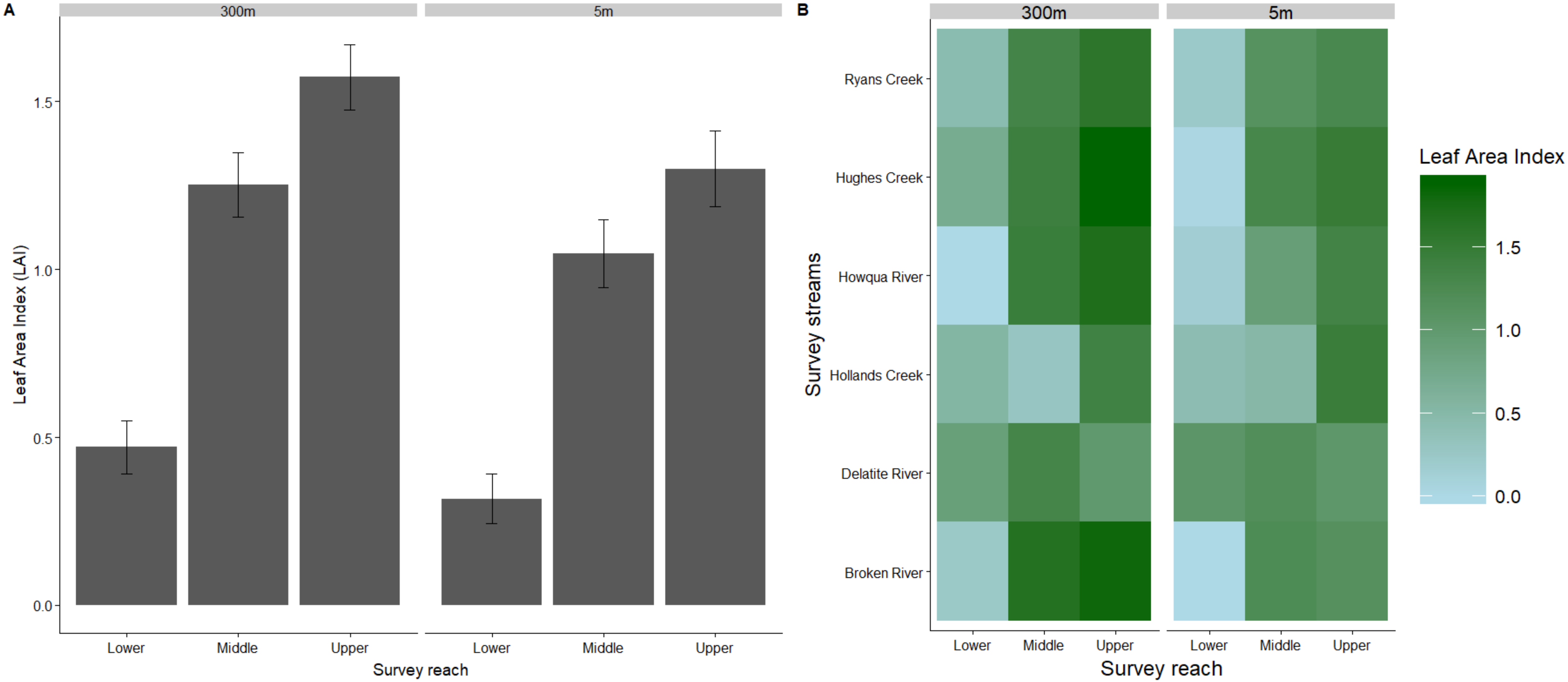

Figure 4.6.2 Mean leaf area index A) between units and B) between sites. Values are presented with standard error bars.

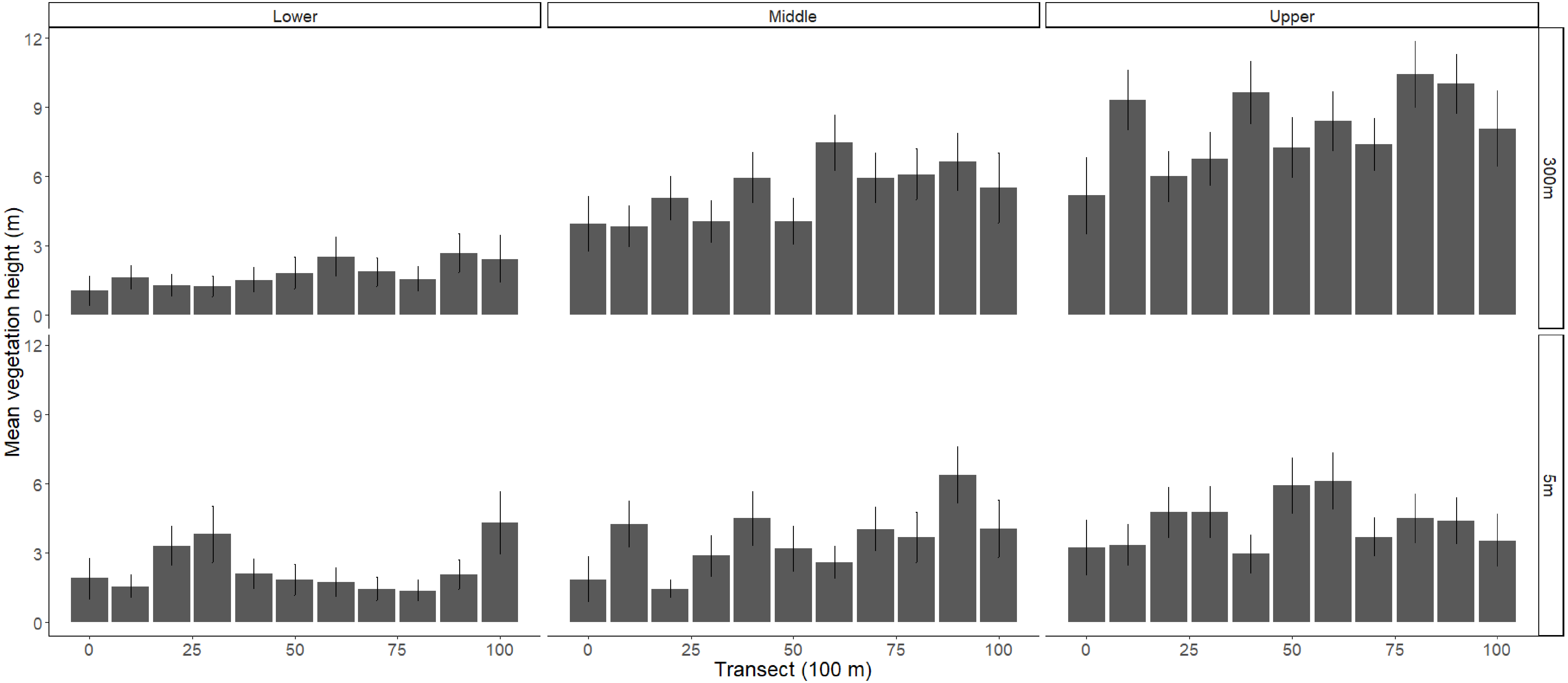

Figure 4.6.3 Mean height of riparian vegetation (m) along 100 m transects at 10 m intervals for survey reaches. Heights are presented with respect to survey reach (upper, middle and lower) and transects (300 m and 5 m). Values are presented with standard error bars.

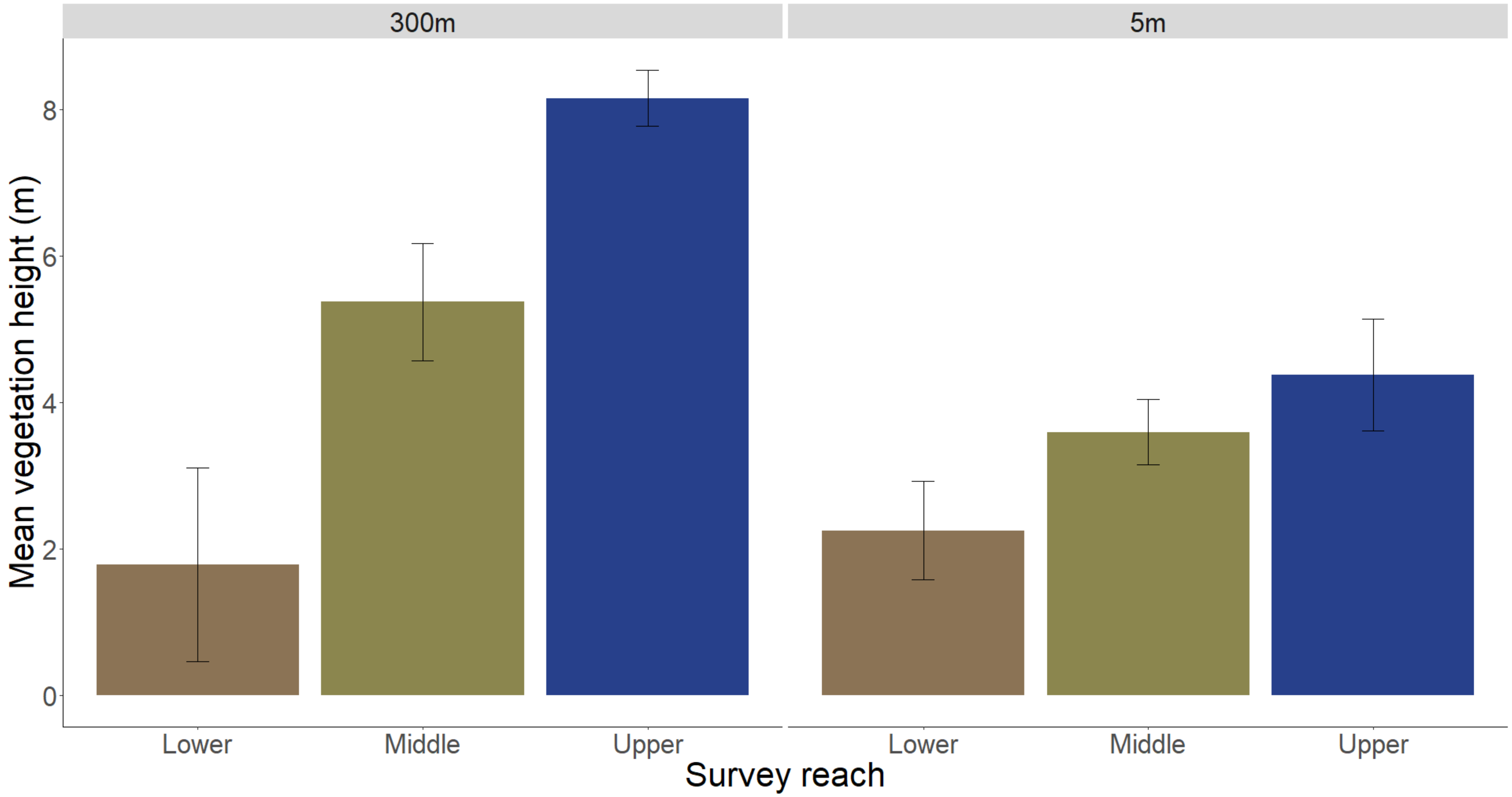

Figure 4.6.4 Mean height of riparian vegetation (m) between units (300 m and 5m). Values are presented with standard error bars.

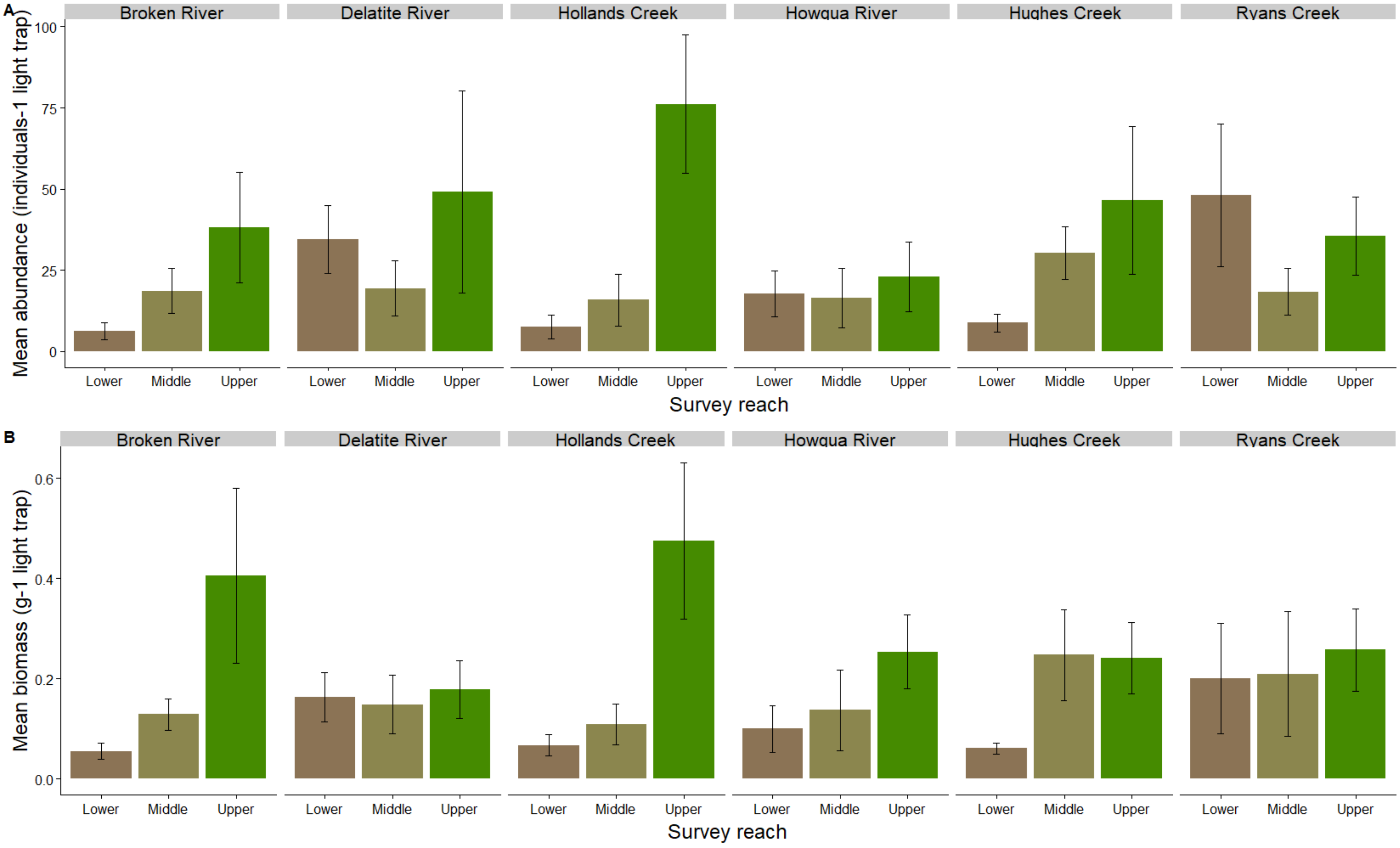

Figure 4.6.5 Mean (A) abundances and (B) biomasses of emergent aquatic invertebrates across streams and survey reaches. Values are presented with standard error bars.

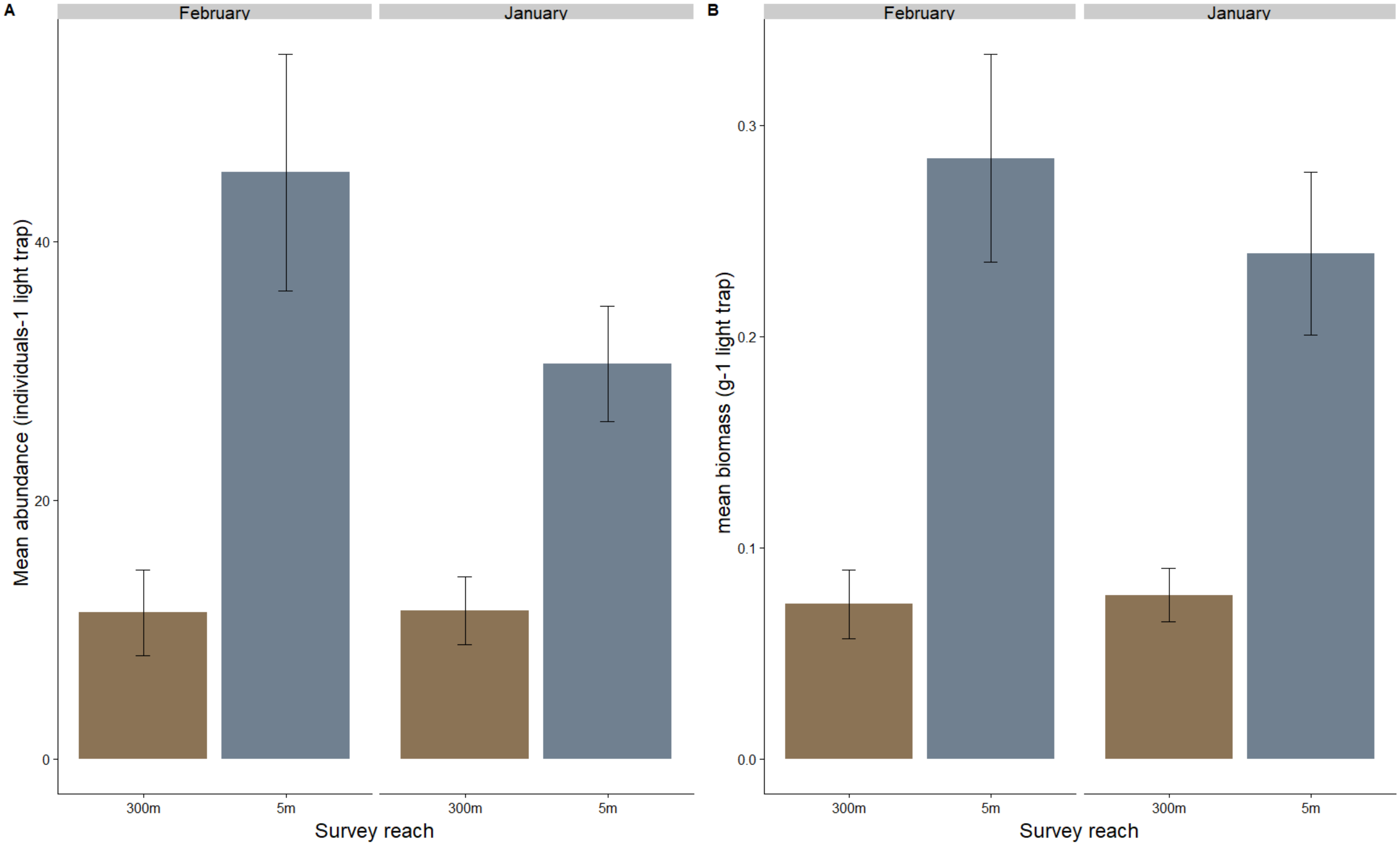

Figure 4.6.6 Mean (A) abundances and (B) biomasses of emergent aquatic invertebrates across survey months and unit (300 m and 5m). Values are presented with standard error bars.

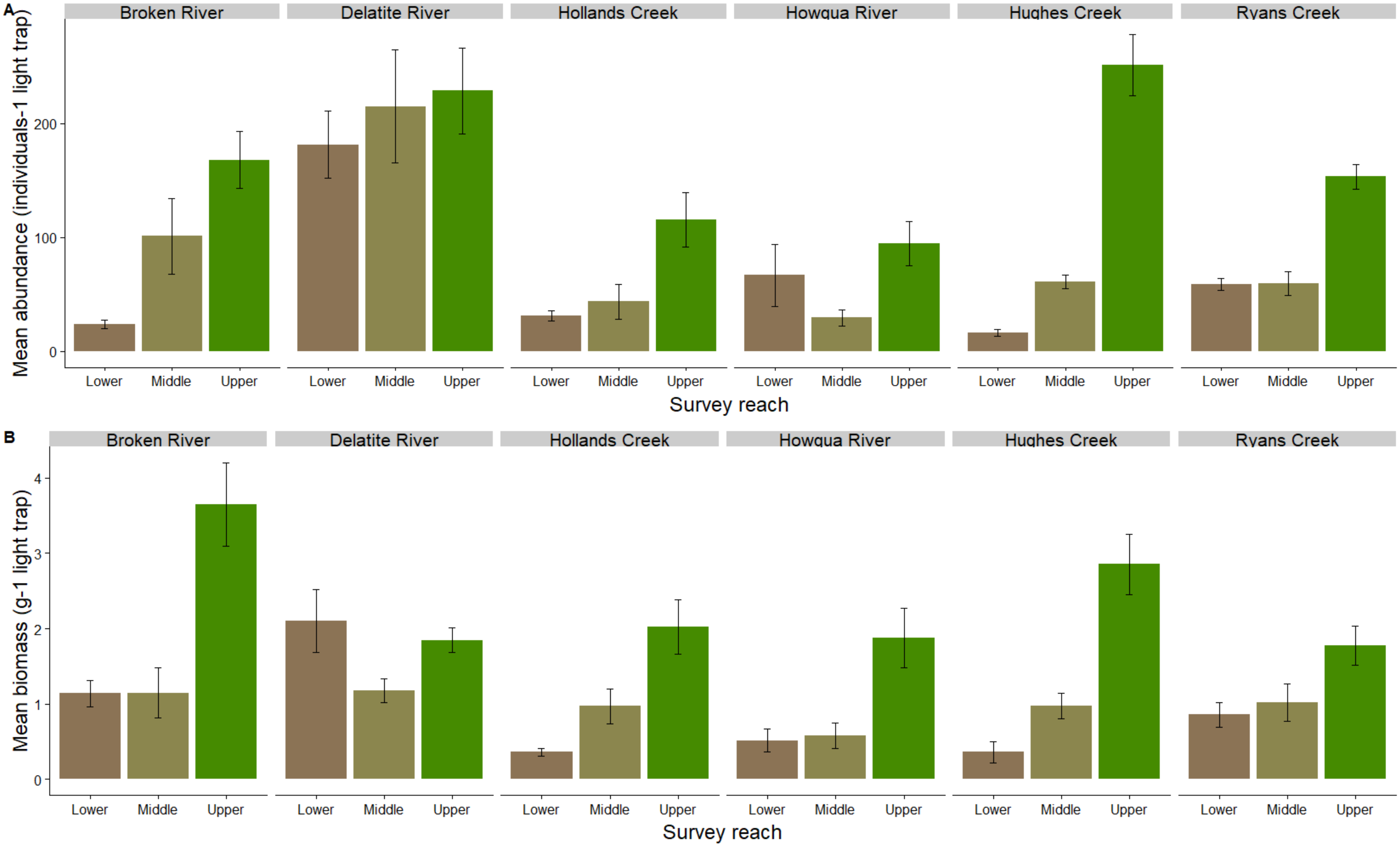

Figure 4.6.7 Mean (A) abundances and (B) biomasses of flying terrestrial invertebrates across streams and survey reaches. Values are presented with standard error bars.

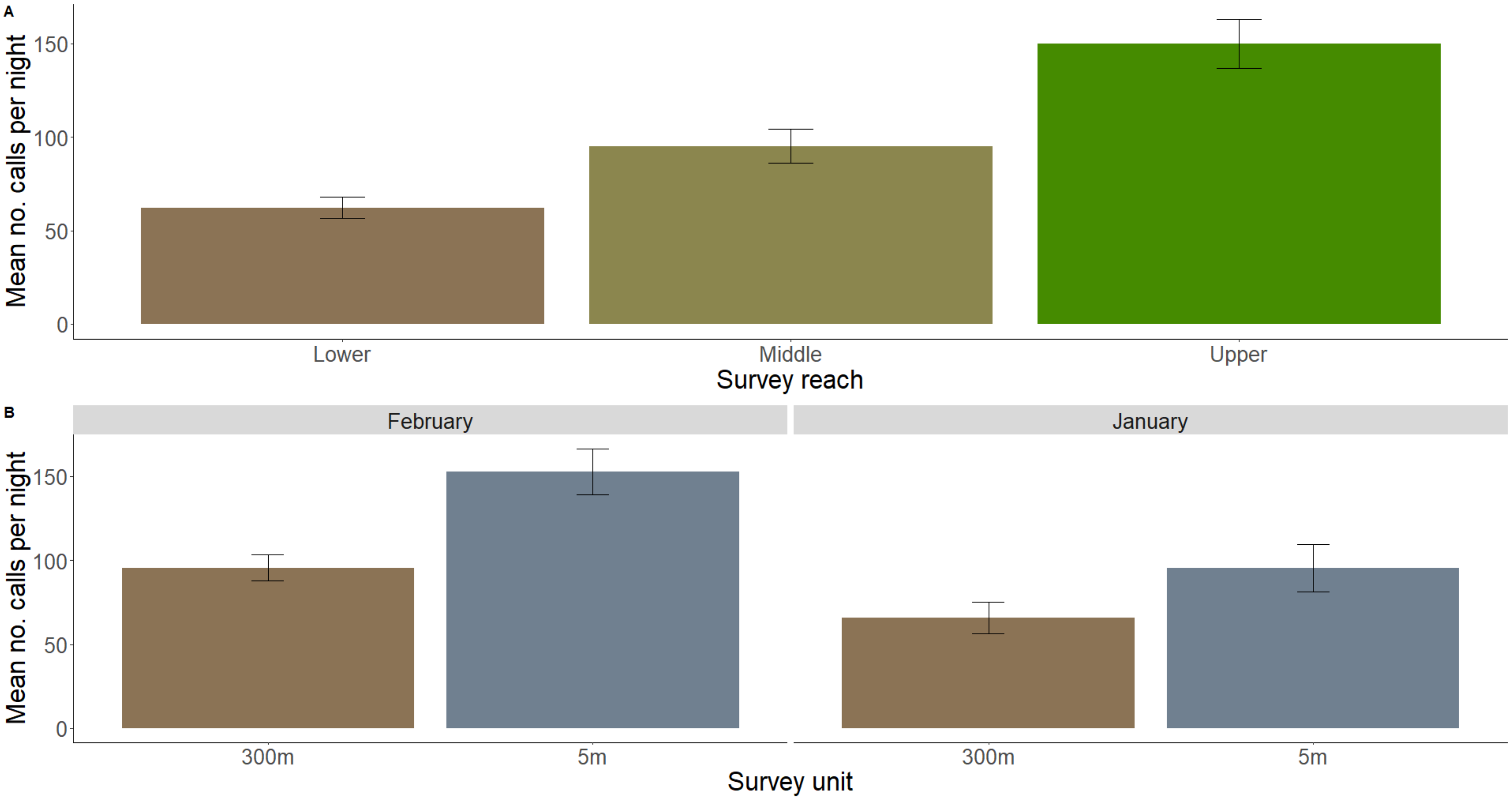

Figure 4.6.8 Mean number of calls per night A) across streams and survey reaches and B) across survey months and unit (300 m and 5m). Values are presented with standard error bars.

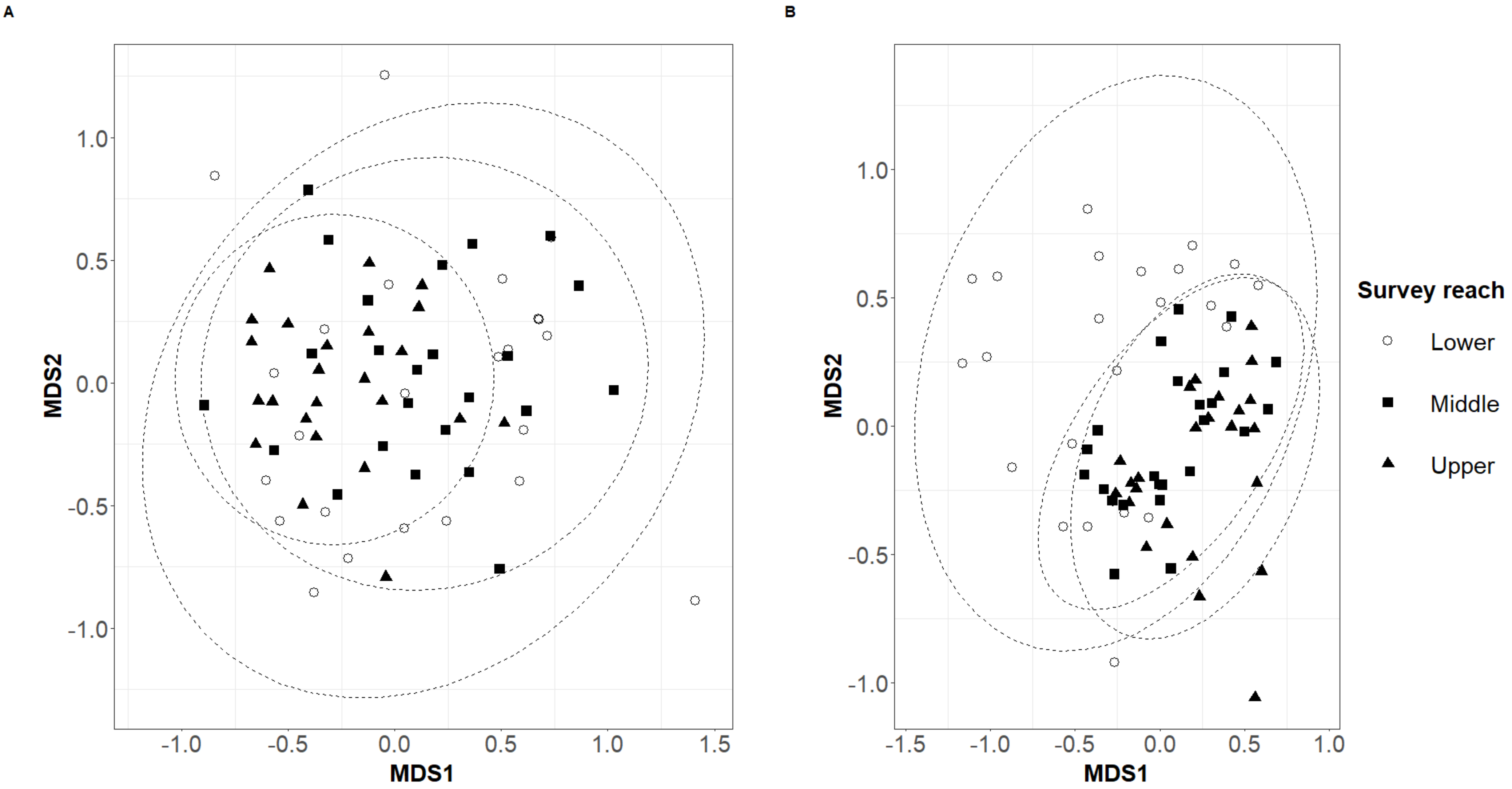

Figure 4.6.9 nMDS plot of A) nocturnal flying invertebrate (Stress=0.2) and B) insectivorous bat community composition (stress = 0.16) with respect to survey reach shown with 95% confidence ellipsoids for each level of survey reach (lower: open circle, middle: closed squares, upper: closed triangles)

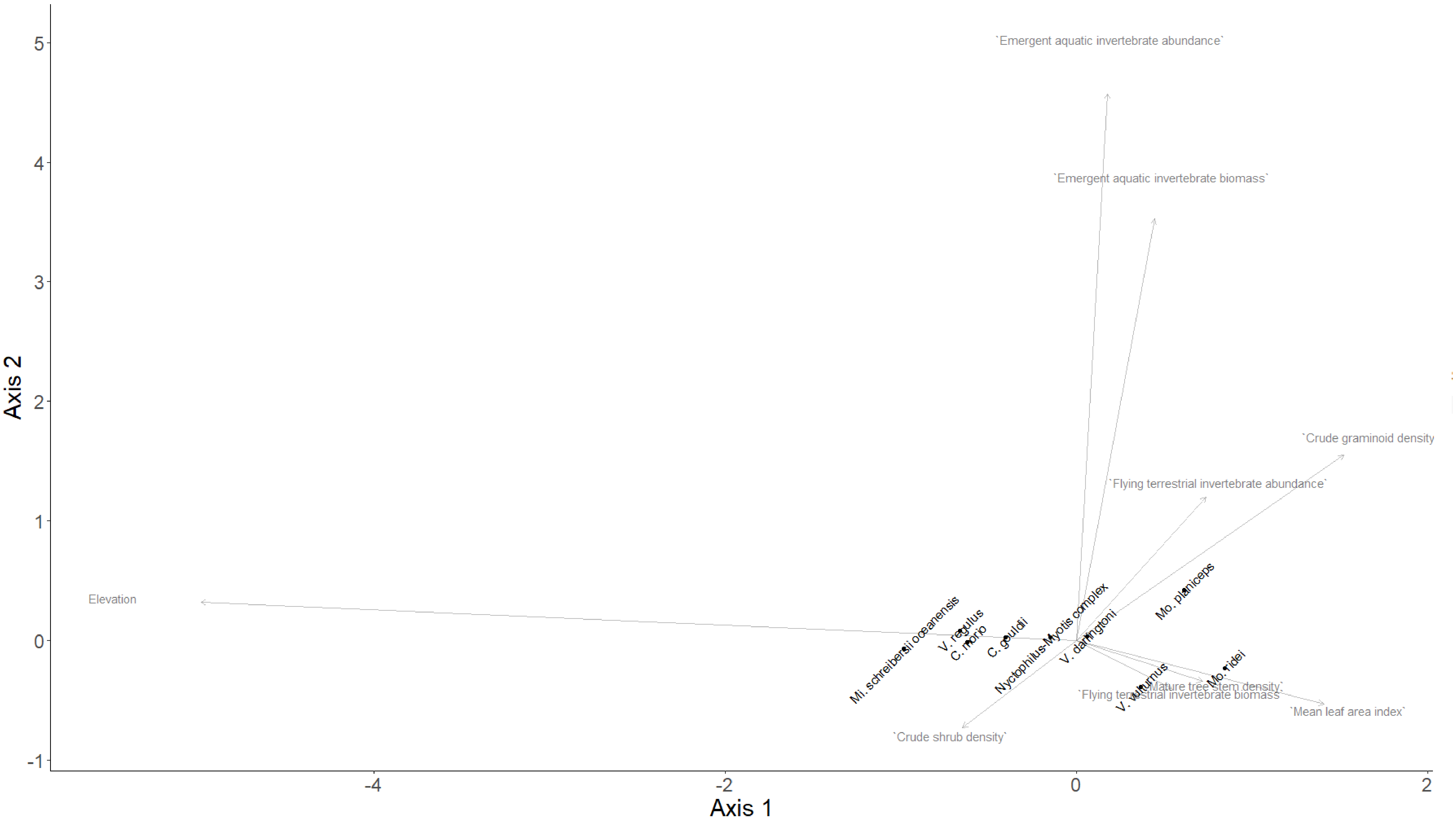

Figure 4.6.10 A Canonical Correspondence Analysis (CCA) ordination for the insectivorous bat activity. Bat taxa are represented by bolded black text and environmental variables are represented by vectors. A bat's positioned closer to or further along an environmental variable vector indicates a stronger relationship with that variable.

CHAPTER 5. CONTINUOUS MONITORING OF INSECTIVOROUS BATS AT A PERENNIAL STREAM REACH IN TEMPERATE AUSTRALIA: A CASE STUDY

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ABSTRACT

Continuous monitoring is crucial for understanding the ecology of insectivorous bats. In order to advance the field, more consideration is needed of temporal aspects to bat foraging. In particular, the dependence of insectivorous bats on freshwater systems across a dry continent, such as Australia needs to be examined over longer periods. In this study, we assessed fluctuating insectivorous bat activity over 148 days as a response to temporal variation in environmental variables. We examined the distribution of bat activity within nights of differing lunar phase and heat accumulated by the perennial stream. By-in-large those lunar phases associated with greater moon illumination (i.e. full and gibbous moons) had higher bat activity. This information supports the need for monitoring programs to incorporate greater temporal scales and contextualise their sampling periods more explicitly.

KEY WORDS: Continuous monitoring, Insectivorous bats, Perennial streams, In-stream temperature, Moon illumination, Australia

5.1 INTRODUCTION

Continuous monitoring is crucial for understanding the ecology of insectivorous bats during times of natural and anthropogenic disturbance (Law, 2018). Continuous monitoring is especially important for exploring the nonlinear, complex and compounding interactions that are prevalent in many ecosystems (Estes et al., 2011; Roberts et al., 2007). Despite this, baseline data for many regions is lacking or absent (Law, 2018; Lintott et al., 2018). Further, continuous monitoring is typically limited to < one month with few datasets available that span a greater temporal range (Bender and Hartman, 2015; Erickson and West, 2002). Temporal variation in bat activity is driven by both seasonal and stochastic events that influence weather, prey availability, and habitat structure (Meyer et al., 2004; Milne et al., 2005). Responses to this variation can be intensely localised (Fischer et al., 2009) with distinct relationships between species and regions (Skalak et al., 2012). In order to advance our understanding of disturbance ecology, more consideration is needed of temporal aspects to bat foraging (Salvarina, 2016). In particular, the dependence of insectivorous bats on freshwater systems across a dry continent, such as Australia (Blakey et al., 2018) needs to be examined over longer periods. This is because site occupancy is seasonal (Gonsalves and Law, 2018) and likely increases in response to various physiological requirements (Law et al., 2015). For example, Law et al. (2015) showed that juvenile bats are weaned and recruited into the general population during mid-summer. This likely results in increase foraging activity during summer (Law et al., 2015) in systems of high productivity including perennial streams (Fukui et al., 2006; Seidman and Zabel, 2001).

Perennial streams and their associated riparian zones provide an important foraging habitat for insectivorous bats (Akasaka et al., 2010; Hagen and Sabo, 2011). Many studies reveal that bat activity, distribution and community composition are related to resources in these habitats (Blakey et al., 2017a; Hagen and Sabo, 2012). Not only do perennial streams provide important prey resources, including emergent aquatic invertebrates, but they are also essential sites for drinking (Grindal et al., 1999). This is particularly important in biomes where permanently flowing water is scarce (Monamy et al., 2013). Despite this, few studies have connected in-stream conditions to bat activity (Salvarina, 2016). In-stream temperature for instance, significantly influences the fecundity of key invertebrate species (Hinton, 1981) as well as the length of their development (Arendt, 2010) and timing of their emergence (Harper and Peckarsky, 2006; McCulloch and Waters, 2018). While many studies have investigated the nutritional links between riparian vegetation, insect prey and insectivorous bats (Clare et al., 2014; Ober and Hayes, 2008c; Weier et al., 2018), few have examined the similar relationship between bat activity and in-stream temperature. Temporal variation in in-stream temperature and its effect on the quantity and quality of aquatically-derived subsidies such as emergent aquatic invertebrates may help explain overall bat activity.

Ambient air temperature (Scanlon and Petit, 2008) and lunar phase (Appel et al., 2017; Law, 1997) are among the most common environmental variables related to insectivorous bat activity. While changes in ambient air temperature is an important determinant of bat activity (Kaupas and Barclay, 2017; Milne et al., 2005), few trends that are consistent across biomes have been observed regarding lunar phase (Saldaña-Vázquez and Munguía-Rosas, 2013; Thomas and Jacobs, 2013). Further, these responses are often species-specific and depend on how light interacts with the landscape (Doty et al., 2019; Gonsalves et al., 2013). Doty *et al.* (2019) documented a surge in activity at sites with dense canopies during a full moon by the aerial-hawking species, *Vespadelus vulturnus*. This shift in foraging behaviour potentially offsets predation risks to bats and reduces the overall influence of moonlight (Doty et al., 2019; Roeleke et al., 2018). In contrast, bats may be negatively associated with moonlight because their insect prey are less active (Lang et al., 2006; Prugh and Golden, 2014). For example, both *Lophostoma silvicolum* and their katydid prey were less active during full moons than new moons (Lang et al. 2006). These results suggest that lunar-phobic behaviour in bats may stem from improved predator detection by prey due to moon illumination (Lang et al., 2006).

With that said, few studies have found a strong relationship between emergent aquatic invertebrates and lunar phase (Corbet, 1958; Ivković et al., 2013). Corbet (1958), for example, found that the mayfly, *Povilla adusta*, emerged consistently after a full moon while the remaining species studied exhibited no strong cyclical fluctuation with respect to lunar phase. Similarly, Ivkovic et al. (2013) found that in-stream temperature superseded moon phase in terms of triggering aquatic invertebrate emergence. Nevertheless, moon illumination is likely to have some influences over the distribution (and dispersal) of emergent aquatic invertebrates given its use in navigation and orientation (Horváth et al., 2009; Perkin et al., 2011).

Hypotheses

In this study, we assessed fluctuating insectivorous bat activity as a response to temporal variation in environmental variables. We examined overall and species-specific activity from spring to autumn at a perennial stream in temperate Australia. We predicted that there will be a strong positive relationship between insectivorous bat activity and nightly ambient air temperature (H_1; Table 5.5.1), where higher foraging activity is expected during warmer nights. Further, we predicted bat activity within nights will be distributed differently within categories of lunar phase and amount of heat accumulated by the perennial stream (H_1; Table 5.5.1). Finally, we predict that local environmental variables including temperature and wind will be more influential on insectivorous bat activity than moon illumination (H_2; Table 5.5.1).

5.2 MATERIALS AND METHODS

5.2.1 Study area

This survey was conducted in Hughes Creek Flora Reserve (WDPA ID 311668; 1.39 km^2), ~120 km north of Melbourne CBD (37°00'15.4"S 145°17'26.2"E; Taungurung Country). The reserve is located within the drainage area of Hughes Creek, a 2nd order tributary of the Goulburn River. A granite batholith, formed in the late Devonian, shapes the landscape (Phillips and Clemens, 2013) with an unconfined gorge straddling Hughes Creek within this reserve. *Eucalyptus viminalis* and *E. ovata* are the dominant canopy species across the reserve with *Acacia*, *Lepidosperma* and *Lomandra* spp. comprising the sparse understory (Department of Environment Land Water and Planning, 2004a). During the study, from March 1st - 9th, 2019, a bushfire occurred on the rocky outcrop to the north of the reserve (~3 km away). While the fire did not enter the reserve, a significant amount of smoke was present in the area.

5.2.2 Continuous monitoring of insectivorous bats

A single Anabat Swift FS Detector (AAAB011, Titley Scientific, Brendale, Qld, Australia) with an attached Anabat US-O Omnidirectional Ultrasonic Microphone (AAAB012, Titley Scientific, Brendale, Qld, Australia) was used to record bat foraging calls. The detector was deployed at the edge of Hughes Creek, and its final location was randomly selected. To do the latter, the extent of the stream within the reserve was mapped with a polyline using ArcMap (v10.5.1; ESRI 2011). The unique identifiers of this polyline were then extracted and assigned a random number. The smallest of these assigned numbers determined the location of the detector (36°59'44.7"S 145°17'28.2"E). In the reserve, the detector was attached to the largest tree, closest to this location at a height of ~170 cm and directed towards the stream (<2 m; Law et al., 2015). The detector was deployed for 148 days from November 14th, 2018 to May 18th, 2019, and the internal clock was adjusted for the end of day-light saving (April 7th, 2019). Bat calls were recorded from dawn to dusk as WAV files, and although two 128 GB SD cards were installed in the detector, the significant memory requirements of this file type resulted in SD cards running out of space four times over the survey period. The detector was serviced, and the data extracted once a month over the survey period.

WAV files were then converted into zero-crossing files, and analysed using AnaScheme (Adams et al., 2010) and the 'Northern Plains' identification key (Lumsden and Bennett, 2005). Calls were identified to species (where possible) and only assessed if they comprised ≥5 buzzes. The threshold for call quality was ≥90%, where each buzz had at least 6 data points. As *Myotis macropus, Nyctophilus gouldii* and *Nyctophilus geoffroyi* calls cannot be reliably separated using AnaScheme, these were aggregated into a 'Myotis-Nyctophilus' species complex. Further, AnaScheme often misattributes ambient noise as *Austronomus australis*, so these calls were manually checked. Calls that could not be assigned to a single species (not including non-identifications) were labelled as 'unknown' and were included in counts of total bat activity.

5.2.3 Environmental sampling

In-stream (Hobo Temp-Light Pendant, UA-002-08, OneTemp Pty Ltd) and ambient air temperatures (Thermochron TC, DS1921G, OnSolution) were recorded every hour using data loggers for 224 and 188 days, respectively. The in-stream logger was affixed to a metal picket and hammered into the streambed of the closest pool to the detector. This data was shared with chapters two and four. We used these values to calculate the accumulated degree-days by summing the mean daily temperature over the survey period. Degree-days (DD) is an expression of the amount of heat emergent aquatic invertebrates must accumulate in order to complete their life-cycle (Bovill et al., 2019). We then determined the number of degree-days 'blocks' available during the survey period to accumulate a thermal constant of ~1000 DD. This was necessary to convert temperature into a categorical variable. Using a probability terciles, we categorised these blocks into periods of 'high' (<44 days to accumulate a thermal constant of ~1000 DD), 'moderate' (44-50 days to accumulate a thermal constant of ~1000 DD) and 'low' (>50 days to accumulate a thermal constant of ~1000 DD) heat accumulation.

The ambient air temperature logger was attached to a wooden stake and hammered into the ground, in the shade adjacent to the detector, at a height of ~1 m. Additional environmental variables, including wind speed was sourced from the Australian Bureau of Meteorology (Mangalore Airstrip, Station ID 088109; http://www.bom.gov.au/climate/data/), while lunar phase (categorical; where full moon = 100%, gibbous = 75%, first quarter = 50%, crescent = 25% and new moon = 0% illuminated) and moon illumination (continuous) were sourced from the United States Naval Observatory (corrected for Australia; https://aa.usno.navy.mil/data/docs/MoonFraction.php). Rain occurred infrequently over the survey period and was not included in our analyses. All environmental data were recorded at the same time as bat sampling.

5.2.4 Statistical approach

Our approach for data analysis had three broad components: 1) simple linear regressions to assess the relationships between local environmental conditions and insectivorous bat activity, 2) a two-sample Kolmorogov-Smirnov test to assess changes in the distribution of bat activity across nights (i.e. from sunset to sunrise and whether activity is skewed closer to sunset or sunrise) based on broad categories: lunar phase and stream heat-accumulation and 3) a forward stepwise regression was used to identify the single "best" explanatory model for bat activity using local environmental factors. Statistical analyses were undertaken in R (i386, v3.5.2; R Core Team 2013).

5.2.5.1 Simple regressions between local environmental conditions and bat activity

Initially, we used simple linear regressions to examine the relationship between continuous environmental variables, and between bat activity and these variables. As much as possible, only those measurements during times where bats were likely to be active were included. For instance, ambient air and in-stream temperature, and wind speed were averaged from ~1 hour before sunset to ~1 hour after sunrise. Bat foraging activity was pooled across the night and the total number of calls were $\log_{10}$-transformed to meet assumptions of normality. Bat activity as a response to hourly changes in environmental conditions was not considered.

5.2.5.2 Two-sample Kolmorogov-Smirnov test of nightly distributions of bat activity

Then, using a two-sample Kolmorogov-Smirnov test (KS test; Daniel 1978; Sokal and Rohlf 1995), we compared the distribution of calls within nights (i.e. from sunset to sunrise and whether activity is skewed closer to sunset or sunrise) during different lunar phases (crescent, full, gibbous, new and quarter) and heat accumulation periods (high, moderate and low). KS tests are sensitive to the location, dispersion and skewness of distribution curves (Sokal and Rohlf, 1995) and thus, were appropriate to measure differences in the nightly distributions of insectivorous bat activity, which are not normally distributed. This test uses the statistic D_{crit}, which indicates the maximum absolute difference between the relative cumulative frequency distributions of each pair-wise comparison among lunar phases and heat accumulation periods, respectively (Sokal and Rohlf, 1995). If the null hypothesis is true and calls are distributed identically within nights of different lunar phases or heat accumulation periods, then D_{crit} should be zero (or close to) and P-values should be insignificant.

5.2.5.3 Environmental variable assessment and forward stepwise regression

Finally, we examined the relative importance of continuous environmental variables to bat foraging activity using a forward stepwise regression (with AIC adjusted for small sample size as the selection criterion; Burnham and Anderson 2003). Those variables included were moon illumination, Julian date and windspeed. As in-stream temperature and ambient nightly air temperature were correlated ($r^2 < 0.50$), they were included as an interaction term (hereafter referred to as "environmental temperature").

Stepwise regression allowed us to construct a model comprising those variables that explained the most variation in bat activity and species richness (Hammerson et al., 2017; Neter et al., 1996). This process can be useful in qualitatively identifying a subset of variables but has been criticized for underestimating P-values (Wilkinson and Dallal, 1981) and struggling with multicollinearity (De Veaux and Ungar, 1994). To limit the effects of multicollinearity, however, we considered the variance inflation factor (VIF) of each environmental variable in a full model (i.e. one containing all environmental variables; Fox and Monette, 1992). As a result, we interpreted the results cautiously (Hammerson et al., 2017). VIFs quantify the severity of multicollinearity and provides an index that measures how much the variance of an estimated regression coefficient is increased due to collinearity (Akinwande et al., 2015; Lindsey and Sheather, 2010). As a general rule, VIFs >5 represent high levels of multicollinearity among environmental variables, where regression coefficients are poorly estimated and resulting p-values are problematic (Lindsey and Sheather, 2010). Environmental variables with a VIF>5 were identified and systematically removed from the analysis. An intercept only model was run as our base model (Neter et al., 1996). The package 'car' was used to complete this analysis (Fox et al., 2019).

To scrutinise the model derived from the stepwise regression process (referred to hereafter as the "best" model), we generated a set of unique models comprising all available combinations of environmental variables before taking a subset of these models that represented <2AIC (Grueber et al., 2011). This subset of models and the best model were then ranked based on their AIC to identify the most parsimonious model. The package 'AICcmodavg' was used to complete this portion of the analysis (Mazerolle, 2019). A model averaging approach was then used to identify the relative importance of each variable (Grueber et al., 2011), using the 'MuMin' package (Barton, 2019). The relative importance of a variable is commonly estimated by summing the weights of models where the variable appears (Galipaud et al., 2014). Variables were deemed relatively important if they had a relative variable importance ≥ 0.73; equivalent to an ΔAIC of 2, a common 'rule-of-thumb' to indicate a significant effect (Richards, 2005).

5.3 RESULTS

5.3.1 Environmental conditions

Average nightly ambient air temperature ranged 6.5 °C to 29.95 °C with an average air temperature over the survey period was 17.1 ± 4.71 °C. In-stream temperatures averaged 18.53 ± 3.82 °C and a close, positive association between this and nightly ambient air temperature was detected ($F_{1,145} = 340.4$, $r^2 = 0.69$, $P < 0.001$). This relationship can be described by the following equation:

Mean in-stream temperature = 6.986 + 0.679(mean nightly ambient air temperature)

With regards to stream heat accumulation, the longest degree-day block (the number of days taken to accumulate 1000 degree-days) within our survey period was 65 days (mean daily in-stream temperature: 10.31 °C; March 16th – May 20th, 2019) and the shortest was 41 days (mean daily in-stream temperature: 27.35 °C; December 16th – January 26th). Overall, 50, 42 and 51 degree-day blocks comprised high, moderate and low heat accumulation periods, respectively.

5.3.2 General bat activity

In total, 74 222 bat passes were recorded over 148 nights (the nightly average was 501.5 ± 480.7). Of these, ~81% (60 478) were positively identified to species or species-complex and ~18% were attributed to an 'unknown' category (Table 5.5.2). Overall, 11 taxa were positively identified (Table 5.5.2). *Vespadelus darlingtoni* was the most active over the survey period with over 27,000 calls recorded. There was only one night where *V. darlingtoni* was not recorded (Table 5.5.2). *Vespadelus regulus* was the least active species with only 39 calls across 49 nights of the survey period. The greatest activity was recorded on January 20th, 2019 with 2, 916 passes recorded during a waxing gibbous moon (Fig. 5.6.1). On this night, ambient air temperatures averaged 27.72 °C. Overall, nightly ambient air temperature explained the most variation in bat activity of any single variable ($F_{1,145}=131.7$, $r^2 = 0.47$, $P<0.001$, Table 5.5.3; Fig. 5.6.2) and this relationship can be described by the following equation:

log(Bat activity) = 1.171 + 0.077(nightly ambient air temperature).

Moon illumination exhibited no associated with bat activity explaining <0.01% in variation ($F_{1,145} = 1.617$, $P<0.21$; Table 5.5.3) and this relationship can be described by the following equation:

log(Bat activity) = 2.39 - 0.16(moon illumination).

A summary of all linear regression models can be found in Table 5.5.3.

5.3.3 Nightly distribution of bat activity

There was a large spike in activity within two and half hours from sunset and additional (smaller) spikes after seven hours from sunset regardless of lunar phase or heat accumulation period (Fig. 5.6.3 & 5.5.6). As indicated by a relatively large D_{crit} and significant P-value, the distribution of insectivorous bat activity during nights with gibbous moons differed significantly from that of crescent, new and quarter moons (Table 5.5.4, Fig. 5.6.4). Similarly, the distribution during full moon nights significantly differed from that of crescent, new and quarter moons (Table 5.5.4, Fig. 5.6.4). No other pairwise combination significantly differed (Table 5.5.4). By-in-large those lunar phases associated with greater moon illumination (i.e. full and gibbous moons) had higher bat activity.

In contrast to lunar phase, the distribution of total activity during periods of high, moderate and low heat accumulation were all significantly different (Table 5.5.4; Fig. 5.6.7). Peaks in activity were prolonged during moderate periods than high periods and prolonged still during low periods (Fig. 5.6.6). Similarly, additional spikes in activity over the night occurred later during moderate and low periods (Fig. 5.6.6).

5.3.4 Relative importance of environmental variables

In the first instance, no variable had a VIF > 5, which would indicate server multicollinearity, and hence were not removed prior to analysis. Of those variables that contributed to our explanatory model of total bat activity: Julian date was negatively associated while environmental temperature was positively associated (Table 5.5.5). These variables were identified as relatively important based on our model averaging method (Table 5.5.6). Similarly, environmental temperature was an important variable (with positive associations) of bat species richness and explained ~19% variation along with moon illumination (Table 5.5.5 & 5.5.6). Overall, environmental temperature contributed to the explanatory models of the nine out of ten most active bat taxa (Tables 5.5.5 & 5.5.7). Moon illumination, however, only appeared in three out of ten explanatory models (Tables 5.5.5 & 5.5.7). Our explanatory model for *V. vulturnus* activity (which comprised Julian date, windspeed and environmental temperature) explained ~55% of variation (Table 5.5.7). See Tables 5.5.5, 5.5.6, 5.5.7 & 5.5.8 for a full outline of explanatory models and the relative importance of these variables.

5.4 DISCUSSION

In this study, we continuously monitored bat activity over ~5 months, from spring to autumn, at a perennial stream in temperate Australia. Simultaneously, we collected environmental variables and related these to bat activity and species richness. We made the following predictions and discuss them below: There should be a positive relationship between insectivorous bat activity and nightly ambient air temperature (H_1; Table 5.5.1). Further, bat activity within nights should be distributed differently depending on the lunar phase and amount of heat accumulated by the perennial stream (H_1; Table 5.5.1). Finally, local environmental variables including temperature and wind should be more influential on insectivorous bat activity than moon illumination (H_2; Table 5.5.1).

5.4.1 Limitations

Some limitations need to be considered with the results and discussion presented here. First, while keys are available that allow for species identification, activity data are pooled across sexes. Any sexual dimorphism in terms of call structure, and in turn responses to environmental variables may therefore be concealed (Grilliot et al., 2009). Further, these keys represent broad geographic regions and while they are the best available tool, regional (and sub-regional) differences in bat calls remain (Law et al., 2002). Next, due to lack of detector replication the scope of this study is limited to the reserve, in the first instance. There is value, however, in the results presented here as they highlight significant relationships with environmental variables over a sizeable temporal scale. We endorse the use of this methodology in future medium- and long-term monitoring of insectivorous bats with greater detector replication. Finally, a significant issue exists where some variables are correlated with each other. Such correlations create issues for multiple (stepwise) regression because correlated environmental variables can artificially inflate the r^2. It then becomes impossible to isolate the effects of "causal" environmental variable on bat activity, and those which are merely correlated with the "causal" ones. For instance, if the "causal" effect is seasonal changes in weather with which environmental temperature and prey availability are associated; the driver for bat foraging may be warmer weather because (a) it is energetically efficient to do so or (b) there is more prey available or (c) for both. As a result, it may be impossible to isolate the effects of these variables as they are naturally associated. If there are naturally, strongly associated environmental variables, then it starts to beg the question of why it is important to assign them separate amounts of explained variation in bat activity models? As much as possible, we limited the effects of such multicollinearity by inspecting the VIFs of environmental variables. We did not need to exclude any, however (based on this rule), as they all exhibited VIFs <5. Further, we included air and in-stream temperature as a pure interaction term in our stepwise regression to acknowledge that these variables are closely associated.

5.4.2 Ambient air temperature

Consistent with our 'within nights' hypothesis, we detected a strong positive relationship between total bat activity and nightly ambient air temperature. The effects of temperature on bat activity is widely documented (O'Farrell et al., 1967). In particular, nightly ambient air temperature has implications for the diets (Kaupas and Barclay, 2017), movement (Chaverri and Quirós, 2017) and roost selection (Czenze et al., 2017) of insectivorous bats. In this study, nightly ambient air temperature was unimodal and peaked on January 24th (71 days into the survey). As with other studies, bat activity also peaked within two hours of dusk when ambient air temperature was highest (Milne et al., 2005), independent of other categories (lunar phase and heat accumulation). Other studies, however, have identified more complex relationships between bat activity and ambient air temperature (Doty et al., 2019; Milne et al., 2005). Doty et al. (2019) for instance, identified a threshold for bat activity at ~17.8 °C, beyond which activity had little association with temperature. In this case, bat activity was monitored within a subtropical coastal environment over a winter-spring transitional period (Doty et al., 2019), illustrating potentially very different dynamics to the present study. Nevertheless, our results did not reflect a similar threshold.

5.4.3 Heat accumulation periods

Emergent aquatic invertebrates are intimately connected to in-stream temperature (Arendt, 2010; Bovill et al., 2019). According to the temperature-size rule, cooler temperatures prolong the developmental phase of stream invertebrates (Atkinson, 1994), which at the community-level results in delayed emergence (Watanabe et al., 1999). As insectivorous bat communities are subsidised by the influx of aquatically-derived prey (Fukui et al., 2006), it follows that they may be indirectly responding to higher in-stream temperatures via relatively high abundances of flying adults. Consistent with our 'within nights' hypothesis during times where heat accumulation by the stream was high, bats were more active. While few studies have coupled bat activity with in-stream temperature, the link between bat activity and other in-stream conditions has been investigated (Korine et al., 2015; Racey et al., 1998). Given the importance of freshwater habitats to insectivorous bat communities (Blakey et al., 2017a; Salvarina, 2016), more work is needed to untangle the relationship of insectivorous bats with the conditions of these systems.

5.4.4 Lunar effects

The relationship between bat activity and moon illumination is highly variable across different spatiotemporal scales (Appel et al., 2017; Doty et al., 2019; Law, 1997; Scanlon and Petit, 2008). A recent review suggests that bats foraging over water were significantly more lunar-phobic than bats that foraged in cluttered (terrestrial) habitats (Saldaña-Vázquez and Munguía-Rosas, 2013). Bats run a high risk of being preyed upon (by owls and other birds of prey) in over water airspace because they are highly visible during well illuminated nights (Appel et al., 2017; Saldaña-Vázquez and Munguía-Rosas, 2013). Saldaña-Vázquez & Munguía-Rosas (2013) further noted that moon illumination was less important for temperate species because these biomes are composed of fast-flying bats, which are less suceptible to predation. Our findings support this as moon illumination only featured in the explantory models for overall species richness, *C. morio, Nyctophilus-Myotis* complex and *Mo. ridei* activity. Further, moon illumination was identified as a relatively important variable for *V. vulturnus* activity despite not featuring in the final explanatory model.

Interestingly and contrary to our ‘within nights’ hypothesis, we did find that bat activity during fuller moons was distributed differently to those with lower illumination, with activity generally higher on full and gibbous moon nights. Discrepancies here may be a product of increased canopy cover (see chapters 2 and 4) or high granitic landforms within the study area, which maintain a dark understorey during illuminated nights (Doty et al., 2019). Additionally, edge-dwelling (e.g. *V. darlingtoni* and *V. vulturnus*) and open-space species (e.g. *M. ridei*) may take advantage of the increased visibility during these nights to intensify their foraging (Doty et al., 2019; Roeleke et al., 2018). Nevertheless, overall species richness was negatively associated with moon illumination.

5.5.5 Conclusions

In the present study, bat activity was influenced by a range of environmental across a broad temporal period, with some species-specific responses detected. Understanding these responses is integral to understanding the ecology of insectivorous bats, particularly within biomes and habitats that are often ill-studied including perennial streams. Increased foraging spurred by optimal environmental temperature or increased prey availability, may supersede any suppressive effects of other environmental variables, such as moon illumination. Further, foraging activity is sustained longer over the night during periods where heat accumulation by the perennial stream was high. Finally, while the effects of moon illumination on overall bat activity was apparently insignificant, some species did respond (both positively and negatively) to this variable and this may inform the ecology of these species. This information supports the need for monitoring programs to incorporate greater temporal scales and contextualise their sampling periods more explicitly.

5.5 TABLES

Table 5.5.1 Two categories of alternative hypotheses (H_{1-2}) that predict different spatial and temporal patterns in invertebrate abundance and biomass, and community composition. Possible underlying mechanisms, and the scale (within nights and within reaches) at which responses are likely to be most variable, are also outlined

	Hypothesis	Source of variation	Statistical approach
H_1	There will be a positive relationship between insectivorous bat activity and nightly ambient temperature *<u>Mechanism:</u> As small endothermic organisms, insectivorous bats consume a lot of energy maintaining a stable body temperature and therefore, may be sensitive to local weather conditions in temperate areas. For example, bat activity should be greater during warmer temperatures.*	Within nights	See Section 5.2.5.1
	Insectivorous bat activity will be skewed later during nights with respect to moon phase. *<u>Mechanism:</u> Increased available light associated with full and gibbous moon phases may drive delayed emergence times of bats (and in turn delayed activity) or suppress bat activity generally.*		See Section 5.2.5.2
	Insectivorous bat activity at a perennial stream will be skewed earlier during nights with respect to the rate at which a perennial stream will accumulate heat *<u>Mechanism:</u> Increased in-stream temperature may drive high prey emergence/ availability and in turn, greater foraging activity at perennial streams*		
H_2	Local environmental conditions will be more influential on insectivorous bat foraging than moon illumination *<u>Mechanism:</u> Local weather including air temperature and wind will supersede risks to predation that increase with greater moon illumination*	Within reach	See Section 5.2.5.3

Table 5.5.2 Total number of passes, average number of passes per night over the sampling period and number of nights recorded per species. 'sd' = standard deviation.

Species	Total number of passes	Average number of passes per night (± sd)	Number of nights recorded
Austronomus australis	240	1.6 ± 3.97	85
Chalinolobus gouldii	1 009	6.8 ± 10.5	128
Chalinolobus morio	4 913	33.2 ± 34.5	145
Mormopterus ridei	6 370	43.04 ± 39.1	128
Mormopterus planiceps	1 120	7.6 ± 12.3	146
Myotis-Nyctophilus complex	385	2.6 ± 3.7	114
Saccolaimus flaviventris	197	1.3 ± 2.95	83
Scotorepens balstoni	256	1.7 ± 3.6	91
Vespadelus darlingtoni	27 379	184.99 ± 250.98	147
Vespadelus regulus	39	0.2 ± 0.6	49
Vespadelus vulturnus	18 570	125.5 ± 140.2	146
Unknown	13 744	92.9 ± 102.1	

Table 5.5.3 Simple regressions between local environmental conditions and bat activity

Equations	$F_{1,145}$	R^2	P-value
log(Bat activity) = 1.171 + 0.077(nightly ambient air temperature)	131.7	0.47	<0.001
log(Bat activity) = 2.39 - 0.16(moon illumination)	1.62	<0.01	0.21
log(Bat activity) = 0.732 + 0.095(in-stream temperature temperature)	131.7	0.46	<0.001
log(Bat activity) = 96.481 – 0.005(Julian date)	67.39	0.31	<0.001
log(Bat activity) = 96.481 – 0.005(windspeed)	10.69	0.06	0.001

Table 5.5.4 Results for two sample Kolmorogov-Smirnov test comparing the distribution of activity within nights between moon phases and heat accumulation periods. This test uses the statistic D_{crit}, which indicates the maximum absolute difference between the relative cumulative frequency distributions of each pair-wise comparison among lunar phases and heat accumulation periods, respectively (Sokal and Rohlf, 1995). If the null hypothesis is true and calls are distributed identically within nights of different lunar phases or heat accumulation periods, then D_{crit} should be zero (or close to).

Moon phase			Heat accumulation period		
	D_{crit}	P		D_{crit}	P
Crescent moon – Full moon	0.44	0.004	High-Moderate	0.4	0.01
Crescent moon – Gibbous moon	0.53	<0.001	High-Low	0.59	<0.001
Crescent moon –New moon	0.28	0.159	Moderate-Low	0.44	0.004
Crescent moon –Quarter moon	0.28	0.159			
Full moon – Gibbous moon	0.09	0.999			
Full moon –New moon	0.34	0.046			
Full moon –Quarter moon	0.34	0.046			
Gibbous moon –New moon	0.38	0.02			
Gibbous moon –Quarter moon	0.38	0.02			
New moon –Quarter moon	0.22	0.43			

Table 5.5.5 Explanatory models for total, *V. darlingtoni*, *V. vulturnus* and Nyctophilus- Myotis complex activity, and species richness using a forward step-wise regression process. Equations are provided for those models that ranked the highest for each response. All models were significant.

Response	Model structure	ΔAIC_c	w_i	R^2
Total bat activity	Julian date + environmental temperature	0	0.38	0.51
	Julian date + moon illumination + windspeed + environmental temperature	0.36	0.32	
	Julian date + windspeed + in-stream temperature : nightly ambient	0.51	0.3	
Bat species richness	Moon illumination + environmental temperature	0	0.54	0.19
	Julian date + Moon illumination + environmental temperature	1.59	0.25	
	Julian date + environmental temperature	3.03	0.12	
	Julian date + moon illumination + windspeed + environmental temperature	3.59	0.09	
V. darlingtoni activity	Environmental temperature	0	0.59	0.47
	Julian date + environmental temperature	1.84	0.24	
	Julian date + moon illumination + environmental temperature	3.04	0.13	
V. vulturnus activity	Julian date + windspeed + environmental temperature	0	0.52	0.55
	Julian date + moon illumination + windspeed + environmental temperature	1.56	0.24	
	Julian date + moon illumination + in-stream temperature : nightly ambient	1.58	0.24	
Nyctophilus-Myotis complex activity	Julian date + moon illumination + windspeed + environmental temperature	0	0.53	0.2
	Julian date + windspeed + environmental temperature	0.33	0.45	

Table 5.5.6 Relative variable importance (RVI) on bat activity and species richness; calculated from Akaike weights. Variables with RVI ≥ 0.73 (indicated in bold) are considered significant predictor variables.

RVI	Total bat activity	Bat species richness	*V. darlingtoni* activity	*V. vulturnus* activity	*Nyctophilus-Myotis* complex activity
Moon illumination	0.32	**0.88**	0.17	**0.96**	0.3
Wind speed	0.62	0.09	0.04	0.27	**0.85**
Julian date	**0.99**	0.46	0.41	**0.98**	**0.92**
Interaction					
Environmental temperature	**0.98**	**0.79**	**0.79**	**0.76**	0.35

Table 5.5.7 Explanatory models for *C. gouldii, C. morio, Mo. ridei, Mo. planiceps and A. australis* activity, and species richness using a forward step-wise regression process. Equations are provided for those models that ranked the highest for each response. All models were significant.

Response	Model structure	ΔAIC_c	w_i	R^2
C. gouldii activity	Environmental temperature	0	0.63	0.09
	Environmental temperature + Julian date	1.53	0.29	
	Julian date + moon illumination + windspeed + environmental temperature	5.85	0.04	
C. morio activity	Julian date + moon illumination + environmental temperature	0	0.61	0.46
	Julian date + moon illumination + windspeed + environmental temperature	0.91	0.29	
Mo. ridei activity	Moon illumination + environmental temperature	0	0.34	0.10
	Moon illumination + Julian date + environmental temperature	0.06	0.33	
	Moon illumination + Julian date + environmental temperature + windspeed	2.11	0.12	
	Julian date + environmental temperature	2.3	0.11	
	environmental temperature	2.47	0.1	
Mo. planiceps activity	Julian date + environmental temperature	0	0.8	0.36
	Julian date	2.78	0.2	
Au. australis activity	Julian date + windspeed	0	0.44	0.15
	Julian date + windspeed + environmental temperature	1.32	0.23	
	Julian date + windspeed + moon illumination	1.53	0.21	
	Julian date + moon illumination + windspeed + environmental temperature	2.55	0.12	

Table 5.5.8 Relative variable importance (RVI) on bat activity; calculated from Akaike weights. Variables with RVI ≥ 0.73 (indicated in bold) are considered significant predictor variables.

RVI	*C. gouldii* activity	*C. morio activity*	*Mo. ridei* activity	*Mo. planiceps* activity	*Au. australis* activity
Moon illumination	0.24	**0.97**	0.29	0.02	0.23
Wind speed	0.05	0.28	0.05	0.41	**0.98**
Julian date	**0.99**	**0.98**	0.21	**0.98**	**0.97**
Interaction					
Environmental temperature	0.23	**0.99**	**0.99**	0.05	0.26

5.6 FIGURE

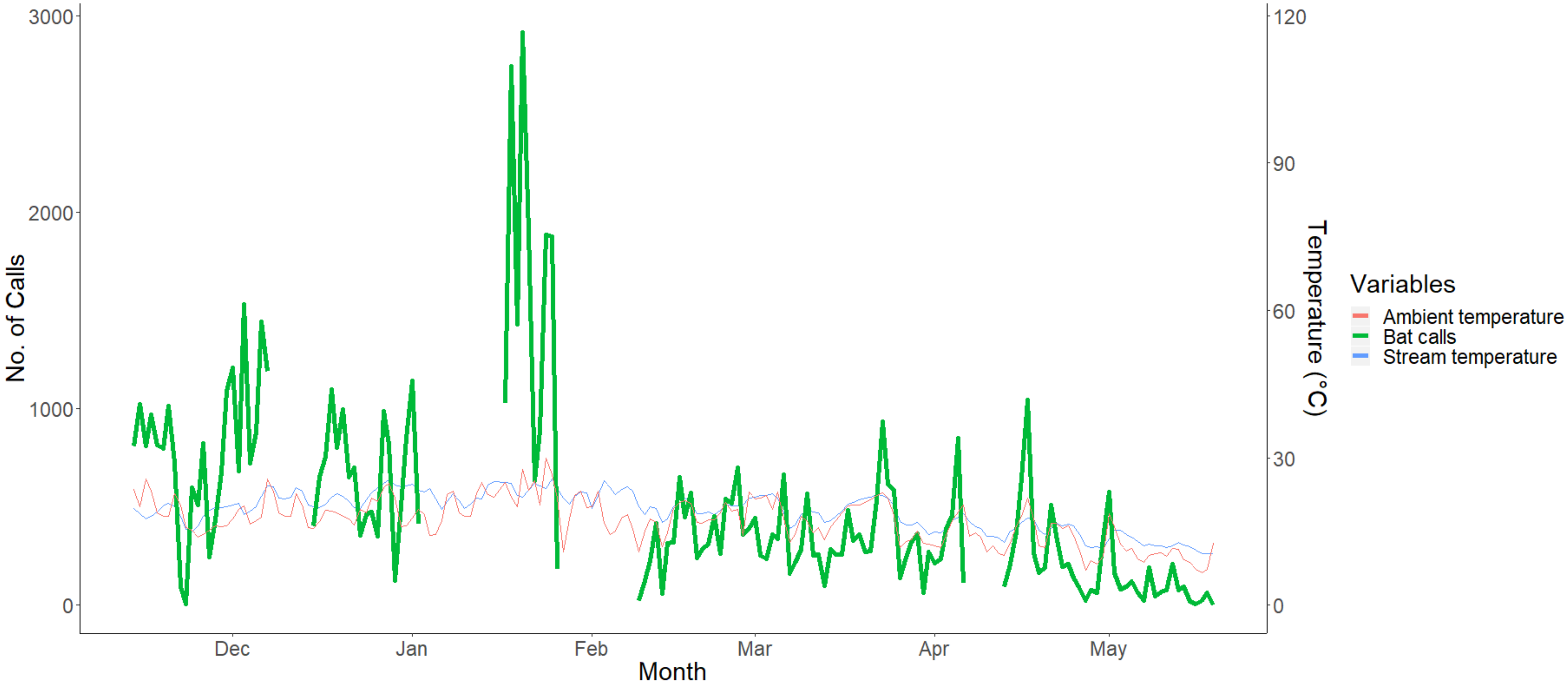

Figure 5.6.1 Bat activity over the survey period. Gaps in the green line indicate where SD cards ran out of memory.

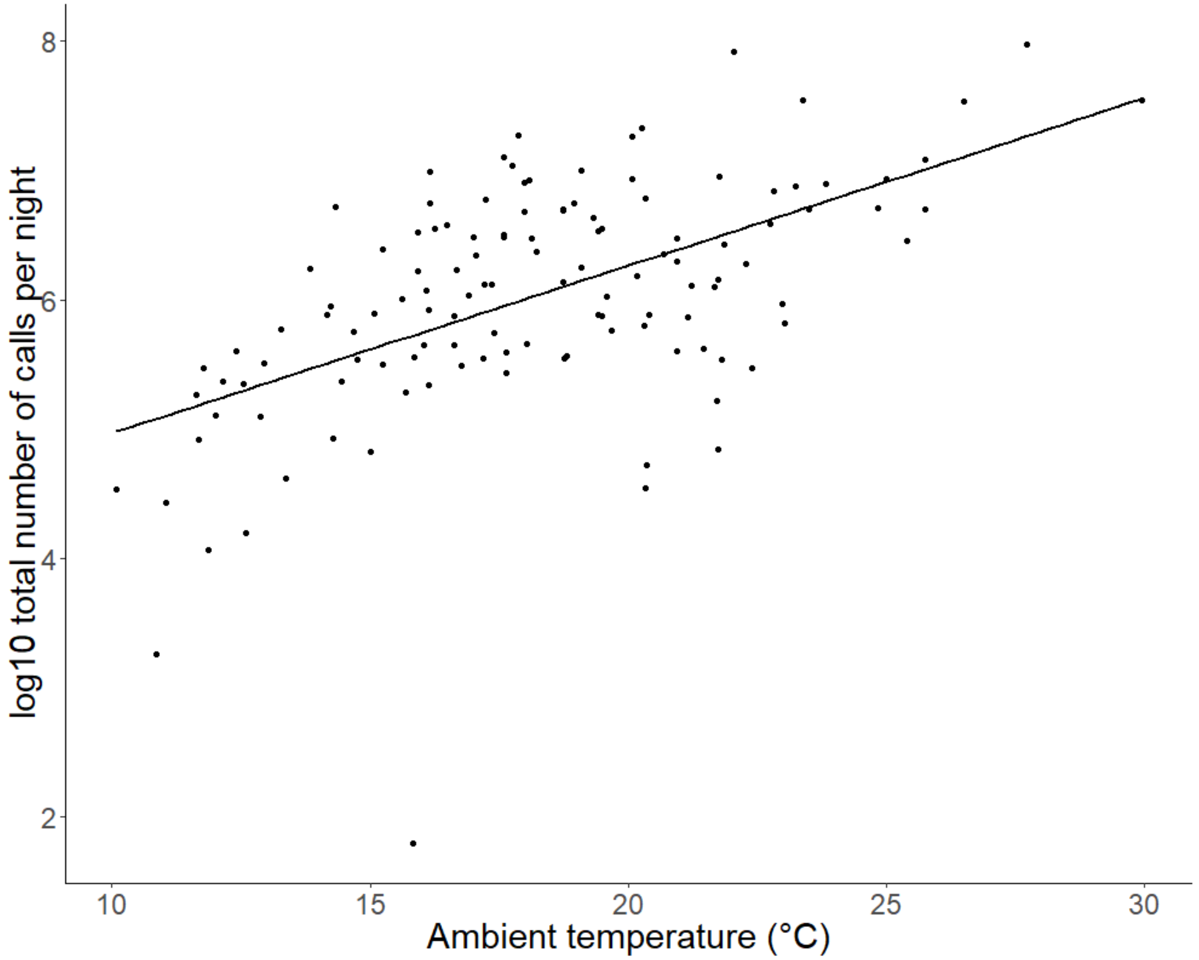

Figure 5.6.2 Bat activity responded positively to nightly ambient temperature. The black line indicates the overall trend and was fitted via a linear regression.

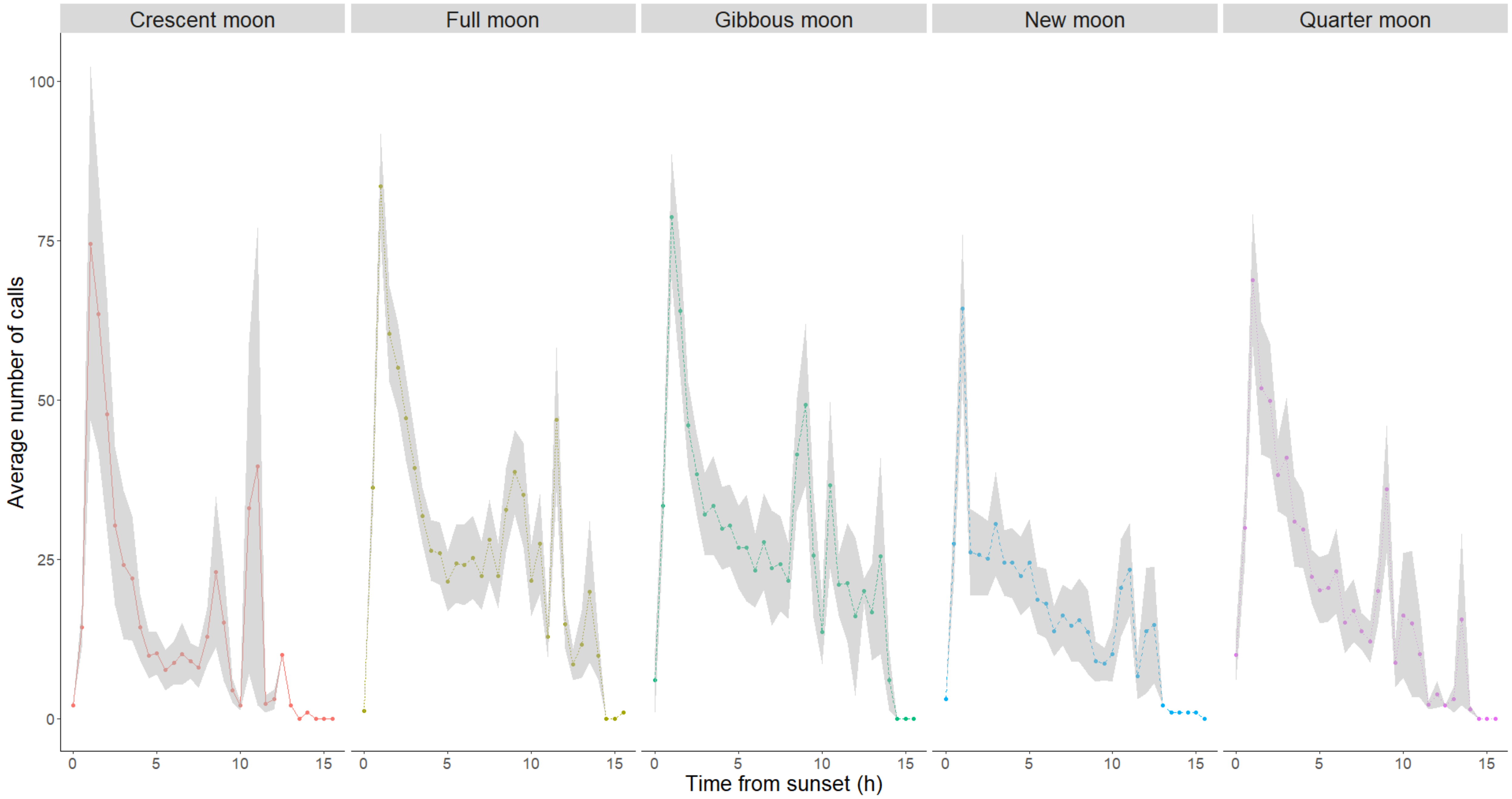

Figure 5.6.3 The within-night distribution of activity per moon phase. Activity during full and gibbous moons were significantly different from that of others. Grey bands indicate standard error.

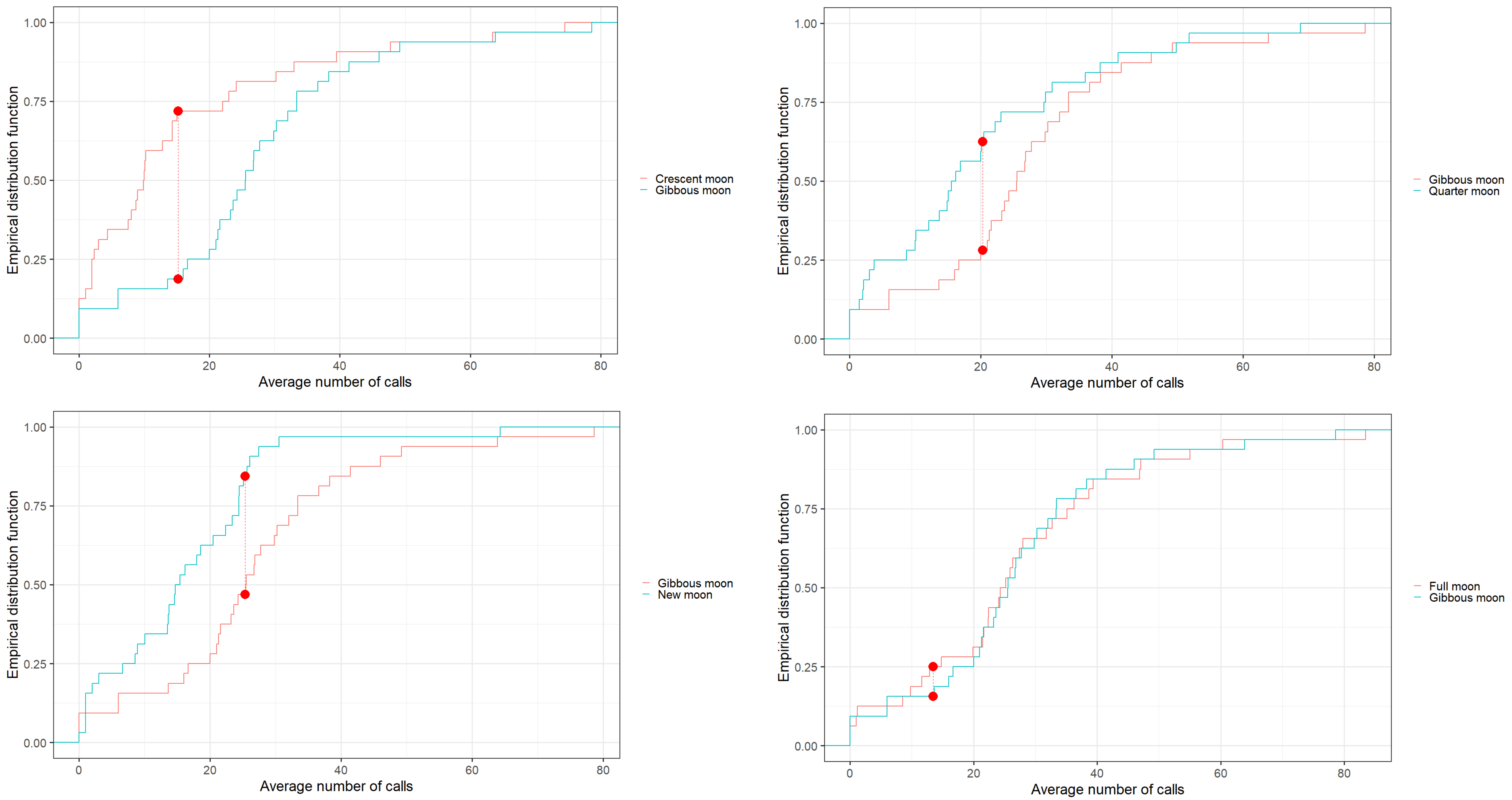

Figure 5.6.4 Empirical distribution functions for bat activity comparing nights with gibbous moons to the other lunar phases. The red points indicate the maximum absolute difference between the relative cumulative frequency distributions of each pair-wise comparison (D_{crit}). If the null hypothesis is true and calls are distributed identically within nights of different lunar phases, then D_{crit} should be zero (or close to). By-and-in-large the gibbous moon values are greater than the other lunar phases (excluding full moons) for the same empirical distribution function.

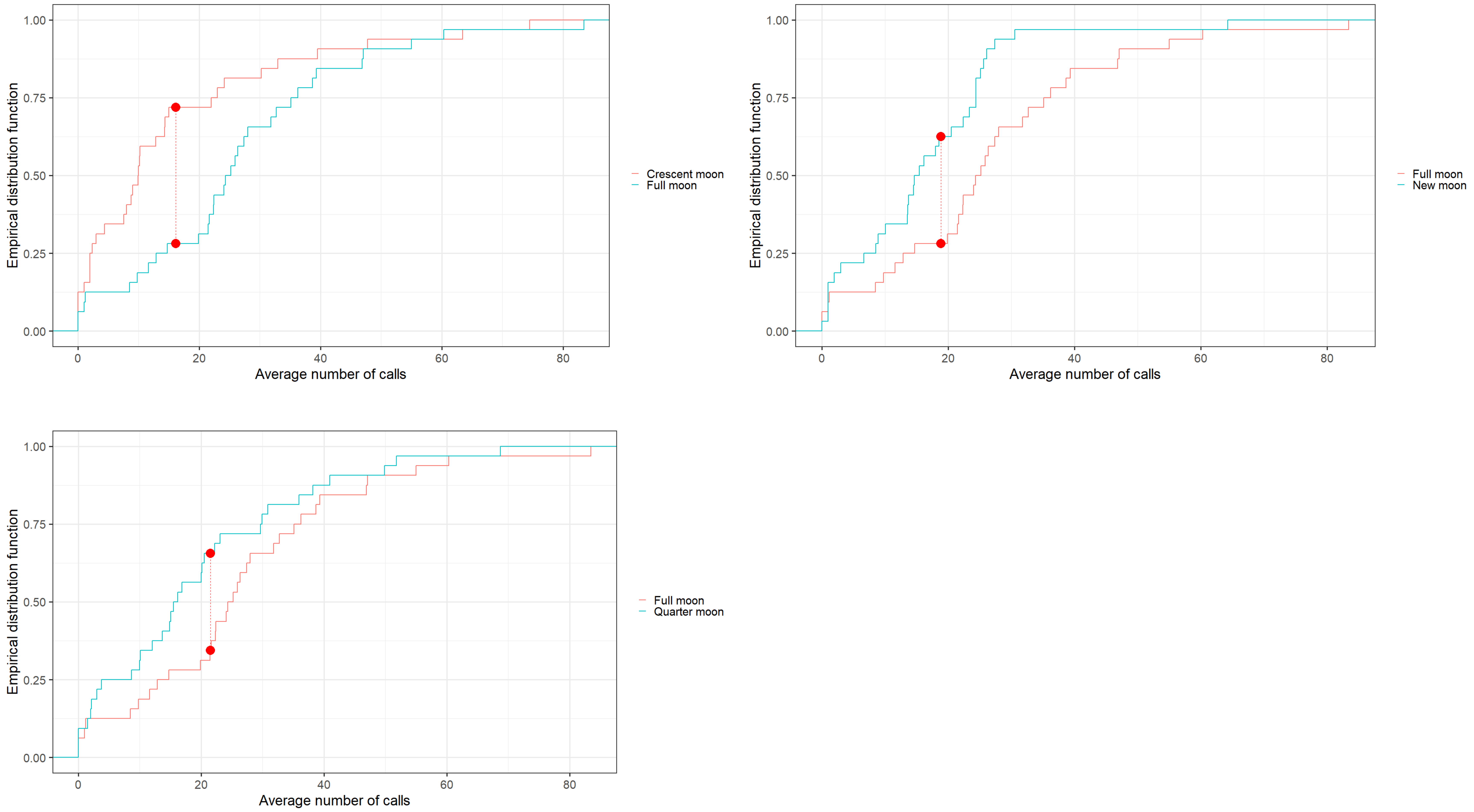

Figure 5.6.5 Empirical distribution functions for bat activity comparing nights with full moons to the other lunar phases. The red points indicate the maximum absolute difference between the relative cumulative frequency distributions of each pair-wise comparison (D_{crit}). If the null hypothesis is true and calls are distributed identically within nights of different lunar phases, then D_{crit} should be zero (or close to). By-in-large activity during a full moon was significantly larger than the other lunar phases for the same empirical distribution function.

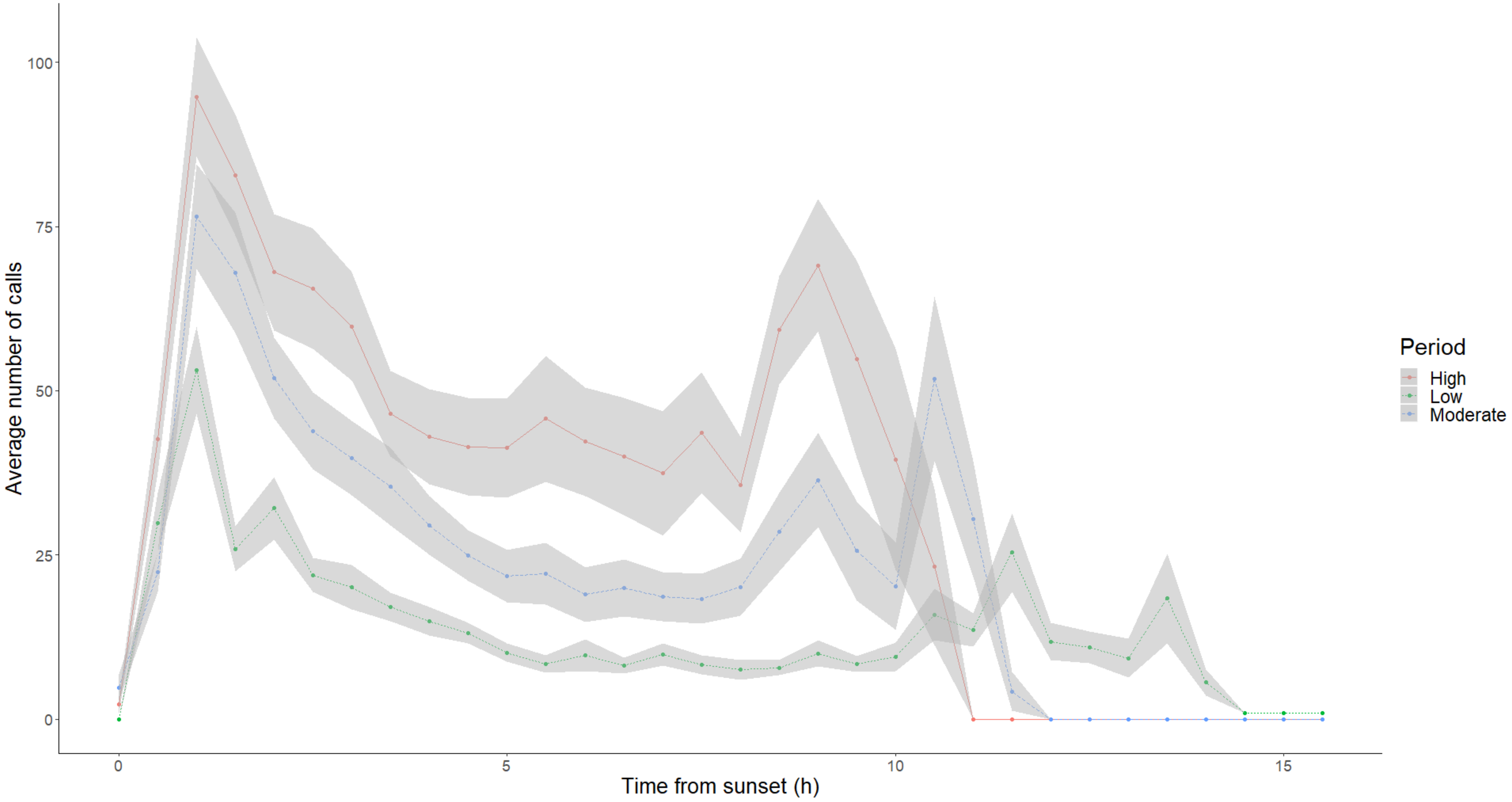

Figure 5.6.6 The within-night distribution of activity per heat accumulation period. Activity during each accumulation period was significantly different from that of others. Grey bands indicate standard error.

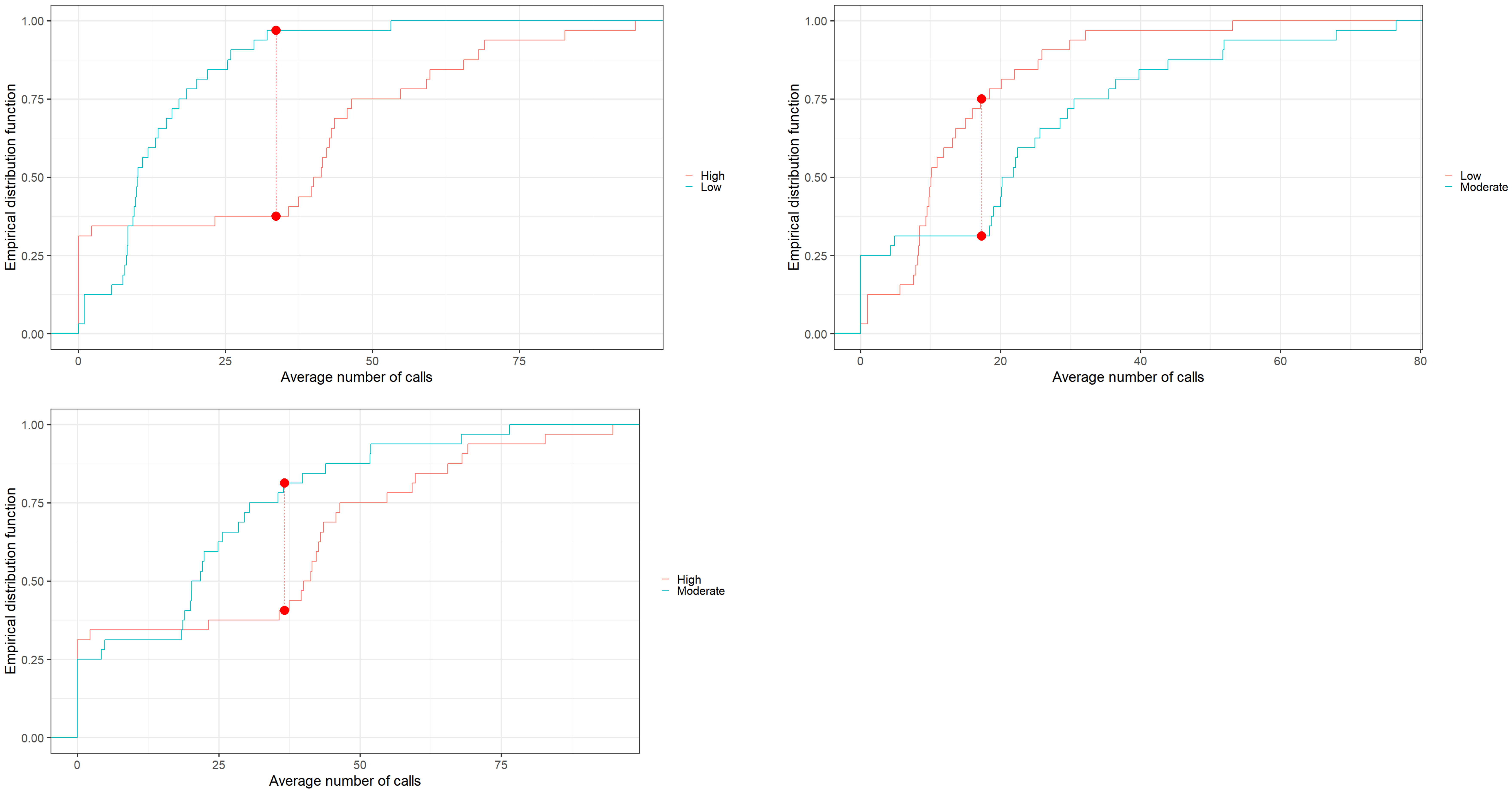

Figure 5.6.7 Empirical distribution functions for bat activity comparing heat accumulation periods. The red points indicate the maximum absolute difference between the relative cumulative frequency distributions of each pair-wise comparison (D_{crit}). If the null hypothesis is true and calls are distributed identically within nights of different heat accumulation periods, then D_{crit} should be zero (or close to). By-and-in-large the higher heat accumulation period values are larger than the other periods for the same empirical distribution function.

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