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How does deforestation affect the functional links between riparian zones and stream channels?

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How does deforestation affect the functional links between riparian zones and stream channels?

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Abstract

Riparian vegetation is essential for headwater streams, as it regulates allochthonous inputs of coarse particulate organic matter (CPOM) delivered into streams. CPOM accumulates in patches across the streambed, these patches are sources of energy and shelter where ecological linkages between aquatic populations occur. This group of studies evaluate such relationships in Hughes Creek, Victoria, southern Australia. The first of these studies evaluates the evidence documented in 45 studies which were undertaken mostly in temperate or subtropical regions of the U.S.A., Canada, Spain and Australia. The main focus of these works was to evaluate the effect of deforestation upon allochthonous inputs of CPOM, often in first and second order streams. Most studies addressed airborne inputs only, while lateral surface inputs, or downstream transport of CPOM were not commonly studied. Hedges' effect size (*g*) was calculated for allochthonous inputs data from the 45 articles and plotted against deforestation. A threshold for airborne inputs and benthic organic matter (BOM) standing stock was observed when deforestation reached 70%. At that level of deforestation, effect sizes decreased by up to -5 standard deviations.

The second study encompassed a field survey where forested and low forested sites along the one stream were evaluated. The survey required the collection of allochthonous inputs monthly for one year, where airborne, lateral surface transfer (LST), and drifting CPOM fractions were collected in sites with contrasting forest cover. Sites with intact vegetation showed high inputs (14 kg m^{-2} DW $year^{-1}$), while deforested reaches showed lower airborne inputs (9.25 kg m^{-2} DW $year^{-1}$). LST inputs represented 42% of allochthonous inputs in forested reaches, and 37.5% in deforested sites. The transport of CPOM downstream was similar between forested and deforested sites (23-25 kg DW $year^{-1}$). Given this similarity in CPOM transportation, and that the majority of streams in Victoria are deforested, patches of riparian forest might be an attractive management option for restoration/management of streams. However, it is necessary to be mindful of the scope and limitations of forested patches along streams, as they might not provide resources to neighbouring areas. Rather, forested sections tend to retain most of their allochthonous inputs within their boundaries.

The third study of this thesis comprises a field survey where patches of CPOM, located on the streambed of forested and deforested reaches, were collected in Summer, Spring and Winter. CPOM was separated intro fractions of leaves, bark and twigs. It was found that the type of cover did not modify the mass of CPOM fractions between forested and deforested reaches ($p > 0.05$). However, the results show significant differences between Sites within Forest Cover for all fractions, with exception of leaf material. The dominant patterns suggest high variation between sites and shifts between seasons. In relation to the contribution of each fraction provided to CPOM benthic standing stock, it was found that during the three sampling seasons, benthic CPOM composition was dominated by, in decreasing order, twigs, bark, leaf, and grass. Additionally, macroinvertebrates found in CPOM patches were separated and sorted into genus and species when possible. The analysis of species densities between forested and deforested sites show that *Simulium ornatipes* and *Ecnomina F* sp. densities differed between the two types of forest cover, while the remaining species showed no differences. However, *Simulium ornatip*es showed strong differences between sites. *Ecnomina F* sp. was the only taxon to show a significant difference related to forest cover, without having a substantial difference between sites within the same forest cover. On the other hand, *Ecnomus continentalis, Notalina* sp., *Chemautopsyche* sp, *Hydroptila*, *Berosus* (larvae), and *Micronecta* sp. showed higher significant differences in summer; whereas *Chemautopsyche* sp. and *Hydroptila* sp. densities were minimal in patches during spring. The regressions between the mass of CPOM and density of species showed that some presented negative relationships between specimens' density and the increase of CPOM mass, as illustrated by *Ecnomia* F sp., *Cheumatopsyche* sp., and *Nousia* sp.

The last study of this thesis was a field experiment where the size and spatial distribution of CPOM patches was manipulated, due to small-scale fragmentation being predicted to affect species densities, particularly where patches are ephemeral or organisms are transported advectively. CPOM patches were deployed in two possible configurations (a) one big patch treatment (BPT), comprised of 12 smaller sub-patches of the same size, and (b) 12 split patches (SPT), which were distributed across the streambed. Patches from the split treatment were of two sizes, double (300 cm^2) and single (150 cm^2). BPT and SPT patches from both treatments were oriented randomly on the stream (parallel or perpendicular) with respect to water flow. After 10 days, samples were collected of 13 common macroinvertebrates which had colonised the patches. It was found that the genera *Offadens* spp. and *Notriolus* spp. had responded to the orientation of patches in both treatments. Moreover, in SPT sites *Offadens* spp., *Cheumatopsyche* spp., and *Notriolus* spp. showed significantly higher densities in small patches, suggesting that species densities, which show no searching strategies for resources, are likely to be affected by patch size.

The knowledge generated in this thesis provides a greater understanding of the effect upon macroinvertebrates densities by deforestation of a creek that flows through agricultural lands in southern Australian.

Declaration

This is to certify that

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

_________________________ Arturo Gonzalez

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Thank you to my supervisor, Barbara Downes, who taught me – by example – the value of having a strong foundation in the discipline of ecology. I appreciated your patience, guidance, your academic rigour, and critical and challenging mind. At this point, I have developed a “think about the question” science approach, in my opinion one extremely useful habit. Moreover, I want to thank you for your statistical guidance and advices, they help me to get most from my sets of data.

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List of abbreviations

ANOVA: Analysis of variance

AVR: Average recurrent interval

BACI: Before-After Control-Impact experimental design

BPT: Big patch treatment

BOM: Benthic organic matter

CPOM: Coarse particulate organic matter

DARs: Density-area relationships

DOM: Dissolve organic matter

Drifting CPOM: CPOM transported downstream by water flow

FPC: Flood pulse concept

FPOM: Fine particulate organic matter

(*g*): Hedges' effect size

(***-k***): Decay rate

LWD: Large woody debris

LST: Lateral surface transfer

OM: Organic matter

RCC: River continuum concept

RPM: Riverine productivity model

RWC: River wave concept

SD^*_{pooled}: pooled and weighted standard deviation

SIMPER: Similarity Percentages analysis

SPT: Split patch treatment

1. Introduction

Riparian vegetation and streams are intrinsically connected by the interchange of energy (Ballinger & Lake 2006). Forested streams depend greatly on the inputs delivered from riparian vegetation (Bilby & Bisson 1998, Cummins 1974, Minshall et al. 1985, Richardson et al. 2005) and many aquatic species depend on them as a source of energy (Li & Dudgeon 2008, Murphy & Giller 2000). In normal conditions, riparian vegetation delivers variable amounts of leaves, bark, and twigs, or allochthonous inputs, into adjacent streams, and these inputs are strongly seasonal (Winterbourn 1976). Once in a stream, allochthonous inputs are either transported downstream by the current or retained by logs, benches, or backwaters. Typically, retained organic matter, such as coarse particulate organic matter, which is defined as pieces larger than 1 mm (Bilby & Bisson 1992, Bilby & Bisson 1998), is large enough to become trapped by such structures.

Smaller fractions of organic material such as dissolved and fine particulate organic matter, are vital resources for bacteria and fungi (Naiman & Sedell 1979), and filter feeder macroinvertebrates (Wallace & Merritt 1980, Wallace & Webster 1996). However, these fractions do not provide shelter or substrate for macroinvertebrates. Further, coarse particulate organic matter (CPOM) does provide energy (Cummins 1974), shelter, or substrate (Kobayashi & Kagaya 2002) for macroinvertebrates. However, human disturbances, such as deforestation of riparian forests, are capable of disrupting the type and amount of energy inputs from riparian forests to streams, which in most cases is expressed as a reduction of CPOM allochthonous inputs (Lorion & Kennedy 2009a). This decrease results in several effects, one of which could be the lower density of CPOM patches and a decrease of the size of such patches across the streambed. The latter is supported by resource flow model (Wallace et al. 1999) which explains that allochthonous inputs from riparian areas should decrease in magnitude as the deforestation of riparian areas increases. The latter could imply that macroinvertebrates would have to search for CPOM across more extensive areas, and the capacity to reach new patches will depend on the dispersal strategy of each species.

The thesis presents a group of studies that evaluate the RFM. The RFM model leaves several questions open, as it is unknown how reduction of allochthonous inputs occur, and how this affects aquatic populations that depend on these sources of energy. Thus, the aim of this thesis is to test whether allochthonous inputs decrease equally in forested and deforested areas located in the same stream, and if these changes affect benthic CPOM standing stock in downstream reaches. On the other hand, the second aim of this thesis is to evaluate how local communities of macroinvertebrates are affected by the potential decrease in the size of CPOM patches, and if higher isolation between patches could constrain the dispersal of species based on their dispersal capacity.

The following section provides an introduction to allochthonous inputs in disturbed streams, and the general explanation of some concepts that, latter in this thesis, will help the reader to understand the effect of deforestation upon allochthonous inputs of CPOM.

1.1. Allochthonous inputs of disturbed headwater streams

Organic matter budgets of small streams flowing through forested watersheds are dominated by inputs of terrestrial organic material (Naiman & Sedell 1979). Several models have been developed to explain what happen to allochthonous inputs when the enter a stream. For example, one initial model was the river continuum concept (Vannote et al. 1980), and subsequent models, such as the flood pulse concept, the river productivity model (Thorp & Delong 1994), and the river wave concept. However, such concepts focus on what happens to organic matter after it has entered the river, but they do not explain how organic matter enters the stream. Thus it is neccesary to explain the mechanisms moving organic matter from riparian areas to streams.

Ecologists have documented at least three direct mechanisms by which CPOM is transported to streams: (I) airborne inputs (Abelho & Graca 1996, Weigelhofer & Waringer 1994), where organic material falls directly from the canopy; (II) lateral surface input (Magana 2001), where wind and ocassional floods transport organic material to streams; and (III) drifting CPOM, which is CPOM that falls upstream and is subsequently transported to downstream reaches (Brown & Timms 2002). These three fractions are responsible for allochthonous inputs in small forested streams (Bilby & Bisson 1992, Cummins 1974, Richardson, Bilby & Bondar 2005, Roberts & Bilby

2009). However, there still are limitations on the knowledge related to these inputs. For example, many studies have focused on evaluating the amount of allocthonous input in a variety of streams simultaneously, sometimes comparing forested and deforested streams (England & Rosemond 2004, Hoover et al. 2011, Kiffney & Richardson 2010, Kreutzweiser et al. 2004). However, the study of a large number of waterbodies in any one time frame limits the amount of samples that can be made per stream, leading to a knowledge gap of how allochthonous inputs work in detail in such streams. Moreover, within deforested streams, management of riparian vegetation has focused on maintaining channel stability by leaving strips of trees along stream banks (Tabacchi et al. 1998, Tabacchi et al. 2000). Further, a stream with few patches of forested riparian areas are considered to be buffer zones, where local population of different species can survive and where downstream export of CPOM ocurr. Yet few studies have evaluated if allochthonous inputs from these forested areas are greater to those in deforested ones within the same stream. Furthermore, it is as yet unknown if there is any export of organic matter downstream from forested areas to deforested ones, and if there is, how important it is to its eventual location.

After allochthonous inputs are delivered and retained on the streambed, then they can be colonized or populated by aquatic fauna. The following section provides initial material for the understanding of CPOM retained on streams and how it supports local communities in macroinvertebrates.

1.2. Benthic CPOM and the ecology of aquatic macroinvertebrates

Retention of CPOM is influenced by particle size (Ehrman & Lamberti 1992), hydrologic regime (Webster et al. 1999), and type of riparian vegetation. Anthropogenic disturbances may modify the amount or quality of allochthonous CPOM, which later is retained. For example, data regarding benthic CPOM from deforested reaches surrounded by grasslands, indicate a higher presence of grass than in reaches where riparian vegetation remains unchanged (Brown & Timms 2002, England & Rosemond 2004, Nyström et al. 2003, Reid et al. 2008a). Such changes are likely to modify species densities in patches of CPOM, due to the type of substrate being inadequate for shelter, or the nutritional value being lower than what is required. For example, it has been documented on the Iberian Peninsula that benthic CPOM in reaches dominated by eucalypt plantations did not provide the energetic requirements needed by native macroinvertebrates (Abelho & Graca 1996, Blackburn & Petr 1979).

Moreover, Canhoto and Graça (1995) demonstrated that at least one native Mediterranean shredder (*Tipula lateralis*) was unable to feed on eucalyptus leaves, which represent a low-quality resource for some insect communities. Likewise, Graça et al (2001) and Molles (1982) found a lower number of aquatic macroinvertebrates in sites where the riparian composition had been changed. These data illustrate that the link provided by energy subsidies from riparian zones, and the ecological features of aquatic communities (i.e. species diversity, densities etc.) depend greatly on the composition and amount of allochthonous inputs.

Aquatic communities are also affected by geomorphological changes that occur in stream channels after deforestation of riparian vegetation. For example, stream channels became wider and more shallow following the removal of trees from or near the banks (Sweeney et al. 2004). Wider and shallower channels promote the growth of algae, and the increase of autochthonous organic matter has also been reported to augment macroinvertebrate densities. Streams with some canopy cover have two limitations; on the one hand, canopy cover prevents the growth of autochthonous sources of energy (Bilby & Bisson 1992, Richardson, Bilby & Bondar 2005, Vannote et al. 1980). However, on the other hand, limited canopy cover is likely to result in shortages of benthic CPOM delivered from riparian areas – although this may be accompanied by more autochthonous production (Menninger & Palmer 2007). Patchy distribution of resources is of great interest in many areas of ecology, and many studies have been developed in to understand species dispersal in patchy landscapes (Earl & Zollner 2014, Ricketts 2001, Tischendorf et al. 2003, Turner 1989, Turner 1998, Wiens 1976). However, the available information for resource patches in streams is limited to few studies (Lancaster & Downes 2014, Lancaster & Downes 2017, Palmer et al. 1997, Palmer et al. 2000).

Two different hypotheses attempt to explain the mobility of macroinvertebrates species between resource patches. The first hypothesis is based on the resource concentration concept proposed by Root (1973), who proposed that higher densities of species are found in larger patches of suitable resources. Contrastingly, the second hypothesis proposed by Bowman et al. (2002), argues that negative relationships between population densities and patch size are to be expected, where immigration is the main process modifying population densities. In newly created patches, this hypothesis explains the dispersal of species at the local level.

The distance between patches, or clusters of patches, has the capacity to constrain the search capacity of an organism, varying between individuals, and on a broader scale between species (Hambäck et al. 2007). Such constriction on species capacity to find resource patches is capable of leading to large mortality rates (Bell 2012). Understanding movement behaviour provides an explanation for the variation of species population density and distribution. Although many of these studies are focused on landscape scales, it still remains unknown what happens at local scales, in areas where the distribution of patches might define the success of individuals of different species to reach resources.

1.3. Thesis scope

In summary, streams throughout the world suffer a lack of CPOM allochthonous resources, due to commercial activities decreasing canopy cover along river banks. Leaves, bark, twigs, and fruit conglomerate in patches along the streambed, due to retentive structures such as rocks and LWD, but retention rates decrease due to the development of simpler stream channels (Vietz et al. 2013).

Stream landscapes with the majority of the riparian vegetation clear-cut produce unique mobility challenges for macroinvertebrates. Research is scant on whether different macroinvertebrate species can disperse across areas in which there are fewer resource patches of CPOM. Moreover, it is yet unknown if taxonomically related species respond differently to the distribution of patches. Consequently, it is vital to understand the causal effects between deforestation, spatial distribution of patches, and macroinvertebrate dispersal.

1.4. Research aims

This study addresses the following questions: How does deforestation of riparian areas modify allochthonous inputs and benthic CPOM, and how do such changes affect the density of macroinvertebrates? To answer these general questions, four secondary questions are posed:

(I) If deforestation decreases allochthonous inputs of CPOM, by how much does deforestation reduce these inputs to headwater streams? This question was addressed through a systematic literature review, where data were extracted from a variety of studies, to ascertain if there was a threshold between percentage of deforestation and allochthonous inputs.

II) In southeast Australia, deforested or partially deforested streams have two types of canopy cover. The first type of forest provides dense canopy cover to the stream. Dense canopy covers are found in patches in some points along streams where most riparian forests haven been deforested. The second forest cover is the one with a thin line of trees along the banks and surrounded by grasslands. If these two types of riparian vegetation deliver different types or amounts of CPOM, are these inputs different, and is it possible to observe changes in the proportions of fractions delivered?

(III) Do changes in riparian forests modify the amount of benthic CPOM in stream channels? Does any change to benthic CPOM modify the densities of macroinvertebrates depending on such resource patches?

(IV) Does the size, orientation. and distribution of CPOM patches affect a species' capacity to reach such resources.

(V) To produce an updated cause-effect model that effectively related deforestation of riparian zones with allochthonous inputs, how the aggregations of CPOM in the stream affect species density

1.5. Thesis layout

Chapter 1 – The Introduction of this thesis is divided into three sections, each of which provides material for the four aims proposed.

Chapter 2 – The Background provides relevant material related to CPOM allochthonous inputs to streams, including different transport mechanisms, and retention of organic matter. Further, the material provided discusses the most common concepts, which explain how the transport of organic matter from the river banks to the stream occurs, and the limitations of these concepts. The background material also discusses the ecology of macroinvertebrate dynamics in patchy landscapes, including the mobility means that different species use to reach resources, and factors that promote, and or, constrain migration of individuals to other resource patches.

Chapters 3, 4, and 6 are presented in journal submission format. Chapter 3 is a systematic literature review that incorporates the first aim and is focused on the gathering of evidence of the effects that deforestation has upon allochthonous inputs.

Chapter 4 provides empirical data of allochthonous inputs, and CPOM dynamics in forested and deforested reaches, thereby encompassing the second aim of this project.

Chapter 5, presented as thesis chapter, covers the third aim, provides empirical data of the effect that changes in the fractions constituting CPOM patches have upon macroinvertebrate species density.

Chapter 6 comprises a field experiment, where the spatial distribution and size of CPOM patches was manipulated – this chapter encompasses the fourth aim of this thesis.

Chapter 7 provides the general implications of the findings obtained in the four result sections. Moreover, this chapter includes a causal model, where the findings of the thesis are condensed.

2. Background: Riparian vegetation, allochthonous inputs, and macroinvertebrate ecology of streams

2.1. Introduction

Most forested headwater streams throughout the world depend on external sources of energy, substrate, and nutrients to support the aquatic communities living in these ecosystems. In such streams, riparian vegetation impacts basal resources of stream food webs by delivering externally derived organic matter subsidies (Bilby & Bisson 1992, Bilby & Likens 1980). Allochthonous inputs are represented by Coarse Particulate Organic Matter (CPOM), Fine Particulate Organic Matter (FPOM), and Dissolved Organic Matter (DOM) (Bilby & Bisson 1998). CPOM is usually defined as pieces of organic matter with a diameter larger than 1 mm (Cummins 1974, Fisher & Likens 1972, Turowski et al. 2013, Webster et al. 1999), and the most common fractions that represent these fractions are leaves, bark, and twigs. When CPOM material is deposited on the streambed, the physical abrasion from water flow can break it down into FPOM and DOM (Graça 2001). Furthermore, as macroinvertebrates feed upon it, they reduce these materials into smaller fractions, while they also use it as substrate.

Diverse studies focused on the removal of riparian vegetation of forested streams have demonstrated the importance of allochthonous inputs for stream food webs where autochthonous production is limited by riparian shading (Wootton & Power 1993). The structure of food webs in headwater streams suggests that productivity and abundance of populations at any given trophic level are controlled by the productivity and abundance of populations in the trophic level below them. The latter phenomenon is defined as bottom-up control. Changes to riparian vegetation have serious implications for bottom-up drivers of consumers via changes in structure, nutrients, substrate, food sources, and temperature (Heaston et al. 2018). In Australia, some studies have shown headwater streams depend greatly on allochthonous CPOM inputs and are the major source of carbon assimilated by aquatic fauna during certain periods of the year (Reid et al.2008a, Reid et al. 2013). However, most studies have focused on CPOM as source of food for aquatic fauna (Sabater et al. 2000).

In recent years, field experiments have shown that CPOM retention, and that the size and densities of CPOM patches across the riverbed affects local densities of aquatic species of macroinvertebrates (Lancaster & Downes 2014, Lancaster & Downes 2017a, Lancaster & Downes 2017). However, such experiments have focused on large scale ecological questions (the effect of deforestation of an entire catchment and the effect on species composition). It is unknown what effect the distribution of patches (i.e. one large patch or several smaller patches) has upon aquatic macroinvertebrates populations at local scales. Aquatic macroinvertebrates have diverse dispersal strategies, which include drift (passive dispersal), crawling/walking, swimming, and flying (active dispersal) (Lancaster & Downes 2013). However, most aquatic macroinvertebrates in their aquatic stage use drift to disperse, or a combination of an active dispersal method with drift (Downes & Lancaster 2018). Consequently, the success of reaching a patch of CPOM for each individual may depend upon the latter's dispersal ability and the geometric and spatial characteristics of the patch (i.e. area, position in respect to waterflow, volume etc.). The present thesis will explore the role of riparian vegetation as a source of CPOM, and the role that the distribution and characteristics of CPOM patches play in dispersal of macroinvertebrates and the potential effect upon local populations.

This thesis focuses on the importance of CPOM allochthonous inputs used by macroinvertebrates as source of food, shelter, or substrate

The main objective of this review is to address two vital research questions:

- How does deforestation of riparian areas modify organic matter allochthonous inputs?
- How do changes in organic matter inputs affect the amount and size of patches and does this affect local macroinvertebrate densities for species that disperse via drift?

Firstly, this review will explore models and mechanisms by which organic matter is delivered into a stream. Secondly, the ecology of macroinvertebrates and their dispersal mechanisms in ecosystems where resources are patchily distributed will be addressed. Finally, the anthropogenic disturbances occurring on streams and riparian areas will be exposed, with special attention to deforestation of riparian forests.

2.2. Riparian areas and their relevance to headwater stream ecology

This literature review will begin by defining what riparian areas are and how they contribute to headwater streams. Riparian areas are vital for headwater streams as they provide diverse services to lotic ecosystems. They regulate water temperature, by providing shade, and the canopy also releases organic matter in the shape of leaves, bark, twigs, et cetera to the stream below (Bilby & Bisson 1992, Bilby & Bisson 1998). Moreover, riparian areas also depend on the stream as they are functions of their geomorphic position in landscapes, and the temporal and spatial variation in the presence and actions of water (Noe 2013). In detail, vegetation impacts river geomorphology by influencing the balance between deposition and erosion along river banks, as well as directly contributing to soil organic matter deposition, thereby influencing vegetation succession (Bledsoe & Shear 2000, Noe 2013). On the other hand, hydrogeomorphic processes such as flood events may lead to an increased abundance of hydrophytic plant species (defined as a plant that grows partly or wholly in water), and to overall increased species richness, cover, and productivity, which influence the ecological succession in stream banks (Bagstad et al. 2005). However, riparian zones are not easily defined, as the concept can vary depending upon the environment and region where they are located. For example, for scientific purposes riparian areas have been defined as having a fixed width alongside designated rivers and streams. In this case, we define the riparian zone as the land which directly influences or is influenced by a body of water (Lovett & Price 2006). By using this definition, the land alongside streams, including those streams with intermittent flow and encompassing the bank itself, is considered the riparian zone. In Figure 2.1. it is shown as a discrete zonation of riparian areas based on the distribution of the dominant vegetation, and how such areas contribute to streams' ecology.

Several studies have been developed to test the importance of riparian vegetation on CPOM export to streams. For example, Merritt et al. (2010) created a flow response guide for riparian vegetation guilds – a guild is defined as a group of species exploiting the same resources in similar ways (Simberloff & Dayan 1991). The guide provides a framework for how flow, or the lack of it, affects riparian vegetation as it stresses plants and increases CPOM inputs from riparian areas. Floods and droughts are a primary disturbance factor in riparian ecosystems (Junk et al. 1989), flow alterations define riparian vegetation life cycles in riverine ecosystems (Corenblit et al. 2011), and if flow alterations are severe, the increasing stress upon vegetation leads to adaptation to new conditions (Corenblit et al.2007). Additionally, these environmental flows modify the temporal and spatial distributions of CPOM inputs, and the amount and quality of them.

The type, amount, and quality of CPOM delivered to streams also depend on the type of riparian vegetation. For instance, in deciduous forests, most of the litter falls in a relatively short period (Pozo et al. 1997). In contrast, the litterfall inputs to streams under evergreen forests are less copious (Campbell et al. 1992b). For example, Pozo et al. (1997) found that along streams where native riparian vegetation had been replaced with less litter producing eucalyptus trees, there were smaller airborne and lateral inputs (*see next paragraph*) compared to those streams under a deciduous forest. In southeastern Australia, many streams rise in forested headwaters and flow into cleared pasture areas; consequently, it is expected that direct allochthonous inputs downstream will be low, due to limited riparian tree cover (Campbell et al. 1992b, Reid et al. 2008a, Reid et al. 2008b). Although differences in CPOM inputs between different riverine regions in Australia exist, CPOM input follows a pattern in quantity, with the largest litter delivery to the stream occurring during summer (Campbell et al. 1992b). Thus, CPOM export in southeastern Australian streams is affected by major droughts and the degree of vegetation clearance in riparian areas (Reid et al. 2013), rather than the manner in which deciduous forests in northern latitudes are affected.

Allochthonous inputs in riparian areas are normally delivered by direct mechanisms. For example, airborne input of litter to the stream is delivered by gravity to the below streambed. This type of input delivers leaves and other fractions, detached from the forest canopy, to streams (Gasith & Hosier 1976, Langhans et al. 2013). Airborne inputs provide sources of energy and substrate to the stream; such inputs can take place all year around and as long as the canopy above the stream is not removed (Lovett & Price 2006). Moreover, there is a secondary mechanism that transports organic matter to the stream called lateral surface transfer (LST), which depends upon wind energy or overland flows to move light material (i.e. leaves, or small particles of other fractions) to the stream (Benson & Pearson 1993, Langhans et al. 2013, Teeri

& Barrett 1975). Finally, CPOM transported in the drift is also considered as an input mechanism for reaches located downstream from where CPOM was deposited initially, as long as it gets retained on the streambed. All these mechanisms are highly sensitive to changes in riparian areas, and define the amount and distribution of CPOM on the streambed useful for aquatic fauna (Minshall et al. 1983, Vannote et al. 1980). The dynamics of allochthonous inputs between riparian areas and streams have been explained through diverse models. However, in the next section a single model that relates to the degree of anthropogenic disturbance of riparian areas and the effect of allochthonous inputs will be considered, because it considers the type of stream where this thesis has been produced.

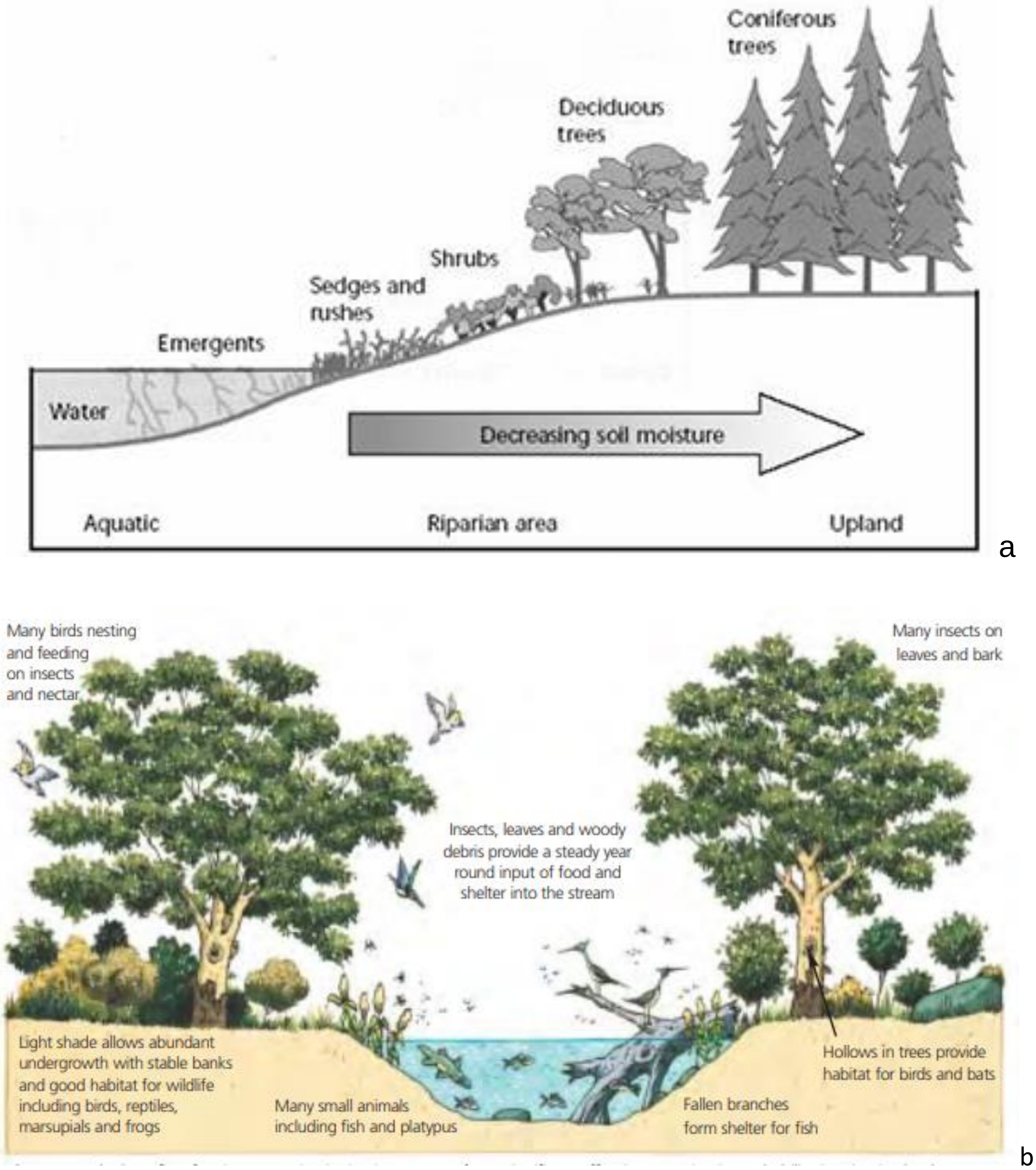

Figure 2 1 a) Discrete zones of stream, riparian areas and upland (Stevens et al. 1995). b) Interactions that occur in the riparian-stream interface (Abernethy & Rutherfurd 1999).

2.3. Riparian vegetation and streams dynamics

2.3.1. Resource flow model

Riparian vegetation plays a key role in the productivity and ecology of headwater streams in forested catchments, which are systems that depend on organic matter delivered from riparian areas (Richardson & Danehy 2007). Riparian forests drive the energy and structure of aquatic food webs by controlling the quantity and quality of allochthonous inputs (Naiman et al. 2005). Moreover, other fractions of organic matter also enter the stream; for instance, dissolve organic matter (DOM) or large woody debris (LWD) play key roles in food web dynamics, production, and nutrient processes (Peterson et al. 2001, Wallace, Eggert et al. 1999). However, a diverse range of anthropogenic activities adversely affect such dynamics in riparian areas, thereby modifying allochthonous inputs and general stream dynamics (Figure 2.2).

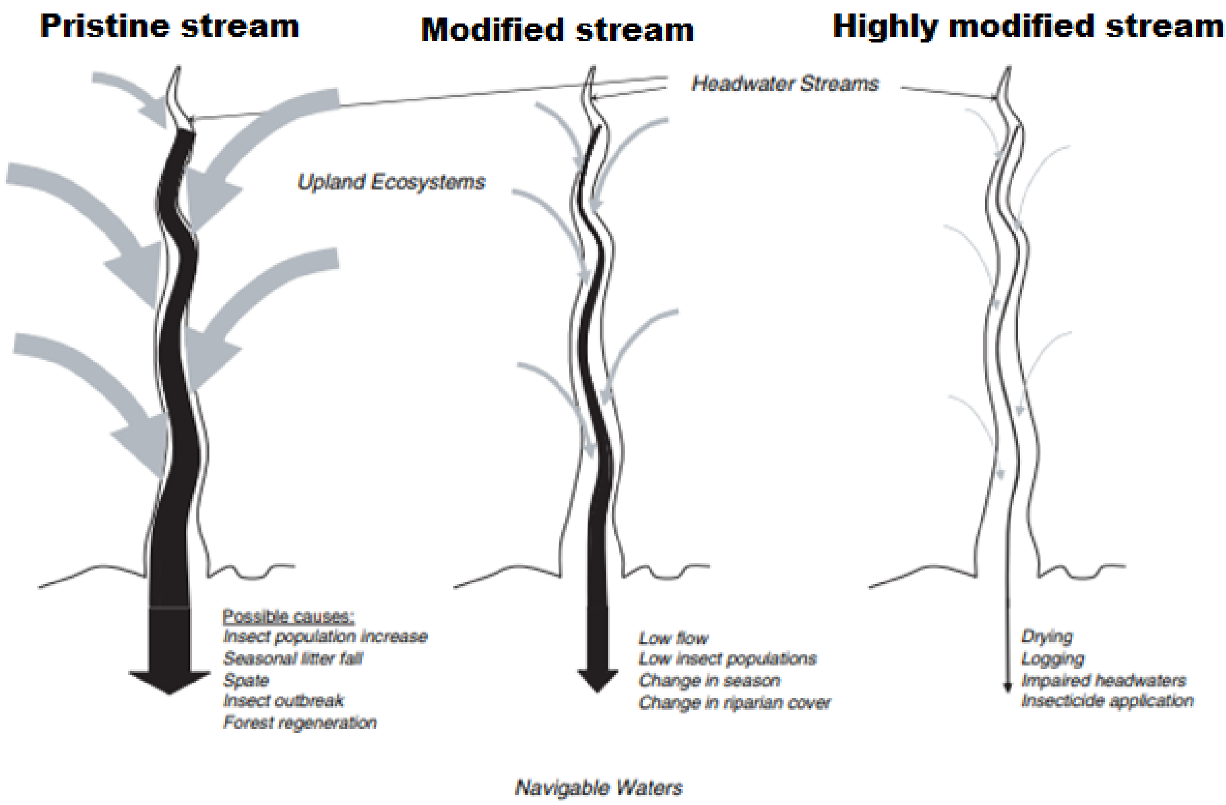

Figure 2 2 The Resource Flow Model: Magnitude of nutrient, and energy flow over time as a function of insect life history, seasonal temperature, rainfall, and anthropogenic disturbances. The figure moves from left to right as the degree of perturbance increases in streams. For example, pristine streams have larger allochthonous inputs (thicker grey arrow), while disturbed streams, with little canopy cover, receiver lesser quantities of allochthonous inputs (far right) (Bincley et al., 2010).

The first obvious relationship between riparian areas and the stream is the quantity of LWD in the stream channel. LWD influences headwaters by affecting channel form, providing sites for storage of organic matter and sediment, and modifying the movement and transformation of nutrients (Bilby & Bisson 1998). Once LWD enters streams, it remains in place until it is biophysically transformed through consumption by aquatic species or it is transported downstream. Generally, large particles of organic matter are broken down into smaller particles by physical water abrasion, or by the biological activity of fungi, bacteria, and macroinvertebrates (Wipfli et al. 2007). Moreover, aquatic invertebrates consume organic matter particles of different sizes, expelling it as faeces, which can be subsequently ingested by other organisms or transported downstream. However, the size or type of fraction consumed is tied to the seasonal timing of species-specific life cycles. (Malmqvist & Rundle 2002).

The resource flow model (RFM) shown in Figure 2.2. presents how the exchange between headwater streams and riparian areas occurs as they get more disturbed by human actions. The RFM includes seasonality as a modifying factor for both organic matter dynamics and the prevalence of species in the stream. Therefore, this causal effect model could be applicable for streams where riparian vegetation has been logged and, potentially, explain the relationship between low CPOM inputs and low density of macroinvertebrates. However, one essential factor of allochthonous inputs is their retention across the streambed, and such retention must occur for aquatic fauna to have sufficient time to use it. The retention of CPOM is product of several structures found in streams. The following section explains in detail the structures where allochthonous CPOM inputs are retained once they enter a stream.

2.4. CPOM distribution in streams

2.4.1. CPOM retention

Retention of allochthonous inputs is a key factor in stream ecology, because if this material is directly transported downstream, the local aquatic community cannot exploit it. The retention time of CPOM in the stream channel increases the consumption of this material by fungi and bacteria, and the residual products of such decomposition, for example DOM and FPOM, can be further exploited by fungi and bacteria. Once CPOM material enters a stream, soluble organic material and other nutrients are rapidly leached. However, if CPOM remains for long periods of time, macroinvertebrates break it down, and the refractory structural biopolymers (e.g. amylose and amylopectin) are slowly consumed by microorganisms (Pettit et al. 2012). These processes show the importance of retention not only for aquatic communities, but also on the ecosystem's carbon cycle (Bilby & Bisson 1998).

CPOM accumulation does not occur uniformly across the river channel. This is due to variable flows, which generate zones wherein CPOM is sorted by its characteristics such as size, weight, and buoyancy. Channel areas in which CPOM has the potential to accumulate include slackwaters (Vietz et al. 2013), benches, and LWD accumulation zones. Furthermore, the shape of a river channel determines the generation of more or less retention area. For example, Kitchingman et al. (2013), found that LWD is more likely to accumulate in meandering rivers than in those with a lower meandering grade. Moreover, seasonality also modifies where these retention structures will form in streams.

As shown before, CPOM distributes within specific areas of the stream, but also it does it in patches, which means that populations of macroinvertebrates need to find the way to these resources, and their capacity to do so might define their densities in different areas of a given stream. The capacity that each species has for reaching resources might affect local populations, because if they are unsuccessful in moving between patches this would mean that they are constrained to specific areas of the stream. On the other hand, if species are successful in dispersing between patches of CPOM, then their distribution and densities along the stream could be expected to be more homogeneous. The latter differences could produce significant effects upon local populations and on metapopulations (at landscape scale). Such ecological relationships occurring in patchy landscapes will be explained further in the next section.

2.5. Ecology of patchy landscapes

Understanding patchy landscapes and the spatial distribution of resources across riverscapes is a prerequisite to understand how movement behaviour of fauna, across patchy landscapes, affects population densities. As explained above, CPOM in headwater streams is clustered into patches, which offer energy sources and shelter for aquatic species (Richardson 1992). Patchiness represents several challenges for individuals moving between patches.

Patchy landscapes have been studied mostly in terrestrial landscapes, particularly those subject to human modification, such as in fragmentation studies (Haila 2002). Patchy resources in the landscape produce unexpected population dynamics within and across them due to the characteristics they provide for biota, as individuals need to disperse in areas where could challenge their survival due to low availability of food sources or predation while dispersing. Some models have been produced to explain such relationships. For example, Lindenmayer et al. (2008) provides a conceptual model where patch scale and landscape scale (habitat amount, patch sizes, and connectivity) interact to produce a landscape classification that complements to the patch-corridor-matrix model proposed by Forman (1995). The latter model defines the components of a patchy landscape, where patches are embedded within a matrix (the matrix refers to the area of a landscape that has no resources or the resources cannot be used by species). However, other authors of models focused on patchy landscapes consider that the characteristics of patches is equivalent in importance to the distribution of them in the landscape (Fahrig 2002, Fahrig 2003, Tischendorf et al. 2003). Moreover, several authors consider patches more than a concentration of resources, as many species use such them for reproductions, shelter, predation etcetera, which alights more with concept of habitat (Fahrig 2007, Lefkovitch & Fahrig 1985).

In ecology, the term habitat broadly refers to the resources and environmental variables present in an area that produces occupancy, and wherein a given organism survives and can reproduce (Hall et al. 1997, Southwood 1977, Whittaker et al. 1973). Moreover, the term habitat is organism-specific, inferring that the study of habitat will depend on the organism, and how resources such as shelter, food sources and reproduction are used by it. However, within a given habitat, resources are not uniformly distributed. Rather, they are typically grouped into patches (Hall et al., 1997). These patches have differing definitions, related to the hypotheses to be addressed. For instance, Levin and Paine (1976) considered a patch as a “a discontinuous area in an homogeneous reference background”. Moreover, Arditi and Dacoronga (1988) define a patch as an area that is well delimited with food uniformly distributed, outside of which there is no food in the nearby vicinity. Regardless of the definition, patches are distinguished by discontinuities in environmental characteristics from their surroundings. Implicit is the notion that the discontinuities have biological significance, and that they matter to an organism’s behaviour. Patchiness is revealed in a nearly endless spectrum of spatial scales from biospheric or continental distributional patterns, to patterns of clonal growth or individual responses to resource distributions (Moelzner & Fink 2015, Wiens 1976). Consequently, CPOM patches can be classified as patches of habitat at local scale, and their origin is given by the interaction between the stream and riparian vegetation. An important question in stream ecology is to what extent patchy distribution of resources affects species densities.

The characteristics of the spatial structure of landscapes is given by the size, shape, inter-patch distance, and quality of patches, including dispersal routes (Fahrig 2003). The distance between patches must be considered relative to species, as a given distance between two patches may be too great for a small insect to reach, yet quite short for birds or mammals. Early studies of populations with high migration rates found significant differences related to patch characteristics. For example, cavity-nesting birds, blackflies, and beetles (Faeth & Kane 1978, Gutzwiller & Anderson 1992) showed significant responses in the number of individuals reaching patches, relative to patch shape and orientation. The dispersal routes between different patches are essential features that allow movement of different species’ populations between such patches. Further, the quality of these routes has the same importance as the quality of patches, upon which the survival of individuals and species survival depend.

The distribution of high-quality resource patches across the landscape is intrinsic to ecological patterns and dynamics. For instance, aggregation of individuals within and across resource patches can promote coexistence of otherwise competing species, and of predators and prey (Chesson 2000). Consequently, the quantity of resources and their spatial distribution can influence those species that actively search for resources across the landscape (Lancaster & Downes 2014). Moreover, resource patches, in streams, are short-lived, as their presence depend on flow conditions (Pringle et al. 1988). The study of the ephemerality of patches in terrestrial landscapes, which highlight the challenge for species dispersal in lotic environments and overall population persistence, has been well documented (Palmer et al. 2000, Silver et al. 2000). The purpose of the following subsections is to provide an understanding of how resource patches of CPOM affect macroinvertebrate densities.

2.5.1. Stream landscape structure

Landscapes can be defined as heterogenous areas of land or water that originate from ecosystems interactions, and in which distances between patches might vary (Hobbs & Humphries 1995). Streams can be considered either a barrier or a corridor within a greater definition of landscape. They can constrain the dispersal of some species, which could find it impossible to cross a waterbody, and, on the other hand, streams could act as a corridor for dispersing species. Therefore, such “riverscapes” fit into the framework of landscape proposed by Turner (1989), as streams are corridors for aquatic fauna, wherein spatial elements and ecological processes produce a dynamic mosaic.

Riverine landscapes are formed by the interaction of three main zones: floodplain, riparian areas, and stream channel, and together these three zones produce spatio-temporal heterogeneity at both terrestrial and aquatic levels (Ward et al. 2002). Components of riverine landscapes include habitat patches, and the matrix in which resource patches are located (Fahrig & Merriam 1994). Consequently, the study of riverine ecosystems requires to be study in terms of ecosystems where resources are distributed patchily.

The analysis of patchy habitats has been studied in diverse landscapes and concepts related to species dispersal have been tested. Some of the concepts that explore patch distribution are island biogeography (MacArthur & Wilson 1967) the habitat fragmentation concept (Bender et al. 2003), and habitat connectivity (Baum et al. 2004, Haddad 2000, Haddad & Nick 1999). These concepts explained that the dispersal of species depends on the structure and how well-connected patches are from each other. On the other hand, other concepts have explored the reason for an individual to disperse, and how the amount of energy and mortality risk are the main factors that define successful dispersal. Two examples of these models are the least-cost path analysis and animal locomotion (Fahrig 2007). However, most studies focused on species dispersal in patchy landscapes have been developed for terrestrial landscapes (Baum et al. 2004, Fahrig & Merriam 1985, Haddad 2000, Tews et al. 2004), although some examples can also be found for aquatic ecosystems (Bellisario et al. 2012, Nielsen et al. 2005, Ning 2010). However, it is important to note that these concepts address questions about metapopulations at landscape scale, where migration/dispersal occur at large scales, but these concepts can be translated to local scale where migration might take place at short distances.

Most animals with locomotion capacities that translate in good dispersal ability disperse across landscapes, whether the landscapes are continuous or patchy. Animals disperse for many reasons such as to acquire resources, for reproductive reasons, or to avoid predators (Dingle 2007, Fahrig 2007). Consequently, to understand animal movement, it is important to analyse why individuals from different species decide to disperse, and if this dispersal implies either to change the population where it lives at or just movement within the same community. This review, however, will address local habitats in which dispersal occurs over a continuum of frequent, short-distance to infrequent, and long-distance movements (out of the local habitat) of individuals. The latter applies to individuals that are more likely to move between patches within the same population than to emigrate to a different breeding population (Bilton et al. 2001b, Diehl et al. 2008). This material raises several questions related to aquatic species dispersal. For example, is the dispersal of species affected by the distribution of CPOM patches, and how are species densities affected in patchy landscapes? Consequently, several models have been developed which aim to extrapolate the effect of resource patchiness on species densities. These have been grouped by Fahrig (1988) into three types (1) dispersal-pool models, (2) grid models, and (3) dispersal-corridor models, which will be explained in the following sections. These models that apply to landscapes where each patch comprises a whole population and in which dispersal reflects proper migration between populations

2.5.2. Dispersal-pool models

In dispersal-pool models, organisms that disperse are assumed to enter a pool of individuals that are dispersing, and that are then redistributed among resource patches following a set of variables such as limitation of resources and patch variability. The pool of dispersing organisms is a concept that allows analytical solutions which explain animal dispersal. This concept describes the pool of individuals as being homogeneous in distribution and in their characteristics (Fahrig 1988). The model has been used to study the role of dispersal in driving population stability and rates of survival (Bolnick et al. 2003, Gustafson & Gardner 1996, Łomnicki 1980). However, dispersal-pool models cannot be used to study the effects of the spatial arrangement of patches, as these models do not consider the relationship between the arrangements of patches and dispersal dynamics.

2.5.3. Grid models

Grid models include spatial landscape heterogeneity of the distribution of resources, within which a theoretical grid is placed over the area that is to be studied, including the matrix where resource patches are distributed (Fahrig 1988). In these models, each subpopulation within the grid is explicitly followed during the total simulation period. For a grid model to be used, it is necessary to obtain detailed data concerning the flow of organisms on the grid, for each simulation. Additionally, it is critical to calculate the probabilities of organisms in each grid reaching other grids (Kitching 1971, McClanahan & Wolfe 1987, Wiens 1976). Although this model can be informative, it requires a lengthy observation period as each patch must be simulated with its own probability of receiving dispersers (Fahrig 1988, Tischendorf & Fahrig 2000). A suggested approach is a mixed model between dispersal-pool and grid models, as the former lacks the sophistication to answer questions regarding dispersal, and the latter model can be too complex to answer a given question.

2.5.4. Dispersal-corridor models

In dispersal-corridor models, resource patches are represented as nodes, which are defined as points in a network of patches at which lines or pathways intersect or branch (Hutchings & Wijesinghe 1997), which might be connected, partially connected, or not connected to another one by corridors or stepping stones (Fahrig 1988). This model has successfully modelled populations of small mammals living on woodlots. Woodlots were interconnected by a fence that produced a corridor that animals used to disperse, thereby increasing their capacity to move between patches of resources (Fahrig & Merriam 1985). Such models have also been successfully used to study rodents, marsupials populations (Baum et al. 2004) and also habitat restoration (Chetkiewicz et al. 2006).

The dispersal-corridor model incorporates three important features: (I) the spatial arrangement of resource patches is explicit (II) corridors and resource patches distribution can be applied to any configuration of patchy landscapes, as these models incorporate most spatial arrangements and species dispersal dynamics, and (III) the model is simple enough to be tested by experimentation on reasonable time and cheaper than other models (Fahrig 1988). Because these important features are taken into account, the model is a robust tool for explaining animal dispersal on stream ecosystems, where water flow creates a directionality of dispersal, making it different to many other ecosystems.

Lotic ecosystems can be considered a corridor where aquatic communities can disperse by using the water flow as a passive transportation method. However, as flow is unidirectional in most cases, and CPOM patches form along the entire length of the stream, then patches could act as stepping stones for aquatic populations.

Patchy resources represent a mobility challenge to populations living in patchy ecosystems, as movement among habitat patches relates not only to mobility of animals, but also depends on the landscape throughout which animals must move (Tischendorf & Fahrig 2000). However, a corridor or stepping stones aid the movement between different patches, with stepping stones defined as a series of small patches partially connecting isolated patches (Baum et al. 2004, Haddad 2000, Saura et al. 2014). Corridors and stepping stones have been proposed as ways in which connectivity is increased across landscapes, that is, in which the distribution of patches promotes the movement of organisms between resource-patches (Fahrig & Merriam 1985, Moilanen & Nieminen 2002, Taylor et al. 1993).

Streams are corridors where are embedded stepping stones (patches) that could help the dispersal of aquatic species, and where they could use waterflow to disperse faster and for longer distances. Also, aquatic species could find shelter or food within CPOM patches during their dispersal. In the following section, I explain how corridors and stepping stones aid the dispersal of species in patchy landscapes

2.5.5. Corridors, stepping stones, and their capacity of connecting patches

Diverse studies on corridors and stepping stones have provided support for the hypothesis that corridors increase connectivity, demonstrating that these connections can increase population sizes (Fahrig & Merriam 1985, Haddad & Baum 1999), and movement among patches (Baum et al. 2004, Gonzalez et al. 1998, Haddad et al. 2003, Haddad & Nick 1999). Although theoretical and empirical evidence supports the role of corridors and stepping stones in conservation efforts in cleared landscapes (Haddad et al. 2003), how they increase connectivity may depend on other factors. For instance, Baum et al. (2004) found in grassy landscapes where corridors and stepping stones of smooth brome (Poaceae) with the same matrix enabled movement by planthoppers, as opposed to planthoppers trying to move across a mudflat matrix. These results show that the types of connections must have particular components such as being of adequate size and with low predation rates, so that fauna can use them as dispersal routes. In general, if a corridor has the same resources as patches, it should not present any barriers to dispersal, and thus may be used as conduits for migration (Haddad, 1999). Notwithstanding this, for some species, these types of connections have no effect on movement, whether measured as emigration from a patch or as a colonization success indicator (Haddad, 1999). Further, there may be negative effects upon populations, as individuals may act as vectors of disease, thereby risking other populations (Simberloff et al. 1992).

Consequently, corridors and stepping stones cannot be considered the consummate solution to interconnected patches. However, if the matrix included physical characteristics such as equivalent vegetation or substrate as there are in patches, these would promote mobility. Furthermore, it is likely that matrix features could increase the distance animals disperse to reach patches that are otherwise isolated (Baum et al. 2004, Haynes & Cronin 2003, Ricketts 2001). Haddad (2000) listed characteristics that corridors and stepping stones should have in order to be effective conduits for dispersing individuals: (I) Animals must be able to detect a stepping stone or corridor from their source patch, (II) animals should not be restricted or directed by habitat boundaries, and (III) individuals should have a low or normal predation rate when moving through stepping stones or a corridor. The lack of these characteristics in corridors or stepping stones may limit the success of individuals to reach new resources, and ultimately fail as a dispersal route.

2.5.6. Corridors and stepping stones in river ecosystems

Corridors and stepping stones have been mostly tested on metapopulations, which have different space and time scales compared to that of the populations of individuals which are distributed across patchy resources. However, the principles of corridors and stepping stones can also be used with individuals as they too must move between patches within the population to obtain resources and shelter, etcetera. For instance, CPOM patches, rocks or pieces of wood can act as stepping stones for dispersal purposes (Marchant et al. 1991). Nonetheless, it is impossible to assume that individuals from different species prefer one habitat over another, or that they use a particular type of corridor to disperse, unless the choice of habitat or corridor amongst other options has been demonstrated (Lancaster & Downes 2010). I argue that corridors in aquatic ecosystems can be created by water flow and its direction, which could effectively connect isolated patches, thereby delivering insects that might drift with stream currents to downstream patches. Notwithstanding that water flow does fit with the general concept of a corridor, it is important to highlight that individuals in the water column are surrounded by a hostile matrix with only the protection of their swimming or drifting skills. Water flow is a physical factor that can effectively displace insects beyond their dispersal capacities to new patches. Although in some cases species could also walk back upstream, but the distance covered by species depends on their size and walking capacity.

2.6. Insect dispersal in streams

River ecosystems represent challenging environmental conditions for animal dispersal, as individuals must cope with several factors that constrain dispersal capacities. For instance, a reduced flow in a river could increase the movement capacity of aquatic macroinvertebrates in colonizing neighbouring patches, as they could walk or crawl between patches without being affect by the water velocity. On the other hand, flow reduction might decrease drifting capacity, thereby constraining the possibility to colonize patches beyond a patchy neighbouring site (Growns 2008). The latter example highlights the complexity of scenarios that the variability of flow can induce in macroinvertebrates, and on their success in colonizing new habitats. Despite changes in hydrology affecting species movement (Lancaster & Downes 2010), there is a common aspect in every animal's movement, which is natural selection (Fahrig 2007). Theoretically, species have adopted different movement strategies to cope with factors that limited their mobility, by displacing individual organisms or a complete population into different patches. With macroinvertebrates, the evolution of dispersal as a strategy in the life cycles of insects reflects a balance between conflicting costs and benefits, particularly in short-term stay movements (Fahrig & Merriam 1985, Roff & Fairbairn 2007). Local mobility of macroinvertebrates depends upon physical conditions, and the adaptations of each species to disperse in river ecosystems. Further, their success in reaching resource patches is determined by such strategies.

2.6.3. Implications of animal movement in stream and management endeavours

Implications of the distribution of resource patches across landscapes and their impact upon species population persistence and density have been illustrated in previous sections. However, dispersal of aquatic macroinvertebrates and the distribution of patches are affected by ecosystem degradation by anthropogenic actions. There has been a concerted effort in recent years to reverse the grave damage that has been exacted on freshwater ecosystems by human beings. Most of this effort has been targeted at restoring physical habitat of impacted ecosystem (England & Wilkes 2018, Lake 2000, Palmer et al. 1997). The management of impacted ecosystems has been addressed for some time (Palmer et al. 1997), albeit mostly has about terrestrial ecosystems, with a paucity of research taking place on aquatic ecosystems. However, degraded streams can be useful tools, as it is possible to deploy large-scale experiments, including manipulation, yet producing minimal impacts to an already damaged system. Managed streams tend to produce less complex communities, from which data of post-restoration communities can be extracted.

Restoration endeavours have been performed without due consideration to the basic components of ecological theory, such as dispersal and colonization of resource patches. This has been addressed by Palmer et al. (1997) in the ‘Field of dreams hypothesis’, which states that restoration projects have a strong focus on habitat structure, assuming that *“if you build it, they will come”* (Tapia-Arboleda 2016). However, if the environmental conditions required for successful dispersal are not accomplished by a restoration project, it is likely that species persistence might be affected, thus threatening the functionality of the ecosystem (Palmer et al. 2014). Several studies have shown that restoration and mitigation measures do not always achieve acceptable environmental conditions. For example, Morandi et al (2014) studied 13 cases of restored streams, where invertebrate densities and species richness suffered further degradation after restoration, while a further 27 streams showed no improvement, based upon reference sites’ values. Due to the limitations of mitigation measures on deforested streams, it is imperative to understand how aggregations of patches affect the capacity of aquatic macroinvertebrates to spread amongst them. The variety of dispersal strategies and locomotion methods of macroinvertebrates requires empirical data on the colonization of resource patches of CPOM. However, it is crucial to understand the nature of human impacts on streams, a summary of which follows.

2.7. Human impacts in streams

Riparian areas are dynamic sections of riverscapes (Allan 2004), and drastic changes in their composition, size, or presence are likely to produce dramatic effects in streams and upland areas (Abernethy & Rutherfurd 1999, Lovett & Price 2006). Natural phenomena such as fires (Pettit & Naiman 2007), major floods (Friedman and Lee 2002), or severe droughts produce impacts on riparian forests, even though such phenomena are infrequent (Lovett & Price 2006), albeit predicted to become more frequent as a result of climate change (Pettit & Naiman 2007). Contrastingly, anthropogenic actions on riparian areas have resulted in gradual changes over longer time scales of years (Malmqvist & Rundle 2002). Human activities at local scales have resulted in large-scale degradation of stream sections, with dramatic effects on their ecosystems. In Australia, such changes have been more drastic in the south-eastern states of New South Wales and Victoria (Reid et al. 2008a). The most common destruction to riparian areas in Australia comprises wide-scale removal of riparian vegetation, and some states have also reported that the presence of feral animals and plants have negative synergetic effects related to deforestation (Price & Tubman 2007).

The consequences of deforestation are clearing of native riparian plants, which decreases the natural source of allochthonous inputs (Reid et al. 2008a) and increases the amount of light and water column temperatures. Consequently, biomass of photosynthetic organisms such as algae and weeds increase (Bunn 1986, Vannote et al. 1980), at times choking the waterways and depriving aquatic organisms of oxygen (Skinner et al. 2012). Removing trees from riparian areas eliminates the source of large branches and trunks, which are two major factors that increase channel complexity (Livers and Wohl 2016). The removal of riparian vegetation destabilises streams and increases channel width and channel erosion (Rutherfurd 2007). Other negative impacts expected, when deforestation of riparian areas is systematized, is the increase of water and land salinization, as salt-saturated water drains into streams, ultimately producing saline waterways (Price & Tubman 2007). Further impacts and their effect on lotic ecosystems are shown in table 2.1.

The restoration of south-eastern Australian streams requires the production of data that can be used in such ecosystems, as most restoration projects have failed to connect allochthonous inputs with an increase in local aquatic fauna (Reid et al. 2008a). Restoration projects do not achieve their goals, in most cases (Morandi et al., 2014). Due to the limited success in restoration projects, several questions related specifically to the restoration of streams, have been raised. For example, Gobster and Hull (2000) posed the following questions: is restoration of nature even possible? What is a natural system and how does that relate to human purpose? Consequently, in recent years, the restoration of ecosystems has been shifting to a position of restoration through the least disturbance required to achieve it (Benayas et al. 2009). This shift is also changing the type of science demanded from restoration ecologists.

For example, the scientific approach focusing on testing population dynamics may be replaced by quantifying the role of a particular species, or group of species, which plays a seminal role in supporting ecosystems processes. Understanding how populations disperse across new resources of patches is but one feature of ecological communities. However, it is an imperative factor to encompass when restoring an ecosystem where resources are patchily distributed.

Table 2-1. Primary anthropogenic factors changing riverine ecosystems. Modified from Allan and Castillo (2007b) and Malmqvist and Rundle (2002).

Forcing factor	Proximate causes	Abiotic alterations	Biotic implications
Habitat alteration	Damming, water extraction, water transfer schemes.	Loss of habitat flow iteration, increased drought potential, severing upstream-downstream linkage	Altered habitat conditions, reduced species dispersal
	Channelization	Reduced habitat and substrate complexity	Reduction of species diversity, favouring species tolerant to drought
	Deforestation, intensive agriculture, urban developments	Altered allochthonous energy sources, increased erosion, promotion of flash floods	Changes in assemblage composition, altered trophic dynamics
Species removal and addition	Fisheries, aquaculture, sport fishing, horticulture (in riparian zones)	Invasive species that have the potential of modifying habitat	Increased/reduced competition, altered energy inputs from riparian areas.
Contaminants	Nutrient enrichment, from agriculture or wastewater, acidification, introduction of heavy metals, organic toxins	Increased N and P, altered nutrient ratios, increased trace metals, reduced pH, increased PCB and pesticides	Increased algal blooms, Physiological and food change effects, Toxic effect through magnification and bioaccumulation.
Climate change	Temperature changes	Milder winters, altered evapotranspiration regimes, changed in flow regimes	Range shifts in accordance with physiological tolerances, higher productivity
	Precipitation changes	Altered flow patterns, greater increases of flash-flows	Greater disturbance effect

2.7.1. Deforestation of riparian areas and its implications on CPOM patches, and dispersal dynamics of macroinvertebrates.

The amount and quality of allochthonous inputs affects the dispersal of aquatic macroinvertebrates, as a decrease of these inputs means that patches where CPOM is accumulated are scarce. Macroinvertebrate disperse using different locomotion strategies, and their success of reaching new patches is affected by the distance between them. Moreover, deforestation of riparian areas affects the amount and type of allochthonous inputs that streams receive. Consequently, it is expected that allochthonous inputs, in streams where riparian vegetation has been partially or completely removed, will decrease. Yet, it is unknown how changes in the distribution and size of patches affect local dispersal of macroinvertebrates. Consequently, a major question in ecology is how areas with a lower number of patches which are associated with human deforestation of riparian areas, affects the capacity of macroinvertebrates to reach them. In the following chapters, specific questions about deforestation of riparian areas, allochthonous inputs, resource patches, and macroinvertebrate species dispersal will aim to connect causal-effects between habitat alteration and species density/dispersal dynamics in streams where external inputs are vital.

2.8. Background summary and research focus

Riparian vegetation is essential for headwater streams as it regulates allochthonous inputs of CPOM. CPOM inputs accumulate in patches, where ecological relationships between aquatic populations occur, and where sources of energy and shelter can be found by aquatic species. However, aquatic macroinvertebrates need to reach these patches in order to obtain the benefits that these accumulations of organic matter provide within streams. Macroinvertebrates reach such CPOM patches by drifting in the water. However, this is not simple, as dispersal strategies employed in navigating the size of patches, and the inter-patch distances, may affect macroinvertebrate capacity to reach patches of resources.,. Thus, a lower or higher presence of patches within a stream could modify the densities of species at a local scale. Furthermore, globally over the last two centuries many riparian forests have been logged. Deforestation of riparian vegetation decreases CPOM allochthonous inputs, which could reduce the size and abundance of patches in deforested streams. Consequently, the dispersal of macroinvertebrate species in streams with fewer available patches, is likely to be adversely affected where strategies are inappropriate for the conditions. The latter may result in a significant decrease of local populations of macroinvertebrates in streams where patch density is low. In the following chapters allochthonous input dynamics in deforested streams will be explored, and whether such deforestation affects the amount and distribution of CPOM patches available, thereby ultimately affecting local macroinvertebrate densities.

3. How much deforestation reduces inputs of plant detritus to headwater streams? A systematic literature review.

Title

How much deforestation reduces inputs of plant detritus to headwater streams? A systematic literature review

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3.1. Abstract

Allochthonous inputs play a dominant role in headwater stream ecosystems, providing relevant energy subsidies to headwater streams. Human commercial activities in riparian forests (i.e. tree plantations, agriculture, cattle grazing) have reduced allochthonous inputs in many streams throughout the world. We reviewed 45 research studies that examined the effects of deforestation on the movement of Coarse Particulate Organic Matter (CPOM) into streams. These studies were concentrated mostly in temperate or subtropical regions (U.S.A., Canada, Spain, and Australia), often in first and second order streams. Most studies focused on airborne inputs only, while lateral surface inputs, or downstream transport of CPOM were not commonly studied. The quality of evidence extracted from articles reporting significant differences between forested and deforested headwater streams, showed strong replication and sufficient sampling length. Hedges' effect size (*g*) was calculated for allochthonous inputs data from the 45 articles and plotted against deforestation. A threshold for airborne inputs and BOM standing stock was observed when deforestation reached 70%. At that level of deforestation, effect sizes decreased by up to -5 standard deviations. Such a decrease potentially affects CPOM dynamics in headwater streams, where aquatic fauna depends on allochthonous inputs to support their nutritional needs.

Keywords: CPOM, allochthonous inputs, benthic organic matter, deforestation, riparian vegetation

3.2. Introduction

In heavily forested headwater streams heterotrophic production is supported primarily by terrestrial coarse particulate organic matter (CPOM). Headwater streams are defined as channels that occur at the edge of any fluvial network with well-developed riparian corridors of vegetation (Richardson & Danehy 2007); these ecosystems often depend on allochthonous inputs of CPOM. For example, some fauna shred leaves, others graze on biofilms that develop on leaves and pieces of wood, while other fauna directly consume particles of CPOM that have been broken down (Benfield 1997, Bilby & Bisson 1998, Minshall et al. 1983). Allochthonous inputs are particularly relevant in small streams located in forested regions, where dense canopy coverage limits light incidence, and subsequently autochthonous production (Vannote et al. 1980). Allochthonous inputs, in addition to providing energy to the stream (Pettit et al. 2012), also provide a stable substrate for aquatic organisms and, at the same time, larger pieces of CPOM (branches, small logs etc.) increase channel heterogeneity. Higher channel heterogeneity implies the development of diverse habitat patches along the stream (Lake 2000). Diversity of habitat patches, in turn, may influence species richness and ecosystem resistance/resilience in the presence of disturbances (i.e. floods or droughts) by providing habitat heterogeneity for the species inhabiting a given stream. Variation of allochthonous inputs affects many aspects of aquatic communities. For example, limited sources of energy, or, more complex effects, whereby homogeneity of the stream due to the removal of retention structures reduces channel complexity, thereby leading to a potential decrease of species richness.

Streams throughout the world are one of the most threatened ecosystems, largely due to agricultural and commercial activities such as cropping, livestock grazing, and tree plantations (Achard et al. 2002). Such activities lead to the deforestation of large sections of riverine vegetation, which can create adverse impacts in streams. For instance, the removal of riparian tree cover adjacent to streams surrounded by pastures, results in lower concentrations of allochthonous inputs (Dala-Corte et al. 2016). Likewise, streams that were adjacent to a natural riparian forest that has been transformed into a tree plantation, are likely to be affected detrimentally by the change in the type and amount of detrital inputs (Molinero & Pozo 2003, Molinero & Pozo 2004). Furthermore, factors such as urbanization of headwater streams increase the ecological pressure on riparian vegetated areas. Although urbanization may cover smaller sections of areas where headwater streams are located, their effects can be considered long-term (Carroll & Jackson 2009, Roberts & Bilby 2009).

Multiple theories aim to explain the relationship between riparian vegetation and the stream. For example, the River Continuum Concept predicts the proportions of functional feeding groups expected according to the inputs of CPOM along rivers (Vannote et al. 1980). Moreover, the Flood Pulse Concept (Junk et al. 1989) and Riverine productivity models (Thorp & Delong 1994) explain how periodic inundation control the lateral exchange of water, nutrients and biota between the stream channel and the adjacent riparian and floodplain areas (Junk et al., 1989). One of the latest models is the River Wave Concept (Humphries et al. 2014). This concept elucidates the location and source of autochthonous production and inputs, and the potential storage, transformation, and transport of the material and food sources derived from such production or inputs (Humphries et al. 2014). Further, the concept argues that production and inputs are directly connected by a river's temporal tidal waves, or, small changes in water levels that are affected by by lunar phases (Humphries et al. 2014). Nonetheless, these models have certain limitations, as they do not explain the effect of removal of terrestrial vegetation, and hence are unable to predict if CPOM allochthonous inputs decrease immediately after deforestation of riparian areas begins, or if there is a threshold between the percentage of canopy cover and the decrease of allochthonous inputs.

In this paper, we use a systematic literature review to pose the following research questions: (i) what types of anthropogenic activities reduce allocthonous detrital inputs? (ii) is the available information based on strong or weak evidence as judged on survey designs? (iii) what is the relationship, if any, between the amount of deforestation and reduction in allochthonous inputs?

3.3. Methods

This review was undertaken following the methods proposed by Pickering et al. (2014), who focused on systematic literature reviews of environmental studies. They proposed three main steps: i) selection of keywords, ii) selection of database and criteria for selection of papers, and iii) reading and assessment of the selected papers. The research articles chosen for this review were published in English-language journals. The papers selected required that the streams researched had riparian zones which had been modified by anthropogenic activities, which otherwise would have had the potential to modify allochthonous CPOM inputs into the stream. The papers were obtained from electronic databases of scientific journals including Academic Search Complete (EBSCO), Environmental Science Collection (Proquest), Environmental Complete (EBSCO), GreenFILE, Science and Geography Education (SAGE), SCOPUS, Web of Science, and Agricola (Proquest). The database search was performed from January 2016 to May 2016, with supplementary searches undertaken until January 2019. The employment of several databases to perform the research was due to the large range of disciplines that examine effects of deforestation. A range of databases ensured that a comprehensive and up-to-date set of papers was found for this review. Keywords used for the searches of organic matter were: ‘allochthonous inputs’ ‘coarse particulate organic matter’, ‘organic compounds’, ‘organic matter’ and ‘canopy cover’. The keywords for anthropogenic activities used for the searches were: ‘agriculture,' ‘agricultural impact’, ‘farm,' ‘countryside,' ‘outback,' ‘backwoods’, It is noted that some studies established that ‘backwoods’ were not necessarily intact, as occasional illegal logging had taken place in such locations. Other keywords for anthropogenic influences on allochthonous inputs included ‘grasslands’, ‘logging impact’, ‘pasture,’ ‘tree plantation’, ‘cattle grazing’, and ‘urbanization’. Additionally, keywords used for aquatic ecosystems were: ‘river,' ‘creek’, ‘stream’, ‘watercourse,’ and ‘river channel’.

The selection of documents published in academic journals was based upon original research which described the results of anthropogenic impact on riparian zones, which potentially affected allochthonous inputs of CPOM. Initial searches meeting the selection criteria included 200 papers, dated from 1989 – 2018. The cited literature of these articles was examined in order to identify other potentially relevant papers. Firstly, paper titles and abstracts were read in order to eliminate papers that were not relevant to this research. This process reduced the number of articles to 100. Secondly, in order for an article to be considered appropriate for our research, it was required to address two or more of the following conditions: 1) sites with different canopy cover had been compared; 2) allochthonous inputs of CPOM from riparian areas into the stream were the focus of the study; and 3) the study examined the effect of deforestation or modification of riparian vegetation for commercial purposes (agriculture) or human settlement (urbanization). These conditions eliminated many studies that focussed predominantly on other factors, such as responses of aquatic biota to CPOM. Examples of studies not considered include Bojsen et al. (2003); Hepp et al. (2016); Lorion and Kennedy (2009b), or those which examined other types of allochthonous inputs (e.g. dissolved organic matter), or focussed on aspects such as storage of CPOM in stream sediments, rather than CPOM transport.

The methods from the selected papers were read and classified as observational studies if they compared disturbed and undisturbed riparian areas, or experimental studies if clear controls and well-defined manipulative treatments were employed. Additionally, we collected data on the following types of inputs and comparisons between forested and deforested sites: (i) airborne (inputs delivered directly from the canopy), (ii) lateral surface transport (LST) inputs (defined as organic matter transported by wind from the banks into the stream channel), (iii) standing stock of benthic CPOM (BOM), (iv) comparisons between CPOM inputs of restored and intact sites. This final process reduced the number of articles to 45 appropriate studies.

The description of the sites provided by the authors, was used to catalogue the type of deforestation present in each study. For example, clear-cut sites were grouped as 100% deforested sites. Additionally, if a strip of trees was left intact along stream banks of deforested sites, then the sites were classified as 90% deforested. This classification is based upon studies which have shown that although a line of trees along river banks will still deliver allochthonous inputs to streams, the input is some 70-80 % lower than forested sites (Sweeney et al. 2004). Where forested strips covered more than 30 m from the banks, deforestation was classified as 60-70%, while restored sites were grouped under 30-40% deforestation, and intact sites were classified as 0% deforested.

The quality of evidence was weighted in each paper by adapting the systems proposed by Norris et al. (2008) and Greet et al. (2011) (Table 3-1). This method tests evidence against a series of criteria and can be used to build an argument for causality through the collective strength of several pieces of individually weak evidence. We modified the criteria provided by Greet et al. (2011) as we weighted the quality of evidence based on the type of methodology employed in each article. For example, the sampling method was set to provide a higher score to those studies that implemented Before-After Control-impact (BACI) designs. This is due to BACI designs having clear controls and samples which were taken before and after disturbance, thereby highlighting the potential effects produced by disturbance (Underwood 1991). Conversely, studies where the sampling did not include reference/control sites had the lowest score possible. Additionally, the length of the study was added, such that higher scores were produced by those studies with the longest sampling campaign (one year ≥), and lower scores were produced by those studies that sampled sites for six or less months. The maximum score possible for the evidence produced in an article was 11 points. This score equated to strong evidence, based on an appropriate sampling design with sufficient replication, which had been sampled over 12 or more months. Articles with scores above seven were considered to provide sufficient evidence, having either sufficient number of replicates, or long sampling periods, but not both. Studies that scored seven had some weaknesses in design, such as low replication or short sampling duration. Scores of six or lower were considered weak studies due to both low replication, and short sampling duration.

Table 3-1 Weights applied to study design types, number of independent control sites and number of independent impact sites to calculate an overall study weight for each relevant study

Study design type	Weight
After impact	1
Reference/control vs impact sites	2
Experiment related to CPOM inputs	3
BACI design	4
Number of independent control sites	
0	0
1	1
≥2	2
Number of independent impact sites	
0	0
1	1
≥2	2
Study length	
≤6 months	1
1 year	2
≥2 year	3

Hedges' effect size (*g*) (Hedges, 1981) was calculated to quantify the sizes of differences in airborne inputs, LST, and BOM values between sites with different densities or types of riparian vegetation, using equation 1.

Equation 1

$$g = \frac{M_1 - M_2}{SD^*_{pooled}}$$

Where:

- M_1-M_2= difference in means, where M_1 is mean of treatment site and M_2 is mean of control/reference site.
- SD^*_{pooled} = pooled and weighted standard deviation (SD) (Cohen, 1988), calculated using standard deviation (SD) from each sample type according to:

$$SD_{pooled} = \frac{\sqrt{SD_1^2 - SD_2^2}}{2}$$

Where SD_1 = standard deviation treatment site and SD_2 = standard deviation control site

Some studies contained multiple comparisons. For example, comparison of reference sites (i.e. forested sites) to other sites that had different degrees of deforestation, or where riparian vegetation had been modified (i.e. clear-cut sites, low canopy cover, farmlands, or tree plantations). In these cases, (*g*) was calculated for each of the comparisons, therefore, some studies contributed multiple values of *g* (Table 3-2). Finally, we plotted (*g*) was plotted against the percentage of deforestation to reveal any relationships between size of effect and degree of deforestation.

Table 3-2. Articles that contributed with more than two points to produce figure 3.1. (g). Some studies compared more than one stream with reference sites, which produced several (g) points of streams with different degrees of negative impacts

Reference	Year	Number of Airborne (g) values contributed by article	(g) values	Number of LST (g) values contributed by article	(g) values	Number of BOM standing stock (g) values contributed by article	(g) values
Golladay et al.	1989					3	-0.483
							-0.206
							-0.690
Melody and Richardson	2007					9	-0.079
							0.096
							-2.397
							-3.176
							-0.69
							-1.30
							0
							0.045
							-3.69
Carroll et al	2008	3	0.108				
			-1.22				
			-1.61				
Reid et al.	2008	3	0.084	3	-0.05	3	-0.064
			-0.686		-0.5		-0.516
			-0.821		0.05		-0.271
Masi and Miserendino	2009					5	-0.319
							-0.057
							-0.097
							-0.507
							-0.389
Roberts and Bilby	2009	3	0.061				
			0.089				
			-0.472				
Kiffney and Richardson	2010	3	-0.335				
			0.015				
			0.109				
Chadwick et al.	2010	3	-0.221	3	-0.44	3	-0.180
			0.009		-0.71		0.0015
			-0.091		-0.08		-0.469
Hagen et al.	2010	3	-0.069				

			0.004
			-0.561
Imberg et al.	2011	5	-0.379
			-0.346
			-0.432
			-0.101
			-0.676

3.4. Results

Most studies focussed on airborne inputs into streams, with measures of benthic standing stock of CPOM being the next most common (Table 3-3). There were scant studies that quantified the amounts of CPOM delivered to sites via drift. As expected, most studies found that tree leaves dominated CPOM, given that research had been undertaken in forests or landscapes with a mix of forest and grasslands. Likewise, standing stock of CPOM was dominated by leaves, with larger fractions also being reported (e.g. twigs and bark).

Most articles focussing on airborne inputs reported decreases of allochthonous inputs after vegetation was altered (Table 3-3). Similarly, in many studies, LST inputs were reported to decrease in deforested areas (Table 3-3). Regarding study design, relatively few studies employed designs that provided strong inference (e.g. BACI-designs), and many were of short duration (6 months – 1 year), albeit many studies did have controls (Table 3-3).

Both airborne inputs and BOM standing stock values declined when deforestation of riparian vegetation was >70% (Figure 3.1). At this level of deforestation, effect sizes measuring relative losses of CPOM increased by up to five standard deviations. LST inputs were relatively sensitive to changes in the riparian zone, as most *g* values were negative whenever the riparian forest was only partially deforested. LST inputs decreased as soon as deforestation reached 10% and it continue dropping until the deforestation reached 40%, where LST inputs decrease -2 standard deviations (Figure 3:1). Moreover, many of the studies that provided evidence of significant decreases of airborne and LST inputs also scored high study weight scores (Table 3-4).

Table 3-3 Number of published studies (1989-2018) that studied the decrease of CPOM allochthonous inputs related to changes in riparian vegetation. Each category represents information extracted from the articles, and by using the Excel filter function, it was possible to isolate each category and the type of evidence provided by 45 articles.

Category	No. of studies	Number of studies showing a decline in CPOM inputs	Number of studies showing no significant change in CPOM inputs
All studies	45		
Source of CPOM			
Airborne inputs	32	31	1
LST inputs	13	8	5
BOM standing stock	11	11	0
Drifted CPOM	5	3	2
Survey or experimental design			
BACI-design experiment	3	1	2
Experiment with controls	3	2	1
Observational studies with control	33	30	3
Observational studies without controls	6	1	5
Dominant allochthonous CPOM fractions			
Leaves	29	20	9
Bark	1	1	0
Needles	1	1	0
Twigs/branches	1	1	0
Dominant BOM standing stock fractions			
Leaves	10	5	5
Bark	1	1	0
Grass	1	0	1
Miscellaneous material	1	1	0
Landscape			
Forest	10	2	8
Grasslands	3	3	0
Mixed landscape (forest and grasslands	16	10	6
Mixed landscape (forest and tree plantation)	7	6	1
Mixed landscape (forest and urban development)	5	4	1
Study Length			
6 months ≤	13	8	5

1 Year	18	11	7
2 Years	7	6	1
2 years ≥	7	5	2
Continent			
Australia/Oceania	8	5	3
Asia	2	1	1
Africa	2	2	0
Europe	8	5	3
North America	19	13	6
South America	6	3	3

Table 3-4 Details of the studies that provided evidence of the effect disturbance of the riparian vegetation on CPOM dynamics, including evidence weight assessment.

	Author/year	Location	Journal	Allochthonous inputs	BOM standing stock	Samples of aquatic fauna were taken	Study weight
1	Smolders et al. (2018)	Australia	Ecological engineering		X		9
2	Inoue et al. (2012)	Japan	Limnology	X		X	9
3	Kiffney and Richardson(2010)	Canada	Forest Ecology and Management	X			9
4	Reid et al. (2008)	Australia	Marine and Freshwater Research	X	X		9
5	Scrimgeour and Kendall (2003)	Canada	Freshwater Biology	X		X	9
6	Roberts and Bilby (2009)	U.S.A.	Journal of the North American Benthological Society	X			8
7	Carvalho and Uieda, (2010)	Brazil	Brazilian Journal of Biology	X			8
8	Hagen et al. (2010)	Canada	Hydrobiology	X			8
9	Chadwick et al.(2010)	U.S.A.	Freshwater forum: A journal of the Freshwater Biological Association	X			8
10	Hoover et al. (2011)	Canada	Canadian Journal of Forest Research	X			8
11	Abelho and Graca (1996)	Portugal	Hydrobiology	X	X	X	8
12	Carroll and Jackson, (2009)	U.S.A.	Fundamental and applied ecology	X			8
14	Alberts et al. (2018)	U.S.A.	Freshwater science		X		8
15	Mineau et al (2012)	U.S.A.	Ecology	X	X		7
16	Masi and Miserendino (2009)	Argentina	Ecologia Austral	X	X		7
17	Santiago et al. (2011)	Spain	Forest Ecology and Management	X			7

18	Webster et al. (1990)	U.S.A.	Journal of the North American Benthological Society	X			7
19	Campbell et al. (1992a)	Australia	Freshwater Biology	X		X	7
20	Delong and Brusven (1994)	U.S.A.	Environmental Management	X			7
21	Ellis et al. (1998)	U.S.A.	Journal of Arid Environments	X			7
22	Molinero and Pozo (2004)	Spain	Hydrobiology	X	X		7
23	Stone et al. (2005)	U.S.A.	Journal of Environmental Quality		X	X	7
24	Imberger et al. (2011)	Australia	Freshwater Biology	X			6
25	Pozo et al. (1997)	Spain	Journal of the North American Benthological Society	X			6
26	Pozo et al. (1997)	Spain	Limnetica	X			6
27	Afonso et al. (2000)	Brazil	Hydrobiology	X			6
28	M'Erimba et al. (2006)	Kenya	African Journal of Ecology	X			6
29	Robertson and Rowling (2000)	Australia	Regulated Rivers: Research & Management	X	X		5
30	Magana (2001)	Kenya	Hydrobiology	X			5
31	England and Rosemond (2004)	U.S.A.	Freshwater Biology	X		X	5
32	Connolly et al. (2016)	Australia	Agriculture, Ecosystems and Environment		X	X	5
33	Franca et al. (2009)	Brazil	Marine and Freshwater Research		X		3

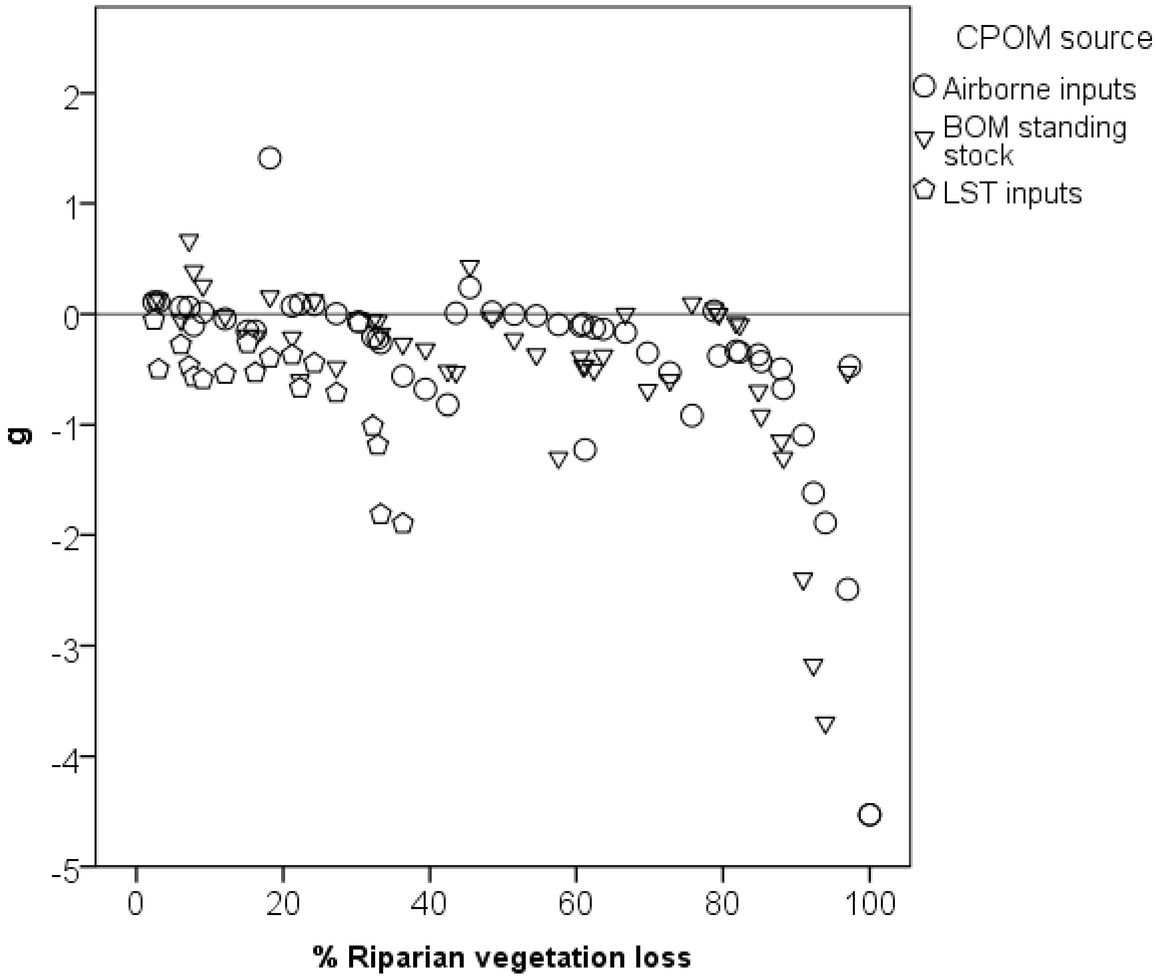

Figure 3 1 Values for Hedges' effect size (g) for airborne, BOM, and LST fractions plotted against the magnitude of deforestation of riparian zones across 45 published studies.

3.5. Discussion

A literature review was conducted in order to investigate the connections between deforestation of riparian zones and its effects on CPOM inputs into headwater streams, and the strength of evidence provided by published research was evaluated. Effect sizes were calculated, thereby revealing relationships between the proportion of vegetation removed and changes in CPOM inputs.

3.5.1. Threshold between riparian vegetation deforestation and allochthonous inputs

The literature pointed to an abrupt decrease of CPOM entering streams via airborne inputs from riparian cover, when such cover was reduced by 70% or greater. Interestingly, standing stocks of benthic organic matter within stream channels showed the same relationship, suggesting that airborne sources are the dominant route by which CPOM enters streams and, potentially, the declines of both fractions are causally related. However, the latter statement should be considered with caution, as the limited number of studies sampling LST and drift CPOM did not extrapolate how much such fractions contribute CPOM inputs into streams. Notwithstanding this, our data shows that when extensive or intensive human activities occurred, (*g*) values decreased sharply. For example, where data provided by studies compared intensive agricultural or extensive deforestation in riparian areas, allochthonous inputs decreased sharply (Carvalho & Uieda 2010b, Molinero & Pozo 2003, Molinero & Pozo 2004). Similarly, streams located in urbanized areas showed sharp decreases of allochothonous inputs, similar to those sites under intensive agriculture. Nonetheless, some studies established that there were increases in allochthonous inputs when deforestation was controlled. Studies of riparian reforestation areas reported canopy recovery to be between 30-40% of the original native canopy cover. For example, Kiffney and Richardson (2010) compiled data from streams where different management practices were applied, and found that streams with riparian vegetation extending 30 m from the stream to inland, produced an increase of allocthonous inputs (g = 0.109). However, when riparian vegetation decreased to 10 m (g), values were slightly lower than those of the reference sites (g= -0.015). Such evidence indicates that when appropiate management practices are performed, allochthonous inputs still remain stable in sections where riparian vegetation has been largely affected, but where the first line of trees is still intact.

CPOM allochthonous inputs provide materials and energy for food webs in headwater streams and many of these inputs remain on the streambed as benthic organic matter (BOM). We found that airborne inputs and BOM standing stock decreased similarly, both showing sharp declines at ~ 70% deforestation. Such a strong relationship between airborne inputs and BOM can be used as a quick method for the identification of streams threatened with a potential lack of BOM. However, we caution that many more studies are required to estimate confidently a deforestation threshold whereby BOM declines. Our results are based on 45 studies, being the total number that met our stringent criteria for inclusion. Additionally, some studies contributed multiple estimates of effect sizes, by comparing multiple sites with different reforestation levels, which thus illustrates that the points in Figure 3.1 are not all strictly independent (Table 3-2).

LST inputs were highly sensitive to deforestation as such inputs decreased. Further, they remained low even when there were small proportions of deforestation. Unfortunately, the number of studies of LST inputs are scant, and further research is required to quantify LST effects. Additionally, studies examining inputs via drifting CPOM are limited. Theoretically, CPOM that drifts from forested to deforested reaches might compensate, to some extent, for local reductions in CPOM allochthonous inputs (Minshall et al. 1983; Vannote et al. 1980). However, there is insufficient evidence to evaluate this hypothesis, as there were only five articles reported drifting CPOM between forested and deforested reaches or streams (Brown & Timms 2002, Carvalho & Uieda 2010a, Inoue et al. 2012, Molinero & Pozo 2003, Molinero & Pozo 2004). Moreover, none of the latter articles examined in detail the effects of deforestation upstream. It is necessary for more studies to be undertaken that consider varying distances between deforested sites and the nearest forested sites. While the findings suggest a threshold relationship between losses of riparian vegetation and declines in CPOM in streams, more extensive research is required to quantify the relative contributions of LST and drifting CPOM.

3.5.2. Methodological limitations and directions for future research

The majority of studies (n = 33) which examined allochthonous CPOM inputs were observational. The weights applied to the design type from many observational studies indicated that those including the collection of samples of different CPOM sources generated the highest values. However, the weight of a study was also influenced by the collection of other samples, such as macroinvertebrates or other types of biota. For example, Scrimgeour and Kendall (2003), Abelho and Graca (1996), and Inoue et al. (2012) showed heavier weights of evidence as they linked CPOM inputs with the effect on local biota (Table 3.3). Although observational studies provide sufficient weight to the quality of the data provided, some weaknesses are inherent. For example, in the hierarchy of evidence quality for environmental studies, observational studies are categorized II-2 (Pullin & Knight 2003). Category II-2 indicates that some difficulties in the design are due to the number of replicates or due to the type of controls. Moreover, observational studies rely on assumptions, such as any change occurring on the treatment sites is the product of human activity (Smith 2002). Thus, it is difficult to prove that changes taking place on an impacted site are the direct result of commercial activities in the area. Therefore, it is important to consider if an alternative sampling design would produce results that directly link deforestation/ disturbance with decreases of allochthonous inputs.

The application of different methodologies, such as BACI designs, offer an excellent option for evaluating changes on the CPOM dynamics caused by human commercial activities. In BACI designs, data is collected from all sites/elements to be evaluated (i.e. Before, After, Control, and Impact sites), and such designs include replication of each of the elements. The specifications of BACI designs are difficult to comply with in impacted streams, as it is required to have at least two similar streams, which should be sampled before and after impact (i.e. deforestation). Finding a pair of streams that meet this requirement is unlikely in the natural world, as each stream may have been affected differently over time. Nonetheless, some cases have been reported; for example, within the 45 articles selected for this review, the studies proposed by Kreutzweiser et al. (2004) and Smolders et al. (2018) were based on a BACI design, whereby different sections of forest were selectively cut down, and the differences in CPOM inputs were measured. The advantage of using BACI designs is that the data is obtained before human perturbation, and such data can then be used to estimate the rate of change of allochthonous inputs into a stream, and more importantly, to identify/isolate the factor that is causing changes to allochthonous inputs (Downes et al. 2002). Moreover, the manipulative approach of BACI designs, being similar to traditionally controlled experiments, allows for validation of outcomes.

Streams can be found with different degrees of degradation in impacted catchments; however, it is unlikely to find control streams to compare them against, thus researches must adapt their designs to the prevailing conditions. For instance, Scrimgeour and Kendall (2003) proposed a block-type experimental design to assess the effect of cattle-grazing over allochthonous inputs. Block designs are used largely in agricultural research, as treatments are confined to specific areas (blocks). Consequently, Scrimgeour and Kendall (2003) proposed the proper identification and manipulation of variables between control and treatments, and from this design it was possible to gather data from experimentation, rather than observation. However, such experiments are not representative of the study of CPOM dynamics, and such experimental manipulation would be complicated to implement, especially when the scale of an experiment increases, as it would not be recommended or ethical to deforest vast extensions of riparian forest to test a hypothesis. Nonetheless, other sampling options can produce sufficient data. Examples include the sampling methods of those studies which focussed on agricultural and tree-plantations which incorporated observational studies with controls (Table 311), and which are used extensively. To illustrate how best control sites might be used, a fencing system could be installed along an impacted stream in order to protect riparian vegetation from cattle.

Some limitations were observed relating to the number of streams sampled in studies, thereby limiting the reliability of the data. For example, some studies were extensive and covered entire basins, albeit this can limit the frequency and amount of data collected from each site. For example, Hoover et al. (2011) covered an entire basin by sampling 20 streams; however, the number of samples collected at each stream was limited to one site per stream x two replicates x three seasons(n=120). This led to several assumptions being made, such that a single site per stream was given to represent the entire riparian system along the stream. Further, two replicates per site also represents a low number of samples, reducing the power in a test of significance, and leading to a Type II error. Therefore, if no information is available of the CPOM dynamics in the streams of a region, we recommend focusing the research on a limited number of streams with multiple replicates, varying accordingly to the hypotheses to be addressed. Apart from the strategic selection of the number of streams to be studied, it is also important to consider streams that will assist in answering related research questions. For instance, only two of the 45 studies examined included regulated streams in which to compare CPOM dynamics. These streams may have had, for example, dams or weirs etc. to regulate flows of water. Structures that regulate waterflow could produce significant changes in the transport of drifting CPOM up and downstream, whereby there may be a decrease in discharge, which increases the depositional rate of CPOM upstream, simultaneously limiting the source of energy in downstream sites. It is possible that the latter scenario may produce two contrasting types of sites, where concentrations of BOM are influenced by the presence of structures regulating waterflow. Thus, we suggest that future studies should focus on the interaction between flow regulation and deforestation, and their effects upon organic matter dynamics.

3.5.3. Implications for management and restoration

Since the importance of stream-vegetation linkage was established (Jones 1949, Minshall 1967), restoration of the riparian vegetation of streams has been advocated by environmental authorities. Analysis of the data provided by studies that compare restored sites where riparian vegetation was re-established, versus impacted sites with some degree of deforestation, or sites where native vegetation was changed to species with commercial value, has enabled allowed us to observe two different trends. These trends indicate that airborne inputs on restored sites had similar values to reference sites (Table 3-4), Hagen et al. (2010) and Kiffney and Richardson (2010). Contrastingly, BOM standing stock values at restored sites were marginal or negative, indicating that BOM standing stock values were similar to those values from before the restoration was performed. However, most of the restoration cases reported no effect. Such limited success has been observed and reported by other authors (Collier 2017, Nilsson et al. 2015). These marginal results could be associated with small sample sizes or other limitations in the sampling design, such as a low number of replicates. A further reason may be related to underestimating the complexity between riparian vegetation and the adjacent stream. Several studies and reviews have produced data showing that restoring habitat does not guarantee the success of a given restoration effort (Michener 1997, Riley & Fausch 1995). The assumption of producing restored habitat is that it will re-establish to pre-disturbance conditions, however, this is unlikely to be achieved, as explained by the "field of dreams' hypothesis proposed by Palmer et al. (1997) and Lake (2001). Restored conditions of streams, and the final ecosystem, are likely to be substantially different to an unaltered ecosystem.

Restoration of the aquatic-terrestrial linkage has specific challenges, summarized by Bond and Lake (2003) whereby the authors provide a detailed review of five factors that influence the effectiveness of any habitat restoration in streams. For example, the introduction of exotic species may out-compete native biota. Studies performed on the Iberian Peninsula (Molinero & Pozo 2003, Molinero & Pozo 2004) reported that exotic eucalypt leaf inputs were higher and lasted longer in the stream, compared to the deciduous leaves provided by native flora. Additionally, the eucalypt leaves had lower nutritional values for local aquatic fauna, than that provided by native trees. In restored sites, allochthonous inputs depend directly on the magnitude of the restoration level and, therefore, it is important to place these inputs into the appropriated scales of space and time. That is to say, that in order to achieve natural allochthonous inputs in a restored riparian area, it is necessary to have trees large enough to provide sufficient organic material to a stream. Moreover, it is necessary that any new vegetation be similar to that which was extant before disturbance. Another factor affecting allochthonous inputs in restored streams is driven by inappropriate scales of restoration. Consequently, it is impractical to expect that a few restored areas along a stream could provide sufficient allochthonous inputs for an entire stream ecosystem, yet many habitat restoration efforts are based at this local scale. The above factors explain why some of the studies used in the present review report no differences between restored areas and deforested ones.

4. Patches of riparian forest as reservoirs of allochthonous inputs: exports and inputs limitations.

Title

Patches of riparian forest as reservoirs of allochthonous inputs: exports, and inputs limitations.

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4.1. Abstract

A study was conducted on a stream flowing through agricultural and forested floodplains in southeast Australia. We quantified whether reductions in riparian forests were associated with a decrease of allochthonous inputs of two delivery methods: airborne and Lateral Surface Transfer (LST), and the downstream transport of Coarse Particulate Organic Matter (CPOM). Comparisons were made between three farmland sites, and three sites with dense canopy cover. Allochthonous inputs were measured monthly for one year. Sites with intact vegetation showed high inputs (14 kg m^{-2} DW $year^{-1}$), while deforested reaches showed lower airborne inputs (9.25 kg m^{-2} DW $year^{-1}$). LST inputs represented 42% of allochthonous inputs in forested reaches, and 37.5% in deforested sites. The transport of CPOM downstream was similar between forested and deforested sites (23-25 kg DW $year^{-1}$). A patch of riparian forests showed increased allochthonous inputs in the vicinity of the river, however no significant exportation of CPOM from the forested area to deforested sites occurred. As most streams in Victoria, Australia, are deforested, patches of riparian forest reservoirs should be increased along such waterbodies. However, it is necessary to be mindful of the scope and limitations of forested patches along the streams, as they might not provide resources to neighbouring areas. Rather, forested sections tend to retain most of their allochthonous inputs within their boundaries.

Keywords: riparian vegetation, allochthonous inputs, headwater streams, deforestation, coarse particulate organic matter.

4.2. Introduction

Riparian forests bordering headwater streams have undergone one of the greatest deforestation rates globally (FAO 2011, Sweeney et al. 2004). Riparian areas are essential for most headwater streams, as allochthonous inputs of coarse particulate organic matter (CPOM), such as leaf litter, bark, and twigs originating from outside the river channel, are important sources of food and habitat for aquatic biota (Allan & Castillo 2007a, Richardson 1992, Sutfin et al. 2016, Vannote et al. 1980, Wallace et al. 1999).

Because headwater streams are small, their importance can easily be underestimated, yet they may represent two-thirds of the total stream length in a river network (EPA, 2006). In many cases, inadequate or infrequent conservation or mitigation strategies have been employed on riparian forests surrounding headwater streams (Lake 2001). For example, since the mid-twentieth century small areas of forest have been reserved along streams, while the remaining forests have been exploited freely or converted to agriculture areas. Furthermore, in some locations valuable forests were harvested and replaced with naturally regenerated, second-growth forests in watersheds, where uplands and stream sides were logged (Carey 2003a, Carey 2003b). Deforestation of riparian forests has simplified these ecosystems (Carey 2003a), enabled invasion by exotic species (Hobbs & Humphries 1995), caused an imbalance in biotic communities (Aubry 2000), and reduced functioning of food webs (Bojsen & Jacobsen 2003). The effects of deforestation of riparian vegetation in streams are several. For example, degraded landscapes no longer produce moderated flows of cool, clear water for fish in temperate regions. Further, streams tend to have fewer complex structures such as pools, riffles, and large woody debris. Such structures provide shelter, and retention of energy sources (i.e. CPOM) which are used by aquatic biota (Carey 2003b).

Although disturbance of streams has long been studied and is considered an important factor in forcing modifications of lotic ecosystem~~s~~ dynamics (Death 1996, Power et al. 1988, Resh et al. 1988), many questions remain unanswered. For example, the role of allochthonous inputs in the carbon budgets of rivers and streams has been explored in detail by river ecologists (Abelho 2001, Abelho & Graca 1996, Anderson & Sedell 1979, Bretschko 1990), but these studies have focused on the dynamics of allochthonous inputs, such as litter accession, patterns of retention, and accumulation of organic matter (Abelho 2001). Little attention has been given in the literature to management strategies for the mitigation of the effects on streams produced by deforestation of riparian forests. Moreover, strategies are yet to be developed in many countries. One exception is in North America, where initiatives have focused on conservation and mitigation of impacts on fish, water, wildlife, and general sustainability (Moeur et al. 2005).

In Australia, two main mitigation strategies have been employed in streams with large deforestation rates: (1) the protection of one line of trees along river banks in deforested areas, and (2) the creation of reserve areas where vegetation remains as natural as possible (Planning & Environment Act 1987; Water Act 1989). Although both strategies were designed for the preservation of streams, they were copied from models used in the northern-hemisphere, with no evidence that such schemes would be effective in increasing allochthonous inputs in Australian deforested streams.

The link between riparian vegetation and the adjacent stream has been well described (Cummins 1974, Minshall et al. 1983). Consequently, ecologists have suggested that one of the aims of mitigation measures taken in areas where riparian vegetation has been compromised should be to re-establish natural allochthonous inputs in the stream. Allochthonous material is delivered to the stream via airborne inputs (organic matter delivered directly from the canopy), and lateral surface transport (LST) by wind or water of CPOM that has accumulated on stream banks. Additionally, in natural forested streams, large amounts of allochthonous CPOM are transported from headwater tributaries (Minshall et al., 1983, Webster et al 1999). Movement of CPOM and other smaller fractions, and invertebrates from headwater reaches, to some extent supports the downstream food web, albeit downstream reaches have their own inputs and primary production (Wipfli & Gregovich 2002). However, data on the amount of organic matter transported downstream is limited. Additionally, it is unknown if CPOM transport is greater from forested sites than from sites with a thin line of trees along the banks. Consequently, the first aim of this study was to evaluate whether CPOM transported downstream in the drift changes as a function of the decrease of canopy cover. The second aim was to test how different percentages of canopy cover affect airborne and LST inputs in a deforested stream where relatively intact patches of riparian forest are surrounded by deforested reaches that have a single line of trees.

4.3. Methods

4.3.1. Study site

The study took place on a 10 km stretch along Hughes Creek (36°59'S; 145°21'E), a tributary of the Goulburn River in central Victoria, south-eastern Australia. Hughes Creek rises in the Strathbogie Ranges and flows across the Ruffy Swamps and connected ponds, before flowing through the Hughes Creek valley via a granite gorge (Catchment-Management-Authority 2013). Hughes Creek discharge dynamics are highly seasonal, as most rainfall occurs during the winter-spring months (Jun-Oct) when could fronts affect Victoria (Bureau of Meteorology www.bom.gov.au/vic). Climatic data used in this study was retrieved from the climatic station number 088109, located 16 km from Hughes Creek (www.bom.gov.au/vic). Figure 4.1 shows the climatic conditions that took place during our sampling year.

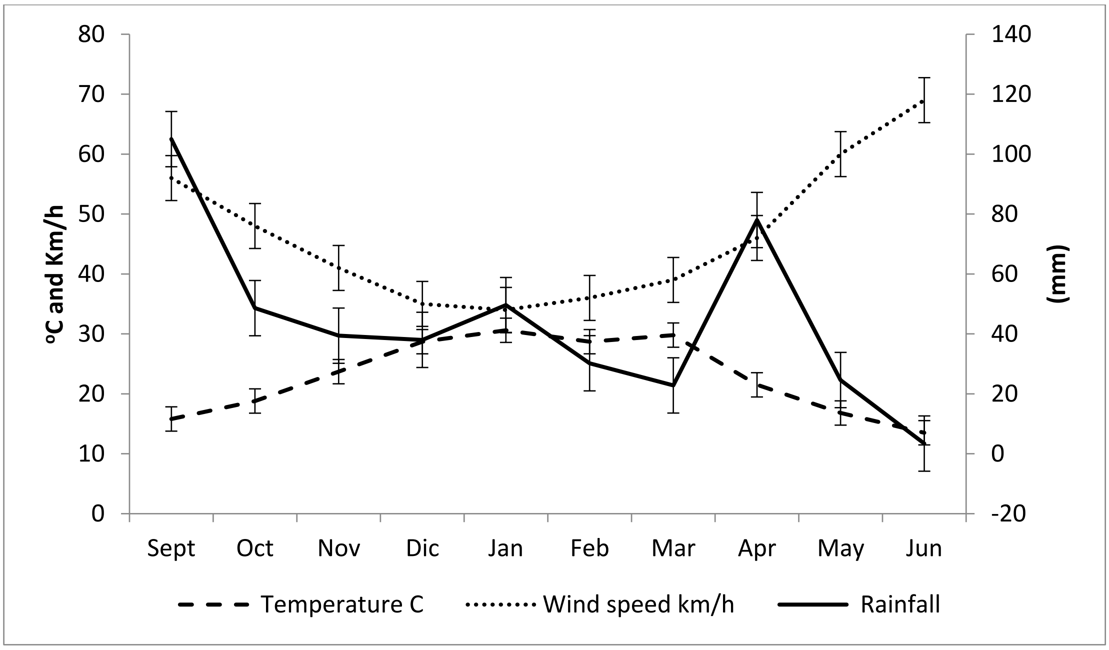


Figure 4 1 Mean climatic conditions on Hughes Creek 2016-2017. Bars represent (SE); wind speed is embedded on the primary Y axis. The heaviest rains and winds in Victoria, Australia occur in Winter. *Data source www.bom.gov.au/vic.*

4.3.2. Vegetation

The natural riparian vegetation in central Victorian streams is dominated by River Red Gum (*Eucalyptus camaldulensis*). The Red Gum understory comprises perennial plant families, with the most common being grasses (*Poaceae*), daisies (*Asteraceae*), sedges (*Cyperaceae*), and peas (*Fabaceae*) (Mackay and Eastburn 1990). In the Strathbogie Plateau region, where Hughes Creek is located, the natural vegetation cover is dominated by *Eucalyptus* spp. (*E. radiata, E. macrorhyncha*, and *E. obliqua*) and small trees (e.g. *Acacia* spp.), and perennial plants (Davis and Finlayson 2000). Nonetheless, riparian vegetation has been cleared for agriculture along most of the length of Hughes Creek wherein one stream section flows through a gorge.

In order to understand how a forested section surrounded by deforested reaches affects CPOM dynamics, six sites were selected along Hughes Creek (Table 4-1, Figure 4.2). The distance between sites of the same pair averaged 1.2 Km. The substrate was predominantly sand (Ø -0.5 to -1, or 1.7 to 2.0 mm) in all sites. Previous studies reported that the middle section of Hughes Creek decreases from 250 m ASL to163 m ASL (Lancaster & Downes 2017), giving a gradient of 0.44 % over 20 km. The gradient between pairs of sites averaged 0.65%, allowing us to compare reaches under similar gradient conditions. On the other hand, channel's width in all sites ranged from 6-8 m, while channels depth ranged between 30-50 cm.

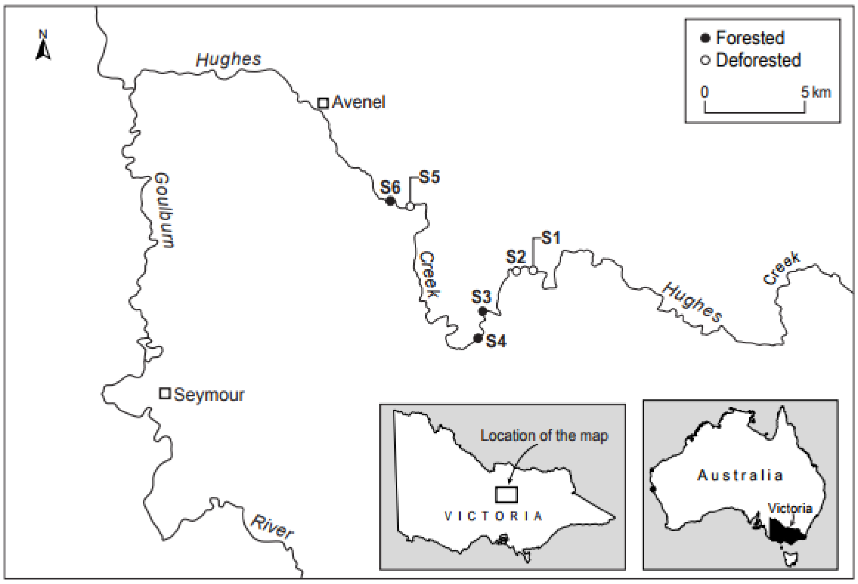


Figure 4 2 Study reaches distributed between forested and deforested sites. Selected sites were placed in the section with higher canopy cover (S1 and S2), in the forested patch (S3 and S4), and in two further sites downstream from the forested area (S5, S6)

Canopy cover was estimated using i-tree canopy (canopy.itreetools.org), where in each of the selected six sites, an area of 100 m^2 was delimited and 50 random points were sampled (Figure 4.3), then the coordinates of each site were introduced in the software to obtain the canopy cover. Three main vegetation strata where observed: ground stratum represented by grasses, mid-stratum by shrubs, and the upper stratum by trees. Additionally, in the field visual percent estimation of vegetation was performed using 10 random points along 100 m on both banks at each site (Table 4-1). Sites were grouped in deforested sites, where the upper stratum cover was under 30 % of the total cover, and forested sites, where the upper stratum cover was over 40 % of the total cover. The grouping decision of sites between forested and deforested categories was made based on the results obtained in the systematic review (section 3.4). Moreover, as the canopy cover located upstream in any reach influences the type and quantities of CPOM transported downstream by lotic systems (Bilby & Likens 1980, Jones & Smock 1991), it was decided to analyse the upstream canopy covers. We estimated the canopy cover for up to 300 m upstream at each of our study sites. The cover for ground (grasses), mid (shrubs), and upper (trees) strata was also estimated at 100 random points (Table 4-2). However, areas covered by trees made visual estimations of ground and mid stratum covers difficult, thus estimations of only the upper stratum cover were made, by employing aerial photos.

Table 4-1 Site general information, canopy cover, and vegetation-covered distance from the stream banks. Canopy cover was estimated using i-tree canopy software (canopy.itreetools.org), sampling 50 random points on each site. ground stratum = grass; mid stratum= shrubs; upper stratum= trees.

General reach information			Percentage cover (±SE)		
Reach	**Location**	**Vegetation conditions**	**Ground stratum %**	**Mid stratum %**	**Upper-stratum %**
S1	(36° 59’ 02.09’’ S, 145° 21’ 11.07’’ E)	Deforested, surrounded by agricultural lands	42.9 (±7.07)	22.4 (±5.96)	26.5 (±6.31)
S2	(36° 59’ 01.24’’ S, 145° 20’ 36.18’’ E)	Deforested, surrounded by agricultural lands	49 (±7.14)	10.2 (±4.56)	28.6 (±6.45)
S3	(37° 00’ 00.07’’ S, 145° 19’ 23.44’’ E)	A forest patch surrounded by agricultural lands	20.4 (±5.76)	8.16 (±4.08)	71.4 (±6.45)
S4	(37° 00’ 44.71’’ S, 145° 19’ 09.03’’ E)	A forest patch surrounded by agricultural lands	16.3 (±5.77)	16.3 (±5.77)	61.2 (±6.96)
S5	(36° 57’ 03.42’’ S, 145° 17’ 00.78’’ E)	Deforested site, surrounded by agricultural lands	45.1 (±6.97)	7.84 (±3.92)	29.2 (±6.84)
S6	(36° 56’ 52.86’’ S, 145° 16’ 18.97’’ E)	A Forested patch, surrounded by agricultural lands	40.8 (±7.02)	10.2 (±4.56)	45.9 (±7.07)

(a)

(b)

Figure 4 3. Contrasting examples, site 1 located in a deforested section (a), and site 3 located in forested reach (b). The rectangle represents the sample area where canopy cover was calculated. Images were generated using i-tree canopy software.

Table 4-2. Upstream canopy cover percentage composition. Canopy cover was estimated from the end of each of our study sites to 300 m upstream, by selecting 100 random points using i-tree software (canopy.itreetools.org).

General information		Percentage cover (±SE)		
Reach	**Vegetation conditions 300 m upstream of study sites**	**Ground stratum %**	**Mid stratum %**	**Upper stratum %**
Upstream S1	Deforested, surrounded by agricultural lands	48.5 (±5.02)	5.05 (±2.26)	30.3 (±4.62)
Upstream S2	Deforested, surrounded by agricultural lands	53.5 (±5.01)	5.05 (±2.26)	24.2 (±4.31)
Upstream S3	A forest patch surrounded by agricultural lands	28.3 (±4.53)	8.08 (±2.86)	60.6 (±4.91)
Upstream S4	A forest patch surrounded by agricultural lands	15.2 (±3.60)	12.1 (±3.28)	70.7 (±4.57)
Upstream S5	Deforested, surrounded by agricultural lands	54.5 (±5.00)	4.04 (±2.02)	39.4 (±4.91)
Upstream S6	A forest patch surrounded by agricultural lands	28.3 (±4.53)	8.08 (±2.86)	54.5 (±5.00)

4.3.3. Field sampling

Allochthonous inputs from riparian vegetation to the stream were collected, and two types were considered, (a) airborne inputs, which were direct inputs from trees to the stream, and (b) lateral surface transfer inputs (LST), which were inputs collected from organic material stored near the banks and moved via aeolian transport (wind) towards the stream. To collect these fractions, ten plastic traps (30 cm long x 18 cm wide x 12 cm deep) were deployed on one of the banks of the six reaches, with the distance between traps being 10 metres. It was decided to use plastic buckets, as previous studies in the same region had reported net-type traps were sometimes damaged by cattle. Also, bucket-type traps were reported to be, to some extent, resistant to floods, and they remain in situ after such events (Langhans et al. 2013), making them ideal for conditions along Hughes Creek, where potential flash floods occur. Further, five holes were drilled in the bottom of the buckets to drain rainwater. Two configurations were designed to collect allochthonous inputs. In configuration one, traps were placed facing the canopy cover above, to facilitate the collection of airborne material. These traps were buried 6 cm in the ground, thereby preventing the edges of the bucket from collecting LST inputs. In configuration two, traps were placed with the bucket opening adjacent to the ground and pointing away from the stream, ensuring collection of only organic material which had been transported laterally by wind from the banks to the stream (i.e. LST inputs). Airborne and LST samples were collected monthly from September 2016 to June 2017, and material retained by traps was collected as separate replicates.

CPOM transported downstream by the river (henceforth referred to as drifting CPOM) was collected by placing three drift nets in the channel at each reach. Drift nets were similar to airborne and LST traps (30 cm long x 18 cm wide). Drift nets were deployed across the channel on each site, being always located in the thalweg (main current area). Nets were deployed for four hours, as longer times resulted in clogged and sometimes lost nets. No measure of flow velocity was calculated along with drifting CPOM, as the intention was to measure the mass of CPOM drifting through sites per unit time, rather than per unit of volume of water. Drifting CPOM trapped by drift nets was homogenised to form one sample per site. Drifting CPOM was collected once each month from October 2015 to June 2016 inclusive. It was decided to cease the collection of samples beyond June, as the winter water currents in August were too strong to situate the drift nets safely. Samples were preserved in 70% alcohol. Although alcohol might produce the leaching of detrital components of the sample, this preservation method was the best option to preserve the samples until they were processed, which were processed within two days after collection.

4.3.4. Laboratory

In the laboratory, airborne and LST fractions were cleaned gently with a soft fibre brush in order to remove dust that might have accumulated between deposition and collection times. Samples were then oven-dried for 24 hours at 105 °C (Matthews 2010). Drifting CPOM samples were rinsed to remove sediment, air-dried for five days, and then oven-dried in the same conditions as employed for LST and airborne samples. When the samples had dried thoroughly, they were sorted into leaves, bark, twigs/branches, fruit, grasses, and miscellaneous material, and weighed to the nearest 0.001 g. Due to the lower fraction of fruit collected, it was combined with the miscellaneous fraction, as employed by Reid et al. (2008a) on similar streams.

4.3.5 Statistical analysis

Data were $\log_{10}$ transformed, a Kolmogorov-Smimov test of normality (SPSS version 26) was performed to the data to ensure its normal distribution. A nested ANOVA model was used to analyse the data (Table 4-3). Forest cover and month were considered fixed crossed factors, and site was considered as a random factor nested within forest cover. Month was considered fixed because sampling times were not a random selection from possible times (and hence cannot be used to draw conclusions about the days that were not sampled). Drifting CPOM samples were grouped in a homogenous sample each time, with one value per month per site. This was due to the highly variable values of trapped CPOM per net. Consequently, there was not a within-site replicate, which excludes the term “site” in the model, as the variation between sites forms the replicates. Thus, a 2-way model was performed. All results were considered significant at $p < 0.05$.

Table 4-3 Nested ANOVA model and F-test calculations

Factor	df	Denominator to use for F-test
Forest cover	1	$Site_{within\ F}$
Si$te_{within\ F}$	4	Residual
Month	9	M x $Si_{within\ F}$
M x F	9	M x $Si_{within\ F}$
M x $Si_{within\ F}$	36	Residual
Residual	240	

4.4. Results

4.4.1. Airborne inputs

Airborne inputs were highly season-dependent and forest-cover affected. Our study demonstrated that inputs of leaves vary throughout the year, and in most sites, such inputs increased during December and January (Summer). Moreover, forested sites showed higher leaf inputs during summer than deforested sites (Figure 4.4; Table 4-4). Further, the highest inputs throughout the year were from the leaf fraction (Figure 4.4). Grass and miscellaneous material inputs increased in forested sites during summer. Fractions dominating allochthonous inputs such as twigs, bark, and leaves, showed interactions between months and cover, whereas miscellaneous material was consistently different between forested and deforested sites, and was influenced by forest cover (Table 4-4).

Table 4-4 Nested ANOVA of airborne inputs. Month and forest cover were crossed, and site was nested within forest cover. Model design is shown in Table 4-2. Significant differences in bold.

Fraction	Factor	Type III Sum of Squares	df	Mean Square	F	p
Leaves	Forest cover	90.413	1	90.413	11.577	**0.027**
	$Site_{withinF}$	31.239	4	7.810	1.541	0.191
	Month	233.484	9	25.943	13.606	**0.001**
	Month*Forest cover	104.852	9	11.650	6.110	**0.001**
	Month* $Site_{withinF}$	68.641	36	1.907	0.376	1.000
	Residual	1216.490	240	5.069		
Bark	Forest cover	27.200	1	27.200	1.644	0.269
	$Site_{withinF}$	66.187	4	16.547	1.315	0.265
	Month	89.060	9	9.896	1.121	0.433
	Month*Forest cover	171.566	9	19.063	2.159	**0.049**
	Month* $Site_{withinF}$	317.912	36	8.831	0.702	0.899
	Residual	3020.006	240	12.583		
Twigs	Forest cover	0.626	1	0.626	0.193	0.683
	$Site_{withinF}$	13.009	4	3.252	1.268	0.283
	Month	10.839	9	1.204	0.682	0.711
	Month*Forest cover	20.452	9	2.272	1.286	0.278
	Month* $Site_{withinF}$	63.606	36	1.767	0.689	0.910
	Residual	615.430	240	2.564		
Grass	Forest cover	7.128	1	7.128	344.440	**0.001**
	$Site_{withinF}$	0.083	4	0.021	0.077	0.989
	Month	23.189	9	2.577	17.666	**0.001**
	Month*Forest cover	7.865	9	0.874	5.991	**0.001**
	Month* $Site_{withinF}$	5.251	36	0.146	0.546	0.984
	Residual	64.130	240	0.267		
Miscellaneous material	Forest cover	0.195	1	0.195	11.304	**0.028**
	$Site_{withinF}$	0.069	4	0.017	0.449	0.773
	Month	0.898	9	0.100	4.559	**0.016**
	Month*Forest cover	0.421	9	0.047	2.138	0.051
	Month* $Site_{withinF}$	0.788	36	0.022	0.571	0.977
	Residual	9.201	240	0.038		

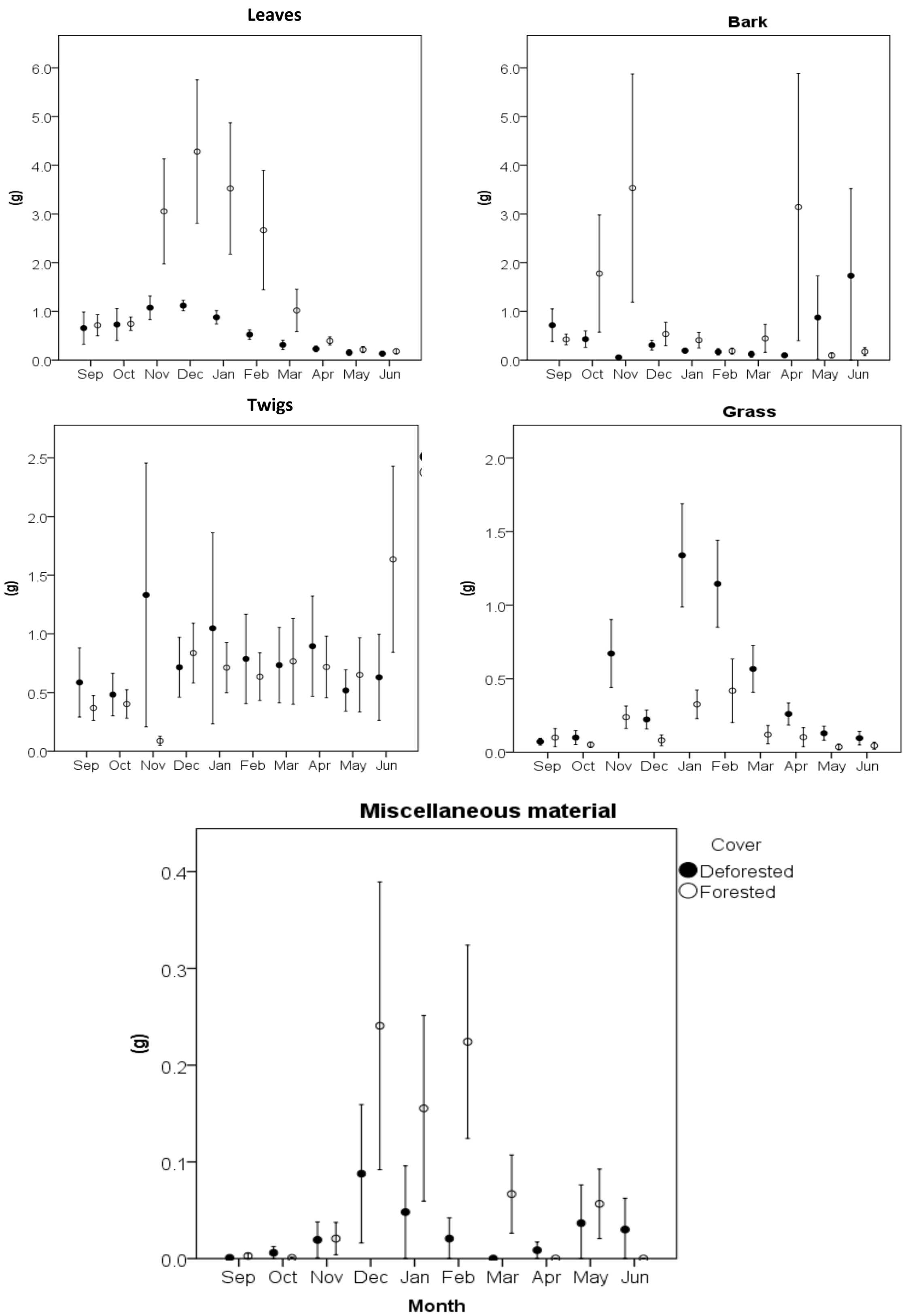


Figure 4 4 Airborne inputs, showing comparisons of various fractions between forested and deforested sites along Hughes Creek throughout one year. Points are displayed with standard error bars

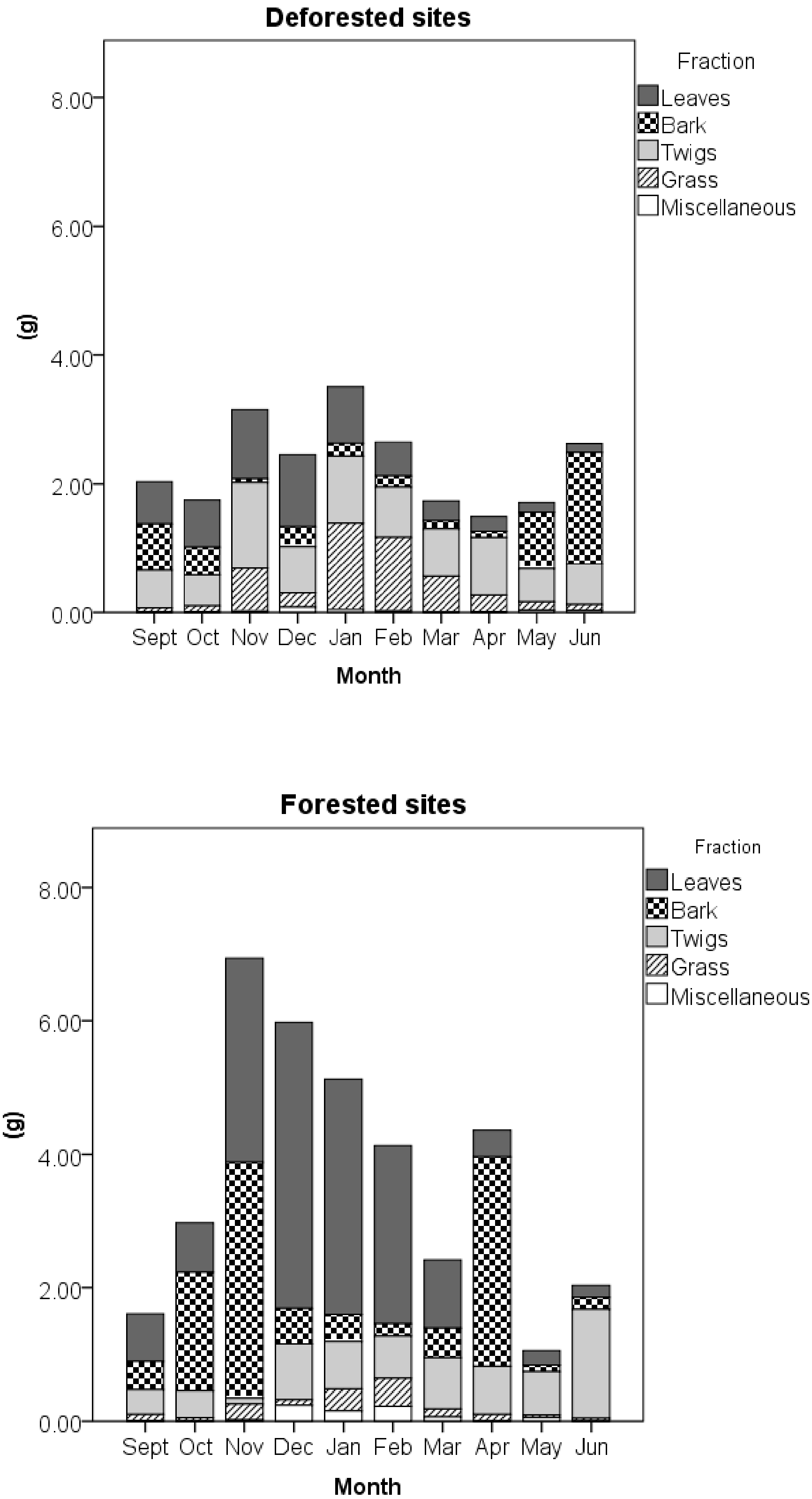


Figure 4 5 Stacked bar showing airborne inputs across the 10-month sampling period. The stacked bar charts show the fractions composition in forested and deforested sites.

4.4.2. LST inputs

LST higher inputs of CPOM occurred during the summer months. Moreover, wind transported all types of fractions; however, leaf material proved to be the most dominant fraction during the entire year. This was anticipated due to the low weight of leaves. However, none of the sampled fractions were sensitive to the type of forest cover, or to any seasonal interactions (Table 4-5). Furthermore, forested sites showed trends of having higher inputs of bark and twigs, with a sharp increase of both fractions occurring during the summer months (Figure 4.6). A significant response to the variable of month was observed with bark, twigs, grass, and miscellaneous material (Table 4-5). The sum of fractions (Figure 4.7) indicates that higher LST inputs occur during summer months, with forested and deforested sites showing similar tendencies. LST inputs were dominated by leaves, twigs, and bark fractions throughout the year, while grass and miscellaneous material provided low contributions via LST inputs.

Table 4-5 Nested ANOVA of LST inputs. The model design is illustrated in Table 4-2. Significant differences in bold.

Fraction	Factor	Type III Sum of Squares	df	Mean Square	F	Sig.
Leaves	Forest cover	12.417	1	12.417	1.658	0.267
	$Site_{withinF}$	29.951	4	7.488	1.111	0.351
	Month	93.587	9	10.399	1.587	0.156
	Month*Forest cover	60.612	9	6.735	1.028	0.441
	Month* $Site_{withinF}$	235.927	36	6.554	0.973	0.518
	Residual	1617.083	240	6.738		
Bark	Forest cover	1.442	1	1.442	1.677	0.265
	$Site_{withinF}$	3.440	4	0.860	1.880	0.114
	Month	9.947	9	1.105	3.709	**0.002**
	Month*Forest cover	3.869	9	0.430	1.443	0.491
	Month* $Site_{withinF}$	10.728	36	0.298	0.652	0.938
	Residual	109.775	240	0.457		
Twigs	Forest cover	4.952	1	4.952	4.173	0.110
	$Site_{withinF}$	4.747	4	1.187	1.262	0.285
	Month	13.428	9	1.492	5.254	**0.001**
	Month*Forest cover	7.203	9	0.800	2.818	0.570
	Month* $Site_{withinF}$	10.223	36	0.284	0.302	1.000
	Residual	225.776	240	0.941		
Grass	Forest cover	0.379	1	0.379	3.942	0.118
	$Site_{withinF}$	0.385	4	0.096	1.300	0.270
	Month	4.644	9	0.516	4.806	**0.001**
	Month*Forest cover	0.619	9	0.069	0.641	0.500
	Month* $Site_{withinF}$	3.865	36	0.107	1.450	0.055
	Residual	17.774	240	0.074		
Miscellaneous material	Forest cover	0.001	1	0.001	0.069	0.805
	$Site_{withinF}$	0.042	4	0.010	0.906	0.461
	Month	0.243	9	0.027	3.048	**0.008**
	Month*Forest cover	0.091	9	0.010	1.137	0.552
	Month* $Site_{withinF}$	0.319	36	0.009	0.766	0.830
	Residual	2.776	240	0.012		

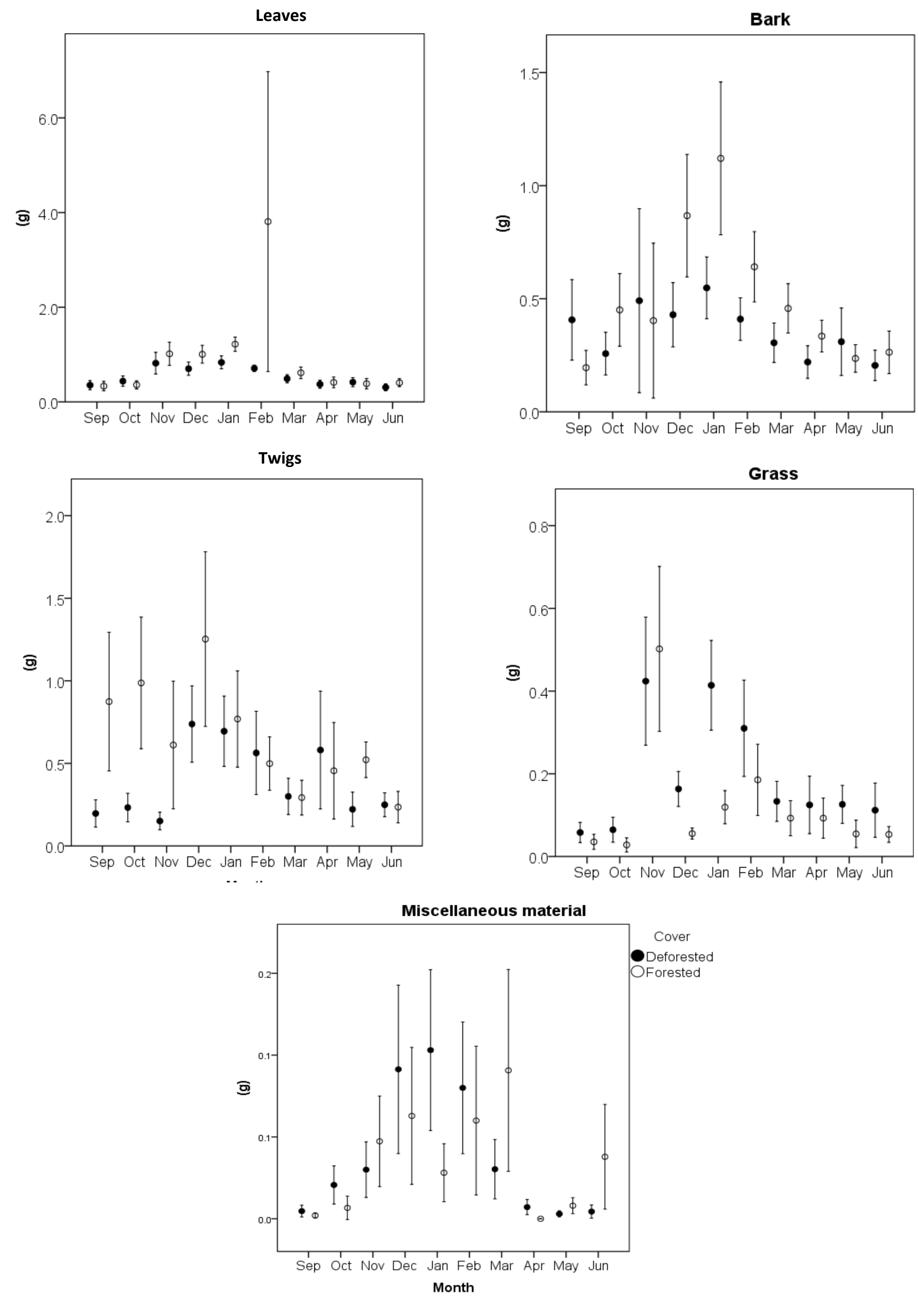
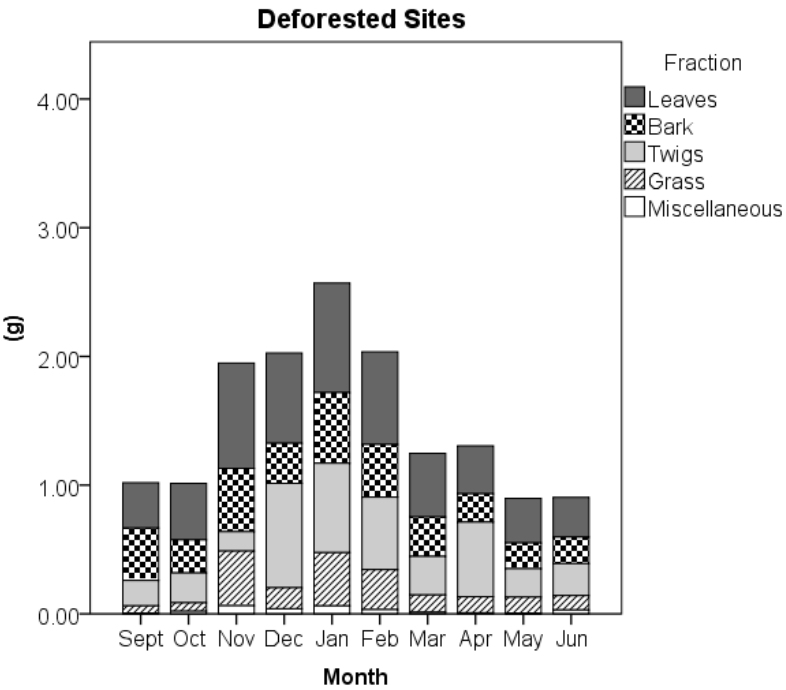


Figure 4 6 LST inputs, comparisons of various fractions between forested and deforested sites along Hughes Creek throughout one year 2016-2017 values are displayed with error bars.



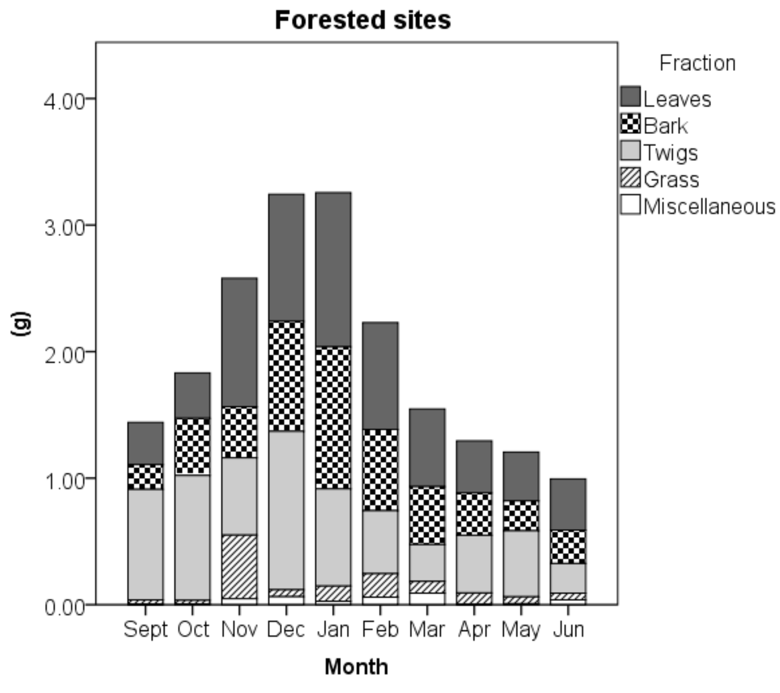


Figure 4 7 Stacked bar showing LST inputs across a 10-month sampling period (2016-2017). The stacked bar charts show the fractions composition in forested and deforested sites.

4.4.3. Drifting CPOM

Trends of higher leaf transport occurred during summer (Figure 4.8), which is consistent with the months where airborne and LST inputs also showed higher allochthonous inputs. Drifting CPOM was dominated by leaf material in all cases (Figure 4.9), and twigs and miscellaneous material fractions were similar at all sites. Contrastingly, bark and grass varied between forested and deforested sites. However, none of the fractions showed any significant interactions between forest cover and month, although some varied between months (Table 4-6).

Drifting CPOM inputs also depend on canopy cover characteristics upstream, where the composition and amount of inputs collected via drifting transport vary in function. Upstream canopy cover was compared with drifting CPOM values to observe trends. For example, sites with low tree cover (upper stratum) upstream (sites 1,2, and 5), showed higher transportation of grass (ground stratum cover) downstream. Conversely, with sites upstream with higher tree cover (sites 3,4, and 6), the CPOM transported downstream was dominated by leaves, bark, and twigs, which originated in the upper stratum (Figure 4.10).

Table 4-6 Drifting CPOM crossed factor design ANOVA. This analysis involves more than one independent variable. Significant differences in bold, while bold and underlined p values were marginally outside the significance boundary.

Fraction	Factor	Type III Sum of Squares	df	Mean Square	F	p
Leaves	Forest cover	9.216	1	9.216	0.026	0.874
	Month	6158.851	8	769.856	2.136	**<u>0.057</u>**
	Forest cover*Month	565.686	8	70.711	0.196	0.990
	Residual	12972.527	36	360.348		
Bark	Forest cover	92.622	1	92.622	6.755	**0.013**
	Month	249.687	8	31.211	2.276	**0.044**
	Forest cover*Month	179.839	8	22.480	1.639	0.148
	Residual	493.654	36	13.713		
Twigs	Forest cover	25.958	1	25.958	3.409	0.073
	Month	98.751	8	12.344	1.621	0.153
	Forest cover*Month	67.369	8	8.421	1.106	0.382
	Residual	274.094	36	7.614		
Grass	Forest cover	68.141	1	68.141	8.742	**0.005**
	Month	55.427	8	6.928	0.889	0.536
	Forest cover*Month	57.923	8	7.240	0.929	0.505
	Residual	280.618	36	7.795		
Miscellaneous material	Forest cover	0.094	1	0.094	0.161	0.690
	Month	3.187	8	0.398	0.682	0.704
	Forest cover*Month	5.215	8	0.652	1.116	0.376
	Residual	21.028	36	0.584		

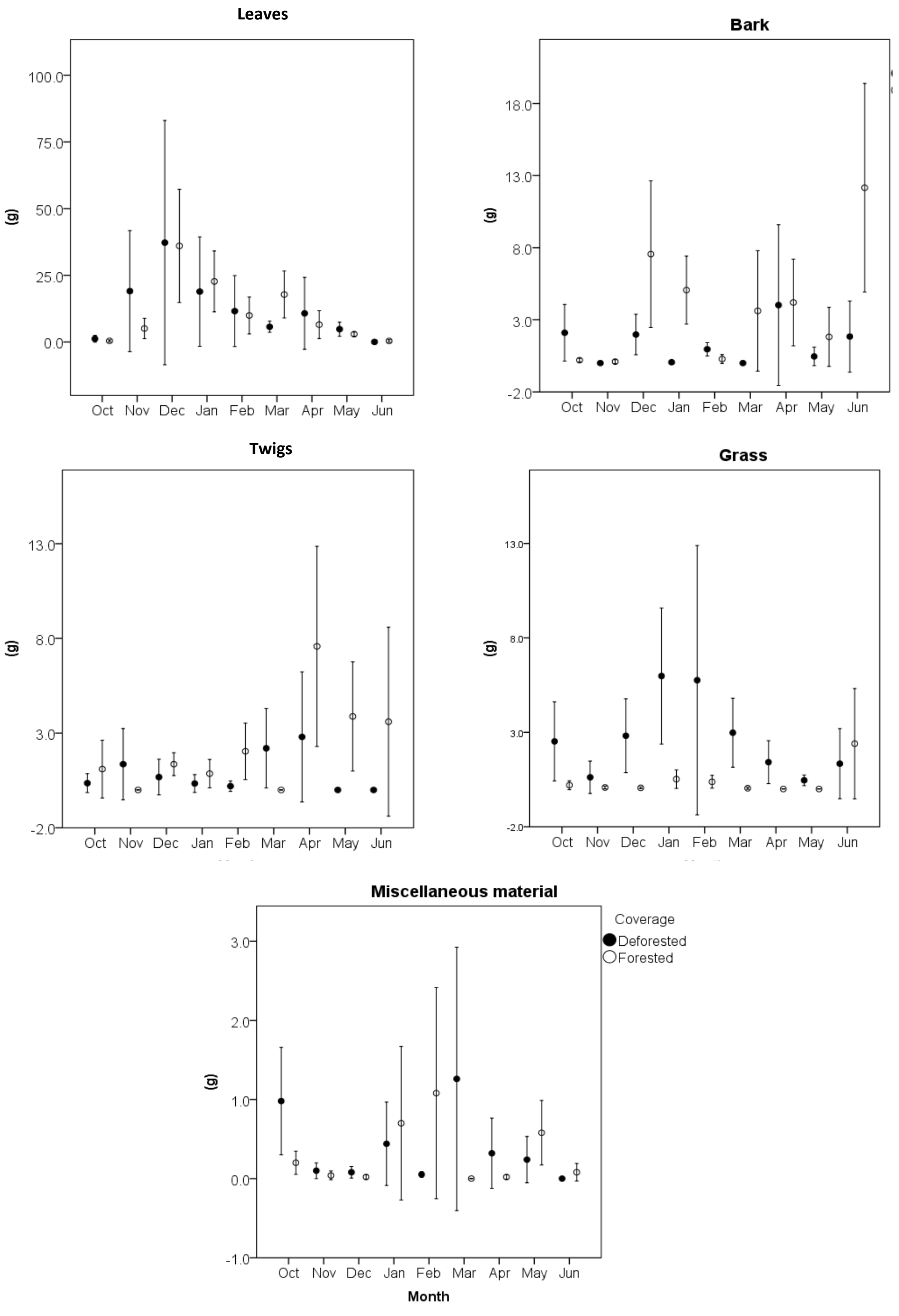


Figure 4 8 CPOM transported downstream divided into fractions. Values were transformed into g d-1 by converting the collection time (four hours) of drift nets into 24 hrs.

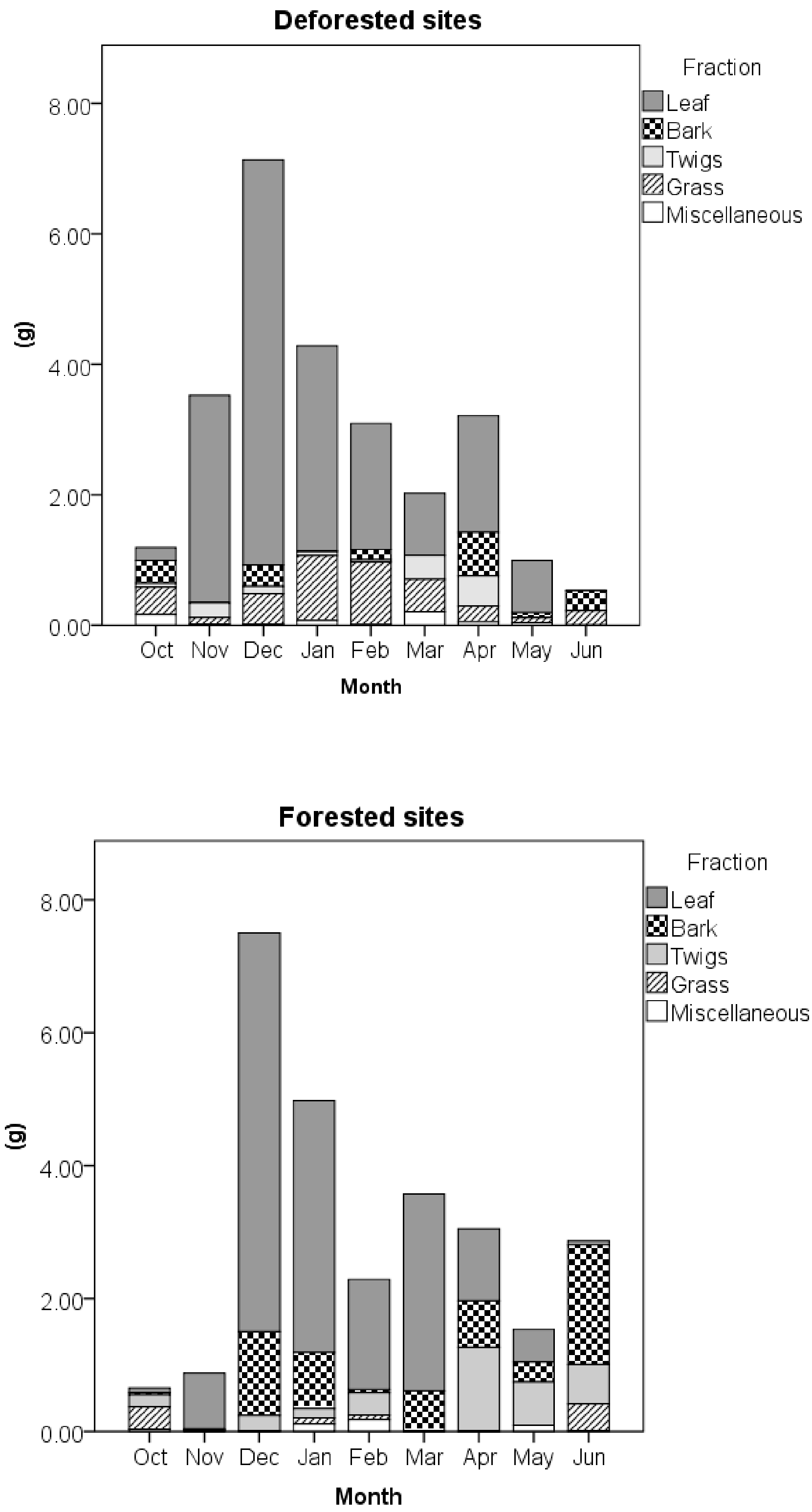
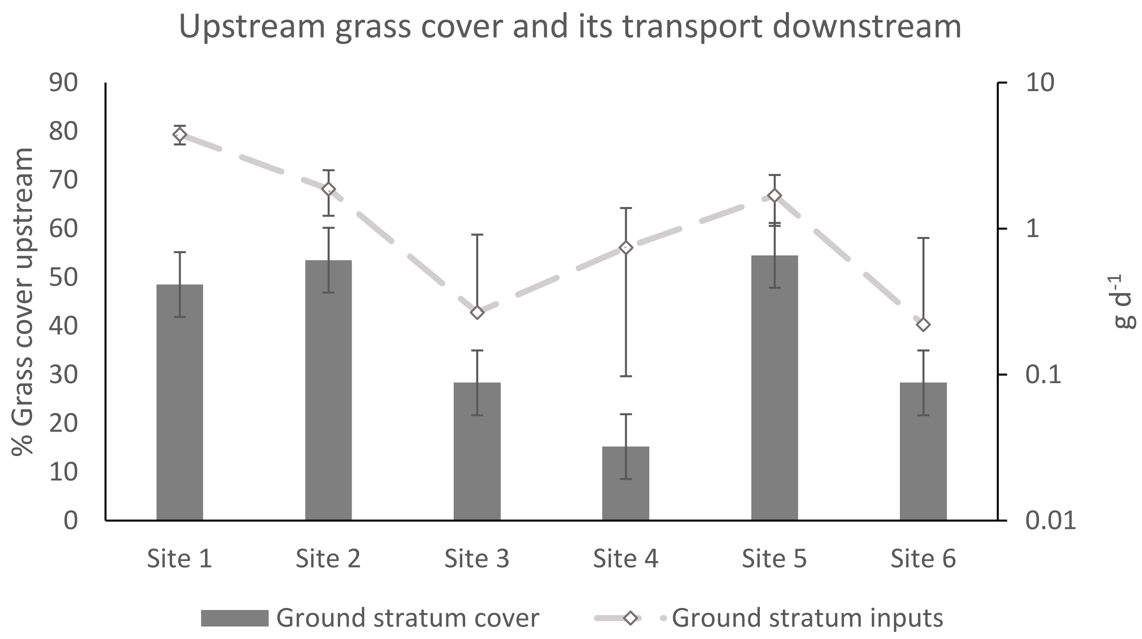


Figure 4 9 Stacked bars showing mean composition of different fractions transported downstream in forested and deforested sites.



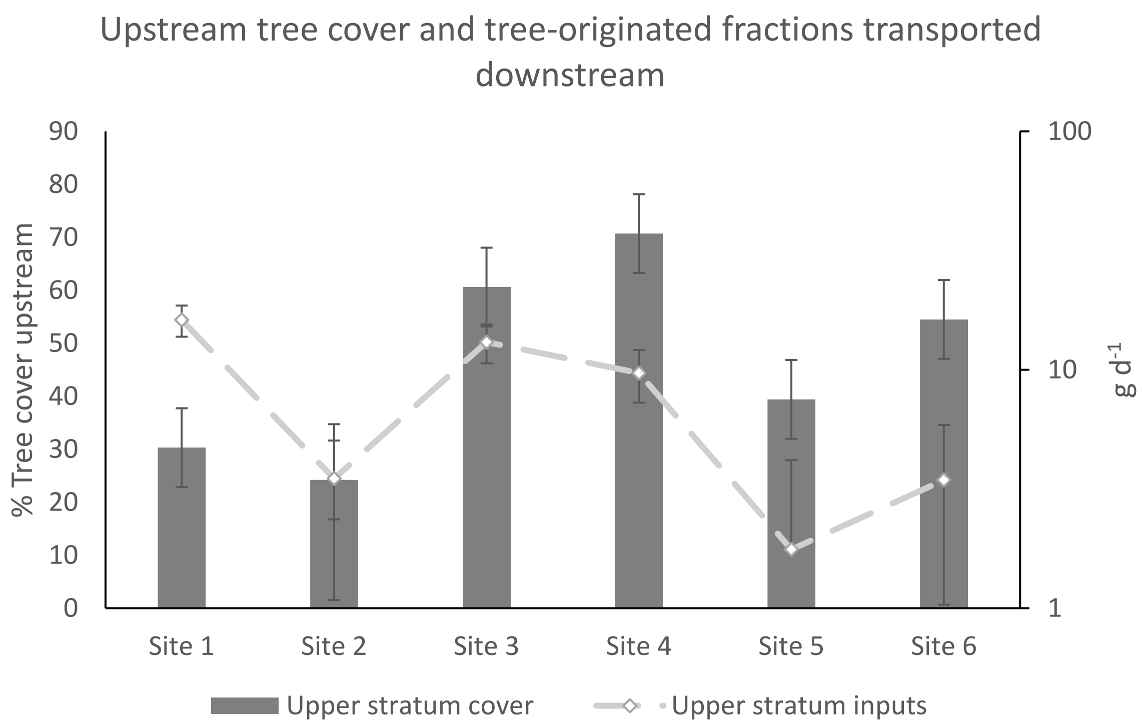


Figure 4 10. Relationship between grass and tree cover in upstream sections of all sites, and the amount of material collected downstream via drifting CPOM. Ground stratum represents mean values of grass. Upper stratum inputs are represented by the sum of individual mean values of leaves, bark, and twigs, with all being delivered by trees.

4.4.4. Total allochthonous inputs and drifting CPOM

The results showed the main mechanism of allochthonous inputs were airborne inputs, which provided almost 40 kg/year of allochthonous inputs in forested sites, while in deforested areas inputs were less than 25 kg/year. LST inputs were similar on both forested and deforested sections, and our estimations indicated that 20 kg/year of CPOM is LST-transported to the stream. Likewise, the amount of drifting CPOM transported downstream was similar on all sites, with an average of 25 kg/year (Figure 4.11)

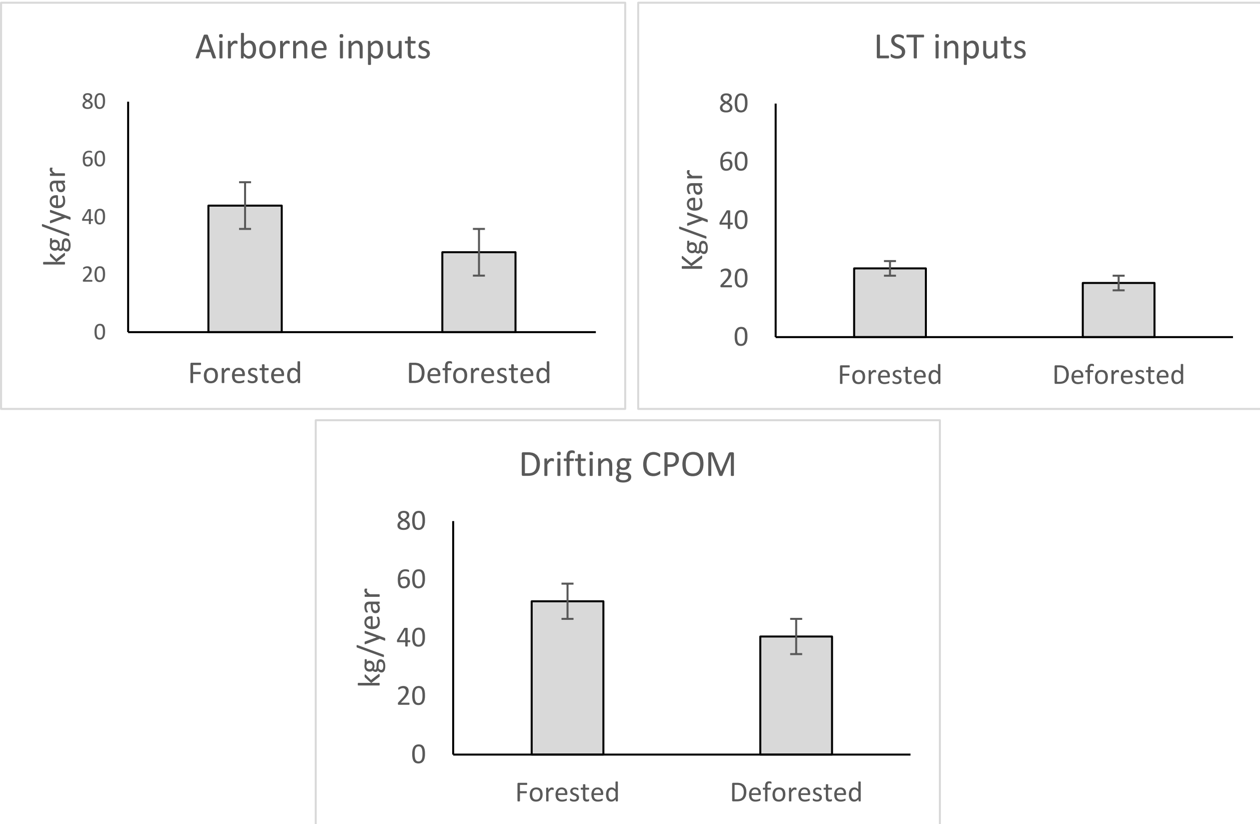


Figure 4 11 Mean annual allochthonous inputs and CPOM transportation. Allochthonous input data was estimated for 100 m transects, representing the section where traps were placed. The estimation for allochthonous inputs was calculated by adding the mean values of CPOM trapped in each trap per month, and then extrapolated to 100 m. Drifting CPOM values were estimated by extrapolating the catching area of traps to the total width of the channel, then mean values of CPOM trapped in four hours were extrapolated to 24 hours.

4.5. Discussion

It was tested whether allochthonous inputs are significantly affected by changes in the amount of canopy cover in a stream where extensive areas of riparian vegetation have been largely removed. We also evaluated the effect upon the amount of CPOM transported downstream in the drift from forested areas. Our results show that allochthonous inputs can be drastically affected by the amount of forest cover available nearby; however, drifting CPOM was not affected in a similar manner.

4.5.1. Airborne inputs

It was found that airborne inputs were highly season-dependent, and forest cover influenced the quantities and proportion of the CPOM fractions delivered to the stream. One of the most important airborne fractions was leaf material, because potentially leaves can travel longer distances from the riparian zone to the stream due to their low weight, making them easily transported by aeolian conditions. Leaf fraction has been reported to be the most dominant material of airborne inputs throughout the world (Abelho & Graca 1996, Delong & Brusven 1994, Kreutzweiser et al. 2004). Although the reserve area along Hughes Creek is not completely free of human disturbance, the results obtained in this study were similar or higher than previous studies of sites with intact *Eucalyptus* forests (Campbell & Fuchshuber 1995, Robertson et al. 1999). Moreover, in other streams in the area, allochthonous inputs are similar to the inputs of well-developed riparian forests (Reid et al., 2008), and show similar results to ours. In most Australian rivers systems, the CPOM fractions that dominate airborne inputs are commonly contributed by the upper-stratum (Campbell et al. 1992a); this could explain why sections with higher canopy cover showed higher inputs than deforested sites. Thus, where Victorian headwater streams have well-developed upper-stratum cover along their banks, the largest contribution of organic matter is delivered via airborne inputs in.

These results show that some fractions dominate allochthonous inputs during different seasons. For example, bark dominated airborne inputs during spring (September-October), whilst leaf inputs dominated during summer (December-February). The results are consistent with the study of Blackburn (1976), whereby airborne input dynamics of bark were greater during middle spring, when winds were stronger (Figure

4.1). Further, where Blackburn (1976) found leaf inputs occurring during summer were related to natural defoliation of eucalypts, our results of benthic CPOM showed that leaves were also found in higher proportions during summer at Hughes Creek (Gonzalez, unpublished data).

4.5.2. LST inputs

Wind transported all types of fractions; however, leaf material proved to be the most dominant fraction at forested and deforested sites during the entire year (2016-2017), which was consistent with the results from other studies throughout the world (Kreutzweiser et al. 2004, Magana 2001, Molinero & Pozo 2003, Molinero & Pozo 2004, Pozo et al. 1997), and in Australian streams (Campbell et al., 1992, Ried et al., 2008). The results for airborne and LST inputs were similar to values reported in eucalypt plantations on the Iberian Peninsula (Molinero & Pozo 2003). It is feasible that any differences could be related to deforested and forested sites lacking obstacles along the banks, thereby having no obstructions to halt aeolian transported material into the stream. Moreover, the grass fraction was higher in deforested sites, as expected, however it provides direct evidence that the type and quantity of LST inputs depends directly on the conditions and the type of vegetation in the adjacent riparian zone. The latter is particularly important for many streams globally, as most of them have been deforested, with grass left to grow freely along the steam banks (Menninger & Palmer 2007). Indeed, our results illustrate that grass is a relevant fraction transported by wind into the stream when riparian forest have been logged.

4.5.3. Relative contributions of airborne and LST inputs,

LST inputs were 50% lower than airborne inputs in forested sites. In contrast, deforested sites had similar LST inputs to the total airborne inputs. However, two previous studies of Australian streams reported lower LST inputs in similar streams. For example, Campbell et al. (1992) reported that 10% of allochthonous inputs were associated with LST inputs, while Reid et al. (2008) estimated LST inputs contributed to 10-15 % of the total allochthonous inputs. In contrast, LST inputs in the northern hemisphere ranged between 10-22 % of the total allochthonous inputs (Molinero & Pozo 2003).

The total allochthonous inputs on both forested and deforested sites were considerably lower in our study than those reported in previous studies (Campbell et al. 1992; Reid et al. 2008). These differences may be related to type of trap we used.

Bucket traps trapped organic matter throughout the year, however the traps are disadvantaged by their small trapping area, as also reported by Langhans et al. (2013). Despite our data finding lower total inputs than in previously reported studies, we observed that airborne and LST inputs showed similar trends between forested and deforested sites.

4.5.4. Upstream vegetation cover and drifting CPOM

The similarity between deforested and forested sites in leaf transport was consistent between both sites. This result was contrary to our hypothesis, as we expected to have larger downstream transport of CPOM in sites with larger allochthonous inputs. However, Brown and Timms (2002), also found the transport between forested and deforested sites was not significantly different, in their work on a New South Wales stream. Moreover, it is likely that the amount of CPOM transported depends on the ability of the trees to deliver organic matter to the stream, and the type of vegetation next to the river channel. The latter is relevant for each fraction, as the energy required to move CPOM from the banks to the stream varies between fractions. Likewise, the upstream distance that CPOM fractions are delivered, and then transported downstream, depend upon the weight and size of each fraction and their resistance to wind velocities.

When the composition of canopy cover upstream from each site and fractions of CPOM transported downstream were compared, we found a likely potential relationship between the type of cover and the composition of CPOM found downstream. For example, in forested sites the composition of CPOM transported downstream was represented by higher amounts of leaf, bark, and twigs, delivered by trees. Contrastingly, in deforested sites higher inputs of grass were collected than in forested sites. Such results are comparable to those found by Clark et al. (1986) in the Amazon River, where the composition of organic matter collected was highly influenced by the type of nearby vegetation. For example, they found higher amounts of woody material in areas dominated by trees, and grass particles where vegetation was dominated by grasslands. The latter dynamics can be explained by drifting CPOM, which is retained soon after been delivered into the stream where it decomposes or breaks into smaller fractions (Bilby & Likens 1980, Jones & Smock 1991, Tank et al. 2010). Further, CPOM composition shifts might influence water quality, macroinvertebrate composition, fisheries production, and ultimately the global carbon budget (Meybeck 1982, Raymond et al. 2007, Schlünz & Schneider 2000).

One prediction was that site 5 (a deforested site), being located downstream of a forested section, would receive large inputs of drifting CPOM from the upstream forested area. However, our results suggest that downstream transportation at this site was not different to the other sites that were in deforested areas. This may be related to a variety of factors. For example, the presence of retentive structures such as large woody debris, macrophytes, sedimentation banks et cetera could be present in the forested section. These structures could trigger higher retention of CPOM (Bilby & Likens 1980, Sutfin et al. 2016). Further, higher retention capacity in the forest section could increase the breakdown of organic matter by shredders or decomposition by bacteria (Allan & Castillo 2007; Wagener et al., 1998). Several studies substantiate CPOM being broken-down before it is transported downstream as fine particulate organic matter or dissolved organic matter (Muotka & Laasonen 2002, Wallace et al. 1991). Consequently, while the amount of CPOM transported downstream in forested areas does not vary greatly, FPOM fractions are likely to increase.

The results from this study showed that allochthonous inputs between forested and deforested stream reaches was similar but the type of forest cover (grass or trees) did influence the quantities of the different fractions of CPOM delivered into the stream. These results show that, at least in Hughes Creek, inputs of CPOM depended on the first line of trees that deliver airborne and LST material to the below stream. Moreover, the export of CPOM from forested sections to downstream reaches was limited by the channel complexity (larger presence of LWD and other retention structures) that prevent the movement of CPOM to these sections. Consequently, it is possible to conclude that deforested sections depend greatly on the allochthonous inputs delivered locally.

5. Headwater streams: the relationships between forest cover, benthic CPOM, and macroinvertebrate densities.

5.1. Introduction

Understanding the factors driving the distribution and abundance of organisms is central to ecological theory. Distributions of organisms in streams are both spatially and temporally heterogeneous across the streambed (Egglishaw 1969, Tavares-Martins et al. 2017). Moreover, resources in streams such as CPOM are often distributed in patches. Various models have been developed that explain how patchiness affects the distribution and dispersal of organisms (Fahrig 1988, Fahrig 2003, Fahrig & Merriam 1985, Fahrig & Paloheimo 1988). Such patchiness is likely to cause disruption in faunal movement frequency and distances travelled, due to the distance and quality of patches changing over time. Patches of resources in streams are found under varying conditions. For example, backwater or slackwaters might provide refuge for macroinvertebrates, as these areas can be used by macroinvertebrates as shelter from water flow (Lancaster 2008). Likewise, stream hydrologic forces distribute allochthonous organic matter in patches, with such resources playing a significant role for aquatic communities in headwater streams (Bilby & Likens 1980, Minshall et al. 1985, Vannote et al. 1980).

Allochthonous inputs of organic matter originate from riparian vegetation (i.e. leaf, bark, twigs etc.) in headwater streams, providing energy, shelter, and substrate for fish, macroinvertebrates, and other aquatic organisms (González-Bergonzoni et al. 2017, Vannote et al. 1980). One of the most important fractions of allochthonous organic matter is coarse particulate organic matter (CPOM) (Bilby & Bisson 1992). CPOM availability and composition is influenced by seasonality, and the type and percentage of canopy cover. For instance, in temperate regions of the northern hemisphere, allochthonous inputs increase during autumn as deciduous forests prepare for winter (Hagen et al. 2010, Hoover et al. 2011, Kiffney & Richardson 2010, Muto et al. 2009). Contrastingly, in Australian streams allochthonous inputs tend to increase when eucalypt trees lose leaves and branches as a response to drought conditions (Campbell et al. 1992a, Lake et al. 1982, Reid et al. 2008a).

The type and condition of canopy cover changes over time, through anthropogenic and natural causes. For example, global riparian forests have undergone drastic changes due to the development of agriculture (Carvalho & Uieda 2010b, Roberts &

Bilby 2009), forest plantations (Molinero & Pozo 2004), and logging (Hoover et al. 2011, Kiffney & Richardson 2010). Such changes modify allochthonous inputs in headwater streams (Bilby & Bisson 1992, Kreutzweiser et al. 2004, Vannote et al. 1980, Webster et al. 1992). Furthermore, the effects of deforestation on riparian areas have long been studied, with findings illustrating the loss of canopy cover adversely influencing allochthonous inputs, (Abelho & Graca 1996, Campbell et al. 1992b, Kreutzweiser et al. 2004, Mayer 2005, Molinero & Pozo 2003, Muscutt et al. 1993, Robertson & Rowling 2000).

Several studies have shown that macroinvertebrates can be affected directly by the availability of CPOM on the streambed. For example, Lancaster and Downes (2017c) reported that macroinvertebrate species richness and densities increased after artificially increasing the retention of CPOM at studied sites. The density of individuals within patches can vary due to density-area relationships (DARs). The concept of DARs states that abundances are almost always reduced with a reduction in patch size, while the effect on density is much more variable among species and depends on diverse factors, such as dispersal mechanisms. Several models have been developed to explain DARs such as the equilibrium theory of island biogeography (MacArthur & Wilson, 1967), the resource concentration hypothesis (Root, 1973), or the single large vs small several reserves debate that was exposed in the island dilemma by Diamond (1975). For aquatic macroinvertebrates, the sizes and distances between patches challenge the success of individuals to reach new resource patches (CPOM); therefore, affecting densities of species. However, each species will be affected differently, and the effect will depend on the dispersal ability that each species has because that will define how far they can disperse successfully.

The disturbance of riparian vegetation along streams has resulted in the transformation of riparian forests into grasslands (Hladyz et al. 2011). Some studies have reported that benthic CPOM with a high concentration of grass leaf material had lower macroinvertebrate colonization rates than that of patches of herbs and leaf matter (Douglas & O'Connor 2003, Fonseca & Tanaka 2015, Menninger & Palmer 2007). However, such studies focused on the grass-originated allochthonous inputs as exotic sources of energy or substrate for macroinvertebrates.

In this study two hypotheses were tested: (1) whether the composition of benthic CPOM patches in deforested sites have a higher presence of grass in comparison to forested reaches. (2) To evaluate if macroinvertebrate species densities and species composition in benthic CPOM patches changes when the amount of CPOM increases, and whether the canopy cover affect macroinvertebrate population parameters.

5.2. Methods

5.2.1. Study sites.

The study was conducted along a 10 km length of Hughes Creek, a predominantly sandy-bed stream, and a minor tributary of the Goulburn River in central Victoria, Australia. Hughes Creek is 70.4 km long and has no major tributaries in the system.

All sites for this study were along the main channel. We selected six reaches located in the middle section of the stream (36°59'S; 145°21'E). The distance between sites averaged 1.2 km, and the substrate at all sites was predominantly sand (Ø -0.5 to -1, or 1.7 to 2.0 mm). Additionally, in the middle section of Hughes Creek the height MASL decreases from 250 m to163 m MASL (Lancaster & Downes 2017) giving a gradient of 0.44 % over 20 km (Figure 5.1). The gradient between pairs of sites averaged 0.65%, which allowed us to compare reaches under similar gradient conditions albeit with sufficient distance between sites to prevent potential cofounding (Figure 5.2).

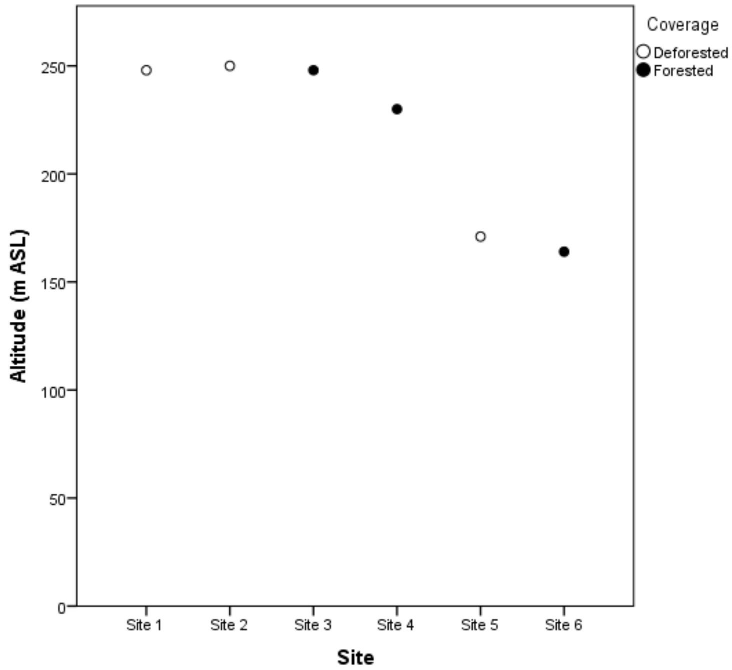


Figure 5 1. Altitudinal profile of the sites selected for this research. The altitude difference between the upper most site and the lowest site is 90 m (AMSL).

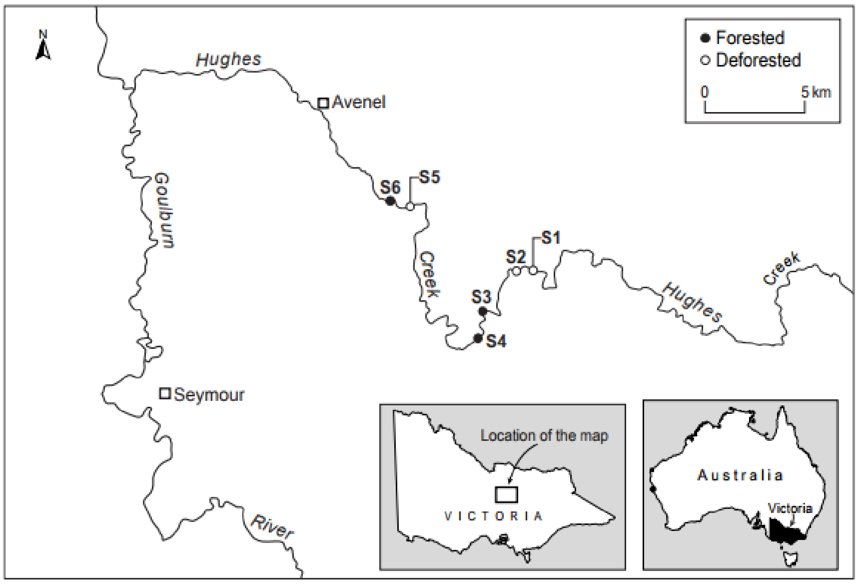


Figure 5 2. Study reaches distributed between forested and deforested sites. Selected sites were placed along the section with higher canopy cover (S1 and S2), in the forested patch (S3 and S4), and along two sites downstream from the forested area (S5, S6)

Along most of the length of Hughes Creek, the majority of riparian vegetation cover was low. However, patches of riparian forests surrounded the stream channel in some locations. In order to quantify vegetation cover and classify sites as forested or deforested, three main vegetation strata where observed: ground stratum represented by grass, mid-stratum represented by shrubs, and upper stratum represented by trees. The complete canopy description is available in Table 4.1 and supplementary material 7.1.

5.2.2. Collection of benthic CPOM

Ten CPOM samples were taken randomly from different patches of CPOM during February, June and November 2016. Sample collection was performed with a Surber sampler (0.09 m^2). The collection of benthic CPOM samples followed two main criteria: (1) CPOM patches had to be in the active channel, and patches should be from at least 3 pieces of CPOM gathered together (two or less leaves or twigs etc. were not considered as a patch) and (2) samples were taken at the centre of any patches larger than the Surber sampler area. Samples where patches were smaller than the area of the Surber sampler (0.09 m^2), were scrubbed around the delineated area of the sampler. This was undertaken in order to ensure uniform sample collection from similar areas. The age of patches was defined under an *in-situ* categorization criteria, whereby patches comprising decomposed organic matter (OM) were considered old (the OM was darkened, soft and decomposing), patches with a combination of new (green leaves) and old OM were classified as ‘mixed age’ patches, and those formed from CPOM recently delivered to the stream were recorded as new patches (dominated by fresh green leaves and twigs). All CPOM samples were preserved in 70% ethanol. In the laboratory, CPOM samples were sorted into fractions and dried and weighed to the nearest significant value (0.00g).

5.2.3. Macroinvertebrates

Macroinvertebrates in the orders Trichoptera, Ephemeroptera, Coleoptera, Diptera, and Hemiptera were removed from samples of benthic CPOM patches in summer (February) and spring (November) 2016. In the laboratory, the specimens were sorted and identified into genus, and when possible to species level. However, due to time constraints, the majority of Diptera species were excluded, apart from two blackflies species: *Austrosimulium furiosum and Simulium ornatipes*. Additionally, the only Coleoptera found, where adults were aquatic as well, were members of the *Austrolimnius* spp. (Elmidae) and *Berosus* spp. (Hydrophilidae) Larvae and adult stages of the former orders were counted separately.

5.2.4. Statistical methods

CPOM data were log-transformed and all CPOM fractions were analysed using nested factorial ANOVA models (IBM SPSS version 24.0), where season and forest cover (i.e. forested or deforested) were crossed, fixed factors, and site, a random factor, was nested within forest cover. Tests used a significance level of $p<0.05$. Patch age data (visual estimation of patch decomposition stage) were analysed through contingency table analysis (cross-tabulation, where cover was crossed with the total number of patches of each age). Macroinvertebrate density data were log-transformed and analysed with the same ANOVA model as CPOM fractions, also using a significance level of $p<0.05$. Scatterplots and linear regressions between CPOM density and species densities were performed in order to evaluate if density increase as the amount of CPOM become greater. To identify which species generated greatest dissimilarities between forested and deforested reaches, the densities of species were log-transformed and a SIMPER analysis was performed in PAST (version 3.26) software (Hammer et al. 2001) - Bray-Curtis distances were used as similarity index.

5.3. Results

5.3.1. CPOM results

The results show significant differences between Sites within Forest Cover for all the fractions with exception of leaf material. Moreover, some species also showed a *site x season* effect. The dominant patterns suggest high variation between sites and shifts between seasons (Table 5-1). In relation to seasonal change, it was found that leaf and twigs were fractions that showed significant variations across seasons but this depended on forest cover. However, all the fractions showed significant variation within sites as showed by Season X site (within Forest cover) factor. However, results illustrate that no fraction showed a response to Forest cover.

In relation to the contribution of each fraction provided to CPOM benthic standing stock, it was found that during the three sampling seasons, benthic CPOM composition was dominated by, in decreasing order, by twigs, bark, leaf, and grass (Figure 5.3). Moreover, it was demonstrated that grass was a small fraction in comparison to rest of fractions, yet it was clear that during summer at most sites, the composition of CPOM patches had low yet consistent amounts of grass. Moreover, between the three sampling seasons, summer showed the largest mass of CPOM standing stock on the streambed, where patches mas was 30g on average (Figure 5.3).

In relation to the age of patches, the results show that the patch age was dominated in both forested and deforested sites by old patches, and this result was consistent across all seasons (Figure 5.4). There were not significant differences between forested and deforested sites in relation to the age of patches (Tables 5-1 and 5-2).

Table 5-1. Nested ANOVA for benthic CPOM. Season and forest cover are crossed fixed factors, and site is nested within forest at a significance level of $p<0.05$. The table shows separate analyses for each fraction.

Fraction	Source	Type III SS	df	Mean Squares	F-ratio	p-value
Leaf	Forest cover	0.23	1	0.23	0.397	0.563
	Site (within Forest cover)	2.321	4	0.58	1.431	0.226
	Season	1.528	2	0.764	0.884	0.45
	Season x Forest cover	9.596	2	4.798	5.551	**0.031**
	Season x Site (within Forest cover)	6.915	8	0.864	2.131	**0.036**
	Error	65.691	162	0.406		
Bark	Forest cover	10.6	1	10.6	2.143	0.217
	Site (within Forest cover)	19.782	4	4.945	4.694	**0.001**
	Season	12.853	2	6.427	2.26	0.167
	Season x Forest cover	6.807	2	3.403	1.197	0.351
	Season x Site (within Forest cover)	22.75	8	2.844	2.699	**0.008**
	Error	170.697	162	1.054		
Twigs	Forest cover	0.297	1	0.297	0.045	0.842
	Site (within Forest cover)	26.398	4	6.599	8.191	**0.001**
	Season	2.776	2	1.388	0.715	0.518
	Season x Forest cover	22.837	2	11.419	5.88	**0.027**
	Season x Site (within Forest cover)	15.537	8	1.942	2.411	**0.017**
	Error	130.519	162	0.806		
Grass	Forest cover	0.038	1	0.038	0.017	0.904
	Site (within Forest cover)	9.23	4	2.307	5.389	**0.001**
	Season	2.797	2	1.398	0.577	0.583
	Season x Forest cover	0.332	2	0.166	0.069	0.934
	Season x Site (within Forest cover)	19.396	8	2.424	5.663	**0.001**
	Error	69.361	162	0.428		
Miscellaneous material	Forest cover	1.196	1	1.196	0.302	0.612
	Site (within Forest cover)	15.834	4	3.958	11.305	**0.001**
	Season	7.326	2	3.663	2.793	0.12
	Season x Forest cover	1.829	2	0.915	0.697	0.526
	Season x Site (Forest cover)	10.493	8	1.312	3.746	**0.001**
	Error	56.724	162	0.35		

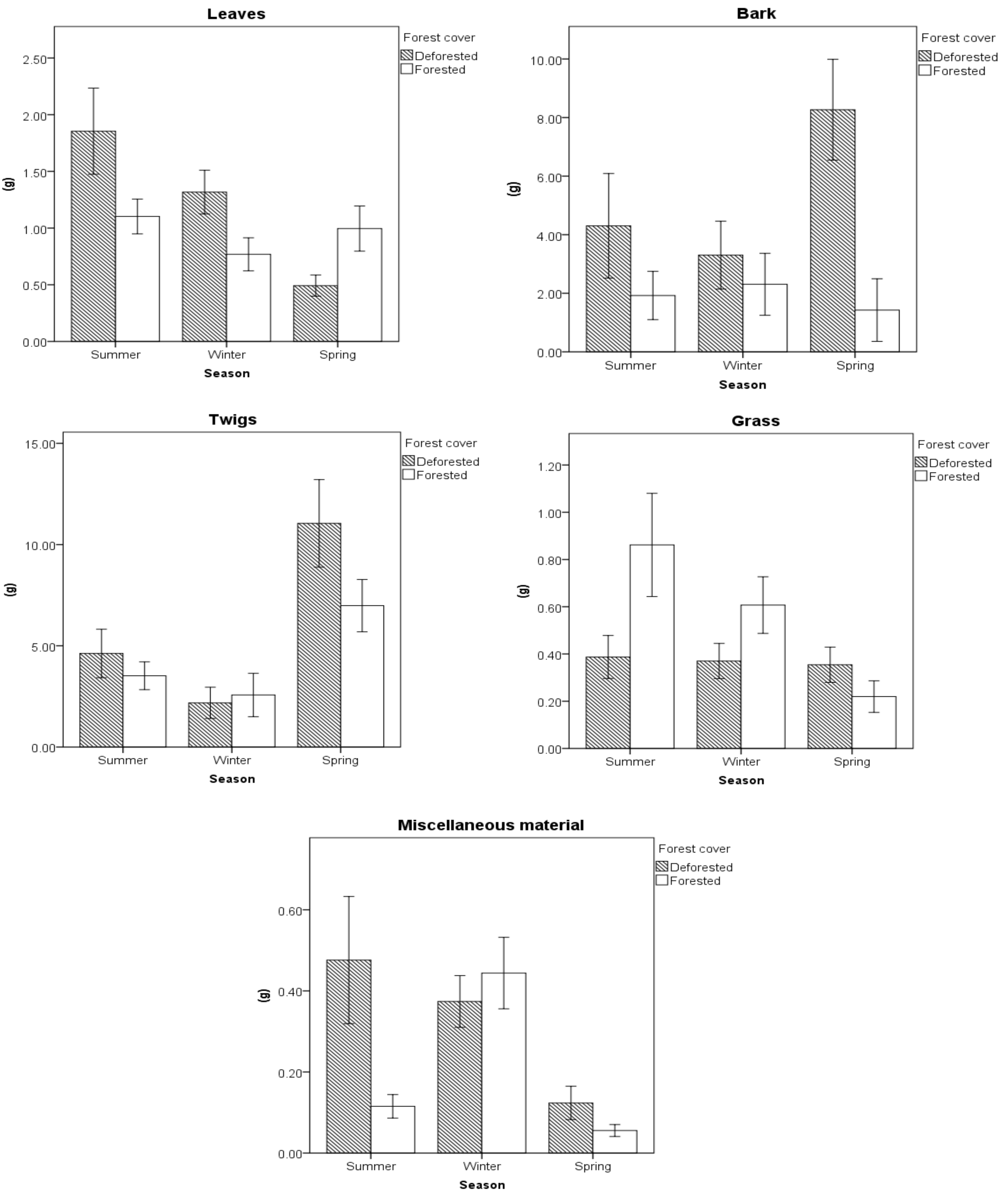


Figure 5 3. Bar charts with error bars illustrating the composition of patches during three sampling seasons in 2016. Bars represent standard error (SE); miscellaneous material refers to CPOM < 0.05 mm.

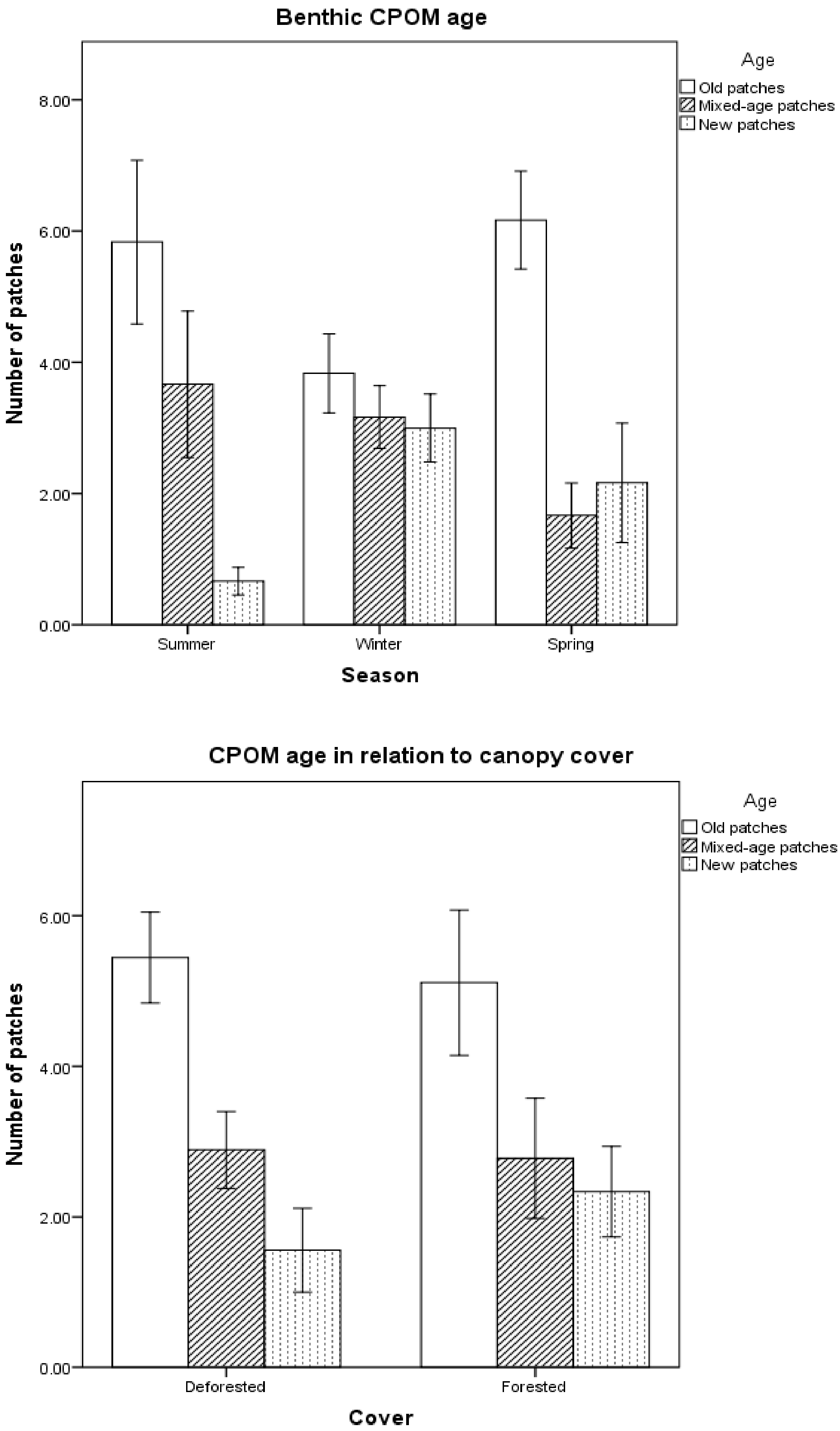


Figure 5 4. Bar charts with error bars of frequencies of benthic CPOM patches of different ages in three different seasons in 2016 (top) and (bottom) plotted vs different canopy covers (summed across seasons).

*Table 5-2. Cover * Patch age contingency table analysis. Count represents average of patches with three different ages across three different seasons and percentages of the total are also given. Chi-Square tests are found in table 5-4*

		Patch age			Total
		Old	Mixed age	New	
Cover	Deforested	50	26	14	90
		55.60%	28.90%	15.60%	100.00%
	Forested	46	25	19	90
		51.10%	27.80%	21.10%	100.00%
Total		96	51	33	180
		53.30%	28.30%	18.30%	100.00%

Table 5-3. Contingency table. Chi-Square results show that patch age is independent of forest cover

	Value	df	Asymptotic Significance (2-sided)
Pearson Chi-Square	.944[a]	2	0.624

5.3.2. Macroinvertebrate results

The analysis of species densities between forested and deforested site show that *Simulium ornatipes* and *Ecnomina F* sp. densities were different between the two types of forest cover, while the rest of species did not show any difference. Yet, *Simulium ornatipes* showed strong differences between sites. *Ecnomina F sp*., however, was the only taxon to show a difference related to forest cover without substantial difference among sites within the same forest cover On the other hand, *Ecnomus continentalis, Notalina* sp., *Chemautopsyche* sp, *Hydroptila*, *Berosus* (larvae), and *Micronecta* sp. showed higher significant differences in summer; where *Chemautopsyche* sp. and *Hydroptila* sp. densities were minimal in patches during spring (Table 5-4; Figure 5.5). However, it was also observed that the spatial and temporal variation dominated in many of the differences between sites, and in some cases with interactions with season

The regressions correlation between the mass of CPOM and density of species showed that some of them presented negative relationships between specimens' density and the increase of CPOM mass. For example, *Ecnomia* F sp., *Cheumatopsyche* sp., and *Nousia* sp. (Figure 5.6); however, some of these species responded to the season factor. Moreover, a SIMPER analysis was performed to evaluate if the former species were responsible of producing differences between forested and deforested reaches. However, the SIMPER analysis showed that *Austrosimulium furiosus*, *Offadens* sp., *Tasmanocoenis* sp., and *Micronecta* sp. were the species that produced the highest dissimilarity between forested and deforested sites, in both Summer and Spring. (Table 5-5).

Table 5-4. Nested ANOVA of macroinvertebrate species found in CPOM patches in forested and deforested reaches. Species are grouped into families. Bold values highlight significant differences. (Species and genera descriptions can be found in supplementary material 2).

Taxa	Factor	Type III Sum of Squares	df	Mean Square	F	p
Simulium ornatipes	Forest cover	87.571	1	87.571	8.499	**0.043**
	Site (Forest cover)	41.213	4	10.303	6.177	**0.001**
	Season	15.139	1	15.139	1.152	0.343
	Season*Forest cover	10.394	1	10.394	0.791	0.424
	Season x Site (Forest cover)	52.578	4	13.144	7.880	**< 0.001**
	Residual	180.152	108	1.668		
Austrosimulium furiosum	Forest cover	23.003	4	5.751	0.016	0.905
	Site (Forest cover)	348.598	1	348.598	251.074	**0.001**
	Season	2.038	1	2.038	0.553	0.498
	Season*Forest cover	19.461	4	4.865	1.319	0.314
	Season x Site (Forest cover)	3.689	1	3.689	2.657	**0.036**
	Residual	149.950	108	1.388		
Ecnomina E sp.	Forest cover	8.906	1	8.906	1.353	0.309
	Site (Forest cover)	26.330	4	6.583	5.505	**0.001**
	Season	2.617	1	2.617	0.405	0.559
	Season*Forest cover	4.915	1	4.915	0.760	0.432
	Season x Site (Forest cover)	25.865	4	6.466	5.408	**0.001**
	Residual	129.146	108	1.196		
Ecnomina F sp.	Forest cover	9.736	1	9.736	39.820	**0.003**
	Site (Forest cover)	0.978	4	0.244	0.401	0.808
	Season	1.820	1	1.820	0.433	0.546
	Season*Forest cover	1.820	1	1.820	0.433	0.546
	Season x Site (Forest cover)	16.808	4	4.202	6.887	**0.001**
	Residual	65.899	108	0.610		
Ecnomus continentalis	Forest cover	4.003	1	4.003	0.670	0.459
	Site (Forest cover)	23.892	4	5.973	3.510	**0.01**
	Season	118.668	1	118.668	11.645	**0.026**
	Season*Forest cover	3.718	1	3.718	0.365	0.578
	Season x Site (Forest cover)	40.761	4	10.190	5.988	**0.001**
	Residual	183.805	108	1.702		
Coenoria sp.	Forest cover	7.859	1	7.859	1.346	0.31
	Site (Forest cover)	23.354	4	5.839	3.573	**0.009**
	Season	12.430	1	12.430	2.414	0.195
	Season*Forest cover	0.953	1	0.953	0.185	0.689
	Season x Site (Forest cover)	20.596	4	5.149	3.151	**0.017**
	Residual	176.481	108	1.634		
Notalina sp.	Forest cover	9.719	1	9.719	5.446	0.079
	Site (Forest cover)	7.138	4	1.785	1.551	0.193
	Season	44.972	1	44.972	25.200	**0.007**

	Season*Forest cover	9.719	1	9.719	5.446	0.079
	Season x Site (Forest cover)	7.138	4	1.785	1.551	0.192
	Residual	124.261	108	1.151		
Chemautopsyche sp.	Forest cover	9.316	1	9.316	0.991	0.375
	Site (Forest cover)	37.619	4	9.405	5.845	**0.001**
	Season	110.549	1	110.549	17.273	**0.014**
	Season*Forest cover	10.203	1	10.203	1.594	0.275
	Season x Site (Forest cover)	25.601	4	6.400	3.978	**0.004**
	Residual	173.767	108	1.609		
Hydroptila sp.	Forest cover	0.898	1	0.898	1.380	0.305
	Site (Forest cover)	2.602	4	0.651	0.748	0.561
	Season	9.852	1	9.852	12.307	**0.024**
	Season*Forest cover	2.236	1	2.236	2.793	0.169
	Season x Site (Forest cover)	3.202	4	0.801	0.921	0.454
	Residual	93.897	108	0.869		
Oecetis sp.	Forest cover	0.300	1	0.300	4.000	0.116
	Site (Forest cover)	0.300	4	0.075	0.500	0.736
	Season	0.000	1	0.000	0.000	1.00
	Season*Forest cover	0.000	1	0.000	0.000	1.00
	Season x Site (Forest cover)	0.900	4	0.225	1.500	0.207
	Residual	16.205	108	0.150		
Asmicridea sp.	Forest cover	0.108	1	0.108	1.000	0.373
	Site (Forest cover)	0.433	4	0.108	1.000	0.411
	Season	0.108	1	0.108	1.000	0.373
	Season*Forest cover	0.108	1	0.108	1.000	0.373
	Season x Site (Forest cover)	0.433	4	0.108	1.000	0.410
	Residual	11.678	108	0.108		
Diplectrona sp.	Forest cover	0.075	1	0.075	1.000	0.373
	Site (Forest cover)	0.300	4	0.075	1.000	0.411
	Season	0.075	1	0.075	1.000	0.373
	Season*Forest cover	0.075	1	0.075	1.000	0.373
	Season x Site (Forest cover)	0.300	4	0.075	1.000	0.410
	Residual	8.102	108	0.075		
Offadens sp.	Forest cover	1.480	1	1.480	0.216	0.666
	Site (Forest cover)	27.453	4	6.863	7.548	**0.001**
	Season	0.020	1	0.020	0.002	0.883
	Season*Forest cover	0.000	1	0.000	0.000	0.99
	Season x Site (Forest cover)	33.686	4	8.421	9.261	**0.001**
	Residual	98.206	108	0.909		
Centroptilumn sp.	Forest cover	0.020	1	0.020	0.026	0.879
	Site (Forest cover)	3.104	4	0.776	2.246	0.069
	Season	0.020	1	0.020	0.026	0.879
	Season*Forest cover	1.532	1	1.532	1.974	0.232
	Season x Site (Forest cover)	3.104	4	0.776	2.246	0.068
	Residual	37.306	108	0.345		
Cleon sp.	Forest cover	0.009	1	0.009	0.043	0.845

	Site (Forest cover)	0.845	4	0.211	1.000	0.411
	Season	0.413	1	0.413	1.957	0.234
	Season*Forest cover	0.009	1	0.009	0.043	0.846
	Season x Site (Forest cover)	0.845	4	0.211	1.000	0.410
	Residual	22.802	108	0.211		
Tasmanocoenis sp.	Forest cover	0.802	1	0.802	0.078	0.793
	Site (Forest cover)	41.164	4	10.291	9.858	**0.001**
	Season	7.008	1	7.008	1.044	0.364
	Season*Forest cover	3.619	1	3.619	0.539	0.503
	Season x Site (Forest cover)	26.857	4	6.714	6.432	0.503
	Residual	112.743	108	1.044		
Nousia sp.	Forest cover	3.188	1	3.188	0.208	0.672
	Site (Forest cover)	61.328	4	15.331	7.316	**0.001**
	Season	19.901	1	19.901	6.115	0.068
	Season*Forest cover	4.610	1	4.610	1.417	0.299
	Season x Site (Forest cover)	13.018	4	3.254	1.553	0.192
	Residual	226.32	108	2.096		
Atalophlebia sp.	Forest cover	0.119	1	0.119	0.212	0.669
	Site (Forest cover)	2.249	4	0.562	1.406	0.237
	Season	0.041	1	0.041	0.108	0.758
	Season*Forest cover	0.797	1	0.797	2.099	0.220
	Season x Site (Forest cover)	1.519	4	0.380	0.949	0.438
	Residual	43.197	108	0.400		
Austrolimnius sp.	Forest cover	0.772	1	0.772	0.041	0.849
	Site (Forest cover)	75.427	4	18.857	12.250	**0.001**
	Season	66.282	1	66.282	5.493	0.079
	Season*Forest cover	0.129	1	0.129	0.011	0.922
	Season x Site (Forest cover)	48.267	4	12.067	7.839	**0.001**
	Residual	166.24	108	1.539		
Berosus sp. (larvae)	Forest cover	5.145	1	5.145	0.528	0.507
	Site (Forest cover)	38.984	4	9.746	10.170	**0.001**
	Season	96.968	1	96.968	8.707	**0.041**
	Season*Forest cover	8.751	1	8.751	0.786	0.425
	Season x Site (Forest cover)	44.545	4	11.136	11.621	**0.001**
	Residual	103.49	108	0.958		
Berosus sp. (adult)	Forest cover	3.072	1	3.072	0.299	0.613
	Site (Forest cover)	41.093	4	10.273	20.166	**0.000**
	Season	11.533	1	11.533	1.579	0.277
	Season*Forest cover	3.072	1	3.072	0.421	0.551
	Season x Site (Forest cover)	29.211	4	7.303	14.335	**0.001**
	Residual	55.019	108	0.509		
Micronecta sp.	Forest cover	32.726	1	32.726	2.574	0.183
	Site (Forest cover)	50.854	4	12.713	8.130	**0.001**
	Season	203.28	1	203.285	47.092	**0.002**
	Season*Forest cover	0.053	1	0.053	0.012	0.917
	Season x Site (Forest cover)	17.267	4	4.317	2.760	**0.031**
	Residual	168.89	108	1.564		

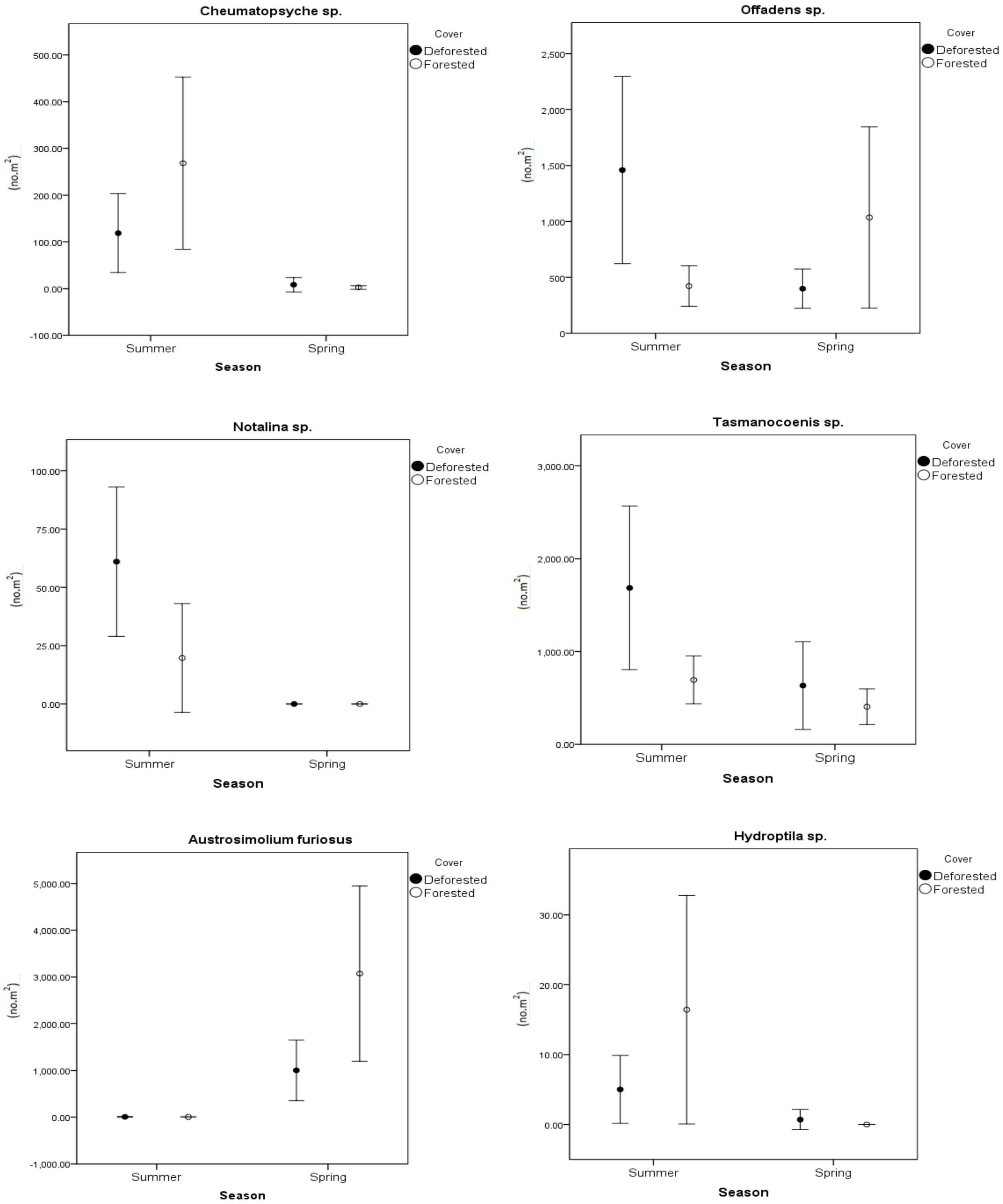


Figure 5 5. Examples of densities of individuals of six taxa in forested and deforested sites at Hughes Creek during summer and spring 2016. Bars represent standard error (SE), where Offadens sp., Tasmanocoenis sp., and Hydroptila sp. showed no significant differences to forest cover, while Cheumatopsyche sp, Notalina sp., and Austrosimolium sp. However, the figures also show strong variation between sites with interactions between sites.

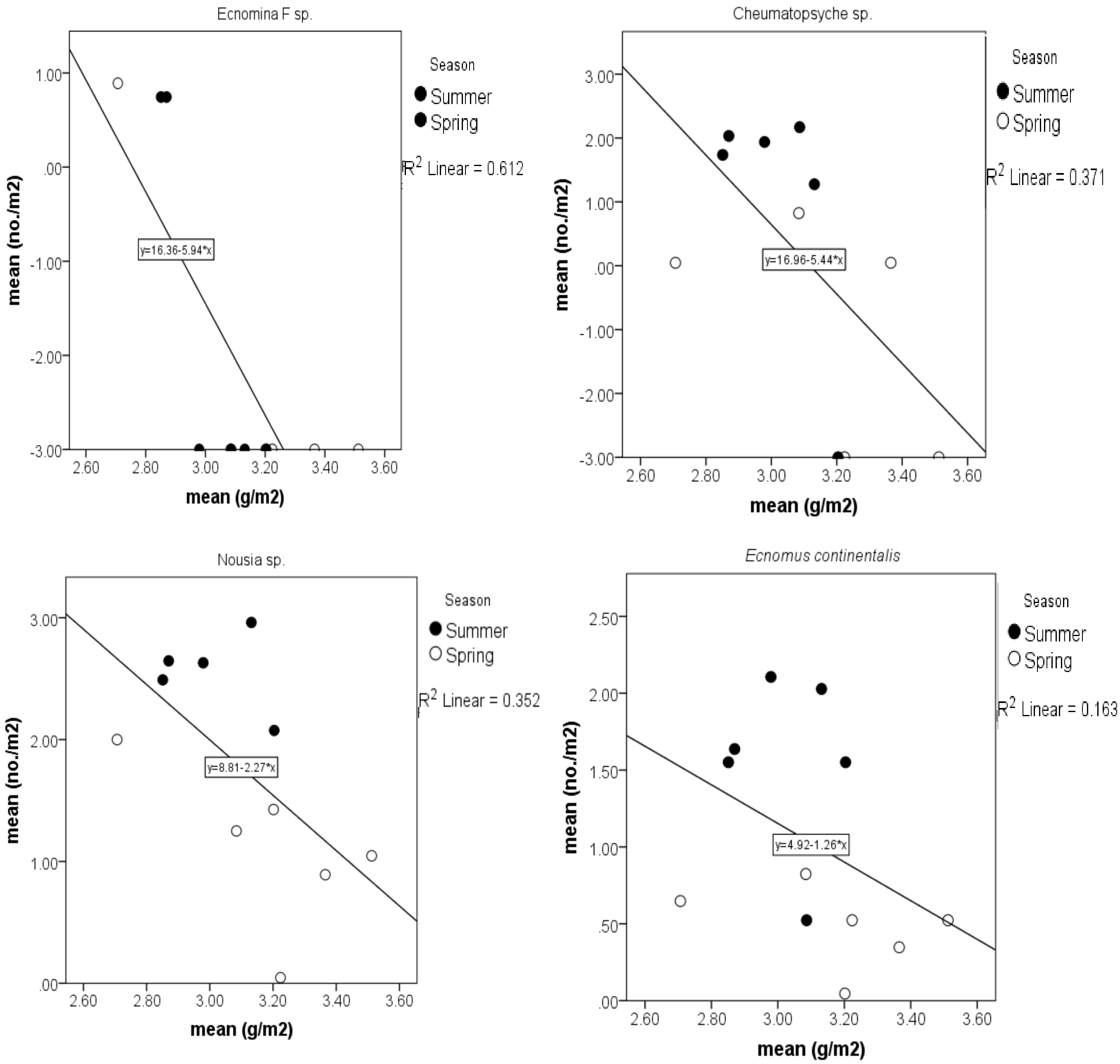


Figure 5 6. Scatterplot examples of species showing negative regressions between species density (no./m^2) and density of CPOM (g/m^2) at Hughes Creek during spring and summer 2016. CPOM and species density values were log$_{10}$-transformed. On this case, regressions were used to evaluate if CPOM mass drove changes on macroinvertebrate densities

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Table 5-5: List of taxa making the largest contributions to dissimilarity in community composition between forest and deforested reaches in spring and summer at Hughes Creek, based on SIMPER analysis. List is in order of decreasing importance. Taxa in bold dominate deforested reaches

Rank	Species code	Summer	Contrib. %	Species code	Spring	Contrib. %
1	A	***Austrosimulium furiosus***	*23.79*	A	*Austrosimulium furiosum*	55.97
2	B	***Offadens* sp.**	*22.5*	B	*Offadens* sp.	19.27
3	C	***Tasmanocoenis* sp.**	*18.31*	C	***Tasmanocoenis* sp.**	18.23
4	D	***Micronecta* sp.**	*15.73*	D	*Nousia* sp.	3.364
5	E	*Cheumatopsyche sp.*	*5.915*	E	***Micronecta* sp.**	1.378
6	F	*Ecnomus continentalis*	*3.482*	F	*Ecno* Simuliidae	0.2616
7	G	***Austrolimnius* sp.**	*2.314*	G	*Ecnomina F* sp.	0.2558
8	H	*Berosini sp.* (Larvae)	1.899	H	***Austrolimnius* sp.**	0.2368
9	I	*Ecnomina E* sp.	0.9337	I	***Coenoria* sp. *AV1***	0.1691
10	J	*Coenoria* sp.	0.9175	J	***Ecnomus continentalis***	0.1614
11	K	***Notalina* sp.**	0.8125	K	*Cheumatopsyche* sp.	0.1605
12	L	*Nousia* sp.	0.73	L	*Leptoperla*	0.1517
13	M	***Berosini sp* (adult)**	0.706	M	***Berosini* sp. (Larvae)**	0.1514
14	N	*Centroptilum* sp.	0.4995	N	*Centroptilum* sp.	0.06928
15	O	*Cleon* sp.	0.3568	O	***Atalophlebia* sp.**	0.06727
16	P	*Ecnomina* sp.	0.3103	P	***Hydroptila* sp.**	0.03339
17	Q	*Hydroptila* sp.	0.3035	Q	*Berosini sp* (adult)	0.03307
18	R	*Ecnomina F* sp.	0.2263	R	*Oecetis* sp.	0.02718
19	S	*Atalophlebia* sp.	0.1405	S	*Notalina* sp.	0
20	T	*Diplectrona* sp.	0.08702	T	*Cleon* sp.	0
21	U	*Asmicridea* sp.	0.01582	U	*Diplectrona* sp.	0
22	V	*Oecetis* sp.	0.01582	V	*Asmicridea* sp.	0
Overall average dissimilarity 46.3				Overall average dissimilarity 59.56		

5.4. Discussion

In this chapter I tested two hypotheses. The first hypothesis was that the composition of benthic CPOM patches have a higher mass of grass when riparian vegetation of deforested reaches has been transformed into grasslands. It was further hypothesized that if macroinvertebrate species densities and composition was affected by the amount of CPOM found in patches. It would be expected a significant variation of densities and type of macroinvertebrate species between patches with different masses of CPOM, and that the type of CPOM fraction (i.e. grass or tree-originated CPOM) would not be a significant factor affecting macroinvertebrates.

5.4.1. CPOM patch composition

The amount of benthic CPOM standing stock in headwater streams, depends upon the allochthonous inputs delivered by riparian vegetation (Bilby & Bisson 1992, Richardson et al. 2005, Webster et al. 1994, Webster et al. 2006). Moreover, the dynamics and composition of benthic CPOM is affected by the type of riparian vegetation available along the banks of streams (Dodds et al. 2004, Matthews 1988). Based on these observations, it was expected that in deforested reaches benthic CPOM composition would have higher amounts of grass. However, our analysis illustrates that the amount of grass between forested and deforested reaches was similar, in contradiction with our hypothesis. Scarsbrook and Townsend (1994) argue that the similarity between forested and deforested reaches is related to the small size of grass, which is likely to drift even when there is a minimal increase in discharge. However, our data does not provide enough evidence to assess whether the latter was the case. Similarly, none of the fractions delivered by trees showed significant differences between the two types of forest cover. However, most fractions, including grass, showed significant differences related to Site (within Forest cover), suggesting that there was strong variability between sites collected in both forested and deforested reaches. Diez et al. (2000) found that higher allochthonous inputs, due to higher canopy cover, do not increase benthic storage of CPOM. This observation could be related to the absence of retention structures such as large woody debris (LWD), which increase both channel heterogeneity and CPOM retention. Lancaster and Downes (2017c) provide evidence that the addition of small stakes on the riverbed of Hughes Creek increased significantly the retention of CPOM on the sites where these structures were added. Thus, it is possible that the lack of retention structures between our studies could influence our results.

5.4.2. Age of CPOM patches

The age of the CPOM patches was dominated by old patches during the three sampling seasons during 2016. In winter, it was expected that patches of CPOM on the river bed would be mostly new, due to high flows transporting CPOM too quickly for decomposition to occur, but our results show a different scenario. Finding more old patches across the three sampling seasons could be a result of the sclerophyllous nature of eucalypt leaves, which are more resistant to breakdown than are leaves of other species (Abelho & Graca 1996, Pozo et al. 1997). However, the breakdown of eucalypt leaves is subject to seasonal variability. For example, Larrañaga et al (2014) found that eucalypt leaves deteriorate 97% faster during winter compared to other seasons, while the decomposition of leaves from other tree species increased by 58% during winter in comparison to other seasons. Such decomposition rates depend upon many factors. For example, Menninger and Palmer (2007) found that monocotyledon species had lower decomposition rates than did dicotyledon species, indicating that plant/leaf physical and chemical properties play a significant role in decomposition rates during different seasons. Additionally, the leaves of some eucalypt species contain more oils and have more resistant cellulose than those of other eucalypt species, and the leaves have different morphologies, colours and other characteristics as the tree matures (Brooker & Kleinig 1999), which may further exacerbate differences in decomposition. Notwithstanding this, the contingency analysis illustrates that forest cover did not affect the age of patches found in the streambed (Table 5-3; 5-4). Further, the presence of old patches was always over 50 % in both forested and deforested sample reaches.

5.4.3. Macroinvertebrates species composition between forested and deforested reaches

The second hypothesis was that macroinvertebrate densities and species composition would vary between patches with different masses of CPOM, irrespective of the type of cover in the reach from where they were collected. Whereas two species responded to the type of cover, such response was conditional upon the interaction between the site and the season, which suggests that variability of macroinvertebrates within each site was greater. In fact, the results from our data show that patterns associated with

Forest Cover or Season are trivial compared to the variation between sites and interactions between sites and seasons.

The species that responded to the type of canopy cover, were species that showed higher densities in deforested reaches. One initial explanation could be the greater availability of food in deforested reaches, as greater amounts of algae associated to sunlight reaching the stream, as exposed by Scrimgeour and Kendall (2002), Passy and Blanchet (2007), or Stevenson et al (1996). However, these studies were all based on rocky streams, whereas Hughes Creek is a sandy stream, and very little algae can be found on the surface, as it gets covered by sand quickly. The latter is supported by the studied performed by Reid et al (2008b), where it is explained that in Hughes Creek terrestrial detritus are the source that supports food webs in Hughes Creek. Thus, as we did not find significant differences between the amount of CPOM found in forested and deforested reaches, and other explanations should be explored to explain densities variations in macroinvertebrates. For instance, it has also been reported that deforested reaches may decrease alpha diversity due to changes in water temperature (Benstead & Pringle 2004, Bojsen & Jacobsen 2003, Lorion & Kennedy 2009a), which ultimately could lead to a decrease in beta diversity in the streams of a given area (Passy & Blanchet 2007). However, we have no evidence to assure what was the factor that produce the densities dissimilarities between the two types of reaches.

The regression between CPOM mass and macroinvertebrate density illustrates two scenarios. Firstly, species showing no correlation to the amount of CPOM (Figure 5.6), which is consistent with their feeding groups. For example, the larvae of *Simulium ornatipes* use detritus as places to filter-feed. On the other hand, the nymphs of *Offadens* spp. scrap algae and fine detritus (Supplementary material 7.2). Contrastingly, we found that *Austrosimulium furiosus* did not respond to the amount of CPOM, which is contrary to findings reported by Lancaster and Downes (2017c), where *Austrosimulium furiosum* responded strongly to the amount of detritus available. However, our scatterplots results show that they were confounded comparisons, because seasons with their different amounts of CPOM are often restricted to one part on the graph – i.e. the differences could be seasonally related rather than directly related to CPOM densities. Consequently, there is no possible way to separate seasonal differences and effects of CPOM densities on densities of invertebrates. This outcome prevents us from concluding that the concentration of CPOM was the main cause for the changes in species densities, even though the pattern from the graphs show a potential tendency to reduce densities as CPOM masses increase.

In regard to species composition, the SIMPER analysis shows that it was only a few species which produced the greatest dissimilarity between forested and deforested reaches, both in summer (average dissimilarity 46.3) and spring (average dissimilarity 59.56). We found the species that promoted the highest dissimilarity during summer were more abundant in deforested reaches (Table 5-6). Moreover, most of the species that produced the greatest dissimilarity fed, or use detritus as a substrate, either from algae (*Offadens* spp.) or were filter-feeders (*Austrosimulium furiosum*). However, in spring the opposite was apparent, whereby many of the species that resulted in the greatest dissimilarities during summer, also dominated in spring but in the forested reaches (Table 5-6). Previous studies deployed in isolated forest ponds have shown that species composition varied seasonally (Batzer et al. 2004, Brooks 2000). Also, early studies that focused on the micro-distribution of benthic communities associated density variability to changes in substrate condition, current, and depth (Minshall and Minshall 1977, Ulfstrand 1967). Yet, these results show that there is a great species density variability in time and space within each sampled reach, and that, at least in Hughes Creek, species densities are sensitive to either forest cover or season.

5.4.4. Survey results and implications for a field experiment

The results of this chapter established that space and time variability of species densities cannot be explained by forest cover or season only. Further, many questions arose from the survey, for example, to what extent do the sizes of CPOM patches affect species densities? It may be that the sampled natural patches in this survey were quite homogenous, as only twice were patches found to be substantially larger than that of the average patch, thereby affecting the response of species to them. In addition, we queried if patch size modifies macroinvertebrate densities, as the models for patchy landscapes suggest. These questions enabled us to develop the field experiment described in the next chapter, where the size, orientation, and the spatial distribution of patches upon the densities of the most common species is tested.

6. The effect of spatial distribution, size, and orientation of resource patches upon aquatic populations with advective dispersal.

Title

The effect of spatial distribution, size, and orientation of resource patches upon aquatic populations with advective dispersal.

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6.1. Abstract

Many macroinvertebrate species in headwater streams depend on coarse particulate organic matter (CPOM) patches, which are randomly distributed in an environment that otherwise may not provide them with, for example, energy or shelter. Effects of patchiness depend upon the characteristics of the spatial distribution of patches, and animal distribution. Small-scale fragmentation is predicted to affect species densities, particularly where patches are ephemeral, or organisms are transported advectively. Macroinvertebrates and lotic streams represent this type of relationship. We deployed CPOM patches in two possible configurations (a) one big patch treatment (BPT), comprised of 12 smaller sub-patches of the same size, and (b) 12 split patches (SPT), which were distributed across the streambed. Patches from the split treatment were of two sizes, double (300 cm^2) and single (150 cm^2). BPT and SPT patches from both treatments were oriented randomly on the stream (parallel or perpendicular) with respect to water flow. After 10 days, it was sampled 13 common macroinvertebrates which had colonised the patches. It was found that, the genera *Offadens* spp. and *Notriolus* spp. had responded to the orientation of patches in both treatments. Moreover, in SPT sites *Offadens* spp., Cheumatopsyche spp., and *Notriolus* spp. showed significantly higher densities in small patches, suggesting that these species did not show search strategies for resources and their densities might be affected by patch size.

Keywords

Density, patch, size, orientation, stream, macroinvertebrates

6.2. Introduction

Many populations occur in complex landscapes where high quality resource patches are distributed within in an environment that represents a lower quality matrix. The quantity and quality of resources and the heterogeneity of these landscapes affect populations in diverse ways, because the landscape structure represents different degrees of risks and benefits for the movement of individuals (Rothermel & Semlitsch 2002, Turner 1989). At the population level, densities of different species may vary with total resources abundance, and size and shape of resource patches (Gutzwiller & Anderson 1992).

The density of individuals within patches can vary due to density-area relationships (DARs). The concept of DARs states that abundances are in most cases reduced with a reduction in patch size, while the effect on density is much more variable among species and depends on the differences of body size or shape and dispersal mechanisms (Hambäck et al. 2007). For example, when patches are clumped, densities can be lower than when patches are distributed randomly, because distances between clumps may exceed the movement capacity of animals (Lancaster & Downes 2014). Theories such as island biogeography (MacArthur & Wilson 1967), the resource concentration hypothesis (Root 1973), or the single large or small several reserves exposed in the island dilemma, by Diamond (1975) have been developed to explain DARs relationships. The theory proposed by MacArthur and Wilson (1967) predicts higher densities on larger islands due to area-related immigration and emigration rates. Moreover, the authors also hypothesize that an increase in island size could decrease extinction rates; however, if distance between islands decreases then the immigration rate increases, with these two factors being defined as "single large or several small" (SLOSS) distributions of islands the authors explain densities variability across landscapes where the distribution of islands vary. Furthermore, Root's hypothesis (1973) also conjectures that population density should be positively correlated with the concentration of resources. The latter means that density of species is also correlated to the amount of the resources or substrate found in patches, which ultimately determines patch size. Furthermore, recent evidence suggests that the spatial arrangement of resource patch arrays might affect movement behaviour and the abundance of species with adventive dispersal (Baum et al. 2004, Bender & Fahrig 2005, Haddad & Baum 1999).

The movement strategy of different taxa and patch sizes in ecosystems can affect species densities differently. Bowman et al. (2002) proposed diverse scenaria according to the dispersal strategies of different taxa, patch sizes, and orientation of patches. (Figures 6.1 and 6.2), which differ from the general idea that densities are linearly correlated to patch area. For example, taxa not searching actively for resources, such as species that reach resources by chance through drift transport, result in immigration proportional to the linear dimension of the patch (Figures 6.1. and 6.2. A). This effect is related to the number of individuals searching for a patch being proportional to the linear dimension of the patch that is perpendicular to the direction of travel (Figure. 6.2). However, the area of the patch increases with the square of the linear dimensions of the patch, thus it is expected that the density of individuals declines as patch size increases. Moreover, taxa dispersing via a random search strategy such as species that move across the landscape for patches (Figure 6.1 and 6.2, B), are likely to show a negative relationship between density and patch area. This is because the likelihood of a specimen reaching a patch is similar to those taxa with no searching strategies, or, a species that moves without a specific pattern across the landscape, yet nonetheless reaches resource patches (Bowman et al. 2002). Likewise, in proportion to the linear dimension of the patch (Figures 6.1 and 6.2), taxa that crawl or walk towards patches would show negative immigration rates. This is due to immigrating individuals facing the same effect of , as in cases A and B, due to the area of patch area increasing exponentially with patch linear dimension (Figure 6.1 and 6.2, C) Conversely, taxon searching actively for larger patches would show a contrasting positive effect in relation to patch area, resulting in A,B, or C would show a constant increase (Figure 6.1 and 6.2. D), ergo, immigration rates would be proportional to the area of the patch, thereby resulting in positive immigration rates in larger patches. Thus, in summary, three search strategies result in negative density-area relationships, while a fourth results in positive density-area relationships.

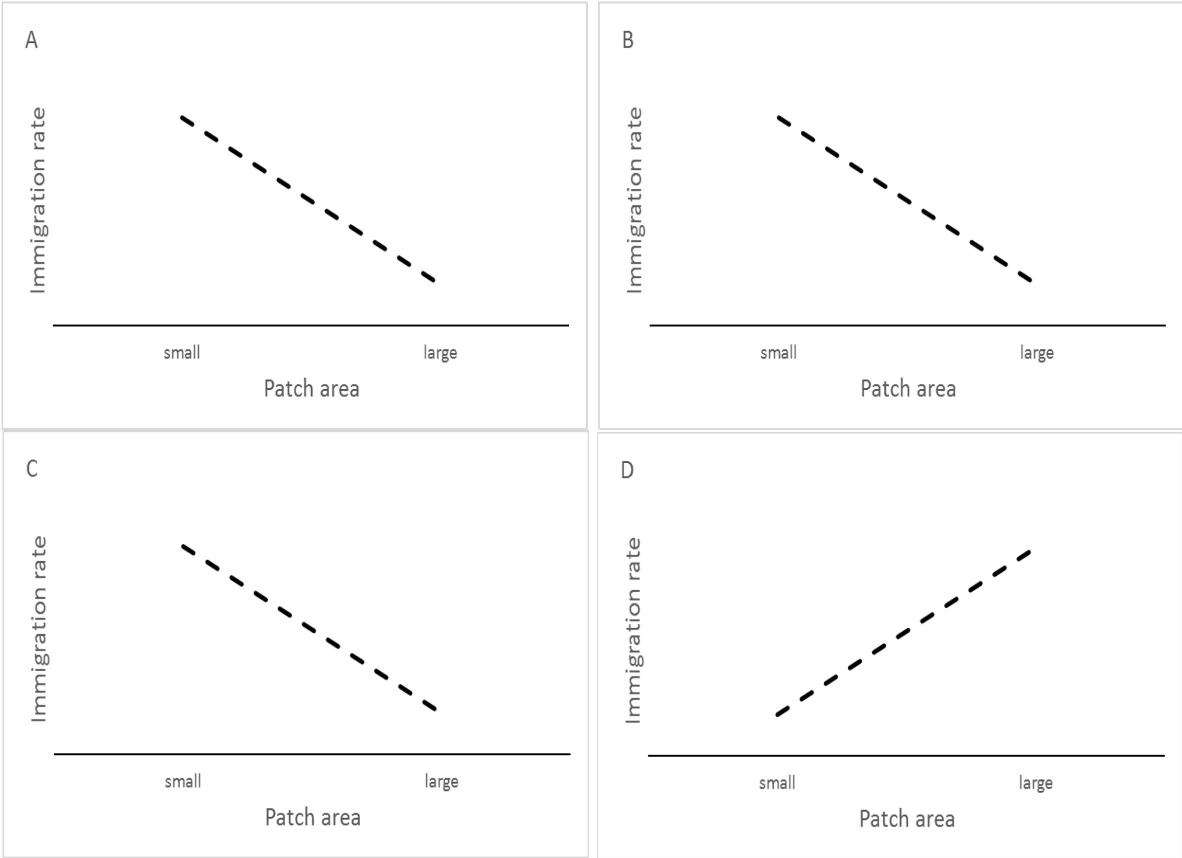

Figure 6 1. Expected relationship between immigration rate and patch area for species that move near the ground. A) No searching, B) Random searching, C) Orientation toward patches proportional to patch size (linear dimension or area), and D) Orientation toward patches increases disproportionately with patch size (linear dimension or area). Figures summarized from the observations of Bowman et al. (2002).

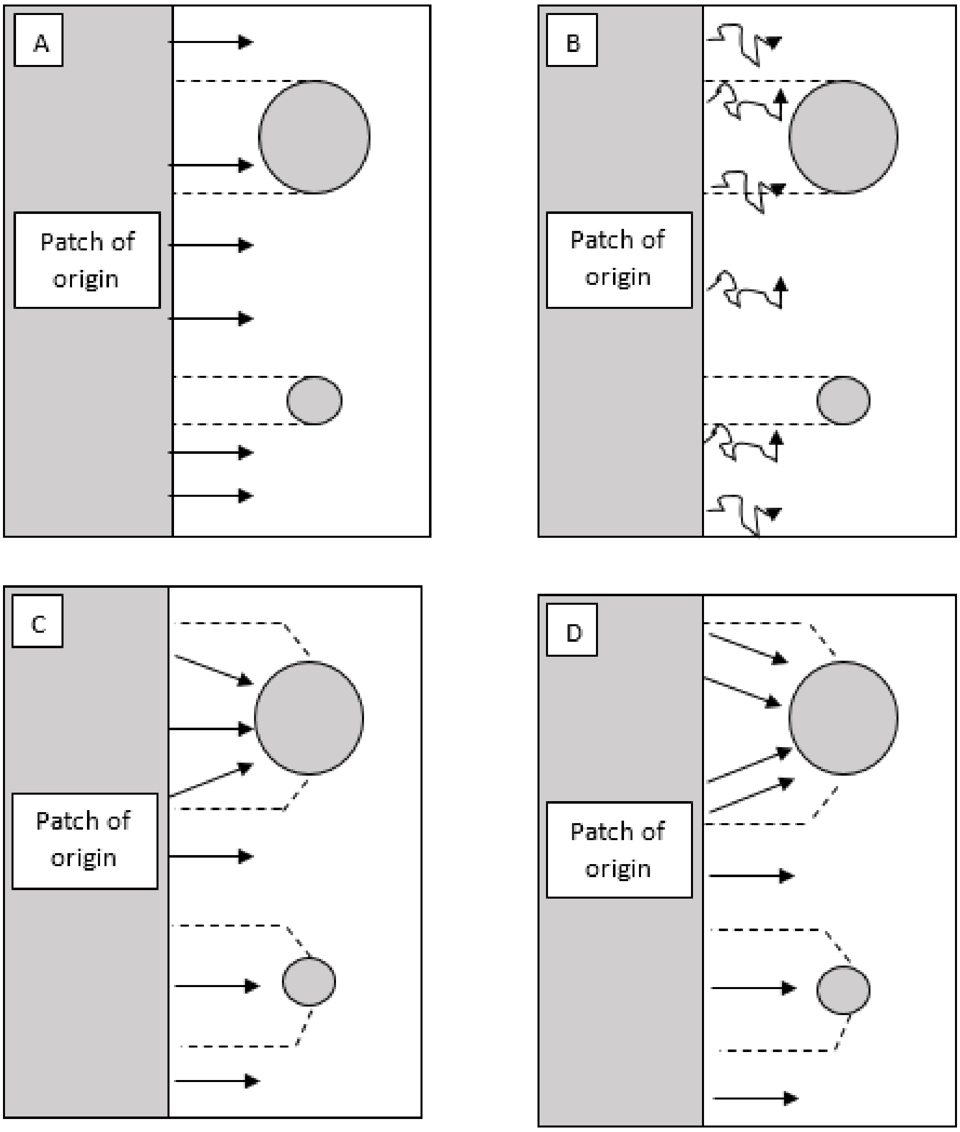

Figure 6 2. Graphic representation of the four dispersal strategies showed in figure 6.1. A) No searching, species that reach patches by chance, B) Random searching, species that search for resources but their movement follows no pattern, C) Orientation toward patches proportional to patch size (linear dimension or area), species that move patches regarding the size of them, and D) Orientation toward patches increases disproportionately with patch size (linear dimension or area), species that move towards patches that have greater area. Figures adapted from figure 1 in Bowman et al. (2002).

The above relationships between patch area and species densities can also be disrupted by human activities, which could increase, decrease or modify the quantity and quality of resource patches. For example, headwater streams globally are in constant change as anthropogenic development modifies them into agricultural or urban areas. The modification of the areas surrounding headwater streams directly affects canopy cover of such lotic systems, due to deforestation. However, in several cases, deforestation does not take place along the entire length of a stream, and some sections remain with contrasting riparian vegetation cover (Reid et al. 2008b). Changes in riparian cover inevitably modify the quantity, quality, or type of allochthonous inputs into streams, which is retained in patches (benthic CPOM) on the streambed by diverse structures, such as benches, large woody debris et cetera (Bilby & Bisson 1998, Bilby & Likens 1980) – further information in Chapter 5.

Lower quantities of allochthonous inputs may decrease the amount of benthic CPOM available, which results in complex landscapes where resource patches are relatively isolated from each other. Such patchy distribution of resources is likely to affect aquatic macroinvertebrates, which depend greatly upon these resources to obtain energy or shelter (Mihuc & Minshall 1995, Minshall 1967, Vannote et al. 1980). In lotic ecosystems, as in terrestrial ones, the balance between the risks and benefits of the movement of macroinvertebrates is affected by landscape structure, and in particular, the amount of habitat in the landscape, habitat patchiness, habitat permanence and matrix quality (Fahrig 2007). However, streams also have the capacity to affect species dispersal due to discharge, and spatial and temporal factors, which create new patterns of patchiness - patches are in constant flux due to flow and other physical and biotic (decomposition) factors which act upon them (Lake 2000). However, stream resource patches and biota are also connected to other patches longitudinally, vertically, and laterally by water flow. All these factors are capable of modifying macroinvertebrate density in streams. On the other hand, it is well established that aquatic macroinvertebrates have evolved in these types of ecosystems, and they have developed different dispersal strategies. For example, some macroinvertebrates disperse using water flow as a transport method between patches (Bilton et al. 2001a, Lancaster & Downes 2013), and this strategy may reflect the no searching strategy as proposed by Bowman et al. (2002) (Figure 6.1; No searching graph). However, it is important to consider that species dispersing by drift could also walk – they may drift into a site and then leave the drift and walk to locate patches (Lancaster & Downes 2013). Moreover, some macroinvertebrates may walk randomly on the streambed (Figure 6.1; Random searching dispersal), whereas others may have the capacity to detect and walk directly toward patches (Figure 6.1; Orientation toward patches), as reported by Chase et al. (2001), where grazing snails were found in larger quantities in large patches or in areas where patches are closed each other. Moreover, it has also been reported that macroinvertebrates have different strategies when colonizing new patches. For instance, Downes and Lancaster (2018) include a new terminology related to how macroinvertebrates colonized new patches, where nomad refers to species that routinely disperse via drift and increase their densities among locations. Invaders refers to species that take advantage of new situations. species that were in the drift, but for which no evidence was found to show that drift drove benthic densities were defined as unsuccessful. However, there is a paucity of studies which have addressed the relationships between spatial distribution of resource patches, patch size, and species densities in streams (Lancaster & Downes 2017, Palmer et al. 2000, Tapia-Arboleda 2016). Although the predictions proposed by Bowman et al. (2002) include species that disperse aerially, in this study attention will be focused only on ground-level dispersal of macroinvertebrates, which is equivalent to drifting and walking. My adaptation of Bowman's study has repercussions on our ability to separate outcomes represented by dispersal strategies A, B, and, C (Figure 6.1 and 6.2) but I can distinguish strategy D from the other three.

New resource patches are colonized by individuals dispersing from other patches. However, it is likely that inter-patch movement limits the persistence and abundance of some species due to inter-patch distances and the size of new patches (Palmer et al. 2000). Thus, there are three components affecting densities of taxa that are considered relevant for this study: (i) dispersal of species into new patches, where the dispersal strategies of different species may modify their density in new patches, as described above. (ii) Spatial patterns of patches - defined by the size and distribution of CPOM patches within sections of the stream. (iii) Whether species respond to CPOM patches aggregations as proposed by Lancaster and Downes (2017C). The aim of this study is to test the following hypotheses: if species show an orientation towards patches that increases disproportionately with patch size, then patches with larger areas might present higher densities (Figure 6.1. D). Additionally, comparisons between faunal densities in SPTs vs BPTs tested whether many smaller patches gained more or less animals than one large patch of the same total area

6.3. Methods

6.3.1. Site description

The study took place along a 1.5 km length of Hughes Creek (36°59'S; 145°21'E) (Figure 6.3), a tributary of the Goulburn River in central Victoria, south-eastern Australia. Hughes Creek rises in the Strathbogie Ranges and flows across the Ruffy swamps and ponds before flowing into the Hughes Creek valley via a granite gorge (Catchment-Management-Authority 2013). The catchment vegetation is dominated by River Red Gum (*Eucalyptus camaldulensis*); with *E. obliqua, E. macrorhyncha, E. radiate and Acacia dealbata* also present. However, in the section where this study was deployed, large woody debris was rare and the presence of other retentive structures (i.e. structures able to decrease water speed, and promoting the precipitation of suspend material) was limited, thereby providing a low-retention environment of CPOM (Lancaster & Downes 2014). Moreover, natural CPOM patches in the area are aggregations of leaf and small pieces of bark and twigs, which are normally distributed across the streambed (Reid et al. 2008b). Patches in Hughes Creek can be short-lived due to movement by water flow or burial by sediments (Downes et al. 2011). Discharge dynamics in Hughes Creek are directly connected to seasonal rainfall, which occurs mostly throughout the winter-spring months (Jun-Oct) (Bureau of Meteorology www.bom.gov.au/vic). The substrate is sand dominated (0.5 to -1 Ø, or 1.7 to 2.0 mm) with occasional bedrock outcrops, mostly in the headwater reaches where the geology is predominantly granitic (Davis & Finlayson, 2000). The river flats are Pliocene-aged alluvium, primarily gravel, sand and clay (Davis & Finlayson 2000).

Figure 6 3. Experiment deployment site located in Hughes Creek central Victoria (36° 59' 01.24'' S, 145° 20' 36.18'' E). Treatments were deployed along a 1.3 km section of the stream channel. The distance between treatment replicates was approximately 60 m. Split Patch Treatment (SPT) and Big Patch Treatment (BPT) represent the locations of the two treatments at the study site.

6.3.2. Experimental design

Two different treatments were designed to test whether the size and orientation of CPOM patches modify the colonization rate of macroinvertebrates in a headwater stream.

There were two treatments deployed: a Split Patch Treatment (henceforth SPT) and a Big Patch Treatment (henceforth BPT). The SPT comprised two sizes of patches, either a small patch or a large patch, which was twice the area of the small patch. These patches were placed either parallel or perpendicular to the current (Figure 6.4). One SPT replicate comprised eight patches of two sizes (small, large) crossed with two orientations (parallel, perpendicular) that were deployed across one site. There were 16 replicates (i.e. SPT sites). These replicates thus allowed us to test hypotheses about the effects of patch size and orientation on faunal densities. However, it should be noted that patches within a site were not strictly independent. Thus, each site was randomly allocated to one of the four treatment combinations (Table 6-1). Only the patches from the assigned treatment combination from each replicate site were used to test the effects of patch size and orientation on faunal densities.

The big patch treatment comprised a single large single patch, that was equivalent in area to the collective area of the patches deployed in the SPT (effectively, 12 small patches) (Figure 6.5). Each BPT was deployed at a single site in one of two possible orientations, parallel or perpendicular. There were ten replicates of each orientation and thus 20 sites in all (Table 6.1). This design enabled testing of the effects of patch orientation with a much larger patch size than those used in the SPT. Additionally, comparisons between faunal densities in SPTs vs BPTs tested whether many smaller patches gained more or less animals than one large patch of the same total area.

Table 6-1 Number of replicates of SPT and BPT deployed in Hughes Creek. Each treatment consisted of 12 onion bags. In the SPT experiment, small patches are one onion bag, while large patches are two onion bags.

Treatment 1	Site name	Number of replicates	Number of bags per site
SPT	"Small perpendicular"	4	12
	"Small parallel"	4	12
	"Big perpendicular"	4	12
	"Big parallel"	4	12
	Total number of replicates	16	
Treatment 2			
BPT	"Parallel"	5	12
	"Perpendicular"	5	12
	Total number of replicates	10	

6.3.3. Field methods

To facilitate the construction of patches, CPOM was collected from the stream banks and dried at 105 °C for 24 hours in the laboratory. This is considered the optimum, temperature for removing the bulk of moisture from eucalypt samples, without eliminating their essential oils (Matthews 2010). Plastic onion bags (mesh size 0.5 mm) were cut and sewn to create the small patch sizes (15 x 10 cm, 150 cm^2). The bags were filled with 10g of a mix of eucalypt leaves (*Eucalyptus camaldulensis* and *Eucalyptus aggregata*), and no more than 2g of small pieces of bark and twigs. It was important to control the amount of organic matter in each bag, as bark and twigs are denser than leaves. Large patches were created by sewing two onion bags together, with the very large patch for each BPT replicate being created by sewing 12 bags together.

Within each SPT replicate, the position of each patch was selected randomly to ensure that the arrangement of the four types was randomised within sites, as well as the actual positions of patches in sites. Wooden stakes were hammered into the stream bed, to which the onion bags attached to prevent them floating away. However, the number of stakes need to attach BPT sites (3) was less than those needed in SPT sites (8). Thus, we added five additional stakes at the BPT sites so that the number of stakes between SPT and BPT sites were uniform (Figure 6.4, 6.5).

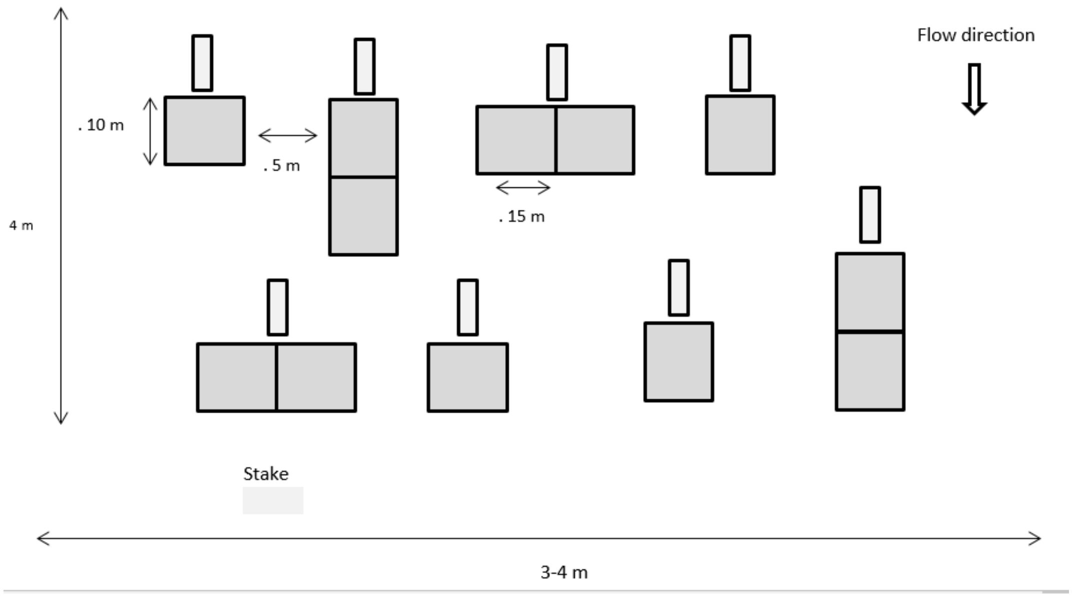

Figure 6 4. The SPT design. Two small and two large patches were placed horizontally to the flow of the creek, whilst the remaining two pairs were parallel. The position of each patch was assigned randomly, starting from the top left row, thereby avoiding configuration homogeneity across the 16 replicates. The downstream row of bags was displaced to the right to minimize interference from the top row. Thin rectangles represent stakes used to fix the bags to the riverbed.

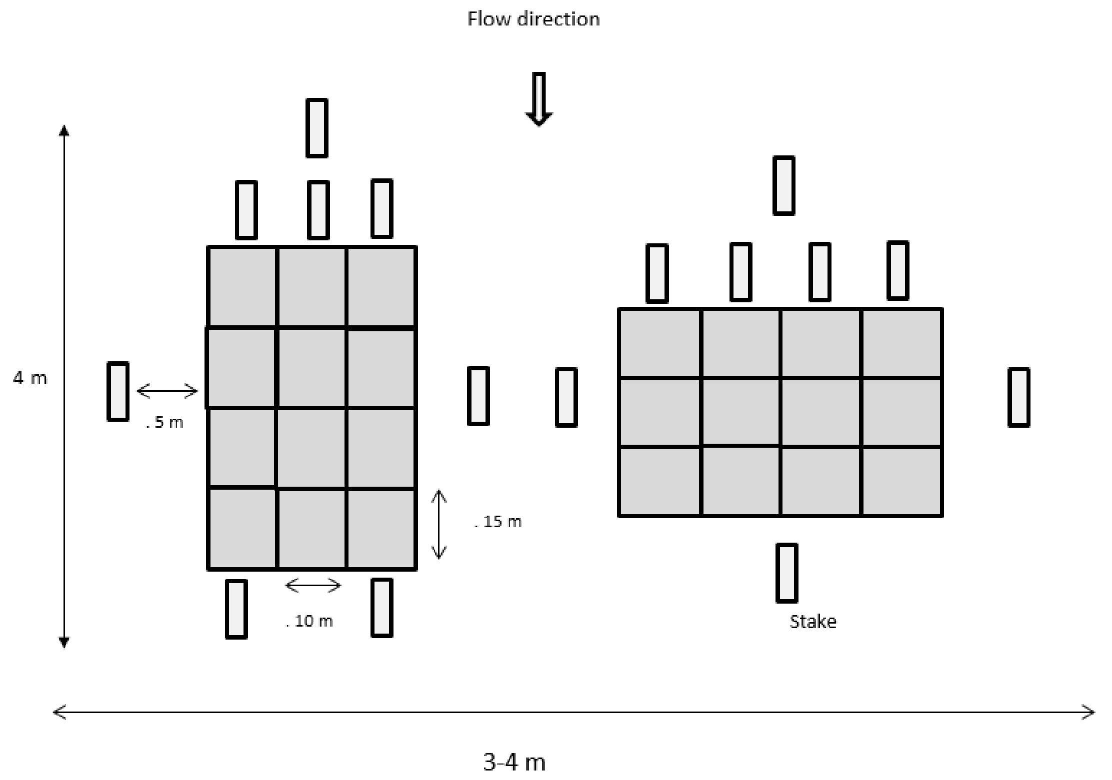

Figure 6 5 The BPT design had two possible configurations vertical (left) and horizontal (right), each configuration had five replicates. Free stakes (thin rectangles) were added to mimic the number of stakes used in SPT design.

Treatments were installed over two days (1-2 February 2017), from downstream to upstream to avoid disturbance to sites. The distribution of treatments across the 26 sites used in total was randomized with a rule that a repeat of any one treatment in consecutive sites was not permitted, in order to avoid clustering of treatments along the stream. Additionally, both treatments were deployed at the stream centre, and in shallow water (30-40 cm) sections. Following deployment of treatments, each experimental site was visited every two days to remove CPOM that had been retained naturally by the onion bags or stakes, and to ensure bags remained attached firmly to the riverbed.

6.3.4. Species selection

The selection of macroinvertebrates species to be sampled in both treatments was made following the criteria that: (a) species should be present at the season when patches were deployed - this requirement was accomplished by performing a field survey a year before. (b) The species selected had also been sampled in the study of Lancaster and Downes (2017), which provided two lists of macroinvertebrates species, being (1) species showing significant responses to sites where CPOM retention was artificially increased, and (2) species that showed no response. The similarity of the latter study to the present one is that both studies evaluate how CPOM-enriched sites modify the density of macroinvertebrates. Finally, the selection of closely related species which fulfilled the two criteria of Lancaster and Downes (2017), species that were sufficiently abundant and with contrasting response to CPOM enriched sites were essential, as the affect upon species was also tested when patch configuration changed.

The focal macroinvertebrates selected for this study included species of mayflies (Baetidae, Caenidae, and Leptophlebiidae), water boatmen (Micronectidae), riffle beetles (families Elmidae and Hydrophilidae), caddisflies (Ecnomidae, Hydropsychidae,), and blackflies (Simuliidae). Diet and foraging mode information for all species selected was retrieved, as a factor for species to be attracted to resource patches is food availability. For example, shredders search for leaf material to ingest. However, whereas Downes et al. (2011) found that a few species were obligate shredders, these were not chosen for the present study as they mainly occur upstream in Hughes Creek, above our study area. Consequently, the selection of species for this study was inherent upon (1) sufficient number of specimens from the selected species, as reported by Lancaster and Downes (2017) (appendix 6), and (2) where possible, species which were taxonomically close were selected, in order to evaluate any similar response to CPOM patches, and (3) species with contrasting capacities when colonising riverbed, as proposed by Downes and Lancaster (2018) were selected. For example, species that had been classified as unsuccessful colonisers were species that were in the drift, but for which no evidence was found to show that drift drove benthic densities – the evidence showed they were in the drift but densities did not increase. The latter suggests that many specimens were unsuccessful at colonising the stream bottom or left immediately. Conversely, nomad species are those that drift, and this dispersal strategy increases benthic densities among locations. Moreover, species classified as invaders are those whereby drift controls their benthic density, but also enables their colonization of any new available substrate. The summary of the previous information can be found in Table 6-2.

Table 6-2. Feeding mode and diet from the species selected in this study. The dispersal ability for each of the species, based on the results provided by Downes and Lancaster (2018), is also included. ***Nomad*** *refers to species that routinely disperse via drift and increase their densities among locations.* ***Invaders*** *refers to species that take advantage of new situations. species that were in the drift, but for which no evidence was found to show that drift drove benthic densities* ***UN****. Locomotion information was retrieved from Lancaster and Downes (2013), Downes et al. (2005), and Downes and Lancaster (2010)*

Taxa that did not respond to increased CPOM	Dispersal ability/Locomotion type	Foraging mode	Diet	Reference
Micronecta annae	Nomad / Swimmer	scraper/gatherer	invertebrates	Tinerella et al. (2013);
Micronecta australiensis	UN/Swimmer	scraper/gatherer	invertebrates	Haedicke et al. (2017);
Tasmanocoenis tillyardi	UN/Swimmer and drifter	Collector/gatherer	fine detritus, algae	Downes et al. (2011);
Austrolimnius waterhousei (Adult)	UN/Crawler and swimmer	scraper/gatherer	detritus/algae	Downes et al. (2011);
Austrolimnius waterhousei (Larvae)	UN/Crawler and swimmer	scraper/gatherer	fine detritus/algae	Downes et al. (2011)
Simulium ornatipes	Nomad/Drifter and walker	filter collector	fine detritus	Crosskey and Zwick (2007)
Berosus spp. (adult)	Invader/Swimmer	Collector/gatherer	dead and decaying vegetable matter	Downes et al. (2011)
Taxa that responded to increased CPOM				
Ecnomus continentalis	Invader/Walker and drifter	net-spinner	invertebrates, fine detritus, algae	Downes et al. (2011)
Cheumatopsyche spp.	Invader/Walker and Drifter	net-spinner/filter-feeder	fine detritus, algae, and invertebrates	Downes et al. (2011)
Asmicridea sp.	Invader/Drifter and waker	net-spinner/filter collector	Fine detritus	Dean (1988)
Atalophlebia sp.	Invader/Swimmer and drifter	Filter collector	Fine detritus/ultrafine detritus	Chessman (1986)
Nousia sp.	Invader/Swimmer and drifter	Collector/gatherer	detritus. Vascular plants	Downes et al. (2011)
Offadens spp.	Invader/Swimmer and drifter	Grazer/collector	fine detritus, leaves algae	Downes et al. (2011)
Notriolus spp.	UN/Crawler	Gougers/scrapers	fine detritus, leaves, wood fragments	Downes et al. (2011)

6.3.5. Sampling

All onion bags were retrieved ten days after deployment (11-12 February 2017), using a Surber sampler fitted with 250µm mesh and a sample jar. Ten days is sufficient time for invertebrate colonisation, and avoids the difficulties created by litter breaking down, which would represent uneven amount of CPOM available across patches. The Surber net was rinsed thoroughly, and the onion bags, their contents and material in the sample jar were placed in a plastic bag and preserved with ethanol. At SPT sites, patches in the allocated treatment were sampled and bagged separately from all other patches, which were also collected (so that total densities could be compared to BPT replicates). Size, orientation, and replicate number (i.e. site, or for small patches, size and orientation) were recorded for each sample.

6.3.6. Laboratory process

In the laboratory, onion bags were rinsed, and macroinvertebrates were sieved with a 250 µm mesh. Each sample was labelled and stored in lidded plastic jars filled with 70% alcohol and stored at room temperature until processed further. CPOM was rinsed and air-dried in plastic trays for 48 hours, then oven-dried for 24 hours at 105 °C (Matthews 2010) and weighed to the nearest value (0.001 g).

As macroinvertebrate samples were very large, they were sub-sampled using the methods reported in previous studies (Lancaster & Downes 2017c, Tapia-Arboleda 2016). The sub-samples consisted of 100 cells arranged in a 10x10 matrix (40x40 cm) in a case with a lid, into which each sample was poured, the lid then closed, and the case shaken thoroughly. Cells were selected at random and the macroinvertebrates removed. The initial sub-sample size was 10% (10 cells randomly selected), however following the processing of the first three sub-samples, it was evident that the sub-sample proportion resulted in too few individuals for meaningful results. Consequently, it was decided to increase the sub-sample size to 50%.

6.3.7. Statistical analysis

The hypotheses in this study test whether the species, either responders and no responders as reported in Lancaster and Downes (2017c), would show similar trends to the CPOM patches in this study. Additionally, the statistical analyses in this study tested the relationships between density of macroinvertebrates, patch orientation (linear dimension of patches), patch size, and the density differences between SPT and BPT treatments (Table 6-3)

It was expected the density of species that responded to CPOM enriched sites which were driven by the drift, should respond to the linear dimensions of patches. Consequently, SPT sites should have greater densities due to the total linear dimension of the patches being greater (Table 6-3, A, B, or C). Contrastingly, if species densities increased exponentially with the increase of total patch area, then the densities should be greater in larger patches (Table 6-3, D).

Table 6-3. The following table was designed based on the predictions proposed by Bowman et al. (2002), where species dispersal ability via drift responded to one of the models based on the relationship between area, or linear dimension of patches and density

Model predictions / Hypothesis	Model A	Model B	Model C	Model D
BPT vs SPT	**Negative** (larger density in SPT)	**Negative** (larger density in SPT)	**Negative** (larger density in SPT)	**Positive** (larger density in BPT)
Patch orientation (linear dimension)	**Negative** (larger density in parallel patches)	**Negative** (larger density in parallel patches)	**Negative** (larger density in parallel patches)	**Positive** (larger density in perpendicular patches)
Patch size	**Negative** (larger density in single patches from SPT)	**Negative** (larger density in single patches from SPT)	**Negative** (larger density in single patches from SPT)	**Positive** (larger density in double size patches from SPT)

To test for differences between BPT and SPT treatments, densities were calculated by dividing abundances of each taxon by the total patch area; these values were log-transformed and compared using a one-way analysis of variance (ANOVA) for each taxon, with alpha set at < 0.05. The comparison of patch orientation of BPT patches (parallel vs. perpendicular) was also evaluated by one-way ANOVA. The analysis of differences between patches of different sizes (small vs large) and orientation (parallel vs perpendicular) within SPT sites was evaluated using a 2 x 2 factorial ANOVA.

It was important to examine CPOM decay rates to test whether they varied greatly between treatments, as such variances may have led to effects on faunal densities. The decay rates of CPOM within patches from CPOM contained in bags from SPT and BPT treatments, were calculated by the CPOM decay rate protocol (Rugenski et al. 2017) (Equation 1) and differences between treatments were tested using one-way ANOVA.

Equation 1

$-k = log_e \frac{(\frac{R}{100})}{t}$, where (R) is the percent remaining of organic matter at any time (t).

6.4. Results

6.4.1. CPOM decomposition

The decomposition of CPOM in onion bags between SPT and BPT sites was not significantly different (Table 6-4). The decomposition rate in BPT patches was slightly lower than SPT patches after 10 days on the streambed, but not big enogh to be significantly different (Figure 6.6).

Table 6-4. One-way ANOVA of CPOM decay rate between SPT and BPT treatments

	Sum of Squares	df	Mean Square	F	Sig.
Treatment	0.803	1	0.803	0.724	0.405
Residual	21.062	19	1.109		

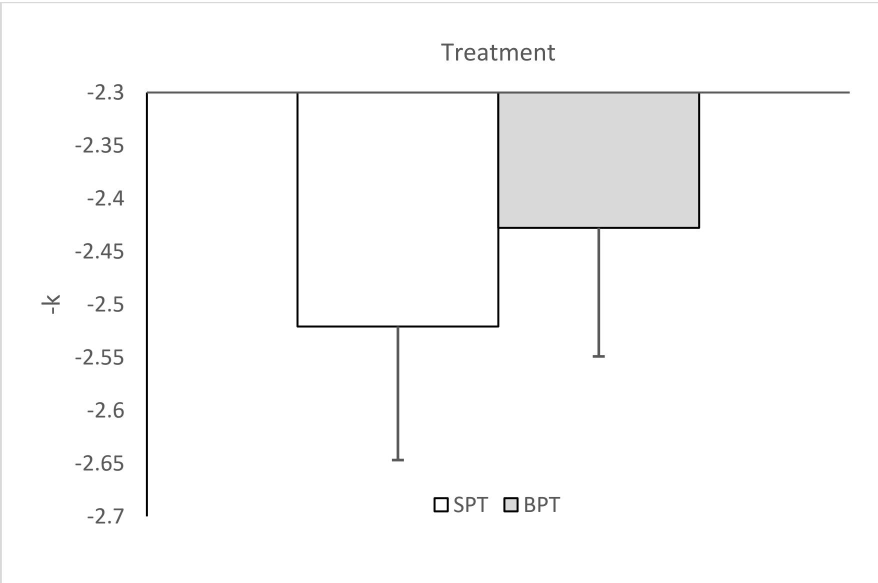

Figure 6 6 Average CPOM decay rate in onion bags from SPT and BPT treatments. Where -k represents the remaining mass of CPOM at any time, compared to the initial mass at time zero. Error bars (SE)

6.4.2. Densities in SPT vs BPT sites

Two taxa responded significantly to whether patches were split or not (Table 6-5). *Offadens* sp. and *Notriolus* sp. had higher densities in the SPT sites than in the BPT sites (Figure 6.7). Most species had higher densities in the SPT sites, however none showed significant differences.

The orientation of patches in BPT sites did not modify the colonisation rate of macroinvertebrates, as none of the species showed significant density differences between parallel or perpendicular orientations (Table 6-6).

*Table 6-5 Results of the one-way ANOVA of macroinvertebrate densities comparing densities between single large (BPT) vs. split patch treatment (SPT). Treatment (df=1) and residual (df=24). The letter **α** represents species that did not respond to CPOM enriched sites in Lancaster and Downes (2017), nor to the distribution of patches offered in BPT and SPT sites. The letter **β** represents species that responded to CPOM enriched sites in Lancaster and Downes (2017) but not to the distribution of patches offered in BPT and SPT sites. The letter **μ** represents species that responded to CPOM enriched sites both in Lancaster and Downes (2017) and to the distribution of patches between BPT and SPT sites. Significant differences shown in bold.*

Species	Source	Mean Square	F	p	*α*	*β*	*μ*
Micronecta annae	Treatment	19.146	0.547	0.467	X		
	Residual	34.997					
Micronecta australiensis	Treatment	0.713	1.538	0.227	X		
	Residual	0.463					
Tasmanocoenis tillyardi	Treatment	0.056	0.344	0.563	X		
	Residual	0.162					
Austrolimnius waterhousei	Treatment	3.66	3.161	0.088	X		
	Residual	1.158					
Simulium ornatipes	Treatment	4.742	3.8	0.053	X		
	Residual	1.248					
Berosus sp.	Treatment	0.001	0.001	0.976	X		
	Residual	0.914					
Ecnomus continentalis	Treatment	0.03	0.146	0.706		X	
	Residual	0.208					
Cheumatopsyche spp.	Treatment	0.404	1.802	0.192		X	
	Residual	0.224					
Asmicridea sp.	Treatment	1.243	1.212	0.282		X	
	Residual	1.026					
Atalophlebia sp.	Treatment	0.753	0.778	0.386		X	
	Residual	0.968					
Nousia sp.	Treatment	0.397	2.721	0.112		X	
	Residual	0.146					
Offadens sp.	Treatment	1.112	9.692	**0.005**			**X**
	Residual	0.115					
Notriolus sp.	Treatment	1.584	3.886	**0.05**			**X**
	Residual	0.408					

Table 6-6. Results of one-way ANOVA comparing parallel and perpendicular orientations for the BPT treatment. Treatment (df=1) and residual (df=8). None of the species sampled in this study responded to BPT orientation.

Genus/species	Source	Mean Square	F	p
Micronecta annae	Treatment	0.001	0.768	0.406
	Residual	0.001		
Micronecta australiensis	Treatment	0.001	1	0.347
	Residual	0.001		
Tasmanocoenis tillyardii	Treatment	0.009	0.044	0.839
	Residual	0.215		
Austrolimnius waterhousei	Treatment	0.001	3.168	0.113
	Residual	0.001		
Simulium ornatipes	Treatment	0.001	0.011	0.92
	Residual	0.002		
Berosus sp.	Treatment	0.001	1.452	0.263
	Residual	0.001		
Ecnomus continentalis	Treatment	0.004	0.117	0.741
	Residual	0.038		
Cheumatpsyche spp.	Treatment	0.205	0.835	0.387
	Residual	0.246		
Asmicridea sp.	Treatment	0.001	0.177	0.685
	Residual	0.001		
Atalophlebia sp.	Treatment	0.001	0.234	0.642
	Residual	0.001		
Nousia sp	Treatment	0.133	1.736	0.224
	Residual	0.076		
Offadens sp.	Treatment	0.134	1.258	0.295
	Residual	0.107		
Notriolius sp.	Treatment	0.004	0.184	0.679
	Residual	0.021		

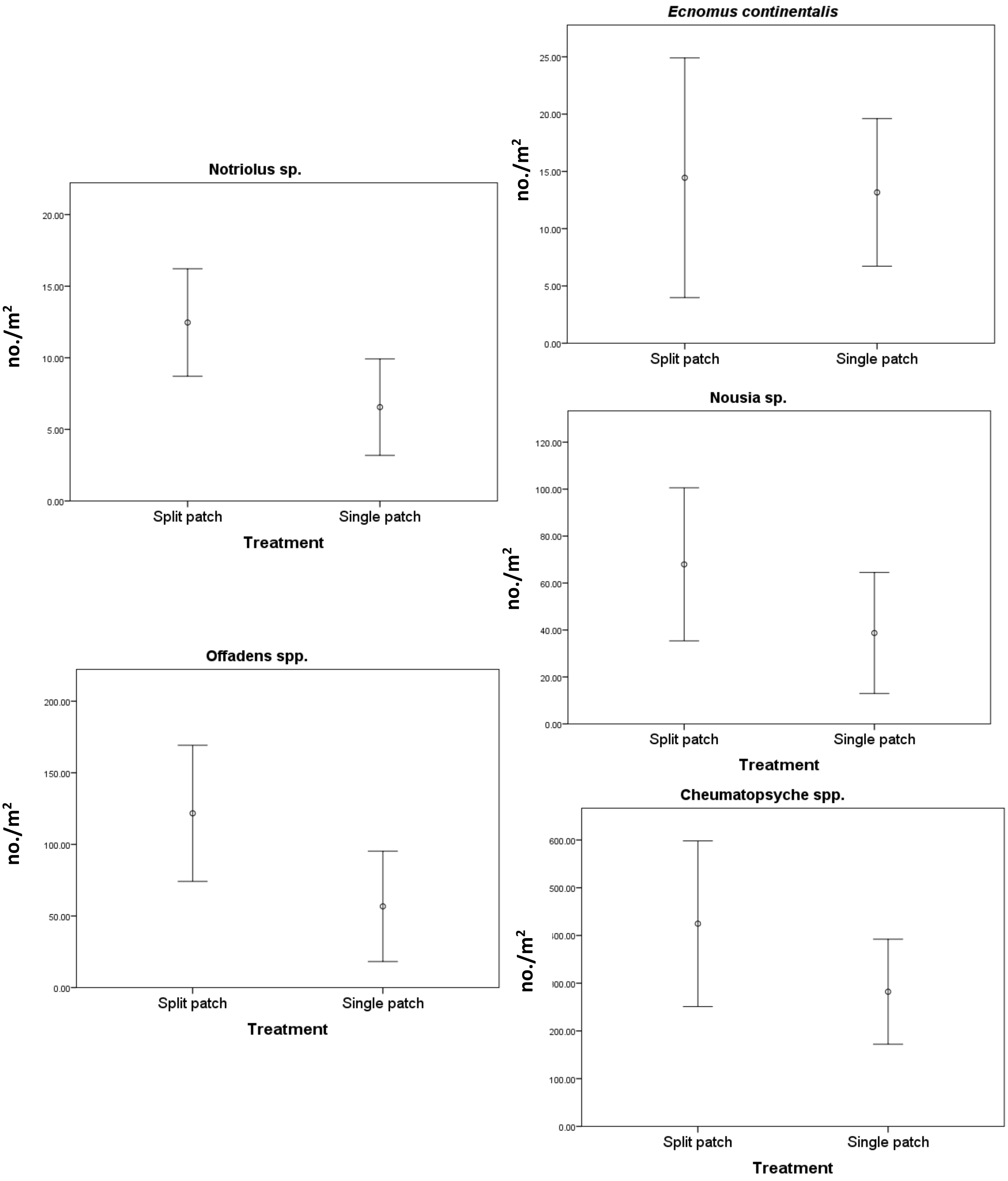

Figure 6 7 Average densities from SPT (split patch) and BPT (single patch). Left column shows graphs of taxa having significantly higher densities in the SPT treatment. Right column shows three examples of species that did not respond to spatial distribution of patches. Error bars represent standard error.

6.4.3. Size and orientation of patches within SPT sites

Three taxa responded to patch size or patch orientation, albeit the interaction between these two factors was not significant for any taxon (Table 6-7). *Offadens* sp. responded to both factors, with higher densities in small patches and parallel patches compared to those patches that were large and perpendicular, respectively. *Notriolus* spp. also attained higher densities in small patches compared to large patches, but in contrast to *Offadens,* achieved higher densities in perpendicular patches compared to parallel ones (Figure 6.8). *Cheumatopsyche* spp. attained higher densities in smaller patches than in larger patches. *Micronecta australiensis* and *Tasmanocoenis tillyardii*, and *Nousia* sp. showed trends for higher densities in large patches, but these species were found in low numbers and differences were not statistically significant.

*Table 6-7 2x2 Factorial ANOVA analysis for patch size and patch orientation from split patch treatment. Patch size (df=1), orientation (df=1), size*orientation (S x O) (df=1), and error (df=12). Significant differences in bold. Species are arranged as in Table 6:1. The letter **α** represents species that did not respond to CPOM enriched sites in Lancaster and Downes (2017), nor to orientation or size from SPT patches. The letter **β** represents species that responded to CPOM enriched sites in Lancaster and Downes (2017), but not to the orientation or size from SPT patches. The letter **μ** represents species that responded to CPOM enriched sites both in Lancaster and Downes (2017), and to the orientation or size from SPT patches. p values in bold represent significant differences.*

Species	Source	Mean Square	F	p	*α*	*β*	*μ*
Micronecta annae	Size	0.839	0.625	0.444	X		
	Orientation	0.007	0.006	0.942			
	S x O	0.839	0.625	0.444			
	Error	1.341					
Micronecta australiensis	Size	0.003	3.857	0.073	X		
	Orientation	0.001	0.429	0.525			
	S x O	0.001	0.429	0.525			
	Error	0.001					
Tasmanocoenis tillyardi	Size	0.372	3.83	0.074	X		
	Orientation	0.009	0.093	0.766			
	S x O	0.022	0.222	0.646			
	Error	0.097					
Austrolimnius waterhousei	Size	0.013	0.448	0.516	X		
	Orientation	0.005	0.187	0.673			
	S x O	0.009	0.31	0.588			
	Error	0.028					
Simulium ornatipes	Size	0.054	1.513	0.242	X		
	Orientation	0.001	0.03	0.865			
	S x O	0.01	0.292	0.599			
	Error	0.035					
Berosus sp.	Size	0.001	2	0.183	X		
	Orientation	0.001	0	1			
	S x O	0.001	0	1			
	Error	0.001					
Ecnomus continentalis	Size	0.128	0.954	0.348		X	
	Orientation	0.001	0.001	0.976			
	S x O	0.01	0.077	0.786			
	Error	0.134					
Asmicridea sp.	Size	0.001	0.133	0.722		X	
	Orientation	0.003	0.846	0.376			
	S x O	0.003	0.846	0.376			
	Error	0.004					
Atalophlebia sp.	Size	2.81E-05	0.005	0.943		X	

	Orientation	0.007	1.293	0.278		
	S x O	0.001	0.15	0.705		
	Error	0.005				
Nousia sp.	Size	0.654	3.815	0.075	**X**	
	Orientation	0.083	0.484	0.5		
	S x O	0.277	1.617	0.228		
	Error	0.171				
Cheumatopsyche spp.	Size	0.945	6.602	**0.025**		**X**
	Orientation	0.052	0.36	0.56		
	S x O	0.174	1.213	0.292		
	Error	0.143				
Offadens sp.	Size	0.873	10.888	**0.006**		**X**
	Orientation	0.57	7.108	**0.021**		
	S x O	0.089	1.114	0.312		
	Error	0.08				
Notriolus sp.	Size	0.627	11.587	**0.005**		**X**
	Orientation	0.331	6.112	**0.029**		
	S x O	0.223	4.121	0.065		
	Error	0.054				

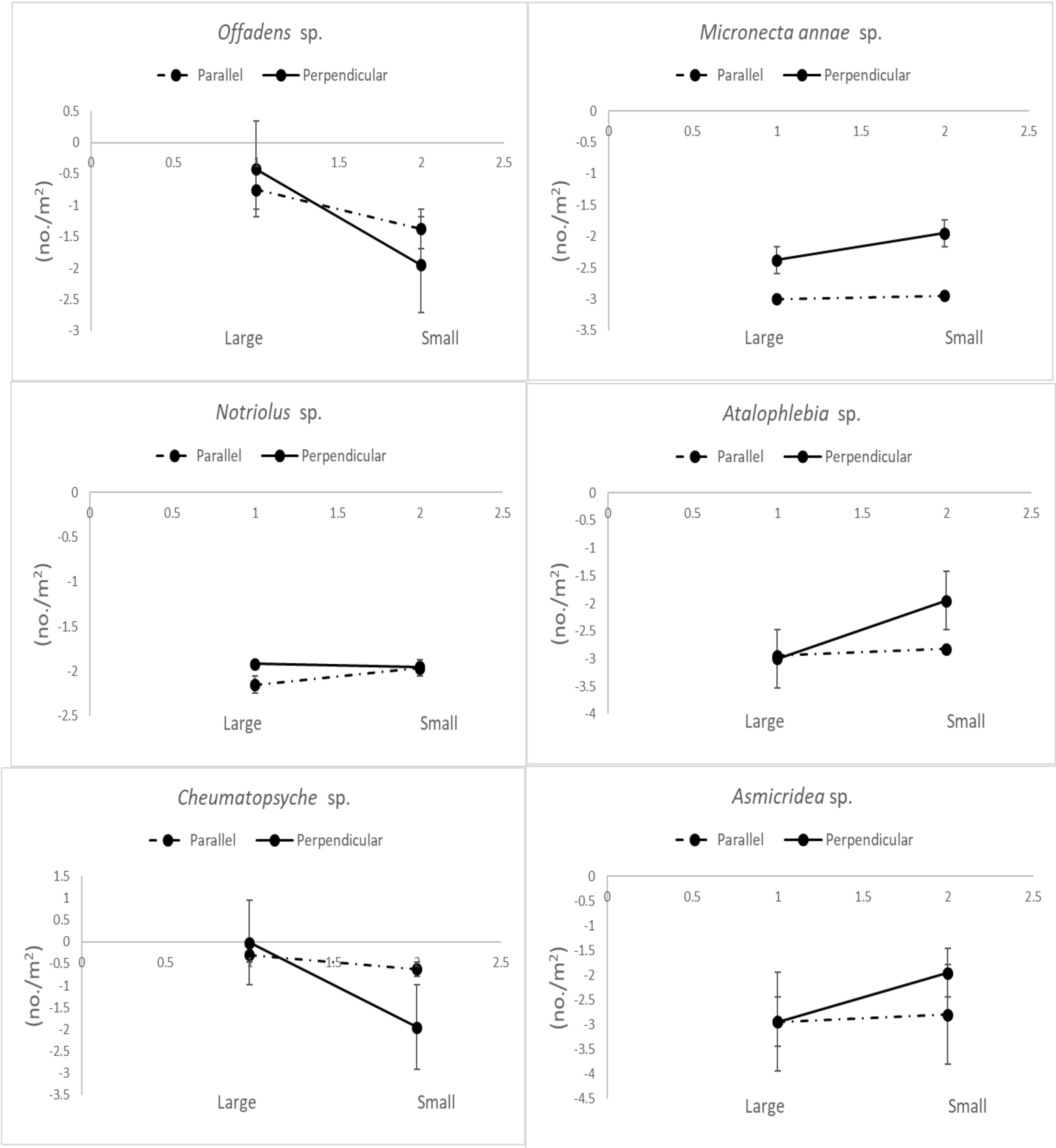

Figure 6 8 Interaction plots for diverse taxa, bars represent standard errors (SE). Left column shows taxa that presented significant differences, either to patch size or patch orientation factors. Right column shows three examples of taxa that showed no differences to the above factors.

6.5. Discussion

In this study was tested whether there is a negative relationship between patch area and densities of species that present no searching, random searching, and orientation toward dispersal strategies as proposed by Bowman et al (2002) models. Contrastingly, it was also tested whether any macroinvertebrate species disperse disproportionately towards patches with larger area, that is macroinvertebrates that could actively search for larger patches, as suggested in Model D by Bowman et al (2002).

6.5.1. Decomposition rate between treatments

Decomposition of patches happens and this could be a cause of variation in CPOM mass between treatments and replicates. Consequently, it was important to explore whether decomposition could affect masses of patches from the two treatments considered in this experiment before considering the macroinvertebrate results. Decomposition of leaf packs has been studied previously, with early works showing that leaf patches have a high initial weight loss (Briggs & Maher 1983). This study found that there were no (-k) value differences between the decomposition of organic matter in SPT and BPT treatments. The differences in weight loss before and after deployment is associated with the leaching of water-soluble organic compounds (Blackburn & Petr 1979), which ends within 24 hours of leaf pack deployment (Petersen & Cummins 1974). Consequently, the amount of substrate available for macroinvertebrates in both treatments was similar throughout the deployment of the leaf packs, and substrate weight can be discarded as a factor that influenced the arrival and colonization of macroinvertebrates into our two treatments.

6.5.2. SPT and BPT linear dimensions and areas: density expectations

Previous studies of populations in patchy landscapes have shown that patch size, orientation, or spatial distribution can affect the densities of species that depend upon such resources. Thus, the dispersal hypotheses in this research have been adapted to encompass lotic patchy landscapes. It was hypothezised that the species showing a response to CPOM-enriched sites in the Lancaster and Downes (2017) study would also respond to our patch-enriched sites. Moreover, for those species that did respond, we evaluated whether they showed significant density differences between SPT and BPT treatments. It was expected that there would be large densities in SPT sites, as most macroinvertebrate taxa living in Hughes Creek disperse via drift mostly (Downes & Lancaster 2018). Consequently, macroinvertebrates that drift mostly do not search for larger patches, rather, they should arrive randomly where bigger linear dimesion within a patch allow for the arrival of greater numbers of macroinvertebrates. Conversely, the density of these macroinvertebrates decreases as the area of the patch increases (Table 6-3, ModelS A-C). In contrast, macroinvertebrates that are able to move directly toward suitable patches should show that either their dispersal is proportional to the linear dimension of resources patches, or that dispersal increases drastically as patches' areas increase (Table 6-3; Model D). In the following sections we will explore such potential area/density relationships.

6.5.3. Split patches vs one very large patch of equivalent area

It was expected that the density of species selected in this study would vary significantly between BPT and SPT treatments - based on the movement predictions for advective taxon proposed by Bowman et al. (2002), and summarized in Table 6-3. However, the results of this study showed that only two species' densities varied between BPT and SPT treatments. The low number of species responding to treatments was similar to the results reported by Lancaster and Downes (2017c). However, of the responding species reported in the latter study, *Offadens* spp. (invader) and *Notrious* spp. (unsuccessful) responded similarly to the different patch distributions provided by the SPT and BPT sites. The results obtained from these two species show that overall densities are higher when detritus is split into many patches, compared with situations where there is a single large patch of equivalent area to that of many smaller patches. That is, both species showed greater densities in SPT treatments compared to BPT sites (Table 6.5). Other studies have found similar results to ours, for example; Bonin et al. (2011), they observed that fragmentation also had positive effects on damselfish survival, and resulted in greater abundance of other recruits in areas where patch available area was greater. Further, in terrestrial and marine environments, similar results have been reported in patchy landscapes. For example, in meadow vole populations living in agricultural-caused patchy landscapes, densities decreased as patch size increased (Collins & Barrett 1997). Likewise, in marine environments, Caley et al. (2001) reported that densities of the crab species *Trapezia cymodoce* increased when artificial habitat fragmentation of coral communities ocurred, whilst the density of the prawn species *Palaemonella* sp. showed no significant density increments. These results are consistent with the prediction of Bowman et al. (2002), who argue that in the colonsation of resource patches in ecosystems where specimens disperse regularly is the dominant process, it is expected that population densities decrease, or remain constant, when the linear dimension of patches increases.

That only two species responded to SPT and BPT distributions raises several questions about the efficacy of Bowman's dispersal models. For example in a field experiment focused on leaf patch composition (Palmer et al. 2002), it was reported that chironomids did not increase as the number and size of leaf patches increased. This may be explained through the observations of Hoffman et al. (2006), where it was found that two species of hervivores macroinvertebrates dispersed over longer distances when patch density decreased. Further, both species moved less in aquatic landscapes where resource patches were closer to each other(Hoffman et al. 2006). Thus, indivuals disperse less when more patches are available in the area, however if patches are scarce, individuals will disperse at a greater rate. Such factors are not considered in Bowman's models, which explain how an individual is affected by patch size, based on their dispersal strategy, but give no consideration to the reasons a specimen disperses initially. Moreover, Bowman et al (2002) focuses at one component of dispersal – the successful immigration of individuals dictated by patch dimensions. Also, their models do not consider number of patches, subsequent or symbiotic relationships. Given the varied evidence obtained, it is valid to conclude that the models of Bowman et al (2002) explain partially the dispersal of species, but they do not encompass the searching strategy in lotic ecosystems.

6.5.4. Patch orientation

It was hypothesized that patch orientation (perpendicular and parallel to water flow) could affect individuals' opportunities of reaching new resource patches. It was expected that species density would decrease as the linear dimension of the patch, exposed to water flow, increased. However, our results suggest that other factors affect species densities in patches more so than does patch orientation.

From the species selected for this study, none responded to the orientation of BPT patches. Even when a larger linear dimension was provided in patches placed perpendicularly, species density did not increase. One interpretation is that when a patch reaches a certain size, it becomes sufficiently large that even the linear dimension of the shorter side is large enough to catch drifting macroinvertebrates. This conclusion is supported by the results from SPT orientation, where *Offadens* spp., *Cheumatopsyche* sp., and *Notriolus* spp, responded to the orientation of patches. The response of these three species followed the predictions of the Bowman et al. (2002) models, whereby *Offadens* spp. and *Cheumatopsyche* sp. showed higher densities in small patches than perpendicular, illustrating that density increased as the linear dimension of patches decreased. Conversely, *Notriolus* spp. showed the opposite response, whereby larger density of individuals were found in perpendicular patches, with density increasing as patch linear dimension increased. That *Notrolious* spp. density increased in patches which offered larger linear dimensions perpendicular to drift illustrates that density of this species decreases when patch area reduces – meaning that they could search actively for larger patches (Bowman et al. (2002), Model D). These results are consistent with a model where densities are related to linear dimension of patches but not to patch area. Thus, there are other factors than the orientation of patches that affect the density of the remaining species studied.

The absence of response to BPT orientation, and the low response to SPT patch orientation by the species that responded to CPOM enriched sites, suggests that in the majority of lotic ecosystems, macroinvertebrate species are not just drifting. Instead, such species employ a combination of strategies, as they could drift but also combined this dispersal method with crawl, walk, or swim to reach patches. These results suggest that the density of macroinvertebrates is more complex than has been considered previously, as it could be that macroinvertebrates drift, land to a patch, and then walk around. Some studies have focused on stream hydraulics and the potential effect on macroinvertebrates densities. For example, Lancaster and Hildrew (1993) reported that densities of *L. nigra* were affected by the type of hydraulic refugia in which patches were located (i.e. fast, variable, or slow flowing areas). The results from this study show that the hydraulics of streams are also important factors in determining densities of species in patches. Moreover, Hildrew et al. (1980) reported that larvae of two species of stoneflies (*Nemurella picteti* and *Leuctra nigra*) were over-represented in patches of CPOM, from which they fed. However, younger larvae of *L. nigra* were more commonly found on stony substrate. As a consequence, the changes in the distribution of larvae during their development varied in function of the availability of substrate more so than from the sources on which they fed. Moreover, the models proposed by Bowman assume that individuals dispersing from each patch distribute equally among all surrounding patches. However, in the natural world, species are not equally distributed, with some species likely be found in larger numbers in different sections of of a given stream (Lancaster & Downes 2017). The latter implies that species show different densities in patches depending on location. In summary, the orientation of patches is likely to be a factor that affects some species densities, notwithstanding that there may be other physical factors which are more relevant than patch orientation.

6.4.5. Patch size

This study tested the concept of patch size, as a factor which could modify species densities when a group of patches increases the recruiting area on landscapes where species dispersed by advectic means. Results showed that patch orientation and patch size had significant effects on *Offadens* spp, *Cheumatopsyche* sp and *Notriolus* sp. only. Moreover, other studies have reported similar trends. For example, Mazerolle and Villard (1999) found that patch orientation explains highes density of individuals from the same species in a few cases only, while patch area explained most of the significant changes, with 11.8 % of the studies on invertebrates showing a response to patch area.

Previous findings suggest that patch orientation may aid in increasing species densities, albeit this only occurs when patch sizes decrease (Bender & Fahrig 2005, Bowman et al. 2002, Fahrig 1988). This suggests that resources arranged in specific configurations, embedded in ecosystems where species have a high migration rate (Fahrig 2003), could retain more individuals of certain species than others. Consequently, it is appropriate in some cases, such as those experiments developed in fragmented forests by Bierregaard et al. (1992), Hagan et al. (1996), Schimiegelow et al. (1997) that the predictions proposed in table 6-3 be used.

6.4.6. Size and orientation of patches might have limited implications on aquatic macroinvertebrates densities.

Historic and more recent literature supports the effects that landscape structure, habitat, patchiness, habitat permanence availability, and patch have upon population dynamics (Fahrig & Merriam 1985, Gadgil 1971, Heino & Hanski 2001). Consequently, it is argued that taxonomically related taxa, or those taxa with similar feeding methods, find their food, resource patches et cetera in a similar manner. The results of the current study demonstrate that patch colonization differs between species, and that patch configurations affect population densities in different ways. For example, of the invader species sampled in this study, *Offadens* spp. was the only species that responded to different arrays of patches (SPT vs BPT) and also responded to the size and orientation of patches within SPT sites. Likewise, among the species that unsuccessfully disperse via drift, *Notriolus* spp. responded to the same factors as did *Offadens* spp – but not to the SPT vs BPT comparison. However, *Notriolus* spp. feeds from fine detritus and leaves, and it was expected that this species would show stronger responses to patch characteristics than results indicate. The latter could be associated with the nature of lotic systems, whereby diverse ecological and physical variables increase the complexity of disperal of macroinvertebrates that drift.

Spatial distribution of patches in lotic systems is dynamic, and in constant change (Palmer and Poff 1997), making them dissimilar to those of terrestrial fragmented ecosystems because they are ephemeral. Terrestrial patches with greater longevity makes them easier to be found by species. Further, it is possible that some species possess a ‘memory’ of where resources can be found, as patches remain in the same location for long periods of time (Fagan et al. 2013). In aquatic small-scale fragmented systems, patches are closer to each other in some other areas, while in other systems, patches are scarce. However, the time and distance required by macroinvertebrates to travel among patches can vary, with such time and distance scales representing a challenge. Moreover, as many studies have shown, the orientation and the time length that patches remain on the river bed varies due to stream hydrology (Brown 2003, Lancaster & Downes 2010, Lancaster & Hildrew 1993). This challenges the capacity of aquatic invertebrates to reach new resources as spatial arragaments vary (de Brouwer et al. 2017). The latter could imply that species densities might vary in short periods of time, as patches are formed or destroyed by stream forces. Such variability could affect our statistical power, and potentially, prevent us to find more species showing similar area-density relationships.

The effect of patchy landscapes on species densities has been studied in the past (Fountain et al. 2016). However, in respect of fragmented landscapes, most questions are related to the sizes and degrees of isolation of patches (Bender et al. 2003). Previous studies of cavity-nesting birds (Gutzwiller & Anderson, 1992), and blackflies and beetles (Faeth & Kane, 1978) with high migration rates, have found significant differences associated with patch orientation and patch area. For example, Gutzwiller and Anderson (1992) found that bird densities were higher in patches that were long, narrow, and with a distribution parallel to the migration direction. Birds, migrating throught vast areas of ocean, find similar spatial dificulties to reach patches as macroinvertebrates, which have also to cover proportinally long distances between patches. However, the overall density of patches relation to the area where stream animals are dispersing is relatively high, thus, the isolation was a minor issue.

The present study presents evidence that (1) within aggregation of patches, the orientation and size of such patches affects the densities *Offadens* spp., *Notriolus* spp., and *Cheumatopsyche* spp. However, (2) the size and orientation of patches creates different effects on these species even though they are all dispersing via drift. (3) *Notriolus* spp. were found in larger proportions in small parallel patches. which suggest a strong response to larger linear dimensions. However, many species did not respond in accordance with the models of Bowman et al. (2002), which could be associated with other ecological factors acting within resource patches

7. Thesis synthesis

7.1. Thesis summary

The study of headwater streams has been moved beyond simplistic models that have focused on the relationship between riparian areas and the stream. However, there are many knowledge gaps to be explored in detail. In this thesis, I focused on two general questions. How does deforestation modify allochthonous input dynamics in headwater streams? How do changes of allochthonous inputs of CPOM affect the distribution of patches of this material and is there any effect upon macroinvertebrate densities? These two questions were divided into four secondary questions, which form the four results chapters of the thesis. In the following section, the main findings will be summarized, which are also illustrated in Figure 7.1.

It is argued that the resource flow model, where a causal effect relationship between changes in riparian forests and allochthonous inputs is posed, is to general and several factors are not considered. For example, the RFM seems to show that the deforestation of streams is the cause for the reduction of macroinvertebrates density, but it does not show how this density decrease takes place, and the factors that trigger such effect. Thus, this thesis focused on testing how the decrease on allochthonous inputs, given by deforestation, might affect CPOM patch size and their spatial distribution across the streambed, and ultimately affect species densities living in patches. The resource flow model suggests that abrasion, retention, decomposition are factors considered to have dominant role in retention of CPOM, but these processes are connected directly to stream hydrology, hydraulics, and canopy cover. The interaction of the latter processes will define the size of the patch, where it was applied Bowman's models (chapter 6) to observe if it could explain the relationships between patch size and species densities. Our results showed that patch size is more important than the orientation of patches, and that the densities of some species depend on this factor. In the following sections, a general conclusion and summary for each of the result chapters will be exposed

7.1.1 Riparian areas and stream biota: updated causal effect model

The Resource Flow Model connects riparian vegetation allochthonous inputs with aquatic biota proposed in figure 2.1 suggests that allochthonous inputs have a direct effect on benthic organic matter standing stock. Likewise, changes in the amount of benthic organic matter will affect the densities of macroinvertebrate, which are subsequently affected by ecological interactions. However, based on the findings from the present work, it was possible to observe that the simple model in figure 2.1 is quite general and many other environmental and ecological factors are missed.

The results from the systematic literature review suggested that a decrease of allochthonous inputs should take place when riparian areas are highly deforested. The results from the field survey showed that some airborne fractions did respond to the decrease of riparian cover. Contrastingly, LST inputs showed no differences, and this was associated with the type of vegetation at ground level on forested reaches, which could prevent organic matter to be transport to the stream. Literature suggests that drifting CPOM depends on the upstream condition of riparian vegetation. However, it was found that upstream forested sections did not necessarily export more drifting CPOM downstream. Instead, forested sections seemed to act as cage (chapter four, section 4.5.4) for drifting CPOM, which could be associated with higher retention of this fractions by diverse structures. Consequently, it is suggested that forested and deforested sections (i) conditioned the route by which vegetation allochthonous inputs get into the stream (forested sections main route airborne inputs; deforested sections: both airborne and LST but in lower quantities). (ii) Forested sections have higher allochthonous inputs, the export of organic matter via drifting CPOM is limited, as the higher the density of riparian vegetation, the higher the presence of retentive structures – due to an increase of channel complexity (Prochazka 1991, Sheldon & Thoms 2006, Speaker et al. 1984). Although I did not measure channel complexity, literature suggests that large woody debris increase the channel complexity and retention of organic materials. The results of the present study suggest similar trends, where less exportation of CPOM occurs as channel complexity increases.

In relation to species' densities and patch size it was possible to observe that some species' densities increase as the density of CPOM did. However, such increases were confounded with season, and it is not possible to say that these increases were given by increasing patches' mass (section 5.4.3.). Consequently, (i) at the site scale it is not possible to associate the observed density increase of macroinvertebrates species, because it varies strongly between seasons. However, from the field survey I was able to produce research questions to be approached in a field experiment were more control over patch size was performed.

In the field experiment was manipulated the size and patch spatial arrangement of patches in order to understand how macroinvertebrate densities are affected by patch size. Dispersal of macroinvertebrates has been largely studied at landscape and reach scales, and various models have been developed. In the case of aquatic macroinvertebrates dispersal, the model selected was developed by Bowman et al (2002). Our results suggest that only some species dispersed following one of the scenarios proposed by Bowman. Within the species that responded to the model, the size of the patch was the main factor that attracted more individuals, while orientation of the patch was a secondary factor. The fact that some species responded to patch size provide some evidence that patch size is important, and here is where stream hydrology plays a significant role. Wide channels are related to deforested reaches, and in these areas water flow velocity decreases as the system gets shallow (Gordon et al. 2004, John 1978, Rubey 1938). For example, Hughes Creek, and other similar Australian streams, is sandy, and erosion of the banks is common due to floods. After rainy season (winter), Hughes Creek becomes extremely shallow due to the accumulation of sediments on the streambed and because it has spread across the entire active channel rather just a portion of it. Erosion is caused by the lack of retentive structures in the river banks; for example, tree roots consolidate material around them (Allan 2004), thus the lack of such structures would imply the instability of banks when floods hit the area, producing wider and shallow streams (Wild et al. 2019), with retention of benthic CPOM distributed in small patches across the stream. The latter would mean that some species might decrease their density as the size of patches decrease.

The evidence collected on this study has helped with identifying cause-and-effect pathways between deforestation of stream banks and subsequent effect on macroinvertebrate densities. This study has suggested some aspects that are being overlooked in research into the effects of deforestation. However, there are some limitations that should be considered. Hughes Creek was deforested many years ago, which could imply the ecological structure of the system has stabilized; the latter could be different in streams that have been recently deforested (e.g. 1-10 years ago). Further, Hughes Creek, as other sandy streams (Fritz et al. 2019, Ginder-Vogel et al. 2019), depends greatly on the retention of material by large wood debris, while other streams might have other ways to retain organic matter. For example, streams where large quantities of boulders are present might play a relevant role of retaining CPOM or other fractions and could be more important than LWD.

The objective of this thesis was to generate a cause-and-effect model, which meant I would need to collected large quantities of organic matter, and macroinvertebrates. I acknowledge since the beginning that I would not be able to work with multiple streams because that would obviate the sort of detailed work performed at Hughes Creek. Even though it is presented evidence about deforestation and the effect at small-scale on benthic standing stock and macroinvertebrate densities, it is difficult to extrapolate these findings to any type of stream with confidence. However, these observations could be applied to creeks of similar morphology, land use history (streams flowing through agricultural lands), and running off the same catchment boundary, such as Seven creeks located just to the north of Hughes Creek location. Another limitation is the fact that three forested and three low-forested sites were examined. This low number of sites might arise doubts related to low statistical power to test the effect of forest cover on allochthonous inputs, benthic CPOM standing stock, or macroinvertebrate densities. However, I was able to find some differences in fractions that represent a significant portion of allochthonous inputs (i.e. leaves). Moreover, the variability within each site was real. The latter suggests that local conditions are important – not just a measure of canopy cover, but other variables are also influencing outcomes. This can be translated to a lesson that future studies would need to be aware of – that is, even when more sites are sampled, the may end up study showing similar results, as the same variability between sites in the same "canopy cover" class are variable and dwarf the effects of local canopy cover.

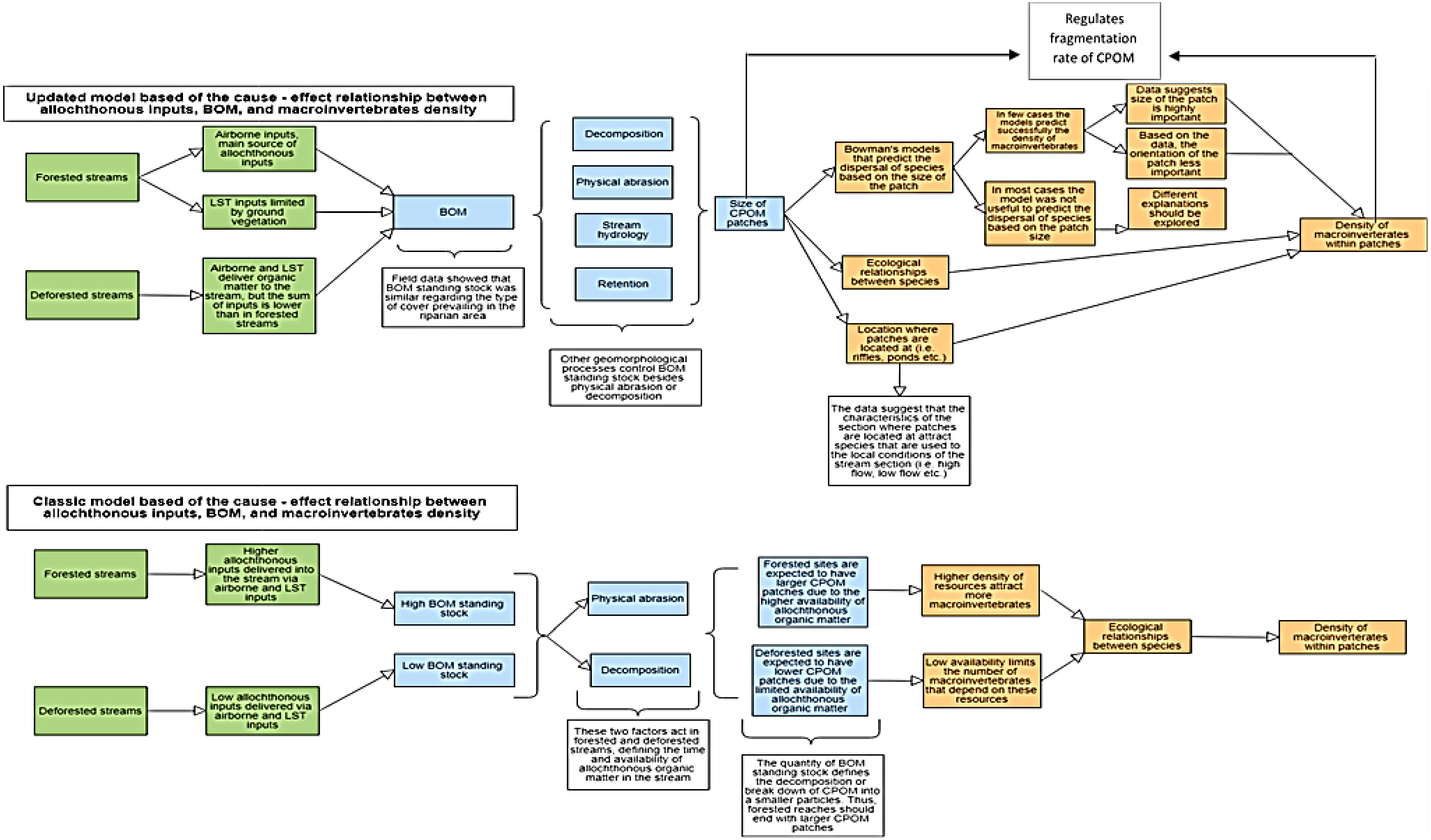
Regulates fragmentation rate of CPOM
Updated model based of the cause - effect relationship between allochthonous inputs, BOM, and macroinvertebrates density
Forested streams
Airborne inputs, main source of allochthonous inputs
LST inputs limited by ground vegetation
Deforested streams
Airborne and LST deliver organic matter to the stream, but the sum of inputs is lower than in forested streams
BOM
Field data showed that BOM standing stock was similar regarding the type of cover prevailing in the riparian area
Decomposition
Physical abrasion
Stream hydrology
Retention
Other geomorphological processes control BOM standing stock besides physical abrasion or decomposition
Size of CPOM patches
Bowman's models that predict the dispersal of species based on the size of the patch
In few cases the models predict successfully the density of macroinvertebrates
In most cases the model was not useful to predict the dispersal of species based on the patch size
Data suggests size of the patch is highly important
Based on the data, the orientation of the patch less important
Different explanations should be explored
Ecological relationships between species
Location where patches are located at (i.e. riffles, ponds etc.)
The data suggest that the characteristics of the section where patches are located at attract species that are used to the local conditions of the stream section (i.e. high flow, low flow etc.)
Density of macroinverterates within patches
Classic model based of the cause - effect relationship between allochthonous inputs, BOM, and macroinvertebrates density
Forested streams
Higher allochthonous inputs delivered into the stream via airborne and LST inputs
Deforested streams
Low allochthonous inputs delivered via airborne and LST inputs
High BOM standing stock
Low BOM standing stock
Physical abrasion
Decomposition
These two factors act in forested and deforested streams, defining the time and availability of allochthonous organic matter in the stream
Forested sites are expected to have larger CPOM patches due to the higher availability of allochthonous organic matter
Deforested sites are expected to have lower CPOM patches due to the limited availability of allochthonous organic matter
The quantity of BOM standing stock defines the decomposition or break down of CPOM into a smaller particles. Thus, forested reaches should end with larger CPOM patches
Higher density of resources attract more macroinvertebrates
Low availability limits the number of macroinvertebrates that depend on these resources
Ecological relationships between species
Density of macroinverterates within patches

Figure 7 1. Updated Resource flow model between the type of canopy cover, benthic organic matter, and the density of macroinvertebrates in CPOM patches. Arrows represent the connection between factors and show how inputs from forested and deforested streams produce a cause-effect relationship wth BOM standing stock, and ultimately with macroinvertebrate species densities. The classic cause- effect model shows a rather superficial explanation of how densities of macroinvertebrate densities respond to variations of allochthonous inputs, where emphasis is given forest cover, and other factors are less represented (i.e. hydrology, retention etc.). On the other hand, the updated model assembles factors of patch size and spatial distrbution of patches that should be considered when explaining the cause-effect model between forest cover, allochthonous inputs, BOM standing stock, and macroinvertebrates. Different colours show the transition between riparian forest, stream dynamics, and the ecological dynamics in CPOM patches.

8. Supplementary material

8.1. Supplementary material

Canopy cover estimation from each reach studied in Chapter 4.

Site 1

Figure 8 8.1-1. The most upstream study site at Hughes Creek, site 1 was catalogue as deforested site. The blue line shows the transect where canopy cover was estimated in the field, it is also the location where airborne and LST traps were placed. Upper canopy cover on this site only cover a thin line at both stream banks (≈ 8 m). Images were produced using nearmap software. (nearmap.com.au)

Site 2

Figure 8 8.1-2. Located downstream from site 1, site 2 was cataloge as deforested site. The blue line shows the transect where canopy cover was estimated in the field, is it also the location where airborne and LST traps were placed. Upper canopy cover on this site only cover a thin line at both stream banks (≈ 6 m). Images were produced using nearmap software (nearmap.com.au)

Site 3

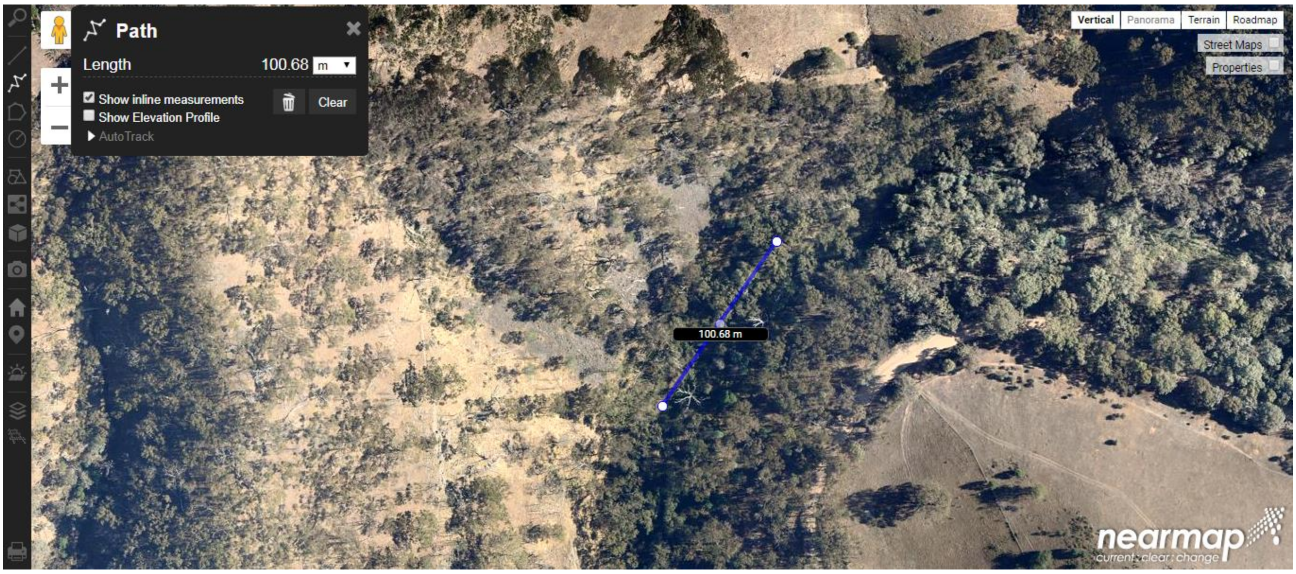

Figure 8 8.1-3. Located in a gorge area of Hughes Creek, site 3 was cataloged as forested site. The blue line shows the transect where canopy cover was estimated in the field, it is also the location where airborne and LST traps were placed. Upper stratum canopy cover on this site covers up to 200 m from the bank to inland direction on the left bank. On the right bank, Upper stratum covers up to 50 m from the bank to inland direction. Images were produced using nearmap software (nearmap.com.au)

Site 4

Figure 8 8.1-4. Located in a gorge area of Hughes Creek, site 4 was cataloged as forested site. The blue line shows the transect where canopy cover was estimated in the field, it is also the location where airborne and LST traps were placed. Upper stratum canopy cover on this site covers more than 200 m from the bank to inland direction on the left bank. On the right bank, Upper stratum covers up to 45 m from the bank to inland direction. Images were produced using nearmap software (nearmap.com.au)

Site 5

Figure 8 8.1-5. Located downstream the gorge area of Hughes Creek, site 5 was cataloged as deforested site. The blue line shows the transect where canopy cover was estimated in the field, it is also the location where airborne and LST traps were placed. Upper stratum canopy cover on this site covers ≈ 6 m from the bank to inland direction on the right bank. On the left bank, Upper stratum covers ≈ 15.72 m from the bank to inland direction. Images were produced using nearmap software (nearmap.com.au).

Site 6

Figure 8 8.1-6. Located downstream from all the study sites of Hughes Creek, site 6 was cataloged as forested site. The blue line shows the transect where canopy cover was estimated in the field, it is also the location where airborne and LST traps were placed. Upper stratum canopy cover on this site covers ≈ 77.35 m from the bank to inland direction on the left bank. On the right bank, Upper stratum covers ≈ 47.59 m from the bank to inland direction. Images were produced using nearmap software (nearmap.com.au)

Table 8-1 Upper stratum canopy cover (tree cover) obtained for site 1. The values were obtained by drawing 10 digital transects perpendicular to the stream channel, each transect crosses with the original transect, and where the allochthonous traps were located. The distance between transects was 10 m. Each transect ran from the stream edge to inland direction, and stopped until it reached grasslands (lower stratum component)

Transect	Extension of Upper stratum left bank	Extension of Upper stratum right bank
1	3	6.63
2	3.25	9.69
3	0.89	8.77
4	6.11	9.69
5	10.77	10.42
6	7.67	4.1
7	7.83	3.6
8	14.67	5.2
9	20.01	0
10	5.87	1.61
Min	0.89	0
Max	20.01	10.42
Mean	8.007	5.971
SD	5.800026916	3.653188714

Table 8-2 Upper stratum canopy cover (tree cover) obtained for site 2. The values were obtained by drawing 10 digital transects perpendicular to the stream channel, each transect crosses with the original transect, and where the allochthonous traps were located. The distance between transects was 10 m. Each transect ran from the stream edge to inland direction, and stopped until it reach grasslands (lower stratum component).

Transect	Extension of Upper stratum left bank	Extension of Upper stratum right bank
1	15	5.96
2	14.68	4.3
3	8.51	20.7
4	6.65	11.2
5	6.07	5.37
6	6.43	19.01
7	6.38	13.13
8	6.07	17.32
9	2.99	11.9
10	4.04	12.05
Min	2.99	4.3
Max	15	20.7
Mean	7.682	12.094
SD	4.055374486	5.722295965

Table 8-3 Upper stratum canopy cover (tree cover) obtained for site 3. The values were obtained by drawing 10 digital transects perpendicular to the stream channel, each transect crosses with the original transect, and where the allochthonous traps were located. The distance between transects was 10 m. Each transect ran from the stream edge to inland direction, and stopped until it reached grasslands (lower stratum component)

Transect	Extension of Upper stratum left bank	Extension of Upper stratum right bank
1	285.57	66.41
2	205.69	57.72
3	200.65	54.9
4	142.53	48.46
5	163.56	50.9
6	139.1	49.61
7	128.35	53.68
8	97.13	57.91
9	91.71	62.61
10	76.88	67.19
Min	76.88	48.46
Max	285.57	67.19
Mean	153.117	56.939
SD	63.5221475	6.711115903

Table 8-4 Upper stratum canopy cover (tree cover) obtained for site 4. The values were obtained by drawing 10 digital transects perpendicular to the stream channel, each transect crosses with the original transect, and where the allochthonous traps were located. The distance between transects was 10 m. Each transect ran from the stream edge to inland direction and stopped until it reached grasslands (lower stratum component).

Transect	Extension of Upper stratum left bank	Extension of Upper stratum right bank
1	204.03	43.19
2	191.97	38.74
3	175.26	37.26
4	194.46	41.06
5	180.2	42.59
6	159.19	41.62
7	150.03	44.7
8	140.08	40.34
9	126.22	39.12
10	118.17	37.74
Min	118.17	37.26
Max	204.03	44.7
Mean	163.961	40.636
SD	29.85134743	2.44426858

Table 8-5 Upper stratum canopy cover (tree cover) obtained for site 5. The values were obtained by drawing 10 digital transects perpendicular to the stream channel, each transect crosses with the original transect, and where the allochthonous traps were located. The distance between transects was 10 m. Each transect ran from the stream edge to inland direction, and stopped until it reached grasslands (lower stratum component)

Transect	Extension of Upper stratum left bank	Extension of Upper stratum right bank
1	20.97	16.07
2	20.8	10.29
3	20.33	10.78
4	16.15	12.33
5	13.13	15.64
6	9.33	12.79
7	5.49	15.04
8	0	14.42
9	0	6.62
10	1.54	7.25
Min	0	6.62
Max	20.97	16.07
Mean	10.774	12.123
SD	8.677423069	3.356810821

Table 8-6 Upper stratum canopy cover (tree cover) obtained for site 6. The values were obtained by drawing 10 digital transects perpendicular to the stream channel, each transect crosses with the original transect, and where the allochthonous traps were located. The distance between transects was 10 m. Each transect ran from the stream edge to inland direction, and stopped until it reached grasslands (lower stratum component)

Transect	Extension of Upper stratum left bank	Extension of Upper stratum right bank
1	33.73	37
2	36.22	56.2
3	43.1	46.6
4	44.9	42.38
5	42.05	40.29
6	38.08	21.11
7	24.4	32.21
8	25.52	9.82
9	86.45	64.74
10	81.4	76.78
Min	24.4	9.82
Max	86.45	76.78
Mean	45.585	42.713
SD	21.3639906	19.83355577

8.2. Supplementary material

Supplementary material 7.2 . Habitat and feeding group of species sampled in Chapter 5. Information was retrieved from Lancaster and Downes (2017).

Species	Habitat	Feeding group
Austrosimulium furiosum	Larvae occur in fast flowing waters	Larvae are filtering collectors
Simulium ornatipes	Larvae occur in fast flowing waters	Larvae are filtering collectors
Ecnomina F	Ecnomid larvae occur in lentic and slow lotic waters. They are found on or under rocks or logs.	Early instar larvae feed on fine organic particles. Later instars are primarily predator
Ecnomina E	Ecnomid larvae occur in lentic and slow lotic waters. They are found on or under rocks or logs.	Early instar larvae feed on fine organic particles. Later instars are primarily predator
Ecnomus continentalis	Ecnomid larvae occur in lentic and slow lotic waters. They are found on or under rocks or logs.	Early instar larvae feed on fine organic particles. Later instars are primarily predator
Coenoria sp.	Coenoria sp. larvae occur in fast flowing	Larvae are herbivores grazing on benthic algae and shredders of leaves and wood
Notalina sp.	Usually found on detritus or aquatic macrophytes	Generalist feeders
Cheumatopsyche sp.	Usually found on detritus or aquatic macrophytes	*Cheumatopsyche* larvae are omnivores
Hydroptila sp.	Not available	Scrapers
Oecetis sp.	They are usually found on detritus or aquatic macrophytes.	Scrapers
Asmicridea sp.	Not available	Filtering collectors
Diplectrona sp.	Fast flowing areas	Filtering collectors
Offadens sp.	Baetid nymphs occur in almost all freshwater habitats, including the fast flowing riffle zone of rivers to the slackwaters of rivers	Baetid nymphs scrape algae and fine detritus from submerged rocks, wood and macrophytes
Centroptilumn sp.	Baetid nymphs occur in almost all freshwater habitats, including the fast flowing riffle zone of rivers to the slackwaters of rivers	Baetid nymphs scrape algae and fine detritus from submerged rocks, wood and macrophytes
Cleon sp.	Baetid nymphs occur in almost all freshwater habitats, including the fast flowing riffle zone of rivers to the slackwaters of rivers	Baetid nymphs scrape algae and fine detritus from submerged rocks, wood and macrophytes
Tasmanocoenis sp.	They typically dwell in leaf packs, on logs or macrophytes.	Nymphs feed on fine particulate detritus.
Nousia sp.	Nymphs are found in log crevices, amongst macrophytes and debris, also on or under cobbles and bedrock	Most nymphs scrape the surface of gravel, rocks and logs feeding on algae and detritus
Atalophlebia sp.	Found in diverses stream areas from backwaters to fast flowing sections	Gathering collectors, shredders
Austrolimnius sp.	Elmid beetles are commonly known as riffle beetles because of their tendency to live in lotic (running water) habitats	Riffle beetles feed on algae and fine detritus
Berosus sp.	Most hydrophild beetles occur in slow moving streams or shallow. Berosus also occur in fast flowing streams	Predators (larvae); shredders (adults)
Micronecta sp.	few species live in streams, and others are found in brackish pools	Shredders

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