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Changes in benthic community structure and function in an Australian regulated upland stream following wildfire

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Abstract The effects of fire on stream ecosystems are mostly indirect and can be attributed to post-fire floods, enhanced sediment and nutrient influxes, and channel morphology changes. Flow regulation will modify water and sediment regimes and thus can be expected to influence the nature and trajectory of post-fire changes in regulated streams. Despite this, few studies have examined how fire-related disturbances interact with flow regulation. This study draws on the results of several previous projects to generate multiple lines of evidence to explore pre- and post-fire benthic metabolism and benthic macroinvertebrate assemblages in an Australian regulated upland stream affected by wildfire during the austral summer of 2003. The benthic metabolism results show increased autotrophy following the fire, probably due to higher nutrient influxes and light availability because of reduced shading in conjunction with reduced respiration due to changes in the quality of carbon inputs and reduced interaction with the hyporheos associated with bed armouring.

Key words macroinvertebrates; benthic metabolism; flow regulation; wildfire

INTRODUCTION

The direct effects of wildfire on stream communities are generally small (Minshall 2003; Vieira *et al.*, 2004; Malison & Baxter, 2010); however, indirect effects can be both substantial and persistent. Indirect effects include hydrological disturbances and channel changes because of the effect of fire on catchment runoff rates and volumes (Minshall, 2003), increases in the delivery of sediment to streams as a result of the loss of ground cover vegetation (Silins *et al.*, 2009; Smith *et al.*, 2011a,b), changes in water and sediment quality (Smith *et al.*, 2010,a,b) and increased primary productivity as a result of reduced shading and higher nutrient fluxes from catchment soils (Fernandez *et al.*, 2011; Rhoades *et al.*, 2011). The effect of wildfires may be evident decades after the initial event (Robinson *et al.*, 2005); nevertheless, several studies have shown that instream aquatic communities can recover substantial structural and functional elements of their pre-fire state within a few years of burning. Benthic communities are thus considered to be resilient to the effects of catchment wildfire (Minshall, 2003; Peat *et al.*, 2005).

Recovery of stream communities following wildfires is hampered in streams whose catchments are subject to other anthropogenic disturbances such as logging, livestock grazing and fragmentation associated with water resource development (Minshall, 2003; Beschta *et al.*, 2004; Mellon *et al.*, 2008). Importantly, despite the evidence that interactions with anthropogenic disturbances strongly influence recovery rates and even trajectories, relatively few studies have examined recovery in streams regulated by dams. Flow regulation directly affects sediment and water regimes, both key drivers of stream disturbance following fire. Moreover, given the important role that longitudinal connectivity is likely to play in facilitating recolonisation of severely disturbed reaches, fragmentation by dams and weirs has the potential to influence further both recovery rates and trajectories.

Here we draw together the results of previous studies of benthic macroinvertebrate communities and benthic metabolism in a regulated, middle-order gravel-bed stream affected by a severe and extensive wildfire with the aim of extending the times series of data on the recovery trajectory of the stream following fire. The original studies from which we draw these data were conducted primarily to investigate questions other than post-fire recovery and, as such, the study designs and available data limit the strength of the inferences that can be made. Nevertheless, the data provide a valuable window into the ways in which flow regulation may modify recovery rates and trajectories in forested stream ecosystems impacted by the occurrence of wildfire.

METHODS

Study area

The Cotter River is an upland cobble and gravel-bed system that drains a catchment of approximately 483 km^2 located within the Brindabella Ranges in the Australian Capital Territory (Fig. 1). Although three dams regulate flow, the catchment itself is largely unmodified by human land use. These dams supply water for the city of Canberra (pop. ~322 000); however, environmental flow releases designed to minimize the impact of the dams and mimic the natural flow regime are made. Sites included in the study are all situated on the reach of the Cotter River between the Bendora and Cotter dams (Fig. 1) at altitudes ranging from ~700 to 500 m ASL. The climate is temperate with hot summers and cold winters. Average precipitation ranges from 990 to 1080 mm, with the wettest months between July and October. During the summer of 2003, the Cotter River catchment was subject to severe and extensive fire. These fires burnt a total of 260 000 ha in the ACT and NSW, including most of the Cotter River catchment above the Cotter Dam (McRae, 2003).

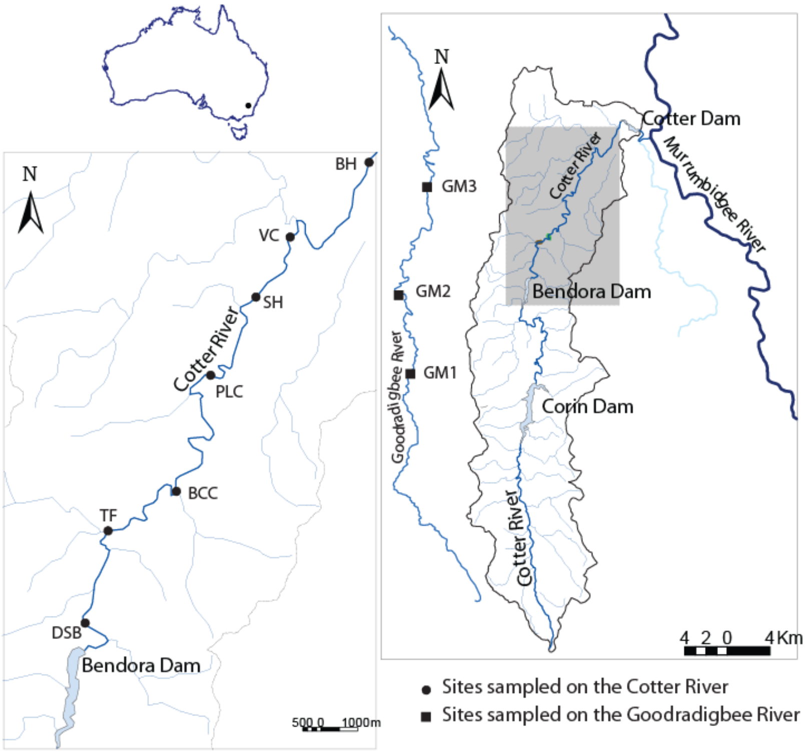


Fig. 1 The study area showing the locations of the Cotter and Goodradigbee rivers and the river locations sampled in Chester (2003), Norris & Thoms (2004), Peat *et al.* (2005), Reid *et al.* (2006) and Reid & Thoms (2008), which are included in this overview.

Study design

This study incorporates data from several previous projects on benthic macroinvertebrates and benthic metabolism collected from the Cotter River (Fig. 1) and from a nearby unregulated stream. The details of the original source data including timing of sampling and the variables collected are summarised in Table 1. The methods used in each case are described in the original publications (Chester, 2003; Peat *et al.*, 2005; Reid *et al.*, 2006; Reid & Thoms, 2008). Comparisons between variables derived from different studies are complicated by the different methods used in the original studies, which reflects the different purposes for which the data were collected in each case. For this reason, variables chosen for comparison were selected to minimise the possible confounding effects of sampling methods. Accordingly, benthic metabolism is compared only

Table 1 Details (variables, sample dates, locations and rivers) of source data used in this study.

Variable		P/R (productivity/respiration ratio)								Macroinvertebrate sampling								
River		Cotter						Goodradigbee		Cotter						Goodradigbee		
Site		VC	TF	SH	PLC	DSB*	BH	GM2	GM1	VC	TF	PLC	DSB*	BH	BCC	GM3	GM2	GM1
	Date																	
Chester (2003)	Feb 2002					×												
	May 2002					X												
Norris & Thoms (2004)	Apr 2003				X	X	X		X									
	May 2003				X	X	X		X									
	Jun 2003									X	X	X	X	X				
	Jul 2003				X		X	X	X									
	Aug 2003				X	X	X	X	X									
	Oct 2003				X	X	X		X									
	Nov 2003											X						
Peat *et al*. (2005)	Oct 2001												X			X	X	X
	Oct 2003												X			X	X	X
	Oct 2004												X			X	X	X
Reid *et al.* (2006)	Nov 2003		X		X													
	Dec 2003		X	X	X													
	Mar 2004		X	X	X													
	May 2004		X	X	X													
Reid & Thoms (2008)	Feb 2006									X	X	X			X			

*referred to as CM2 in Chester (2003) and *Peat et al.* (2005) and as 4102005 in Norris & Thoms (2004).

using productivity/respiration (P/R) ratios rather than primary productivity and/or respiration rates. In the case of benthic macroinvertebrates, sampling in the different studies varied somewhat: Norris & Thoms (2004) and Peat *et al.* (2005) followed the AusRivAS protocol for riffle sampling (Coysh *et al.*, 2000; Peat *et al.*, 2005); whereas Reid *et al.* (2008) sampled benthic macroinvertebrates in different surface flow types, which included habitat types not associated with riffles (Newson & Newson, 2000; Reid & Thoms, 2008). Accordingly, the analyses in this study only utilise assemblage data from Reid & Thoms (2008) collected from surface flow types associated with riffles (chute flow, standing broken waves, standing unbroken waves and ripple flow). In addition, benthic macroinvertebrate assemblages are compared through relative abundances of families and functional feeding groups rather than absolute abundances. Finally, in all cases, only informal analyses are applied to the data and interpretations are made with due consideration of the underlying limitations of making comparisons across the individual studies.

RESULTS

Benthic metabolism varied considerably in space and time (Fig. 2). Overall, P/R ratios were lower before the wildfire and in the first few months after the fire. In both the unregulated and regulated stream there was a general increase in P/R ratios in the months after the fire. Although this change was inconsistent between sites, most site P/R averages from the spring of 2003 onwards (~10 months after the fire) were in excess of 1, and half were more than 2.5 (Fig. 2). Comparisons of trajectories of change in benthic metabolism between unregulated and regulated streams over this period are limited by the lack of data from the unregulated Goodradigbee after spring 2003.

Overall, the number of benthic macroinvertebrate families recorded was higher before the fire than in the samples taken in the first year after the fire for both rivers (Fig. 3). Samples taken in the second year indicated recovery in the number of benthic macroinvertebrate families recorded in the unregulated stream to near pre-fire levels. In contrast, the number of benthic macroinvertebrate families recorded remained low in the unregulated stream in the second year (Fig. 3). After three years, however, the number of benthic macroinvertebrate families recorded in the unregulated stream exceeded those of pre-fire levels in both the regulated and unregulated stream (Fig. 3).

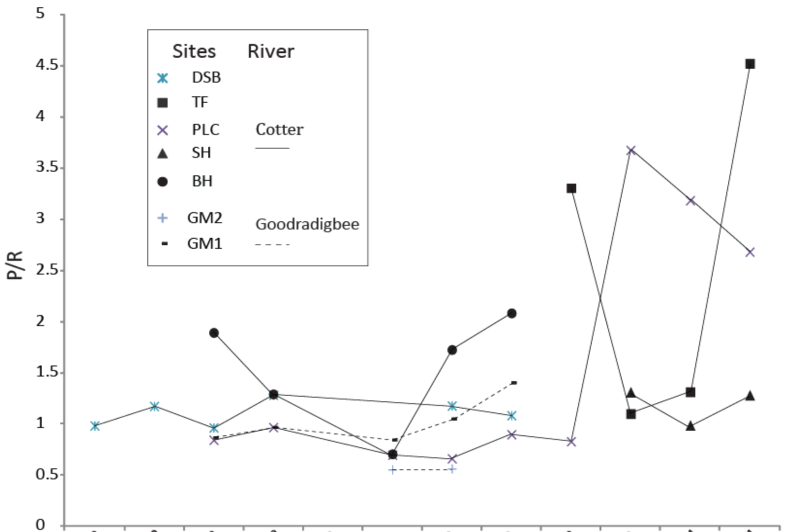


Fig. 2 Primary productivity/respiration ratios (P/R) recorded by Chester (2003), Norris & Thoms (2004) and Reid *et al.* (2006) at various locations on the Cotter and Goodradigbee rivers between February 2002 and May 2004.

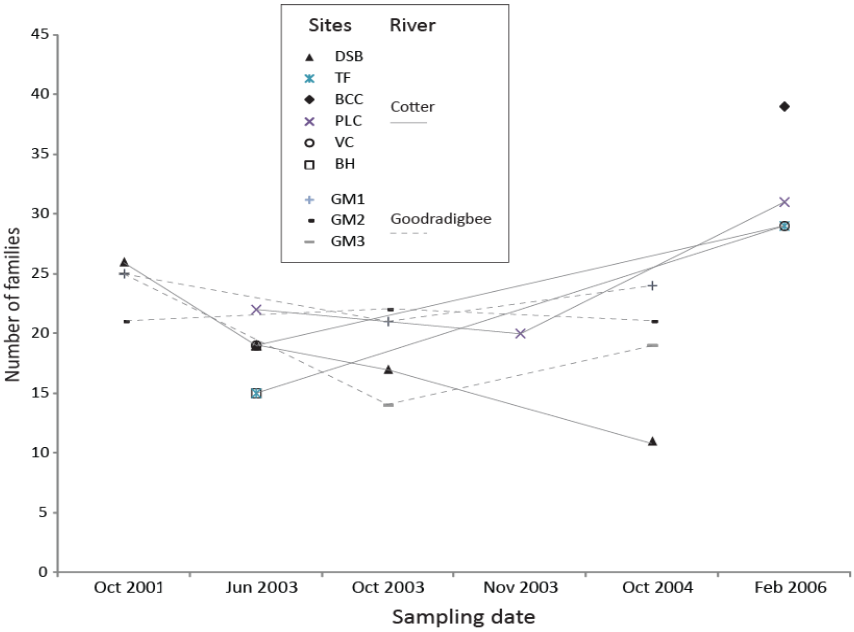


Fig. 3 Number of macroinvertebrate families recorded in riffle samples by Norris & Thoms (2004), Peat *et al.* (2005) and Reid & Thoms (2008) at various locations on the Cotter and Goodradigbee rivers between October 2001 and February 2006.

Assemblage level comparisons could only be made for post-fire macroinvertebrate assemblages in the regulated stream due to the limited amount of raw data available in Peat *et al.* (2005). These comparisons were made using MDS ordinations of family level and functional feeding-group level assemblages (Fig. 4). Both ordinations show clear separation of benthic macroinvertebrates assemblages in samples taken during the first year after the fire from those taken three years after the fire. In the case of the family-level ordination, this separation reflects the higher numbers of oligochaete worms and Caenidae (Ephemeroptera) in assemblages from June and November 2003 and the higher numbers of Gomphidae, Telephlebiidae (Odonata), Leptophlebiidae (Ephmeroptera), Hydropsychidae (Tricoptera) and Corydalidae (Megaloptera) in assemblages sampled in February 2006 (Fig. 4(a)). For the functional feeding group ordination, the separation reflects the higher abundances of “gatherers” and to a lesser extent “shredders” in the 2003 samples, and higher numbers of “scrapers” and “filterers” in the 2006 samples (Fig. 4(b)).

DISCUSSION

It is often difficult to make reliable direct comparisons of data collected by different studies. Taken individually, the benthic metabolism, benthic macroinvertebrate family number and benthic macroinvertebrate assemblage data do not offer a strong basis for making robust inferences about the impact of fire on stream benthic communities in a regulated stream; this is because there is confounding of the factors of interest (pre- *vs* post-fire, regulated *vs* unregulated stream) with the different studies, which each utilised different methods. However, collectively, the data are confirmatory and suggest that the benthic communities that established after 3 years following the fire in the regulated stream are distinct from those prior to the fire and to those that might have been expected in an unregulated stream. The benthic metabolism results from 2004 show a strongly autotrophic benthic community (Reid *et al*., 2006); this finding is consistent with the later findings of Reid & Thoms (2008) which showed that the macroinvertebrate communities in this reach of the Cotter River are dominated by scraper taxa (Fig. 5) that feed on periphyton communities. Thus, multiple lines of evidence suggest the system is supported by high levels of periphyton production. Increasingly, multiple lines of evidence are being employed in river

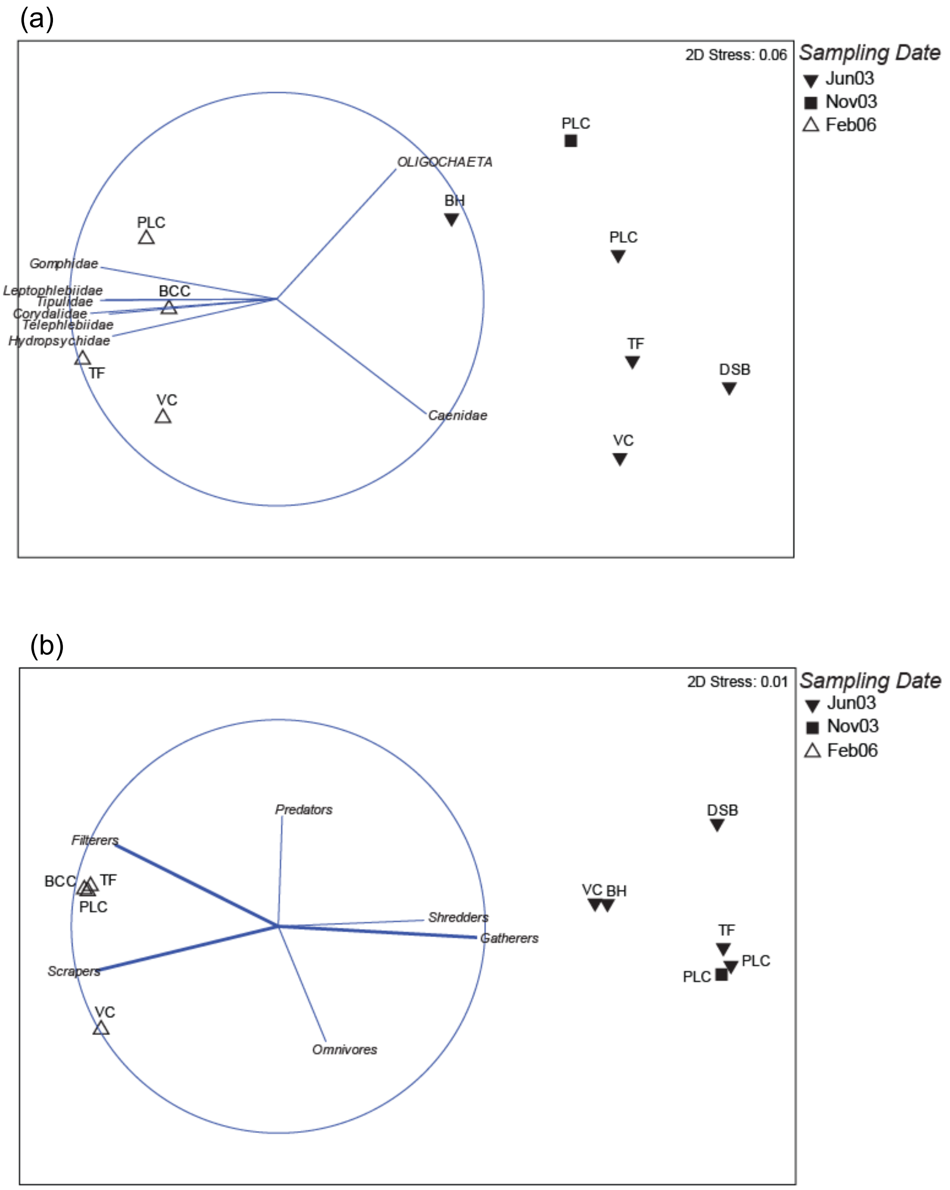
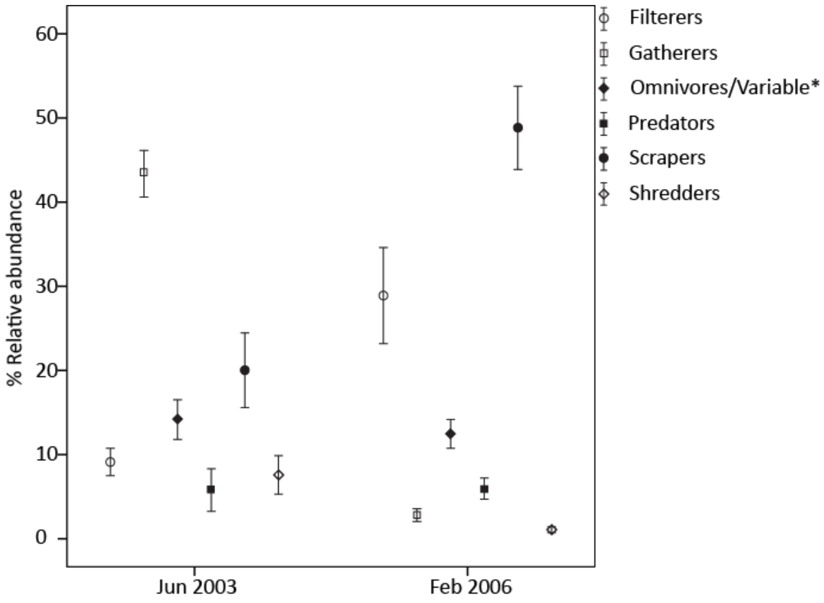


Fig. 4 Multi-Dimensional Scaling (MDS) ordinations of benthic macroinvertebrate assemblages recorded in riffle samples by Norris & Thoms (2004), and Reid & Thoms (2006) at various locations on the Cotter River between June 2003 and February 2006. Ordinations are based on resemblance matrices of Bray-Curtis similarity indices calculated using relative abundances of families (a) and functional feeding groups (b). Vectors indicate the direction of Pearson correlations >0.8 for individual taxa (a) and >0.5 (thin lines) and >0.8 (thick lines) for individual functional feeding groups (b).

science, particularly when exploring ecosystem responses to complex arrays of direct and indirect drivers (Norris *et al.*, 2004) associated with pressures on catchments and water resources.

The Cotter benthic periphyton community appears to have taken some time to become established following the fire. The early post-fire assemblages recorded in the Cotter River in 2003 were similar to those that have been recorded in other streams subject to fire where high catchment runoff and sediment inputs resulted in an abundance of taxa such as chironomids and oligochaete worms that are associated with high concentrations of fine sediment (Mihuc & Minshall, 1995; Minshall, 2003, Norris & Thoms, 2004, Vieira *et al.*, 2004, Peat *et al.*, 2005). However, since this period, it would seem that much of this fine material has been removed from riffle habitats leaving an armoured, highly stable substrate (Southwell *et al.*, 2012; Thoms, 2012). Coupled with reduced



*Families that include taxa with a range of feeding ecologies.

Fig. 5 Relative abundances of macroinvertebrate functional feeding groups recorded in riffle samples by Norris & Thoms (2004), and Reid & Thoms (2006) at various locations on the Cotter River in June 2003 and February 2006. Error bars are standard errors of the means.

shading caused by the opening of the riparian forest canopy and, potentially, high influx of dissolved nutrients from the disturbed catchment (Minshall, 2003; Townsend & Douglas, 2004), these conditions would appear to have facilitated a productive periphyton community that, in turn, supports a large biomass of scraper and filterer macroinvertebrates.

The apparently strongly autotrophic nature of the benthic communities in the Cotter River three years after the fire can be partly attributed to high primary productivity, but may also reflect relatively low levels of respiration in the disturbed system. The quantity and quality of allochthonous material is likely to have been greatly affected by the fire. While post fire influxes of sediment and organic allochthonous materials are generally higher due to increased runoff and availability of material for mobilisation and delivery to river channels, much of the organic debris is likely to be refractory charcoal (Minshall *et al.*, 2001). Moreover, allochthonous organic material may not be retained for long periods due to the armouring of the stream bed (Petts, 1988). The armouring of the bed may also reduce interaction with hyporheic communities where much of the respiration occurs (Petts, 1988).

The results of this study indicate that the interaction of the indirect effects of fire with the effects of flow regulation have resulted in an altered recovery trajectory following the disturbance created by the extensive wildfire in the Cotter River catchment. While it is possible that forest succession and the associated gradual increase in shading of the stream may result in reduced benthic primary productivity in the system, the effect of bed armouring in reducing organic matter retention and fluxes to, and from, the hyporheic zone are likely to persist and thus contribute to the maintenance of an autotrophic system.

CONCLUSION

This study, synthesising the results of several previous projects that examined benthic communities in a regulated stream impacted by wildfire, has shown that the effects of wildfire are likely to be modified under regulated flow regimes. Under natural flow regimes, the principal effects of wildfire relate to the subsequent hydrological disturbances, which deliver high peak flows, high volumes of sediment and changes to channel morphology. Under the regulated flow regime of the Cotter River, these disturbances appear to have been mitigated to a large degree and, as a result, the principal effect of wildfire was a shift to a strongly autotrophic benthic community supported by reduced shading and a stable, armoured substrate that limited interaction with the hyporheos. However, we stress that, given the possible confounding associated with the use of data from several different studies, these conclusions require testing in integrated Before–After/Control–Impact (BACI) studies.

Acknowledgements This manuscript is dedicated to the memory of Prof. Richard Norris, who, through his enthusiasm and dedication to high quality research, made an enormous contribution to stream ecology in Australia.

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