Restoring connectivity:
the effect of riparian replanting on in-stream organic carbon dynamics in a degraded agricultural landscape

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Remnant and replanted river red gums (*Eucalyptus camaldulensis*) lining the banks of Seven Creeks, Victoria, Australia.

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Summary

Streams and rivers are intrinsically linked to the terrestrial environment by the exchange of water, nutrients, organic matter and biota. Terrestrial-aquatic connectivity has been disrupted by the degradation and removal of riparian vegetation due to widespread agricultural development. Loss of terrestrial vegetation modifies channel shading, in-stream habitat, and the quantity and composition of organic carbon (i.e. energy) subsidies provided to stream food webs. Collectively, these changes result in biodiversity loss and altered ecosystem functioning.

Replanting riparian vegetation aims to alleviate the adverse ecological effects of riparian clearance. Replanting is already commonly used for ecological restoration, but revegetation may become more widespread if restoration activities are driven by economic forces, such as payments for planting trees to mitigate climate change. However, replantings currently are often spatially limited and isolated, so the plantings may not have a large effect on halting or reversing ecological degradation.

Riparian clearance and revegetation are likely to alter carbon dynamics, which is a critical process underpinning biodiversity and ecosystem functioning in streams. We have little knowledge of if, and when, riparian replanting will restore in-stream organic-carbon processes towards pre-clearance conditions, or of the broad-scale effects on carbon balances. The integration of aquatic fluxes into regional carbon budgets is an important component of regional, national and global carbon accounting.

I sought to:

(1) quantify the reach-scale effects of replanting on in-stream organic carbon dynamics;

(2) assess the potential for organic matter properties to reflect the success of restoring terrestrial-aquatic connectivity; and

(3) upscale organic carbon fluxes to project the consequences of revegetation for carbon balance and atmospheric feedback at watershed (= catchment) scales.

I assessed the dynamics of aquatic organic carbon (input, standing stock, export and metabolism) in 15 streams (1^{st}-3^{rd} Strahler order) of an agricultural landscape in south-eastern Australia. Ten of the streams had reaches that were replanted with native woody vegetation 8 to 22 years prior to the study; I refer to these restored reaches as ‘replanted’ and other reaches in which there had been no plantings, pasture reaches, as ‘untreated’.

Replanted stream reaches had greater inputs and accumulation of terrestrial organic carbon on the stream-bed than did untreated reaches. Replanting was correlated with a reduction in net ecosystem productivity and a shorter organic carbon turnover length. Within two decades of planting, metabolic rates in replanted reaches had values more typical of those in natural, forested streams, supporting the use of ecosystem metabolism as a functional indictor of restoration success at reach-scales. Metabolic measures could be combined with pattern-based measures, such as biodiversity, to demonstrate the ecological value of replanting.

The export of organic carbon was governed by land-use and climatic variables at spatial scales larger than typical replanting projects. Watershed tree cover affected the composition of dissolved organic matter, but not its quantity. A greater proportion of the dissolved organic matter in agricultural streams was from within the stream and a reduced proportion was from terrestrial vegetation, compared to streams in forested watersheds. The characteristics of dissolved organic matter potentially provide an aggregate measure of aquatic and terrestrial connectivity over large spatial scales. The quantity of total organic carbon transported was controlled by discharge. Projected increases in rainfall variability will affect the timing and magnitude of storm-flows, altering the fluxes of energy subsidies among ecosystems in landscapes.

The estimated organic carbon budget showed that replanted reaches potentially were a greater source of carbon than were untreated reaches (net change -0.52 g C m^{-2} day^{-1} ± 0.80 SD). At a watershed scale, this increased carbon loss per unit area of stream was small compared to organic carbon export from 3rd-order streams.

Riparian restoration at reach spatial scales (i.e. 100s of m) can restore ecosystem processes towards pre-clearance condition, within two decades. However, the effects of replanting at small scales may be overwhelmed by changes to hydrologic processes arising from probable increased climate variability in the future. Addressing land-use effects requires a landscape perspective that incorporates spatial context and connectivity at multiple scales to guide restoration activities into the areas likely to provide the greatest ecological return for investment.

General Declaration

In accordance with Monash University Doctorate Regulation 17.2 Doctor of Philosophy and Research Master's regulations the following declarations are made:

I hereby declare that this thesis contains no material which has been accepted for the award of any other degree or diploma at any university or equivalent institution and that, to the best of my knowledge and belief, this thesis contains no material previously published or written by another person, except where due reference is made in the text of the thesis.

This thesis includes two original papers published in peer reviewed journals and three unpublished publications. The core theme of the thesis is the effect of replanting native riparian vegetation on aquatic organic carbon dynamics. The ideas, development and writing up of all the papers in the thesis were the principal responsibility of myself, the candidate, working within the School of Biological Science, Monash University under the supervision of Professor Ralph Mac Nally and Professor Ross M. Thompson.

The inclusion of co-authors reflects the fact that the work came from active collaboration between researchers and acknowledges input into team-based research.

In the case of Chapters 2-6 my contribution to the work involved the following:

Thesis chapter	Publication title	Publication status	Nature and extent of candidate's contribution
2	Detecting reach-scale restoration success in stream ecosystems: are macroinvertebrate indices enough?	Submitted	I performed 70% of the fieldwork, 70% of the laboratory work, all the statistical analyses and was the primary author of the manuscript.
3	The influence of native replanting on stream ecosystem metabolism in a degraded landscape: can a little vegetation go a long way?	Published	I performed all the fieldwork, all the laboratory work, 75% of the statistical analyses and was the primary author of the manuscript.
4	Effect of native vegetation loss on stream ecosystem processes: dissolved organic matter composition and export in agricultural landscapes	Published	I performed 90% of the fieldwork, all the laboratory work (except for some outsourced chemical analyses), 50% of the statistical analyses and was the primary author of the manuscript.
5	Projecting cross-system subsidies under changing climates	Submitted	I performed 90% of the fieldwork, all the laboratory work (except for some outsourced chemical analyses), 90% of the statistical analyses and was the primary author of the manuscript.
6	Aquatic organic carbon dynamics in massively altered landscapes: past, present and future	In prep.	I performed 95% of the fieldwork, all the laboratory work (except for some outsourced chemical analyses), 90% of the statistical analyses and was the primary author of the manuscript.

I have renumbered sections of submitted or published papers in order to generate a consistent presentation within the thesis.

Signed: …… [redacted] ………

Date: 11-04-2014 ………………………………

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Chapter 1

General introduction

Background

Ecological effects of global land-use change

Clearing native forests for crop and pasture land to support an expanding human population has pervasive adverse ecological effects. A projected doubling in global food production by 2050 means these negative effects will not abate (Tilman *et al.*, 2011). Habitat loss and degradation as a result of land clearance are major drivers of biodiversity loss (Stoate *et al.*, 2009), while irrigating and fertilizing agricultural land substantially alters biogeochemical and hydrological processes (Foley *et al.*, 2005). Collectively, these effects have produced agricultural landscapes that consist of fragmented and isolated habitat patches with greatly altered ecosystem boundaries and disrupted connectivity (Polis *et al.*, 1997).

Streams and rivers are linked intrinsically to the terrestrial environment by the transfer of water, nutrients, energy and biota, and so, are sensitive to change in their watersheds (= catchments) (Stoate *et al.*, 2009). Agricultural development degrades stream ecosystems through increasing runoff, channel modification, inducing eutrophication and salinization, and the clearing of riparian vegetation (Foley *et al.*, 2005). Vegetation clearing is particularly detrimental in riparian zones, which form an ecotone between the terrestrial and aquatic ecosystems. Here, we consider the riparian zone the area that directly influences stream ecosystem ecological and geomorphological processes. This differs among streams, and includes the zone directly adjacent to the channel together with occasionally inundated floodplains if they are present in the stream valley (following Goodwin *et al.*, 1997). Vegetation in the riparian zone filters nutrients and pollutants, stabilizes banks and provides energy subsidies (e.g. leaf litter) to stream food webs (Naiman & Décamps, 1997). Riparian plant communities in agricultural landscapes have a dissimilar suite of functional traits to those prior to intense human management (Kominoski *et al.*, 2013).

Changes in riparian functions have large effects on aquatic ecosystems, including altered water quality and greater erosion (e.g. Sweeney *et al.*, 2004). Variation in the quantity, composition and timing of terrestrial organic-matter inputs greatly affects in-stream biodiversity and function (Kominoski *et al.*, 2013). Reduced terrestrial connectivity affects aquatic macroinvertebrate assemblages (e.g. Eggert & Wallace, 2003; Thompson & Townsend, 2004) and alters trophic interactions (Wallace *et al.*, 1999), with consequences for processes such as leaf litter decomposition and nutrient processing (Bernot *et al.*, 2006; Kominoski *et al.*, 2010). The loss of canopy cover reduces shading and increases water temperatures (Rutherford *et al.*, 1997), facilitating increased growth of aquatic primary producers (Bunn *et al.*, 1998).

Restoring stream ecosystems

Watersheds and river networks provide key ecosystem services to humans, including clean drinking water, irrigation water, mitigation against flood, and nutrient and pollutant processing (Postel & Carpenter, 1997). Consequently, stream and riparian restoration has become more commonplace to militate against the effects of agriculture (Follstad Shah *et al.*, 2007). Billions of US dollars have been spent on stream restoration activities such as channel reconfiguration, bank stabilization, providing more natural flow regimes and replanting riparian vegetation (Bernhardt *et al.*, 2005).

Despite the apparent scale of these investments, the effectiveness of riparian restoration is not well understood. Many restoration projects do not have pre-defined ecological goals, and outcomes rarely are monitored (Brooks & Lake, 2007; Follstad Shah *et al.*, 2007). Even when aims are defined, the motivation often is to improve water quality and to reinstate habitat for biodiversity, with success gauged by measuring biodiversity responses (Follstad Shah *et al.*, 2007). However, these responses are often difficult to detect and are highly variable (e.g. Parkyn *et al.*, 2003; Collins *et al.*, 2013). Instead of focusing on particular taxa, there has been a shift in emphasis to restoring whole ecosystems and their associated processes (Poiani *et al.*, 2000).

One of the challenges in assessing ecosystem responses to restoration is that the extent of stream restoration usually is spatially mismatched from its intended outcomes (Bernhardt & Palmer, 2011). Riparian replanting has been restricted by logistics and cost to relatively small patches in terms of linear length (< 1 km), and in terms of width of replanting on each side of channels (Bernhardt *et al.*, 2005). In contrast, stream degradation generally occurs over larger spatial scales (often at whole-watershed or sub-watershed scales), meaning that local-scale replanting may not produce the desired outcomes at larger spatial scales (Greenwood *et al.*, 2012).

Maximizing restoration effectiveness: The case for in-stream carbon

A growing recognition of whole-of-watershed influences on streams and rivers has informed our current conceptual view of how hydrology and geomorphology influence aquatic habitats and processes at nested spatial scales (Frissell *et al.*, 1986; Allan, 2004). Maintaining ecosystem condition and providing ecological services in future landscapes requires river networks to be considered as integrated into landscapes (Allan, 2004), and the importance of connectivity to be considered explicitly (Jansson *et al.*, 2007). The longitudinal, lateral and vertical linkages of organic matter in watersheds are central to freshwater ecological theories that explain the assembly and trophic interactions of aquatic communities (Ward, 1989).

The provision, processing and transport of aquatic organic matter are crucial ecological processes in streams and rivers. Aquatic organic matter originates from terrestrial and in-stream sources, and is classified into size fractions that range from dissolved molecules (such as humic and fulvic acids) to particulate forms, such as detrital leaf litter and large wood (Thurman, 1985). The characteristics (i.e. size, quantity and composition) of aquatic organic matter depend on stream, riparian and watershed processes, such as hydrology, terrestrial litter inputs, in-stream primary production and decomposition (Stanley *et al.*, 2012). Organic matter characteristics integrate aquatic-terrestrial connectivity at multiple spatial scales, from local riparian condition (e.g. Sakamaki & Richardson, 2011) to land use or geomorphology at watershed (e.g. Wilson & Xenopoulos, 2009), continental or global (Aitkenhead & McDowell, 2000) scales. In turn, organic matter quantity and quality have a strong regulatory effect on in-stream biota and trophic dynamics because terrestrial aquatic organic carbon (a major component of organic matter) is an important basal energy source and substrate for aquatic heterotrophs (Wiegner *et al.*, 2005; Reid *et al.*, 2008).

Monitoring fluxes of aquatic organic carbon is a realistic means to measure restoration success (Kominoski & Rosemond, 2012). The effects of land-use change on in-stream organic matter fluxes (e.g. metabolism and export) have been described by studies comparing pasture and forested reaches (e.g. Gücker *et al.*, 2009; Wilson & Xenopoulos, 2009). However, we have little knowledge of if, and when, riparian replanting could shift aquatic organic carbon dynamics towards that typical of reference condition. Further understanding of how energy flow in aquatic systems responds to riparian-zone restoration will inform future management, such replanting location, extent of replanting and time lags required to achieve ecological goals.

Regional carbon balance will be affected by changes in aquatic organic carbon dynamics. Fluxes from agricultural watersheds are an important link in the global carbon cycle because agriculture covers more than a third of Earth's ice-free land surface (Ramankutty *et al.*, 2008), but these fluxes often are not included in regional budgets (Cole *et al.*, 2007). About half of the terrestrial organic carbon entering streams is processed or stored, while the remainder is transported to the oceans (Cole *et al.*, 2007). A greater understanding of the biogeochemical implications of altered fluxes of aquatic organic carbon is required to address global challenges, such as land-use and climate change.

Watershed-scale restoration may become feasible in future landscapes. There is a growing awareness of the multiple benefits provided by native vegetation, such as supporting regional biodiversity and as windbreaks for stock (Jose, 2009; Gilvear *et al.*, 2013). Economic forces, such as payment for sequestering carbon by planting trees (‘carbon farming’) may induce broad-scale revegetation in the future (Harper *et al.*, 2007; Bradshaw *et al.*, 2013), affecting aquatic organic carbon dynamics. Further, exports are linked strongly to discharge (Royer & David, 2005) and so, will respond to hydrologic changes such as those associated with drought and climate variability. Managing interacting global changes (i.e. land-use and climate change) requires a large-scale, integrated approach and comprehensive estimates of aquatic carbon fluxes that incorporate inland waters (Battin *et al.*, 2009). This includes upscaling smaller-scale measurements to assess how anthropogenic change will affect aquatic organic carbon storage and processing at regional scales (Battin *et al.*, 2009; Tank *et al.*, 2010).

Study aims and hypotheses

I place the restoration of aquatic processes into a landscape context by examining the effect of land-use degradation and restoration on aquatic organic carbon fluxes at multiple spatial scales (Fig. 1). I sought to:

(1) quantify the reach-scale effects of replanting on in-stream organic carbon dynamics;
(2) assess the potential for organic matter properties to reflect the success of restoring terrestrial-aquatic connectivity; and
(3) upscale organic carbon fluxes to project the consequences of revegetation for carbon balance and atmospheric feedback at watershed scales.

I measured organic carbon dynamics, including inputs, standing stock, transport and metabolism, at 20 sites on 15 unregulated streams (1st-3rd Strahler order) in an agricultural landscape of south-eastern Australia over two years (2010-2012). This region has been extensively cleared, and revegetation for multiple benefits may be a feasible and possibly desirable land-use option in the future (Bradshaw *et al.*, 2013). Ten of the stream sites had reaches replanted with native woody vegetation 8-22 years ago, while three sites were ‘untreated’ sites with degraded riparian vegetation. Seven other sites were selected to incorporate the full range of watershed-scale land-use variability to provide a more complete understanding for Aim 3 (Table 1). These seven sites are termed 'watershed land-use' sites (or 'organic matter quality' sites in Chapter 4). The replanting ages are defined by the year of the study's completion (2012), except for Chapter 3, which were defined in 2011 (i.e. one year younger). The focal streams historically were perennial or intermittent, but have recently experienced extreme hydrologic variation, from long-term drought (1997 – early 2010; Leblanc *et al.*, 2012) to more recent widespread flooding (late 2010; Leblanc *et al.*, 2012).

Study sites differed in both local riparian condition (restored and untreated) and watershed-scale land use (watershed areal tree cover). This 'scale of vegetation' (Fig. 1, far left) was crucial for understanding the broad-scale ecological and biogeochemical implications of future land-use options because various organic carbon processes are governed by terrestrial-aquatic connectivity at different spatial scales. I hypothesized that reach-scale organic matter inputs will be coupled with local effects on basal processes such as metabolic rates and benthic standing stocks (Fig.1, bottom). In contrast, watershed-scale land use and hydrologic regime may drive the export and spiralling (i.e. the relationship between turnover and transport) of organic carbon, particularly for mobile forms such as dissolved molecules (Fig. 1, top). Watershed condition and discharge could affect basal processes and turnover and by influencing the composition and accumulation of organic carbon (Fig. 1, middle and right).

In Chapters 2 – 5, I examine the effect of vegetation (reach- and watershed-scale) and hydrology on biodiversity and organic carbon fluxes, while in Chapter 6, I investigate whether aquatic organic-carbon processes in replanted stream networks will become more similar to reference condition using a budget approach. Lowland, forested stream sites were not available in the study region for direct comparison, so I defined reference condition as values closer to those that typify intact, forested systems elsewhere. Throughout this thesis I use the term 'organic matter' to denote all organic material (e.g. dissolved organic carbon and dissolved organic nitrogen) where appropriate, such as when measurements were made on entire samples (predominantly Chapter 4) or when all elements were potentially available as an ecological resource. The term ‘organic carbon’ is used to specify only the carbon component of the organic matter, and is used when measurements are taken of this fraction only or for carbon accounting. Note that the terms ‘watershed’ and ‘catchment’ are equivalent, and are used as such in this thesis.

Thesis structure

Chapter 2 - Detecting reach-scale restoration success in stream ecosystems: are macroinvertebrate indices enough? I investigated whether reinstating aquatic biodiversity is an appropriate goal for reach-scale restoration projects (Fig. 1, middle left). I examined the effects of both reach- and watershed-scale characteristics on macroinvertebrate assemblages and indices. I sought to determine the relative importance of local and watershed physicochemical variables on macroinvertebrate assemblages and if macroinvertebrate biodiversity and sensitivity measures respond to replanting within two decades, which was the longest duration available in this region.

Chapter 3 (Giling et al., 2013) - The influence of native replanting on stream ecosystem metabolism in a degraded landscape: can a little vegetation go a long way? I sought to determine if the typical spatial extent of riparian replanting affects in-stream ecosystem processes within two decades of replanting (Fig. 1, bottom left). This was assessed using stream-ecosystem metabolism, a functional indicator that incorporates the production (gross primary productivity; GPP) and utilization (ecosystem respiration; ER) of aquatic carbon. I tested if restored reaches had altered rates of GPP and ER, and if this were due to changes in canopy shading and terrestrial organic-matter supply.

Note this manuscript has been published and is referenced within the thesis as Giling *et al.* (2013).

Chapter 4 (Giling et al., 2014) - Effect of native vegetation loss on stream ecosystem processes: dissolved organic matter composition and export in agricultural landscapes. I assessed the effects of loss of native vegetation at watershed scales on dissolved organic matter (DOM) quantity and quality (Fig. 1, top). I measured DOM concentration, export, composition and lability to microbial consumers across a forest-to-pasture land-use gradient. I aimed to determine if there was a difference in the quantity and quality (i.e. ease of breakdown to microbial consumers) of DOM exported from intact and agricultural watersheds.
Note this manuscript has been published and is referenced within the thesis as Giling *et al.* (2014).

Chapter 5 - Projecting cross-system subsidies under changing climates. I investigated the contribution of extreme flows to organic carbon transport (dissolved and particulate) (Fig. 1, top right). I sought to provide a conceptual framework for projecting how future hydrologic patterns will interact with land use to affect the dynamics of terrestrial-aquatic subsidies.

Chapter 6 - Aquatic organic carbon dynamics in massively altered landscapes: past, present and future. I assimilated data on organic carbon provision, processing and transport to build a budget for untreated and replanted agricultural stream reaches. I sought to determine if replanting riparian vegetation can restore in-stream organic carbon dynamics to those that typify forested streams within two decades (Fig. 1, right). I upscaled my findings to assess the probable biogeochemical implications (i.e. transport and turnover of organic carbon) of broad-scale replantings in future agricultural landscapes.

Chapter 7 - General discussion. I summarize and synthesize the major findings and provide recommendation for restoring terrestrial-aquatic connectivity in degraded landscapes.

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Table 1. Table describing which of the 20 sites were sampled for each chapter (shown by '✓') in this thesis. A subset of sites was used for chapters where it was necessary to maintain particular variables (e.g. watershed area or discharge) within a small range to aid interpretation. Sites are grouped into 'untreated', 'replanted' and 'watershed land-use' categories. Untreated and replanted sites had a downstream [either untreated (pasture, age=zero) or replanted] and an upstream (untreated) reach (shown on the left and right of each chapter column respectively). Some streams have an upper and lower site where there are multiple sites on that stream. MDF = mean daily flow (Ml day^{-1}).

Site (stream name)	Site type	Reaches per site	Lat.	Long.	Replanting age (d.s. reach)	Watershed tree cover (%)	MDF	Ch. 2		Ch. 3		Ch. 4		Ch. 5		Ch. 6	
								d.s.	u.s.	d.s.	u.s.	d.s.	u.s.	d.s.	u.s.	d.s.	u.s.
Creightons	untreated site	2	-36.88	145.53	0	15	25.7	✓		✓	✓	✓		✓		✓	✓
Faithful (lower)			-36.74	145.66	0	22	26.9	✓						✓		✓	✓
Hollands			-36.71	146.09	0	73	157.3	✓				✓		✓		✓	✓
Castle (lower)	replanted site	2	-36.86	145.58	8	10	12.4	✓						✓		✓	✓
tributary of Broken			-36.92	145.98	8	72	1.9	✓				✓		✓		✓	✓
Camerons Well			-36.86	145.42	10	20	0.1	✓								✓	✓
Harrys			-36.70	145.74	11	36	8.3	✓				✓		✓		✓	✓
Honeysuckle			-36.65	145.74	13	30	21.8	✓		✓✓		✓		✓		✓✓	✓
Seven (lower)			-36.71	145.54	13	15	240.5	✓						✓		✓	✓
Wombat			-36.87	145.63	15	58	22.2	✓				✓		✓		✓	✓
Warrenbayne (lower)			-36.70	145.88	18	67	30.3	✓		✓	✓			✓		✓	✓
Moonee (lower)			-36.74	145.99	22	70	49.6	✓		✓	✓			✓		✓	✓
Ryans			-36.64	146.19	22	86	98.7	✓				✓		✓		✓	✓
Castle (upper)	watershed land-use site	1	-36.90	145.59	-	15	6.7	✓				✓		✓			
Faithful (upper)			-36.75	145.75	-	32	3.7	✓				✓		✓			
Moonee (upper)			-36.84	145.94	-	97	8.4	✓				✓		✓			
Seven (upper)			-36.81	145.82	-	48	18.1	✓				✓		✓			
Two Mile			-36.65	145.78	-	26	2.9	✓				✓		✓			
Warrenbayne (upper)			-36.72	145.85	-	70	17.9	✓				✓		✓			
White Gum Gully			-36.80	145.89	-	85	8.4	✓				✓		✓			

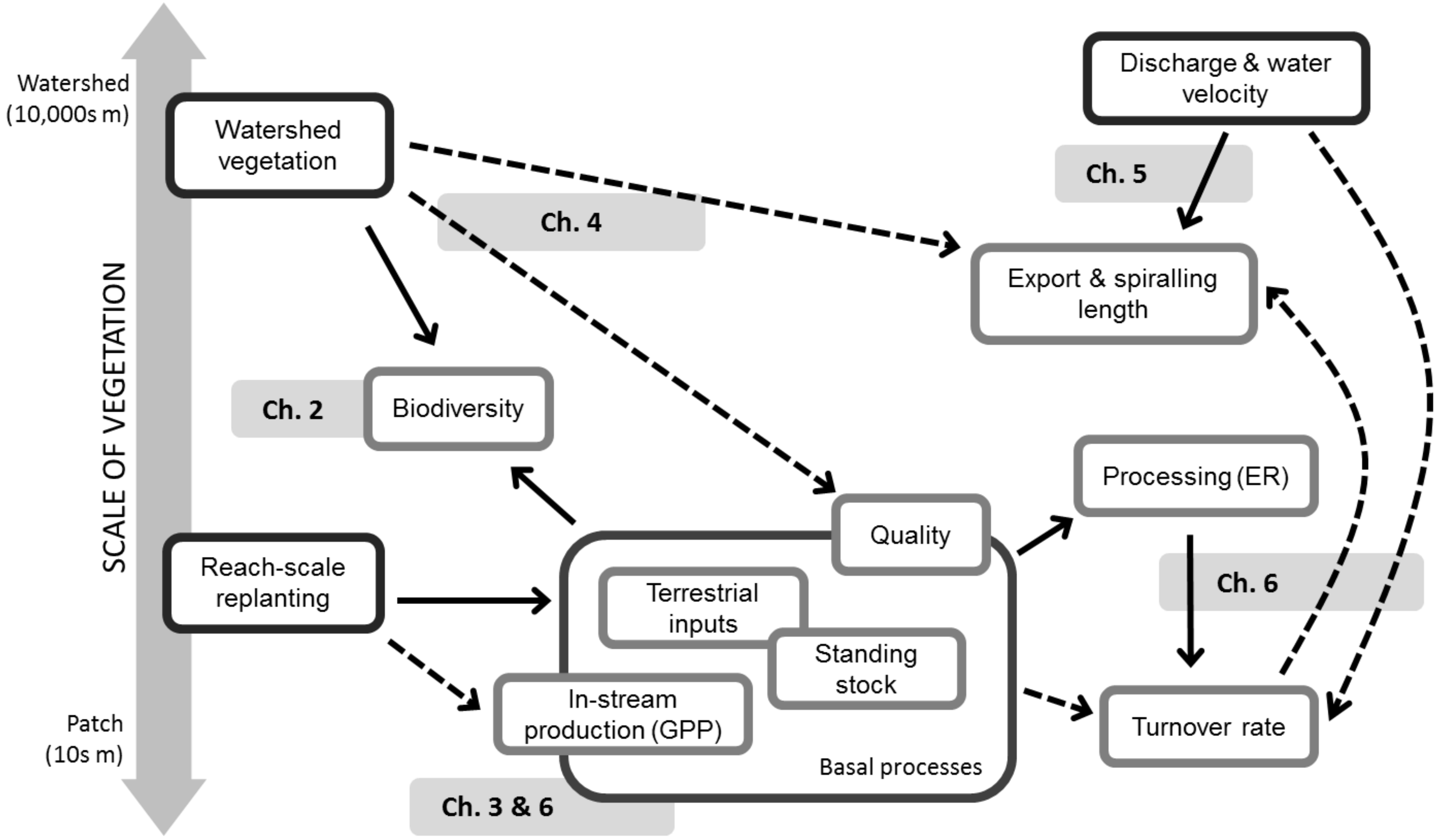

Figure 1. Conceptual model describing the effect of native vegetation (at reach- and watershed-scales) on in-stream organic carbon dynamics. Hypotheses are shown as arrows, where solid lines indicate positive effects and dashed lines indicate negative effects. Carbon processes are influenced by scale of vegetation as indicated by arrows, but their placement on the model is not indicative of scale.

Declaration for Thesis Chapter 2

Declaration by candidate

In the case of Chapter 2, the nature and extent of my contribution to the work was the following:

Nature of contribution	**Extent of contribution (%)**
I performed 70% of the fieldwork, 70% of the laboratory work, all the statistical analyses and was the primary author of the manuscript.	80%

The following co-authors contributed to the work. If co-authors are students at Monash University, the extent of their contribution in percentage terms must be stated:

Name	**Nature of contribution**	**Extent of contribution (%) for student co-authors only**
Ralph Mac Nally	Input of ideas and contributed to writing the manuscript.	
Ross M. Thompson	Input of ideas and contributed to writing the manuscript.	

The undersigned hereby certify that the above declaration correctly reflects the nature and extent of the candidate's and co-authors' contributions to this work*.

Candidate's Signature	[redacted]	**Date** 11.4.14
Main Supervisor's Signature	[redacted]	**Date** 11.4.14

*Note: Where the responsible author is not the candidate's main supervisor, the main supervisor should consult with the responsible author to agree on the respective contributions of the authors.

Chapter 2

Detecting reach-scale restoration success in stream ecosystems: are macroinvertebrate indices enough?

Abstract

1. Clearing native vegetation for crop and pasture land has pervasive effects on stream and river ecosystems worldwide. Loss and degradation of riparian vegetation alters bank morphology, lowers water quality and reduces terrestrial litter inputs to streams, with effects for stream biota and food webs. Restoring riparian zones is a commonplace restoration action that is expected to alleviate agricultural effects.
2. Replanting native vegetation is often conducted to return water quality and re-establish biotic assemblages that perform important ecological functions. However, reach-scale restoration may do little to combat watershed-scale degradation. Whether reinstating macroinvertebrate biodiversity is an appropriate goal of restoring riparian zones (as opposed to directly measuring water quality or whole-ecosystem function) over intermediate timeframes is currently unclear.
3. We measured the response of aquatic macroinvertebrate assemblages and indices to riparian restoration across a chronosequence of replanted reaches on agricultural streams in south-eastern Australia. Sites were replanted with native vegetation 8 to 22 years prior to the study.
4. Indices of macroinvertebrate sensitivity did not respond to replanting within two decades, perhaps because replanting did not appear to benefit local water quality or in-stream habitat. The invertebrate assemblages were influenced mainly by indirect watershed-scale effects and geomorphological characteristics, but were closer to reference condition at sites with lower total watershed agricultural land cover.

5. The expected restoration trajectory and feasible endpoint of biodiversity response to reach-scale restoration over longer time scales is central to ecological restoration theory. However, our findings suggest restoration must address the large scale drivers of agricultural degradation to return biodiversity in lowland reaches to pre-clearance condition. Restoration goals, and the spatial and temporal scale of processes required to meet them, should be carefully considered, and monitoring methods explicitly matched to desired outcomes.

Introduction

Clearing natural land for agriculture has pervasive effects on ecosystems worldwide (Tilman *et al.*, 2011). Globally, crop and pasture land constitutes the largest land-cover category, and has caused widespread habitat loss (Asner *et al.*, 2004). Habitat loss has contributed to a dramatic decline in biodiversity and significant alteration to ecosystem services (Stoate *et al.*, 2009; Cardinale *et al.*, 2012). Remaining habitat is usually fragmented, which not only leads directly to species loss, but creates edge effects that influence biotic processes (Fahrig, 2003). For example, fertilizer application to agricultural land can alter nutrient cycling in both the recipient habitat and in adjacent habitats (Caraco & Cole, 1999; Bennett *et al.*, 2001).

Streams and rivers are heavily degraded ecosystems (Bernhardt & Palmer, 2011). Agricultural runoff lowers water quality, whilst water impoundment affects hydrologic regimes, downstream water temperatures and the movement of biota (Tilman, 1999; Scanlon *et al.*, 2007; Liermann *et al.*, 2012). River channels have been straightened and incised; simplifying habitats (Blann *et al.*, 2009). Riparian vegetation has been degraded, leading to riparian-plant communities with an altered suite of functional traits to pre-clearance communities (Kominoski *et al.*, 2013). Reduced canopy shading increases water temperatures and the loss of stabilizing roots leads to widespread soil erosion and sedimentation of river benthos (Webb *et al.*, 2008; Dosskey *et al.*, 2010). Terrestrial litter inputs (e.g. leaves and twigs) from riparian vegetation support aquatic food webs (Wallace *et al.*, 1997), and altering the quantity and quality (e.g. nutrient content) of available basal resources affects in-stream trophic dynamics (e.g. Thompson & Townsend, 2004) and community composition (e.g. Motomori *et al.*, 2001).

Stream and river restoration has become commonplace over the last 25 years in response to increasing anthropogenic pressures (Follstad Shah *et al.*, 2007). Restoration projects include physical manipulations (such as channel reconfiguration and bank stabilization), hydrological restoration (e.g. dam removal and the provision of environmental flows), managing water quality and replanting riparian vegetation (Bernhardt *et al.*, 2005). Reinstating aquatic biodiversity by enhancing in-stream habitat is one of the most common motivations for restoration (Follstad Shah *et al.*, 2007; Bernhardt & Palmer, 2011). However, we have limited knowledge of its effectiveness, despite substantial investment (> US$14 billion in the United States since 1990; Bernhardt *et al.*, 2005), as the outcomes of restoration projects are often not monitored. Brooks and Lake (2007) reviewed thousands of restoration projects and found that only 14% included monitoring some measure of ecological success. Consequently, accounts of biodiversity response (usually measured with aquatic macroinvertebrates) to restoration are uncommon relative to the number of undertaken projects. Existing evidence suggests response(s) of aquatic biodiversity to river restoration is variable over intermediate (< 30 years) time scales (Table 1).

Replanting riparian vegetation is already among the most common restoration activities and may become increasingly widespread in future, carbon economies (Bradshaw *et al.*, 2013). Increased shading, nutrient interception and terrestrial litter inputs are expected to provide food and habitat benefits, shifting aquatic biodiversity assemblages towards reference condition (Orzetti *et al.*, 2010), which is deemed important to returning ecosystem functions (e.g. decomposition; Covich *et al.*, 2004). Indices based on macroinvertebrate assemblages (e.g. richness and sensitivity) are expected to give an overall indication of water and habitat quality (Orzetti *et al.*, 2010). However, whether reinstating macroinvertebrate assemblages is an appropriate goal of restoring riparian zones rather than directly measuring water quality or whole-ecosystem function over intermediate timeframes is unclear (Table 1).

A particular challenge of restoring aquatic biodiversity is in the spatial mismatch between agricultural degradation and restoration projects. Agricultural effects occur at watershed (= catchment) scales, while most replanting work is conducted at reach scales (Bond & Lake, 2003; Bernhardt *et al.*, 2005). Macroinvertebrate biodiversity or sensitivity measures often are correlated more strongly to watershed-scale variables than to local riparian condition (e.g. Death & Collier, 2010; Thomson *et al.*, 2012). If we are to continue aiming to improve in-stream biodiversity by replanting riparian vegetation, we require a greater understanding of the mechanistic relationships between biodiversity and the spatial and temporal factors that influence macroinvertebrate resilience (Parkyn & Smith, 2011; Feld, 2013).

We measured macroinvertebrate biodiversity across a chronosequence of replanted agricultural stream reaches. Riparian zones were replanted with native vegetation 8 to 22 years previously. We assessed whether reach-scale restoration improved stream ecological condition over several decades, when measured with the standard biomonitoring technique employed in the region of interest. We hypothesized that an improvement in macroinvertebrate metrics would not be evident based on the variable responses found in studies of similarly aged replanted riparian zones. We expect that watershed-scale factors have a greater influence, and aimed to identify which factors may impede the response of macroinvertebrates to riparian restoration in agricultural landscapes.

Methods

Study region and design

We sampled the macroinvertebrate assemblage at 20 stream reaches (15 streams, 1st-3rd Strahler order; Table S1 in Supporting Information), four times over a two year period. Streams were situated in an agricultural landscape within the Goulburn-Broken watershed in south-eastern Australia (Fig. 1). Ten of the agricultural reaches had been replanted with native vegetation between 8 and 22 years prior to sampling (‘replanted’ reaches). These replantings (*c.* 270-1200 m long corridors) had been replanted with mixed stands of *Eucalyptus* spp. and *Acacia* spp., which are endemic for the area. The replantings were fenced, but livestock had occasional access. Three sites were agricultural ‘untreated’ control sites (age = 0) where the riparian vegetation was typical of lowland agricultural streams in the area; i.e. a ground cover of pasture grasses with occasional large native trees (predominantly river red gum; *Eucalyptus camaldulensis*). Following the first sampling period (autumn 2011), another seven sites were added to better capture the full range of watershed-scale land-use variability, termed the ‘watershed land-use’ sites. Two of these sites had 85 and 97% watershed cover of trees, mostly native vegetation with some pine plantation beyond extensive buffers, and acted as ‘reference’ sites (Table S1, Fig. 1).

Reach physicochemical variables

At each site, a reach approximately ten times stream width was identified (minimum 50 m) and physical variables characterized following standard stream assessment guidelines for biomonitoring in Victoria (Environment Protection Authority Victoria, 2003) (Table 2). At replanted sites this reach was located at the downstream end of the replanting. Stream wetted width, channel width and riparian width (to maximum 30 m) were measured and riparian longitudinal extent was assessed (i.e. how continuous tree cover is parallel to the channel). The percentages of reach length characterized by riffle (fast flow), run (medium-slow flow) and pool (little to no flow) habitats were recorded. Substrate percentage cover at the reach scale was estimated in size categories: bedrock, boulder (> 256 mm), cobble (> 64 mm), pebble (> 16 mm), gravel (> 2 mm) sand (> 0.06 mm) and silt/clay (< 0.06 mm). The percentage cover of moss, filamentous algae and macrophytes (= aquatic plants; total of all growth forms) was assessed and categorized on an ordinal scale (low-high; 0-4). The percentage areal cover of coarse particulate organic matter (CPOM; > 1 mm) and large wood (LW; > 10 cm diameter) in each reach was characterized and expressed on an ordinal scale (low-high; 1-3). Canopy shading of the stream channel at midday was estimated and expressed on an ordinal scale (low-high; 1-5).

Point measurements of pH, electrical conductivity (EC) and turbidity were taken at each sampling visit over the study using a U-50 Water Quality Meter (Horiba; Kyoto, Japan). Nutrient measurements were made quarterly over the study period. We collected duplicate water samples for measurements of total phosphorus (P) and total nitrogen (N), and analyzed using the alkaline persulphate digestion method (APHA, 2005) with a Quick-Chem 8500 (Lachat Instruments; Loveland, USA). Water for ammonium (NH_4^+), filterable reactive phosphorus (FRP) and nitrate plus nitrite (NO_x) was filtered (0.45 µm PES; Advantec; Dublin, USA) onsite. Concentrations of FRP, NH_4^+ and NO_x were determined using flow-injection analysis with the standard phosphomolybdenum blue, phenate and Griess methods, respectively (APHA, 2005).

Stream height was measured with TruTrack water level/temperature loggers (Intech Instruments; Auckland, New Zealand). Stream height was converted to discharge with a rating curve built by measuring instantaneous stream discharge 7-13 times at each site across the range of observed stream heights. Instantaneous discharge was calculated by dividing the stream into ≥ 5 cells of equal width and measuring water velocity with a Marsh-McBirney Flo-Mate water velocity meter (Hach; Maryland, USA). The slope-area method (Dalrymple & Benson, 1967) was used to estimate discharge when maximum stream height exceeded the measured range of discharges. Depth loggers were deployed for 24 months at most sites, but for shorter periods (about 18 months) at some sites due to equipment damage. Mean daily flow (MDF) was calculated over the entire period for each site.

Watershed morphology and land-use variables

Watershed land-use and topography variables were obtained from a digital elevation model (DEM; 250-m resolution) derived stream network and associated data sets (Stein *et al.*, 2002). Upstream riparian land use was assessed using Google Earth (version 6.0). The riparian zone was classified as having ‘continuous’ canopy cover, ‘scattered’ trees or ‘cleared’. The longitudinal distance of each riparian category upstream of the site was expressed as a proportion of total upstream channel length. The upstream channel extent was determined from the DEM-derived stream network. We measured the minimum upstream distance to continuous ‘intact’ forested habitat (i.e. native tree cover extending well beyond the riparian boundary) for each site using ArcMap (version 10; ESRI, Redlands, CA, USA) as a measure of potential minimum dispersal distance for drifting invertebrates in headwater source habitats.

Biological sampling

The invertebrate assemblages were sampled in autumn and spring 2011 and autumn and spring in 2012 using the rapid bioassessment (RBA) methods (Environment Protection Authority Victoria, 2003). One replanting site (Camerons Well Creek) was inaccessible in spring 2012 and was only sampled three times. A sweep sample was taken at each visit, using a dip net (250 μm) to sample all available habitats (e.g. overhanging vegetation, wood, macrophytes and bare substrata) at a site in areas of slow flow or no current. Riffle habitats were avoided because they are associated with a distinctive set of invertebrates and riffles were not available at all sites. Each sweep sample integrated 10 m of habitat. Samples were emptied into trays and invertebrates were 'live sorted' on-site for at least 30 min, which was extended for 10 min if a new taxon was found in the last 5 min, to a maximum of 60 min. Invertebrates were preserved in 70% ethanol for processing.

Invertebrates were identified to family with some exceptions (Oligochaeta and Acarina to class, Chrironomidae to sub-family). Taxa not included in the calculation of RBA indices were discarded, including Nematoda, Collembola, terrestrial Coleopteran families and planktonic crustacean orders (Cladocera, Ostracoda and Copepoda). Three indices were calculated. Total taxa richness described the total number of taxa found on a sampling occasion at a site. Proportion of EPT taxa was calculated as the number of families belonging to the Ephemeroptera, Plecoptera and Tricoptera insect orders as a proportion of total taxa richness. The Stream Invertebrate Grade Number – Average Level (SIGNAL) average score was calculated based on Chessman (2003). Each family was assigned a score (between 1 and 10; using SIGNAL 2) based on its sensitivity to anthropogenic disturbance (10 being most sensitive) (Chessman, 2003). The average of these scores for all present taxa is the site's SIGNAL2 score, an indication of water and habitat quality (Chessman, 2003).

Biological traits

The effect of habitat characteristics on the invertebrate assemblage was investigated by assigning family-level sensitivity, dispersal and feeding traits to each taxon (Table 3). These traits were obtained from existing trait databases compiled for family groups in south-eastern Australia (Chessman, 2009; Schäfer *et al.*, 2011). Some traits were a combination of interval and ordinal data; here the interval data were assigned a category. For tolerance to salinity, the values were taken as the mean from the range reported by Schäfer *et al.* (2011) and given an ordinal values according to the scale: 0-17 mS cm^{-1} = low, 18-34 = low-medium, 35-43 = medium, > 43 = high. These intervals were based on species being considered 'at risk' when tolerance was low or low-medium or < 35 mS cm^{-1} (Schäfer *et al.*, 2011). Invertebrates play an important role in ecosystem functions such as decomposition, so that the effect of replanting on invertebrate functional groups was assessed independently of biodiversity metrics. Invertebrates families were assigned to functional feeding groups: shredders (detritivores feeding primarily on leaf litter), scrapers (primary consumers and detritivores that graze on surfaces), collectors (detritivores that filter or gather organic matter) and predators (feeding on other invertebrates) (Schäfer *et al.*, 2011). Data on dispersal ability and drought resistant life stages were not available for all taxa present. The mean of each trait for all taxa present in each sample was taken as a measure of assemblage sensitivity or capacity.

Statistical analysis

The effect of replanting age (replanting and control sites; n = 13) and season on water and habitat quality variables, invertebrate indices, and functional feeding groups was assessed with a linear mixed model that included random effects for site and season where appropriate:

$$R_{ij} \sim Normal\left(\mu_{ij}, \sigma_o^2\right);\ \mu_{ij} = \alpha + \beta_1 \times\ Age_{ij} + \beta_2 Season_i + \epsilon_j;$$

$$\sigma_o \sim Uniform(0.01, \text{maxsd } \times 2); \alpha, \beta_{1,2} \sim Normal(0, \sigma^2 = 10000);$$

$$\epsilon_j \sim Normal(0, \sigma_s^2);\ \sigma_s \sim Uniform(0.01, \text{maxsd } \times 2).$$

Here, R_{ij} is the measured response in season i in site j, which are distributed normally with means μ_{ij} and a common variance σ_o^2. The μ_{ij} are modelled as a linear function of Age_{ij} , which is the replanting age corresponding to the responses, α and β are the regression coefficients, and the ε_j are random effects for sites, which are drawn from a common distribution with mean 0 and variance σ^2. The upper bound of σ^2 was set as twice the maximum standard deviation (maxsd) of *R*.

Change in invertebrate indices over successive sampling periods (i.e. the effect of season) was important because the communities may have been affected by recent hydrologic disturbance (long term drought and recent flooding; Leblanc *et al.*, 2012). The effect of distance to continuous forest habitat on assemblage change over time was modelled as above with the response variable being the difference in SIGNAL, EPT or richness between the first and fourth sampling period (an 18 month interval).

We examined the effect of reach- and watershed-scale water quality, habitat and land-use variables (other than replanting age) on the whole invertebrate assemblage and traits using non-metric multidimensional scaling (NMDS) and Bayesian model averaging (BMA). A Bray-Curtis dissimilarity ordination was used to represent macroinvertebrate assemblages in R (R Development Core Team, 2011). This was based on mean abundance over the sampling periods ($n = 3$ or 4) at all sites (i.e. replanting, untreated and watershed land-use sites, $n = 20$). The NMDS ordination was fitted with vectors separately for environmental and invertebrate trait predictors to determine which variables best predict the assemblages. We excluded highly co-linear ($R > 0.8$) variables from vector fitting and BMA analyses (e.g. watershed area and stream width were removed because they were highly correlated with discharge), leaving the variables in Table 2. Only one variable was included in vector fitting when two were the inverse of another variable and hence correlated (e.g. small and large substrate cover; Table 2).

We took the environmental variables considered important to the whole assemblages (13 variables, log-transformed where necessary) and used BMA to identify which were the most important to explaining variation in taxa richness, proportion of EPT and SIGNAL2 score. BMA yields posterior model probabilities for each model structure (combination of predictors) that indicate the relative weight of evidence for each model. Summing the posterior model probabilities for all models that include a particular variable (maximum number of variables allowed in a candidate model at one time = 5) yields an integrated probability that the variable is a useful predictor (i.e. has a non-zero coefficient). The BMA included a random effect for stream because some of the additional 'watershed land-use' sites were at different locations on the same stream as replanting and untreated sites. The upper bound for σ_S priors was set as the maximum standard deviation of the response. We re-ran all BMA analyses to test that moderately correlated (i.e. $0.7 > R > 0.8$) variables did not affect results.

Analyses were conducted using WinBUGS (version 1.4; Lunn *et al.*, 2000). We used the odds ratio (OR) to indicate an important effect of model parameters. The OR is the ratio of posterior odds to prior odds, where OR > 3 indicates an important effect in BMA and OR > 10 indicates 'strong' evidence of an effect in linear mixed models (Jeffreys, 1961). A stricter criterion is required for the linear mixed models because the variables are forced into the model versus true model selection as in BMA. We used uninformative priors, so the prior odds were unity.

Results

Effect of reach-scale replanting on water quality and habitat

Mean water quality and habitat variables over the sampling periods were not related to riparian replanting age (n = 13 sites, Table 2). There was a positive relationship between replanting age and longitudinal extent of riparian vegetation (i.e. continuity of trees parallel to the channel) (Table 2), but this was not observed when control sites (replanting age = 0) were removed from the analysis.

Effect of reach-scale replanting on invertebrate indices

There was no effect of replanting age on total taxa richness (slope = 0.005 ± 0.013 SD, OR = 1.7, $R^2 < 0.01$; Fig. 2), the proportion of EPT taxa (slope = -0.002 ± 0.002 SD, OR = 6.8, $R^2 = 0.06$) or SIGNAL2 score (slope = 0.02 ± 0.10 SD, OR = 1.5, $R^2 = 0.01$). We found no effect of replanting age on the proportion of taxa that were shredders (slope = -0.00088 ± 0.00085 SD, OR = 1.2, $R^2 < 0.01$), scrapers (slope = -0.002 ± 0.002 SD, OR = 8.1, $R^2 = 0.05$), collectors (slope = 0.00059 ± 0.0015 SD, OR = 2.0, $R^2 < 0.01$) or predators (slope = 0.0006 ± 0.0016 SD, OR = 1.9, $R^2 = 0.29$).

Some of the invertebrate indices increased over succussive sampling periods. There was a positive effect of sampling period on proportion of EPT taxa (slope = 0.021 ± 0.0061 SD, OR = 1999, $R^2 = 0.15$; Fig. 2) and SIGNAL2 score (slope = 0.13 ± 0.03 SD, OR = 9999, $R^2 = 0.13$). However, there was no effect of sampling period on taxa richness (slope = 0.23 ± 0.53 SD, OR = 2.0, $R^2 < 0.01$). We did not find a relationship between the distance to upstream ‘intact’ habitats and total change proportion of EPT taxa (slope = 0.001 ± 0.003 SD, OR = 2.1, $R^2 = 0.02$) or in SIGNAL2 score (slope = 0.008 ± 0.026 SD, OR = 1.6, $R^2 < 0.01$) over time.

Effect of physicochemical variables on invertebrate assemblage

The potential driving factors of invertebrate assemblage health can be assessed using a plot of taxa richness versus SIGNAL2 and defining quadrants based on reference sites (Fig. 3; Chessman, 2003). This provides context to results for that particular study region and method (Chessman, 2003). Most agricultural stream sites were in quadrant 2 on the richness versus SIGNAL2 plot (Fig. 3). Some of the stream sites in watersheds with more pasture land (i.e. low watershed tree cover) were in quadrant 4, indicating more severe watershed-scale agricultural influences.

Analysis of patterns in the entire assemblage suggests watershed-scale processes were important to invertebrate distributions. The NMDS fitted with reach- and watershed-scale physicochemical vectors showed the invertebrate assemblage was influenced by a wide range of land-use, chemical and hydrologic variables (Fig. 4). There was no evidence that assemblages in replanted sites are more similar to those in reference sites than the untreated or watershed land-use sites.

Macroinvertebrate traits were correlated with reach and watershed characteristics, although many of these relationships were explained by a site's position in the stream network. Shredders were positively associated with sites that had high watershed and upstream riparian tree cover and greater large wood cover, while scrapers were more common in faster, shaded and higher altitude sites (Fig. 4). Invertebrates with high thermal and saline tolerance were associated with unshaded and lower-flow sites. Sites that were long distances from intact forest had assemblages characterized by taxa with greater dispersal ability (Fig. 4).

There were few environmental vectors (from those determined important in vector fitting) that had an important influence on macroinvertebrate indices, but percentage riffle and run cover was important to mean SIGNAL2 score (Table 4).

Discussion

Aquatic biomonitoring indices (taxa richness proportion of EPT taxa and SIGNAL2 score) and functional feeding group representation did not appear to be related to riparian replanting age (Fig. 2). Across all 20 reaches we did not find strong associations between invertebrate indices and reach-scale variables that may be controlled by reach-scale riparian vegetation (Table 4). Restoration had not returned water and habitat quality within 22 years, or macroinvertebrates are not responding to these changes. The response of the invertebrate assemblage to restoration may depend on watershed context. Most of the influential physicochemical variables (i.e. water chemistry, flow characteristics and geomorphology) were probably indirect effects of watershed-scale processes or to geographical location (such as elevation or watershed tree cover; Fig. 4).

It is possible that age of the plantings (maximum 22 years) is insufficient for restoration to provide suitable habitat and food resources for aquatic biodiversity. Studies in New Zealand have also failed to detect changes in invertebrate indices towards reference condition in similar aged replantings (up to 24 years; Parkyn *et al.*, 2003; Collins *et al.*, 2013). Those studies described a shift towards reference condition in some water-quality variables (e.g. turbidity), but no change in nutrients, conductivity or contamination. Others have reported shifts in macroinvertebrate indices towards reference condition within 5 to 10 years of riparian restoration (Jowett *et al.*, 2009; Orzetti *et al.*, 2010). These differences are probably due to the successful restoration of water quality and habitat characteristics. Restored sites in successful projects had lower temperatures, conductivity and levels of some nutrients associated with increasing replanting age (Orzetti *et al.*, 2010). Replanting age did not appear to affect water and habitat quality at our sites, although replanted reaches had greater coarse organic matter when compared to nearby unrestored sites (Chapter 6). The response of water quality to replanting may depend on regional land use, channel morphology or restoration characteristics (e.g. length and width of replanting), not just replanting age. This finding is similar to previous work that has shown that watershed-scale effects often are more important than are reach-scale variables in determining macroinvertebrate assemblages (Townsend *et al.*, 2003; Harding *et al.*, 2006; but see Sponseller *et al.*, 2001).

The macroinvertebrate assemblages in our streams may have been affected by high salinity or nutrient levels (Figs. 3, 4) (Chessman, 2003), but these levels were not extreme (Table S1; ANZECC, 2000) and individually did not influence invertebrate indices (Table 4). Invertebrate assemblages may not be under physiological stress because conductivity was below macroinvertebrate tolerance values for sensitive Australian taxa (e.g. Baetidae and Chironomidae; minimum EC 5.5 mS cm^{-1}) even at the most saline site (maximum EC 1.4 mS cm^{-1}) (Kefford *et al.*, 2003). Instead, difference from reference conditions may reflect the integrated signal of a range of agricultural effects and watershed spatial context, given the wide range of watershed variables that affect invertebrate assemblages (Fig. 4).

The typical scale of replanting in riparian restoration projects (i.e. < 1 km; Bernhardt *et al.*, 2005) is unlikely to influence the degradation of water quality and habitat that results from watershed-scale land-use change in either agricultural (Scarsbrook & Halliday, 1999; Bernhardt & Palmer, 2011) or urban (Imberger *et al.*, 2011) landscapes. Addressing these indirect effects and reinstating sensitive macroinvertebrates to stream communities would be most effective with riparian management at watershed scales (Parkyn *et al.*, 2003). Streams with a greater proportion of native tree cover in the whole watershed had invertebrate assemblages more like those of reference sites and greater mean SIGNAL2 scores (Figs. 3, 4), which suggests that broad-scale replanting may provide benefits for downstream aquatic biodiversity. High watershed tree cover (> 60%) is beneficial to maintaining stream invertebrate assemblages closer to reference condition (Death & Collier, 2010; Thomson *et al.*, 2012). It is unclear whether replanting to achieve this level of cover would improve biodiversity because revegetation work at watershed scales has not been attempted.

We observed a modest increase in macroinvertebrate sensitivity indices (SIGNAL2 and EPT proportion) across all sites (regardless of riparian vegetation) over the duration of the sampling period. This defies a longer term decline in indices (Thomson *et al.*, 2012), and may reflect the degradation and subsequent recovery of invertebrate assemblages from 13 years of drought in this region (1997 – early 2010; Leblanc *et al.*, 2012). It is unlikely we observed any legacy of flooding, which occurred in late 2010 (Leblanc *et al.*, 2012), because recovery generally is rapid (i.e. < 3 months) through high resilience or strong dispersal (Fritz & Dodds, 2004; Sponseller *et al.*, 2010). Recovery is quicker for better dispersers (Boulton, 2003). We did not observe a relationship between distance to intact source habitat, a potential measure of dispersal distance, and the change in proportion of EPT or SIGNAL2 score over time. This suggests these sensitive taxa had enough time to colonize following disturbance, are not limited by dispersal capacity, or had closer refugia.

Whole macroinvertebrate assemblages were further from reference condition at sites more distant from continuous forest (Fig. 4). This suggests, in contrast to sensitivity indices, that the proximity to potential source populations should be considered when planning restoration activities (Parkyn & Smith, 2011). However, separating upstream vegetation condition and the effects of dispersal distance from physical and chemical conditions related to site elevation or location of a site in the stream network is problematic (King *et al.*, 2005). In the absence of pre-clearance and pre-restoration data, information for reference sites in the study watershed are restricted to higher elevation areas where tree clearing has not occurred. These may not represent the nature of invertebrate assemblages in lower-altitude, low bed-slope, restored reaches. The importance of fast-flowing habitats to SIGNAL2 score (Table 4) suggests adding in-stream habitat to downstream reaches may increase the representation of sensitive species, but evidence from elsewhere is lacking (Table 1).

Managing expectations in riparian restoration

We found no effect of reach-scale riparian management on invertebrate indices, but there only were 10 restored sites with a maximum project age of 22 years, and we assumed a linear relationship between age and invertebrate indices. Whether replanted riparian corridors more consistently shift stream biodiversity towards reference condition after longer time periods is unresolved. There is strong evidence that isolated patches of riparian zones in better condition can be beneficial to macroinvertebrate richness (Scarsbrook & Halliday, 1999; Arnaiz *et al.*, 2011), and that maintaining riparian zones is effective at ameliorating wider watershed-scale degradation (e.g. Wilkerson *et al.*, 2009). However, assessing effects in restored sites over short to intermediate time periods remains problematic. It is of ongoing importance to restoration theory to determine the likely trajectory of restoration that can be expected (Hobbs, 2007; Lake *et al.*, 2007). In this case, it appears the response of invertebrates to stream restoration activities within the context of whole-of-watershed degradation is relatively slow.

Given the need to demonstrate benefits of restoration investments on relatively short time scales, there is a need to reconsider restoration goals or to focus on metrics other than macroinvertebrate community composition. An alternative is to focus on ecosystem-scale ecological processes (Gessner & Chauvet, 2002), which integrate all biotic components and not just the functional roles played by macroinvertebrates. Often used functional metrics (e.g. leaf breakdown and ecosystem metabolism) respond to restoration at reach and whole-of-watershed scale in agricultural landscapes (McTammany *et al.*, 2007; Giling *et al.*, 2013). These processes generally have been overlooked when monitoring stream restoration (Lake *et al.*, 2007), and may be more appropriate when restoration actions have a greater influence on aspects of ecosystems (e.g. microbial processes) other than on the traditionally measured responses (e.g. macroinvertebrates) (Sandin & Solimini, 2009). Restoration indicators should be explicitly matched to desired outcomes, and not selected because they are known to respond to restorative actions.

The spatial scale of mechanisms most important for restoring ecological condition (e.g. better water quality, water temperature regulation) requires further investigation (Hutchens *et al.*, 2009; Feld, 2013). It is clear that restoration of aquatic systems will be more effective if broader-scale agricultural effects are addressed (Greenwood *et al.*, 2012). We advocate that restoration activities to limit or reverse adverse agricultural effects on biodiversity need to occur on larger spatial scales, such as contiguous planting in upstream riparian zones. Restoration should initially focus on upstream riparian areas that have watersheds in better condition (Greenwood *et al.*, 2012). These reaches have reduced nonpoint effects of agriculture and are close to intact source areas for macroinvertebrate colonists, making restoration success more likely if returning assemblages closer to reference condition is the measure of success. Placing river networks into a landscape context and considering the effect of land-use at multiple spatial scales is essential for the restoration of aquatic health in degraded agricultural landscapes.

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Table 1. Review of recent studies of aquatic macroinvertebrate response (abundance, richness or sensitivity indices) to waterway and riparian restoration compared to unrestored sites. BACI = Before-after control-impact.

Restoration activity	Location; dominant land use	Period of sampling following action (design)	Macroinvertebrate response	Reference
Riparian zone management				
Willow removal and replanting	Australia (temperate); agricultural	8 years (space-for-time)	No response	Becker & Robson 2009
Replanting riparian zones	New Zealand; agricultural	2-20 years (space-for-time)	Variable	Collins *et al.* 2013
Replanting riparian zones	New Zealand; agricultural	2-24 years (space-for-time)	Variable; most sites had no response	Parkyn *et al.* 2003
Replanting buffers and reducing dairy effluent discharges	New Zealand; agricultural	max. 4 years (temporal replication)	No response	Wilcock *et al.* 2009
Restoration of riparian zones	Maryland, USA; forest and agriculture	0 - 25 years (space-for-time)	Positive	Orzetti *et al.* 2010
Fencing and tree coppicing	UK; rural	7 years (temporal replication with controls)	No treatment response	Clews & Ormerod 2010
Fencing and replanting	New Zealand; agricultural	10 years (BACI)	Positive	Jowett *et al.* 2009
Hydrogeomorphic manipulation				
Install natural channel features and connectivity	Germany; mixed	1-12 years (space-for-time)	No response	Haase *et al.* 2013
Increased substrate and flow heterogeneity	Finland; forestry	6 years (BACI); 15-17 years (space-for-time)	No response	Louhi *et al.* 2011
Channel reconfiguration	North Carolina, USA; forested & urban	1-7 years (space-for-time)	No response	Violin *et al.* 2011
Habitat creation				
Addition of large wood	Mississippi, USA; agricultural and forest	2 years (BACI)	No response	Testa *et al.* 2011
Modifying habitat heterogeneity (includes e.g. channel reconfiguration; adding boulders, riffles and logs)	US, Australia, Asia, Europe	< 2 to 16 years (mixed)	Variable, habitat heterogeneity generally not the leading factor	Palmer *et al.* 2010 (review)

(Table 1 continued)

Flow management				
Aqueduct decommission	Australia (temperate)	3 years (modified BACI)	No response	Brooks *et al.* 2011
Environmental flow regime	Australia (temperate); agriculture	Samples taken during release season (total duration of 5 years; BACI)	Variable	Lind *et al.* 2007
Environmental flow regime	Australia (temperate); forested	1-4 weeks (modified BACI)	Positive	Mackie *et al.* 2013
Mixed				
Stormwater retrofit; channel reconstruction; replanting	Maryland, USA; urban	4-11 years (space-for-time)	No response	Stranko *et al.* 2012

Table 2. Reach and watershed variables considered across study streams (*n* = 13 sites) of varying extent and age of riparian vegetation (and abbreviations). 'Linear model' shows the estimated slope (*β*) of relationship between replanting age (0-22 years) and the variable, where an odds ratio (OR) > 10 indicates an important effect (bold type).

Variable	(abbreviation)	Units	Type	Measurement scale	Linear model (response = replanting age)		Included in vector fitting
					β (mean ± SD)	OR	
pH	pH		water quality	reach	-0.02 ± 0.02	6.0	Y
Electrical conductivity	Cond	mS cm^{-1}	water quality	reach	0.00 ± 0.00	2.4	Y
Turbidity	Turb	NTU	water quality	reach	-0.20 ± 0.30	2.2	Y
Dissolved oxygen	DO	mg l^{-1}	water quality	reach	0.00 ± 0.10	2.2	Y
Mean daily water temperature	Temp	°C	water quality	reach	0.00 ± 0.10	2.0	Y
Filterable reactive phosphorous	FRP	mg l^{-1}	water quality	reach	0.00 ± 0.00	1.5	Y
Nitrate/nitrite	NO_x	mg l^{-1}	water quality	reach	0.00 ± 0.01	2.4	Y
Ammonia	NH_3	mg l^{-1}	water quality	reach	0.00 ± 0.00	1.9	Y
Days since spate	Days.spate	days	hydrology	reach			Y
Mean daily flow	MDF	Ml day^{-1}	hydrology	reach			Y
Riffle and run cover	RiffRun%	%	habitat	reach			Y
Pool cover	Pool%	%	habitat	reach			
Small substrate cover (< pebble)	SubSmall%	%	habitat	reach	-0.80 ± 0.90	5.1	Y
Large substrate cover (≥ pebble)	SubLarge	%	habitat	reach			
Algae cover	Algae	ordinal	habitat	reach	-0.02 ± 0.06	1.9	Y
Silt cover	Silt	ordinal	habitat	reach	0.01 ± 0.04	1.7	Y
Macrophyte cover	Macro	ordinal	habitat	reach	0.00 ± 0.04	1.1	Y
CPOM cover	CPOM	ordinal	habitat	reach	0.00 ± 0.02	1.0	Y
Large wood cover	LW	ordinal	habitat	reach	-0.01 ± 0.02	3.3	Y
Midday shading	Shading	ordinal	habitat	reach	0.00 ± 0.03	1.0	Y
Mean riparian width	RipWidth	m	physical	reach	0.30 ± 0.40	4.3	Y
Longitudinal extent riparian vegetation	RipLongExt	m	physical	reach	**0.20 ± 0.10**	**332.3**	Y
Reach elevation	Elevation	m	physical	reach			Y
Watershed total tree cover	WSTrees	%	physical	watershed			Y
Watershed mean slope	WSSlope	%	physical	watershed			Y
Upstream riparian zone with continuous canopy cover	USRipCont	%	physical	watershed			Y
Distance upstream to continuous forest	DistContFor	km	physical	watershed			Y

Table 3. Description of family-level sensitivity, dispersal and feeding traits assigned to each taxon sampled across the study sites.

Taxa or community trait	(abbreviation)	Scale	Source
Physiological sensitivity to organic toxicants	SalTol	ordinal scale: low (1); low-medium (2); medium (3); high (4)	Schäfer *et al.* 2011
Physiological sensitivity to organic toxicants	S_{org}	ratio scale (-2.09 - 1.0)	Schäfer *et al.* 2011
Dispersal capacity	Disp*	ordinal scale: low (1); some member with strong drifting or flying (2); strong drifting or flying (3); high (4)	Schäfer *et al.* 2011
Maximum body size	MaxBody	ratio scale (1.5 - 200 mm)	Schäfer *et al.* 2011
Availability of drought-resistant life stages	DrghtRes*	ordinal scale: yes (1) or no (0)	Schäfer *et al.* 2011
Preference for fast flowing areas	Rheophily	ratio scale (0 - 4.1)	Chessman 2009
Preference for higher water temperatures	Thermophily	ratio scale (0.48- 1.44)	Chessman 2009
Proportion of total taxa richness that are scraper taxa	prop scraper taxa	proportion (0.0 - 1.0)	Schäfer *et al.* 2011
Proportion of total taxa richness that are shredder taxa	prop shredder taxa	proportion (0.0 - 1.0)	Schäfer *et al.* 2011
Proportion of total taxa richness that are collector taxa	prop collector taxa	proportion (0.0 - 1.0)	Schäfer *et al.* 2011
Proportion of total taxa richness that are predatory taxa	prop pred taxa	proportion (0.0 - 1.0)	Schäfer *et al.* 2011
Proportion of total abundance that are Chironomidae individuals	prop chironomidae ind	proportion (0.0 - 1.0)	

* denotes data not available for all families

Table 4. Bayesian model averaging (BMA) results showing the estimated slope (*β*) and the probability of inclusion in the best model for reach- and watershed-scale physicochemical variables (abbreviations are defined in Table 2). Important effects (i.e. OR > 3) are shown in bold type.

Response	Variable	Slope (β) (mean ± SD)			Inclusion probability	OR
Taxa Richness	RiffRun%	0.09	±	0.28	0.20	0.84
	Macro	0.07	±	0.25	0.18	0.77
	USRipCont	-0.06	±	0.26	0.18	0.76
	SubSmall%	0.06	±	0.23	0.17	0.72
	Shading	-0.05	±	0.26	0.17	0.70
	Elevation	0.06	±	0.26	0.16	0.69
	LW	-0.03	±	0.18	0.15	0.62
	MDF	-0.03	±	0.18	0.15	0.62
	DistContFor	-0.03	±	0.18	0.14	0.61
	Cond	0.00	±	0.16	0.14	0.57
	WSTrees	0.00	±	0.16	0.13	0.56
	NH$_3$	0.01	±	0.15	0.13	0.56
	DO	0.00	±	0.12	0.12	0.52
Proportion of EPT taxa	NH$_3$	-0.018	±	0.017	0.64	2.69
	LW	0.007	±	0.012	0.33	1.40
	RiffRun%	0.006	±	0.011	0.32	1.34
	Cond	-0.007	±	0.012	0.31	1.32
	SubSmall%	-0.003	±	0.008	0.18	0.77
	Macro	-0.001	±	0.005	0.12	0.50
	WSTrees	0.001	±	0.005	0.12	0.50
	DO	0.001	±	0.005	0.12	0.49
	Shading	0.001	±	0.004	0.10	0.44
	Elevation	0.000	±	0.004	0.10	0.41
	DistContFor	0.000	±	0.004	0.09	0.40
	USRipCont	0.001	±	0.004	0.09	0.40
	MDF	0.000	±	0.004	0.08	0.36
SIGNAL2	**RiffRun%**	**0.18**	**±**	**0.09**	**0.87**	**3.68**
	WSTrees	0.13	±	0.11	0.67	2.81
	Elevation	0.07	±	0.10	0.38	1.58
	Shading	0.04	±	0.08	0.32	1.34
	LW	0.04	±	0.07	0.30	1.28
	NH$_3$	-0.02	±	0.06	0.17	0.72
	USRipCont	0.02	±	0.06	0.15	0.65
	SubSmall%	-0.02	±	0.05	0.13	0.57
	Macro	-0.01	±	0.04	0.12	0.52
	Cond	-0.01	±	0.03	0.09	0.39
	DistContFor	-0.01	±	0.03	0.08	0.34
	MDF	0.00	±	0.02	0.06	0.26
	DO	0.00	±	0.01	0.03	0.11

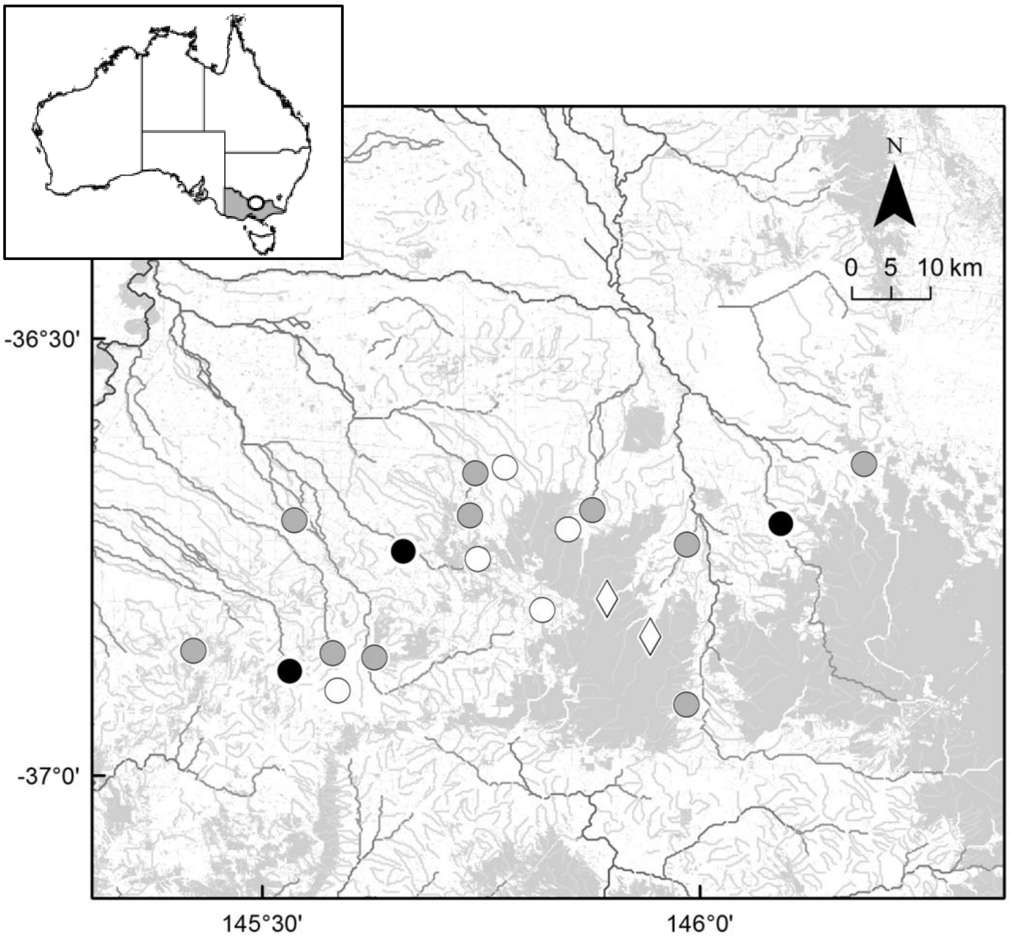

Figure 1. Map of the Goulburn-Broken watershed, south-east Australia (insert), showing 'replanted' study sites (light grey circles) and 'untreated' study sites (black circles). Additional 'watershed land-use' sites are shown in white, and 'reference' sites represented by diamonds. Shaded areas indicate remnant forest, while unshaded areas are dominated by pasture grasses with sparse *Eucalyptus* spp. cover.

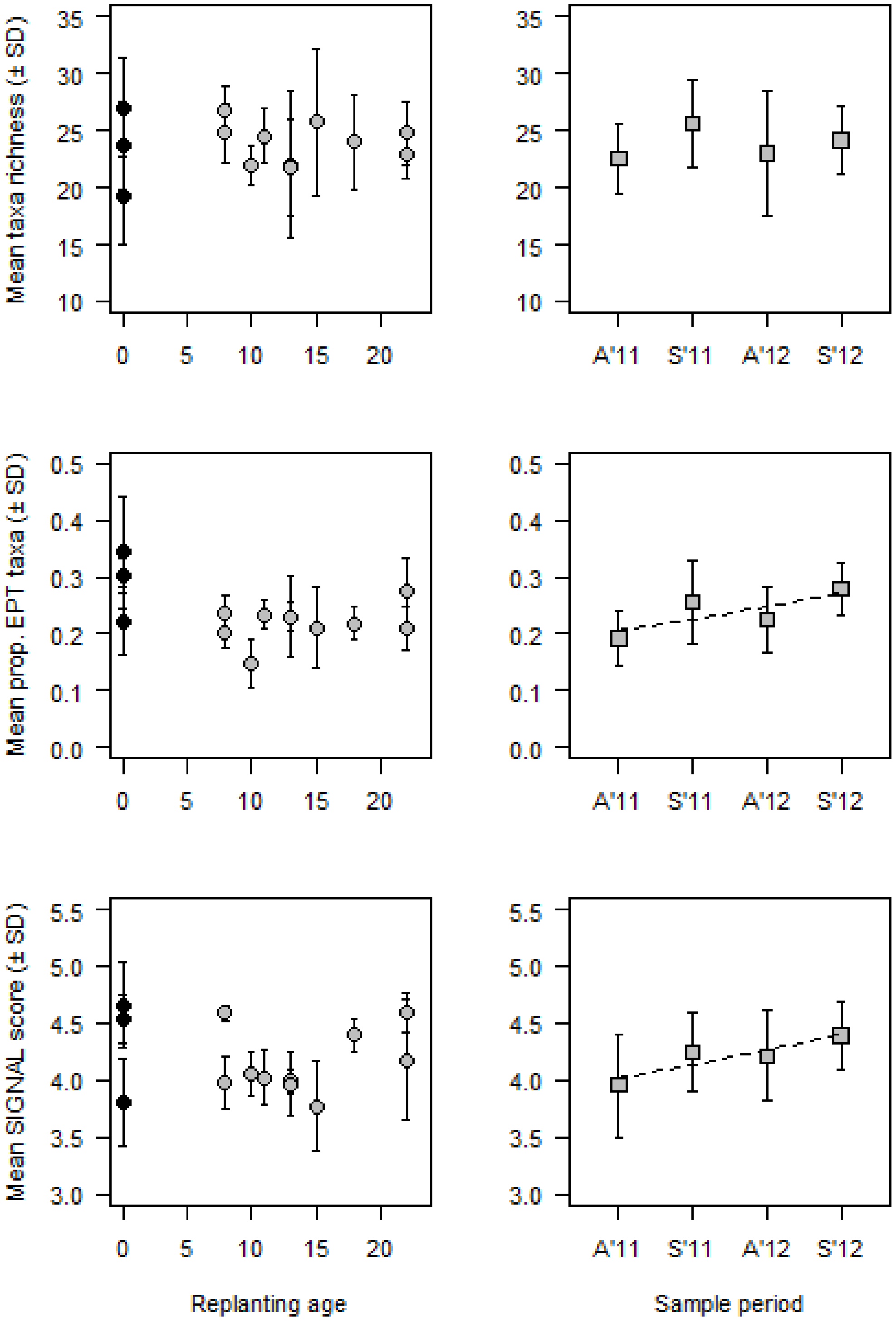

Figure 2. Effect of replanting age (*n* = 13 sites; left) and sampling period (*n* = four periods, A = autumn, S = spring, '11 = 2011 and '12 = 2012; right) on taxa richness, proportion of EPT taxa and mean SIGNAL2 score. Shades on replanting age plots (left) indicate 'replanted' sites (grey) and 'untreated' sites (black). Dashed lines indicate a significant effect in linear mixed models.

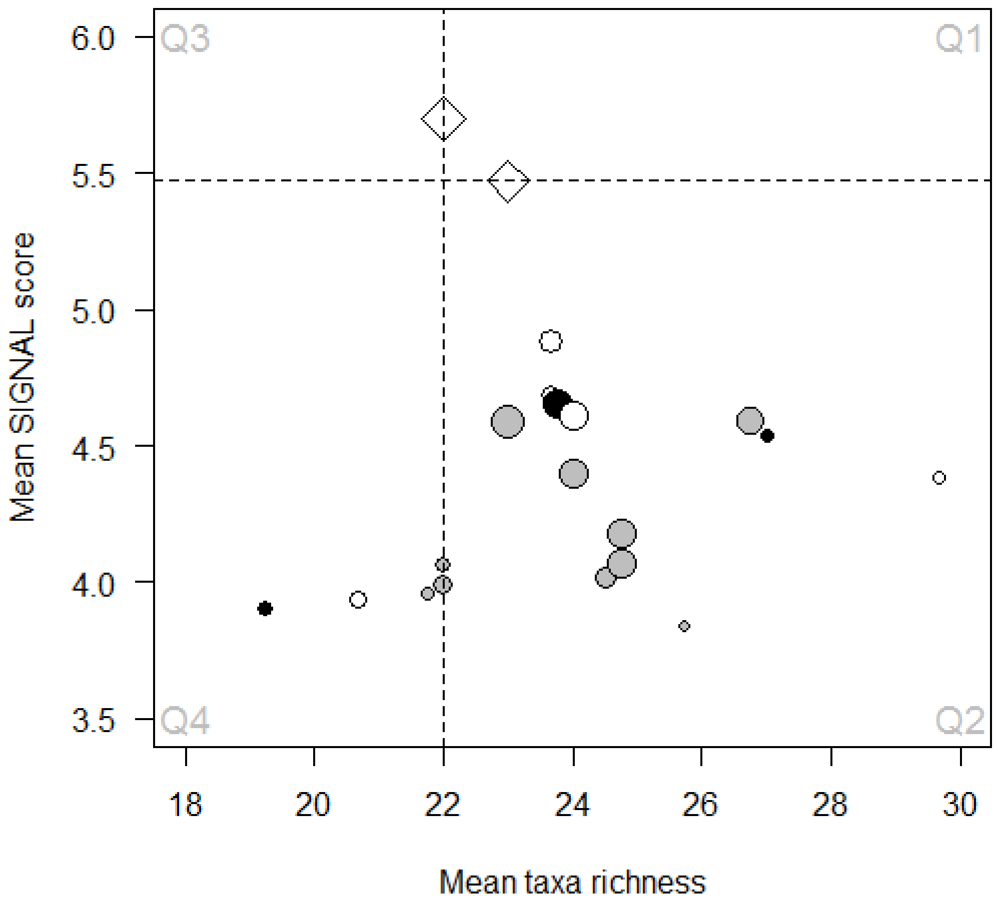

Figure 3. Plot showing mean taxa richness against mean SIGNAL2 score across four sampling periods. Quadrants (Q1-4) are defined by the minimum of the two reference sites (white diamonds) on each axis. Shades indicate ‘replanted’ sites (grey), agricultural ‘untreated’ sites (black) and ‘watershed land-use’ sites (white). Point size is relative to whole-of-watershed areal tree cover.

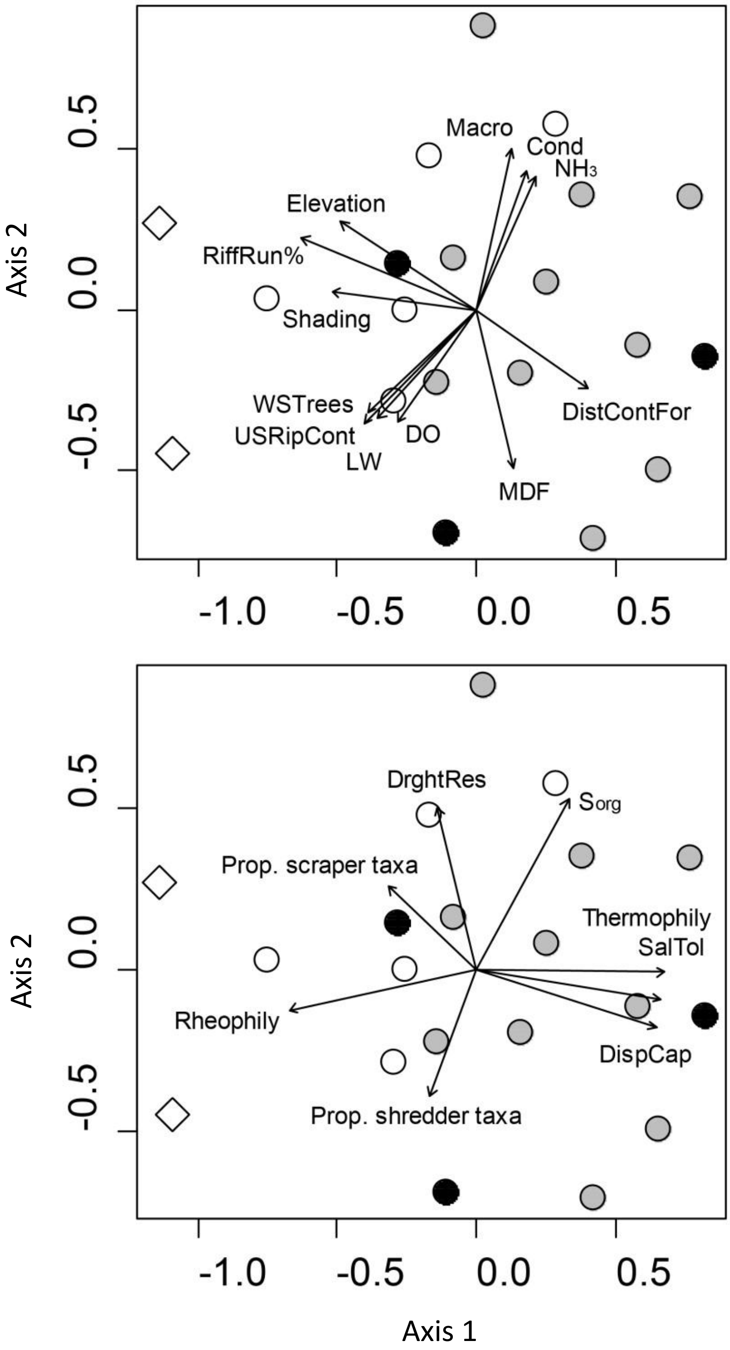

Figure 4. Multidimensional scaling plots showing assemblage dissimilarity (based on mean relative abundance of invertebrates over three or four sampling periods) at 20 sites. Shades indicate ‘replanted’ sites (grey), agricultural ‘untreated’ sites (black) and additional ‘watershed land-use’ sites (white, with reference sites shown as diamonds). Environmental vectors show important ($p < 0.05$) effects of (a) reach- and watershed-scale physicochemical variables; and (b) invertebrate assemblage feeding and resilience traits to the invertebrate assemblage (for abbreviations of physicochemical variables and traits, see Tables 2 & 3). Vector length indicates strength of relationship and direction shows the assemblages they were associated with.

Supporting Information

Table S1. Summary statistics of reach and watershed characteristics at each site. Abbreviations are defined in Table 2.

Variable (*n* samples)	Units	Camerons Well	Castle (lower)	Castle (upper)	Creightons	Fatihful (lower)	Faithful (upper)	Harrys
Lat.	° S	36.86	36.86	36.90	36.88	36.74	36.75	36.70
Long.	° E	145.42	145.58	145.59	145.53	145.66	145.75	145.74
pH (3-4)		6.4 (0.2)	7.2 (0.1)	7.4 (0.2)	7.3 (0.2)	7 (0.1)	6.8 (0.3)	7.5 (0.1)
Cond (3-4)	mS cm^{-1}	0.38 (0.11)	0.27 (0.02)	0.19 (0)	0.14 (0.01)	0.19 (0.02)	0.06 (0)	0.26 (0.04)
Turb (3-4)	NTU	14 (6)	13 (3)	34 (30)	22 (5)	27 (9)	43 (19)	11 (5)
DO (3-4)	mg l^{-1}	6.7 (5.4)	8.1 (1.2)	9 (1)	10.1 (2.2)	9.6 (5.1)	9.1 (0.6)	9.5 (1.1)
Temp (529-808)	°C	13.8 (4.2)	13.9 (5.3)	12.7 (4.1)	14.6 (4.6)	14.1 (4.9)	12.1 (3.9)	13.2 (4.8)
FRP (6-22)	mg l^{-1}	0.01 (0.006)	0.009 (0.007)	0.019 (0.006)	0.021 (0.009)	0.032 (0.056)	0.011 (0.001)	0.043 (0.017)
NO_x (6-22)	mg l^{-1}	0.284 (0.284)	0.041 (0.057)	0.138 (0.124)	0.387 (0.217)	0.112 (0.119)	0.316 (0.087)	0.053 (0.076)
NH_3 (6-22)	mg l^{-1}	0.09 (0.074)	0.024 (0.028)	0.031 (0.008)	0.036 (0.022)	0.026 (0.011)	0.029 (0.009)	0.023 (0.015)
Days.spate (3-4)	days	72 (41)	41 (11)	36 (4)	42 (12)	48 (23)	37 (3)	27 (15)
MDF (529-808)	Ml day^{-1}	0 (0)	12 (46)	7 (11)	26 (44)	27 (20)	4 (4)	8 (40)
RiffRun%	%	10	5	80	80	5	90	30
Pool%	%	90	95	20	20	95	10	70
SubSmall%	%	80	98	95	100	100	100	100
SubLarge	%	20	2	5	0	0	0	0
Algae	ordinal	5	1	1	1	0	0	0
Silt	ordinal	0	2	3	1	2	1	1
Macro	ordinal	2	2	1	2	0	1	2
CPOM	ordinal	1	2	1	1	1	1	2
LW	ordinal	1	1	1	1	1	2	1
Shading	ordinal	3	2	2	1	2	4	3
RipWidth	m	7	12	15	0	6.5	30	30
RipLongExt	m	5	4	4	0	2.5	1	5
Elevation	m	383	245	305	250	214	450	303
WSTrees	%	20	10	15	15	22	32	36
WSSlope	%	-	4	5	4	5	3	8
USRipCont	%	66	34	65	18	78	89	29
DistContFor	km	1	10	5	5	3	0	4

(Table S1 continued)

Variable (*n* samples)	Units	Hollands	Honeysuckle	Moonee (lower)	Moonee (upper)	Ryans	Seven (lower)	Seven (upper)
Lat.	° S	36.71	36.65	36.74	36.84	36.64	36.71	36.81
Long.	° E	146.09	145.74	145.99	145.94	146.19	145.54	145.82
pH (3-4)		7.7 (1.1)	7.6 (0.2)	6.6 (0.2)	6.5 (0.2)	6.9 (0.2)	7.1 (0.2)	6.3 (0.3)
Cond (3-4)	mS cm^{-1}	0.09 (0.01)	0.2 (0.02)	0.07 (0.01)	0.05 (0)	0.05 (0.01)	0.12 (0.01)	0.05 (0)
Turb (3-4)	NTU	7 (2)	17 (8)	24 (16)	11 (5)	6 (2)	31 (12)	26 (3)
DO (3-4)	mg l^{-1}	9.8 (1.1)	9.2 (1.6)	8.5 (1.8)	9.8 (0.4)	8.9 (0.3)	8.3 (1)	8.8 (0.8)
Temp (529-808)	°C	14.6 (5.6)	14.5 (5.3)	13.7 (4.6)	11.7 (3.2)	17 (5.4)	14.4 (5.6)	10.8 (4.3)
FRP (6-22)	mg l^{-1}	0.008 (0.003)	0.025 (0.008)	0.021 (0.006)	0.027 (0.018)	0.007 (0.003)	0.011 (0.004)	0.012 (0.002)
NO_x (6-22)	mg l^{-1}	0.089 (0.105)	0.091 (0.055)	0.203 (0.02)	0.037 (0.015)	0.057 (0.049)	0.297 (0.196)	0.151 (0.049)
NH_3 (6-22)	mg l^{-1}	0.013 (0.006)	0.016 (0.005)	0.022 (0.007)	0.013 (0.007)	0.015 (0.009)	0.025 (0.006)	0.017 (0.004)
Days.spate (3-4)	days	36 (6)	36 (6)	49 (23)	69 (17)	68 (12)	38 (10)	37 (3)
MDF (529-808)	Ml day^{-1}	157 (179)	22 (53)	50 (48)	8 (4)	99 (63)	241 (280)	18 (29)
RiffRun%	%	20	10	0	90	80	30	50
Pool%	%	80	90	100	10	20	70	50
SubSmall%	%	70	95	100	60	29	70	55
SubLarge	%	30	5	0	40	71	30	45
Algae	ordinal	1	0	0	0	1	0	3
Silt	ordinal	1	1	3	1	0	1	2
Macro	ordinal	0	2	0	1	1	1	1
CPOM	ordinal	1	2	1	2	1	1	2
LW	ordinal	2	2	1	2	1	1	2
Shading	ordinal	2	2	2	5	1	1	4
RipWidth	m	3	8.5	9	30	6.5	25	25
RipLongExt	m	1	5	5	5	5	4.5	4
Elevation	m	222	193	205	925	229	166	532
WSTrees	%	73	30	70	97	86	15	48
WSSlope	%	8	6	7	10	7	4	4
USRipCont	%	87	45	49	100	80	64	78
DistContFor	km	6	10	4	0	10	24	6

(Table S1 continued)

Variable (n samples)	Units	trib. of Broken	Two Mile	Warrenbayne (lower)	Warrenbayne (upper)	White Gum Gully	Wombat
Lat.	° S	36.92	36.65	36.70	36.72	36.80	36.87
Long.	° E	145.98	145.78	145.88	145.85	145.89	145.63
pH (3-4)		7 (0.2)	7.6 (0.1)	7.2 (0.3)	7 (0.3)	6.7 (0.5)	6.9 (0.3)
Cond (3-4)	mS cm^{-1}	0.19 (0.04)	1.15 (0.27)	0.26 (0.32)	0.09 (0)	0.05 (0)	0.13 (0.02)
Turb (3-4)	NTU	22 (20)	24 (23)	17 (4)	14 (1)	16 (3)	10 (2)
DO (3-4)	mg l^{-1}	7.2 (2.5)	5.9 (1.4)	9.9 (1.3)	11.2 (2.2)	10.3 (0.7)	9.4 (1.5)
Temp (529-808)	°C	13.6 (4.9)	13.7 (4.2)	13.2 (4.9)	12.2 (4.5)	11.6 (3.2)	13.7 (4.8)
FRP (6-22)	mg l^{-1}	0.013 (0.006)	0.016 (0.007)	0.022 (0.014)	0.014 (0.003)	0.018 (0.003)	0.017 (0.005)
NO_x (6-22)	mg l^{-1}	0.017 (0.019)	0.064 (0.113)	0.087 (0.05)	0.096 (0.071)	0.037 (0.02)	0.118 (0.099)
NH_3 (6-22)	mg l^{-1}	0.024 (0.016)	0.028 (0.033)	0.022 (0.018)	0.015 (0.005)	0.009 (0.004)	0.02 (0.011)
Days.spate (3-4)	days	32 (9)	37 (3)	28 (15)	37 (3)	69 (16)	52 (32)
MDF (529-808)	Ml day^{-1}	2 (6)	3 (7)	30 (35)	18 (17)	8 (5)	22 (45)
RiffRun%	%	25	20	5	40	80	40
Pool%	%	75	80	95	60	20	60
SubSmall%	%	100	90	98	85	60	87
SubLarge	%	0	15	2	15	40	13
Algae	ordinal	2	2	0	3	0	0
Silt	ordinal	1	3	2	1	2	1
Macro	ordinal	3	1	1	1	0	2
CPOM	ordinal	1	2	1	2	2	1
LW	ordinal	1	1	1	1	2	1
Shading	ordinal	2	2	2	2	4	2
RipWidth	m	7	3	12	15	22.5	7.5
RipLongExt	m	4	1	4.5	2	5	2.5
Elevation	m	315	197	230	270	359	570
WSTrees	%	72	26	67	70	85	58
WSSlope	%	8	5	7	6	7	6
USRipCont	%	55	36	72	88	100	74
DistContFor	km	1	7	4	1	0	1

Declaration for Thesis Chapter 3

Declaration by candidate

In the case of Chapter 3, the nature and extent of my contribution to the work was the following:

Nature of contribution	Extent of contribution (%)
I performed all the fieldwork, all the laboratory work, 75% of the statistical analyses and was the primary author of the manuscript.	60%

The following co-authors contributed to the work. If co-authors are students at Monash University, the extent of their contribution in percentage terms must be stated:

Name	Nature of contribution	Extent of contribution (%) for student co-authors only
Ralph Mac Nally	Input of ideas and contributed to analysis and writing of the manuscript	
Michael R. Grace	Input of ideas and methods, and contributed to writing the manuscript.	
Ross M. Thompson	Input of ideas and contributed to writing the manuscript.	

The undersigned hereby certify that the above declaration correctly reflects the nature and extent of the candidate's and co-authors' contributions to this work*.

Candidate's Signature	[redacted]	**Date** 11.4.14
Main Supervisor's Signature	[redacted]	**Date** 11.4.14

*Note: Where the responsible author is not the candidate's main supervisor, the main supervisor should consult with the responsible author to agree on the respective contributions of the authors.

Chapter 3

The influence of native replanting on stream ecosystem metabolism in a degraded landscape: can a little vegetation go a long way?

Please note this manuscript is a reformatted version of the published paper:

Giling D.P., Grace M.R., Mac Nally R. & Thompson R.M. (2013) Influence of native replanting on stream ecosystem metabolism in a degraded landscape: can a little vegetation go a long way? Freshwater Biology, ***58****, 2601-2613.*

Abstract

1. The effectiveness of revegetation is usually gauged by responses in biodiversity, which differs among isolated replanted patches. The ecological value of revegetation may be detected more effectively by monitoring ecosystem processes. In-stream metabolism has been much modified by the degradation of riparian vegetation in agricultural landscapes around the world. We sought to determine if the spatial scale typical of most riparian replanting projects (i.e. < 1 km long) influences stream metabolism.
2. Metabolism is a functional measure that incorporates gross primary production (GPP), ecosystem respiration (ER) and the difference between them (net ecosystem productivity, NEP). We hypothesized that replanted reaches would have lower GPP (due to greater canopy shading) and greater ER (governed by larger terrestrial-energy inputs) compared to pasture reaches.
3. We measured metabolism in paired reaches within four agricultural streams. Two streams had an untreated pasture reach contrasted with a reach replanted with native woody vegetation > 17 years ago. The other two streams had similar riparian vegetation condition adjacent to both reaches to act as reference sites.

4. Mean daily GPP (0.27 to 4.9 g O_2 m^{-2} day^{-1}) and ER (1.1 to 22 g O_2 m^{-2} day^{-1}) were within the range of values recorded previously in agricultural streams elsewhere in the world. Replanted reaches had rates of NEP lower than upstream untreated reaches at treatment sites, but NEP was similar between reaches at reference sites.
5. The effects of replanting on stream ecosystem processes are detectable even when the spatial scale of restoration is relatively small in a whole-of-catchment context. Land managers can protect and restore vegetation at feasible spatial scales and benefit ecosystem processes. Ecosystem metabolism should be included in the range of responses that need to be monitored to provide a complete picture of the effectiveness of stream restoration.

Introduction

Human activity has pervasive effects on ecosystems, one of the most extensive being the conversion or removal of native vegetation for agriculture. Cropland and pasture now constitute the largest land-use category on the planet, and food production will have to increase to support a projected 50% increase in population by 2050 (Asner *et al.*, 2004; U.S. Census Bureau, 2004). Land-use change has modified biogeochemical cycling and water availability, and is a leading contributor to high extinction rates through habitat loss, fragmentation and degradation (Stoate *et al.*, 2009). These land-use effects also affect adjacent stream ecosystems (Kominoski *et al.*, 2013); the loss of riparian vegetation reduces the supply of terrestrial organic matter, and alters in-stream biodiversity and food web structure (Thompson & Townsend, 2004).

Revegetation is intended to reverse effects of land-use change and to provide favourable ecological outcomes. However, many revegetation projects have ill-defined goals, and are rarely monitored (Follstad Shah *et al.*, 2007). When outcomes are assessed, success is often gauged by surveying biodiversity responses (Follstad Shah *et al.*, 2007). However biodiversity responses may be highly variable or difficult to detect on short (years to decades) time scales (e.g. Parkyn *et al.*, 2003; Munro *et al.*, 2007). An alternative approach to demonstrate ecological outcomes is to measure ecosystem processes.

There has been a shift from activities aiming to restore biodiversity towards the restoration of entire ecosystems (Poiani *et al.*, 2000). The latter includes ecosystem processes, their natural variability, and the biodiversity that they support (Poiani *et al.*, 2000). There have been several calls for a greater emphasis on the effects of restoration on ecosystem function (Bunn & Davies, 2000; Gessner & Chauvet, 2002), and even isolated patches of revegetated land in degraded landscapes may provide ‘ecosystem services’ (e.g. flood mitigation, nutrient cycling). For example, bioturbation by invertebrates increased soil-water infiltration and restored local hydrological processes in a replanted open forest of Australia within 11-20 years (Colloff *et* *al.*, 2010). Monitoring the response of ecosystem processes to revegetation should be an important aspect of assessing replanting design and spatial arrangement.

Riparian vegetation is important for stream ecosystems, providing terrestrial organic matter that subsidises stream metabolism (Roberts *et al.*, 2007). Stream metabolism incorporates gross primary production (GPP; the production of organic carbon) and ecosystem respiration (ER; the consumption of organic carbon). The balance between these two processes can be expressed as a ratio GPP/ER (henceforth referred to as P/R) or as the difference between them, GPP – ER (net ecosystem production, NEP). This balance indicates whether a system is net heterotrophic (NEP < 0, more organic carbon is respired than is fixed), or net autotrophic (NEP > 0, surplus carbon is fixed and stored or exported) (Lovett *et al.*, 2006). Natural forested stream ecosystems have NEP << 0 (e.g. Hagen *et al.*, 2010), although secondary consumers may still obtain their energy needs from carbon produced in-stream (e.g. McCutchan & Lewis, 2002).

The effect of agriculture on the rates of ER and GPP in streams has been assessed across forested-agricultural land-use gradients (e.g. Gücker *et al.*, 2009; Young & Collier, 2009) but rarely used to assess the success of reach-scale restoration (but see Riley & Dodds, 2012). The primary determinants of ER and GPP are light, organic matter, nutrients and hydrology (Bernot *et al.*, 2010). Of these, shading (reduced light supply) and the provision of terrestrial organic matter are expected to be modified by local replanting of riparian vegetation and changed towards values more characteristic of undisturbed systems; i.e. lower NEP. Terrestrial organic matter is an important energy source and substrate supporting in-stream ER, while GPP can be light-limited (Young & Huryn, 1999; Mulholland *et al.*, 2001).

We aimed to determine if the typically small scale (i.e. 100s of m long) of most riparian replanting projects affects stream ecosystem function. Therefore, we measured whole-ecosystem metabolism in untreated and replanted reaches of four streams in degraded agricultural catchments of south-eastern Australia. We hypothesized that restored reaches would have a greater rate of ER, due to increased organic matter supply, and a decreased rate of GPP, due to greater shading. We assessed whether whole-stream metabolism could be a feasible indicator to monitor restoration at reach-scales over the mid-term (17–20 years), which is the age of many of the older replantings in this region and elsewhere.

Methods

Study design

In-stream metabolism was measured in four low-gradient, second and third Strahler order (Table 1) agricultural streams in the Goulburn-Broken catchment of south-eastern Australia. The dominant land use adjacent to the four study streams was dryland grazing by sheep and cattle. Stream substrata were dominated by gravel and sand. Comparisons were made between contiguous paired reaches on each stream (reach lengths 210–510 m). The riparian condition of each reach was classified as replanted (‘R’) or untreated and largely denuded of native vegetation (‘U’). Replanted reaches had been revegetated through planting with of *Eucalyptus* spp., *Acacia* spp. and *Melaleuca* spp. native to the area. The replantings were fenced, but livestock had occasional access. Untreated reaches were not fenced and had riparian vegetation typical of agricultural areas in the region; a ground cover of pasture grasses with occasional large remnant native trees (primarily *E. camaldulensis*). The density of large remnant trees (in either U or R reaches) was similar between each pair of reaches (data not shown). Sites were not located close to any large areas of unmodified remnant forest.

In two treatment streams (Warrenbayne Creek and Moonee Creek), the downstream reach was replanted 17 and 21 years ago respectively, while the upstream reach was untreated (Fig. 1). These were termed the ‘UR’ (untreated-replanted) streams. The other two streams were selected to control for longitudinal metabolic variation, although there were no *priori* reasons to expect a difference in the rates of ER or GPP between reaches based on riparian condition. One stream (Honeysuckle Creek) had replanted trees (12 years old) in the riparian zone of both reaches, and was termed the ‘RR’ (replanted-replanted) stream. The riparian zone of the fourth stream (Creightons Creek) had untreated riparian vegetation in both the upstream and downstream reach, termed ‘UU’. There were no ‘reference’ lowland forested streams available in the study region for direct comparison. Our response variables were the mean difference in daily metabolic rate between reaches. The questions we posed in the Introduction can be stated formally as:

ER and GPP $\mathrm{UU}_{\mathrm{downstream}} - \mathrm{UU}_{\mathrm{upstream}} = 0$ (1)

ER and GPP $\mathrm{RR}_{\mathrm{downstream}} - \mathrm{RR}_{\mathrm{upstream}} = 0$ (2)

ER $\mathrm{UR}_{\mathrm{downstream}} - \mathrm{UR}_{\mathrm{upstream}} > 0$ (3)

GPP $\mathrm{UR}_{\mathrm{downstream}} - \mathrm{UR}_{\mathrm{upstream}} < 0$ (4)

That is, metabolic rates between paired reaches at UU and RR will not differ, while replanted reaches at UR sites are hypothesized to have higher ER and lower GPP.

Reach physicochemical characteristics

Measurements of physical, chemical and biotic variables required to inform metabolic calculations or interpret results were made for each reach. Stream height was measured continuously using a TruTrack water level logger (Intech Instruments; Auckland, New Zealand). Stream width and mean water depth were measured at 10 haphazardly selected locations along each reach. Five evenly spaced hemispherical photos were taken from the water surface mid-stream. Percentage canopy closure was estimated using Gap Light Analyzer software (version 2, Simon Fraser University, Burnaby, Canada). Spot measurements of pH, electrical conductivity (EC) and turbidity were taken using a U-50 Water Quality Meter (Horiba; Kyoto, Japan). Duplicate water samples were collected for measurements of total phosphorus (P) and total nitrogen (N), and analysed using the alkaline persulphate digestion method (APHA, 2005) using a Quick-Chem 8500 (Lachat Instruments; Loveland, USA). Water was filtered onsite (0.45 µm PES; Advantec; Dublin, USA) for ammonium (NH_4^+), filterable reactive phosphorus (FRP) and nitrate plus nitrite (NO_x). Concentrations of FRP, NH_4^+ and NO_x were determined using flow injection analysis with the standard phosphomolybdenum blue, phenate and Griess methods, respectively (APHA, 2005).

Water samples for total and dissolved organic carbon were taken from mid-stream. Dissolved samples were filtered onsite through GF-75 glass fibre filters (Advantec; Dublin, USA) into pre-combusted, amber-glass jars and acidified (to $pH < 2$) with concentrated (32%) HCl. These samples were refrigerated immediately for return to the laboratory, where they were split into two sub-samples. For one sub-sample DOC concentration was analysed using a Shimadzu TOC-V CPH/CPN Total Organic Carbon Analyzer (Shimadzu; Tokyo, Japan) following APHA (2005) standard methods.

The source (terrestrial or aquatic) of the dissolved organic matter (DOM) was determined by fluorescence spectrophotometry performed on the second DOC subsample. Fluorescence spectrophotometry characterizes the complex mixture of DOM using the fluorescence index (FI; McKnight *et al.*, 2001). FI was calculated as the ratio of emission intensity at 470 nm to emission intensity at 520 nm, at excitation wavelength of 370 nm on a Cary Eclipse fluorescence spectrophotometer (Varian; Melbourne, Australia) (McKnight *et al.*, 2001). A FI of 1.3-1.5 indicates DOM originating from a terrestrial vegetation source, whilst FI of 1.7-1.9 indicates DOM of in-stream microbial origin (McKnight *et al.*, 2001).

Benthic coarse particulate organic matter (CPOM; > 1 mm) was sampled by taking 15 cores from a range of water depths in each reach at haphazardly selected locations. A 25-cm diameter core was inserted into the sediment, and all CPOM to a depth of 10 cm was removed and frozen. Samples were sieved, dried to a constant weight at 60°C for 5-7 days, then ashed (4 hours, 550°C) to calculate ash-free dry mass (AFDM). Standing stock of benthic fine particulate organic matter (FPOM; 0.45 μm to 1 mm) was estimated by taking 10 haphazardly selected cores in each reach by inserting a 7-cm diameter core and removing all sediment and organic material. This material was sieved over nested 1 mm and 250 μm sieves. A well-mixed subsample of the material passing through the 250 µm sieve was filtered through a pre-ashed and weighed filter paper (Whatman GF/C). The sieved (250-1000 µm) and residue (0.45-250 µm) fractions were oven dried, ashed and the AFDM summed to calculate total benthic FPOM AFDM.

Water-column and benthic chlorophyll concentrations were measured using the two-wavelength method (Nusch, 1980) with a UV-1700 UV-visible spectrophotometer (Shimadzu; Sydney, Australia). Triplicate water column chlorophyll samples were collected by filtering 500-1000 ml of stream water onto glass fibre filters (Whatman GF/C) and then freezing. Benthic chlorophyll samples were collected by taking 15 haphazardly selected 3 cm diameter cores per reach. In soft sediments, a scraping of the top 3 mm of sediment was collected. On harder surfaces, a portion of the substratum was isolated and scrubbed before material was removed with a syringe and filtered. Chlorophyll-a was extracted from filter paper or sediment scraping with acetone (cold extraction at 4°C for 12 hours). Macrophyte (aquatic plant) areal cover was visually assessed at each width transect to the nearest 5%. Dominant macrophytes included *Juncus* spp., *Percicaria* spp. and *Phragmites australis*.

Metabolism measurements

Metabolism estimates were made over a single diel period at three streams in February 2011 (late summer) as a pilot study, and subsequently over a longer deployment (6-16 days per site) in March/April 2012 (early autumn). We measured stream ecosystem metabolism using a whole-ecosystem, two-station approach (Odum, 1956), following a single station analysis that enabled calculation of the reaeration coefficient (Atkinson *et al.*, 2008). Dissolved oxygen (DO) and water temperature were logged at 5 min intervals using D-Opto dissolved oxygen sensors (Zebra-Tech; Nelson, New Zealand). Probes were positioned mid water column at three locations (up, mid and down; Fig. 1) on each stream to integrate dissolved oxygen change over the upstream (up-mid probe) and downstream (mid-down probe) reaches. Equipment limitations meant the reaches were contiguous (i.e. the middle oxygen probe was the bottom of the upstream reach and at the top of the downstream reach). Measurements were made at each stream consecutively. Before and after placement, the loggers were put in an O_2 saturated solution and then together in the stream for 1 hr to account for probe drift and, if required, linear corrections were applied prior to metabolism calculations.

Photosynthetic active radiation (PAR) was measured at 5-min intervals using photosynthetic irradiance loggers (Odyssey; Christchurch, New Zealand). Light intensity was measured in an unshaded location and at the water-surface in one location of the upstream and downstream reaches. Barometric pressure was logged with a Silva Atmospheric Data Centre Pro (Silva; Sollentuna, Sweden).

Solute injection

The average time taken for water to travel between the DO probes is used to estimate two-station areal rates of metabolism. Reach travel time was calculated using a solute slug of NaCl. Salt was dissolved and injected into a well-mixed area upstream of the probe location. Electrical conductivity (EC) was logged continuously at the reach boundaries using a HQd Portable Meter probe (Hach; Loveland, CO, USA) and a 90-FLT probe (TPS; Springwood, Australia) until EC returned to background values. The mean reach travel time was the time difference between half the salt (measured as EC) passing the upstream and downstream probes.

Calculation of metabolic rates

Diel O_2 and PAR data were used to estimate single-station rates of GPP, ER and the reaeration coefficient (*K*) for each DO probe on each day. We used Bayesian estimation to calculate the metabolic parameters in the day-time regression model (Kosinski, 1984):

$$\frac{\Delta[O_2]_i}{\Delta t} = AI_i^p - R\left(\theta^{(temp_i - temp_{ave})}\right) + K\left(1.0241^{(temp_i - temp_{ave})}\right)D_i \ ,$$

where *A* = photosynthetic constant, *I* = surface PAR (µEs m^{-2} s^{-1}), *p* = photo-saturation exponent, *R* = respiration rate (mg $l^{-1}d^{-1}$), *K* = reaeration coefficient (d^{-1}), *D* = O_2 saturation deficit or surfeit (mg l^{-1}) and θ = temperature-dependence factor. Data sets resulting in non-convergence of model parameters or poor model fits ($R^2 < 0.8$) between measured and modelled DO for the single-station method were discarded from two-station calculations.

Two-station metabolic estimates were made at each reach for days with successful single-station DO model fits for all three probes (between 5–8 days per stream). Two-station calculations were made using the diel oxygen mass balance approach (following Marzolf *et al.*, 1994) in an Excel spreadsheet (initially provided by C. Fellows, Griffith University, Australia). Upstream and downstream diel O_2 data, the reaeration coefficient (determined by day-time regression model described above), barometric pressure, temperature, reach travel time and discharge were used to calculate the metabolic flux for each 5-min interval. Daily ER was calculated as the sum of metabolic flux for all night-time intervals, plus a temperature-corrected estimate for daytime (PAR > 0.5 μmol m^{-2} s^{-1}) intervals. Daily GPP was calculated as the sum of daytime metabolic flux less the estimated daytime ER. These rates were divided by the stream-bed area to convert to areal units.

Statistical analysis

We analysed the effect of replanting treatment (i.e. UR, RR or UU) by using the difference between reaches (downstream – upstream) for each stream as the response variable to account for among-stream variation. A positive difference indicates that the variable was higher in the downstream reach. The effect of replanting treatment on predicted determinants of stream metabolism (i.e. benthic CPOM, benthic FPOM and canopy cover) between reaches was assessed with a two-object comparison. Multiple samples for each object provided means and variances for the comparison using WinBUGS (version 1.4; Lunn *et al.*, 2000). Benthic CPOM mass and FPOM mass were log-transformed to improve distributional properties. Light at the stream surface was not included as a determinant because of low replication (one light intensity logger per reach).

We analysed the effect of riparian treatment on metabolic variables for each stream and day (2012 data) using a linear mixed model:

$$response_i \sim Normal(\mu_i, \sigma_o^2); \qquad (likelihood)$$

$$\mu_{ij} = \alpha + \beta_1 T_i + \beta_2 PAR_{ij} + \beta_3 \overline{Temp}_{ij} + \epsilon_i;$$

$$\sigma_o \sim Uniform(0.001, 0.2); \alpha, \beta_i \sim Normal(0, \sigma^2 = 4); \qquad (priors)$$

$$\epsilon_i \sim Normal(0, \sigma_s^2);\ \sigma_s \sim Uniform(0.001, 0.2).$$

Here, response is the daily difference in the metabolic variable between the downstream and upstream reach and treatment is the replanting category (UR, RR or UU). The model included covariance terms for total daily PAR and mean daily water temperature to account for differences due to non-concurrent measurements at different sites. A random effect for stream was included to account for the repeated daily sampling. We estimated treatment means and tested our hypotheses at the overall mean water temperature and mean total daily PAR. We excluded P/R from statistical analyses because ratios can be misleading and have poor distributional properties for statistical analysis (i.e. positively skewed and no upper boundary). We used the odds ratio to indicate an important effect of model parameters. The OR is the ratio of posterior odds to prior odds where 3 < OR < 10 indicates 'substantial' evidence and OR > 10 indicates 'strong' evidence of an effect (Jeffreys, 1961). An OR of infinity (inf.) indicates that there is virtually no doubt that the parameter differs from zero given the uninformative prior (equally likely to be positive or negative). We used uninformative priors, so the prior odds were unity.

Results

Reach physicochemical characteristics

Riparian vegetation affected the determinants of in-stream metabolism (i.e. light and organic matter availability). The difference in canopy closure between reaches was > 0 (i.e. the canopy was more closed over the stream channel in replanted reaches) at UR sites (Fig. 2a; mean difference 25% ± 3.8 SD, OR = inf.). The difference in canopy closure between up- and downstream reaches was not different from zero at the UU site (mean difference 4.8% ± 3.7 SD, OR = 9.4). The difference in canopy closure between reaches was less than zero (i.e. more open in downstream reach) at the RR site (mean difference 6.9% ± 5.0 SD, OR = 11), but was still much less than that between the reaches in the UR sites.

The difference in benthic FPOM mass (AFDM g m^{-2}) between reaches was > 0 (i.e. greater in replanted reaches) at UR streams (Fig. 2b; mean difference 992 ± 402 SD, OR = 19). The difference in benthic FPOM between reaches was not different to zero at the UU (mean difference 93.6 ± 269 SD, OR = 2.0) or RR site (mean difference 74.3 ± 515 SD, OR = 1.2).

The difference in benthic CPOM mass (AFDM g m^{-2}) between reaches was not greater than zero at UR streams (Fig. 2c; mean difference 292 ± 88.2 SD, OR = 4.8). There was also no difference between reaches at the UU site (mean difference 1.50 ± 29.7 SD, OR = 1.2) or RR site (mean difference 47.2 ± 125 SD, OR = 1.4).

There was little variation in stream nutrient and organic carbon concentration between reaches in each stream (Table 1). Water temperature (measured by DO probes at 5 min intervals) also exhibited little variation among reaches (Table 1). Fluorescence index (FI) results were also similar across all reaches and were consistent with DOM being from terrestrial sources (Table 1).

Stream metabolic rates

There was large among-stream variation in mean daily two-station metabolism estimates (Table 2). Among all eight study reaches, daily GPP ranged from 0.06 to 5.7 g O_2 m^{-2} day^{-1} and ER ranged from 0.38 to 27 g O_2 m^{-2} day^{-1}. Given that ER was generally greater than GPP, NEP was mostly negative, and ranged from –25 to 0.21 g O_2 m^{-2} day^{-1}. Stream reaches were mostly heterotrophic, with only one reach on one day (from 65 reach-days) being autotrophic (P/R = 1.32; Warrenbayne Creek untreated reach).

Effect of riparian replanting on stream ecosystem metabolism

The mean daily difference in metabolic rates (ER and GPP) between reaches was not different to zero at the UU site (Table 3; Fig. 3), in agreement with hypothesis 1. Similarly, there was no statistical difference in ER or GPP between reaches at the RR site (Table 3), in agreement with hypothesis 2.

A mean 150% increase in ER rate was seen in replanted reaches compared to untreated reaches at UR sites (Table 2). Although not a strong effect in the overall model, the difference in mean daily ER between reaches was greater than zero at UR sites (Table 3; Fig. 3a), in agreement with hypothesis 3. The difference in GPP between reaches at UR sites was negative (i.e. smaller in replanted reaches), but the magnitude of this effect differed between the two sites. The mean daily difference in GPP between UR reaches was not different to zero (Table 3; Fig. 3b), refuting hypothesis 4.

Riparian replanting affected NEP (Fig. 3c). There was no difference in mean daily NEP between reaches at UU or RR streams. In contrast, replanted reaches at UR streams had lower NEP than untreated reaches (Table 3; Fig. 3c). There were effects of the mean temperate covariate on the difference in ER and NEP between reaches (Table 3).

Discussion

Ecosystem respiration (ER) and gross primary production (GPP) in our four agricultural streams in south-eastern Australia were within the range of previous observations (Mulholland *et al.*, 2001; Bernot *et al.*, 2010). We found that replanted reaches had reduced net ecosystem productivity (NEP) compared to untreated pasture reaches.

Effect of riparian replanting on ecosystem respiration

Replanted reaches had greater canopy cover and fine organic matter standing stock. This organic matter resource probably provided an energy source and substratum for microbes and invertebrates. Associations between organic matter supply and increased microbial respiration have been reported in New Zealand forest streams (Young & Huryn, 1999). Large ER rates (up to 32 g O_2 m^{-2} day^{-1}) were observed in a Mediterranean forested stream when leaf-fall led to large amounts of benthic organic matter, but rates were reduced the following year when high flows prevented accumulation (Acuña *et al.*, 2004). Accrual of coarse organic matter in replanted reaches of the current study was variable (Fig. 2c). Increased supply of leaf inputs combined with lower average water velocity probably contributed to the accumulation at one replanted reach (Table 1).

The variation in our data is not surprising given that the effects of land use on in-stream ER in agricultural catchments compared to forested or low-intensity land-use catchments are still unclear (Young & Huryn, 1999; Young & Collier, 2009; Bernot *et al.*, 2010). Ecosystem respiration (ER) was similar in streams draining Appalachian agricultural catchments compared to catchments with 50 years of vegetation recovery (McTammany *et al.*, 2007). Few studies have compared metabolic rate between paired reaches with contrasting riparian condition on one stream. Vegetation removal to restore the natural open-canopy state of USA prairie streams reduced ER in some seasons by a magnitude comparable with our results (Riley & Dodds, 2012). Ecosystem respiration was *c.* 1.6 times greater in meadow reaches compared to forested reaches of some USA streams (Bott *et al.*, 2006), in contrast to the results from the current study. This may be due to deposition of fine organic matter and increased hyporheic respiration in meadow reaches in the USA streams (Bott *et al.*, 2006), whereas benthic FPOM in our streams was greater in replanted reaches.

Microbial respiration of dissolved organic carbon (DOC) contributes much to whole-stream respiration (Wiegner *et al.*, 2005). Although DOC is generally recalcitrant, the addition of labile DOC increased microbial respiration rates and secondary production in a forested headwater (Wilcox *et al.*, 2005). It is unlikely the replanted reaches of the current study are sufficiently extensive to influence DOC quantity detectably. Similar DOC concentrations were observed in the up- and downstream reaches of the UR sites, along with fluorescence index (FI) values indicating dissolved organic matter was from terrestrial vegetation. Labile DOM, leaching from fresh leaf inputs, is readily consumed by the microbial community (Baldwin, 1999). Pulsed inputs of fresh terrestrial organic matter (e.g. from storms), or upstream algal carbon, could increase DOC respiration in replanted reaches. An important distinction is whether energy from microbial respiration in the replanted reaches is transferred into secondary production, or exported quickly from the reach. This will influence food web dynamics and affect the effectiveness of replanting on other in-stream functions.

The effect of riparian replanting on gross primary production

We detected only marginal evidence of lower rates of GPP at replanted reaches compared to untreated reaches at UR streams, despite an increase in canopy cover. Canopy cover, affecting the amount of light reaching the water, often explains a large proportion of variation in GPP (Bunn *et al.*, 1999). Canopy cover of the replanted reaches was *c.* 25% more than upstream untreated reaches, and approached the 73% threshold value of canopy cover to yield a P/R value indicating a healthy stream in Australia (Bunn *et al.*, 1999). The mean daily proportion of full sunlight reaching the stream surface in all untreated and replanted reaches was 84% and 39%, respectively. This light available below the canopy is much greater than that in many small forested or plantation streams on other continents, which typically have more closed canopies and/or vegetation with denser foliage (e.g. 1.3% of above-canopy light; Davies-Colley & Quinn, 1998). Benthic-chlorophyll concentrations were similar between reaches at UR sites, suggesting that canopy cover did not affect standing crops of algae or that autotrophs (e.g. diatoms) adapted to lower light conditions are selected for in replanted reaches (Lange *et al.*, 2010).

Our results differ from studies from the USA and South America, which reported greater GPP in agricultural than in forested streams (Gücker *et al.*, 2009; Bernot *et al.*, 2010). This suggests that other land-use effects, unaffected by small-scale replanting, were important for GPP (see also Riley & Dodds, 2012). A stronger effect of replanting on GPP may not have been detected because considerable channel incision, and hence bank shading, may have limited GPP in all reaches (Young & Huryn, 1999). Erosion has resulted in the deposition of sand and gravel that is unstable and constantly being transported, resulting in low attachment and growth of autotrophs (Atkinson *et al.*, 2008). Total nitrogen and phosphorus exerts an important control on GPP (e.g. Frankforter *et al.*, 2010). Nutrient concentrations in our study reaches were not extreme, but generally were indicative of disturbed ecosystems (ANZECC, 2000). Any further increases in stream-nutrient concentration may affect the interaction of GPP and ER between untreated and replanted reaches. This is highly relevant for management because clearance of land for agriculture is associated with increased nutrient concentrations in stream water (Buck *et al.*, 2004). Reducing catchment-scale effects (e.g. erosion and nutrient additions) requires intervention at larger spatial scales than typical replanting projects, which are mostly < 1 km in length (Bernhardt *et al.*, 2005).

The effect of riparian replanting on NEP and P/R

Replanted reaches were more heterotrophic (lower NEP) than untreated pasture reaches, as a result of the shift in both ER and GPP. All study reaches were heterotrophic (mean daily NEP < 0; P/R < 1). Systems with P/R < 1 are not necessarily completely reliant on energy sources from outside the stream because P/R does not account for the source of carbon supporting secondary-consumer respiration (Rosenfeld & Mackay, 1987). The transition to a reliance on energy produced in-stream has been estimated to occur when 0.5 < P/R < 1.0 (Meyer, 1989). All reaches (apart from one untreated reach) had mean daily P/R < 0.5, indicating a reliance on terrestrial or upstream energy sources. This is consistent with results from moderately and some heavily modified pasture streams in the USA (Hagen *et al.*, 2010). A shift towards reliance on in-stream sources (e.g. Warrenbayne Creek upstream reach; mean P/R = 0.75) in heavily degraded agricultural streams may depend on other factors, such as livestock disturbance or fertiliser inputs (Hagen *et al.*, 2010).

The P/R ratio, interpreted appropriately, can indicate the relative importance of organic carbon sources in streams. However, we recommend caution in using P/R to compare paired reaches on different streams because this ratio is sensitive to the magnitude of ER and GPP rates. A small-magnitude difference in opposite directions can have a large effect on the ratio when GPP and ER rates are small, but little effect if GPP and ER are large. The difference in NEP between reaches is a more robust measure.

A set of criteria to classify stream ecosystem health based on metabolic rates was developed by Young *et al.* (2008). The metabolic rates in most reaches of our study would indicate streams unaffected or mildly affected by land use (Young *et al.*, 2008). Only the downstream reaches of Honeysuckle Creek (low ER rates) and Moonee Creek (high ER rates) could be regarded as being ‘impaired’ (Young *et al.*, 2008). Nevertheless, we saw shifts indicating that replanted reaches had lower NEP rates more typical of un-affected forested streams. Metabolic rates are affected by many proximate factors (e.g. light, nutrients, temperature, organic matter), meaning responses to interacting stressors can be unclear (e.g. Young & Collier, 2009). This emphasizes the importance of using paired reaches to monitor and to assess restoration success.

The number of replicate streams places an important limitation on the generality of our results. Longitudinal variation in the direction of response was observed at UU and RR streams, although the effect was small. The response of ER and GPP to vegetation in both UR streams was consistent, suggesting replanting was responsible. Unidirectional flow means the reaches were not independent, but the vast majority of particulate organic matter transport occurs during storm-flow conditions (Wiegner *et al.*, 2009). Warming can influence NEP (Shurin *et al.*, 2012), but there was no difference in temperature between upstream untreated and downstream replanted reaches at our sites, potentially due to bank shading. Metabolic calculations were made with the change in DO between probes, and the response variable in our statistical analyses was the difference between reaches, which was independent among treatments.

What do these results mean for riparian vegetation management?

We observed a shift in stream ecosystem processes in response to isolated, reach-scale (i.e. 100s m) patches of riparian vegetation replanting in degraded agricultural catchments. Revegetation can restore the effects of a natural riparian strip, such as shading and organic matter subsidies, even though it is unlikely to influence non-point effects such as nutrient inflows and altered hydrology (McTammany *et al.*, 2007). These landscape scale land-use effects must be addressed because they may influence metabolic drivers such as sedimentation and DOC availability. Restoring in-stream retentive features (e.g. substratum heterogeneity, debris dams and large wood) in agricultural streams will also be important to ensure that the ecologically beneficial in-stream effects of replanting are realized. Measuring stream-ecosystem metabolism integrates organic matter processes but is less labour intensive than many other biodiversity or functional (e.g. leaf breakdown) measures. We advocate that metabolism should be widely implemented as a functional measure of riparian and stream restoration success (Young *et al.*, 2008; Tank *et al.*, 2010). Recent advances in dissolved-oxygen sensors and data processing make long-term installations for monitoring stream health affordable and feasible (Staehr *et al.*, 2010).

The influence of stream size on successfully restoring in-stream processes by riparian management is an important issue. Small to moderate sized streams, such as those in the current study (2nd and 3rd order), are expected to respond to riparian restoration more rapidly than large streams and rivers (Craig *et al.*, 2008; Greenwood *et al.*, 2012). We detected changes in metabolic process rates within two decades in streams up to 7.5 m wide. This timeframe agrees with simulations of canopy closure following replanting in small channels (Davies-Colley *et al.*, 2009). Smaller or shallower channels have a greater capacity to retain coarse and fine organic matter resources (Quinn *et al.*, 2007; Ock & Takemon, 2010). Therefore, we expect metabolic response would take longer and be less pronounced in larger channels. At present, there is little evidence for determining the length of riparian corridor relative to channel width that is needed to influence stream function. The most effective location of restoration for in-stream metabolic process, smaller channels, is also predicted to promote in-stream biodiversity (Death & Collier, 2010). However, we contend that revegetating relatively small and isolated patches may influence stream function, in contrast to recommendations for restoration of biodiversity outcomes (Death & Collier, 2010).

The time lag for response of stream ecosystem processes to riparian replanting was shorter than lags observed for recovery of in-stream biodiversity (e.g. Parkyn *et al.*, 2003; Munro *et al.*, 2007). This is important because land required for optimal spatial arrangement of revegetation for biodiversity (i.e. productive, close to existing patches; Thomson *et al.*, 2009) may not always be available for purchase, meaning that restoration may proceed in a 'piece-meal' manner. Our results show that, when opportunities arise, land managers should work at a landholder scale to restore riparian vegetation patches and to produce responses in ecosystem processes over short to medium terms (decades). Older replantings can be important for biodiversity (Munro *et al.*, 2007), suggesting that revegetated patches may hold biodiversity benefits in the future and could form important habitat networks. Monitoring responses in both biodiversity and ecosystem processes to revegetation together over longer times and in a range of landscape contexts will better inform management decisions and provide insights into the expected timing of responses to ecosystem restoration.

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Table 1. Physical, chemical and biotic site characteristics (mean ± SD) for the eight study reaches measured during the 2012 data collection period.

Site		Creightons Creek		Honeysuckle Creek		Warrenbayne Creek		Moonee Creek	
Reach		up	down	up	down	up	down	up	down
Treatment		Untreated	Untreated	Replanted	Replanted	Untreated	Replanted	Untreated	Replanted
Parameter	unit								
Travel Time	min	34	31.7	110	129	23	52.2	25.8	65.1
k	day^{-1}	11 (3.0)	7.1 (0.8)	10 (1.6)	5.2 (1.1)	16 (1.3)	6.8 (0.7)	12 (3.4)	9.0 (4.4)
Length	m	430	380	510	540	210	250	350	350
Width (n = 10)	m	2.1 (2.1)	2.4 (2.4)	5.8 (2.3)	5.6 (1.9)	4.8 (1.2)	5.3 (1.6)	5.3 (0.8)	7.5 (1.3)
Mean depth (n = 10)	m	0.20 (0.09)	0.19 (0.06)	0.37 (0.16)	0.37 (0.26)	0.41 (0.16)	0.39 (0.14)	0.48 (0.08)	0.65 (0.14)
Discharge	l s^{-1}	77 (2.7)		59 (7.0)		145 (13)		1058 (66)	
Velocity	m s^{-1}	0.21	0.2	0.08	0.07	0.15	0.08	0.23	0.09
Bed slope (n = 3)	cm m^{-1}	-0.221 (0.001)	-0.215 (0.000)	-0.468 (0.006)	-0.298 (0.005)	-0.110 (0.001)	-0.032 (0.001)	-0.358 (0.006)	-0.010 (0.000)
Replanting age	years	-	-	12	12	-	17	-	21
Canopy cover (n = 5)	% closed	21.1 (1.7)	16.3 (0.9)	69.1 (4.7)	62.2 (2.2)	39.3 (4.2)	71.4 (3)	47.6 (1.6)	66.1 (3.8)
Surface PAR	mols m^{-2} day^{-1}	34.6 (2.5)	33.5 (2.7)	12.8 (3.3)	21.4 (4.6)	32.4 (11.5)	10.6 (3.7)	15.9 (0.4)	13.5 (1.1)
Average temperature	°C	13.6 (1.9)	13.8 (1.9)	15.9 (0.7)	16 (0.7)	15.3 (2.7)	15.3 (2.7)	16.8 (0.5)	16.8 (0.5)
Turbidity	NTU	5.6	6.7	19.9	31.5	15.1	13.1	17.2	10.5
pH		7	6.54	7.36	7.28	7.08	7.02	6.12	5.89
Electrical conductivity	mS cm^{-1}	0.144	0.146	0.164	0.164	0.09	0.09	0.067	0.069
NH_4^+ (n = 2)	mg l^{-1}	0.022	0.019	0.011	0.014	0.01	0.014	0.016	0.017
NO_x (n = 2)	mg l^{-1}	0.305	0.3	0.077	0.091	0.069	0.069	0.205	0.22
FRP (n = 2)	mg l^{-1}	0.017	0.019	0.024	0.024	0.015	0.017	0.019	0.019
Total N (n = 2)	mg l^{-1}	0.71	0.69	0.77	0.78	0.308	0.308	0.565	0.575
Total P (n = 2)	mg l^{-1}	0.065	0.065	0.095	0.095	0.048	0.05	0.09	0.09
Dissolved Organic C (n = 2)	mg l^{-1}	5.7	8.9	9.4	9.7	3.7	3.8	4.6	5
Fluorescence index (n = 2)		1.46	1.47	1.44	1.44	1.41	1.45	1.42	1.41
Total Organic C (n = 2)	mg l^{-1}	6.6	10	9.8	9.8	4	4.3	5	5.2
Fine Particulate OM (n = 10)	g m^{-2}	160 (94)	260 (230)	670 (490)	740 (670)	680 (340)	1100 (1000)	250 (160)	1800 (1300)
Coarse Particulate OM (n=15)	g m^{-2}	11 (23)	9.0 (20)	250 (290)	300 (470)	49 (86)	90 (120)	66 (150)	610 (1200)
Macrophyte cover (n = 10)	%	13 (6.7)	9.5 (5.1)	14 (18.5)	19 (16)	4.8 (4.3)	3.9 (3.9)	17 (13)	2.4 (2.1)
Water column Chl-a (n = 3)	ug l^{-1}	2.3 (1.2)	2.3 (0.0)	1.2 (0.0)	1.2 (1.2)	0.86 (1.0)	0.89 (1.0)	0.0 (0.0)	0.38 (0.66)
Benthic Chl-a (n = 15)	mg m^{-2}	5.6 (4.8)	5.9 (9.2)	0.6 (0.6)	24 (51)	13 (12)	14 (20)	4.6 (5.2)	2.5 (1.5)

Table 2. Estimated metabolic rates (mean ± SE g O_2 m^{-2} day^{-1}) for diel periods during the 2011 and 2012 collection periods with successful ($R^2 > 0.8$) dissolved oxygen model fits.

	Site	Creightons Creek		Honeysuckle Creek		Warrenbayne Creek		Moonee Creek	
	Reach	up	down	up	down	up	down	up	down
	Treatment	Untreated	Untreated	Replanted	Replanted	Untreated	Replanted	Untreated	Replanted
Summer 2011	Start date	-		08-Feb-11		24-Feb-11		22-Feb-11	
	n days	0	0	1	1	1	1	1*	1
	ER	-	-	2.6	4.5	6.8	14.0	-	8.4
	GPP	-	-	0.14	0.49	2.6	0.87	-	0.87
	NEP	-	-	-2.5	-4.0	-4.2	-13.0	-	-7.5
	P/R	-	-	0.06	0.11	0.38	0.06	-	0.10
Autumn 2012	Start date	05-Apr-12		22-Mar-12		29-Mar-12		18-Apr-12	
	n days	7	12	6	6	9	9	6	5
	ER	1.9 (0.42)	3.5 (0.31)	0.84 (0.10)	1.3 (0.06)	1.7 (0.24)	5.7 (0.60)	22 (1.0)	24 (0.99)
	GPP	0.55 (0.07)	0.41 (0.04)	0.29 (0.03)	0.25 (0.01)	1.2 (0.11)	0.29 (0.09)	4.9 (0.19)	2.1 (0.12)
	NEP	-1.4 (0.37)	-3.1 (0.29)	-0.54 (0.11)	-1.0 (0.06)	-0.47 (0.19)	-5.5 (0.55)	-17 (0.93)	-22 (1.0)
	P/R	0.38 (0.09)	0.12 (0.01)	0.37 (0.06)	0.20 (0.01)	0.79 (0.08)	0.05 (0.01)	0.23 (0.01)	0.09 (0.01)

*Metabolic rates could not be estimated for this day due to poor single-station diurnal DO curve fit at one probe location.

Table 3. Linear mixed model results showing mean effect size (± SD) of each model parameter (treatment effect, total daily PAR and mean daily water temperature) on the difference in metabolic rates between reaches (downstream – upstream). The estimate for each treatment is the difference between reaches predicted at the overall mean PAR and water temperature. Important effects and estimates different from zero (OR > 10) are indicated by bold font.

Response	Parameter	Mean	SD	OR
ER	Treatment (UU)	-0.30	1.45	1.4
	Treatment (RR)	-0.32	1.46	1.5
	Treatment (UR)	1.53	1.40	6.4
	PAR	0.04	0.05	3.6
	Temperature	**-0.41**	**0.27**	**14**
	Estimate (UU)	0.58	1.38	2.2
	Estimate (RR)	0.56	1.41	2.1
	Estimate (UR)	**2.41**	**1.23**	**22**
GPP	Treatment (UU)	0.18	1.45	1.3
	Treatment (RR)	0.27	1.46	1.4
	Treatment (UR)	-0.98	1.39	3.4
	PAR	0.00	0.01	2.5
	Temperature	0.00	0.05	1.1
	Estimate (UU)	-0.35	1.40	1.5
	Estimate (RR)	-0.25	1.41	1.3
	Estimate (UR)	-1.50	1.22	9.2
NEP	Treatment (UU)	0.49	1.46	1.8
	Treatment (RR)	0.61	1.48	2.1
	Treatment (UR)	**-2.46**	**1.49**	**16**
	PAR	-0.05	0.05	5.4
	Temperature	**0.38**	**0.26**	**14.1**
	Estimate (UU)	-0.88	1.41	3.2
	Estimate (RR)	-0.76	1.43	2.6
	Estimate (UR)	**-3.82**	**1.38**	**54**

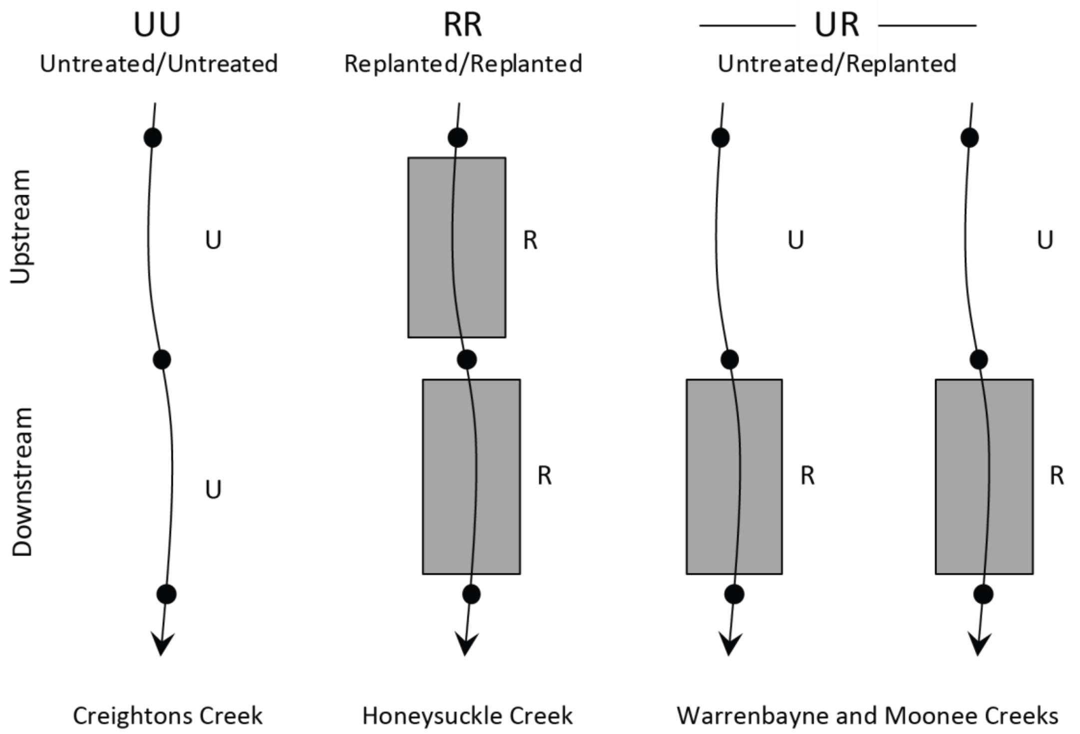

Figure 1. Design of metabolism experiment: grey boxes indicate replanted reaches (‘R’) and black circles show the location of dissolved oxygen loggers.

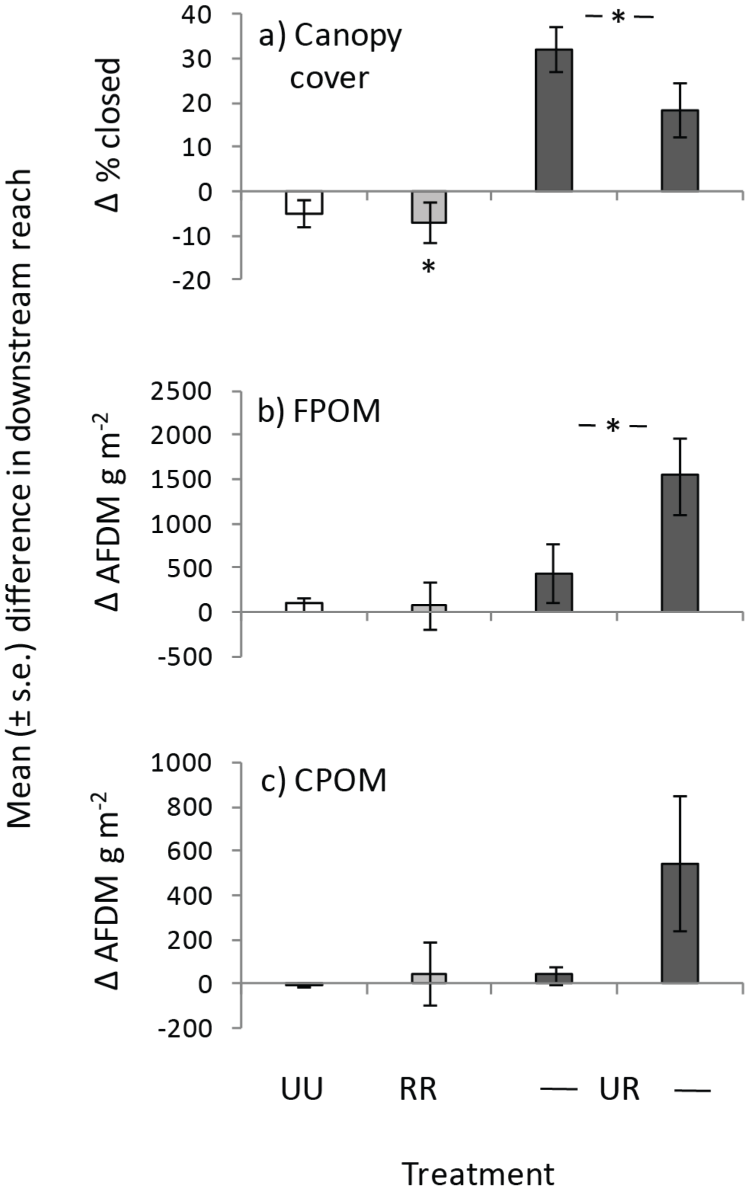

Figure 2. Mean (± SE) difference (downstream – upstream) in canopy closure (*n* = 5 hemispherical photos per reach) and benthic organic matter standing stock between reaches at each of the four streams. Organic matter is split into the fine and coarse fractions (FPOM and CPOM, *n* = 10 and 15 cores per reach respectively). Positive differences indicate the value was greater in the downstream reach. Asterisks indicate estimates different to zero at untreated-untreated (UU; white), replanted-replanted (RR; light grey) and untreated-replanted (UR; dark grey) from a linear mixed model at an odds ratio > 10.

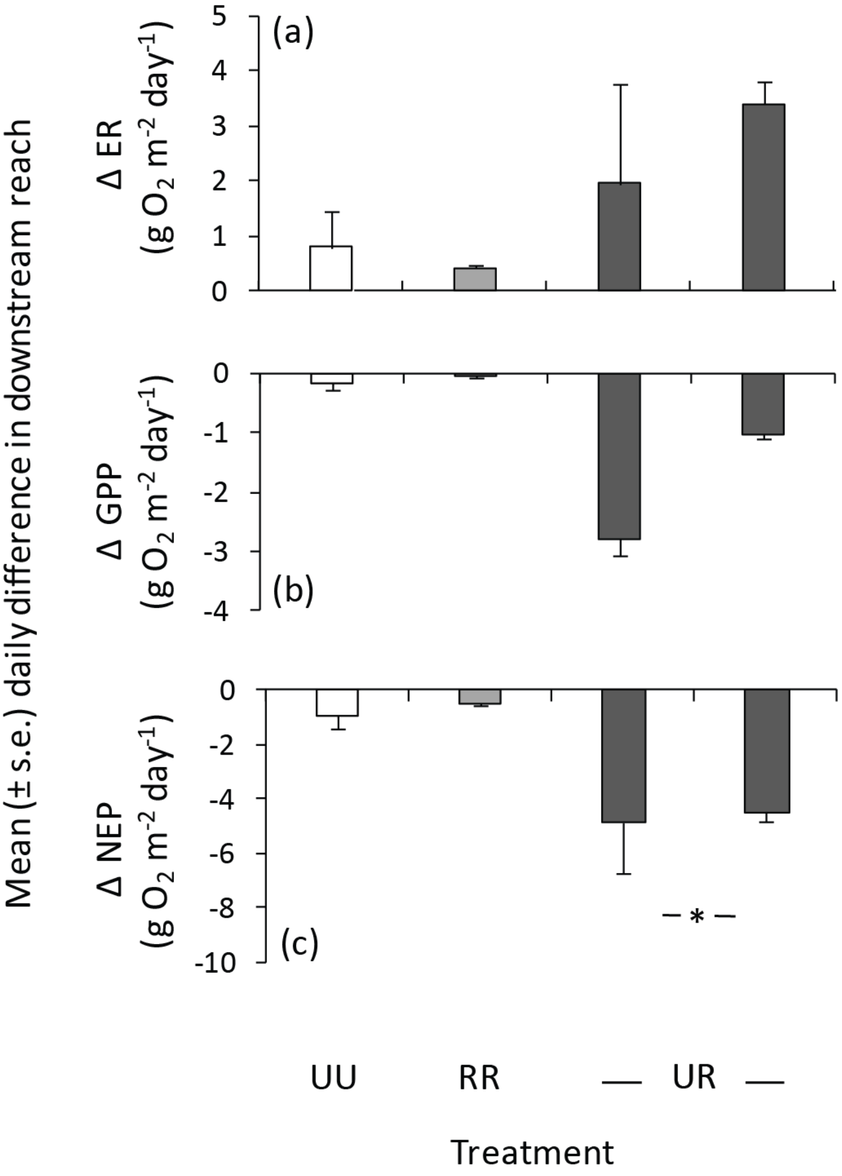

Figure 3. Mean (± SE) daily difference in two-station metabolic rates (ecosystem respiration, gross primary production and net ecosystem productivity) between downstream and upstream reaches at the four streams [*n* = 7, 6, 8 and 5 days for untreated-untreated (UU), replanted-replanted (RR), untreated-replanted (UR) and UR, respectively]. Positive differences indicate greater rates in downstream reaches while negative values show smaller rates in downstream reaches. Asterisks indicate treatment effects different to zero at UU (white), RR (light grey) and UR (dark grey) from a linear mixed model at an odds ratio > 10.

Declaration for Thesis Chapter 4

Declaration by candidate

In the case of Chapter 4, the nature and extent of my contribution to the work was the following:

Nature of contribution	Extent of contribution (%)
I performed 90% of the fieldwork, all the laboratory work (except for some outsourced chemical analyses), 50% of the statistical analyses and was the primary author of the manuscript.	60%

The following co-authors contributed to the work. If co-authors are students at Monash University, the extent of their contribution in percentage terms must be stated:

Name	Nature of contribution	Extent of contribution (%) for student co-authors only
Ralph Mac Nally	Input of ideas and contributed to writing the manuscript.	
Michael R. Grace	Input of ideas and contributed to writing the manuscript.	
James R. Thomson	Contributed to statistical analyses	
Ross M. Thompson	Input of ideas and contributed to writing the manuscript.	

The undersigned hereby certify that the above declaration correctly reflects the nature and extent of the candidate's and co-authors' contributions to this work*.

Candidate's Signature	[redacted]	**Date** 11.4.14
Main Supervisor's Signature	[redacted]	**Date** 11.4.14

*Note: Where the responsible author is not the candidate's main supervisor, the main supervisor should consult with the responsible author to agree on the respective contributions of the authors.

Chapter 4

Effect of native vegetation loss on stream ecosystem processes: dissolved organic matter composition and export in agricultural landscapes.

Please note this manuscript is a reformatted version of the published paper:

Giling D.P., Grace M.R., Thomson J.R., Mac Nally R. & Thompson R.M. (2014) Effect of native vegetation loss on stream ecosystem processes: dissolved organic matter composition and export in agricultural landscapes. Ecosystems, ***17****, 82-95.*

Abstract

Stream and river ecosystems are dependent on energetic inputs from their watersheds and thus shifts in land use from forest cover to agriculture will affect stream community composition and function. The disruption of forest-aquatic linkages alters the organic matter resources in agricultural streams. Dissolved organic matter (DOM) is the dominant form of organic matter in aquatic ecosystems, and a microbial energy source that is important for stream respiration. The concentrations and characteristics of DOM are regulated by both terrestrial (for example, terrestrial organic matter supply) and in-stream processes (for example, microbial respiration and periphyton production) that are influenced by land management. The effects of watershed land use and topographic, soil and climatic variables on DOM quantity (dissolved organic carbon concentration and load), source (terrestrial or in-stream) and quality (composition and lability) were measured in 14 streams across an agricultural land-use gradient. DOC concentration was positively correlated with watershed pasture cover and negatively correlated with watershed relief. No watershed variables were important correlates of DOC load. Stream DOM was

primarily of terrestrial origin, but DOM in agricultural streams had a greater proportion of sources from in-stream sources. This may be due to reduced connection with riparian vegetation and increased in-stream primary production. We suggest that maintaining watershed tree cover > 52% and ensuring < 10% of the length of riparian corridors is cleared for pasture could minimize changes to DOM composition. This is important to avoid effects for stream ecosystem processes that are mediated by DOM. Long-term DOM monitoring will be valuable for assessing the functional impacts of land-use change.

Introduction

Crops and pastures cover 34% of Earth's ice-free land surface (Ramankutty *et al.*, 2008). Clearing of vegetation for agriculture has profound consequences for biodiversity and ecosystem processes; these effects will intensify as global food demand increases (Tilman *et al.*, 2011). Streams and rivers are dependent on inputs from their watersheds (= catchments) (Allan, 2004). Lotic ecosystems respond to changes in the broader landscape, such as those that arise from agricultural intensification (Junk *et al.*, 1989; Allan, 2004). Change in riparian vegetation alters the availability of energy and nutrients in stream ecosystems, and induces changes in community composition and food webs (Wallace *et al.*, 1997; Kominoski & Rosemond, 2012).

The riparian zone is critical to stream-ecosystem function (e.g. Sweeney *et al.*, 2004). Inputs of terrestrial organic matter over the terrestrial-aquatic interface provide substrates and energy sources for consumers (Wallace *et al.*, 1997). Intact riparian zones intercept pollutants and nutrients, and the vegetation provides shading that reduces in-stream primary production (Naiman & Décamps, 1997; Roberts *et al.*, 2007). These processes affect biodiversity and foodwebs, and they interact with other ecosystem components to provide ecosystem services (e.g. clean drinking water; Palmer & Febria, 2012). However, ecological processes are often overlooked in favor of biodiversity metrics when assessing ecosystem condition (Follstad Shah *et al.*, 2007; Lake *et al.*, 2007). Biodiversity indices do not necessarily indicate a properly functioning ecosystem (Hooper *et al.*, 2005; Palmer & Febria, 2012), so attention to ecological processes is necessary.

The quantity and characteristics of in-stream organic matter are a function of in-channel, riparian and watershed processes, including the provision of terrestrial organic matter, invertebrate and microbial processing, and in-stream primary production (Sakamaki & Richardson, 2011; Stanley *et al.*, 2012). These processes are affected by land management (Townsend *et al.*, 1998). However, measuring the characteristics of naturally derived (as opposed to introduced material such as leaf packs) organic matter present in aquatic ecosystems has rarely been used to assess the functional consequences of riparian land-use change (but see Sakamaki & Richardson, 2011). Assessing effects on stream ecosystems requires identifying measures appropriate to the expected spatial scale of land-use effects (Sakamaki & Richardson, 2011). At a reach scale (100s of m), properties of in-stream fine-particulate organic matter (FPOM) are correlated with local riparian condition, but may be less influenced by watershed-scale effects (Sakamaki & Richardson, 2011).

Dissolved organic matter (DOM) is the dominant form of organic matter in stream ecosystems and reflects the effects of upstream characteristics (e.g. land cover, soils, and hydrology) at watershed scales (e.g. Mattsson *et al.*, 2009; Wilson & Xenopoulos, 2009). DOM is a key energy source for the microbiota, such as bacteria. Microbes play a vital role in energy and nutrient cycling, and so the dissolved carbon fraction comprises a large proportion of total organic carbon demand and is important for stream respiration (Wiegner *et al.*, 2005). DOM affects microbial assemblage composition and the availability of nutrients and light in stream ecosystems (Mulholland, 2003; Docherty *et al.*, 2006). Despite its importance to stream ecosystem function, little is known about the controls on DOM dynamics in agricultural landscapes (Royer & David, 2005; Yang *et al.*, 2012).

Assessing land-use effects on DOM requires an understanding of both DOM quantity (concentration and load) and quality to microbial consumers (composition and lability) (Jaffé *et al.*, 2008). Stream DOM primarily is composed of high molecular-weight (MW) humic and fulvic acids leached from soil and terrestrial litter. The reduction of riparian vegetation along agricultural stream corridors reduces these high-MW sources of DOM, with a concomitant increase in the proportion of lower MW DOM (e.g. sugars, and proteins) produced by aquatic microbes (Wilson & Xenopoulos, 2009). This change in MW may affect in-stream DOM processing because low-MW compounds are generally more labile to microbial consumers.

We assessed the effects of native vegetation removal at several spatial scales (upstream riparian and whole-of-watershed) on DOM quantity and quality across a land-use gradient from ‘pasture’ to ‘forested’ in south-eastern Australia. We expected that increased pasture cover would affect DOM quantity and quality. Degraded, homogeneous agricultural streams may export greater amounts of organic matter (i.e. ‘leak’ carbon), have less terrestrial DOM, and a higher bioavailability of DOM to the microbial community. We sought to determine the effect of agricultural land use on the quantity, source, composition, and lability of exported DOM. We provide management recommendations for the total watershed or riparian zone tree cover required to minimize impacts on stream organic matter processes.

Methods

Study design

Dissolved organic matter (DOM) dynamics were measured at 14 stream sites (1st-3rd Strahler order) in the Goulburn-Broken watershed in south-eastern Australia (Fig. 1; Table 1). DOM quantity was measured at all sites over 12 months as DOC (dissolved organic carbon; the main component of DOM) concentration and watershed yield. Measurements of DOM quality, including source (excitation-emission matrices), composition (molecular weight) and lability (% biodegradable) were taken at ten of the 14 streams (Fig. 1). These ten ‘organic matter quality sites’ were similar to each other in terms of watershed areas but ranged in watershed pasture cover (< 1-83%; Table 1). The remaining cover was mostly native dry sclerophyll *Eucalyptus* forest. Watersheds with greater tree cover were steeper and had higher maximum altitudes. There are no large (> 1 ha), permanent wetlands upstream of our study sites.

Data on watershed land use and topography (Table 2) were obtained from a digital elevation model-derived stream network (Stein *et al.*, 2002). Upstream riparian land use (20 m buffer) was assessed using aerial photography (Google Earth). The riparian vegetation was classified as having ‘continuous’ canopy cover, ‘scattered’ trees or cleared for pasture. The longitudinal distance of each riparian category upstream of the site was expressed as a proportion of total upstream channel length. The upstream channel extent was determined from the digital stream network. Climatic and soil data were obtained from the Environmental Systems Modelling Platform (EnSym, Victorian Department of Sustainability and Environment, 2012). Rainfall and soil moisture were modelled as a daily time-series (1/2/2011 to 31/1/2012). Watershed soil characteristics were calculated by determining the proportion of soil types in each watershed with ArcMap (ESRI; Redlands, CA, USA) and producing an area-weighted mean from the properties reported by McKenzie and others (2000).

Hydrology

Stream height was measured with a TruTrack water level/temperature logger (Intech Instruments; Auckland, New Zealand). Stream height was converted to discharge with a rating curve built by measuring instantaneous stream discharge 7–13 times at each site across the range of observed stream heights. Discharge was estimated using the slope-area method (Dalrymple & Benson, 1967) when maximum stream height exceeded the measured range of discharges.

Water chemistry

Grab samples were collected seasonally for one year. Unfiltered water samples were collected for total phosphorus (P) and total nitrogen (N), and filtered (0.45 μm) samples for ammonium (NH_4^+), filterable reactive phosphorus (FRP) and nitrate plus nitrite (NO_x). Total N and P were analyzed using the alkaline persulphate digestion method (APHA, 2005) using a Quick-Chem 8500 (Lachat Instruments; Loveland, USA). Concentrations of FRP and NO_x were determined using flow-injection analysis; NH_4^+ concentration was measured using the phenate method (APHA, 2005). Water-quality variables (pH, electrical conductivity, turbidity, dissolved oxygen) were measured with a U-50 Water Quality Meter (Horiba; Kyoto, Japan).

Dissolved organic matter quantity - DOC concentration and yield

Dissolved organic carbon was sampled by taking water from the centre of each stream every 4 weeks. Additional samples were taken during storm flows (including up to the 99th flow percentile at some sites). Samples were filtered through GF-75 glass fiber filters (Advantec; Dublin, USA) into pre-combusted 60-ml amber-glass jars and acidified (to pH < 2) with 32% HCl. These were refrigerated immediately and DOC concentration analyzed using a Shimadzu TOC-V CPH/CPN Total Organic Carbon analyzer (Shimadzu; Tokyo, Japan).

Dissolved organic matter source - excitation-emission matrices (EEMs)

Excitation-emission matrices (EEMs) are merged emission spectra that allow fractions of the DOM to be traced through the region of the spectrum in which they exhibit peak fluorescence (Stedmon *et al.*, 2003). Duplicate filtered (Whatman GF/C) samples were collected from the ten organic matter quality sites seasonally for 1 year at baseflow conditions. Samples were acidified, refrigerated, and analyzed within 4 days. Scans were performed on stream samples and MilliQ water blanks with a Cary Eclipse fluorescence spectrophotometer (Varian; Melbourne, Australia; xenon lamp). Fluorescence intensity was measured at excitation wavelengths 250–400 at 10 nm increments and emission wavelengths 400–550 at 2 nm increments (following McKnight *et al.*, 2001).

Spectra were corrected for instrument and inner-filter effects before being Raman-normalized (following McKnight *et al.*, 2001; Stedmon *et al.*, 2003). Corrected blanks were deducted from spectra and the region affected by second-order Rayleigh scattering was set to zero (Stedmon *et al.*, 2003). The fluorescence index (FI) indicates the source of DOM. Fulvic acids from terrestrial vegetation have FI values *c.* 1.4, while the FI of in-stream microbial DOM is *c.* 1.9 (McKnight *et al.*, 2001). FI was calculated as the ratio of emission intensity at 470 to 520 nm at an excitation wavelength of 370 nm (McKnight *et al.*, 2001). Changes in FI of *c.* 0.1 indicate a shift in DOM source (McKnight *et al.*, 2001).

Dissolved organic matter composition - specific UV absorbance (SUVA)

Molecular weight and aromatic content of humic materials in water were assessed using specific UV absorbance ($SUVA_{280}$) (Chin *et al.*, 1994). Triplicate filtered (Whatman GF/C) water samples from the ten organic matter quality sites were collected in pre-combusted amber glass jars in autumn and spring 2011. These were frozen in 15-ml polypropylene tubes and slowly defrosted prior to analysis. The UV-visible absorbance of each sample was measured at 280 nm with a UV-visible spectrophotometer (Unicam; Cambridge, England) using a quartz cuvette with a path-length of 1 cm. $SUVA_{280}$ was calculated as $SUVA_{280} = Abs_{280} / DOC$ (mol l^{-1}) (Chin *et al.*, 1994).

The weight-averaged molecular weights of the DOC compounds in the sample were: MW (g mol^{-1}) = 3.99 ($SUVA_{280}$) + 490 (Chin *et al.*, 1994). Humic acids have average molecular weights between 2,000 and 3,000, while fulvic acids have average molecular weights < 1,000 g^{-1} mol (Zeng *et al.*, 2002).

Dissolved organic matter lability - biodegradable dissolved organic carbon (BDOC)

The proportion of DOM bioavailable (= ease of breakdown) for the microbial community (biodegradable DOC or %BDOC) was assessed by incubation (following Servais *et al.*, 1989). Incubations were performed in autumn and spring (2011) with triplicate samples from the ten organic matter quality sites. Water samples were filtered (GF-75, Adventec; Dublin, USA) into 125 ml pre-combusted amber glass jars and refrigerated. An inoculum of stream water containing the micro-organisms responsible for utilizing bioavailable DOM was collected from one site. This sample was filtered (2.0 μm GE polycarbonate membrane) and refrigerated. Additional incubations showed source of inoculum sample had no effect on BDOC (Table S1 in Supporting Information).

Each sample was split into three 40-ml sub-samples. One sub-sample was acidified for analysis of DOC concentration. The other sub-samples had 0.8-ml of inoculum added. One inoculated sub-sample was incubated, while the other was acidified and analyzed to ensure the amount of DOC added in the inoculum did not differ between sub-samples. The incubated sub-samples were placed in a dark temperature-controlled cabinet at 15°C (mean stream temperature prior to autumn sampling) for 30 days. The concentration of BDOC (mg l^{-1}) was calculated as the difference between the pre- and post- incubation DOC concentrations, and BDOC (%) = [BDOC (mg l^{-1}) / pre-incubation DOC (mg l^{-1})] × 100.

Statistical analyses

Discharge was incorporated in DOM quantity calculations because storm flows exert a strong affect on DOM concentration and export (Fellman *et al.*, 2009). We used a hierarchical Bayesian model to calculate the effect of instantaneous stream discharge (Ml day^{-1}) on mean DOM concentration (mg l^{-1}) at each site j:

$$DOC_{ij} \sim N\left(\mu_{ij,}\sigma_1^2\right);\ \mu_{ij} = a_j + b_j * \ln(discharge_{ij})\,;$$

$$a_j \sim N(\bar{a}, \sigma_2^2);\ b_j \sim N\left(\bar{b}, \sigma_3^2\right);\ \bar{a}, \bar{b} \sim N(0{,}0.001);\ \sigma_{1:3} \sim U(0{,}10).$$

Here, there are multiple measurements on stream j (ij) that are modelled as functions of the discharge. The model produces stream-specific intercepts (a_j) and slopes (b_j) that are drawn from common distributions of intercepts and slopes with means $\bar{a}$ and $\bar{b}$. N() and U() indicate normal and uniform distributions. All priors are uninformative.

The site-specific relationships (and uncertainties in parameter estimates) were used to predict mean daily DOM concentration for the daily hydrologic time-series at each site. Estimated concentrations and volumes were used to calculate DOM load and watershed DOM yield (DOM load/watershed area) for 12 months (1/3/2011 – 28/2/2012). A time-series of DOM predictions was made with baseflow discharge only by partitioning out the surface-flow contribution (Nathan & McMahon, 1990) to ensure the high surface runoff during storms did not mask the effect of watershed characteristics.

The importance of the topographic, climatic, and land-use watershed variables on DOM concentration and yield were assessed using Bayesian model averaging (BMA; Table 2). BMA yields posterior model probabilities for each model structure (combination of predictors), which indicate the relative weight of evidence for each model. Summing the posterior model probabilities for all models that include a particular variable yields an integrated probability that the variable is a predictor (i.e. has a non-zero coefficient). The candidate watershed variables were derived from results of past research. If two variables of interest were highly correlated ($R > 0.7$), residuals of one variable regressed against the other were used (Table 2) as a predictor.

Relationships between DOM quality measurements (FI, MW and %BDOC) and watershed pasture cover or percentage upstream riparian pasture cover were analyzed with Bayesian linear mixed models (with season as a covariate and a random site effect) using WinBUGS (version 1.4; Lunn *et al.*, 2000). In the case of the non-linear relationship between FI and riparian pasture cover, a logarithmic model was used. Relationship between predicted watershed DOM load (kg y^{-1}) and water yield (Ml y^{-1}) was analyzed with linear regression. Water yield and DOM load were log-transformed to improve distributional properties. We used the odds ratio (OR) to inform importance of model parameters. The OR is the ratio of posterior odds to prior odds. OR > 3 for BMA indicates an important effect and OR > 10 an important effect for other analyses.

Results

Dissolved organic matter quantity - DOC concentration and yield

There was a positive linear relationship between instantaneous discharge and DOM concentration (measured as DOC) at each site (minimum OR = 2,499). When interpolated over the full year, mean daily DOM concentration ranged between 2.9 and 11.5 mg l^{-1} among sites (mean 6.7 mg l^{-1}; Table 1). The most important variables were a positive effect of the percentage of watershed pasture cover and a negative effect of watershed relief on mean DOM concentration (Table 3a; Fig. 2). There was no relationship between total watershed discharge (Ml y^{-1}) and watershed pasture cover (slope = -0.02 ± 0.01 SD, OR = 8.9, $R^2 = 0.13$) or watershed relief (slope = 1.4 ± 4.5 SD, OR = 1.7, $R^2 = 0.01$).

Watershed DOM yield ranged between 289 and 2318 kg DOC km^{-2} y^{-1} (mean 980 kg DOC km^{-2} y^{-1}, Table 1). There was little evidence that any of the selected watershed characteristics were important predictors of DOM watershed yield in either the full hydrology (Table 3b) or baseflow hydrology models (Table 3c). Instead, the annual export of DOC was related mainly to hydrology (Fig. 3). There was a strong positive correlation between water yield and DOM load (slope = 1.08 ± 0.11 SD, OR = inf., $R^2 = 0.91$, Fig. 3).

Dissolved organic matter source - excitation-emission matrices (EEMs)

There were distinct humic-like peaks in the excitation-emission matrices that were shifted to lower emission maxima (i.e. lower on the ordinate) at stream sites with high watershed pasture cover (Fig. 4). Mean FI values ranged from 1.33 to 1.51, indicating that the majority of the DOM from all watersheds was of terrestrial source. However, increasing pasture cover at both an upstream riparian and watershed spatial scale reduced the terrestrial influence. A positive effect of watershed pasture cover on FI (slope = 0.052 ± 0.013 SD, OR = 1,999, $R^2 = 0.77$, Fig. 5), indicated there was a greater contribution of in-stream microbial DOM sources at sites with low watershed tree cover. There was also an important positive non-linear effect of the percentage of upstream riparian zone completely cleared for pasture (mean effect = 0.037 ± 0.013 SD, OR = 1999, $R^2 = 0.62$, Fig. 5). The effect of season was consistent in each mixed model. Mean FI was lower in autumn (mean = 1.42 ± 0.05 SD) than in spring (mean difference = 0.03 ± 0.01 SD, OR = 178), summer (mean difference = 0.03 ± 0.01 SD, OR = 999) and winter (mean difference = 0.03 ± 0.01 SD, OR= 184). Spring, summer, and winter all did not differ from each other (OR <

10). The magnitude of seasonal differences was not sufficient to indicate a shift in fulvic acid source.

Dissolved organic matter composition - specific UV absorbance (SUVA)

Weight-averaged molecular weight ranged from 1,555 to 2,585 g mol^{-1} (mean 2,090 g mol^{-1}; Fig. 5). Humic acids were the dominant component of the DOM from all sites. There was no effect of watershed pasture cover on mean molecular weight (slope = -22 ± 68 SD, OR = 1.8, Fig. 5). There was also no effect of the percentage of upstream riparian zone completely cleared for pasture on mean molecular weight (slope = -0.3 ± 6.3 SD, OR = 1.1, Fig. 5). Season influenced DOM molecular weight in both the watershed and upstream riparian pasture cover mixed models, which was greater in spring than in autumn (mean difference = 294 ± 27 SD g mol^{-1}, OR = inf.).

Dissolved organic matter lability - biodegradable dissolved organic carbon (BDOC)

Agricultural streams had similar lability compared to streams in forested watersheds. Percent BDOC ranged from 1.0 to 27% (mean = 10.6% ± 5.6 SD; Table S1, Fig. 5) in the two 30-day incubation experiments. Watershed pasture cover did not appear to influence %BDOC (slope = -0.13 ± 1.48 SD, OR = 1.2), but season influenced %BDOC, which was higher in autumn (mean difference = 6.83% ± 0.80 SD, OR = inf.). There was also no effect of the percentage of upstream riparian zone completely cleared for pasture on %BDOC (slope = -0.1 ± 1.3 SD, OR = 2.8, Fig. 5). There was an effect of initial DOC concentration on %BDOC but this explained little of the variation (slope = 1.73 ± 1.28 SD, OR = 10.9, R^2 = 0.09), and season again was an important covariate (OR = inf.).

Discussion

Effect of proportion of agricultural land use on DOM quantity

Agricultural land cover and watershed relief affected DOM concentration. High DOM concentration in streams with flatter agricultural watersheds results from increased contact time between water and the soil in terrestrial flowpaths (Mulholland, 1997). Wetlands are often important sources of DOM production (e.g. Mattsson *et al.*, 2009) but probably contributed minimally in this landscape. The positive relationship between agricultural land use and DOM concentration is consistent with some comparisons between agricultural and forested watersheds (Quinn & Stroud, 2002; Molinero & Burke, 2009), although other studies reported negative relationships (e.g. Mattsson *et al.*, 2009).

The DOM yields (289–2318 kg C km^{-2} y^{-1}) were within the range of other estimates in agricultural watersheds (e.g. Dalzell *et al.*, 2011). There was no consistent effect of watershed land use on DOM yield, which suggests that the highly degraded agricultural watersheds exported a quantity of dissolved organic carbon similar to watersheds with intact native vegetation. This was the case in full and baseflow hydrology models, so that smaller inputs of DOM due to reduced terrestrial vegetation in agricultural watersheds may be offset by increased contributions from in-stream sources, as suggested by the EEM results (Hagen *et al.*, 2010). Reports from elsewhere have been inconsistent; agriculture has been shown to both increase and decrease DOM exports compared to un-impacted or forested watersheds (Cronan *et al.*, 1999; Quinn & Stroud, 2002). This variation may be due to regional differences in watershed characteristics such as soil type and farming practices (Stanley *et al.*, 2012), or the strong hydrologic control on DOM export (e.g. Royer & David, 2005).

Annual discharge explained 91% of the variation in total annual DOM load (Fig. 3). Therefore, interannual variability in precipitation and runoff has large effects on DOM export. Annual watershed rainfall did not greatly affect DOM export, suggesting subtle interactions among rainfall, watershed land use, soil, and topographic characteristics. One’s ability to detect an effect of pasture cover or agriculture on DOM export may be limited by the correlation among rainfall, altitude and watershed tree cover in the existing configuration of watersheds. The climatic and geophysical characteristics that control stream hydrology seem to determine DOM yield.

Effect of proportion of agricultural land use on DOM character

Our results are consistent with findings that agricultural streams are less well connected to terrestrial sources of DOM (Williams *et al.*, 2010). Our fluorescence index (FI) values were similar to those from other agricultural landscapes, in which FI was positively correlated with increasing watershed cropland (Wilson & Xenopoulos, 2009). Reduced terrestrial contribution to DOM in predominantly agricultural watersheds may reflect reduced provision of organic matter by terrestrial vegetation. Increased in-stream microbial or algal productivity due to greater nutrient availability, and increased DOM photodegradation, is important to DOM composition (Wilson & Xenopoulos, 2009; Williams *et al.*, 2010). FI values from both forestry clear-cut and reference headwater streams were indicative of terrestrial sources (1.15-1.35, Yamashita *et al.*, 2011), suggesting that effects of agriculture other than vegetation removal, such as nutrient enrichment, may have contributed to the greater contribution by in-stream DOM sources (i.e. FI > 1.4) in the current study.

Clear-cut and urbanized watersheds have a greater contribution of low-MW protein-like molecules to the DOM (Yamashita *et al.*, 2011; Yang *et al.*, 2012). These labile components have been associated with increased nutrient availability and algal production (Yang *et al.*, 2012), suggesting protein-like DOM may be present in agricultural watersheds. However, protein-like DOM is strongly correlated with DOM bioavailability (Fellman *et al.*, 2009). Bioavailability and MW were not related to watershed or upstream riparian tree cover in this study, so that the contributions of these low-MW components were inconsistent along the land-use gradient. Rapid use of the small amounts of low-MW DOM by microbes may be responsible for the lack of a relationship. Low-MW compounds may be in a rapid production-consumption cycle, being both produced and consumed during microbial metabolism (Cammack *et al.*, 2004). The small fraction could explain the greater microbial contribution to the overall DOM pool at agricultural sites, but the lack of detectable effect on mean MW.

DOM from some agricultural watersheds in the USA had lower MW than forested streams, which differs from our results (Cronan *et al.*, 1999). This may be due to the large extent of scattered or continuous remnant riparian vegetation (predominantly large *Eucalyptus camaldulensis*) close to the agricultural stream channels upstream of our sites. Leaf litter from this remnant riparian vegetation may have contributed to the relatively homogeneous MW observed even in heavily cleared watersheds.

Implications for restoring stream ecosystem processes

All streams received terrestrial DOM subsidies but agricultural streams had greater contributions from in-stream sources. Agricultural activities probably affected the terrestrial and in-stream organic matter processes that control DOM characteristics. Whether this effect is due to vegetation removal at riparian or at a whole-of-watershed scales (or other factors such as nutrient addition) can be difficult to discern because these variables are often correlated (e.g. Williams *et al.*, 2010). Despite this, our results support findings that upstream riparian land-use characteristics explain similar or slightly more of the variation in DOM character than do whole-of-watershed land-use predictors (Gergel *et al.,* 1999; Wilson & Xenopoulos, 2008; Molinero & Burke, 2009). Processes affecting DOM composition could be restored by replanting vegetation in riparian zones. However, there is still a range of watershed-scale processes that influence DOM dynamics and may not be addressed by the current scale of management (reach-scale). In this case, there is a spatial mismatch between restoration activities and their desired outcomes (Stanley *et al.*, 2012).

Our work suggests that upstream removal of riparian vegetation alters the source of DOM at low levels of clearing, with large changes up to 10% clearance, then little change thereafter (Fig. 5). Therefore, changes to organic matter processes may be minimized by restricting the proportion of riparian zone that is completely cleared for pasture to less than 10%. Replanting riparian vegetation at this scale is feasible in many agricultural landscapes given that remnant vegetation often already lines many agricultural streams. Land and stream management at whole-of-watershed scales is becoming more policy-relevant and potentially feasible (e.g. forest and agricultural management to sequester carbon; Ramachandran Nair *et al.*, 2009). Future agricultural developments should aim to maintain native vegetation > 52% watershed areal tree cover. This will maintain FI within *c.* 0.1 units of undisturbed catchments based on our observed relationship (Fig. 5), indicating a maintenance of DOM source. Whether these guidelines maintain the terrestrial and in-stream organic matter processes that determine DOM composition is an important and unresolved issue. We do not think that these measures would have a strong effect on the quantity of exported DOM, which is predominantly under hydrologic control.

The ways in which watershed-scale land cover affects aquatic DOM fluxes have been well established (e.g. Mulholland, 1997; Wilson & Xenopoulos, 2009). The proximate drivers of change in DOM character are less clear (Williams *et al.*, 2010). While we did not directly establish how agriculture affects DOM properties, DOM character probably provides an aggregate measure of a range of factors associated with intact riparian zones. These are commonly measured in many places around the world by stream-condition surveys at small spatial scales, and include canopy cover, organic litter, bank condition, turbidity, and nutrient concentration. In a land-use change context, there is a need to disentangle the effects of these on DOM character. This detailed understanding is needed to focus restoration actions at the appropriate spatial scale and to parts of the ecosystem that are having the largest effect on in-stream function.

Long-term monitoring of DOM character could be incorporated in the assessment of ecosystem condition. This would enable managers to detect changes in organic-matter properties, and hence ecological processes, over time (Kominoski & Rosemond, 2012; Stanley *et al.*, 2012). Modelled DOM export also could contribute to developing environmental policy (e.g. forestry-harvesting regimes; Öhman *et al.*, 2009). Measures of organic matter processes have recently been applied to detecting continental-scale patterns of habitat degradation (Woodward *et al.*, 2012). DOM itself has a strong regulatory effect on other stream ecosystem functions. Changes in DOM concentration and lability have consequences for downstream biota, nutrient cycling, and microbial respiration (Bernhardt & Likens, 2002; Cory *et al.*, 2006). Restoring natural organic matter dynamics will minimize the resultant effects for other aspects of stream ecosystem functioning.

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Table 1. Watershed characteristics of variables included in models, summary statistics for measured variables, and modelled DOM export for the 14 stream sites.

Stream			Castle	Creightons	Faithful	Harrys	Hollands	Honeysuckle	Moonee	Ryans	Seven	trib. of Broken	Two Mile	Warrenbayne	White Gum Gully	Wombat
Organic matter quality site			✓	✓	✓	✓			✓		✓		✓	✓	✓	✓
Latitude (° S)			36.90	36.88	36.75	36.70	36.71	36.65	36.84	36.64	36.81	36.92	36.65	36.72	36.80	36.87
Longitude (° E)			145.59	145.53	145.75	145.74	146.09	145.74	145.94	146.19	145.82	145.98	145.78	145.85	145.89	145.63
Catchment pasture cover (%)			83.1	82.3	59.3	54.3	20.7	64.2	0.6	11.5	42.5	26.8	71.2	22.5	3.4	40.1
Length of upstream riparian zone pasture (%)			4.0	36.1	5.6	18.0	0.0	2.0	0.0	0.4	5.4	18.9	14.8	1.1	0.0	0.0
Watershed relief			0.51	0.55	0.53	0.51	0.4	0.48	0.49	0.5	0.28	0.36	0.3	0.5	0.52	0.49
Maximum watershed elevation (m)			512	530	572	597	1132	661	944	972	822	758	640	719	791	797
Watershed area (km^2)			22	44	8	13	172	60	22	105	27	6	38	37	12	16
Total annual rain (mm)			711	746	1100	1041	1135	1057	1119	1267	1142	907	1076	1100	1217	836
Mean daily total soil moisture (Ml ha^{-1})			3.4	3.5	5.1	5.1	5.6	5.0	3.3	6.8	5.4	4.1	5.0	6.0	7.4	3.8
A horizon K_{sat} (%)			252	279	300	300	208	286	300	279	300	100	200	299	300	293
Hydrology	Mean daily flow (Ml)	*n* = 365	4.6	10.0	3.3	4.4	110.5	9.9	7.6	80.7	17.4	0.9	2.1	15.5	7.7	4.6
	Flow variability (C_v)		1.2	0.8	1.1	6.4	1.2	2.5	0.5	0.6	2.0	1.7	2.4	0.8	0.4	1.2
DOM quantity model results (mean ± SD)	DOC concentration (mg l^{-1})		7.22 (0.82)	7.90 (0.70)	5.26 (0.80)	8.53 (0.69)	3.75 (0.76)	7.87 (0.73)	4.07 (0.82)	2.95 (0.77)	7.84 (0.80)	9.90 (0.78)	11.5 (0.86)	5.12 (0.80)	3.46 (0.85)	8.53 (0.72)
	DOM export (kg DOC km^{-2})		638.4 (65.6)	752.7 (55.2)	950.1 (121.9)	1824 (195)	1314 (185.9)	655.1 (47.8)	544 (103.4)	942.9 (216.4)	2317 (227)	621.8 (44.3)	289 (22.12)	900.4 (124.1)	879.3 (202.1)	1097 (72.8)

Measured chemical variables (mean ± SE)	Temp. (°C)	319 - 365	13.4 (4.12)	14.0 (4.77)	12.8 (3.89)	13.4 (4.73)	14.9 (5.76)	15.1 (5.24)	12.2 (3.18)	17.5 (5.67)	11.5 (4.38)	13.9 (4.76)	14.9 (4.08)	13.0 (4.50)	12.0 (3.12)	14.1 (4.87)
	pH	16 - 26	7.07 (0.59)	6.79 (0.66)	6.80 (0.38)	6.96 (0.51)	7.08 (0.71)	7.16 (0.46)	6.51 (0.39)	6.68 (0.41)	6.46 (0.41)	6.63 (0.72)	7.41 (0.34)	7.08 (0.39)	6.67 (0.47)	6.73 (0.57)
	EC (mS cm^{-1})	16 - 26	0.20 (0.03)	0.14 (0.02)	0.06 (0.01)	0.23 (0.09)	0.07 (0.02)	0.17 (0.06)	0.05 (0.00)	0.05 (0.00)	0.04 (0.00)	0.17 (0.04)	1.10 (0.72)	0.08 (0.01)	0.05 (0.00)	0.14 (0.08)
	Turbidity (NTU)	16 - 26	44.5 (58.2)	41.4 (43.4)	92.8 (155.)	60.1 (114)	60.6 (119)	59.2 (142)	17.6 (25.4)	37.0 (53.9)	37.9 (30.9)	52.5 (88.1)	148 (194)	81.0 (156)	36.9 (93.2)	76.8 (118)
	DO (% sat.)	15 - 25	8.84 (1.41)	9.14 (1.50)	9.21 (1.24)	8.02 (2.62)	9.69 (1.22)	8.86 (1.64)	9.19 (0.80)	9.84 (2.25)	8.61 (1.17)	7.60 (2.38)	5.86 (2.51)	9.62 (1.14)	10.1 (1.13)	9.02 (1.41)
	NH3 (mg l^{-1})	6 - 12	0.03 (0.00)	0.04 (0.02)	0.02 (0.00)	0.02 (0.01)	0.01 (0.00)	0.01 (0.00)	0.01 (0.00)	0.01 (0.00)	0.01 (0.00)	0.02 (0.01)	0.02 (0.03)	0.01 (0.00)	0.00 (0.00)	0.02 (0.01)
	NOx (mg l^{-1})	6 - 12	0.13 (0.12)	0.38 (0.23)	0.31 (0.08)	0.05 (0.07)	0.06 (0.08)	0.07 (0.06)	0.03 (0.01)	0.04 (0.04)	0.15 (0.04)	0.01 (0.02)	0.06 (0.11)	0.09 (0.07)	0.03 (0.01)	0.10 (0.09)
	Total N (mg l^{-1})	6 - 12	0.78 (0.31)	1.16 (0.33)	0.80 (0.08)	0.91 (0.38)	0.36 (0.29)	0.67 (0.19)	0.23 (0.09)	0.32 (0.26)	0.78 (0.10)	0.73 (0.31)	1.08 (0.34)	0.43 (0.14)	0.21 (0.02)	0.90 (0.73)
	FRP (mg l^{-1})	6 - 12	0.01 (0.00)	0.02 (0.01)	0.01 (0.00)	0.04 (0.01)	0.00 (0.00)	0.02 (0.00)	0.02 (0.01)	0.00 (0.00)	0.01 (0.00)	0.01 (0.00)	0.01 (0.00)	0.01 (0.00)	0.01 (0.00)	0.01 (0.00)
	Total P (mg l^{-1})	6 - 12	0.09 (0.05)	0.10 (0.03)	0.07 (0.02)	0.21 (0.15)	0.03 (0.02)	0.09 (0.02)	0.07 (0.02)	0.03 (0.04)	0.08 (0.03)	0.10 (0.07)	0.15 (0.06)	0.06 (0.03)	0.04 (0.00)	0.12 (0.11)

Table 2. Description of candidate variables in explanatory models. Ticks indicate which variables were included as parameters.

Variable description	Category	Range	Unit	Included	
				Conc.	Yield
Catchment tree cover[1]	Land use	15 - 97	%		
Catchment pasture cover[1]	Land use	1 - 83	%	✓	
Length of upstream riparian zone with continuous remnant vegetation[3]	Land use	18 - 100	%		
Length of upstream riparian zone with scattered remnant vegetation[3]	Land use	0 - 53	%		
Length of upstream riparian zone cleared for pasture[3]	Land use	0 - 36	%	✓	✓
Catchment relief (mean upstream elevation / max upstream elevation)[1]	Topography	0.3 - 0.6		✓	
Reach elevation max[1]	Topography	193 - 925	m		
Maximum catchment elevation[1]	Topography	512 - 1132	m		✓
Catchment area[1]	Topography	6.5 - 172.3	km^2	✓	
Catchment mean slope[1]	Topography	3.0 - 10.5	%		
Total annual rain[2]	Climate	711 - 1267	mm		✓
Mean daily total soil moisture[2]	Climate	3.3 - 7.4	Ml ha^{-1}	✓	
Mean soil water holding capacity of A horizon[2]	Soil	37.0 - 59.5	%		✓
Mean soil water holding capacity of B horizon[2]	Soil	36.0 - 47.9	%		
Mean soil saturated hydraulic conductivity (Ksat) of A horizon[2]	Soil	100 - 300	mm h^{-1}	✓	✓
Mean soil saturated hydraulic conductivity (Ksat) of B horizon[2]	Soil	4.0 - 42.1	mm h^{-1}		
Tree cover residuals (against annual rainfall)	Land use	-31.3 - 35.2	%		✓
Annual rainfall residuals (against pasture cover)	Climate	-202 - 160	mm	✓	
Pasture cover residuals (against catchment slope)	Land use	-29 - 29	%		
Catchment slope residuals (against pasture cover)	Topography	-2.5 - 2.3	%	✓	✓

Reference: [1]Digital elevation model (Stein *et al.*, 2002), [2]EnSym (Victorian Department of Sustainability and Environment, 2012), [3]Google Earth.

Table 3. Bayesian model averaging results for DOM concentration model (a) and DOM yield model under full hydrology (baseflow and surface flow; b) and baseflow (c). Odds ratio > 3 indicates an important effect (bold type).

Variable	Inclusion probability	Coefficient	Odds ratio (OR)
a) ln(DOC concentration) model			
Catchment pasture cover	**0.87**	**0.16**	**6.8**
Catchment relief	**0.79**	**-0.12**	**3.7**
Catchment area	0.70	-0.09	2.3
Rainfall residuals (against pasture cover)	0.36	-0.01	1.8
A horizon saturated hydraulic conductivity	0.40	-0.03	1.5
Proportion of upstream riparian zone cleared for pasture	0.42	0.03	1.4
Catchment slope residuals (against pasture cover)	0.43	0.03	1.3
Mean daily total soil water	0.44	-0.03	1.3
b) ln(DOC yield) model: full hydrology			
A horizon saturated hydraulic conductivity	0.51	0.04	1.0
A horizon soil water holding capacity	0.48	0.03	1.1
Catchment elevation max	0.46	0.02	1.2
Total annual rainfall	0.44	0.01	1.3
Pasture cover residuals (against rainfall)	0.44	-0.01	1.3
Catchment slope residuals (against pasture cover)	0.43	-0.01	1.3
Catchment relief	0.43	0.00	1.3
Proportion of upstream riparian zone cleared for pasture	0.43	0.00	1.3
c) ln(DOC yield) model: baseflow hydrology			
Catchment slope residuals (against pasture cover)	0.64	-0.11	1.7
Pasture cover residuals (against rainfall)	0.59	-0.09	1.4
A horizon saturated hydraulic conductivity	0.54	0.07	1.2
Catchment elevation max	0.51	0.06	1.1
A horizon soil water holding capacity	0.43	-0.01	1.3
Catchment relief	0.41	0.01	1.4
Total annual rainfall	0.41	0.00	1.5
Proportion of upstream riparian zone cleared for pasture	0.41	-0.01	1.5

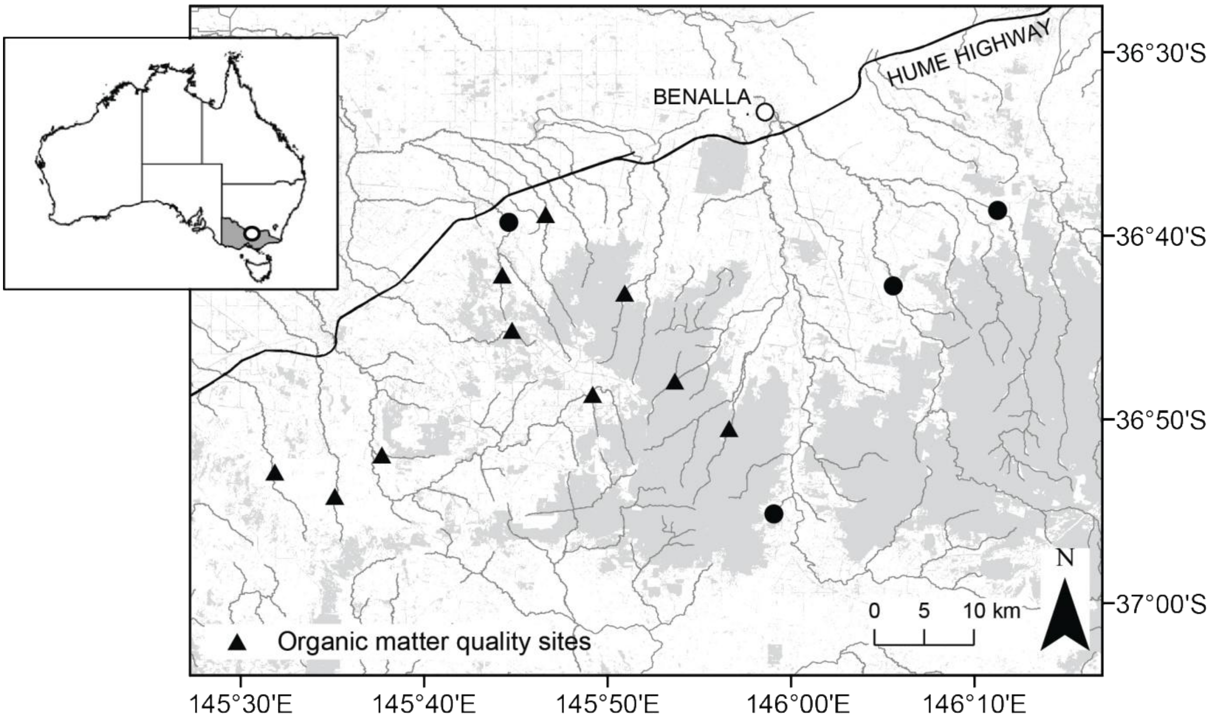

Figure 1. Study design and stream site locations within Victoria, Australia. Black markers (circles and triangles) represent the full set of 14 DOM quantity sites. The subset of ten ‘organic matter quality sites’ are shown as triangles. Light grey is remnant tree cover and white indicates cleared pasture land.

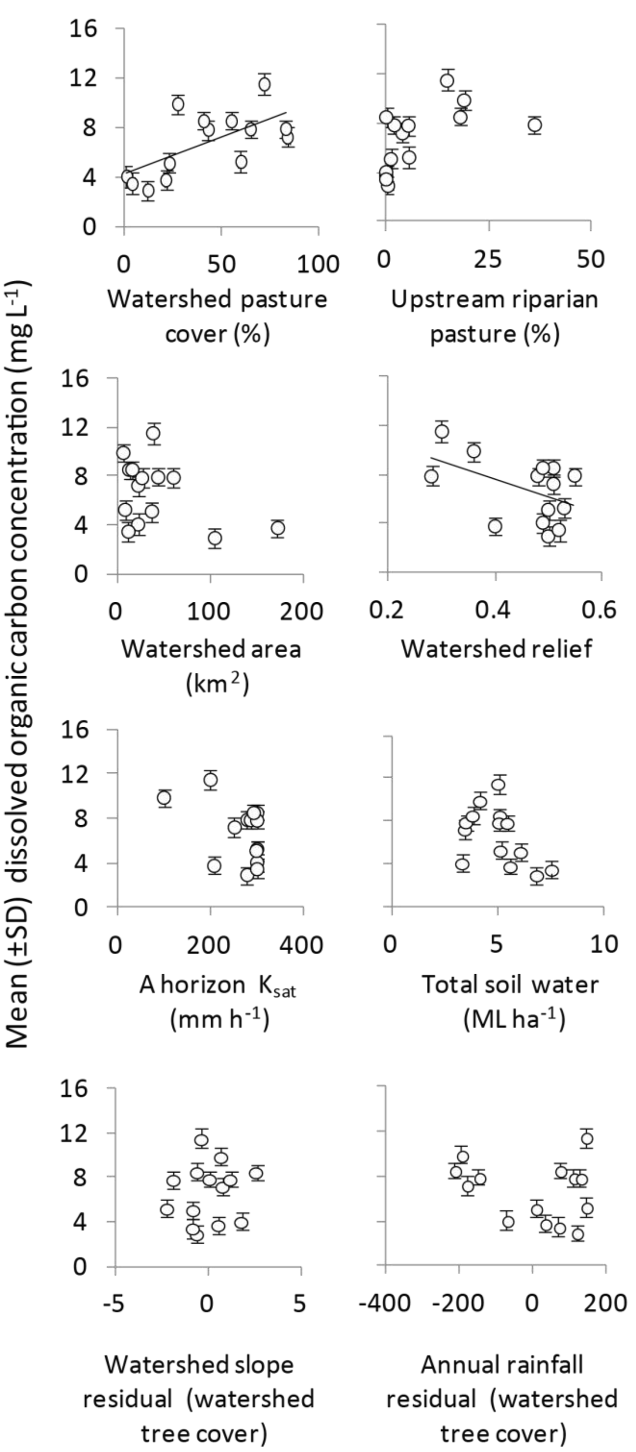

Figure 2. Relationships between mean (±SD) DOM concentration (from hierarchical model; mg DOC l^{-1}) and predictor variables (Table 3) included in BMA analysis of DOM concentration. Important effects (OR > 10) indicated by regression line.

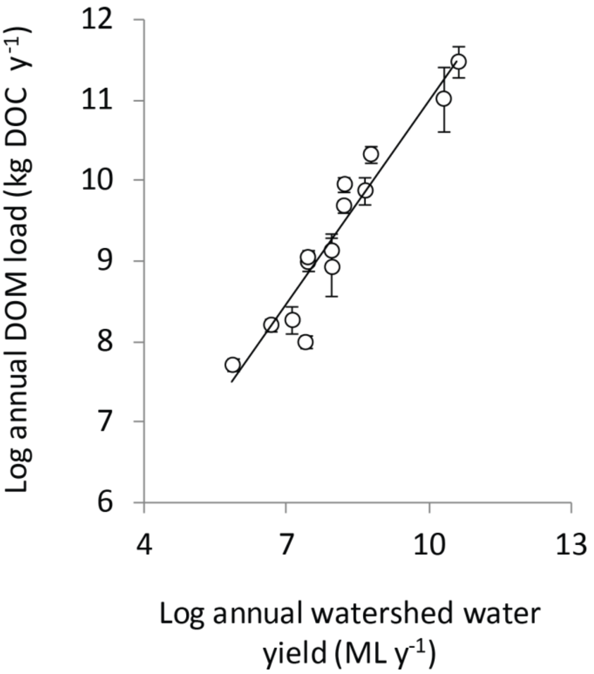

Figure 3. Relationship between mean log annual water yield (Ml y^{-1}) and log total DOM load (kg DOC y^{-1}).

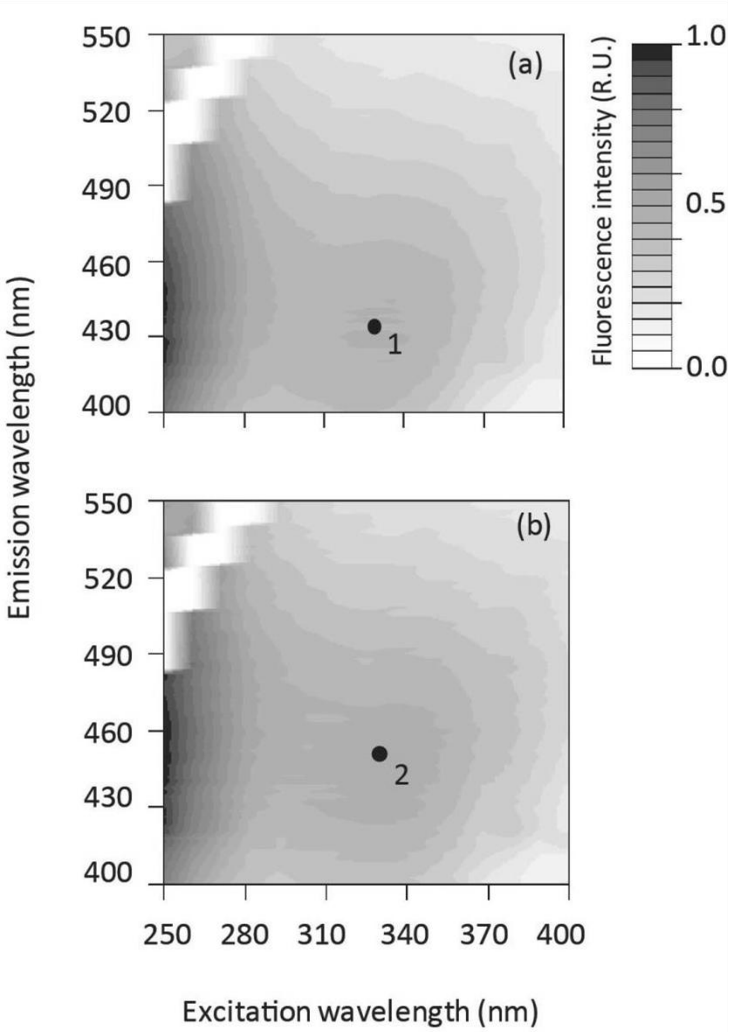

Figure 4. Example excitation-emission matrices (EEMs) from high watershed pasture cover (a) and low watershed pasture cover (b) stream sites. Grey contours show fluorescence intensity (Raman units). High watershed pasture cover sites have the humic-like peak (point 1) shifted toward lower emission wavelength compared to the signature at high tree cover watersheds (point 2).

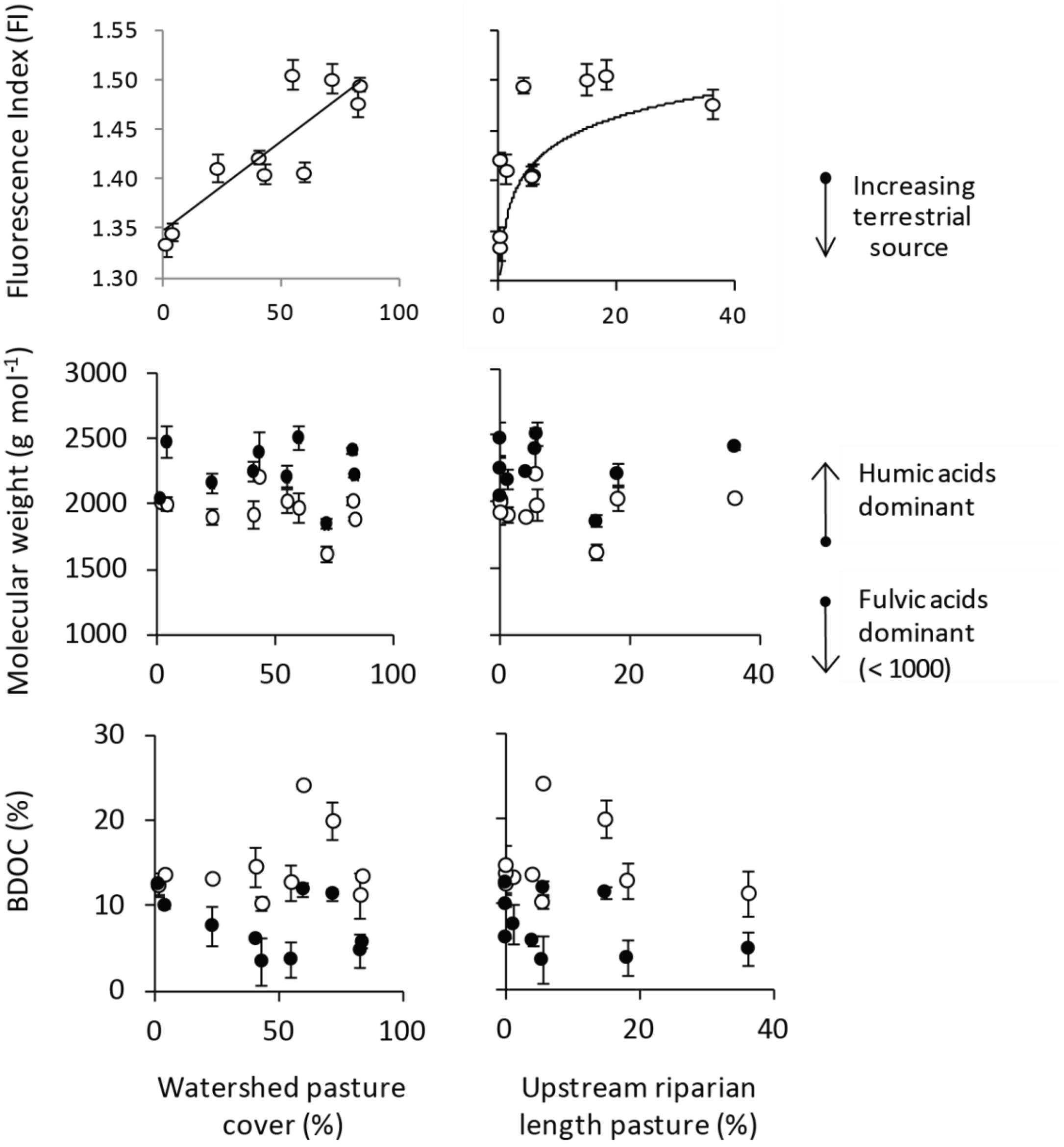

Figure 5. Correlation between whole-of-watershed (left) and upstream riparian (right) pasture cover with DOM character. Plots show mean (± S.E.) DOM source (fluorescence index; *n* = 4 seasons), composition (weight-averaged molecular-weight (MW); g mol^{-1}), and lability (%BDOC). Mean MW and %BDOC (*n* = 3 samples per site per season) are shown for autumn (open circles) and spring (solid circles).

Supporting Information

Effect of inoculum source on %BDOC

A pilot study result suggested inoculum source may have a strong affect on the proportion of DOC that is available to the microbial community (%BDOC). Hence an additional set of triplicate filtered samples were taken in spring 2011 to test for an effect of inoculum source. One set of triplicates were inoculated with a stream water sample from the study region but not one of the study sites. The other set of samples were self-inoculated with a water sample taken at the same site and time of each %BDOC sample (i.e. ten different inoculates).

There was no difference in %BDOC between independently-inoculated and self-inoculated samples (two-group comparison, mean difference = 0.16% ± 0.69 SD, OR = 1.44; Table S1).

Table S1. Comparison of inoculum source on percent BDOC

Site	%BDOC (mean ± SD)	
	Independent inoculum (*n* = 3)	Self-inoculum (*n* = 3)
Castle	13 (4.7)	14 (5.5)
Creightons	11 (0.6)	11 (0.6)
Faithful	24 (3.5)	24 (4.7)
Harrys	13 (1.9)	13 (1.9)
Moonee	12 (1.3)	12 (1.4)
Seven	10 (3.8)	10 (3.7)
Two Mile	20 (0.4)	20 (0.5)
Warrenbayne	13 (0.8)	12 (0.9)
White Gum Gully	14 (3.9)	14 (3.8)
Wombat	15 (1.6)	15 (1.4)

Samples were inoculated with stream water from an independent site and with a water sample from the same location.

Declaration for Thesis Chapter 5

Declaration by candidate

In the case of Chapter 5, the nature and extent of my contribution to the work was the following:

Nature of contribution	Extent of contribution (%)
I performed 90% of the fieldwork, all the laboratory work (except for some outsourced chemical analyses), 90% of the statistical analyses and was the primary author of the manuscript.	70%

The following co-authors contributed to the work. If co-authors are students at Monash University, the extent of their contribution in percentage terms must be stated:

Name	Nature of contribution	Extent of contribution (%) for student co-authors only
Ralph Mac Nally	Input of ideas and contributed to analysis and writing of the manuscript	
Ross M. Thompson	Input of ideas and contributed to writing the manuscript.	

The undersigned hereby certify that the above declaration correctly reflects the nature and extent of the candidate's and co-authors' contributions to this work*.

Candidate's Signature	[redacted]	**Date** 11.4.14
Main Supervisor's Signature	[redacted]	**Date** 11.4.14

*Note: Where the responsible author is not the candidate's main supervisor, the main supervisor should consult with the responsible author to agree on the respective contributions of the authors.

Chapter 5

Projecting cross-system subsidies under changing climates.

Abstract

1. All ecosystems exchange energy and nutrients with other ecosystems. Human activity has markedly altered cross-system exchanges (‘subsidies’) through reconfiguring landscapes, altering the permeability of ecosystem boundaries and the availability of resources and vectors. Climate change modifies patterns of precipitation and snowmelt, affecting the magnitude and timing of discharge in streams and rivers. In particular, flow extremes (e.g. overbank flows and prolonged drought) may increase in frequency or magnitude with more variable climates, disrupting longitudinal, lateral and vertical connectivity in river networks.
2. The effect of floods on the transport of energy subsidies (i.e. organic carbon) are not well understood because watershed (= catchment) budgets often overlook flow extremes. We measured the effect of storm flows on dissolved and particulate organic carbon fluxes in 19 streams over two years in south-eastern Australia.
3. The highest flow events (5% of time) dominated the annual export of dissolved (mean 39%) and fine particulate (mean 59%) organic carbon. High flows increased the transport of particulate relative to dissolved organic carbon.
4. In temperate regions of the world, high flows are predicted to occur during warmer months more commonly, coinciding with warmer water temperatures and peak litterfall from riparian trees. Organic carbon dynamics of currently perennial streams may become more like those of temporary streams; long periods of drawdown with retention favoured over export, net autotrophy and consumer reliance on local energy sources. These periods will be interspersed with sharp ‘blooms’ of longitudinal and lateral energy transfer, organic-matter processing and

net heterotrophy. These blooms may be associated with high tannin concentrations, increased microbial respiration and the development of anoxic water conditions depending on inter-flood frequency.

5. Climate change will have strong effects on metabolic processes and food webs in many ecosystems where subsidy quantity, quality or vectors are mediated by precipitation, temperature, and wind or storm events. Ecosystem management in future climates requires a landscape perspective, and the role of connectivity and cross-system subsidies need to be explicitly incorporated.

Introduction

All ecosystems exchange subsidies of energy, nutrients and biota with other ecosystems (Elton, 1927). Meta-ecosystems, or landscapes, consist of a series of ecosystems connected by subsidies (Loreau *et al.*, 2003). Subsidies involve a donor and a recipient system, with fluxes transported by a vector (e.g. water, wind or biota) across intervening boundaries between ecosystems (Fig. 1; Polis *et al.*, 1997). These subsidies can exert strong effects within ecosystems on primary production (Hocking & Reynolds, 2011), community interactions (Stoler & Relyea, 2013) and food-web dynamics (Takimoto *et al.*, 2002). There is much interest in how the spatial configuration of landscape elements (e.g. terrestrial and aquatic ecosystems), permeability of ecosystem boundaries, and food-web properties determine the influence of biotic or energetic subsidies on recipient ecosystems (Polis *et al.*, 1997). Much of this work has focused on how human activities affect fluxes among ecosystems (Table 1).

Human effects such as land-cover change and water management can influence any component of subsidy linkages (Table 1; Fig. 1). These disruptions operate from landscape to global scales and have important effects on recipient ecosystems (Riley & Jefferies, 2004). For example, salmon runs have been severely disrupted by overfishing and river-channel obstructions, altering the density, growth and survival of freshwater and terrestrial organisms dependent on the marine-derived subsidy of nutrients in salmon carcasses (Gende *et al.*, 2002).

Over the past two centuries, human activities have markedly increased the concentrations of greenhouse gases in the Earth's atmosphere (IPCC, 2007). The resulting changes in global climate are predicted to alter physical and biotic processes that drive internal functioning of ecosystems, and the linkages among them (Palmer, 2009). Altered physical processes may include changes to temperature and precipitation, increased UV-B radiation, higher CO_2 concentrations and altered atmospheric circulation patterns (Riley & Jefferies, 2004). In freshwaters, climate change affects hydrologic processes by altering atmospheric circulation patterns, evapotranspiration rates, snowmelt timing and the magnitude and seasonality of precipitation (Neff *et al.*, 2000; Cao *et al.*, 2011). Collectively these factors will influence river discharge and flood magnitude (e.g. Varanou *et al.*, 2002), which, in turn, will potentially alter supply, transport and retention of subsidies such as leaf litter (Ballinger & Lake, 2006).

River watersheds are one example of a meta-ecosystem that consists of interacting sets of terrestrial and aquatic source and recipient ecosystems in three spatial dimensions: longitudinal, lateral and vertical (Fig. 2; Ward, 1989). Stream- and river-ecosystem function is influenced by subsidies among ecosystems because streams and rivers are low points in the landscape and have large edge-to-area ratios (Leroux & Loreau, 2008; Richardson *et al.*, 2010). Understanding the relative magnitudes of these linkages, and the importance of energy sources at different locations in the river network, have been central to theoretical development in freshwater ecology in recent decades (Table 2).

Fluxes in river-network linkages are dynamic, and river discharge is the primary driver of temporal variability in the connectivity between ecosystems (Ward, 1989). Both the high (storm-flows) and low (cease-to-flow) extremes of flow magnitude, and their seasonal timing, are critical determinants of the accumulation, availability and transport of terrestrially derived and aquatic organic-matter subsidies (Vidon *et al.*, 2010; Ylla *et al.*, 2010). Shifts in storm frequency, water runoff, flood potential and drought likelihood are expected under climate change (IPCC, 2007), but the resulting effects for cross-ecosystem subsidies have not been described. Changes in subsidy supply as a result of altered hydrology are likely to alter the dynamics of aquatic organic matter (Köhler *et al.*, 2008), with implications for food-web structure (e.g. Townsend *et al.*, 1998) and ecosystem processes, such as litter-decomposition rates and whole-stream metabolism (e.g. McTammany *et al.*, 2007; Kominoski *et al.*, 2010).

In many regions around the world (e.g. south-west USA, South Africa, northern China, and parts of Europe), there are projections of reduced precipitation and runoff by the end of the 21st century (IPCC, 2007). Downscaled climate-change projections suggest that south-eastern Australia, our focal area, will experience as much as a 30% reduction in precipitation by 2070 and an increase in drought frequency (Chiew *et al.*, 2011). This is expected to be associated with a shift in the seasonality of precipitation, with a reduction in autumn and winter rainfall (Chiew *et al.*, 2011). The drier climate probably will be punctuated with a higher frequency of events such as storms and floods (IPCC, 2007). Storm events have major effects on stream ecosystems but their influence on cross-system subsidies has not been widely evaluated (but see e.g. Greenwood & McIntosh, 2008).

Here, we present a conceptual model and case study to highlight how cross-system subsidies may be influenced by future climates. There is a need to better understand the effects of climate, hydrology and land-use changes on organic carbon processes in stream and river ecosystems to respond to rapid global changes (Tank *et al.*, 2010; Trimmer *et al.*, 2012). Storm flows have been incorporated poorly in aquatic carbon and nutrient budgets (Tank *et al.*, 2010), so we investigated the contribution of flow extremes to organic carbon export [both dissolved (DOC) and particulate (POC) organic carbon]. We sought to determine the contribution that storm flows make to the quantity and composition of organic carbon subsidies transported downstream. We project how predicted hydrologic changes will interact with land use to affect the composition, timing and retention of energy subsidies for stream and river ecosystems in future climates.

Methods

Study region and design

We assessed organic carbon export from 19 sites (in 15 streams; 1st-3rd Strahler order) in the Goulburn-Broken watershed (= catchment), south-eastern Australia (Table S1 in Supporting Information). The study streams are in a temperate climate (average annual rainfall 900 mm; Victorian Department of Sustainability and Environment, 2012) and their watersheds differ in proportions of land uses. The watersheds for the study streams range from being used primarily for cropping and livestock grazing (90% areal cover) to being dominated by native dry sclerophyll *Eucalyptus* forest and some pine plantation (up to 97% cover).

Hydrology

Stream height was measured with a TruTrack water level/temperature logger positioned at each site (Intech Instruments; Auckland, New Zealand). Height was converted to discharge with a rating curve built by measuring instantaneous stream discharge 7–13 times at each site over the range of observed stream heights. Instantaneous discharge was calculated by dividing the stream into at least five cells of equal width and measuring water velocity with a Marsh-McBirney Flo-Mate water velocity meter (Hach; Maryland, USA). Discharge was estimated using the slope-area method (Dalrymple & Benson, 1967) when maximum stream height exceeded the measured range of discharges. Depth loggers were deployed at sites between August 2010 and September 2012. Annual estimates of organic matter transport were made using two full years of daily discharge data at nine sites and one full year of daily discharge data at ten sites due to equipment loss.

Organic carbon measurement and modelling

Estimates of organic carbon transport were calculated for three size classes: dissolved organic carbon (DOC; < 0.45 μm), fine particulate organic carbon (FPOC; 0.4-1000 μm) and coarse particulate organic carbon (CPOC; 1 mm to 10-cm diameter). Duplicate 60-ml water samples for DOC and FPOC concentration were taken every four weeks. Additional samples were taken during storm-flow events and low-flow periods. Dissolved organic carbon samples were filtered (GF-75 glass fiber filters; Advantec, Dublin, USA) into pre-combusted amber-glass jars and acidified (to pH < 2) with 32% HCl. All samples (DOC and FPOC) were refrigerated immediately and organic carbon concentration analyzed using a Shimadzu TOC-V CPH/CPN

Total Organic Carbon analyzer (Shimadzu; Tokyo, Japan). FPOC concentration was calculated as total organic carbon (unfiltered) minus the DOC concentration.

CPOC export was measured by placing drift nets (600 × 600 mm opening; 1 mm mesh) in the stream channel for a known period of time. This was conducted at seven sites and replicated four to seven times at a range of stream discharges. Time of deployment depended on discharge and varied from several hours during high flows to > 24 hr at low flows. Water velocity at the mouth of the net was measured with a Marsh-McBirney water velocity meter to calculate the volume of water sampled through the net. Multiple nets were placed in the stream to sample the entire water column and surface transport when depth exceeded 600 mm. All organic material trapped was collected and frozen. The sample was dried (60°C, 1 week), weighed and incinerated (550°C, 4 hr) to calculate ash-free dry mass (AFDM). Carbon content was assumed to be 50% of AFDM (Meyer & Edwards, 1990) and CPOC concentration was expressed as mg C l^{-1}. We did not extrapolate CPOC measurements over the hydrologic time series given the inaccuracy of sampling CPOC export at high discharges and strong influence of other physical processes (e.g. previous hydrologic conditions, litterfall timing) on export.

Dissolved organic matter composition - specific UV absorbance (SUVA)

Small protein-like DOC molecules are more bioavailable to microbial consumers than are large, aromatic molecules (Balcarczyk *et al.*, 2009). The average molecular weight (MW) of humic materials in DOC samples was assessed using specific UV absorbance ($SUVA_{280}$) (Chin *et al.*, 1994). Triplicate filtered (Whatman GF/C) water samples were collected from a subset of nine sites during base flow conditions in Spring 2011 and again one week later during a storm spate (mean discharge 2.1 times greater). Samples were frozen in 15-ml polypropylene tubes and slowly defrosted prior to analysis. The UV-visible absorbance of each sample was measured at 280 nm with a UV-visible spectrophotometer (Unicam; Cambridge, England) using a quartz cuvette (path-length 1 cm). $SUVA_{280}$ was calculated as $SUVA_{280} = Abs_{280} / DOC$ (mol l^{-1}) (Chin *et al.*, 1994). The weight-averaged molecular weights of the DOC compounds in the sample were: MW (g mol^{-1}) = (3.99 × SUVA$_{280}$) + 490 (Chin *et al.*, 1994). Humic acids have average molecular weights between 2000–3000, whilst fulvic acids have average molecular weights < 1,000 g mol^{-1} (Zeng *et al.*, 2002).

Data analysis

We modelled the annual export of DOC and FPOC using a two-step process. First, we used a hierarchical Bayesian model to calculate the effect of instantaneous stream discharge (Ml day^{-1}) on mean DOC or FPOC concentration (mg l^{-1}) at each site *j*:

$$DOC_{ij} \sim N\left(\mu_{ij,}\sigma_1^2\right);\ \mu_{ij} = a_j + b_j \times \ln(discharge_{ij})\,;$$

$$a_j \sim N(\bar{a}, \sigma_2^2);\ b_j \sim N\left(\bar{b}, \sigma_3^2\right);\ \bar{a}, \bar{b} \sim N(0{,}0.001);\ \sigma_{1:3} \sim U(0{,}10).$$

There were multiple measurements at site *j* (*ij*) that are modelled as functions of the discharge. The model produces site-specific intercepts (a_j) and slopes (b_j) that are drawn from common distributions of intercepts and slopes with means $\bar{a}$ and $\bar{b}$. *N*() and *U*() indicate normal and uniform distributions and all priors for model parameters were uninformative.

The site-specific relationships (and uncertainties) then were used to predict the mean DOC or FPOC concentration for the daily flow time-series at each site. The estimated concentrations and volumes were used to calculate DOC or FPOC load and watershed yield (load/watershed area) for 12 or 24 months. The contributions of surface runoff from precipitation events to export of DOC and FPOC were calculated by predicting concentrations at base-flow discharge using the same model as above. The surface-flow contribution to discharge was apportioned from total discharge using the recursive digital filter method (Nathan & McMahon, 1990). Estimates of CPOC export were collected over a range of discharges, and yearly estimates reported in Table S1 are based on mean concentration and water volumes only.

The effect of river discharge (Q_{ij}, expressed as a proportion of base-flow to compare among different sized streams) on DOC, FPOC and CPOC export was analysed with a linear model:

$$R_{ijk} \sim Normal\left(\mu_{ijk}, \sigma_o^2\right);\ \mu_{ijk} = \alpha + \beta \times Q_{ij} + \varepsilon_j^{site} + \varepsilon_k^{stream}\ ;$$

$$\sigma_o \sim Uniform(0.001{,}10); \alpha, \beta \sim Normal(0, \sigma^2 = 1000);$$

$$\epsilon_j \sim Normal(0, \sigma_s^2);\ \sigma_s \sim Uniform(0.001{,}10).$$

Here, R_{ijk} is the measured response at time i in site j and stream k, which are distributed normally with means μ_{ijk} and a common variance σ_o^2. The μ_{ijk} are modelled as a linear function of Q_{ij} , which are the flows corresponding to the response measurements, α and β are the regression coefficients, $\varepsilon_j^{site}$are the random effects for sites, and the ε_k^{stream} are random effects for stream (to account for multiple sites on one stream), which are drawn from a common distribution with mean 0 and variance σ^2.

The effect of season on the relationship between discharge ($\log_{10}$ proportion of base-flow) and export was modelled by including a season term in the slope of the above model:

$$\mu_{ijk} = \alpha + \beta_1[Season]_i \times Q_{ij} + \varepsilon_j^{site} + \varepsilon_k^{stream}\ ;$$

$$\beta \sim Normal(0, \sigma^2 = 1000).$$

The effect of discharge (Q, $\log_{10}$ proportion of base-flow) on the proportion of total organic carbon as DOC [i.e. DOC/(DOC+FPOC)] was modelled using an exponential model:

$$R_{ij} \sim Normal\left(\mu_{ij}, \sigma_o^2\right); \mu_{ij} = \alpha - e^{(\beta_j Q_{ij})} + \varepsilon_k^{stream} + \ \varepsilon_j^{site};$$

$$\sigma_o \sim Uniform(0.001{,}0.5); \alpha, \beta \sim Normal(0, \sigma^2 = 1000)\mathrm{I}(0,);$$

$$\epsilon_j \sim Normal(0, \sigma_s^2);\ \sigma_s \sim Uniform(0.001{,}0.5).$$

Where parameters are as described above.

The difference in mean MW of DOC samples taken during base-flow and storm-flow was modelled with a two-group comparison:

$$Y_{ij} = \alpha + \beta I_j + \varepsilon_i;\ \alpha, \beta \sim N(0, \sigma^2 = 1000);$$

$$\alpha, \beta \sim Normal(0, \sigma^2 = 1000);$$

$$\varepsilon_i \sim U(0, \sigma_\varepsilon^2); \sigma_\varepsilon \sim U(0.01,10).$$

Here, Y_{ij} is the measured value in stream i in flow j, I_j is an indicator variable that is 0 for base-flow and 1 for storm-flow, α is the intercept and the estimate of the mean for base-flow, β is the estimate of the difference of values for storm-flow relative to base-flow, and the ε_i are the random effects for sites.

OpenBUGS (version 3.2.2; Lunn *et al.*, 2009) was used for all analyses. We used the odds ratio (OR = posterior odds:prior odds) to indicate an important effect of model parameters, where OR > 10 indicates ‘strong’ evidence of an effect (Jeffreys, 1961). An OR of infinity (inf.) indicates that there is virtually no doubt that the parameter differs from zero. We used uninformative priors, so the prior odds were unity.

Results

Relationship between flow and organic carbon export

Mean daily flow ranged from 1.82 to 230 Ml day^{-1} (corresponding to the 66th to 89th flow percentiles) among the 19 study sites (Table S1). Surface runoff (storm flows) contributed substantially to annual runoff. Some 31% ± 7 SD of the annual discharge came from surface runoff following rain events (Table S1).

There was a positive relationship between discharge (Ml day^{-1}) and DOC concentration (mean slope = 2.2 ± 0.2 SD; OR for all sites = inf.) and FPOC concentration (mean slope = 0.77 ± 0.14 SD; OR for all sites > 14). There was a strong positive relationship between log(discharge as a proportion of base-flow) and log(DOC export) (Fig. 3a; slope = 2.7 ± 0.04 SD, OR = inf.)

and between log(discharge) and log(FPOC) export at all sites (Fig. 3a; slope = 2.8 ± 0.14 SD, OR = inf.). There was a positive relationship between log(discharge as a proportion of base-flow) and log(CPOC export) (Fig. 3a; slope = 0.52 ± 0.12 SD, OR = inf.).

There was little seasonal variation in the slope of the linear relationship between log(DOC export) and log(discharge as a proportion of base-flow), which ranged from 2.6 to 2.8 among seasons. There was a small difference between autumn and summer (difference in slope 0.17 ± 0.09 SD; OR = 40). The slope of the relationship between log(FPOC export) and log(discharge relative to base-flow) differed seasonally. Increased discharge produced greater increases in FPOC concentration in autumn (slope = 2.9 ± 0.23) and summer (slope = 3.1 ± 0.21) compared to spring (slope = 1.5 ± 0.48; ORs of differences = 237 and 673 respectively) and winter (slope = 2.3 ± 0.38; ORs of differences = 13 and 28 respectively).

Organic carbon transport

DOC was the dominant form of organic matter exported from all watersheds (Table S1). On average, 87% ± 6 SD (mean export 2841 kg C km^{-2} yr^{-1}) of the carbon was in the dissolved form, while 12% ± 6 SD was FPOC (mean export 480 kg C km^{-2} yr^{-1}) and 0.49% ± 0.93 SD for CPOC (mean export 1.36 kg C km^{-2} yr^{-1}).

Much of the export of organic carbon occurred during storm flows. Surface runoff (31% of discharge) contributed on average 57% ± 14 SD of DOC export and 75% ± 14 SD of FPOC export. Export quantity was disproportionately great in flows occurring 5% of the time (39% ± 15 SD and 59% ± 15 SD for DOC and FPOC respectively).

Discharge affected the relative contribution of dissolved to particulate organic carbon exported from the watersheds. At base-flow, almost all of the organic carbon was dissolved, but the proportion of FPOC increased with rising discharges to *c.* 25% of the total organic carbon at the highest discharges sampled (up to 1,000 times base-flow, Fig. 3b; $\beta = -0.078 \pm 0.008$ SD, OR = inf.).

Dissolved organic carbon composition

The molecular weight of DOC samples (overall mean 2,230 g mol^{-1} ± 176 SD) indicated molecules were composed mostly of humic acids (Zeng *et al.*, 2002). These aromatic compounds typically dominate freshwater DOC and are not readily bioavailable (Fellman *et al.*, 2009). The bulk of DOC in the streams has a terrestrial origin, although there is some contribution by in-stream sources at agricultural sites (Giling *et al.*, 2014). There was little difference in the molecular weight of DOC sampled in nine sites during base-flow and storm-flow conditions (two-group comparison; mean difference = 0.17 g mol^{-1} ± 31 SD; OR = 1.00). Bacterial uptake rates can increase during storm-flows, but this does not have a strong effect on total export (Buffam *et al.* 2001). Therefore, the contribution of storm-flow to the transport of labile DOC will be approximately proportional to its contribution of total DOC export (i.e. 57%).

Discussion

Organic carbon transport

Our findings contribute to the growing global body of evidence that changing climates are strongly influencing watershed biogeochemical cycles (Köhler *et al.*, 2009). Increases in both discharge and organic carbon concentration from the 19 stream sites indicated additional sources of carbon from the channel or terrestrial environment were being mobilized (Dalzell *et al.*, 2005). There was temporal variation in the discharge-export relationship, with stronger relationships between discharge and FPOC export during summer and autumn, coinciding with peak litterfall (Chapter 6), high temperatures and periods of lower total discharge. Fine particulate organic carbon probably accumulates between the less frequent high summer discharge, greatly increasing concentrations and export when high flows occur. This illustrates the potential for interactions between changes in seasonal flow regimes arising from climate change and a fundamental ecosystem process (carbon flux).

Carbon export from the watersheds was dominated by DOC (often > 90% of export; Waterloo *et al.*, 2006). However, there were significant effects of weather events. The region experienced its largest flooding events for > 20 years during the two-year study period (the ‘Big Wet’; Leblanc *et al.*, 2012). The proportion of annual DOC load that was exported in storm-flows (57%) in our watersheds was comparable to storm-flow or peak-flow (top 10% discharge) estimates from watersheds in the Northern Hemisphere (e.g. Clark *et al.*, 2007; Dalzell *et al.*, 2007). There were greater quantities of particulate organic carbon exported during floods, and the export of fine particulate organic carbon (FPOC) increased relative to DOC at higher discharges (Fig. 3a; Wiegner *et al.*, 2009). Similar results have been shown elsewhere; export of CPOC from two Caribbean headwater streams increased after hurricane conditions, with long term ecological effects (Scalley *et al.*, 2012). Our findings demonstrate that high-flow periods and extreme weather events are crucial for organic-carbon transport in river networks. The potential role of increases in the frequency and intensity of extreme weather events under climate-change scenarios on ecosystem processes has been little explored, but is likely to be an important driver of ecological change (Jentsch *et al.*, 2007; Thompson *et al.*, 2013).

Forecasting the effect of future flow variability on subsidies

The case study presented here is one component of how connectivity in multiple spatial dimensions of riverine landscapes will be altered under more variable future climates (Fig. 4). An increase in storm-flow frequency and magnitude will increase the total longitudinal export of organic carbon (Fig. 2 arrow 2 & 4, Fig. 4c; Trimmer *et al.*, 2012). Increased storm-flow frequency also will increase the relative proportion of the particulate fraction of annual carbon net export from forested and agricultural watersheds. These effects are likely to be important globally; climate scenario modelling predicts a 1.5–2.5 mg l^{-1} increase in total organic carbon concentrations in Swedish streams (Köhler *et al.*, 2009), and changes in the spatial patterns and timing of snow fall and rain events increase sediment export from watersheds in north-east Asia

(Park *et al.*, 2010). Altered subsidy dynamics are not limited to carbon; modelled rainfall-runoff in Denmark using downscaled climate models suggest a 7.7% increase in total nitrogen export under climate change by the end of the century (Andersen *et al.*, 2006). Altered transport of subsidies will affect recipient ecosystems, such as altered estuarine and oceanic phytoplankton production, as shown in China and the USA (Paerl *et al.*, 2006; Gong *et al.*, 2011).

In the lateral dimension (Fig. 2 arrow 3), floods will increase deposition of FPOC and CPOC onto floodplains (Tockner *et al.*, 1999) and move leaf litter and large wood from the floodplain into river channels (Neatrour *et al.*, 2004; Pettit & Naiman, 2005) (Fig. 4c). Leaf-litter breakdown, an important process for energy transfer to food webs, can be retarded by smothering sediments, or elevated through increased moisture, nutrient availability and mechanical stress (Chauvet, 1988; Neatrour *et al.*, 2004). Discharge can affect the source and ‘quality’ (= ease of breakdown) of DOC subsidies because DOC entrained during storm flows from outside the channel may be less bioavailable compared to that of base flow (Wiegner *et al.*, 2009; Vidon *et al.*, 2010, but see this study). These differences in bioavailability are likely to contribute to the influence of flooding on whole-ecosystem rates of organic carbon consumption (ecosystem respiration) and production (gross primary production) (Roberts *et al.*, 2007). Floods also promote lateral and vertical connectivity with hyporheic and groundwater zones (Fig. 2 arrow 1; Harvey *et al.* 2012), providing another strengthened conduit for energy, nutrients and biota (Fig. 4c).

Drought conditions, such as those experienced across much of south-eastern Australia for a prolonged period between 1997 and early 2010 (Verdon-Kidd & Kiem, 2009; Leblanc *et al.*, 2012), reduce stream flow and hydrologic connectivity (Lake, 2003) with effects for energy subsidies (Fig. 4b). Prolonged low-flow conditions favour retention over export (Bernal *et al.* 2013), where leaf litter accumulates in shallow channels and on floodplains, and microbial processing is low in the dry conditions (Corti *et al.*, 2011). These low-flow and cease-to-flow conditions may increase in duration in the future because precipitation is expected to decline by up to 20% in mid-latitudes (IPCC, 2007), reducing overall transport (Fig. 4b) and processing of organic-carbon subsidies (Larned *et al.*, 2010). Longitudinal and lateral connectivity may be maintained by hyporheic flows during periods of surface water disconnection (Daltry *et al.* 2007). These sub-surface linkages are important relative to other fluxes during cease-to-flow events, but are spatially variable depending on river bed topology and substrate porosity (Boulton *et al.* 1998), so that this linkage may not be strong compared to its capacity at base or storm flow (Fig. 4b).

Altered timing, frequency or duration of floods and low flow periods will have considerable consequences for ecosystem responses. Longer inter-flood frequencies will shift the annual balance between production and consumption of organic carbon (Young & Huryn 1996; Uehlinger 2000). Bed-moving spates have a greater effect on primary production than on respiration, so that floods shift systems towards net heterotrophy (Uehlinger 2000). Autotrophs may become more prolific during low flow periods with shallower depths and lower turbidity (Young & Huryn 1996). The altered timing of low-flow periods relative to litterfall and seasonal temperature variation is critical to hydrological effects on organic carbon dynamics and metabolism on floodplains (Robertson *et al.*, 1999; Roberts *et al.*, 2007; Köhler *et al.*, 2009). The predicted increase in summer rainfall in south-eastern Australia under climate change coincides with the availability of fresh *Eucalyptus* litter (Chapter 6). This leaf material leaches large quantities of bioavailable organic carbon compounds when wetted (Baldwin, 1999), particulalry following prolonged periods of disconnection between channels and floodplains (Valett *et al.* 2005). The leachate stimulates intense ‘blooms’ of wetland microbial activity on floodplains that transport labile material to river channels during overbank flows (Boon *et al.*, 1997; Fig. 4c).

Altered subsidy dynamics may be exacerbated in landscapes degraded by land-use change, particularly during low-flow periods. When streams dry into a series of disconnected pools, surface-water longitudinal and floodplain linkages are disrupted, and the influence of directly adjacent riparian vegetation greatly increases (Fig. 4b). Different densities and canopy cover of riparian zone vegetation adjacent to disconnected pools can lead to divergence in aquatic organic-matter characteristics, even over small spatial scales (Lake, 2005; Bond *et al.*, 2008). Intact local riparian vegetation can cause accumulation and concentration of dissolved and particulate organic matter in isolated stream pools during periods of drawdown (McMaster & Bond, 2008; Giling *et al.*, 2009). Conversely, pools with little canopy cover may have greater macrophyte and algal growth (Dahm *et al.*, 2003; Giling *et al.*, 2009). Thus, local riparian condition and drought may interact to affect resource quantity and quality (Giling *et al.*, 2009).

There are many other ways in which climate change will affect cross-system subsidies in watersheds. Flooding and drying influences subsidies in aquatic ecosystems by altering ecosystem boundaries (Greenwood & McIntosh, 2008) and abundances of aquatic insects (Greenwood & McIntosh, 2010; Walters & Post, 2010). Increases in mean water temperature affects DOC dynamics (Striegl *et al.*, 2005; Laudon *et al.*, 2012), raises bacterial respiration rates (Sand-Jensen *et al.*, 2007) and may alter species' distributions (Davies, 2010). Elevated concentrations of atmospheric CO_2 may increase labile DOC emissions by wetland plants (Freeman *et al.*, 2004) and change the quality of riparian leaf litter inputs (Kelly *et al.*, 2010). Although warming and CO_2 concentration affect a range of processes that affect DOC dynamics, it is likely the DOC budget will be more strongly controlled by variation in discharge (Acuña & Tockner, 2010).

Managing subsidies under changing climates

Both transported organic material and locally-produced aquatic sources of energy can be important to aquatic food webs, but the relative contribution of subsidies in different dimensions differs temporally based on current and previous hydrologic conditions (Pingram *et al.*, 2012). The predicted changes in precipitation will manifest in future hydrologic regimes of some regions becoming increasingly variable (Fig. 4). Organic-carbon dynamics in some systems may become more like those of temporary rivers (see Larned *et al.*, 2010), with long periods of water drawdown associated with terrestrial organic matter accumulation, greater autotrophy and increased importance of algal or phytoplankton production to food webs (Bunn *et al.*, 2003; Reid *et al.*, 2008) (Fig. 4b). These periods of disconnection may be interspersed with rapid ‘blooms’ of organic matter leaching, microbial respiration and transport of terrestrial subsidies during and immediately following high flows, which may be exacerbated when associated with high temperatures (Roach, 2013) (Fig. 4c). The magnitude of these effects will be highly dependent on the frequency and timing of high and low-flow events (Vehlinger *et al.* 2000; Valett *et al.* 2005). Climate-change-induced reductions in total rainfall, but increased probability of summer rainfall, may increase the intensity of algal blooms, tannin concentrations and microbial respiration, with an associated reduction in dissolved oxygen concentration that can lead to fish kills (Whitehead *et al.*, 2009; Hladyz *et al.*, 2011).

While the processes described here are for stream ecosystems, there are likely to be comparable effects of extreme climate events for subsidy dynamics in other ecosystems. Altered sea level, wave direction and storm frequencies decrease beach width, reducing the accumulation of macroalgal food subsidies and reducing beach invertebrate abundance (Revell *et al.*, 2011). Productivity of terrestrial systems on islands may be altered by changes in the intensity and frequency of pulse events of rain that mobilize nutrients in bird-guano subsidies (Anderson *et al.*, 2008). Extreme climatic events play major roles in the delivery of spatial subsidies, and the inclusion of storm-event sampling is critical for understanding (Tank *et al.*, 2010). To better manage stream and river systems, the predicted shifts in the extremes of hydrological variability must be considered to ensure lateral, longitudinal and vertical connectivity (Jansson *et al.*, 2007; Chiu *et al.*, 2013). From a management perspective, successful maintenance and restoration of ecosystems must employ a meta-ecosystem perspective, and explicitly incorporate cross-ecosystem subsidies and predicted changes to those subsidies that are likely to arise with climate change.

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Table 1. Examples of anthropogenic effects on components of the cross-system subsidy pathway in freshwater meta-ecosystems. The numbered components are described in Fig. 1.

Component	Example of component	Driver of disruption	Effect on flux (5)	Consequence for recipient habitat (6)	Reference
(1) Donor habitat	riparian vegetation	vegetation loss	reduced terrestrial inputs to streams	altered community structure and food webs	Wallace *et al.* 1997
	inland waters	invasive fish alters food source of native fish	reduced emergence of aquatic invertebrates	decline in riparian spiders	Baxter *et al.* 2004
	inland waters	warming and nutrient increases	increased insect emergence, increased decomposition rates	potential effects for terrestrial food webs and carbon balance	Greig *et al.* 2012
(2) Boundary	forest edges	clearing and fragmentation	altered atmospheric deposition and canopy-water throughfall of nutrients and inorganic compounds	potential indirect effects for nutrient cycling and seedling establishment	Weathers *et al.* 2001
	aquatic-terrestrial boundary	altered flood disturbance	low level of disturbance reduces potential loose-rock habitat by facilitating greater plant growth	reduced number and biomass of fishing spiders	Greenwood & McIntosh 2008
	riparian vegetation	high-severity wildfire	increased in-stream productivity, greater biomass of generalist *r*-strategist larvae, increased aquatic insect emergence	increased insect availability for terrestrial food webs	Malison & Baxter 2010
(3) Corridors	river channels	dams and other obstructions	blocks salmon migration	reduced survival, growth, abundance of aquatic and terrestrial consumers	Gende *et al.* 2002
			reduced export of dissolved silicon to oceans	altered proportion of diatoms and flagellates in oceans with potential indirect effects for food web structure	Humborg *et al.* 2000
		channelization	reduced benthic invertebrate abundance and terrestrial-aquatic connectivity	altered richness and density of terrestrial invertebrate predators	Kennedy & Turner 2011
(4) Vectors	freshwater	global change, water extraction	more variable discharge alters downstream subsidies and floodplain connectivity	altered biogeochemical cycles, reduced insect density at low flows	Park *et al.* 2010; Walters & Post 2010
	freshwater	river regulation	reduced aquatic insect emergence	altered terrestrial invertebrate biomass	Jonsson *et al.* 2013
	oceans	altered atmospheric circulation patterns	changes oceanic upwellings that transport phytoplankton resources	reduced mussel recruitment	Menge *et al.* 2009

Table 2. Spatial dimensions of subsidies in river meta-ecosystems, and the theoretic work that describes them. Dimension numbers (1-4) refer to the subsidy pathways shown in Fig. 2.

#	Dimension	Donor and recipient systems			Vectors	Major fluxes	Boundaries
1	**Vertical (HCC)** (Hyporheic Corridor Concept; Stanford & Ward 1993)	Groundwater (upstream and lateral); hyporheic zone	↔	surface waters (downstream)	water; biota	organic carbon, nutrients, biota	water-sediment interface
2 & 4	**Longitudinal (RCC)** (River Continuum Concept; Vannote *et al.* 1980)	headwater streams; rivers	→	rivers; estuaries and oceans	water; biota	detrital energy sources (e.g. FPOC)	
3	**Lateral (FLC)** (Flood-Pule Concept; Junk *et al.* 1989)	riparian zone and floodplain	↔	streams and rivers	water; biota; wind; gravity	organic carbon, inorganic material and sediments, nutrients, biota	riparian zone, littoral zone

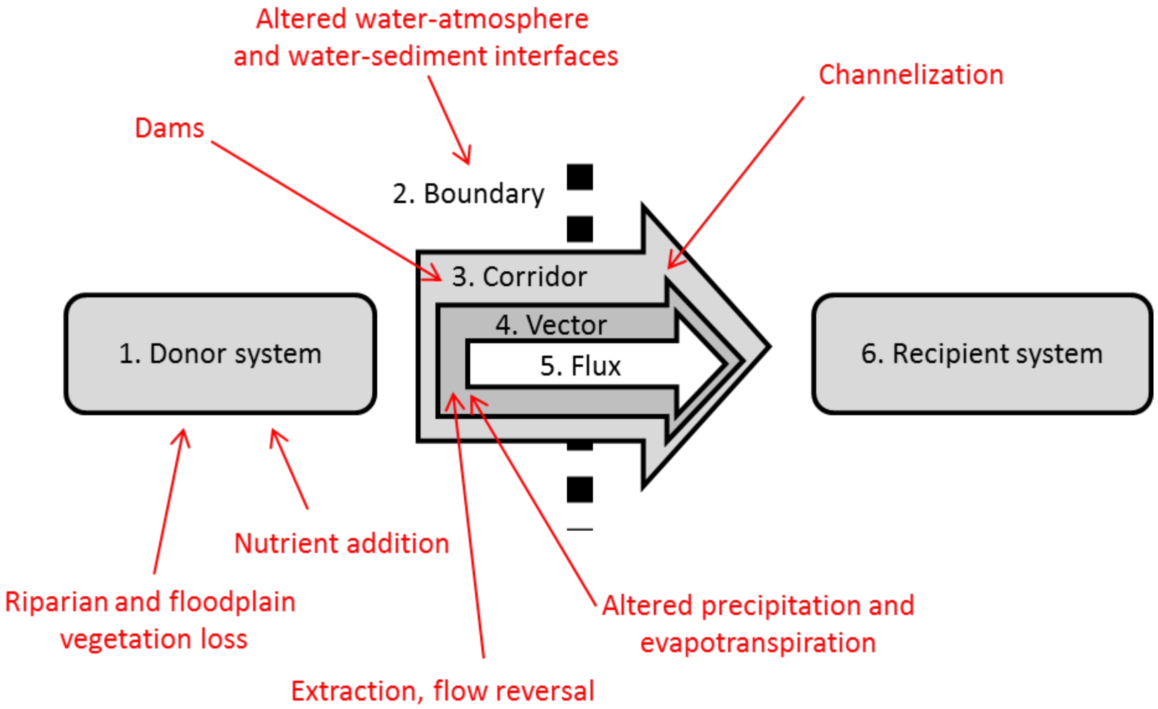

Figure 1. Schematic representing each component of a subsidy pathway (adapted from Polis *et al.*, 1997). The pathway consists of a donor system (1), which controls a resource flux (5) that is transported by a vector (e.g. water or biota; 4) across an system boundary (2) to a recipient system (6). This vector may occur within a defined corridor (3), such as a river channel. Boundaries can have a range of structural and functional attributes that affect resource fluxes (Strayer *et al.*, 2003). Here we define the boundary as a zone that separates two distinct ecosystems. The boundary has an area, and the edges of this boundary may be diffuse (e.g. forest edges; 100s m) or more abrupt (e.g. terrestrial-aquatic boundaries). The boundaries considered here generally are 10s of m wide, but may be many km long. Red arrows indicate how anthropogenic effects can affect any component of the pathway, using river systems as an example. These disruptions ultimately lead to altered subsidy quantity and/or quality being delivered to the recipient system.

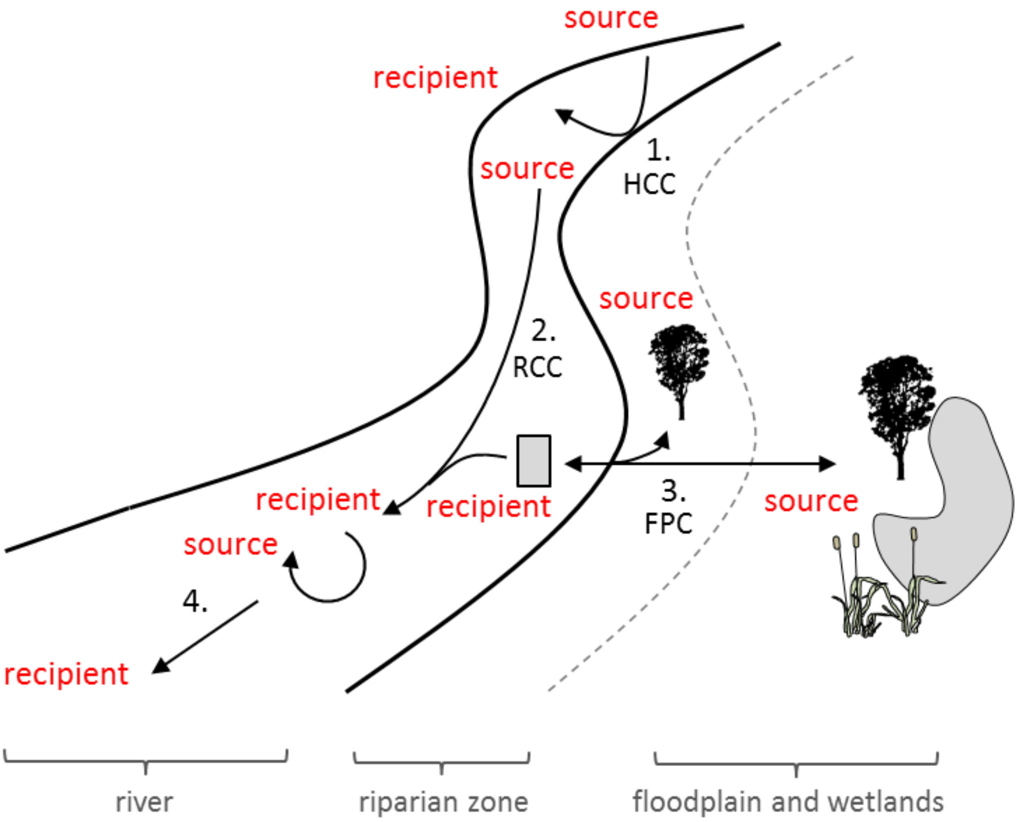

Figure 2. Generalized subsidy transfers and organic-carbon pathways in the stream and river meta-ecosystem. Acronyms (HCC, RCC and FPC) refer to ecological theories describing the dimensions of transport in lotic systems (Table 2). Arrows indicate directional pathways of organic carbon movement between source and recipient systems (red text). The grey box indicates benthic storage of organic carbon that is consumed and recycled (as shown by circular arrow) as it moves downstream (i.e. organic carbon spiralling). Note that arrow 1 (HCC) is drawn once for simplicity; this subsidy occurs repeatedly along the entire channel in downwelling and upwelling zones, and includes lateral groundwater inputs. Arrow 3 (FPC) is strongest where geomorphology and hydrology enable large floodplain areas that are occasionally inundated.

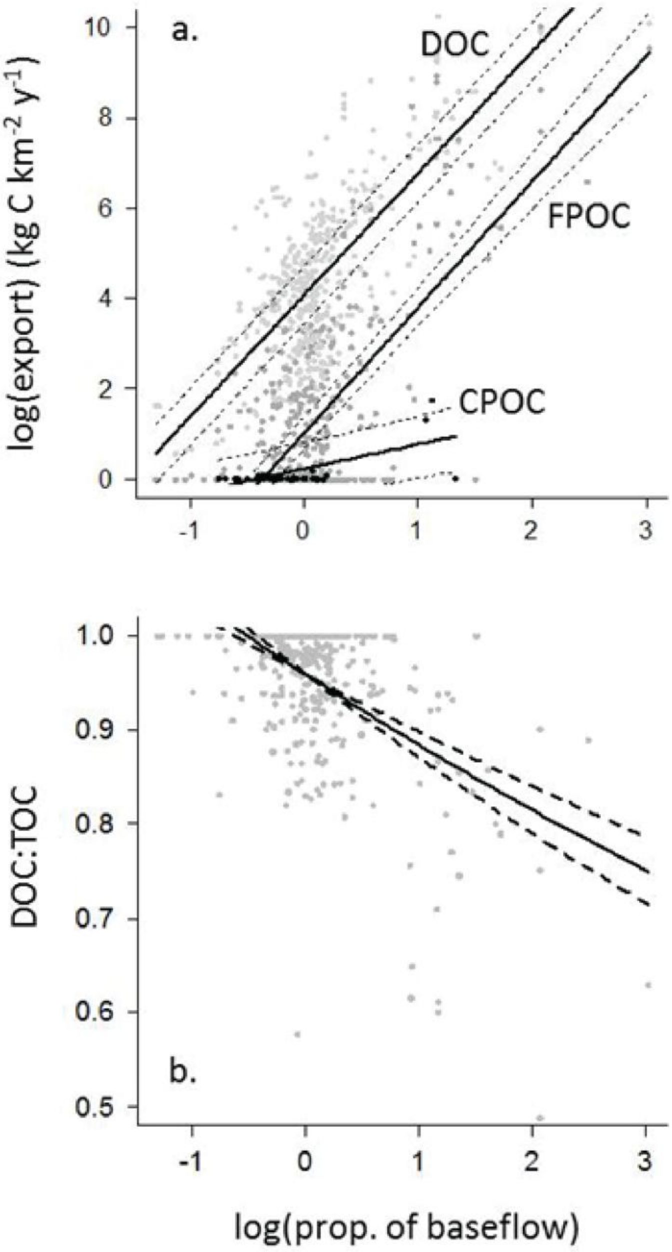

Figure 3. Scatterplots showing relationship and mixed model fit (dashed line shows 95% credible interval) between proportion of base-flow and a. export of DOC (light grey points), FPOC (medium grey points) and CPOC (black points), and b. proportion of DOC to TOC (i.e. DOC/(DOC+FPOC)).

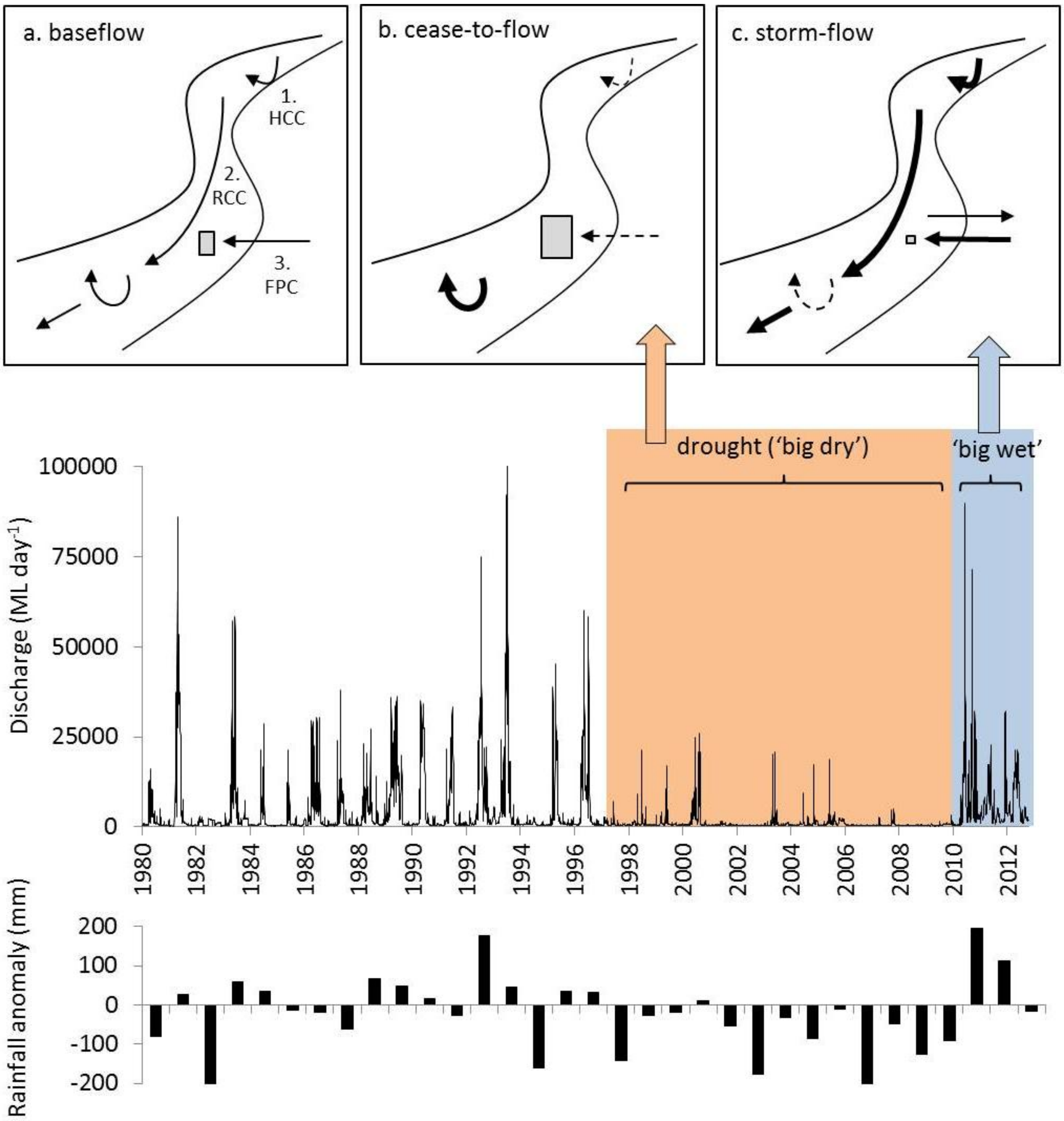

Figure 4. Conceptual model showing the predicted relative strength of subsidy interactions in the river meta-ecosystem as hydrologic conditions vary over time due to rainfall variation (data: Thiess Environmental Monitoring and Australian Bureau of Meteorology). Inserts show subsidy dynamics at: a. baseflow; b. cease-to-flow (such as during the 'big dry' drought) and; c. storm-flows (such as during the 'big wet' flooding). In panels b and c the dashed lines indicate weak interactions and thicker solid lines indicate strong energy subsidy transport relative to a. baseflow conditions (shown as thin solid lines) for each arrow. Size of grey boxes indicates relative accumulation of benthic material, and circular arrows indicate the processing of carbon as it moves downstream.

Supporting Information

Table S1. Summary of hydrology measurements and the mean (SD) estimates of modelled dissolved (DOC) and fine particulate (FPOC) organic carbon export from the 19 study sites. Coarse particulate organic carbon (CPOC) results show the mean (SD) of replicate measurements at seven sites.

				Hydrology			DOC model			FPOC model			Measured CPOC		
Site	Data period (yr)	Latitude (° S)	Longitude (° E)	Mean daily flow (Ml day^{-1})	Flow variability (C_v)	Surface runoff contribution (%)	Mean DOC concentration (mg l^{-1})	Mean DOC export (kg C km^{-2} yr^{-1})	Surface runoff contribution (%)	Mean FPOC concentration (mg l^{-1})	Mean FPOC export (kg C km^{-2} yr^{-1})	Surface runoff contribution (%)	Mean CPOC concentration (mg l^{-1}) *n* = 4 - 7	Mean CPOC export (kg C km^{-2} yr^{-1}) *n* = 4 - 7	Mean temp. (°C; logger)
Castle (lower)	2	36.86	145.58	11.8	4.0	40	9.24 (0.83)	4019 (321.1)	77	0.08 (0.16)	421.4 (165.9)	93			14.3 (5.32)
Castle (upper)	1	36.90	145.59	5.9	1.4	30	7.46 (0.82)	910.6 (93.64)	56	0.31 (0.29)	93.92 (48.8)	86			13.4 (4.12)
Creightons	2	36.88	145.53	24.3	1.8	31	9.06 (0.62)	5124 (336.7)	55	0.49 (0.27)	597.0 (165.8)	70	0.0027 (0.0040)	0.1466 (0.2038)	14.0 (4.77)
Faithful (lower)	2	36.74	145.66	25.8	0.8	25	9.98 (0.69)	2679 (183.3)	40	0.67 (0.32)	235.5 (91.2)	60			14.6 (4.91)
Faithful (upper)	1	36.75	145.75	3.4	1.4	30	5.12 (0.81)	1016 (128)	60	0.18 (0.24)	102.0 (58.9)	89			12.8 (3.89)
Harrys	2	36.70	145.74	8.6	4.8	46	9.15 (0.64)	7598 (693.8)	91	0.49 (0.29)	1785 (314.9)	97			13.4 (4.73)
Hollands	1	36.71	146.09	125.7	1.4	33	3.71 (0.75)	1662 (223.7)	67	0.78 (0.34)	476.1 (1101.)	74			14.9 (5.76)

(Table S1 continued)

Honeysuckle	2	36.65	145.74	22.6	2.4	37	9.03 (0.66)	3508 (224.4)	68	0.76 (0.30)	869.1 (111.3)	82	0.0016 (0.0014)	0.0536 (0.0579)	15.1 (5.24)
Moonee (lower)	2	36.74	145.99	48.4	1.0	26	6.43 (0.73)	2502 (264.4)	48	0.33 (0.28)	182.2 (122.7)	66	0.0001 (7.2264)	0.0122 (0.0098)	14.0 (4.60)
Moonee (upper)	1	36.84	145.94	8.6	0.6	16	4.27 (0.84)	666.9 (121.5)	32	0.31 (0.30)	59.7 (48.6)	50			12.2 (3.18)
Ryans	1	36.64	146.19	96.6	0.7	23	3.16 (0.77)	1281 (267.9)	47	0.47 (0.32)	219.9 (119.4)	59			17.5 (5.67)
Seven (lower)	2	36.71	145.54	230.0	1.2	31	9.38 (0.68)	5116 (379.2)	54	0.37 (0.29)	303.5 (179.0)	69	0.0016 (0.0034)	2.2734 (5.8962)	15.5 (5.81)
Seven (upper)	1	36.81	145.82	18.8	1.9	29	7.91 (0.78)	2585 (246.1)	55	0.24 (0.26)	154.7 (113.9)	79			11.5 (4.38)
trib. of Broken	2	36.92	145.98	1.8	3.6	36	9.44 (0.81)	3008 (241.3)	68	0.13 (0.21)	342 (127.6)	90	0.0006 (0.0005)	0.2098 (0.3624)	13.9 (4.76)
Two Mile	1	36.65	145.78	3.3	2.3	39	11.1 (0.88)	476.5 (38.24)	71	0.25 (0.29)	62.5 (20.7)	92			14.9 (4.08)
Warrenbayne (lower)	2	36.70	145.88	29.4	1.2	33	6.29 (0.65)	2658 (234.5)	64	0.52 (0.28)	339.5 (112.9)	80	0.0069 (0.0148)	6.0740 (14.650)	13.8 (4.97)
Warrenbayne (upper)	1	36.72	145.85	18.3	1.1	25	5.31 (0.81)	1177 (153.8)	50	0.31 (0.29)	108.9 (68.8)	74			13.0 (4.50)
White Gum Gully	1	36.80	145.89	8.6	0.7	19	3.58 (0.84)	1101 (225.2)	40	0.46 (0.34)	179.5 (101.8)	59			12.0 (3.12)
Wombat	1	36.87	145.63	20.1	1.6	31	10.6 (0.65)	6886 (481.4)	52	2.15 (0.31)	2585 (278.4)	59	0.0077 (0.0072)	0.7522 (0.7730)	14.1 (4.87)

Declaration for Thesis Chapter 6

Declaration by candidate

In the case of Chapter 6, the nature and extent of my contribution to the work was the following:

Nature of contribution	**Extent of contribution (%)**
I performed 95% of the fieldwork, all the laboratory work (except for some outsourced chemical analyses), 90% of the statistical analyses and was the primary author of the manuscript.	70%

The following co-authors contributed to the work. If co-authors are students at Monash University, the extent of their contribution in percentage terms must be stated:

Name	**Nature of contribution**	**Extent of contribution (%) for student co-authors only**
Ralph Mac Nally	Input of ideas and contributed to analysis and writing of the manuscript.	
Ross M. Thompson	Input of ideas and contributed to writing the manuscript.	

The undersigned hereby certify that the above declaration correctly reflects the nature and extent of the candidate's and co-authors' contributions to this work*.

Candidate's Signature	[redacted]	**Date** 11.4.14
Main Supervisor's Signature	[redacted]	**Date** 11.4.14

*Note: Where the responsible author is not the candidate's main supervisor, the main supervisor should consult with the responsible author to agree on the respective contributions of the authors.

Chapter 6

Aquatic organic carbon dynamics in massively altered landscapes: Past, present and future.

Abstract

1. Restoring native vegetation has occurred at small spatial scales, with limited ability to reverse the watershed-scale degradation caused by agriculture. Extensive replanting may become feasible if restoration is driven by economic forces, such as payments to plant trees for carbon sequestration. Replanting often occurs in riparian zones, where clearing has reduced the provision of organic carbon to aquatic ecosystems. Altered terrestrial-aquatic linkages affect in-stream processing and energy flow, with implications for watershed carbon export, an important component of global carbon budgets.
2. We examined whether riparian replanting shifted fluxes of aquatic organic carbon towards pre-clearance condition. Organic carbon inputs, standing stock, metabolism and transport were measured in replanted (≤ 22 years old) and pasture reaches of streams in an agricultural landscape in south-eastern Australia. We upscaled fluxes to similarly-sized streams of a seventh-order watershed to estimate the effect of replanting on broad-scale carbon balance.
3. At reach scales, replanting increased canopy closure, terrestrial inputs and in-channel benthic leaf litter. Replanting was associated with lower net ecosystem productivity and more efficient organic carbon processing, nearer to values typical of forested systems. Organic-carbon budgets suggested that replanted streams may become more heterotrophic (-0.52 g C m^{-2} day^{-1} ± 0.80 SD; autumnal rate). At a regional scale (*c.* 24,000 km^2), the increased carbon loss was similar to above-ground storage by replanted trees per unit area, but an order of magnitude lower than total watershed export, which was governed by hydrology.

4. Replanting will restore many aquatic organic carbon processes towards pre-tree-clearance condition within decadal timescales. Replanting should focus on 2nd and 3rd order streams in agricultural landscapes because they are well connected to the terrestrial environment and will have a positive ecological response to restoration more quickly than will larger systems. Incorporating river networks in the landscape and focusing on restoring processes that provide connectivity between terrestrial and aquatic ecosystems is vital to managing the effects of global changes.

Introduction

The conversion of natural forested ecosystems to agricultural land has resulted in massively altered landscapes on all inhabited continents (Foley *et al.*, 2005). Agricultural regions are characterized by fragmentation of natural habitats, transformed ecosystem boundaries (Fahrig, 2003), altered hydrologic cycles and greatly increased nutrient availability (Stoate *et al.*, 2009). These effects have collectively resulted in widespread biodiversity loss (Stoate *et al.*, 2009), and have modified the availability and transport of energy and nutrients within and among landscape compartments (Polis *et al.*, 1997). Alteration to energy fluxes has important consequences for biological communities and ecological processes in surrounding ecosystems, such as streams and rivers, which are sensitive to the modification of their watersheds (= catchments) (Stoate *et al.*, 2009).

Replanting native vegetation is a restoration action that seeks to mitigate negative agricultural effects, and commonly occurs in riparian zones (Brooks & Lake, 2007). Riparian vegetation supports terrestrial and aquatic biodiversity (Sabo *et al.*, 2005; Arnaiz *et al.*, 2011). Many stream-ecosystem processes are mediated by riparian vegetation, including organic-matter breakdown rates (Tank *et al.*, 1998), filtering of nutrients and pollutants, stabilization of banks, and the provision of shade and leaf litter inputs (Naiman & Décamps, 1997). Over the last decade, restoration activities have shifted from a focus on restoring the physical stream environment (often for single taxon, e.g. fish) to restoring the biotic and abiotic processes that maintain functioning aquatic ecosystems (Bernhardt & Palmer, 2011).

Alleviating non-point-source agricultural effects, such as altered hydrology and nutrient pollution, requires management actions at watershed scales (Greenwood *et al.*, 2012). However, the spatial extent of most replanting projects has been small (i.e. < 1 km corridors) due to logistic and cost constraints (Bernhardt *et al.*, 2005). Addressing the spatial mismatch of degradation and restoration may be feasible in future agricultural landscapes; there is an emerging social awareness of the benefits of native vegetation in the landscape for multiple values, including biodiversity and agricultural services (Gilvear *et al.*, 2013), such as windbreaks (Jose, 2009). Economic forces, such as payment for sequestering carbon (‘carbon farming’) are likely to play an important part in subsidizing future revegetation activities (Harper *et al.*, 2007; Bradshaw *et al.*, 2013). Carbon-driven economies may cause future agricultural landscapes to become an increasingly heterogeneous matrix of pasture, forest and agroforestry, with the potential for concurrent benefits to stream-ecosystem function.

Broad-scale reforestation is one option to deal with climate change but the ecological and biogeochemical implications are unclear. Mitigating climate change requires a large-scale, integrated approach that explicitly incorporates connections among inland waters, hydrology and the global carbon cycle (Battin *et al.*, 2009). This integrated approach includes how riparian restoration will affect organic carbon storage, processing and outgassing in river networks (Battin *et al.*, 2009). Comprehensive estimates of aquatic carbon fluxes in aquatic ecosystems (and upscaling these) will help to manage the ecological effects of land-use and climate change on aquatic ecosystem function (Staehr *et al.*, 2010; Tank *et al.*, 2010). Much of the pioneering research on aquatic organic carbon dynamics has focused on small forested streams (e.g. Fisher & Likens, 1973). However, aquatic carbon processes are expected to differ based on land use and position in the river hierarchy (Fig. 1; Townsend, 1989).

The provision, processing and downstream transport of terrestrial organic carbon (Fig. 1) are influenced strongly by agricultural land use, and have major effects on ecosystem functions and biodiversity (Tank *et al.*, 2010). Differences in organic carbon fluxes between intact and agricultural watersheds have been documented (e.g. Wilson & Xenopoulos, 2008; Gücker *et al.*, 2009), but there are few data to assess the response of stream organic carbon fluxes to riparian restoration (but see e.g. Lennox *et al.*, 2011). This is despite considerable investment in riparian restoration (> US$14 billion in the USA over the past two decades; Bernhardt *et al.*, 2005) and the importance of terrestrial organic matter to stream ecosystems (Tank *et al.*, 2010). Consequently, we have little knowledge of if, and when, riparian restoration will restore aquatic organic carbon processes (i.e. inputs, standing stocks, processing and transport) in agricultural streams (Fig. 1b) towards pre land-clearance condition (i.e. greater native tree cover; Fig. 1a).

Here, we use data from replanted agricultural stream reaches in a massively altered agricultural landscape to address how replanting native riparian vegetation might affect in-stream organic carbon dynamics at reach scales within decadal time frames. We upscale our findings to assess how organic carbon budgets may respond to potential land-use change (i.e. extensive replanting) in future landscapes. Last, we discuss the implications of altered aquatic organic carbon fluxes for stream-ecosystem processes and regional carbon balances.

Methods

Study design and sites

Riparian and aquatic organic carbon fluxes were measured over two years in 13 agricultural streams (1st-3rd Strahler order) of the Goulburn-Broken watershed (= catchment), south-eastern Australia (Fig. 2). The areas of the study stream watersheds ranged from 6-371 km^2 and land-use consisted of cropping and grazing mixed with remnant dry *Eucalyptus* forest (Table S1 in Supporting Information; Fig. 2).

Each study stream had a paired upstream and downstream reach (26 reaches; Table S2). In ten of the agricultural streams, the margins of the downstream reach had been replanted with native vegetation between 8 and 22 years prior to the study period (‘replanted’ reaches). These replantings (*c.* 270-1200 m long corridors, mean width 12.5 m; Table S2) had been revegetated through planting native *Eucalyptus* spp. and *Acacia* spp. appropriate to the area. The replantings were fenced, but livestock had occasional access. The other three downstream reaches, and all upstream reaches, were ‘untreated’ (i.e. unplanted) and unfenced. Riparian vegetation of untreated reaches was typical of agricultural areas in the region; a ground cover of pasture grasses with some large remnant native trees (predominantly river red gum; *Eucalyptus* *camaldulensis*). Downstream riparian plantings had similar numbers of large remnant trees to their paired upstream reach (Table S2).

Watershed characteristics

Data on watershed topography, land use (at riparian and whole-of-watershed scales) and climate (Table S1) were obtained from a digital elevation model (DEM) derived stream network (Stein *et al.*, 2002), Google Earth (version 6.0) and the Environmental Systems Modelling Platform (EnSym, Victorian Department of Sustainability and Environment, 2012). Details are available in the Supporting Information.

Reach characteristics

Physical properties including reach length, mean width, mean depth, percent habitat class cover (riffle, run and pool), canopy closure and macrophyte cover were measured in each reach (Table S2). Measurements of water quality (pH, conductivity and turbidity) and nutrients (total P, total N, FRP, NH_4^+ and NO_x) were made monthly to quarterly. Discharge was measured over 18-24 months at each site using depth loggers. Details are available in the Supporting Information.

Effect of reach-scale replanting on organic carbon fluxes

The methods for measuring the inputs, standing stocks, transport and metabolism of aquatic organic carbon are described in the following sections. Here we use ‘flux’ to describe the transport (e.g. exported downstream) or transformation (e.g. organic carbon evaded as carbon dioxide) of carbon within reaches, among reaches or among landscape components (e.g. terrestrial, aquatic, atmospheric).

Inputs

Vertical litterfall and lateral leaf litter inputs were measured with litter traps deployed between February 2011 and February 2012. The vertical litter traps were made from plastic buckets with mesh collars (1 mm, diameter 36 cm). When multiple replanted plant genera were present (i.e. *Eucalyptus* and *Acacia)*, litter traps were associated with a tree or group of trees (distant from remnant vegetation), and litter from that genus was separated and quantified independently. Three replicate traps were used for each replanted genus at each site. Traps located on the stream bank (and not over the water) may overestimate vertical inputs (Cillero *et al.*, 1999) but were necessary to accurately measure inputs from specific replanted trees and avoid remnant vegetation. To assess lateral inputs, five 0.5 m wide lateral litter traps (1 mm mesh) were anchored at the channel edge within each replanting reach (following Benstead *et al.*, 2009). Where possible, lateral litter traps also were located distant to remnant vegetation. Density of large remnant trees was similar between paired reaches, so that we assumed this input was equivalent. Contents of litter traps were collected monthly and the organic material dried (60°C, 1 week) and ashed (550°C, 4 hours) to calculate ash-free dry mass (AFDM). Carbon content was assumed to be 50% of AFDM (Meyer & Edwards, 1990).

Terrestrial litter mass in the riparian zone (riparian coarse particulate organic carbon; riparian CPOC) in all reaches was measured once in winter 2011. All terrestrial detrital material was taken from ten haphazardly selected 0.25 m^2 quadrats placed on the stream bank. Organic material was dried (60°C, 1 week) and ashed (550°C, 4 hours) to calculate AFDM.

Aquatic standing stocks

Benthic organic carbon standing stock was separated into two size classes: fine particulate organic carbon (FPOC; 0.45-1000 μm) and coarse particulate organic carbon (CPOC; 1-100 mm diameter). Benthic CPOC was sampled four times (winter 2010, summer 2011, winter 2011 and summer 2012) by taking 15 cores from a range of water depths in each reach (n = 26 reaches) at haphazardly selected locations. A 25-cm-diameter core was inserted into the sediment, and all organic material to a depth of 10 cm was removed and frozen. Samples were sieved (1 mm), dried (60°C, 1 week), then ashed (550°C, 4 hours) to calculate AFDM. Standing stock of benthic FPOC was estimated by taking cores in summer 2012. Ten haphazardly selected cores were taken in downstream reaches only (*n* = 13 reaches) by inserting a 7-cm-diameter core and removing all material. This material was sieved over nested 1 mm and 250 µm sieves. A well-mixed subsample (5-180 ml depending on filter capacity) of the material passing through the 250 µm sieve was filtered through a pre-ashed and pre-weighed filter paper (Whatman GF/C). The sieved (250 - 1000 µm) and residue (0.45 – 250 µm) fractions were dried, ashed and the AFDM summed to calculate total benthic FPOC AFDM.

Large wood (> 10-cm diameter and 1 m in length) volume was calculated using the line-intercept method (Lamberti & Gregory, 2006). In each reach, 20 transects were haphazardly placed perpendicular to the stream. The channel width, wet width and average diameter of all large wood pieces intersecting the transect were measured. The volume of large wood on each transect was calculated according to:

$$m^3 m^{-2} = \pi^2 \sum \frac{d^2}{8L}.$$

Where: d is the average diameter of a piece of wood and L is the transect length. This volume was converted to mass by taking samples of wood, drying (60°C, 1 week), calculating dry wood density and ashing (550°C, 4 hours) to build a linear relationship and estimate AFDM (g C m^{-2}) from volume (m^3 m^{-2}).

Transport

Organic carbon was separated into three size classes for calculating transport: dissolved organic carbon (DOC; < 0.45 µm), FPOC and CPOC. Water samples for DOC and FPOC concentration were taken from each stream every 4 weeks. Other samples were taken during storm-flow events and low flow periods. DOC samples were filtered (GF-75 glass fiber filters; Advantec, Dublin, USA) into pre-combusted 60 ml amber-glass jars and acidified (to pH < 2) with 32% HCl. Samples were refrigerated and organic carbon concentrations analyzed using a Shimadzu TOC-V CPH/CPN Total Organic Carbon analyzer (Shimadzu; Tokyo, Japan). FPOC concentration was calculated as total organic carbon (unfiltered) minus the DOC concentration. The annual yield (export / watershed area) of DOC and FPOC was modelled as a function of hydrology over the 24 month period (for details see Giling *et al.*, 2014). The export was not calculated for the smallest stream, Camerons Well, because the logger height to discharge relationship was too poor to estimate annual flow.

Export of CPOC was measured by placing drift nets (600 x 600 mm square opening; 1 mm mesh) in the stream channel for a set period of time. Export of CPOC was sampled at seven sites and repeated 4-7 times over a range of stream discharges. For full details of sampling see Chapter 5. We did not extrapolate CPOC measurements over the hydrologic time series given the inaccuracy of sampling CPOC export at high discharges and strong influence of other physical processes (e.g. antecedent hydrologic conditions and litterfall) on export. Estimates of annual yield are based on mean concentration and water volumes only.

Metabolism and spiralling

Stream metabolism is the production of organic carbon (gross primary production; GPP) and consumption of organic carbon (ecosystem respiration; ER). Metabolism was measured at two reaches on four of the agricultural streams in early autumn 2012. The replanted and untreated reaches were measured on two streams (Warrenbayne Creek and Moonee Creek). The other two streams were selected to control for longitudinal variation in metabolism, although there were no *a priori* reasons to expect a difference in the metabolic rate between reaches. On one stream (Honeysuckle Creek), we divided the replanted reach equally in two, and metabolism measured in each sub-reach. The riparian zone of the fourth stream (Creightons Creek) had untreated riparian vegetation in both the upstream and downstream reach (Table S2). Full details of experimental methods are described in Giling *et al.* (2013). Briefly, we measured stream ecosystem metabolism using a whole-ecosystem, two-station approach (Odum, 1956) that followed single station analysis to calculate the reaeration coefficient (Atkinson *et al.*, 2008). Metabolism estimates were converted to carbon units using (Bott, 2006):

$$mg\ C\ L^{-1} = mg\ O_2\ L^{-1} \times \frac{12}{32} \times \frac{1}{PQ} \qquad (GPP);$$

$$mg\ C\ L^{-1} = mg\ O_2\ L^{-1} \times \frac{12}{32} \times RQ \qquad (ER).$$

Where: the photosynthetic quotient (*PQ*; mol of O_2 released per mol CO_2 incorporated) = 1.2, and the respiratory quotient (*RQ*; mol of CO_2 released per mol of O_2 consumed) = 0.85 (Bott, 2006). The term $\frac{12}{32}$ is the atomic mass of C divided by the molecular mass of O_2.

Organic carbon spiralling metrics incorporate organic carbon turnover (i.e. processing) and transport to describe the downstream movement, cycling and retention of organic carbon (Newbold *et al.*, 1982). We used the organic carbon standing stocks and metabolic fluxes to calculate organic carbon velocity (V_{OC}; m day^{-1}) and turnover rate (K_{OC}; day^{-1}). Combined, these metrics estimate organic carbon turnover length (‘spiralling’; S_{OC}), which can vary from < 1 km in small forested streams to > 10,000 km in large rivers (Webster & Meyer, 1997). We also calculated the index of retention (IR), which is close to 1 in streams that retain little organic carbon, and is >>1 in more retentive streams (Minshall *et al.*, 1992). These were calculated according to (Newbold *et al.*, 1982; Minshall *et al.*, 1992):

$$V_{OC} = \frac{TOC \times Q}{BOC \times w}; \quad K_{OC} = \frac{R_{het}}{BOC + (TOC \times z)};$$

$$S_{OC} = \frac{V_{OC}}{K_{OC}}; \qquad IR = \frac{V_{water}}{V_{OC}}.$$

Where: *TOC* = total transported organic carbon (g m^{-3}), *Q* = discharge (m^3 day^{-1}), *BOC* = benthic organic carbon standing stock (fine and coarse) (g m^{-2}), *w* = mean stream width (m), R_{het} = heterotrophic respiration (g C m^{-2} day^{-1}, calculated as ER – 0.2 × GPP; Young & Huryn, 1999) and *z* = mean stream depth (m). These measures were calculated using a subset of storage, concentration, transport and discharge values obtained at the same time as the metabolism estimates, not the annual means.

Scaling organic carbon fluxes to future landscapes

The potential effect of extensive riparian vegetation was assessed by upscaling fluxes to the Goulburn-Broken watershed (*c.* 24,000 km^2), in which the smaller study watersheds are located. We upscaled reach estimates of aquatic organic carbon fluxes to all similar-sized ‘patches’ of stream. Similar patches were defined as stream reaches in the DEM network that were 2nd or 3rd Strahler order and located in areas of low density *Eucalyptus* vegetation (< 10% canopy cover) or in cleared areas dominated by grasses (i.e. collectively the unshaded portions of Fig. 2). ArcMap (ESRI; Redlands, CA, USA) was used for the spatial characterization. The width of each reach was estimated using a linear relationship between average stream width (n = 10) and watershed area (known from DEM network) from sites within the region ($R^2 = 0.84$, $n = 33$). This width was multiplied by the length of each reach (total 2,800 km; *c.* 30% of the stream network), and summed to estimate total benthic area of all patches potentially available to be affected by riparian restoration.

We calculated the potential watershed-scale change in response to replanting the riparian area of all patches using the ‘direct extrapolation’ method (King, 1991; Wu & Li, 2006). This method has been widely used to scale ecosystem processes to landscapes in ecological studies (Wu *et al.*, 2006; Zhang *et al.*, 2007). The effect of replanting was scaled using the mean difference (and error) between replanted and untreated reaches for variables that were affected by replanting treatment. The included data were litter inputs, benthic CPOC and NEP (Table 1). The differences and uncertainties were summed over the appropriate patch length or area (incorporating width-estimate error) to estimate daily change in organic carbon fluxes at a watershed scale (using WinBUGS version 1.4; Lunn *et al.*, 2000). Autumnal metabolic measurements were made at close to mean 2011-2012 annual water temperature (mean 1.1 times higher) and PAR intensity (mean 1.2 times higher); hence an annual rate was estimated by multiplying mean daily flux by 365 days. Daily budget calculations of autumn rates used autumn litterfall, while annual estimates used annual mean litterfall (at mean replanting age, assuming age zero has no additional inputs). The total watershed area drained by 3rd-order streams (including 1st-order and vegetated areas, > half of the Goulburn-Broken watershed area) was calculated from the stream network to estimate watershed-scale organic carbon export (for 1st-3rd order streams) from yield estimates.

Statistical analysis

The effects of replanting age and treatment (replanted or untreated) on organic carbon fluxes were analyzed using Poisson-distributed or normally-distributed linear mixed models. Response variable for inputs and standing stocks were means per reach and season (where measured). Response variables for metabolic and spiralling models were daily rates. Models included terms for season (where measured) and random effects for site, reach and replanted species where appropriate. Metabolic and spiralling models included covariate terms for total daily PAR and mean water temperature to account for non-concurrent measurements. Model descriptions are available in the Supporting Information.

The importance of replanting and reach characteristics to organic carbon fluxes was analyzed using Bayesian model averaging (BMA). BMA indicates the relative importance of predictors (i.e. their inclusion probability) by running a large number of linear combinations and summing the posterior model probabilities. Watershed-scale variables govern organic carbon yields (Giling *et al.*, 2014), so candidate variables for DOC and FPOC yield were corresponding watershed climatic, soil and land-use characteristics.

All analyses were conducted using WinBUGS (version 1.4; Lunn *et al.*, 2000). We used the odds ratio (OR) to indicate an important effect of model parameters. The OR is the ratio of posterior odds to prior odds, where OR > 3 indicates an important effect in BMA and OR > 10 indicates ‘strong’ evidence of an effect in linear mixed models (Jeffreys, 1961). A stricter criterion is required for the mixed models because variables are forced into the model (hence meeting OR > 3 is easier) versus true model selection, as in BMA. An OR of infinity (inf.) indicates that there is virtually no doubt that the parameter differs from zero. We used uninformative priors, so the prior odds were unity for all analyses.

Results

Effect of reach-scale replanting on organic carbon fluxes

Inputs

Replanting riparian vegetation increased canopy cover and terrestrial inputs to streams. Canopy closure was greater in replanted reaches than in untreated reaches (mean difference = 11% ± 3.9 SD, OR = 539), and closure increased with replanting age (coefficient = 0.71 ± 0.26, OR = 312; Fig. 3a). Litterfall was greater in summer than spring, autumn or winter by factors of 1.1, 1.7 and 3.6 times respectively (OR = 15, inf. and inf.). There was little evidence for a relationship between replanting age and vertical litterfall (coefficient = 0.21 ± 0.20 SD, OR = 6.8; Fig. 3b). However, the accumulation of terrestrial vegetation litter (riparian CPOC) was greater in replanted reaches than in untreated reaches (mean difference 64 g C m^{-2} ± 52 SD, OR = 26, Table 1) and increased linearly with replanting age (coefficient = 10.29 ± 0.28 SD, OR = inf.; Fig. 3d). Canopy closure was an important predictor for riparian CPOC (Table 2). Lateral litter movement increased with replanting age (coefficient = 0.80 ± 0.39 SD, OR = 40; Fig. 3c).

Aquatic benthic standing stocks

There was no effect of replanting treatment on benthic fine particulate organic carbon (FPOC; mean difference = 16 g C m^{-2} ± 130 SD, OR = 1.5). The percentage of reach that was pools was an important predictor of FPOC standing stock (Table 2). Standing stock of benthic coarse particulate organic carbon (CPOC) was greater in replanted reaches than in untreated reaches (mean difference = 50 g C m^{-2} ± 14 SD, OR = inf.); this was positively associated with reach canopy closure (Table 2). Benthic CPOC standing stock varied seasonally; it was greater in the first sampling period (winter 2010) than in the three subsequent sampling periods (by factors of 2.7, 1.4 and 1.8 times; OR = inf. in each case). This sampling period was before large-scale flooding in spring 2010. In-channel large wood mass was similar in replanted reaches and untreated reaches (mean difference = 110 g C m^{-2} ± 420 SD, OR = 1.1, Table 1), and was positively correlated with the density of large remnant trees (Table 2).

Transport

The majority of transported organic carbon from the 13 watersheds was the dissolved organic carbon (DOC) fraction (mean 86% of annual export). We did not detect any effect of upstream watershed variables (morphology, land use, and climatic) on DOC or FPOC yield (Table 2).

Metabolism and spiralling

Measurements from eight reaches (two in each of four sites) showed that the autumnal rate of net ecosystem productivity (NEP) was lower in replanted reaches compared to that in untreated reaches (mean difference 1.1 g C m^{-2} day^{-1} ± 0.6 SD, OR = 24, Table 1). This was driven by replanted reaches having marginally greater ecosystem respiration (ER; mean difference 0.7 g C m^{-2} day^{-1} ± 0.6 SD, OR = 6.7) and marginally lower gross primary production (GPP; mean difference 0.5 g C m^{-2} day^{-1} ± 0.4 SD, OR = 9.5) than did untreated reaches.

Spiralling metrics indicated replanting affected organic carbon processing efficiency. Replanted reaches had lower organic-carbon velocity (V_{OC}; mean difference 210 m day^{-1} ± 51 SD, OR = 4999, Table 1) and turnover rate (K_{OC}; mean difference 0.009 day^{-1} ± 0.005 SD, OR = 23) than untreated reaches. Organic carbon turnover length (‘spiralling’; S_{OC}) was lower in replanted reaches (mean difference 13 km ± 7.0 SD, OR = 40). There was no difference in the index of retentiveness (IR), which was highly variable in both replanted and untreated reaches (mean difference 11 ± 240 SD, OR = 1.1). Spiralling metric trends were driven by replanted reaches having greater total benthic organic carbon (BOC; mean difference 430 g C m^{-2} ± 7.8 SD; OR = inf.) and lower water velocity (mean difference 9.6 km day^{-1} ± 2.3 SD; OR = 832) than untreated reaches (Table S2). Total transported organic carbon (TOC; mean difference 0.42 g m^{-3} ± 2.2 SD; OR = 1.4) and heterotrophic respiration (R_{het}; mean difference 0.06 g C m^{-2} day^{-1} ± 1.80 SD; OR = 1.0) were similar between replanted and untreated reaches.

Scaling organic carbon fluxes to future landscapes

We estimated that 3rd-order watersheds within the Goulburn-Broken watershed exported 28 kg C ha^{-1} yr^{-1} ± 18 SD, or a total of 36,000 t C yr^{-1} ± 22,000 SD. When mean differences (and error) in standing stocks between replanted and untreated reaches were upscaled, much additional carbon was estimated to be stored as CPOC (740 t C ± 220 SD) in the benthos of 2nd and 3rd order streams of the Goulburn-Broken watershed. Terrestrial inputs were estimated to increase by 12 t C day^{-1} ± 6.3 SD, while ER increased by 11 t C day^{-1} ± 10 SD. Carbon fixed by in-stream producers (GPP) over stream benthic area decreased by 7.3 t C day^{-1} ± 6.1 SD. From the budget estimates, replanted streams may become more heterotrophic (a greater net source of carbon) within two decades of replanting, with a net carbon loss of 0.52 g C m^{-2} day^{-1} ± 0.80 SD in the stream benthic areas on an average autumn day. At a watershed scale, loss of aquatic organic carbon from streams was estimated to be 2,300 t C yr^{-1} ± 4,700 SD (or 1.6 t C ha^{-1} yr^{-1} ± 3.1 SD) if all sparsely vegetated 2nd and 3rd order stream riparian zones were to be replanted (calculated using annual litter-fall estimates).

Discussion

We measured the effect of replanting riparian vegetation on aquatic organic carbon fluxes and upscaled results to an entire agricultural watershed in south-eastern Australia. At reach scales, replanting increased terrestrial inputs (Fig. 3), the standing stock of aquatic coarse particulate organic carbon (CPOC), and reduced net ecosystem productivity (NEP; Table 1). The aquatic organic carbon budget suggested that replanting will lead to systems becoming more heterotrophic (i.e. greater sources of carbon). These replanted streams (i.e. 'future' landscapes) have organic carbon inputs, processing and turnover distances more similar to streams typical of watersheds with intact forest cover (Fig. 4).

Effect of reach-scale replanting on organic carbon fluxes

There was a positive linear relationship between planting age and riparian litter mass (riparian CPOC), consistent with results for replantings in California of ≤ 39 years (Lennox *et al.*, 2011). Replanted reaches had greater in-stream benthic CPOC than did untreated reaches, and canopy closure was an important predictor of benthic CPOC accumulation (Table 2). Previous studies in similar streams of the same region have showed that benthic CPOC was consistently low when canopy closure was < 35% (Reid *et al.*, 2008). All replanted reaches in the current study (except the widest stream, Seven Creeks) had > 50% canopy closure. However, three-quarters of the untreated reaches, which are typical of the lowland streams in the region, had < 50% closure, with some < 35% (average = 45%; Table S2), indicating probable impairment of CPOC inputs that are important for stream food webs. A difference in benthic CPOC between replanted and untreated paired reaches was not evident at all sites (Table S3), perhaps due to low retention in steeper, fast-flowing reaches.

Replanting did not have a large effect on total benthic organic carbon (BOC, i.e. fine and coarse organic carbon) because fine particulate organic carbon (FPOC) makes up a large fraction of BOC (Table 1). The proportion of pool areas in a reach is important to benthic FPOC mass (Table 2). Pools have low velocity and organic matter travels short distances and is deposited (Hoover *et al.*, 2010). The importance of pools is consistent with results that suggest benthic FPOC dynamics are affected by geomorphological characteristics or hydrologic processes (e.g. water velocity and spate frequency), which occur at larger spatial scales than typical replanting projects (Houlahan & Findlay., 2004; Opperman *et al.*, 2005). This hydrologic control also is true for the export of DOC (Chapter 4; Wilson & Xenopoulos, 2008).

Large wood was positively correlated with greater density of large remnant trees (Table 2). There was a relatively short legacy effect of clearing vegetation on large wood; reaches that were largely cleared of remnant vegetation < 100 years ago had little in-channel wood. Much of this may have been transported or deposited on floodplains by strong flows in the simplified channels, or removed by humans, given the long residence time of large wood (Wallace *et al.*, 2001). It may take centuries for replantings to provide comparable amounts of large wood to those seen in natural forested reaches (Meleason & Hall, 2005). Large wood provides habitat for biota and facilitates ecological functions, such as reducing storm flow velocity and limiting sediment transport (Gregory *et al.*, 2003). Replanting and protecting riparian zones is important to ensure these functions are present in future landscapes because recruitment of native trees is low in grazed riparian zones (Jansen & Robertson, 2001).

Replanted reaches had altered whole-stream metabolism rates and shorter turnover lengths despite high among-stream variation in observations. Metabolic processes were shifted towards that of un-impacted systems (i.e. lower NEP; Fig. 4) through the restoration of riparian vegetation functions, such as shading and organic carbon inputs (Giling *et al.*, 2013). Effects of restoration on stream metabolism have also been found in a prairie stream where riparian canopy was removed to restore the naturally open canopy state, resulting in lower ER and higher GPP (Riley & Dodds, 2012), and previously agricultural streams where forest has regenerated after clearance (McTammany *et al.*, 2007).

The organic carbon downstream velocity (V_{OC}; m day^{-1}), turnover rate (K_{OC}; day^{-1}) and turnover lengths (‘spiralling’; S_{OC}) of streams in this study (discharge 59-1080 l s^{-1}) were similar to degraded cropland streams in the north-west USA (1-1,120 l s^{-1}; Griffiths *et al.*, 2012). Spiralling metrics indicated that all reaches had fairly low IR (mean = 275; autumn) for 2nd and

3rd order streams (Minshall *et al.*, 1992; Griffiths *et al.*, 2012). The two streams with more highly modified watersheds (Creightons Creek and Honeysuckle Creek), had slightly greater organic carbon spiralling lengths than would be expected given their size (i.e. were inefficient, Webster & Meyer, 1997), which is consistent with other agricultural streams (Young & Huryn, 1999; Griffiths *et al.*, 2012). Low retention may be due to reduced terrestrial inputs, altered hydrologic regimes and channel modification (Young & Huryn, 1999). Spiralling lengths in our streams may be even longer (and metabolic rates lower) during winter, when discharge is higher and processing rates are lower in cooler water (Griffiths *et al.*, 2012).

Although reaches were generally unretentive, altered V_{OC} and K_{OC} contributed to replanted reaches having shorter S_{OC} compared to untreated reaches (Table 1). Lower turnover length indicates replanted reaches were processing organic carbon more efficiently, and acting more similarly to those of undisturbed streams in forested watersheds (Griffiths *et al.*, 2012). The index of retention (IR) did not follow the same trend as S_{OC}, and indicated a variable relationship between water velocity and V_{OC} (Tables S2 & S3). Our results suggest that replanting is valuable, but other restoration actions, such as reducing channelization and incorporating retentive features, will contribute to restoring organic carbon transport and processing dynamics in agricultural systems. The metabolism findings at four sites probably are generalizable to other replanting sites given the broadly consistent effect of riparian treatment on canopy cover and organic-matter accumulation. Future stream ecosystems are predicted to have lower organic carbon standing crops, high organic carbon turnover and altered microbial processes, driven predominantly by changes in the input and retention of organic matter (Kominoski & Rosemond, 2012). Replanting riparian vegetation can feasibly contribute to minimizing these changes to inputs and retention.

Organic carbon fluxes of future landscapes

There were no evident effects of watershed physical, climatic or land-use characteristics on the quantity of DOC exported from our watersheds, despite a large range in watershed-scale tree clearance (12-88%) and upstream riparian zone clearance (0-36%; Table S1). We expect that the proportion of DOC inputs that are exported would be higher in more modified watersheds that have longer turnover lengths. However, a range of factors that affect organic carbon fluxes differ widely across this land-use gradient, such as nutrient concentrations, hydrology and geomorphology. These factors may contribute to the effect of land-clearance and pasture on DOC concentration being highly variable (e.g. Cronan *et al.*, 1999; Quinn & Stroud, 2002). Hydrology has an overarching influence on retention (Griffiths *et al.*, 2012), and replanted reaches had lower water velocity. Forested watersheds have greater geomorphic complexity, are wider, and have lower average velocities than do pasture channels (Sweeney *et al.*, 2004; Gooseff *et al.*, 2007). It was not the purpose of this study to determine those underlying mechanisms, but rather, to describe the watershed-scale consequences of future replantings in an agricultural landscape.

The biogeochemical effects of riparian replanting on aquatic fluxes are imprecise but were potentially high per unit area of stream (net -0.52 g C m^{-2} day^{-1} ± 0.80 SD in autumn; *c.* a third of current NEP). Change in annual carbon outgassing at watershed scales was substantial when upscaled to the benthic area of 2nd- and 3rd-order streams (-1.6 t C ha^{-1} yr^{-1} ± 3.1 SD), and reflects changes to stream-ecosystem processes. This carbon loss is the same order of magnitude as the terrestrial storage of carbon by the replanted trees (2.9 t C ha^{-1} yr^{-1} of above-ground carbon; S. C. Cunningham, pers. comm. 20/08/2013). However, more land area potentially is available for replanting than there is stream channel area. In a watershed context, carbon loss from aquatic systems due to broad-scale planting (2,300 t C yr^{-1} ± 4,700 SD) would be an order of magnitude smaller (and more uncertain) than export from 3rd-order watersheds (36,000 t C yr^{-1} ± 22,000 SD) because 2nd- and 3rd-order agricultural reaches account for < 0.1% of their watersheds in area. The effect of land-use and hydrologic change on carbon export should be examined and included in regional carbon balances because changes in this flux could be large compared with aquatic fluxes or terrestrial sequestration.

Extrapolating ecosystem processes from patches to watershed or landscapes scales remains a critical challenge in ecology (Turner, 2005; Wu *et al.*, 2006). Our linear scaling assumed there were no horizontal effects (i.e. replanting did not affect adjacent ‘patches’), or feedbacks in organic carbon fluxes. The directional nature of fluvial ecosystems means that biogeochemical effects of planting may be displaced downstream. This is particularly true for processes that are under larger-scale or hydrological control, which may gain additive effects as replanting extends. Autumnal metabolic rates can be greater than spring rates because algal biomass is more established, and nutrient concentrations vary temporally. Therefore, the annual change in metabolism may be an overestimate. Several mechanisms may have contributed to the effect of replanting on carbon fluxes to be imprecise. Vertical and lateral litter traps occupied a small fraction of riparian area and length respectively (<0.01 %). The effect of emergent macrophyte density, patch size or spatial arrangement on in-stream processes was not incorporated in our ecosystem-scale approach. Macrophyte beds can influence channel geomorphology, hydrology, atmospheric gas exchange and retain organic matter (Wilcock *et al.*, 1999; Imberger *et al.*, 2011), so that they should be incorporated in future carbon budgets.

Managing future massively-altered landscapes

Defining the endpoint or ‘success’ for riparian replanting can be problematic and in many cases the availability of appropriate reference conditions is limited (Palmer *et al.*, 2005). Few stream-restoration activities are effectively monitored (Brooks & Lake, 2007), so trajectories and expectations are not well understood. We showed organic carbon fluxes (e.g. terrestrial inputs and metabolism) in replanted agricultural streams were more like pre-clearance stream ecosystems within two decades (Fig. 4). This time period is similar as for stream shading and temperature to be restored in smaller channels (Davies-Colley *et al.*, 2009), but the time lag will be much longer for some components (e.g. large wood), and will vary based on network position, which influences stream width, flow and geomorphology.

Many restoration policies disregard small streams (e.g. Lassaletta *et al.,* 2010) even though they make up the bulk of river networks (e.g. 1st-3rd order streams accounted for 82% of our network length). Small streams are well connected to terrestrial vegetation, are expected to respond to riparian restoration more rapidly than are large channels, and contribute to downstream ecosystem function (Craig *et al.*, 2008; Greenwood *et al.*, 2012). The 'agricultural future' depicted in Fig. 4c and the economic advantage of sequestering carbon in agricultural landscapes is not yet a reality, so watershed-scale restoration may be unattainable at present. Beginning to restore massively altered landscapes with replanting riparian corridors along small (i.e. 1st-3rd order) streams will have a range of benefits for biodiversity, ecological services and climate-change mitigation (Jose, 2009; Bradshaw *et al.*, 2013).

Future agricultural landscapes that incorporate broad-scale replanting will be more efficient at processing aquatic organic carbon within two decades of planting (Fig. 4). This shift in organic carbon fluxes reflects a return of terrestrial and aquatic processes to those more similar to pre-clearance watersheds, which will influence aquatic trophic dynamics and biodiversity. The response of watersheds to longer durations and extents of replanting is a pertinent issue as one addresses land-use issues at management-relevant spatial scales. Future waterways in massively altered landscapes would benefit from a landscape focus and with the restoration of connectivity between terrestrial and aquatic ecosystems.

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Table 1. Organic carbon budget for the replanted and untreated reaches of the agricultural streams. ‘Treatment effect’ shows whether an important effect (*) or not (-) of treatment (replanted vs. untreated) was present in a linear mixed model. Unit areas indicate benthic stream area, except for transport, which is expressed per unit area of watershed.

Organic carbon fluxes and standing stocks		Untreated reaches mean ± SD (*n* reaches)		Replanted reaches mean ± SD (*n* reaches)		Treatment effect	Sampling regime
Inputs							
GPP	g C m^{-2} day^{-1}	0.5 ± 0.6	(4)	0.2 ± 0.3	(4)	-	Autumn 2012 (*n* = 5-12 days per reach)
Litterfall	g C m^{-2} mo^{-1}			24 ± 8	(6)		Monthly (*n* = 12; Feb 2011 - Feb 2012)
Lateral movement	g C m^{-1} mo^{-1}			7 ± 8	(6)		
Standing crops							
Riparian CPOC	g C m^{-2}	48 ± 49	(16)	180 ± 130	(10)	*	Winter 2011 (*n* = 1 sampling period)
Benthic FPOC	g C m^{-2}	390 ± 280	(3)	370 ± 130	(10)	-	Summer 2012; downstream reaches (*n* = 1)
Benthic CPOC	g C m^{-2}	48 ± 36	(16)	100 ± 56	(10)	*	6-montly from winter 2010 (*n* = 4)
Large wood	g C m^{-2}	270 ± 460	(16)	240 ± 310	(10)	-	Winter 2011 (*n* = 1)
Outputs							
ER	g C m^{-2} day^{-1}	1.9 ± 4.5	(4)	2.4 ± 3.2	(4)	-	Autumn 2012 (*n* = 5-12 days per reach)
DOC transport	kg C km^{-2} y^{-1}	1900 ± 640	(3)	2500 ± 1700	(10)		Monthly from winter 2010 (& event sampling)
FPOC transport	kg C km^{-2} y^{-1}	300 ± 180	(3)	550 ± 760	(10)		
CPOC transport	kg C km^{-2} y^{-1}	0.15	(1)	0.19 ± 0.28	(6)		Replicates at varying discharge (*n* = 4-7)
Spiralling metrics							
Velocity (V_{OC})	m day^{-1}	260 ± 210	(4)	27 ± 18	(4)	*	Autumn 2012 (*n* = 5-12 days per reach)
Turnover (K_{OC})	day^{-1}	0.012 ± 0.014	(4)	0.002 ± 0.002	(4)	*	
Turnover length (S_{OC})	km	35 ± 23	(4)	20 ± 15	(4)	*	
IR		220 ± 310	(4)	330 ± 150	(4)	-	
NEP	g C m^{-2} day^{-1}	-1.4 ± 2.0	(4)	-2.2 ± 3.0	(4)	*	Autumn 2012 (*n* = 5-12 days per reach)

Table 2. Treatment coefficient parameter (*β*) and probability of inclusion in the best model (inc. prob.) for predictors of organic carbon fluxes from Bayesian model averaging (BMA) analyses. Important effects (i.e. OR > 3) of reach- or watershed-scale physicochemical variables on the response are shown in bold.

Response	Predictor variable	*β* mean ± SD	inc. prob.	OR
Riparian CPOC (g C m^{-2})	Replanting age	0.05 ± 0.14	0.17	0.2
	Large remnant tree density	-0.01 ± 0.07	0.09	0.1
	Canopy closure	**1.43 ± 0.22**	**1.00**	**inf.**
	Replanted tree density residuals (against replanting age)	0.00 ± 0.05	0.07	0.1
	Replanting width residuals (against replanting age)	0.00 ± 0.06	0.07	0.1
Benthic FPOC (g C m^{-2})	Replanting age	0.00 ± 0.01	0.05	0.1
	Large remnant tree density	0.00 ± 0.01	0.04	0.0
	Canopy closure	0.00 ± 0.01	0.05	0.0
	Percentage of reach length with pool flow regime	**0.47 ± 0.05**	**1.00**	**inf.**
	Mean daily flow	0.00 ± 0.02	0.06	0.1
Benthic CPOC (g C m^{-2})	Replanting age	0.11 ± 0.16	0.44	0.8
	Large remnant tree density	0.21 ± 0.23	0.57	1.3
	Canopy closure	**0.51 ± 0.26**	**0.91**	**11**
	Percentage of reach length with pool flow regime	0.13 ± 0.21	0.44	0.8
	Mean daily flow	0.05 ± 0.13	0.28	0.4
LW (g C m^{-2})	Replanting age	0.01 ± 0.14	0.11	0.1
	Large remnant tree density	**1.85 ± 0.47**	**0.99**	**158**
	Canopy closure	0.11 ± 0.29	0.21	0.3
	Percentage of reach length with pool flow regime	0.02 ± 0.16	0.12	0.1
	Mean daily flow	0.32 ± 0.45	0.42	0.7
Watershed DOC yield (g C km^{-2} yr^{-1})	A horizon saturated hydraulic conductivity	0.07 ± 0.12	0.52	1.1
	A horizon soil water holding capacity	0.00 ± 0.09	0.40	0.7
	Watershed elevation max	-0.08 ± 0.13	0.55	1.2
	Total annual rainfall	-0.17 ± 0.17	0.72	2.6
	Pasture cover residuals (against rainfall)	-0.01 ± 0.08	0.38	0.6
	Watershed slope residuals (against pasture cover)	0.05 ± 0.10	0.47	0.9
	Watershed relief	0.02 ± 0.08	0.39	0.6
	Prop. of upstream riparian zone cleared for pasture	0.01 ± 0.07	0.37	0.6
Watershed FPOC yield (g C km^{-2} yr^{-1})	A horizon saturated hydraulic conductivity	0.18 ± 0.30	0.58	1.4
	A horizon soil water holding capacity	0.09 ± 0.28	0.47	0.9
	Watershed elevation max	-0.01 ± 0.16	0.41	0.7
	Total annual rainfall	-0.09 ± 0.25	0.47	0.9
	Pasture cover residuals (against rainfall)	-0.18 ± 0.26	0.62	1.6
	Watershed slope residuals (against pasture cover)	0.10 ± 0.20	0.50	1.0
	Watershed relief	0.19 ± 0.30	0.58	1.4
	Prop. of upstream riparian zone cleared for pasture	-0.07 ± 0.20	0.46	0.8

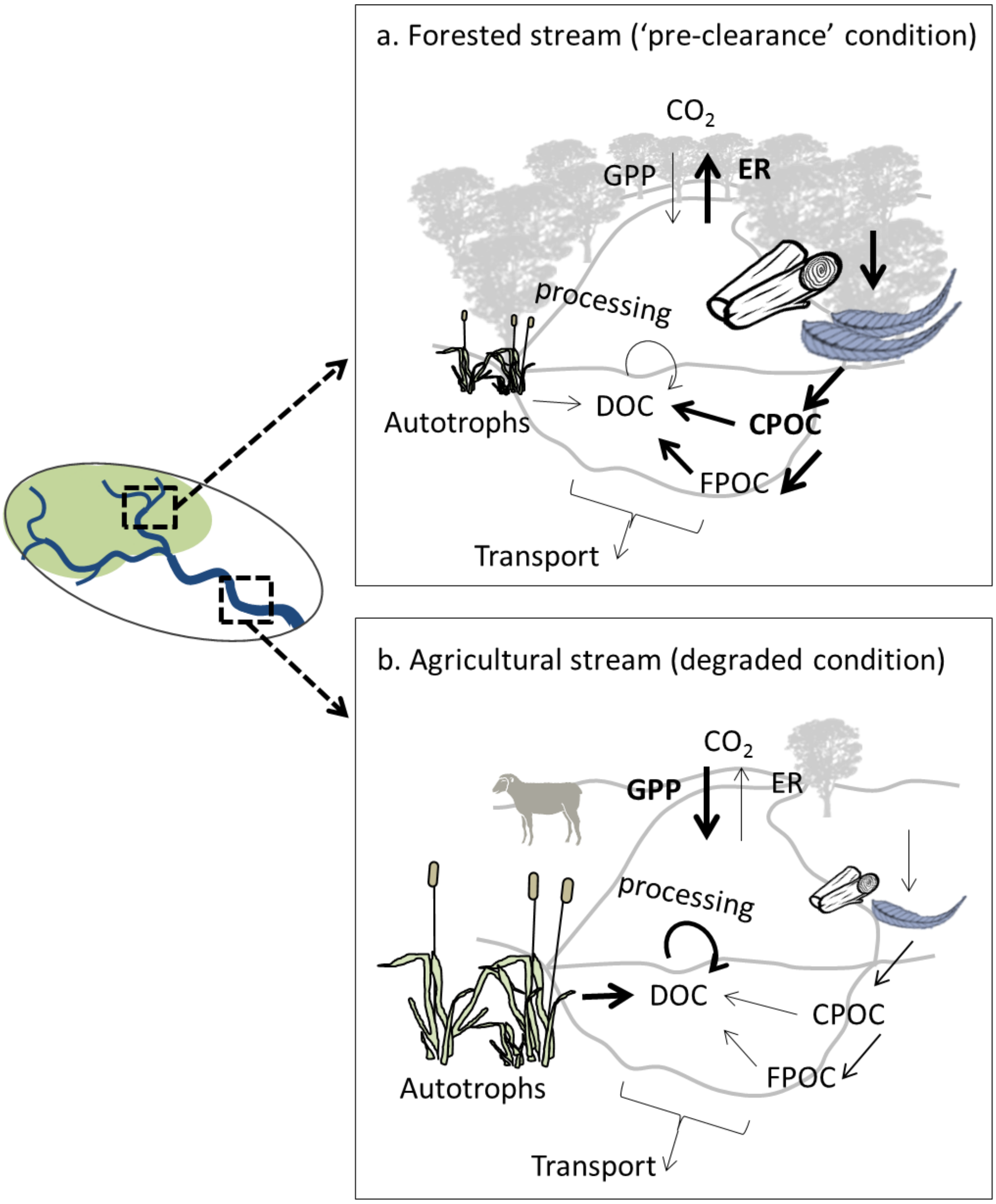

Figure 1. Conceptual diagram of riparian and organic carbon fluxes in a) forested 'pre-clearance' headwaters and b) lowland agricultural streams. Arrow widths, icon sizes and bold text show relative differences between stream types. Terrestrial subsidies in small forested streams include inputs of coarse particulate organic carbon (CPOC; e.g. leaf litter), which are processed by biotic and physical mechanisms into fine particulate organic carbon (FPOC). Dissolved organic carbon (DOC) is sourced mainly from terrestrial leaching, soils and biotic exudates, and is the major form of carbon transported to downstream systems. Much of this is an energy source for ecosystem respiration (ER) in lowland streams, and is processed through microbial pathways as it travels downstream. Degraded lowland systems have greater light and nutrient availability, hence greater gross primary production (GPP) by autotrophs compared to forested headwaters.

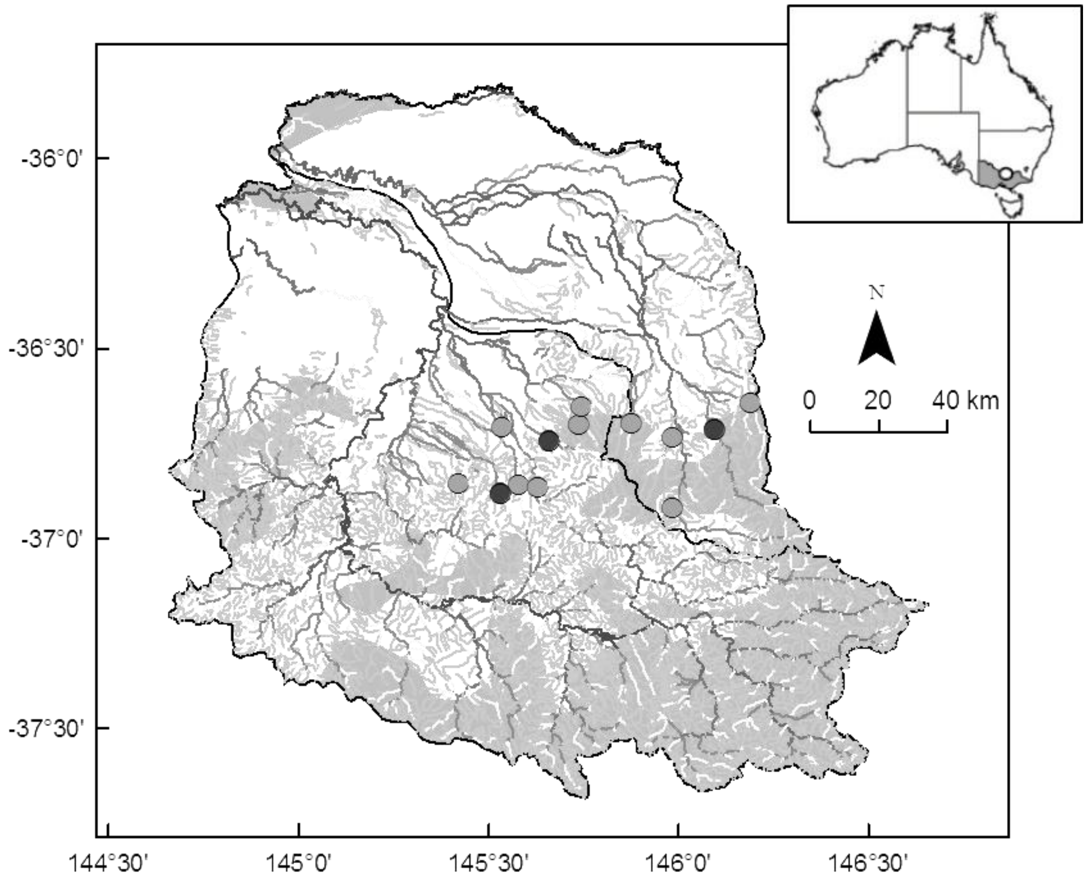

Figure 2. Map of the Goulburn-Broken watershed in south-east Australia (insert) showing replanted study sites (light grey) and untreated study sites (dark grey). Each study site has an upstream and downstream reach. Shaded areas indicate remnant forest, while unshaded areas are dominated by pasture with sparse *Eucalyptus* spp. cover.

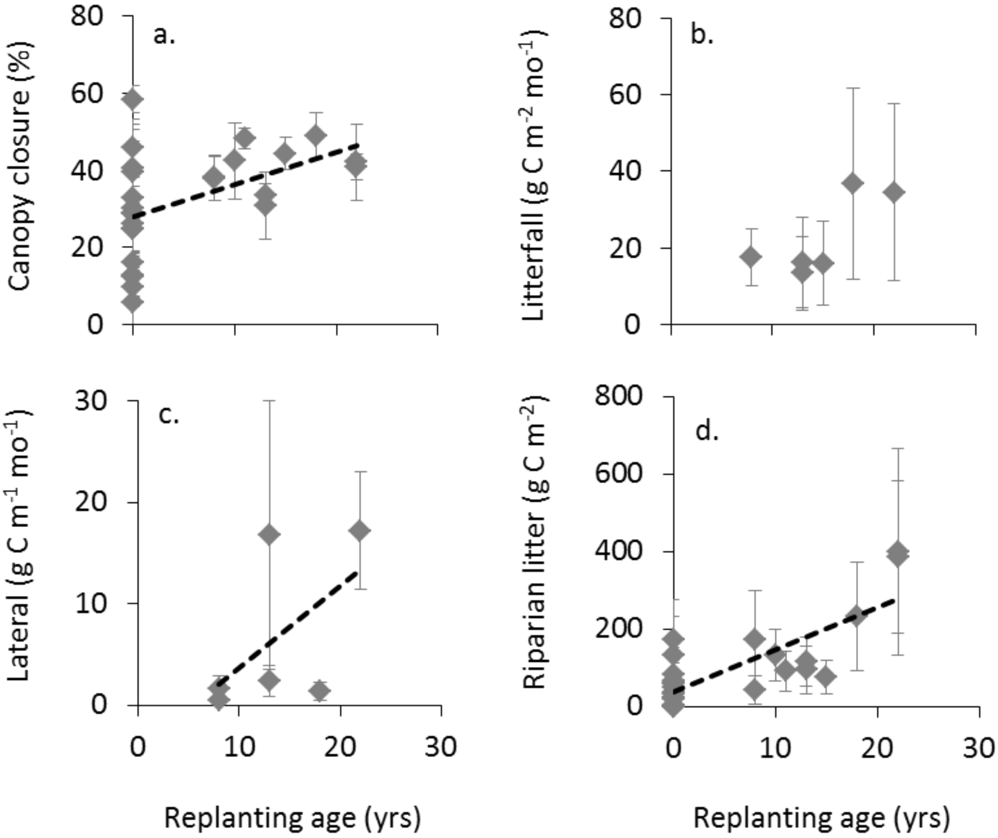

Figure 3. Scatterplots showing the effect of replanting age on mean (± SD): a. canopy cover (*n* = 26 reaches), b. vertical litterfall (*n* = 6 reaches), c. lateral litter movement (*n* = 6 reaches, and d. riparian zone leaf litter (riparian CPOC) standing stock (*n* = 26 reaches). Dashed black lines indicate important effects in linear mixed models.

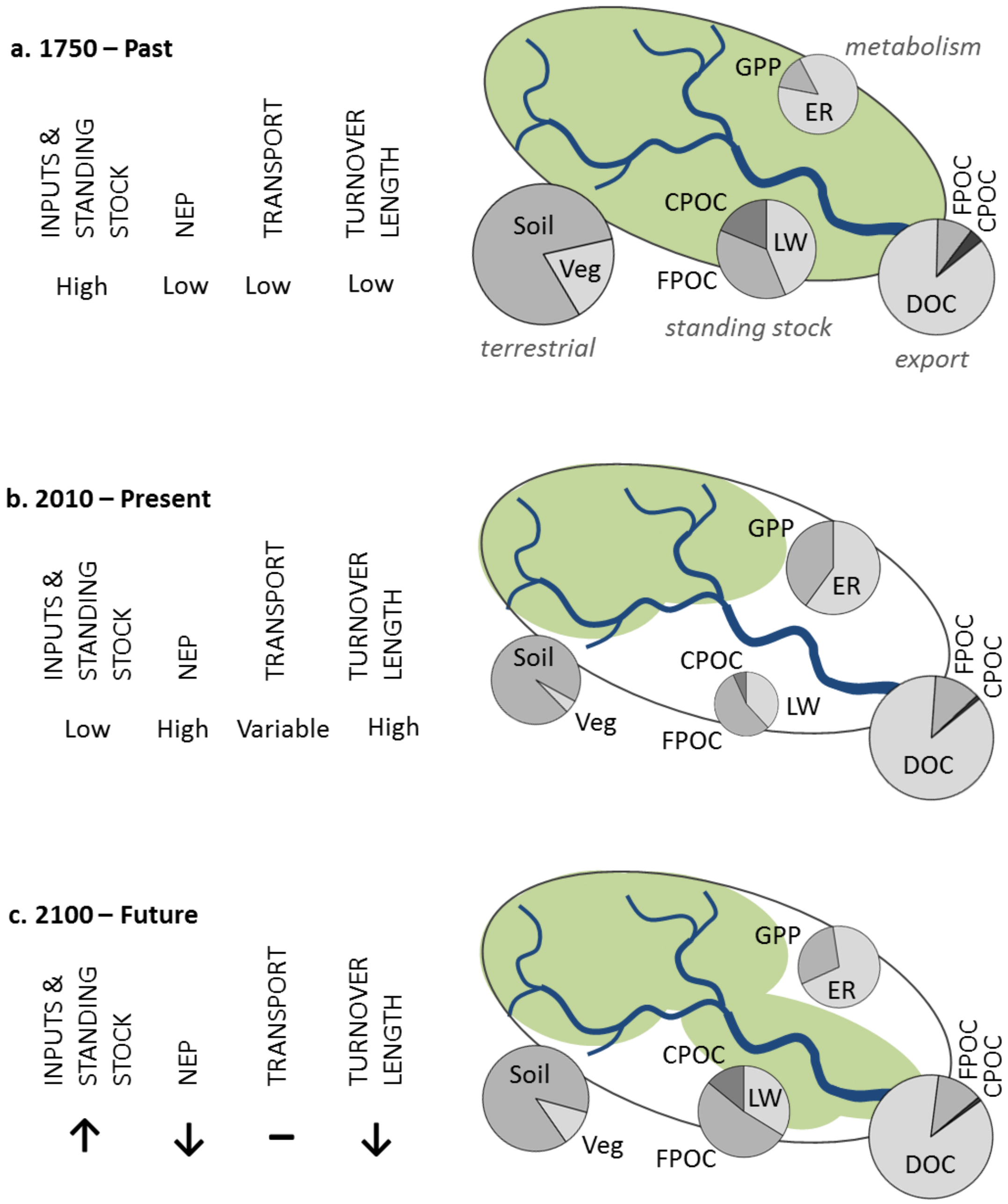

Figure 4. Conceptual figure of organic matter standing stocks and fluxes in: a. 'past' (forested); b. 'present' (cleared); and c. 'future' (replanted) landscapes. Shaded areas indicate idealized remnant or revegetated forest while unshaded areas indicate cleared agricultural land. Pie charts show the relative contribution of processes or components to groupings of the carbon budget: storage in terrestrial and in aquatic systems, aquatic metabolism and downstream export. The difference in pie chart size among the three diagrams for each grouping represents the relative overall change in that storage or flux, based on the effect of revegetation in our study region on aquatic fluxes (this study), above-ground carbon storage (S. C. Cunningham; pers. comm. 20/08/2013) and carbon storage in soils (Hoogmoed *et al.*, 2012). Relative differences in organic carbon inputs, net ecosystem productivity (NEP), transport, and turnover length ('spiralling') are summarized on the left. The predicted effects of replanting at watershed-scales from observations (relative to b; present) are shown as arrows (change) or dashes (no change).

Supporting Information

Methodological details

Watershed characteristics

Data on watershed land use and topography were obtained from a digital elevation model (DEM) derived stream network (Table S1) (Stein *et al.*, 2002). Upstream riparian land use was assessed using aerial photography (Google Earth). Riparian vegetation was classified as having ‘continuous’ canopy cover (no breaks in canopy for 50 m), ‘scattered’ trees or cleared for pasture (no trees for 50 m). The longitudinal distance of channel with each riparian category upstream of the site was expressed as a proportion of total upstream channel length. The upstream channel extent was determined from the digital stream network. Climatic and soil data (for analysis of carbon export) were acquired from the Environmental Systems Modelling Platform (EnSym, Victorian Department of Sustainability and Environment, 2012). Rainfall and soil moisture were modelled as a daily time-series (1/2/2011 to 31/1/2012) using EnSym. Watershed soil characteristics were calculated by determining the proportion of soil types in each watershed with ArcMap (ESRI; Redlands, CA, USA) and producing an area-weighted mean from the properties reported by McKenzie *et al.* (2000).

Reach physicochemical characteristics

At each reach, stream wet width and maximum water depth was measured at 20 haphazardly selected transects (Table S2). The length of each reach was measured at baseflow. Reach lengths were the length of the stream which had had the riparian zone replanted and a similar length for the corresponding upstream reaches (expect where confluences or access difficulties interrupted). For each reach, we measured the proportion of the length that was in the following habitat classes; riffle (fast, turbulent water surface, bed slope > 5%), run (smooth, medium flow, bed slope 1-5%) and pool (low flow and stagnant areas, bed slope < 1%). Five evenly spaced hemispherical photos were taken from the water surface mid-stream in each reach. Percentage canopy closure was estimated from photos using Gap Light Analyzer software (version 2). The number of large (> 15 m tall) remnant (non-replanted natives) trees in the riparian zone of each reach was counted. Macrophyte (aquatic plant) areal cover was visually assessed at each width transect to the nearest 5%. Dominant macrophytes included *Juncus* spp., *Percicaria* spp. and *Phragmites australis*.

Spot measurements of pH, electrical conductivity (EC) and turbidity were taken monthly using a U-50 Water Quality Meter (Horiba; Kyoto, Japan). Duplicate water samples were collected quarterly from midstream for measurements of total phosphorus (P) and total nitrogen (N), and analyzed using the alkaline persulphate digestion method (APHA, 2005) using a Quick-Chem 8500 (Lachat Instruments; Loveland, USA). Water was filtered onsite (0.45 μm PES; Advantec; Dublin, USA) for ammonium (NH_4^+), filterable reactive phosphorus (FRP) and nitrate plus nitrite (NO_x). Concentrations of FRP, NH_4^+ and NO_x were determined using flow injection analysis with the standard phosphomolybdenum blue, phenate and Griess methods, respectively (APHA, 2005).

TruTrack water level/temperature loggers were used to measure stream height (Intech Instruments; Auckland, New Zealand). Height was converted to discharge using a rating curve built by measuring instantaneous stream discharge at each site across the range of observed stream heights (7-13 times per site). Instantaneous discharge was calculated by dividing the stream into cells of equal width and measuring depth and water velocity with a Marsh-McBirney Flo-Mate water velocity meter (Hach; Maryland, USA). Discharge was estimated using the slope-area method (Dalrymple & Benson, 1967) when maximum stream height exceeded the measured range of discharges. Depth loggers were deployed for 24 months between August 2010 and September 2012 at all sites except for Hollands Creek, Wombat Creek and Ryans Creek due to lost equipment, for which 12 months of flow data were included in analyses.

Statistical models

Effect of replanting age on terrestrial leaf litter (riparian CPOC) and canopy cover was analyzed with a linear mixed model:

$$R_i \sim Normal(\mu_i, \sigma_0^2);$$

$$\mu_i = \alpha + \beta Age_i + \varepsilon_i;$$

$$\sigma_0 \sim Uniform(0.001{,}10); \alpha, \beta \sim Normal(0, \sigma^2 = 1000);$$

$$\varepsilon_i \sim Normal(0, \sigma_s^2);\ \sigma_s \sim Uniform(0.001{,}10). \qquad \text{(Eq. S1)}$$

Here: R_i is the measured response (litter mass or canopy cover %) at replanting age *i* (8 – 22 years), which is distributed normally with means μ_i and a common variance σ_0^2. α and β are the regression coefficients, and ε_i are random effects for site.

The effect of replanting age on vertical litterfall was analyzed with a generalized linear mixed model:

$$R_{ij} \sim Poisson(\mu_{ij});$$

$$log(\mu_{ij}) = \alpha + \beta_1 Age_i + \beta_{2,j} + \varepsilon_i^{genus} + \varepsilon_i^{site};$$

$$\alpha, \beta_{1,2} \sim Normal(0, \sigma^2 = 4);$$

$$\varepsilon_i^{site}, \varepsilon_i^{genus} \sim Normal(0, \sigma_s^2);\ \sigma_s \sim Uniform(0.001{,}1). \qquad \text{(Eq. S2)}$$

Where: R_{ij} is the measured response (mean leaf litter mass per site, season and genus) at replanting age *i* (8 – 22 years) and season *j* (*n* = 4), which has a Poisson distribution with mean μ_{ij}. α is the intercept and β_1 is a regression coefficient for planting age. The β_2 are three seasonal effects (winter, spring, summer), which are expressed as deviations relative to winter (i.e. $\beta_{2,winter} = 0$). ε_i^{genus} is the effect for replanting genus (i.e. *Eucalyptus* or *Acacia*, with the latter being expressed relative to the former). ε_i^{site} is a random effect for site, which are drawn from a common distribution with mean 0 and variance σ^2. The upper bound of the σ_s prior is smaller for the Poisson model compared to the normal model (Eq. S1) because the logarithmic link function is associated with lower variation. Lateral litter movement was analyzed in the same way, without the random effect for genus.

The effect of riparian treatment (replanted or untreated) on standing stock of coarse particulate organic carbon (CPOC) was analyzed with a hierarchical generalized linear mixed model:

$$R_{ij} \sim Poisson(\mu_{ij});$$

$$log(\mu_{ij}) = \alpha + \beta_{1,j} + \varepsilon_i^{reach} + \varepsilon_i^{site};$$

$$\alpha, \beta_{1,2} \sim Normal(0, \sigma^2 = 4);\ \varepsilon_i^{site} \sim Normal(0, \sigma_s^2);$$

$$\varepsilon_i^{reach} \sim Normal(\beta_{2j}, \sigma_{rj}^2);$$

$$\sigma_{r,j} \sim Uniform(0.001,1);\ \sigma_s \sim Uniform(0.001,1). \qquad \text{(Eq. S3)}$$

Here, R_{ij} is the measured response (mean reach standing stock) in reach *i* (*n* = 8) with treatment *j* (replanted or untreated), which is Poisson distributed with mean μ_{ij}. α is the intercept, and the β_1 are three seasonal effects (winter, spring, summer), which are expressed as deviations relative to winter (i.e. $\beta_{1,winter} = 0$). The ε_i^{site} are random effects for site. The ε_i^{reach} are random effects for reach, with reaches having different means depending on treatment (β_{21} for untreated, β_{22} for treated) and treatment-specific standard deviations. β_{21} was set to 0 so that the effect of treatment was estimated by β_{22}.

The effect of riparian treatment (replanted or untreated) on large wood (LW) and on riparian CPOC was analyzed with a generalized linear mixed model:

$$R_i \sim Poisson(\mu_i); log(\mu_i) = \alpha + \beta_i + \varepsilon_i^{site};$$

$$\alpha, \beta \sim Normal(0, \sigma^2 = 4);$$

$$\varepsilon_i^{site} \sim Normal(0, \sigma_s^2);\ \sigma_s \sim Uniform(0.001,2). \qquad \text{(Eq. S4)}$$

Where: R_i is the measured response (mean reach standing stock) at treatment *i* (replanted or untreated), which is Poisson distributed with mean μ_i. α is the intercept and β is the treatment effect. ε_i^{site} are random effects for site. Initial models for the effect of treatment on LW and riparian CPOC were over-dispersed. We added a random effect for each response to the model to account for over-dispersion, which was disturbed normally with mean 0 and variance σ_s^2.

The importance of replanting and reach characteristics to organic carbon standing stock and transport was analysed using Bayesian model averaging (BMA). BMA yields posterior model probabilities for each model structure (linear combinations of predictors), which indicate the relative weight of evidence for each model. Summing the posterior model probabilities for all models that include a particular variable yields a marginal probability that the variable is a predictor (i.e. has a non-zero coefficient). The candidate variables for BMA of standing stocks are physical characteristics of the replantings and stream channel expected to influence organic carbon input and retention. Watershed-scale variables control watershed yields (Giling *et al.*, 2014), so candidate variables for DOC and FPOC yield were corresponding watershed climatic, soil and land use characteristics. Variables were removed if two variables of interest were highly correlated ($R > 0.7$), or the residuals of one regressed against the other were used in the model.

We analysed the effect of riparian treatment on metabolic and spiralling variables for each stream and day using a hierarchical linear mixed model:

$$R_{ij} \sim Normal\left(\mu_{ij}, \sigma_0^2\right);$$

$$\mu_{ij} = \alpha + \beta_1 PAR_{ij} + \beta_2 \overline{Temp}_{ij} + \varepsilon_i^{reach} + \varepsilon_i^{site};$$

$$\varepsilon_i^{reach} \sim Normal\left(\beta_{3j}, \sigma_{rj}^2\right);\ \varepsilon_i^{site} \sim Normal(0, \sigma_s^2);$$

$$\alpha, \beta_{1,2,3} \sim Normal(0, \sigma^2 = 4); \sigma_0 \sim Uniform(0.001,1);$$

$$\sigma_{rj} \sim Uniform(0.001,1);\ \sigma_s \sim Uniform(0.001,1). \qquad \text{(Eq. S5)}$$

Here, R_{ij} is the measured metabolic or spiralling response (daily rate) in reach i in treatment j, which are distributed normally with means μ_{ij} and a common variance σ_0^2. α is the intercept and $\beta_{1,2}$ are regression coefficients for dependence on PAR and mean temperature respectively. The ε_i^{site} are random effects for site to account for repeated daily sampling – there were 60 reach-days used in analyses – which are drawn from a common distribution with mean 0 and variance

σ_s^2. The ε_i^{reach} are random effects for reach, with reaches having different means depending on treatment (β_{31} for untreated, β_{32} for treated) and treatment-specific standard deviations. β_{31} was set to 0 so that the effect of treatment was estimated by β_{32}.

The difference in benthic organic carbon (BOC), transported organic carbon (TOC) and water velocity (i.e. variables used to calculate spiralling metrics) and treatment (replanted or untreated) was modelled:

$$R_i \sim Normal(\mu_i, \sigma_0^2);$$

$$\mu_i = \alpha + \beta_j + \varepsilon_i;$$

$$\sigma_0 \sim Uniform(0.001,10);\ \alpha, \beta \sim Normal(0, \sigma^2 = 1000);$$

$$\varepsilon_i \sim Uniform(0, \sigma_s^2); \sigma_s \sim Uniform(0.001,10). \qquad \text{(Eq. S6)}$$

Where: R_i is where the measured value in reach *i*, which are drawn from a common distribution with mean 0 and variance σ_0^2. α is the intercept, β is the estimate of the difference of values in replanted reaches compared with untreated, and the ε_i are random effects for sites.

Heterotrophic respiration (R_{het}) was measured daily, and so was compared between treatments as for metabolic rates (Eq. S5), without covariates for temperature and light. The difference in benthic fine particulate organic carbon (FPOC) between treatments (replanted or untreated) was analyzed with the same model.

Table S1. Mean watershed characteristics from the 12 study sites (NB: not available for Camerons Well Creek due to resolution of GIS data).

Stream	Watershed tree cover[1] (%)	Watershed pasture cover[1] (%)	Watershed relief[1]	Reach elevation[1] (m)	Maximum watershed elevation[1] (m)	Watershed area[1] (km^2)	Strahler order[1]	Distance to source[1] (km)	Watershed slope[1] (%)	Total annual rain[1] (mm)	Mean daily total soil moisture[1] ($Ml\ ha^{-1}$)	Mean soil water holding capacity of A horizon[2] (%)	Mean soil water holding capacity of B horizon[2] (%)	Mean soil saturated hydraulic conductivity (K_{sat}) of A horizon[2] ($mm\ h^{-1}$)	Mean soil saturated hydraulic conductivity (K^{sat}) of B horizon[2] ($mm\ h^{-1}$)	Length of upstream riparian zone cleared for pasture[3] (%)	Length of upstream riparian zone with scattered remnant vegetation[3] (%)	Length of upstream riparian zone with continuous remnant vegetation[3] (%)
Castle	10	88	0.43	245	512	35	2	14	4.5	716	3.5	37	37	222	16	9	57	34
Creightons	15	82	0.55	250	530	44	2	12	4.4	746	3.5	39	38	279	23	36	46	18
Faithfuls	22	74	0.40	214	750	76	3	23	4.6	955	5.0	58	45	283	39	3	19	78
Harrys	36	54	0.51	303	597	13	2	7	8.0	1041	5.1	59	45	300	42	18	53	29
Hollands	73	21	0.40	222	1132	172	3	44	7.9	1135	5.6	50	43	208	25	0	13	87
Honeysuckle	30	64	0.48	193	661	60	3	21	6.3	1057	5.0	58	45	286	40	2	53	45
Moonee	70	28	0.37	205	944	108	3	25	7.2	1100	4.1	40	38	255	21	20	32	49
Ryans	86	12	0.50	229	972	105	2	38	7.5	1267	6.8	59	48	279	39	0	19	80
Seven	15	82	0.36	166	822	371	3	74	3.7	850	4.5	48	42	252	29	2	34	64
trib. of Broken	72	27	0.36	315	758	6	2	5	8.1	907	4.1	37	36	100	4	19	26	55
Warrenbayne	67	26	0.46	230	747	67	3	16	7.4	1159	5.1	54	43	269	35	3	25	72
Wombat	58	40	0.49	570	797	16	1	11	6.0	836	3.8	46	42	293	31	0	26	74

Source: [1]Digital elevation model (Stein *et al.*, 2002), [2]EnSym (Victorian Department of Sustainability and Environment, 2012), [3]Google Earth.

Table S2. Mean (± SD) physicochemical reach characteristics from the 26 study reaches.

Stream	Reach	Treatment	Replanting age (yr)	Reach length (m)	Riparian width (m)	Replanting density (trees ha^{-1})	Above-ground C (t ha^{-1})	Canopy closure (%)	Large remnant tree density (km^{-1})	Mean daily flow (Ml day^{-1})
Creightons	us	untreated		419				21	5	24 (44.7)
	ds	untreated	0	436	0			16	0	
Faithfuls	us	untreated		468				23	11	26 (19.8)
	ds	untreated	0	458	6.5			40	76	
Hollands	us	untreated		310				49	65	125.7 (173)
	ds	untreated	0	390	3			62	92	
Castle	us	untreated		482				32	35	11.8 (46.9)
	ds	replanted	8	680	12	552	7.5	62	7	
trib. of Broken	us	untreated		224				29	9	1.8 (6.6)
	ds	replanted	8	486	7	611	22.3	53	0	
Camerons Well	us	untreated		193				45	10	0.1 (0.1)
	ds	replanted	10	825	7	907	26.5	76	6	
Harrys	us	untreated		389				50	36	8.6 (40.8)
	ds	replanted	11	376	30	448	40.6	69	128	
Honeysuckle	us	untreated		675				69	61	22.6 (54)
	ds	replanted	13	893	8.5	552	14.9	62	89	
Seven	us	untreated		578				48	142	230 (275)
	ds	replanted	13	1221	25	659	14.1	45	31	
Wombat	us	untreated		480				69	110	20.1 (32)
	ds	replanted	15	523	7.5	693	33.3	72	258	
Warrenbayne	us	untreated		250				39	4	29.4 (35.9)
	ds	replanted	18	329	12	344	32.3	71	61	
Moonee	us	untreated		288				48	14	48.4 (48.6)
	ds	replanted	22	272	9	1056	70.9	66	7	
Ryans	us	untreated		316				81	0	96.6 (67.8)
	ds	replanted	22	330	6.5	430	44.8	64	0	

(Table S2 continued)

Stream	Reach	Treatment	Riffle (%)	Run (%)	Pool (%)	Macrophyte cover (%)	Wet width (m)	Maximum depth (m)	Water velocity (km day^{-1})	BOC (g m^{-2})	TOC (g m^{-3})	R_{het} (g C m^{-2} day^{-1})
Creightons	us	untreated	0	99	1	3.9 (4.9)	2.5 (0.8)	0.4 (0.1)	18.1	87	6.6	0.1 (0.1)
	ds	untreated	0	100	0	4.1 (5.7)	2.2 (0.5)	0.4 (0.1)	17.3	132	10	0.2 (0.1)
Faithfuls	us	untreated	0	2	98	7.2 (21)	9.0 (2.4)	0.8 (0.5)				
	ds	untreated	0	12	88	70 (28)	7.8 (4.1)	0.5 (0.3)				
Hollands	us	untreated	10	84	6	1.6 (2.5)	7.8 (1.8)	0.9 (0.3)				
	ds	untreated	18	61	21	2.7 (5.0)	8.4 (1.0)	0.8 (0.3)				
Castle	us	untreated	0	33	67	85.7 (39)	6.7 (3.0)	0.5 (0.5)				
	ds	replanted	4	17	79	70.8 (35)	5.9 (2.1)	0.5 (0.4)				
trib. of Broken	us	untreated	0	100	0	39.4 (42)	1.4 (0.9)	0.2 (0.1)				
	ds	replanted	2	89	9	40.9 (42)	1.5 (0.9)	0.2 (0.1)				
Camerons Well	us	untreated	0	100	0	91.8 (28)	0.7 (1.5)	0.1 (0.1)				
	ds	replanted	3	85	12	7.9 (19)	1.4 (1.8)	0.1 (0.1)				
Harrys	us	untreated	23	60	17	23.3 (29)	4.0 (2.0)	0.3 (0.1)				
	ds	replanted	11	11	78	63.6 (42)	4.2 (2.3)	0.6 (0.4)				
Honeysuckle	us	untreated	3	87	10	28 (40)	4.9 (1.4)	0.3 (0.1)				
	ds	replanted	16	45	39	13 (24)	6.2 (1.6)	0.7 (0.3)	6.9 6.0	457 518	9.8 9.8	0.1 (0.0) 0.1 (0.0)
Seven	us	untreated	0	36	64	0.4 (0.5)	16 (3.6)	0.9 (0.2)				
	ds	replanted	5	24	71	2.2 (3.7)	22 (6.0)	1.0 (0.3)				
Wombat	us	untreated	4	95	1	0.7 (1.5)	2.4 (1.0)	0.2 (0.1)				
	ds	replanted	2	97	1	22 (31)	2.1 (0.6)	0.2 (0.1)				
Warrenbayne	us	untreated	0	100	0	1.3 (2.1)	4.1 (1.1)	0.4 (0.1)	19.9	367	4.0	0.1 (0.0)
	ds	replanted	1	59	40	3.7 (5.9)	5.9 (2.8)	0.7 (0.4)	7.8	610	4.3	0.4 (0.1)
Moonee	us	untreated	0	95	5	11 (22)	5.2 (1.1)	0.6 (0.2)	13	158	5.0	1.4 (0.2)
	ds	replanted	0	0	100	1.6 (2.9)	9.0 (1.0)	1.0 (0.2)	6.9	1202	5.2	1.5 (0.1)
Ryans	us	untreated	38	62	0	13 (16)	7.7 (1.1)	0.5 (0.1)				
	ds	replanted	10	90	0	14.2 (21)	8.1 (1.2)	0.5 (0.1)				

Table S3. Mean (± SD) organic carbon standing stocks and fluxes for each stream and reach. Shaded rows indicate replanted reaches.

Site	Reach	Treatment	Replanting age	Replanted litterfall g C m^{-2} mo^{-1} *n* = 12 mo	Lateral movement g C m^{-1} mo^{-1} *n* = 12 mo	Riparian CPOC g C m^{-2} *n* = 10 quadrats	Benthic FPOC g C m^{-2} *n* = 10 cores	Benthic CPOC g C m^{-2} *n* = 4 seasons	Large wood g C m^{-2} *n* = 20 transects
Creightons	us	untreated				1 ± 1		17 ± 23	88 ± 371
	ds	untreated	untreated			0 ± 0	153 ± 59	4 ± 2	0 ± 0
Faithfuls	us	untreated				4 ± 8		10 ± 11	0 ± 0
	ds	untreated	untreated			35 ± 44	693 ± 508	70 ± 43	169 ± 363
Hollands	us	untreated				24 ± 35		54 ± 58	416 ± 639
	ds	untreated	untreated			83 ± 68	312 ± 350	114 ± 70	244 ± 453
Castle	us	untreated				3 ± 6		22 ± 16	99 ± 271
	ds	replanted	8			174 ± 127	470 ± 302	107 ± 53	754 ± 1433
trib. of Broken	us	untreated				23 ± 63		5 ± 8	7 ± 30
	ds	replanted	8	18 ± 7	0.0 ± 1.0	43 ± 36	279 ± 138	13 ± 13	0 ± 0
Camerons Well	us	untreated				51 ± 94		59 ± 61	0 ± 0
	ds	replanted	10			134 ± 67	391 ± 198	73 ± 50	9 ± 35
Harrys	us	untreated				33 ± 49		38 ± 25	457 ± 1212
	ds	replanted	11			92 ± 51	440 ± 359	171 ± 96	154 ± 325
Honeysuckle	us	untreated				60 ± 54		50 ± 35	284 ± 810
	ds	replanted	13	13 ± 10	2.0 ± 2.0	118 ± 63	457 ± 324	134 ± 53	165 ± 596
Seven	us	untreated				66 ± 47		125 ± 80	1771 ± 2621
	ds	replanted	13	16 ± 12	17 ± 15	96 ± 62	485 ± 656	100 ± 60	399 ± 653
Wombat	us	untreated				133 ± 101		48 ± 72	761 ± 1311
	ds	replanted	15	16 ± 11	2.0 ± 1.0	76 ± 43	169 ± 98	70 ± 88	785 ± 1550
Warrenbayne	us	untreated				19 ± 47		52 ± 40	14 ± 63
	ds	replanted	18	37 ± 25	1.0 ± 1.0	233 ± 142	374 ± 141	146 ± 69	46 ± 110
Moonee	us	untreated				60 ± 59		78 ± 47	11 ± 36
	ds	replanted	22	35 ± 23	18 ± 8.0	400 ± 267	483 ± 659	167 ± 205	40 ± 117
Ryans	us	untreated				174 ± 102		18 ± 10	17 ± 44
	ds	replanted	22			386 ± 198	154 ± 109	20 ± 11	2 ± 11

(Table S3 continued)

DOC transport kg C km^{-2} y^{-1}	FPOC transport kg C km^{-2} y^{-1}	CPOC transport (baseflow) g C km^{-2} day^{-1} *n* = 4-7	ER	GPP	NEP	Velocity (V_{OC}) m day^{-1}	Turnover (K_{OC}) day^{-1}	Turnover length (S_{OC}) km	Index of retention (IR)
			g C m^{-2} day^{-1} *n* = 7, 12, 6, 6, 5, 6, 9, 9 days (Autumn 2012)			*n* = 7, 12, 6, 6, 5, 6, 9, 9 days (Autumn 2012)			
2567 ± 171	299 ± 83	0.40 ± 0.56	0.4 ± 0.2 1.0 ± 0.3	0.1 ± 0.0 0.1 ± 0.0	-0.3 ± 0.2 -0.9 ± 0.3	240 ± 4 210 ± 7	0.0046 ± 0.0027 0.0074 ± 0.0026	69 ± 36 32 ± 12	76 ± 1 83 ± 3
1339 ± 92	118 ± 45								
1654 ± 225	475 ± 110								
2010 ± 161	210 ± 83								
1503 ± 121	172 ± 64	0.57 ± 0.99							
3782 ± 340	892 ± 156								
1751 ± 114	435 ± 55	0.15 ± 0.16	0.2 ± 0.1 0.4 ± 0.0	0.1 ± 0.0 0.1 ± 0.0	-0.2 ± 0.1 -0.3 ± 0.0	19 ± 2 17 ± 2	0.0005 ± 0.0001 0.0007 ± 0.0001	40 ± 7.0 25 ± 1.0	375 ± 45 355 ± 43
2558 ± 187	154 ± 89	0.12 ± 0.22							
6867 ± 490	2591 ± 279	2.06 ± 2.12							
1329 ± 115	170 ± 57	0.26 ± 0.35	0.6 ± 0.2 1.7 ± 0.3	0.4 ± 0.1 0.1 ± 0.1	-0.2 ± 0.3 -1.6 ± 0.3	29 ± 3 17 ± 2	0.0014 ± 0.0006 0.0028 ± 0.0005	23 ± 8 6.0 ± 2.0	687 ± 73 474 ± 45
1250 ± 132	92 ± 62	0.03 ± 0.03	5.5 ± 0.9 7.0 ± 0.8	1.3 ± 0.1 0.6 ± 0.1	-4.2 ± 0.9 -6.4 ± 0.8	541 ± 35 54 ± 3	0.0334 ± 0.0059 0.0058 ± 0.0007	17 ± 4 9.0 ± 1.0	24 ± 2 129 ± 7.0
1288 ± 261	220 ± 121								

Chapter 7

General discussion

I took a landscape approach to examine the degradation and restoration of aquatic processes. I assessed the effect of terrestrial-aquatic interactions on the provision, processing and transport of aquatic organic matter at multiple spatial scales (Fig. 1). This was conducted at 20 stream sites across an agricultural landscape of south-eastern Australia that differed in local riparian condition (some revegetated with native trees 8-22 years previously) and watershed land use (a gradient of pasture to native forest). I sought to quantify the reach-scale effects of replanting riparian vegetation on biodiversity and organic carbon processes, and to project the biogeochemical implications of broad-scale replanting in future agricultural landscapes.

Aquatic biodiversity responded mainly to indirect watershed influences on water chemistry and geomorphology, suggesting their use as an indicator of reach-scale restoration success is limited. Aquatic macroinvertebrate indices were not sensitive to riparian replanting (within 22 years), consistent with previous results (Parkyn *et al.*, 2003; Collins *et al.*, 2013; but see Orzetti *et al.*, 2010). I found little evidence that replanting at the reach scale mediated an increase in biodiversity by altering basal resources and processes (Fig. 1), contrary to my initial conceptual model (pg. 16). Macroinvertebrates probably integrated a range of indirect agricultural effects, such as nutrient enrichment and higher conductivity, in addition to geomorphology (Fig. 1, red text on middle left). The composition of invertebrate assemblages were closer to those of the reference condition at sites with high watershed vegetation cover, suggesting that watershed condition is more important to macroinvertebrates than is local riparian condition (Thomson *et al.*, 2012). However, watershed tree cover was spatially confounded by stream size and altitude, a common challenge in land-use studies (Allan, 2004).

There was a reach-scale effect of riparian replanting on whole-ecosystem metabolism, which was measured at a subset of the older replanting sites (17 and 21 years replanted at time of sampling). In-stream gross primary production (GPP) was marginally lower, and ecosystem respiration (ER) marginally higher, in replanted reaches compared to ‘untreated’ (unplanted, largely cleared) reaches at two streams. Together, these differences resulted in lower net ecosystem productivity (NEP) in replanted reaches, nearer to values more typical of forested streams. Reduced NEP was probably due to greater canopy closure and increased accumulation of fine particulate organic carbon (FPOC), which provided an energy source and substrate for microbial consumers (Young & Huryn, 1999; McTammany *et al.*, 2007). These findings allowed specific mechanisms for linkages between processes to be defined on the updated conceptual model (Fig. 1). Litter accumulation in riparian zones increased with replanting age (consistent with Lennox *et al.*, 2011), and in-stream coarse particulate organic carbon (CPOC) standing stocks generally were greater in replanted reaches compared with upstream untreated reaches. This was not evident at all paired reaches; and although not considered in our original model, the effect of channel slope and flow conditions potentially led to low retention of CPOC at some sites (Fig. 1, bottom middle). Large remnant trees were identified as an important provider of large wood (Fig.1, bottom right).

Native vegetation cover at larger spatial scales (i.e. watersheds) influenced organic carbon dynamics. Concentrations of dissolved organic carbon (DOC) were greater at agricultural sites compared to forested sites, and this organic matter partly originated from a different source. The dissolved organic matter (DOM) in streams with a high percentage of watershed tree cover (at both an upstream riparian and whole-of-watershed scale) mostly originated from terrestrial sources (e.g. leaf litter and soil organic matter). Sites draining predominantly pasture watersheds had a substantial terrestrial component, but there was a greater contribution from in-stream sources (e.g. aquatic microbes and in-stream production). These results suggest a watershed-scale change in terrestrial-aquatic linkages or in-stream production of DOM (e.g. Wilson &

Xenopoulos, 2009). A greater in-stream contribution was expected to increase microbial processing because DOM from in-stream sources (often smaller, protein-like molecules) generally is more labile than the more recalcitrant molecules of terrestrial origin (often larger humic and fulvic acids) (Fellman *et al.*, 2009). There was no difference in the mean DOC molecular weight or bioavailability over the land-use gradient, which is represented by the weaker than hypothesized influence of watershed vegetation on organic matter quality in the updated model (Fig. 1, middle). This suggests the contribution from in-stream sources was small or inconsistent, or that microbes were quickly recycling a small pool of low molecular-weight organic matter (Cammack *et al.*, 2004). Alternatively, the availability of labile material at forested sites may not have limited microbial consumption; DOC could be continually recycled through viral lysis of bacterial biomass, allowing high rates of respiration through a bacterial-viral loop (Pollard & Ducklow 2011). Based on the results, replanting considerable portions of an agricultural landscape would affect the source of DOM, but not the metabolism of DOM.

Hydrology was more important than land-use cover in determining the quantity of organic carbon exported to downstream ecosystems (represented by the strong influence in Fig. 1, top right), which was mostly in the dissolved form (mean 87%). There was no consistent effect of watershed tree cover on yield (i.e. load / watershed area) of DOC or suspended FPOC, and as such this hypothesized effect is absent in my updated conceptual model (Fig. 1). Any losses of DOC or FPOC associated with reduced terrestrial inputs probably were subsidized by in-stream autotrophic production. Organic carbon transport was controlled by discharge (Royer & David, 2005); and the top 5% of discharge times contributed > 39% of the DOC and > 59% of the FPOC export. Antecedent hydrologic conditions appeared to be important to CPOC dynamics. Leaf matter probably accumulated during the long drought from 1997-early 2010 and benthic standing stock was greatest before the widespread flooding (largest in > 20 years) of late 2010. Future rainfall patterns, including a predicted increase in extreme events such as those occurring in 2010, will have a substantial effect on subsidy transport, potentially affecting downstream ecosystems by altering the availability of energy and nutrients (e.g. Gong *et al.*, 2011).

Replanted reaches had shorter organic-carbon spiralling lengths (i.e. organic-carbon velocity / organic-carbon turnover) than untreated reaches, and were more similar to typical forested systems (Griffiths *et al.*, 2012). This suggests replanted reaches more efficiently process carbon and that a lower proportion of the organic carbon entering replanted streams would be exported compared with pasture streams. However, there was no difference in the index of retention (IR) between replanted and untreated reaches, indicating that water velocity played a more important role than did in-stream processing in regulating the retention of all size classes of organic carbon (Fig. 1, far right arrow). Some revegetated reaches in my study did not retain as much organic carbon as would be expected given their discharge (Webster & Meyer, 1997), so that the large-scale adverse effects of agriculture were not fully reversed by local replanting, at least on the temporal scale of this study.

Large-scale replanting in agricultural landscapes is a feasible and possibly desirable land-use option in the future if restoration is driven by economic forces, such as replanting trees to sequester carbon (Thomson *et al.*, 2009; Bradshaw *et al.*, 2013). The potential biogeochemical consequences of large-scale replanting were investigated by assembling an aquatic organic carbon budget for the replanted and untreated stream reaches. Riparian replanting may have a large influence on carbon fluxes per unit area of stream. Replanted reaches may become more heterotrophic, with my budget estimating a mean net carbon loss of 0.52 g C m^{-2} day^{-1} ± 0.80 SD (autumnal rate), a magnitude similar to about a third of mean untreated-reach NEP. By scaling the magnitude of my findings (annual litter inputs, autumnal ER and GPP rates) to similar streams (2^{nd} and 3^{rd} order agricultural reaches of the Goulburn-Broken watershed), I estimated this carbon loss over stream benthic area (1.6 t C ha^{-1} yr^{-1} ± 3.1 SD) was comparable to above-ground carbon storage by replanted trees (2.9 t C ha^{-1} yr^{-1}; S. C. Cunningham, pers. comm. 20/08/2013). Organic-carbon export in all 3^{rd}-order watersheds was smaller (0.028 ± 0.018 SD t

C ha^{-1} yr^{-1}), but stream benthic area covers a small proportion of the watershed area, so that total export was an order of magnitude larger (with less uncertainty) than the implications of replanting for aquatic fluxes. Changes to export from land-use or an increase in extreme hydrologic events could have a large effect on carbon balances.

Maximizing restoration effectiveness: The case for in-stream carbon

Ecological processes may be used to assess ecosystem condition because structural metrics (e.g. biodiversity) do not necessary correlate with functioning ecosystems (Palmer & Febria, 2012). Organic-carbon processes have been used as measures of stream health (Young *et al.*, 2008; Woodward *et al.*, 2012), and might be applied to monitor restoration success. Organic-carbon properties or fluxes are useful when altered microbial processes are the mechanisms underlying the achievement of successful restoration (Sandin & Solimini, 2009). Various organic-carbon fractions and fluxes can integrate riparian and in-stream processes at different spatial scales. Stream metabolism responded to riparian replanting at reach-scales within two decades, probably reflecting a return to terrestrial organic matter dynamics and the closure of the canopy to a more natural state. At watershed-scales, the characteristics of DOM may provide insight into riparian and in-channel organic-matter processes (Stanley *et al.*, 2012). A change in the source of DOM may be indicative of shifts in riparian or aquatic organic matter processes over large scales, such as a greater provision of terrestrial organic material. Whole-ecosystem metabolism and DOM source could be used to monitor riparian restoration success.

Restoring stream ecosystems

Investment in replanting should begin adjacent to small streams (1st-3rd order). These systems are well connected to their riparian zones and are a functionally important component of the river continuum for transporting energy resources downstream. Small streams lack extensive floodplains and therefore have smaller functional riparian zones. Restoring a threshold level of canopy closure may be an important step to return in-stream processes (Bunn *et al.* 1997). This will be achieved in shorter timeframes for narrow channels, so that small streams are expected to respond more rapidly to restoration than are larger streams (Greenwood *et al.*, 2012). Some in-stream organic-matter processes (e.g. metabolism, litter inputs) were more typical of forested streams within two decades of the replanting of native riparian vegetation. Replanting probably will assist to avoid a forecast reduction in organic-matter standing crop and increased turnover in future stream ecosystems (Kominoski & Rosemond, 2012). Other components of the organic carbon will take much longer to converge to more natural values, notably large wood standing stock (Meleason & Hall, 2005).

The expected endpoint for restoration of organic carbon fluxes remains unresolved, given that available replantings were ≤ 22 years old. I made treatment contrasts and analyzed the effect of replanting age as a linear process. Additional monitoring may provide greater understanding of potential thresholds in replanting age that may be required to restore ecological processes for a given stream size and topography. I found little evidence of thresholds over the current temporal scale (e.g. in canopy cover), but the oldest two sites did have greater (but more variable) vertical litter inputs (Chapter 6). Appropriate lowland reference sites do not exist, so I assumed a shift towards typical forested systems (i.e. greater organic matter inputs, low NEP) was indicative of a positive response. Understanding restoration trajectory and the best expected outcomes are pivotal to advancing restoration ecology (Hobbs, 2007; Lake *et al.*, 2007). Long-term and pre-restoration monitoring, combined with continuing to incorporate ecosystem processes, are crucial to achieving this goal.

Isolated replantings at reach scales (i.e. 100s of m) shifted stream ecosystem processes towards pre-tree-clearance condition. Land owners and managers could revegetate at small scales when opportunities arise, even in degraded watersheds. Despite this, there is a need for a landscape perspective to fully restore stream-ecosystem health. DOM characteristics and aquatic biodiversity were influenced by processes operating at whole-of-watershed scales. Managers might aim to maintain > 50% watershed tree cover, and preserve or restore nearly continuous riparian corridors (> 90% stream length) to avoid large shifts in ecological processes. These recommendations are broadly consistent with previous suggestions to maintain macroinvertebrate diversity (e.g. Thomson *et al.*, 2012) and will help mitigate other effects such as warming (Chessman, 2009). Remnant trees should also be protected.

Stream ecosystems are strongly influenced by variation in discharge. Restoration sites and actions should be considered in a watershed context, particularly in relation to geomorphology and hydrology (Fig. 1, top). Water velocity and organic matter retention are vital to organic carbon dynamics and partly will determine restoration trajectories. Some effects of restoration in lotic systems may be displaced downstream, particularly in non-retentive reaches. Quantifying downstream biogeochemical changes will assist in incorporating horizontal interactions among patches in scaling models and making recommendations for restoration priorities. The effect of restoration on hydrologic variability (and vice-versa) was outside the scope of my work, but should be a priority for further research over longer time scales (Cooper *et al.*, 2013). Successful restoration may require a combination of activities, such as replanting and incorporating retentive structures in streams channels. My work also confirms that storm flows must be included in sampling regimes to avoid great underestimates of fluxes (Tank *et al.*, 2010). The effect of timing and duration of low flows on processes should also be explicitly considered and would benefit ecological management in many regions worldwide experiencing a drying climate (IPCC, 2007).

Conclusions

Human pressures will continue to have pervasive adverse effects on natural ecosystems. Restoration work at small scales can provide benefits to aspects of ecosystem functioning, but addressing many effects requires a landscape mind-set. I demonstrated that the incorporation of connectivity at multiple spatial scales enhances understanding of how ecosystems respond to management actions. Long-term monitoring of ecological processes will be valuable to gaining an understanding of how global drivers of change, such as land degradation and climate variability, interact to affect connectivity among ecosystems. Indicators of terrestrial-aquatic connectivity could be incorporated in stream ecosystem monitoring at reach- and watershed-scales to provide a more complete picture of restoration effectiveness.

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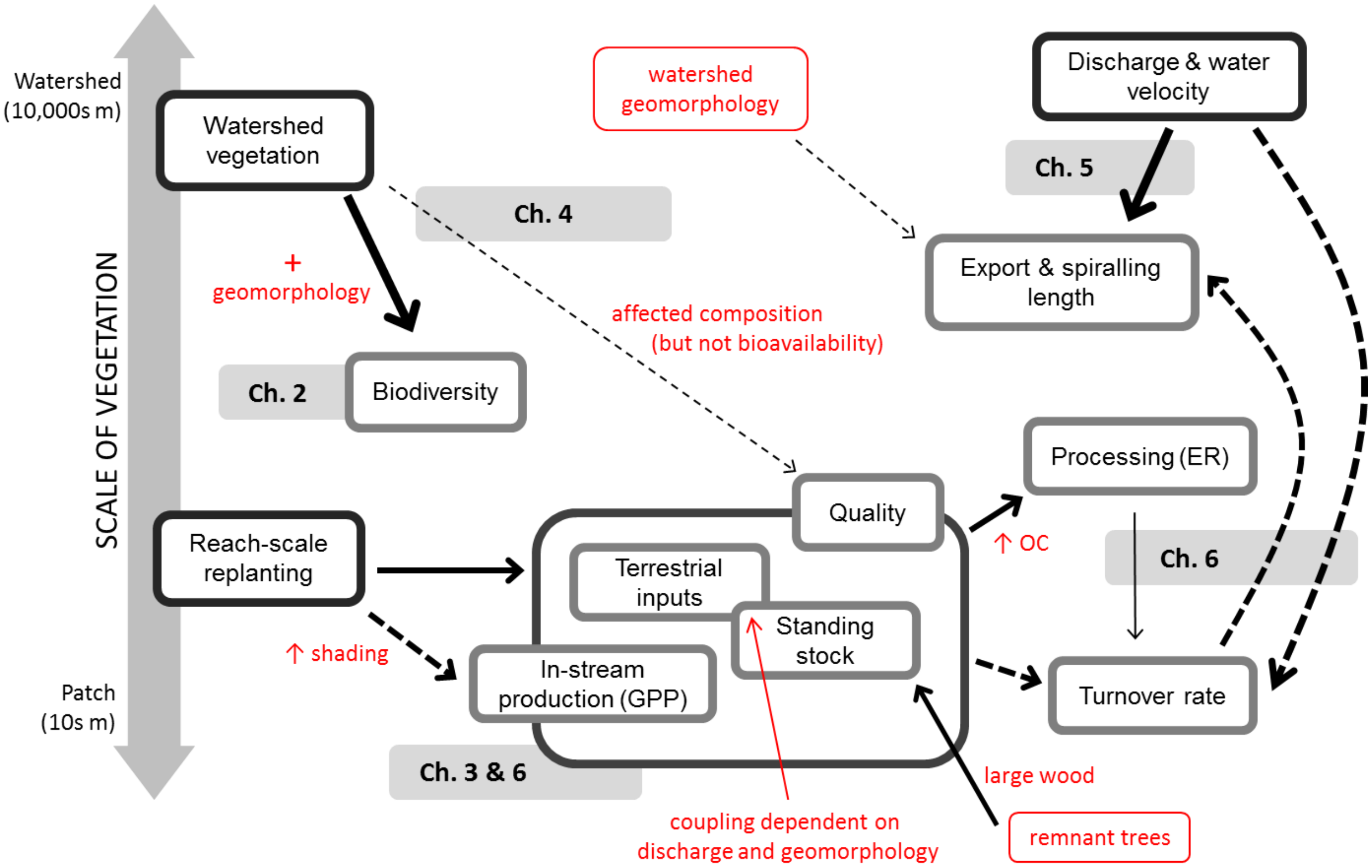

Figure 1. Updated conceptual model of the effects of vegetation at multiple spatial scales on organic carbon dynamics. Thesis findings are shown as arrows, where solid lines indicate positive effects and dashed lines indicate negative effects. The thickness of arrows indicates relative importance of the effect based on results of the current study, and is relative to the original conceptual model (pg. 16). Mechanisms that did not form part of initial hypotheses are shown in red text. Carbon processes are influenced by scale of vegetation as indicated by arrows, but their placement on the model is not indicative of scale.