Changes in benthic macroinvertebrate communities in upper catchment streams across a gradient of catchment forest operation history

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ABSTRACT

The effects of forest harvesting on wet eucalypt forest stream macroinvertebrates were examined in Tasmania, Australia. Sites were selected in second to fourth order streams across a gradient of catchment forest harvesting history and in paired reference catchments. Historical data for every forest parcel (coupe) were obtained for each catchment, detailing forest operational type, area and year of operation, length of roads and number of stream road crossings.

We observed substantial differences in macroinvertebrate community composition and abundance across the 14 site pairs. We observed higher abundances of orthoclad midges, Leptophlebiid mayflies and Elmid and Scirtid beetles, and reduced abundances of worms and Notonemourid stoneflies at forestry test sites, than at their paired reference sites. A consistent shift in community composition was observed for 12 of the 14 site pairs. This was accompanied by a shift in functional feeding group representation away from shredders at test compared to reference sites. Community compositional similarity was substantially higher between test than reference sites, with a reduction in community diversity among streams due to a history of upstream forestry.

Community dissimilarity between paired test and reference sites was negatively correlated with the average parcel age and time since initial harvesting. We observed declines in abundance with increasing average coupe age of the mayfly family Leptophlebiidae and midge sub-family Chironominae at test sites relative to reference sites. Time since initial disturbance and the number of road crossings jointly accounted for 52% of the variance in paired-site Bray-Curtis dissimilarity values, with both variables negatively correlated with dissimilarity.

We observed a shift related to catchment forestry disturbance in macroinvertebrate community composition away from taxa typical of south-east Australian 'depositional' headwater stream environments to greater representation of taxa characteristic of higher power, more 'erosional' stream reaches. This support the hypothesis of a transition from predominantly degradational responses to forest harvesting operations (in the geomorphological sense) in headwater streams toward transient 'aggradational' effects further downstream with concomitant biological responses.

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1. Introduction

A number of factors account for forestry-induced changes in stream ecosystems. Changes to hydrology, sediment transport, nutrient dynamics, carbon budgets and stream habitats can result from forest clearing, conversion to plantations and roading. These can cause secondary impacts such as changes in diversity of macroinvertebrates, fish and other vertebrates (see for example, Michaelis, 1984; Growns and Davis, 1991), and in community composition, growth rates, reproductive success and behaviour of aquatic biota (Davies and Nelson, 1994; Growns and Davis, 1994; Hynes, 1994; Newbold et al., 1980; Ormerod et al., 1993; Silsbee and Larson, 1983).

Spatial variation in geological, groundwater, geomorphological, soil and vegetation characteristics can contribute to diversity of channel forms, and of meso- and micro-habitats in headwater streams of even a relatively small region or catchment (Gooderham et al., 2007). The nature and intensity of effects of forest operations on stream systems are therefore likely to be highly dependent on the physical context of both the operation (soil type, hill slope, proximity to stream channel, catchment geomorphology) and the drainage system (hydrological regime, stream power, channel slope, fluvial geomorphological character).

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Biological responses to forestry-induced changes in upper catchment stream ecosystems are quite variable as a result. For example, total macroinvertebrate abundance and biomass can increase as a result of forest harvesting (Silsbee and Larson, 1983; Noel et al., 1986; Fuchs et al., 2003), accompanied by increased representation of shredder, collector-filterer, collector-gatherer and collector-scraper functional feeding groups (Wallace, 1990; Kedzierski and Smock, 2001; Liljaniemi et al., 2002), but may also decrease (Newbold et al., 1980; Silsbee and Larson, 1983; Ormerod et al., 1993; Growns and Davis, 1994; Hynes, 1994), or remain static (Noel et al., 1986). Silsbee and Larson (1983) observed more taxa in logged streams and related the increase to changes in the structure of the allochthonous inputs (leaf-litter or other terrestrially derived organic matter) into the stream. Haynes (1999) found that species diversity was higher in unlogged streams. Noel et al. (1986) found no change in the number of taxa between logged and un-logged streams. Growns and Davis (1994) found that taxon richness declined in logged streams immediately after logging due to the increase in suspended solids, but recovered when suspended solid load subsided.

We contend that local geomorphological context is significantly responsible for some of this variation in the nature of the ecological response to forest disturbance. Many small headwater streams in South Eastern Australia (including Tasmania) have low stream power and sediment transport competence, associated with their small catchment size and varying local slope conditions (Gooderham et al., 2007). Davies et al. (2005a) recorded differences in instream channel morphology, sediment composition and habitats between upland Tasmanian first order streams which were ascribed to the influence of clearfell logging (with poor riparian protection) 15 years previously. In their undisturbed state these streams were characterised by significant storage of sands and silts and organic matter, coupled with diffuse and shallow channel complexes. Logged streams had shifted toward a coarser grained, simpler and more incised channel form. These differences were associated with changes in macroinvertebrate communities (Davies et al., 2005b) away from a typically 'depositional' fauna dominated by nematodes, worms and microcrustaceans and toward a fauna typical of higher power, coarser substrate streams, with increased representation of stoneflies and mayflies, and reduced abundances of taxa associated with depositional habitats. These effects were related to loss of backwater and pool meso-habitats, as well as an overall loss of fine particulate organic matter, presumably because of more intense peak flows after logging.

These effects contrasted markedly with previously reported effects of forest operations on higher order Tasmanian streams (Davies and Nelson, 1994), in which aggrading siltation effects from upstream forest operations were identified as a primary cause of reduced benthic macroinvertebrate diversity and abundance.

The sediment dynamics and geomorphology of a headwater stream reach are strongly influenced by its position relative to the location of the colluvial–alluvial boundary in the drainage system (Church, 2002; Gomi et al., 2002; Montgomery, 1999). This boundary (sometimes sharp, though often diffuse) marks a significant change in the dominant mode of sediment delivery to, and transport within, the stream. First order headwater streams are frequently above this boundary. Here, hill slope processes dominate sediment movement and stream power (controlled by channel slope and discharge) is often low enough for the stream to lack competence (Gooderham et al., 2007) This can result in significant storage of inorganic and organic fine sediments, both within and adjacent to the channel. This was certainly the situation in the headwater streams studied by Davies et al. (2005a,b) at Ben Nevis, Tasmania, Australia.

We postulate a transition from predominantly degradational responses to forest harvesting operations (in the geomorphological sense) in small headwater streams of low stream power, and hence competence, toward transient 'aggradational' effects further downstream. The degradational processes are characterised by raised levels of sediment and organic matter export driven primarily by increased peak flows. These may be partially controlled by higher relative incompetence of particle transport processes in those headwater reaches with relatively lower gradients. Exported fine sediment is deposited in reaches downstream, often transitorily, between periods of higher flow, with varying degrees of accumulation and aggradation. Intermediate stream reaches (typically second to fourth order streams) may show either type of effect, depending on stream power and geomorphological context (such as the nature and complexity of hydraulic controls, and substrate and channel sediment composition).

In order to evaluate this transition, we evaluated differences between benthic macroinvertebrate communities in stream reaches downstream of logging operations and in reference reaches (with no catchment logging history) in second to fourth order streams which were intermediate between first order, low power streams of the type evaluated by Davies et al. (2005a) and larger streams studied by Davies and Nelson (1994). We also wanted to evaluate the relationship between differences in benthic macroinvertebrate communities and the history of upstream forestry operations. The sites were therefore selected across a gradient of intensity of historical forest management within the upstream catchments. We characterised this in terms of catchment area harvested and/or converted to plantation, length or roads, and the time since of logging. We then related differences in macroinvertebrate community characteristics between paired reference and logged test stream reaches to variables describing the intensity of headwater catchment forest management.

2. Methods

2.1. Site selection

Sites of stream order 2–4 (sensu Strahler, 1952, at 1:25,000 map scale), and of greater channel slope than those described by Davies et al. (2005a,b) were selected, independent of sub-catchment fluvial geomorphological types, across a gradient of intensity of forest operations. For each site affected by forestry, a paired reference site was also chosen, with a history of no or minimal (selective) logging operations or other significant level of human landuse (Fig. 1), and with comparable stream geomorphology. Sites were selected using 1:25,000 scale spatial data layers sourced from Forestry Tasmania. These layers had features and attributes representing topography, roads, land tenure, and coupe age, area and forestry/silvicultural history.

Catchment areas ranged from 54 to 346 ha, averaging 148 ha. Stream slopes ranged from 0.02 to 0.52, with a mean of 0.19. These were five times steeper on average, than the first order streams described by Davies et al. (2005a,b) at Ben Nevis. Sites were located only in native wet sclerophyll State Forest (dominated by Eucalpytus sp.). The paired stream reach sites were adjacent or as close to each other as possible, with the same aspect, and of the same geomorphological type. The fluvial geomorphological type was characterised by the 'mosaic' approach developed for Tasmanian stream systems by Jerie and Houshold (2003), which characterised development of riverine features based on topography, geology, climate and process history. Site locations and features are shown in Table 1.

A raster-based GIS watershed analysis was conducted by overlay of parcel (coupe) map and history data onto stream
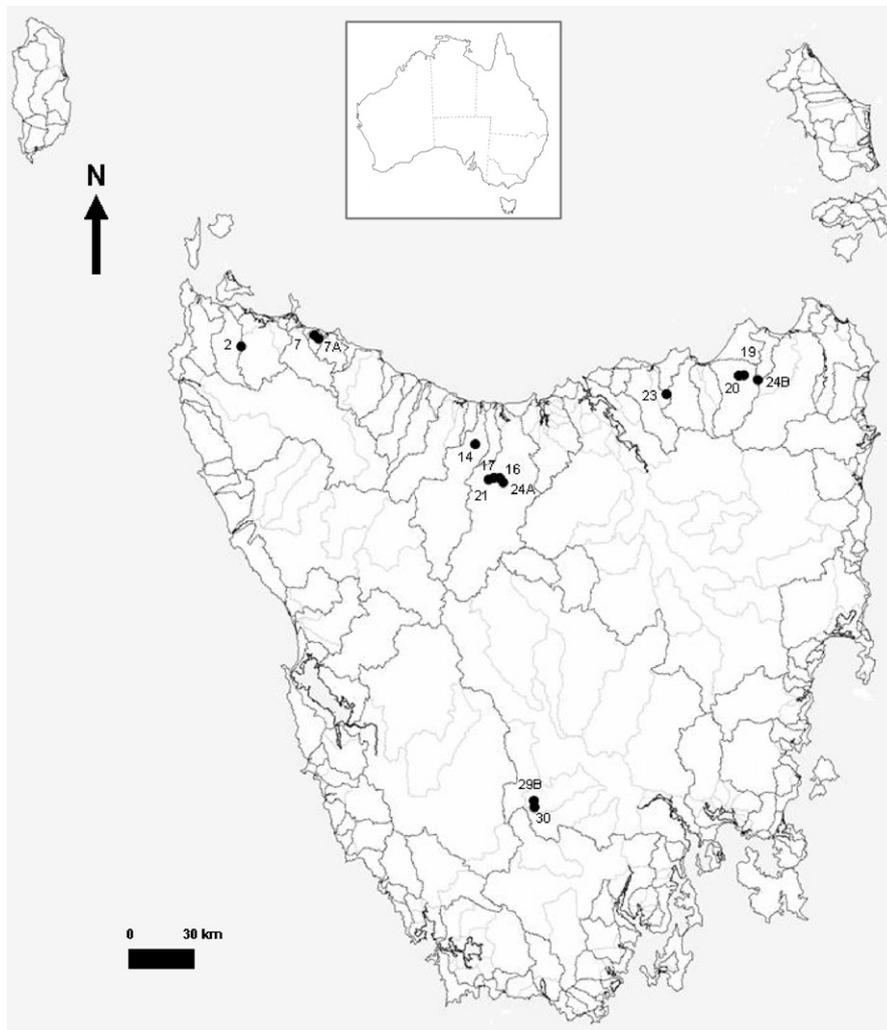
Fig. 1. The locations of studied stream site pairs in Tasmania, Australia. Numbers indicate test sites affected by previous forestry operations. Major river catchments and sub-catchments are indicated by black and grey lines.

drainage and topographic map layers (using ArcGIS®). Data on catchment area, the area of catchment logged and/or cleared, the area, time since harvest and identity of all upstream parcels (coupes) and the area of private land upstream cleared of native vegetation were derived for each stream site. The number of road crossings and the length of roads in the catchment were derived from 1: 25,000 scale maps using a mechanical curvimeter. Differentiation was made between forest operations which occurred prior to and after the establishment of the Tasmanian Forest Practices Code (Forest Practices Board, 1997/2000), a code of environmental practice enforced under the Tasmanian *Forest Practices Act* (1995). Key variables derived by GIS and map analysis and related statistically to instream observations are listed in Table 2.

A summary of the forestry history of each test site catchment is provided in Table 3. An attempt was made to select test sites with a range of time since peak harvesting and conversion (in years prior to the survey), area of catchment logged and converted (to plantation or regenerated native *Eucalyptus* species forest), and short vs. long periods of intensive forest management. The number of wet sclerophyll forest catchment sites available which met these requirements, and which had similar and adjacent minimally impaired reference stream sites, was limited. Sites were also screened to exclude other (primarily agricultural) land uses. A final selection of 14 site pairs was made, comprising a total of 26 sites.

2.2. Sampling regime

2.2.1. Macroinvertebrates

Benthic macroinvertebrate and organic matter samples were collected from random locations within mid-channel riffle habitats at each site using a standard Surber sampler (33 cm × 33 cm quadrat, 500 μm mesh, Lind, 1974; Wetzel and Likens, 1991) during autumn, under baseflow conditions. The benthos was disturbed by hand, and dislodged material captured in the downstream net. 10 samples were collected at each site, then combined and preserved in 10% formalin solution.

2.2.2. Stream habitat data

Riparian canopy density was measured using a Spherical Densiometer, as percentage of overhead cover, with 10 readings mid-channel per site spread evenly over a 100 m reach. Data were also collected for the 100 m study site reach on riffle substrate composition (by visual estimate of percent area of dominant bed material) and mean depth and width (wetted and bankfull). Visual estimates were also made of % benthic cover of algae, silt and organic detritus. Stream temperature (°C) and conductivity (μS/cm) were recorded at the time of sampling using hand-held YSI® water quality instruments.

Table 1
Sample site details. Test and reference sites are shown paired. Strahler stream order derived at the 1: 25,000 map scale. *, + = test sites with shared reference site.

Site	River catchment	Description	Location (AGD66)		Catchment area (ha)	Order	Bankfull width (m) (mean, m)	Channel slope (mean rise/run)	Elevation (of site, m)
			Easting	Northing					
2	Arthur River	Test	332612	5468283	295	4	3.0	1.06	40
		Reference	331612	5465083	140	2	3.5	2.18	60
7A	Black River	Test	366799	5472300	217	3	1.5	1.75	30
		Reference	367088	5469147	109	2	4.0	7.37	50
7	Black River	Test	365147	5473099	155	2	4.0	2.58	20
		Reference	364687	5470717	186	2	1.5	3.41	45
14	Forth-Wilmot Rivers	Test	437158	5423150	72	2	3.0	16.90	80
		Reference	437319	5422826	56	2	5.0	20.47	60
16	Mersey River	Test	446878	5407642	154	3	3.0	7.63	240
		Reference	444727	5408791	346	2	4.0	6.94	245
17	Mersey River	Test	443775	5407650	75	2	8.0	10.20	260
		Reference	443136	5407991	203	2	3.5	16.32	300
21	Mersey River	Test*	448255	5408286	129	2	5.0	6.34	215
24		Test*	448725	5407150	224	3	3.0	8.03	240
2124A		Reference	450403	5405646	110	2	2.0	22.58	330
19	Great Forester	Test+	559265	5451767	330	2	3.5	4.11	205
20		Test+	557310	5452974	127	2	1.7	4.33	200
1920		Reference	554488	5454417	97	2	1.5	15.09	80
23	Little Forester	Test	522079	5445288	90	2	1.0	7.59	125
		Reference	523312	5445523	54	2	1.0	5.81	90
24B	Great Forester	Test	564607	5453735	201	3	3.0	7.55	170
		Reference	563677	5450485	107	2	2.5	4.10	170
29B	Lower Derwent	Test	462662	5262650	87	2	5.0	9.24	340
		Reference	465125	5262425	75	2	3.0	20.96	390
30	Lower Derwent	Test	464854	5260674	144	2	3.4	3.05	480
		Reference	463025	5260675	64	2	4.5	5.22	490

2.3. Sample processing

Benthic macroinvertebrate samples were elutriated with a saturated calcium chloride solution prior to being sub-sampled in the laboratory using a Marchant box sub-sampler (Marchant, 1989) to 10% of the total sample. The sub-samples were then hand-sorted under magnification and all macroinvertebrates identified and counted. Identification was to family level, with the exception of Turbellaria, Nematoda, Hirudinea, Oligochaeta, Acarina, Copepoda, Cladocera, Ostracoda and Collembola, which were not identified to a lower taxonomic level. Individuals of the Dipteran family Chironomidae were identified to sub-family level. Each macroinvertebrate taxon was assigned a dominant functional feeding group (FFG) based on information provided by Chessman (1986), Cummins and Klug (1979), and Gooderham and Tsyrlin (2002).

Table 2
Variables derived from GIS and map analysis.

Variable	Unit of measurement
Total catchment area	Hectares
Plantation area	''
Native regeneration area (clearfell–burn–sow)	''
Area logged before the Forest Practices Code (>1987)	''
Area logged after the Forest Practices Code (<1987)	''
Total area harvested	''
Cleared private land	''
Average years since logging (overall, pre-Code, post-Code)	Years
Range of years of logging activity (overall, pre-Code, post-Code)	''
Time since initial logging activity (overall, pre-Code, post-Code)	''
Number of road crossings over the upstream catchment drainage	Count
Total length of roads in the upstream catchment	Metres

The organic residue remaining after elutriation with saturated calcium chloride solution and hand-picking for macroinvertebrates was sieved at 1 mm into two portions—fine particulate organic matter (FPOM, 0.5–1.0 mm size fraction) and coarse particulate organic matter (CPOM, >1 mm size fraction). The two fractions were dried to a constant weight at 60 °C and weighed.

2.4. Statistical analysis

Macroinvertebrate data were ordinated using non-metric multi-dimensional scaling (NMDS) of a matrix of Bray-Curtis dissimilarity values derived from $\log(x + 1)$ transformed abundance data (in the PC-ORD package, McCune and Grace, 2002). Ordination was considered successful when global stress was less than 20%. The non-parametric multi-response permutation procedure (MRPP, McCune and Grace, 2002) was used to test for the significance of multivariate differences between the test and reference sites in the ordinations. For each pair of test and reference sites we derived Bray-Curtis dissimilarity values. Ordination biplots were used to initially explore which taxa were potentially responsible for differences between test and reference sites.

Habitat variables were subject to redundancy analysis using the Principal Components Analysis (PCA) procedure in SYSTAT 10.0 (Wilkinson et al., 1996). All the following analyses were conducted using the relevant procedures in SYSTAT 10.0. Inter-site paired differences in habitat variable values (test minus reference) were regressed against the macroinvertebrate Bray-Curtis dissimilarities for reference and test site pairs. Similarly, inter-site paired differences in macroinvertebrate taxon abundance (test minus reference) were regressed against inter-site paired differences in the scores for the first habitat PCA factor.

Table 3
Summary of forest management within test site catchments.

Test site	%Catchment area logged	Conversion	Age of operations (before survey)
2	52	Mostly hardwood plantations conversion	2–14 years
7	39	Mix of hardwood and natural regeneration coupes	1–3 years
7A	8	Hardwood plantations conversion	1 year
16	44	Mix of hardwood and softwood plantations, and natural regeneration.	1–2 years
17	71	Mix of hardwood and softwood plantations, and natural regeneration.	6–7 years
21	85	Mix of hardwood and softwood plantations, and natural regeneration.	10–20 years
24A	85	Mix of hardwood and softwood plantations, and natural regeneration.	1–22 years
14	26	Natural regeneration	3 years
23	13	Mix of hardwood and softwood plantations	4 years
19	26	Mix of hardwood and softwood plantations	1–4 years
20	85	Mix of hardwood and softwood plantations	2–4 years
24B	24	Mix of hardwood and softwood plantations, and natural regeneration.	1–2 years
29B	14	Mix of hardwood and softwood plantations, and natural regeneration.	14 years
30	83	Mix of hardwood and softwood plantations, and natural regeneration.	1–14 years

Paired t-tests were conducted on taxon richness, total abundance, the abundance for each of the taxa present at every test site, as well as on values of individual habitat variables, with pairing by test-reference site pair. Variance in abundance and habitat data was frequently observed to increase with mean values (Sokal and Rohlf, 1995), requiring $\log(x + 1)$ transformation to correct for non-normality prior to t-tests. t-Tests were conducted using an alpha of 0.1, due to the small number of sample pairs, decreasing the risk of Type I error, but increasing the risk of Type II error. Tests for individual taxa were conducted with a Bonferroni correction applied to alpha values.

Correlation and multiple linear regression were used to explore the relationships between macroinvertebrate variables (abundance, taxon richness and Bray-Curtis similarities), habitat variables (sediment composition, CPOM, etc.) and the forestry related variables listed in Table 2. Residual and predicted values were plotted to check that the variance of the dependant variable was homogeneous across observations.

3. Results

3.1. Habitat and disturbance

The mass of FPOM was significantly higher at test than reference sites, by an average of 2.6 times (paired t-test, $p < 0.05$, Fig. 6). The mass of CPOM was also higher at test than reference sites, by a factor of 2.2, though with marginal statistical significance (paired t-test, $p = 0.10$, Fig. 6). No significant differences between test and reference sites were detected for the remaining habitat variables.

3.2. Macroinvertebrates

A total of 58 taxa were collected and 4893 individuals counted from the 14 site-pairs. Taxon richness at sites ranged from 7 to 27, with a mean of 18 (Table 4). Oligochaeta, Paramelitidae, and Chironominae were the most abundant taxa across all sites, accounting for almost half (47.5%) of all individuals counted. Orthocladiinae, Leptophlebiidae, Scirtidae, Sphaeriidae, Simulidae and Tanypodinae were the next most common taxa, accounting for a total of 31.5% of all individuals. Rare taxa, taxa for which <10 individuals were observed across all sites, accounted for 46.5% of the taxa found, but only 1.8% of the individuals.

There was no significant difference in total invertebrate abundance between the test and reference sites when compared by unpaired t-test ($p > 0.1$). Both the overall number of taxa and the number of rare taxa were significantly higher in test than reference streams (paired t-test, both $p < 0.05$, Fig. 2). Mean

numbers of taxa for all test and reference sites were 19.6 and 15.7, respectively.

MRPP analysis confirmed a significant difference between test and reference site community composition, even when un-paired (chance-corrected within group agreement, $A = 0.018$, $p = 0.03$). Bray-Curtis dissimilarities of test sites were also significantly

Table 4
Total macroinvertebrate abundance and number of taxa for each site pair. Data from 10% sub-samples of 10 pooled Surber sample units per site i.e. standardised to 0.09 m^2 stream bed area.

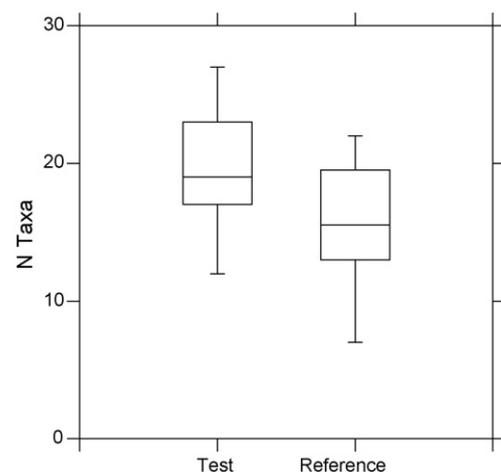| Site pair	Abundance		N taxa	
	Test	Reference	Test	Reference
2	275	103	26	14
7	338	139	18	7
7A	293	158	12	13
14	310	83	19	13
16	149	156	22	20
17	56	52	14	16
21	243	473	23	19
24A	93		19	
19	313	160	25	22
20	294		27	
23	202	83	12	20
24B	132	241	21	12
29B	91	182	17	17
30	194	80	19	15

Fig. 2. Number of macroinvertebrate taxa observed in test and reference stream site samples. Box plots with centre lines at the median, box covering the interquartile range, and whiskers showing outliers.
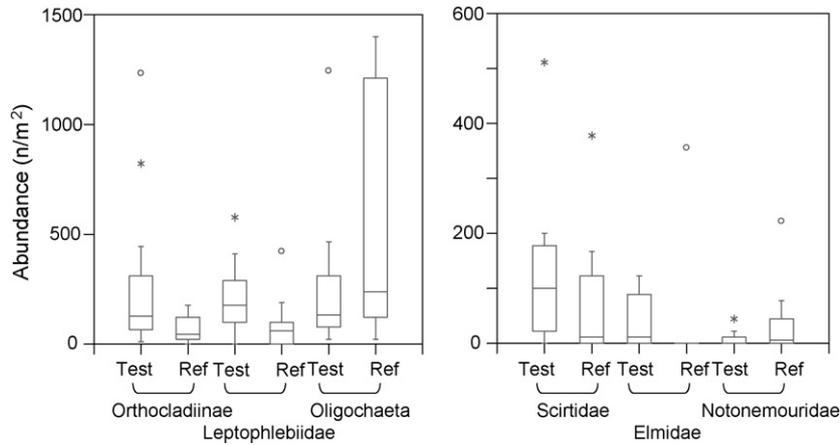
Fig. 3. Boxplots showing abundances of macroinvertebrate taxa which differ significantly between paired test and reference sites.

smaller than those of reference sites (unpaired t-test, $p < 0.05$), indicating that macroinvertebrate communities at test sites were more uniform in overall composition than at reference sites.

The abundances of four families were substantially and statistically significantly higher at test than at paired reference sites (paired t-test, all $p < 0.1$). Midges of the sub-family Orthocladiinae, mayflies of the family Leptophlebiidae, and beetles of the families Elmidae and Scirtidae were 1.5 to 4 times more abundant at the test sites than at paired reference sites. Three taxa were significantly less abundant in test than reference sites (paired t-test, all $p < 0.1$, Fig. 3). Oligochaeta (worms) and Notonemouridae (stoneflies) were two and six times more abundant at reference than at paired test sites, while Janiiridae (isopods) were present at five of the 14 reference sites, but absent at all test sites.

Inspection of vectors linking paired test and reference sites in ordination space revealed that, 12 of the 14 test-reference pairs differed with a similar orientation (along axis 2 in Fig. 4), i.e. their

compositions differed in a systematic way. A biplot (Fig. 4) indicated that these differences were associated with higher abundances of Leptophlebiidae mayflies, Elmidae beetles, Orthocladiinae midges, Scirtidae beetles and Hydrobiidae snails, and lower abundances of freshwater worms (Oligochaeta) at test than at reference sites.

Bray-Curtis Dissimilarities between test sites based on functional feeding group data were significantly smaller than between control sites (paired t-test, $p < 0.05$) indicating that macroinvertebrate FFG community composition at test sites was significantly more uniform than at reference sites. There were significant overall differences between test and reference sites in their FFG composition ($p = 0.008$, by MRPP analysis).

The abundance of collector-gatherer and scraper FFGs were both significantly higher in the test than reference sites (paired t-test, all $p < 0.07$, Fig. 5). The shredder feeding group was considerably more abundant in reference than test sites (paired t-test, $p < 0.03$, Fig. 5) (Fig. 6).

Macroinvertebrate Bray-Curtis dissimilarity between paired test and reference sites was negatively correlated with both the average age of coupes and the time since initial harvesting in the coupes, both overall and following the inception of the Forest Practices Code ($r = -0.55$ to -0.65, $p = 0.01–0.04$, by Pearson correlation, $n = 14$, Fig. 7). The proportional difference in total macroinvertebrate abundance between paired test and reference sites ($A_{test} - A_{reference}/A_{reference}$) was negatively correlated with average coupe age ($p < 0.05$, $r = -0.57$, $n = 14$, Fig. 8).

These two results indicate an initial post-harvesting response in community composition followed by recovery over time. Significant negative correlations were observed between the change
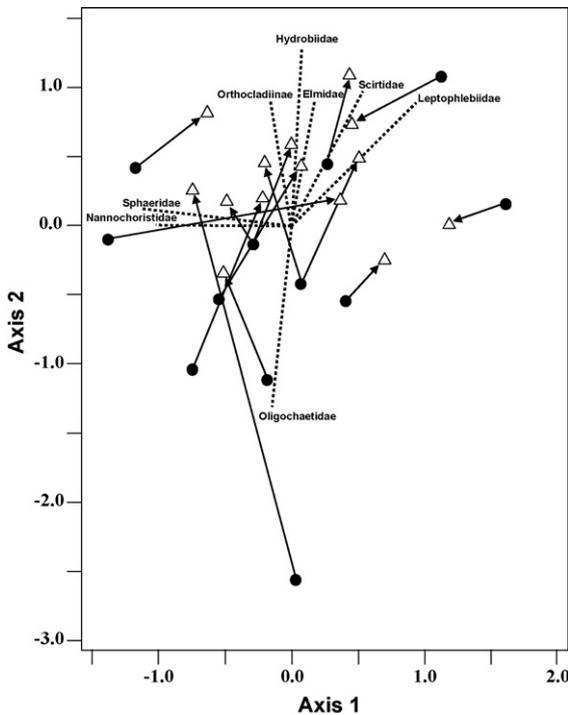

Fig. 4. NMDS ordination and biplot of test (triangles) and reference (circles) sites. Arrows indicate pairing. Biplot vectors (dashed lines) indicate direction in ordination space associated with increased abundance of key taxa (only significant taxon vectors are shown). Stress = 2.7.
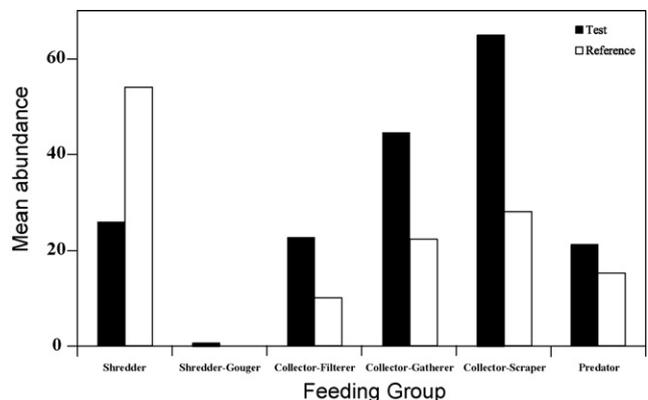

Fig. 5. Mean abundance per sample of functional feeding groups (FFGs) at test and reference sites. Numbers are equivalent to $n/0.09$ m^2 of stream bed area.
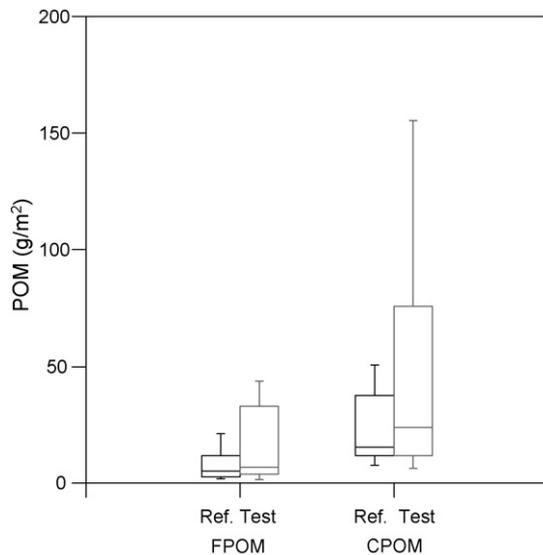
Fig. 6. Box plots of values for FPOM and CPOM substrate loads in test and reference sites. Note the increase in median and maximum values at test sites.

in abundance of both Leptophlebiidae and Chironominae and average coupe age (both $r = -0.54$, $p < 0.05$, $n = 14$), with declines in abundance at test sites relative to reference sites with increasing average coupe age. A similar negative correlation was observed for Orthocladiinae, but with marginal statistical significance ($r = -0.46$, $p < 0.1$, $n = 14$). There were no significant relationships between differences in taxon richness between paired test and reference sites and any forestry disturbance related variable (all $p > 0.1$).

Time since initial disturbance and the number of road crossings jointly accounted for 52 % of the variance in paired-site Bray-Curtis dissimilarity values (adjusted $r^2 = 0.52$, $p = 0.02$, by multiple linear regression), with these variables negatively and positively correlated with Bray-Curtis dissimilarity, respectively.

4. Discussion

We observed a shift related to forestry disturbance in macroinvertebrate community composition away from taxa typical of 'depositional' headwater streams toward a greater representation of taxa more characteristic of higher power stream environments. The principal response was a reduction in the relative abundance of worms, isopods and Notonemourid stone-
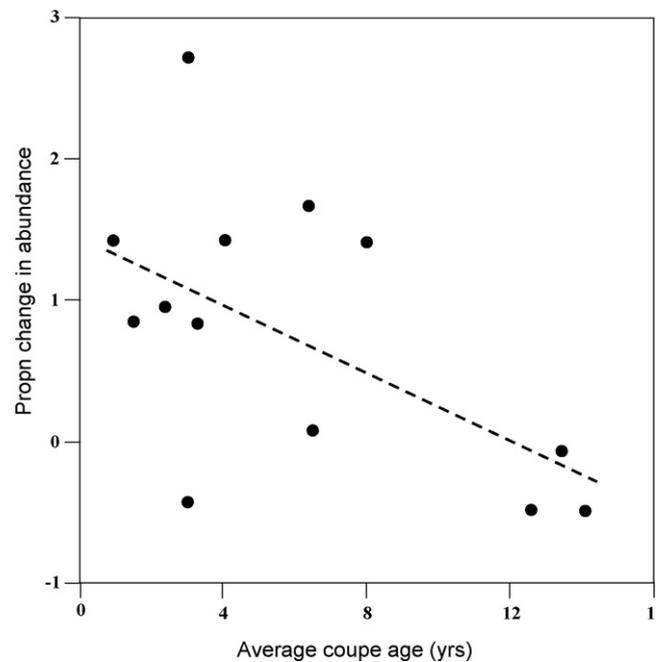

Fig. 8. Relationship between difference in abundance between test and reference sites as a proportion of reference site abundance, $(A_{test} - A_{reference})/A_{reference}$, and the average age of coupes in the test stream catchment for the 14 stream site pairs. Dashed line indicates least squares linear regression.

flies, and increases in the relative abundance of mayflies, beetles, hydrobiid snails and Orthoclad midges. There were also fewer shredder invertebrates and significantly higher abundances of collector-gatherer taxa at logged sites compared to reference sites. These differences occurred in 12 of the 14 paired sites.

Forestry disturbance also reduced the heterogeneity of test stream macroinvertebrate communities relative to those of reference streams. From this work, and our previous observations (Davies et al., 2005a,b; Davies and Nelson, 1994), it appears that in Tasmanian headwater catchments, forestry-induced disturbance causes a shift from more heterogeneous depositional stream environments, whose character is likely to be strongly influenced by local geomorphological features (Gooderham et al., 2007), toward more uniform, though slightly more biodiverse, 'riffle' stream habitats.

The forestry related variables that correlated strongly with biological change in our study streams were those that described the average age of forest operations in the catchment and the time
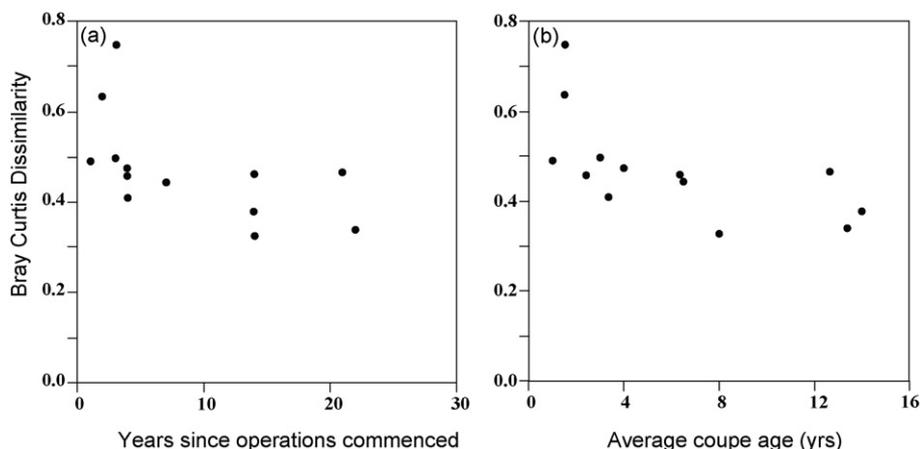

Fig. 7. The relationship between Bray-Curtis dissimilarity of macroinvertebrate communities between test and reference site pairs and years since forest harvesting commenced in the catchment (a), and the average age of all parcels (coupes) in the catchment (b).

since logging commenced. The changes we observed in macro-invertebrate abundance and community composition were negatively correlated with the time since logging commenced in the catchment, and suggested a recovery process over a period of approximately 10–15 years. The proportion of the catchment logged or roaded was not strongly related to the level of biological or physical response—despite the proportion of test catchments logged ranging from 8 to 85%. This may be due to masking by operations occurring at different times within the one catchment. Dispersed timing of logging operations could influence the magnitude and timing of responses regardless of the proportion of catchment logged, with the most likely mechanism being via alteration to the overall catchment hydrological response to logging operations and subsequent re-growth.

The shift in the macroinvertebrate community we observed here suggests a change in the energy of the hydrological regime in the logged catchments. Peak stream flow increases following logging of headwater catchments (Taylor, 1990), with water and sediment yield and discharge increasing with the proportion of catchment area logged (Michaelis, 1984; Clinnick, 1985; Cornish, 1993). This change in hydrology reduces with age after logging, as forest regeneration progressed. Martin et al. (2000) found that water yield increased by 150 mm immediately following logging but declined again over the following 4–6 years. Borg et al. (1988) found that stream flow increased following logging and persisted for 2 years, reducing as coupe vegetation regenerated. They suggested that yield was likely to return to pre-logging levels within 15 years. Return to pre-logging forest water yield is largely driven by forest-controlled changes in evapotranspiration (see Beets and Oliver, 2007).

We observed that test sites in the study described here stored larger amounts of organic matter in the benthos than the reference sites. This may be due to increased organic inputs following logging and/or changes in hydrology. An increased input of organic material to streams following logging is well recognized (Campbell and Doeg, 1989). Stone and Wallace (1998) also found that FPOM increased significantly in logged streams in the USA. Growns and Davis (1991) found higher levels of FPOM and CPOM in streams passing through clear felled logging coupes in Western Australia. They related variation in FPOM and CPOM to size of streamside buffer.

We had observed a marked relationship between macroinvertebrate community composition and the load of FPOM in small headwater streams at Ben Nevis, Tasmania (Davies et al., 2005b). In that study, logging had resulted in erosion of naturally 'depositional' channels with loss of fine sediment and organic material accompanied by a shift in faunal composition away from detritivore-dominance.

Collector taxa feed primarily on deposited FPOM, which is commonly colonised by bacteria, whilst scraper taxa feed on periphyton attached to the surface of the substrate (Cummins and Klug, 1979; Boulton and Brock, 1999; Davies unpublished data). According to the River Continuum Concept (Vannote et al., 1980), an increase in scrapers (grazers) is associated with a shift from allochthonous to autochthonous energy inputs in higher order streams. Newbold et al. (1980) reported increases in scraper taxa abundance in logged streams, due to increases in primary productivity (Wallace and Gurtz, 1986, in Wallace, 1990). Noel et al. (1986) and Davies and Nelson (1994) reported increases in benthic algae in logged streams. Kedzierski and Smock (2001) also observed increased abundance of collector-filterers and collector-gatherers in logged streams.

Shredder taxa feed on coarse particulate organic matter, which is colonised by micro-organisms (Cummins and Klug, 1979). This feeding group is common to low order streams where allochthonous material dominate energy inputs (Vannote et al., 1980). Scrapers and collectors dominated the functional feeding groups in

the test sites in the present study. The observed shift in FFGs between test and reference sites indicates a shift toward a stream ecosystem with greater autochthonous production and higher fine organic particulate loads. The shift in FFG we observed here may relate to the dominance of primarily allochthonous inputs in our unlogged streams, supporting a greater abundance of shredder taxa. The test streams were characterised by a mix of shredder and scraper taxa (including taxa that exploit autochthonous material), which also declined in representation over time after logging.

This study detected a time-dependent difference between test and reference streams, which suggests a non-linear process of recovery within a 10–20 year time span. Reported rates of recovery of macroinvertebrate communities toward a pre-logging state vary widely, and are likely to be controlled by both the intensity of forestry operations and the hydrological and geomorphological context of the stream ecosystem. Macroinvertebrate community composition will track changes in stream hydrology, sediment dynamics, food resource availability and channel form. Time scales of recovery of instream biota will largely be commensurate with the temporal scales of recovery of the physical and energetic aspects of the stream ecosystem. Stone and Wallace (1998) demonstrated that the macroinvertebrate community in logged streams resembled control streams 16 years after the disturbance. Growns and Davis (1991) found that buffered streams were more similar to control streams after 8 years than streams where no buffer was retained. Davies et al. (2005b) observed marked differences in stream macroinvertebrate community structure 15 years after headwater catchment clear-felling forest operations. It should be noted that those operations resulted in significant damage to riparian vegetation, whereas current logging practice in Tasmania requires mandatory riparian reserves (Forest Practices Board, 1997/2000).

We observed a broadly systematic difference in community composition and diversity between upper catchment stream sites with a recent history of forest management in their catchment. These streams, while still essentially headwater systems, were of higher order (2–4) and steeper than the first order Tasmanian streams whose response to logging disturbance had been described by Davies et al. (2005a,b) at Ben Nevis. The nature of the instream biological response was, however, similar to those at Ben Nevis, despite the set of streams having varied geomorphological contexts. This type of response to the influence of forest harvesting, a shift to an instream macroinvertebrate community more typical of higher energy fluvial habitats, differs markedly from the response previously described for Tasmanian main-stem streams (Davies and Nelson, 1994), and appears to be characteristic of Tasmanian headwater stream systems. We believe that these differences in response are due to differences in stream power and sedimentary behaviour within the stream drainage. Further research is underway to evaluate this question in more detail.

Acknowledgements

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