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# Changes in stream biota along a gradient of logging disturbance, 15 years after logging at Ben Nevis, Tasmania

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**Abstract**

We compared the instream biota of five first-order granitic headwater streams and five similar streams which had experienced a range of intensity of clearfell operations 15 years previously. We observed substantial differences in benthic macroinvertebrate community composition and abundance, aquatic insect emergence rates and abundance of macrophytes and algae between the two stream groups. Differences in the riparian vegetation structure, stream channel form and habitats and sediment composition of these streams had previously been ascribed to the effects of the clearfell operations and related to the intensity of historical forestry-induced disturbance. Instream biological responses (changes in macroinvertebrate assemblage composition and declines in abundance) were correlated with both a measure of the intensity of the degree of historical clearfell disturbance and with the amount of fine particulate organic matter (FPOM) in the stream substrate. Differences in macroinvertebrate abundance between channel and pool habitats were also associated with inter-habitat differences in substrate FPOM loading. We suggest that the magnitude of the response of benthic fauna along the disturbance gradient is mediated by the effect of disturbance on the storage of FPOM, which is both a habitat and food source, and that the clearfelling has induced long-lasting deficits of bioavailable organic carbon stores and backwater habitats in these streams.


*Keywords:* Logging; Headwater streams; Macroinvertebrates; Emergence; Diversity; Algae; Australia; Forest practices code; First-order streams; Tasmania; Disturbance

## 1. Introduction

Short to medium-term impacts of logging on streams have been well documented worldwide (Campbell and Doeg, 1989; Dignan et al., 1996). They include primary changes to hydrology, geomorphology, sediment transport, nutrient dynamics, carbon budgets and stream habitats. Secondary impacts include declines in diversity of macroinvertebrates, fish and other vertebrates, as well as changes in community composition, growth rates, reproductive success and behaviour of aquatic biota. These impacts are often moderated by the use of riparian buffers and setbacks, and limits on the slopes and proportions of

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catchments logged and on the nature and timing of logging and roading activities near stream channels (e.g. Bren, 1995; Quinn et al., 2004).

Longer-term (decadal and above) impacts are less well documented. Large and small scale changes in geomorphology have been observed (e.g. Stott, 1997; Slaymaker, 2000), and have been associated with some shifts in instream biological assemblages (Liljaniemi et al., 2002).

The faunal communities of small first-order forest streams and the impacts of forest harvesting operations on them are now starting to receive some attention (Moore and Richardson, 2003; Price et al., 2003; Haggerty et al., 2004), though not in Australia. Headwater stream geomorphology is highly heterogeneous (Gomi et al., 2002). It is, therefore, likely that the response of both their physical and biological characteristics to land clearing disturbance will be both spatially and temporally variable. This study attempts to evaluate long-term impacts of forest clearance on a particular headwater stream type – granitic upland first-order forest streams with moderate gradient.

The pattern of forestry-induced impacts on stream habitats and macroinvertebrates has been generally described from studies of steep headwater streams with substrates of large grain sizes (Campbell and Doeg, 1989; Dignan et al., 1996). Here, impacts are dominated by heightened delivery of fine sediments and exacerbated by flashy hydrological responses with extreme high flows and low baseflows, often coupled with increased insolation and stream temperatures. Such effects are accompanied by declines in macroinvertebrate diversity, attended by loss of water quality sensitive taxa, such as mayflies, stoneflies and caddis (e.g. Davies and Nelson, 1994; Growns and Davis, 1991, 1994). However, patterns of impact in headwater streams of quite different geomorphologies and stream power may follow a substantially different course (Gomi et al., 2002; Jackson and Sturm, 2002).

Headwater streams can store significant quantities of organic material (Gomi et al., 2002) and are significant sources of allochthonous carbon for downstream reaches (Cummins et al., 1983; Kiffney et al., 2000). Many upland Australian headwater streams are typified by fine-grain substrates and high levels of organic carbon storage, accompanied by relatively low stream power. In such streams, forest clearance will increase flow flashiness, and this may be accompanied by channel adjustment, coarsening of bed material and export of coarse and fine particulate organic material (CPOM and FPOM). Responses of the macroinvertebrate community may be substantially different to those in higher power streams, with a general shift from a community dominated by allochthonous processing (shredders and detritivores) to one more typical of coarser bed streams with increased representation of mayflies and stoneflies.

Differences in vegetation and the physical characteristics of first-order stream channels in the Ben Nevis area, in north-east Tasmania, Australia, have been linked to the impact of clearfell logging 15 years previously (Davies et al., 2005; McIntosh and Laffan, 2005). These studies noted marked changes in vegetation persisting in both the riparian and slope areas which were typical of vegetation shifts reported following clearfell logging on poor soils.

Previously clearfelled stream channels were deeper, more uniform in internal morphology and contained more coarse sediments, exposed boulders and less fine organic material than control streams. This response was interpreted as indicating a shift from shallow, braided ill-defined and organic-rich channels to incised sand-bed channels due to a combination of erosional scouring following clearfelling and gradual infilling over the ensuing period of vegetation regrowth and reduced stream energies.

This paper evaluates the differences in benthic macroinvertebrate communities between two sets of small headwater streams at Ben Nevis in terms of community composition, abundance and emergence of adult aquatic insects. These changes are interpreted in relation to a gradient of the degree of disturbance experienced by the streams during historical logging operations. Implications of the observed changes in stream habitat and macroinvertebrate assemblages for platypus populations at Ben Nevis are explored elsewhere (Koch et al., submitted for publication).

## 2. Study Sites

The 10 first-order study streams at Ben Nevis, north-east Tasmania, are shown in Fig. 1 and described

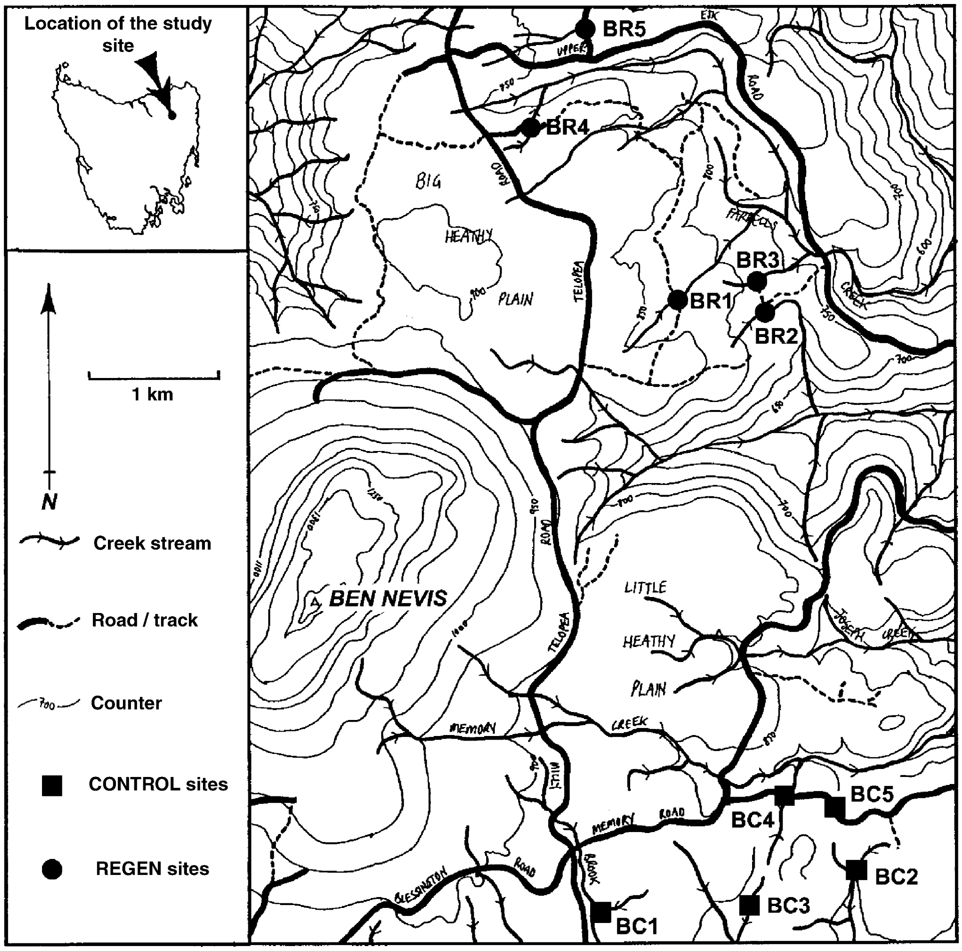


Fig. 1. Map of study site at Ben Nevis, Tasmania, showing location of study reaches in each REGEN (BR1–BR5) and CONTROL (BC1–BC5) headwater stream. Stream channels shown as defined on 1:25,000 scale 'Tasmap' map.

in detail by Davies et al. (2005). The streams were sub-alpine, at altitudes between 800 and 900 m, had a mean catchment area of 20 ha (range 8–40 ha) and were all on granite/adamellite bedrock geology draining eastward into the upper South Esk River catchment. Overall study stream gradients ranged between 0.024 and 0.07, with a mean of 0.05. In each stream, a single 50 m reach was selected for study, identified as representative of overall channel conditions within the lower reaches of the streams, with similar positions within the stream catchment and lying upstream of any road crossings. These reaches were jointly sampled for physical characteristics (McIntosh and Laffan, 2005) and biota (this study, Koch et al., submitted for publication).

## 3. Methods

### 3.1. Benthic macroinvertebrate sampling

Two quantitative samples of macroinvertebrates were collected at six equidistant locations within each 50 m study reach. One sample was taken in mid-channel, and the second in backwaters along the channel margins at the same site. These two locations corresponded to the 'channel' and 'backwater' habitats (morphological units) identified in the physical assessment (Davies et al., 2005). Each sample was taken with a modified 'surber' sampler, with a 250 μm mesh net in a frame immediately downstream of a 10 cm × 10 cm steel quadrat. All the substrate within the quadrat was disturbed by hand to a depth of 10 cm and all material washed into the net. The six sample units from each habitat within each reach were then combined and preserved with neutral-buffered 10% formalin to provide a single composite sample per habitat type per stream.

### 3.2. Emergence sampling

At the midway point along each study reach, one standard Malaise trap was pitched across the main channel perpendicular to the direction of flow. Ninety percent ethanol (with 5% glycerol) was used to fill the trap preserving bottle. Trapping was conducted for two 6-week periods ending on 9 August and 4 October 2001, respectively, corresponding to the peak winter and spring emergence periods. Trap contents were preserved in 90% ethanol until processed.

### 3.3. 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 20%. The sub-samples were then hand-sorted under magnification and all macroinvertebrates counted and identified. Identification was to family level for all aquatic insects and crustaceans. All other taxa were identified to order, with the exception of Turbellaria, Nematoda, Hirudinea, Oligochaeta, Acarina, Copepoda, Cladocera, Ostracoda and Collembola, which were not identified further. Individuals of the Dipteran family Chironomidae were identified to sub-family level.

Emergence trap samples were sub-sampled by gentle mixing in a 90% ethanol suspension and pouring over a 100 cell grid marked on a sorting tray. The tray was then agitated by hand. Ten cells were randomly selected and all insects within these cells counted and identified. Identification was to family level only.

### 3.4. Instream flora

For each of 20 m × 2.5 m sections along each 50 m study reach, the percentage of stream bed covered by benthic algae, moss and macrophytes was estimated visually. The number of discrete algal and macrophyte patches were also counted throughout each study reach.

### 3.5. Physical variables

Data on physical characteristics of the study stream reaches were collected and described by Davies et al. (2005) and used in this study (Table 1).

This data set, however, only included measurements of the overall area of organic silt deposits within stream reaches. The mass per unit area of fine particulate organic matter (FPOM) was therefore measured by passing the residues from the elutriated stream macroinvertebrate surber sub-samples through a 250 μm sieve, and drying the residue to constant weight. The dried residues were placed in a muffle furnace and loss on ignition was derived as a measure of FPOM per unit stream area, with one mean value derived per stream habitat sampled. One FPOM sample set was lost during this analysis, resulting in values for only nine streams in total.

### 3.6. Disturbance index

A single index of the degree of stream disturbance from the 1985 forest harvest operations was derived for all study streams from aerial photograph and field observations, as described by Davies et al. (2005). The rating was based on the degree of disturbance from forest operations within the catchment and riparian zone.

At the REGEN sites, fire was used to induce regeneration following clearfelling, but the regeneration pattern indicated that burns were patchy. The relative area of forest and under-storey removed and/or burnt, and the intensity of snig (harvestor) tracking was estimated for the catchments from aerial photographs taken immediately after harvesting in 1985. The relative area of forest removed and/or burnt, and the number of snig track stream crossings was also estimated for the riparian zones. It was not possible to assess stream channel condition from aerial photographs due to the dense riparian canopy cover. Index

Table 1
Mean values (and standard deviations) of stream morphology and habitat variables for the five CONTROL and five REGEN streams at Ben Nevis

| | | CONTROL | | REGEN | |
|---|---|---|---|---|---|
| | | Mean | S.D. | Mean | S.D. |
| Stream gradient | Overall site gradient* | 0.040 | 0.016 | 0.049 | 0.010 |
| | CV of local gradient | 0.735 | 0.279 | 1.102 | 0.328 |
| Channel dimensions | Wetted width (m) | 1.413 | 0.089 | 1.150 | 0.162 |
| | Bankfull width (m) | 1.915 | 0.138 | 1.866 | 0.291 |
| | Bank height (m) | 0.229 | 0.032 | 0.320 | 0.045 |
| | CV of Bankfull Width | 0.370 | 0.078 | 0.517 | 0.106 |
| *N* logs | Overlying# | 18.200 | 2.756 | 36.400 | 9.422 |
| | Instream# | 19.400 | 3.361 | 36.800 | 9.150 |
| % of channel area as | Channel | 43.446 | 7.068 | 58.600 | 12.500 |
| | Bar | 18.886 | 4.924 | 16.926 | 4.121 |
| | Pool | 37.668 | 9.172 | 24.848 | 11.150 |
| % of channel area as | Sand | 17.856 | 9.095 | 20.554 | 10.526 |
| | Gravel | 21.293 | 3.208 | 21.796 | 5.996 |
| | Cobble | 1.698 | 1.669 | 4.512 | 2.907 |
| | Boulder | 0.876 | 0.863 | 6.537 | 3.530 |
| | CPOM | 30.917 | 4.001 | 17.306 | 2.736 |
| | Organic silt | 21.157 | 4.711 | 14.191 | 3.983 |
| | Root mass | 3.159 | 3.028 | 3.385 | 0.807 |
| | Mosses | 1.782 | 1.131 | 3.709 | 2.877 |
| | Algae | 0.320 | 0.444 | 4.661 | 3.066 |
| | Macrophytes | 0.000 | 0.000 | 2.484 | 1.479 |
| *N* patches | Algae# | 0.320 | 0.716 | 4.661 | 4.938 |
| | Macrophytes# | 0.000 | 0.000 | 2.484 | 2.383 |
| | Mosses# | 3.000 | 2.236 | 4.400 | 4.722 |

S.D., standard deviation. Values derived from 20 measures per stream, except (#) measured over whole reach and (*) summed over whole reach.

values were also derived for CONTROL streams by field observation of historical cut stumps and snig tracks.

An overall relative disturbance rating for each REGEN stream catchment was then assigned to each catchment, giving a final score ranging between 0 (undisturbed) and 3 (intensely disturbed). The ratings and catchment and riparian descriptions are shown in Table 2.

### 3.7. Data analysis

Benthic macroinvertebrate (BM) data were analysed separately by habitat (channel and backwater). These data were also combined to represent overall stream macroinvertebrate community structure. The BM data for each habitat within a reach were sub-sampled in proportion to the % area of the habitat using the virtual Marchant sub-sampler (Marchant, 1989, Walsh, 1997). The sub-sampled data were then summed for each study reach. These data are hereafter referred to as 'combined habitat' BM data.

Overall % cover of moss, algae and macrophytes were derived for each stream by averaging % cover data from all 20 (2.5 m) sections within each study reach.

#### 3.7.1. Macroinvertebrate abundance and richness

Differences in benthic macroinvertebrate abundance and richness between CONTROL and REGEN streams were explored by one-way analysis of covariance (ANCOVA), with overall stream gradient within the study reaches as a covariate. Stream gradient had been shown to be a significant determinant of variance across streams for a number of the physical attributes (Davies et al., 2005), and was also believed to potentially influence macroinvertebrate attributes. Abundance data was $\log(x + 1)$ transformed prior to analysis. Correlations between

Table 2
Study stream features and logging disturbance rating

| Treatment | Stream | Catchment area (ha) | Mean stream gradient | Mean bankfull width (m) | Description of logging disturbance | Disturbance rating |
|---|---|---|---|---|---|---|
| CONTROL | BC1 | 22.56 | 0.0318 | 2.052 | Intact open canopy forest across catchment, light selective logging | 0.25 |
| | BC2 | 11.8 | 0.0332 | 2.168 | Closed, intact riparian canopy, minimal selective logging | 0.125 |
| | BC3 | 18.11 | 0.0234 | 1.815 | Closed intact riparian canopy, one side of catchment lightly selectively logged | 0.25 |
| | BC4 | 21.55 | 0.0534 | 1.945 | Open canopy forest in catchment, selectively logged, intact riparian forest | 0.25 |
| | BC5 | 8.04 | 0.0571 | 1.595 | Closed, intact riparian canopy, lightly selectively logged | 0.125 |
| REGEN | BR1 | 40.41 | 0.0310 | 1.950 | 80% of catchment cleared, one side of study reach with scrub retained | 2.00 |
| | BR2 | 26.48 | 0.0478 | 2.473 | 70% of catchment logged but still with scrub cover, two snig track crossings | 1.50 |
| | BR3 | 8.49 | 0.0636 | 2.095 | 65% of catchment logged, still with scrub cover, riparian trees retained | 1.00 |
| | BR4 | 19.25 | 0.0654 | 1.521 | 50% of catchment severely logged, no understorey, and burnt through stream. 50% a marsh, lightly burnt | 2.50 |
| | BR5 | 22.73 | 0.0341 | 1.290 | 90% of catchment cleared and burnt, minimal understorey retention, some scrub retained adjacent to study reach | 3.00 |

benthic macroinvertebrate and physical variables were determined by Pearson correlation. Differences in emergent macroinvertebrate abundance and richness between CONTROL and REGEN streams were explored by one-way ANCOVA, with overall stream gradient within the study reaches as a covariate.

The null hypotheses for all ANCOVA analyses were that no significant difference existed between CONTROL and REGEN streams, at an alpha of 0.05. Those differences significant at alpha of 0.1 were also examined, recognising the potential for Type II error due to small sample sizes. All univariate analyses were conducted using SYSTAT Version 10.0 (Wilkinson, 2001).

### *3.7.2. Community composition*

A matrix of inter-sample distances was prepared using the Bray-Curtis (BC) Similarity distance measure based on $\log_{10}(x+1)$ transformed data, separately for both benthic and emergent macroinvertebrate sample sets. Non-metric multi-dimensional scaling ordination (MDS) was performed on both data sets (using the PRIMER-5 package, Clarke and Warwick, 2001). MDS ordination was conducted for emergent macroinvertebrate data and for benthic macroinvertebrate data, both separately for each habitat ($n = 20$), and also for the combined habitat data ($n = 10$). One-way multivariate analysis of similarity (ANOSIM, in PRIMER-5) was conducted to assess overall community compositional differences between CONTROL and REGEN sites.

The distance of each sample in the BM ordination from the centroid of all CONTROL streams was calculated. Davies et al. (2005) had conducted Principal Components Analysis (PCA) on within-reach stream channel attributes (within-reach slope variability; number of logs; area of habitat types, substrates, tree roots, CPOM and FPOM; channel width and bank height; tree roots; area and number of patches of algae, moss and macrophytes), and had derived PCA factors. The BM ordination inter-site distances were then correlated with the PCA Factor 1 score as well as the disturbance index to assess relationships between deviation in community composition and these environmental factors.

Indicator Species Analysis (Dufrene and Legendre, 1997) was used to identify any taxa whose abundance was significantly representative of either of the two habitat types (i.e. backwater or channel) sampled in CONTROL or REGEN streams, using the PC-ORD package (McCune and Grace, 2002). This technique calculates relative abundances (RA) and relative frequencies (RF) of taxa in each group and derives an indicator value for each taxon across the groups (where IV = 100 × RA × RF, and IV ranges from 0 to 100). The significance of this IV is evaluated for each taxon by Monte Carlo randomisation of all taxa across the groups (with 1000 random reassignments).

## 4. Results

### 4.1. Macroinvertebrate community composition

A total of 67 benthic aquatic macroinvertebrate taxa were recorded from the 20 benthic sample sets, with a total of 18,094 specimens counted and identified. The BM communities across the study area were char-

Table 3
Mean abundances of all benthic macroinvertebrate taxa (per m$^2$), total abundance and number of taxa from all study streams, by habitat

| Group | Family/sub-family | Channel[a] | | Backwater[a] | |
|---|---|---|---|---|---|
| | | Control[b] | Clearfell[b] | Control | Clearfell |
| Nematoda | | 7481 | 1170 | 11911 | 7081 |
| Oligochaetae | | 6689 | 3726 | 3030 | 6985 |
| Diptera | Aphroteniinae | 1778 | 74 | 459 | 59 |
| | Chironominae | 1556 | 341 | 3289 | 1837 |
| | Orthocladiinae | 1304 | 563 | 2770 | 1333 |
| | Ceratopogonidae | 519 | 474 | 1452 | 859 |
| | Tipulidae | 444 | 237 | 1348 | 593 |
| | Tanypodinae | 237 | 119 | 252 | 222 |
| | Simulidae | 119 | 15 | – | 15 |
| | Empididae | 104 | 30 | 178 | 119 |
| | Podonominae | 15 | – | 15 | – |
| | Epihydridae | – | – | 15 | – |
| | Muscidae | – | – | 15 | – |
| | Syrphidae | – | – | 74 | – |
| | Tanyderidae | – | 15 | – | – |
| | Thaumelatidae | – | 15 | – | – |
| Crustaceae | Copepoda | 1674 | 222 | 5452 | 904 |
| | Ostracoda | 1422 | 178 | 6785 | 2593 |
| | Parameletidae | 800 | 237 | 2459 | 2222 |
| | Phreatoicidae | 133 | 74 | 104 | 193 |
| | Cladocera | 59 | – | – | 30 |
| | Janiridae | – | – | 15 | 15 |
| | Syncaridae | – | – | – | – |
| Plecoptera | Gripopterygidae | 770 | 1126 | 696 | 993 |
| | Notonemouridae | 74 | 326 | 59 | 548 |
| | Eusthenidae | – | – | – | 15 |
| Coleoptera | Scirtidae | 607 | 652 | 133 | 281 |
| | Elmidae (adult) | 30 | 15 | – | – |
| | Circulionidae (adult) | – | 15 | – | – |
| | Elmidae | – | 133 | – | 30 |
| | Psephenidae | – | – | – | 15 |
| | Dytiscidae | – | – | 15 | 15 |
| Acarina | | 474 | 89 | 1126 | 770 |

Table 3 (*Continued*)

| Group | Family/sub-family | Channel[a] | | Backwater[a] | |
|---|---|---|---|---|---|
| | | Control[b] | Clearfell[b] | Control | Clearfell |
| Mollusca | Sphaeriidae | 341 | 296 | 919 | 415 |
| | Glacidorbidae | 89 | 15 | 74 | 119 |
| | Hydrobiidae | 15 | 15 | 74 | 30 |
| | Planorbidae | – | 59 | – | 15 |
| Ephemeroptera | Leptophlebiidae | 296 | 311 | 178 | 207 |
| Trichoptera | Calocidae | 178 | 44 | 252 | 59 |
| | Hydropsychidae | 59 | – | – | – |
| | Hydrobiosidae | 30 | 74 | 15 | 15 |
| | Philopotamidae | 15 | – | – | – |
| | Philorheithridae | 15 | – | 15 | – |
| | Unidentified | 15 | 44 | 44 | 30 |
| | Psychodidae | – | – | 281 | 44 |
| | Linmephilidae | – | – | – | 30 |
| | Athericidae | – | – | 30 | – |
| | Conoesucidae | – | – | 44 | – |
| | Helicophidae | – | – | 30 | – |
| | Hydroptilidae | – | – | 15 | – |
| | Leptoceridae | – | – | 44 | – |
| Collembola | | 59 | 104 | 133 | 326 |
| Turbellaria | | 15 | 44 | 207 | 148 |
| | Total abundance | 27415 | 10852 | 44007 | 29163 |
| | Number of Taxa | 33 | 33 | 39 | 36 |

Taxa listed in order of decreasing abundance in control stream channel habitats.

[a] Habitat.

[b] Treatment.

acterised by high abundances of nematodes and oligochaetes, comprising 54 and 64% of total BM abundance in CONTROL and REGEN streams, respectively (Table 3). The remaining fauna was dominated by microcrustaceans (Copepoda, Ostracoda) and chironomids (Orthocladiinae and Chironominae), with these groups totalling 27% of the overall faunal abundance in CONTROL streams.

Total BM abundance in CONTROL streams was substantially (60%) higher in FPOM and CPOM-rich backwater habitats than in the more sandy channels, with an additional six taxa recorded (Table 3). BM abundance was almost twice that (97% higher) in CONTROL backwaters than in channels when worms (oligochaetes, for whom estimation of abundance is problematic) are excluded.

Total BM abundance, and the abundance of Chironomiin midges, Nematodes and Ostracods were all significantly more abundant in backwater-pool habitats in both CONTROL and REGEN streams (all $p < 0.05$ by two-way ANOVA, Fig. 2). Worms were also more abundant in backwater-pool than channel habitats, but only in REGEN streams. There were no differences between habitat types in the number of taxa (Fig. 2, $p > 0.2$). Larval beetles of the family Scirtidae were significantly more abundant in channel than backwater-pool habitats in both stream treatments ($p < 0.01$ by two-way ANOVA).

In CONTROL streams, copepods were significant indicator taxa for backwater habitats (indicator value of 76.5 out of a possible 100, and $p = 0.050$ by Monte Carlo randomisation with 1000 permutations), while simuliids were significant indicator taxa for channel habitats (indicator value of 80.0, $p = 0.049$). In REGEN streams, ostracods and mites (Acarina) were both significant indicator taxa for backwater habitats (indicator values of 83.9 and 90.2, and $p = 0.024$ and 0.035, respectively), but no taxa were significant indicators of channel habitats.

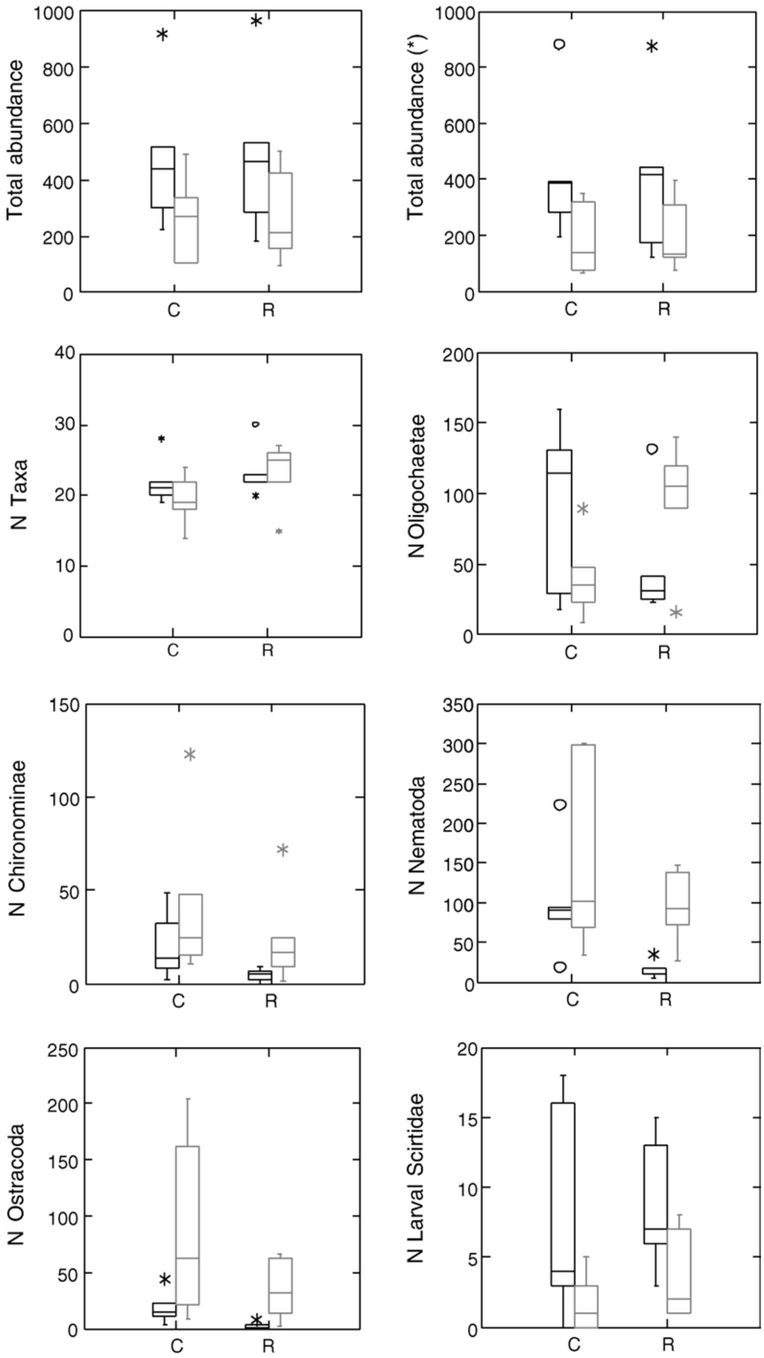


Fig. 2. Total BM abundance with and without oligochaetes (*); number of BM taxa and abundance of Oligochaetae, larval Chironominae, Nematoda, Ostracoda and larval Scirtidae in CONTROL (C) and REGEN (R) stream channel (black) and pool (grey) habitats.

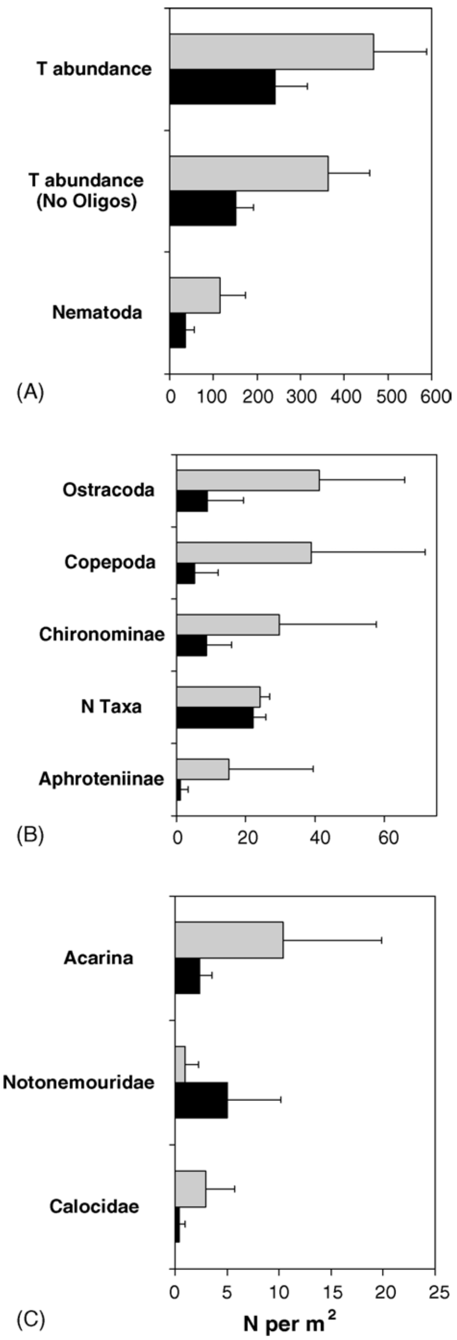


Fig. 3. Mean (and S.D.) of: (A) total benthic macroinvertebrate abundance with and without oligochaetes and nematodes; (B) aquatic microcrustacean and Chironomid abundance and number of all taxa and (C) mite, Notonemourid stonefly and Calocid caddis abundance; in CONTROL (grey) and REGEN (black) streams at Ben Nevis (both habitats combined).

### *4.2. Emergent macroinvertebrates*

Emergence rates were high, averaging 5557 individuals per trap per 6-week period across all streams, with means of 7371 (±S.D. 3101) and 3742 (±S.D. 1814) for CONTROL and REGEN streams, respectively. Emergence trap catches were dominated by Chironomid midges, which comprised 85.5% of the total catch across all streams, reflecting their dominance of the aquatic insect community. The next most abundant aquatic groups, the dipteran families Psychodidae and Chaoboridae, comprised only 6.2 and 2.6%, respectively. Collembola comprised 3.8% of trap catches.

### *4.3. Differences between control and clearfelled streams*

#### *4.3.1. Macroinvertebrates*

*4.3.1.1. Abundance and diversity.* Overall, REGEN streams had lower abundances of nematodes, chironomids, crustaceans and mites, and a higher absolute and relative abundance of stoneflies. Total BM abundance and total BM abundance excluding Oligochaetes (worms) were significantly lower in REGEN streams, with an overall reduction in abundance of 48 and 59%, respectively ($p < 0.05$ by ANCOVA, Table 3, Fig. 3). The abundance of nematodes, ostracods, calocidae, copepods and acarinids were all significantly (at $p < 0.05$) and substantially lower in the REGEN streams, being 68, 78, 87, 86 and 77% lower, respectively, than in CONTROL streams (Fig. 3). Chironominae and Aphroteniidae were also less abundant (by 70 and 93%, respectively) in the REGEN streams, but these were only significant at the 0.1 alpha level (Fig. 3). Only Notonemouridae were more abundant in REGEN than in CONTROL streams (by a factor of 5.0, $p < 0.1$ by ANCOVA).

The two groups of streams also differed significantly in aquatic insect emergence rates (Table 4, Fig. 4). Total abundance in traps, and the abundance of Chironomidae and Trichoptera of the family Psychodidae were significantly lower in clearfelled streams (by 49, 50 and 23%, respectively), while only Empididae were higher in abundance, by a factor of 2.2 (all $p < 0.03$, by

Table 4
Total Malaise trap catch of aquatic macroinvertebrate adults (*n*/6 weeks) across all streams winter and spring 2001

| Order | Family | CONTROL | | | | | REGEN | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | BC1 | BC2 | BC3 | BC4 | BC5 | BR1 | BR2 | BR3 | BR4 | BR5 |
| Plecoptera | Austroperlidae | – | – | – | – | – | – | – | – | 1 | – |
| | Gripopterygidae | 13 | 3 | – | – | 2 | 1 | 18 | – | 3 | 3 |
| | Notonemouridae | 58 | 23 | 4 | – | 5 | 1 | 11 | 12 | 15 | 35 |
| Ephemeroptera | Leptophlebiidae | 2 | – | 1 | – | – | – | – | – | 2 | – |
| Mecoptera | Nannochoristidae | 2 | 4 | 10 | – | – | – | 46 | 4 | 6 | 10 |
| Diptera | Ceratopogonidae | 20 | – | 220 | – | 10 | – | – | – | 10 | – |
| | Chaoboridae | 170 | 430 | 110 | 70 | 330 | 190 | – | 50 | 70 | – |
| | Chironomidae | 5717 | 10490 | 7250 | 3551 | 4817 | 2881 | 2490 | 2203 | 2142 | 5960 |
| | Dixidae | – | 10 | 10 | – | – | – | 10 | – | – | 20 |
| | Dolichophidae | 10 | – | – | – | 75 | – | – | – | 20 | – |
| | Empididae | 3 | 21 | 20 | 34 | 86 | 30 | – | 2 | 20 | 10 |
| | Tipulidae | 3 | 26 | 16 | 2 | 1 | 5 | 18 | 3 | 11 | 1 |
| | Psychodidae | 70 | 960 | 580 | 170 | 180 | 340 | 230 | – | 190 | 740 |
| | Simuliidae | 10 | – | – | – | – | – | 10 | – | – | – |
| Trichoptera | Calocidae | – | – | – | – | 5 | – | – | – | – | – |
| | Hydrobiosidae | – | – | – | – | – | 1 | 2 | – | – | 4 |
| | Philopotamidae | 1 | – | – | – | – | – | – | 10 | 1 | – |
| | Philorheithridae | 2 | 4 | 1 | – | – | – | – | – | – | – |
| | Plectrotarsidae | – | 4 | – | – | – | – | – | – | – | – |
| Collembola | | 650 | 160 | 60 | 60 | 310 | 90 | 360 | 30 | 290 | 100 |
| Total abundance | | 6731 | 12135 | 8282 | 3887 | 5821 | 3539 | 3195 | 2314 | 2781 | 6883 |
| Number of Taxa | | 15 | 12 | 12 | 6 | 11 | 9 | 10 | 8 | 14 | 10 |

ANCOVA). The number of emergent taxa did not differ significantly between treatments (means of 11 and 10 for CONTROL and REGEN streams, respectively).

*4.3.1.2. Community composition.* Ordination of the combined habitat BM data in two-dimensions revealed two distinct groups, with a low level of stress (Fig. 5A). These groups corresponded with the two forest treatment groups, which therefore differed significantly in composition. Mean Bray-Curtis similarity within groups (68.5 and 66.9%) was significantly greater ($p < 0.05$ by ANOSIM) than mean similarity between groups (36.14%).

Ordination of the backwater BM data also clearly distinguished REGEN from CONTROL streams (Fig. 5B). Ordination of the channel BM data also revealed two groups (Fig. 5C), with REGEN streams showing a substantially greater variation in BM composition than CONTROL streams. One site in particular (BR3) was more similar in composition to that of CONTROL streams.

Indicator Species Analysis revealed that ostracods were significant indicator taxa for CONTROL streams in the channel habitat (indicator value of 83.5 out of a possible 100, and $p = 0.04$). In backwater habitats, Notonemourids were significant indicator taxa for REGEN streams (indicator value of 90.2 and $p = 0.029$) as were copepods for CONTROL streams (indicator value of 85.8 and $p = 0.030$). These were therefore key taxa in discriminating CONTROL and REGEN streams in these two habitats.

*4.3.1.3. Relationships with disturbance index.* The positive correlation of inter-site ordination distances from the centroid of the CONTROL streams in benthic macroinvertebrate ordination space with the disturbance index was highly significant ($r = 0.85$, $p < 0.002$, Fig. 6), and essentially monotonic. Site BR3 had the lowest disturbance index value, due to the

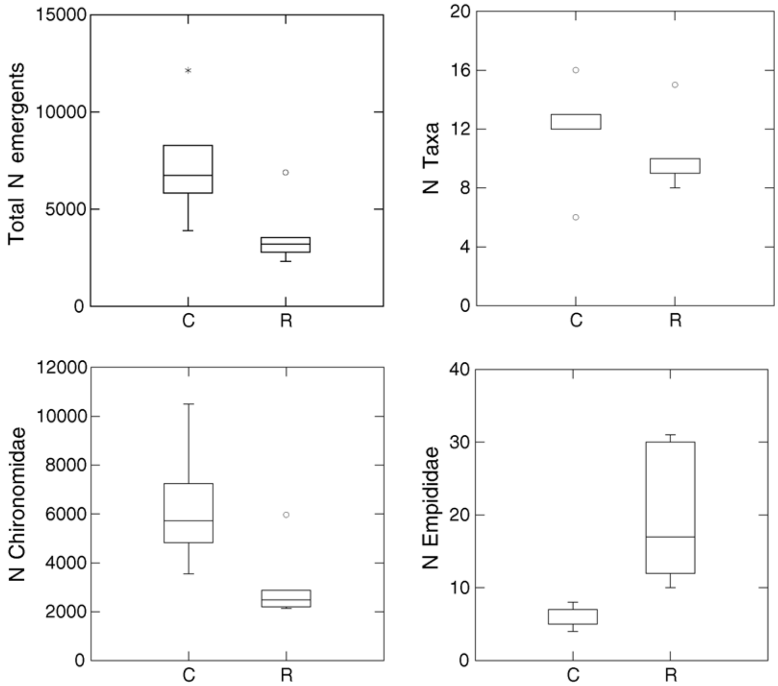


Fig. 4. Box plots of total Malaise trap catch (*n*/6 weeks) of aquatic insects for the CONTROL (C) and REGEN (R) streams, showing total abundance of all insects, number of taxa, abundance of Chironomidae and Empididae.

relatively low degree of disturbance of the riparian vegetation from logging.

*4.3.1.4. Relationships with physical attributes.* The first factor produced by PCA of physical attributes (Factor 1), which explained 36% of the variance in the physical data, was significantly different for CONTROL and REGEN sites (Davies et al., 2005). This factor was positively correlated with slope variability, number of logs, channel area, mean channel width and bank height, and percent area of cobble and boulder substrate, as well as with the number of patches of macrophytes per 50 m of stream length. This factor was also negatively correlated with mean channel width, backwater area, organic debris and organic silt substrate. Factor 1 was also highly correlated with the disturbance index (Davies et al., 2005, Fig. 7, $r = 0.93$, $p < 0.001$). Factor 1 therefore represents the overall physical channel response to historical disturbance by forestry.

PCA Factor 1 was significantly positively correlated with inter-site ordination distances from the centroid of the CONTROL streams in ordination space ($r = 0.67$, $p < 0.03$, $n = 10$). It was also strongly negatively correlated with Surber-derived FPOM content ($r = 0.87$, $n = 9$, $p < 0.002$). Stream FPOM storage was strongly negatively correlated with the disturbance index ($r = 0.94$, $p < 0.001$, $n = 9$, for combined habitats, Fig. 8), and was significantly lower in REGEN than CONTROL streams ($p = 0.006$, by ANCOVA). FPOM storage was 3.4 times higher across all streams in backwater-pool habitats than in channels. Channel habitat FPOM storage was significantly lower in REGEN than CONTROL streams ($p < 0.005$) but this was not the case for backwater-pool habitats (Fig. 9).

Total BM abundance was strongly positively correlated with sample FPOM content ($p < 0.01$, Fig. 10). All the dominant taxa—nematodes, mites, copepods, ostracods, Chironominae, Tanypodinae, Ceratopogonidae, Psychodidae—had significant posi-

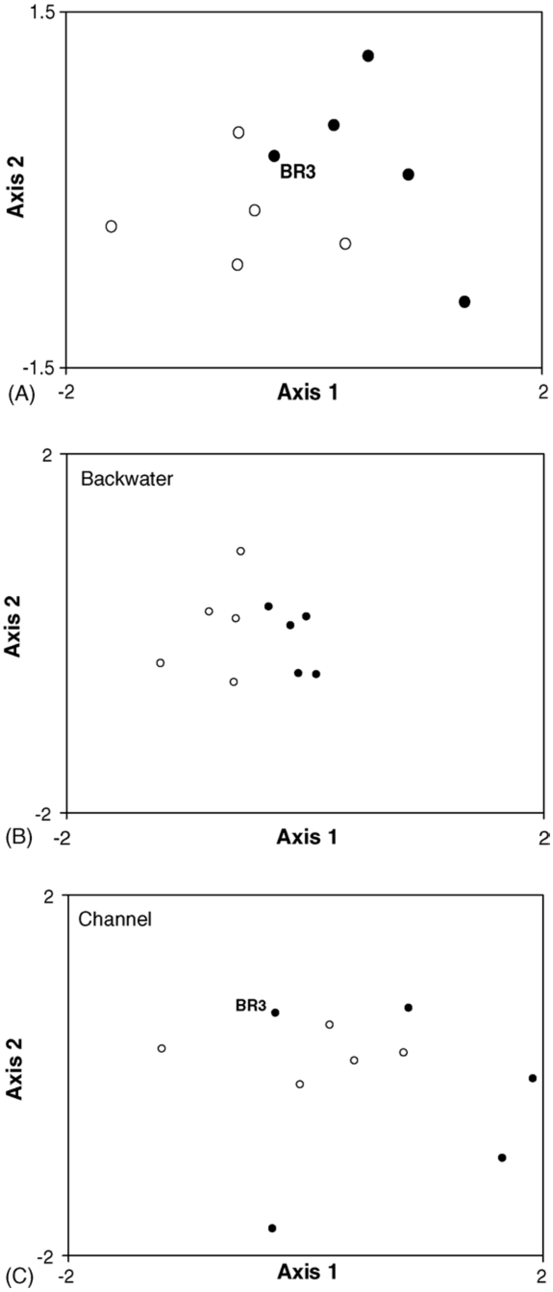


Fig. 5. MDS ordination plots of: (A) combined habitat benthic macroinvertebrate samples, and benthic macroinvertebrate samples from (B) backwater and (C) channel habitats from CONTROL (clear circle) and REGEN (filled circle) headwater streams at Ben Nevis. Note the distinction between site groups with the exception of stream BR3. Stress = 0.09 (A) and 0.13 (B). Ordinations plotted to same scale and in same space in (B) and (C).

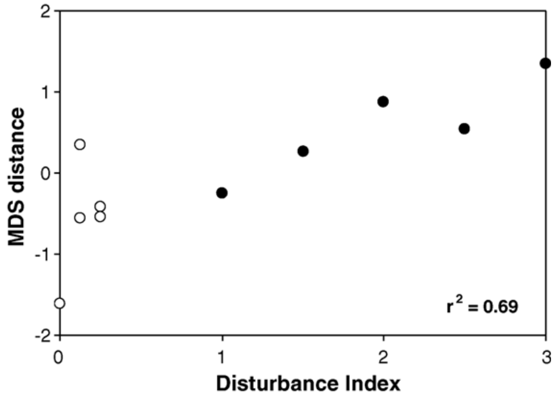


Fig. 6. Relationship between distance on ordination axis 1 of benthic macroinvertebrate MDS (combined habitats) from centroid of control streams and the disturbance index value. $r^2$ shown for Pearson correlation. Filled circles, REGEN; clear circles, CONTROL sites.

tive correlations with FPOM content across all samples (all $p < 0.05$). Two taxa—Notonemouridae and Grypopterygidae—were significantly negatively correlated with FPOM (both $p < 0.01$).

### 4.3.2. Instream flora

REGEN streams had 14.5 times higher algal cover than CONTROL streams (Fig. 11), with a mean of 4.7

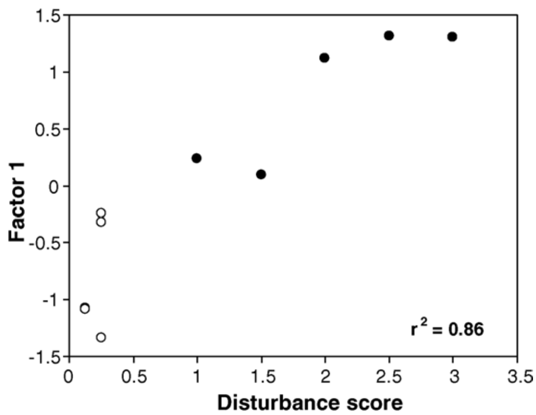


Fig. 7. Relationship between value of Factor 1 derived from PCA of physical variables and disturbance index value. $r^2$ shown for Pearson correlation. Filled circles, REGEN; clear circles, CONTROL sites. From Davies et al. (2005).

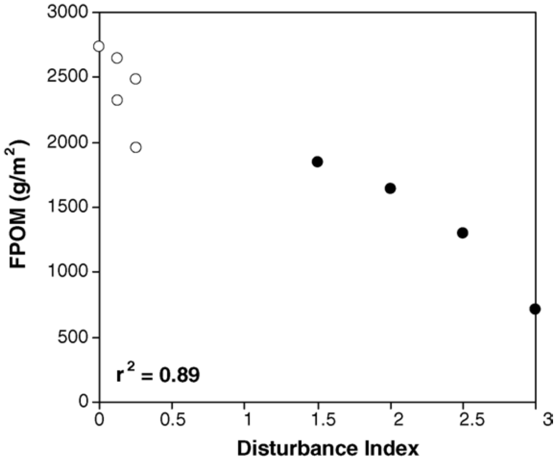


Fig. 8. Correlation of FPOM with disturbance grade in CONTROL (clear circle) and REGEN (filled circle) headwater streams at Ben Nevis.

algal 'patches' per 50 m of stream compared to 0.2 patches per 50 m in CONTROL streams ($p < 0.1$ by ANOVA). REGEN streams also had a substantially greater macrophyte cover than CONTROL streams, with a mean of 2.1 'patches' per 50 m of stream compared to 0.2 per 50 m in CONTROL streams.

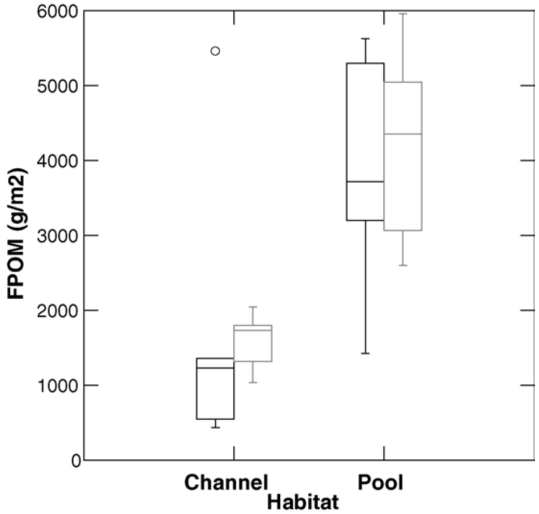


Fig. 9. FPOM storage (mass per unit area) in channels and pools. Left-hand (black) boxes refer to REGEN streams; right-hand (grey) boxes refer to CONTROL streams. Mid-lines represent medians, box and whiskers represent inner and outer hinges.

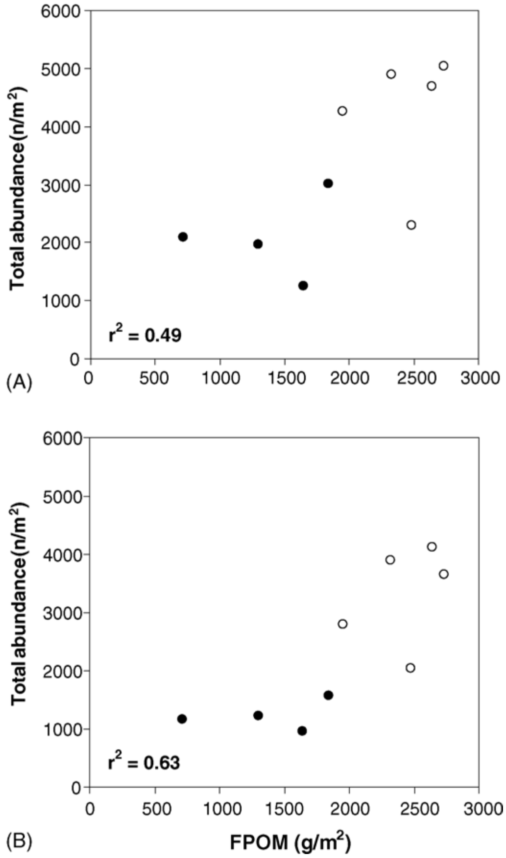


Fig. 10. Relationship between total abundance of benthic macroinvertebrates, with (A) and without (B) oligochaetes included, and FPOM in CONTROL (clear circle) and REGEN (filled circle) headwater streams at Ben Nevis. Combined habitat data presented (see text).

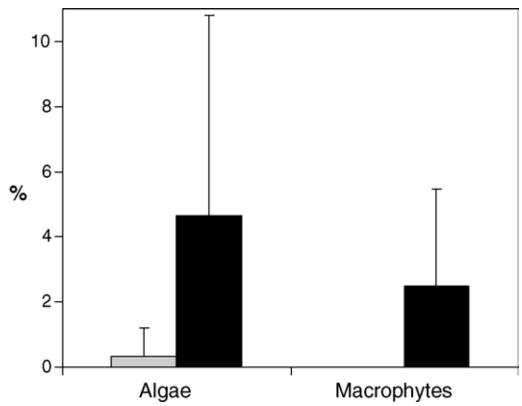


Fig. 11. Box plots of % cover of algae and macrophytes within study reaches in CONTROL (gray) and REGEN (black) streams. Bars show means and two standard deviations.

## 5. Discussion

We observed substantial differences in the faunal composition, abundance and emergence rates of benthic macroinvertebrates between historically clearfelled and control granitic headwater streams. The number and nature of biological and physical differences between the two groups of streams, coupled with the consistency of the responses with our conceptual understanding of the nature of stream disturbance from forest operations, and the correlations with the gradient of historical forest disturbance intensity all provides strong inferential evidence for a persistent and ongoing environmental impact from forest operations 15 years later.

The study does not conform to a before–after impact assessment or formal design with a temporal component, which may have better supported the case for impacts due to historical logging activities. However, these streams were selected on the basis of having maximum similarity in geology, climate, catchment characteristics (aspect, area, slopes) and vegetation structure prior to clearfell operations, and they are all in close proximity to one another. Both multivariate and univariate analysis failed to discriminate the two stream groups on the basis of natural drainage characteristics stream slope, catchment area and elevation, mean annual runoff and pre-logging forest vegetation (Davies et al., 2005). We believe that the only substantial difference between these streams is the occurrence of clearfell logging in one group and its absence in the other.

The degree of response is strongly related to the intensity of historical disturbance, supporting other observations (Davies et al., 2005; McIntosh and Laffan, 2005) that the amount of catchment clearance, combined with the intensity of disturbance in the riparian zone as well as the amount of snig track formation, all combine to result in long-term instream impacts on the receiving streams that persist in proportion with the intensity of the original disturbance.

The faunal composition observed in the unlogged streams was characteristic of shallow, first-order, infilled sand and silt-dominated streams of south-eastern Australia (Boulton and Brock, 1999), and differs markedly from that found in larger, higher gradient Tasmanian forest streams (e.g. Davies and Nelson, 1994).

The observed shift in macroinvertebrate community composition is consistent with a change to a coarser grained stream environment with a degraded channel profile. Forest harvesting operations on alluvial or depositional headwater streams in which riparian zones are not protected can cause a long-term shift in both channel form and aquatic faunal composition and production.

The changes observed here contrast substantially from the shorter-term (1–3 year post-logging) responses observed by Davies and Nelson (1994) in larger, cobble-dominated Tasmanian streams, where fine sediment accumulation, increased temperatures and increased loads of CPOM were associated with declines in diversity and loss of abundance of mayflies, caddis and stoneflies (as well as fish).

We propose that this contrast in response is mainly related to differences in stream power and geomorphology, which determine the dominant grain size. The predominant impact in the streams in this study was related to down-cutting, channelisation and loss of organic material, (Davies et al., 2005). Jackson and Sturm (2002) observed that the geomorphological context is an important determinant of the nature of headwater stream responses to logging disturbance, and headwater channel dynamics are strongly controlled by a combination of soil, geomorphological, hillslope and climatic characteristics (Montgomery, 1999; Gomi et al., 2002).

Other Australian sand-bed forest streams show similar effects to those observed at Ben Nevis. Growns and Davis (1991, 1994) observed shifts in macroinvertebrate community composition immediately following harvesting, and also 8 years later in higher order lowland sand-dominated West Australian streams. Trayler and Davis (1998) documented the nematode-dominated nature of the stream fauna in these West Australian streams, which were reduced in diversity and abundance in the period immediately after clearfelling.

The impact on macroinvertebrates at Ben Nevis has resulted in a shift away from a partially depositional, fine-sediment stream fauna toward one with elements more typical of steeper, coarser grained and higher energy streams. This shift appears to be at least partially controlled by changes in the amount of FPOM stored in the channel, which remains greatly reduced in the previously clearfelled streams 15 years after the primary disturbance. Differences in the abundance and community composition of benthic macroinvertebrates and aquatic insect emergence were strongly correlated with the amount of FPOM present in the substrate. FPOM storage was greater in pool habitats, and these habitats were associated with greater abundances of macroinvertebrates. When coupled with the dominance by detritivorous feeding groups, this indicates that FPOM is both a primary habitat and also a significant food source for most of the taxa present (e.g. for nematodes, oligochaetes and detritivorous insects). Storage of FPOM is likely to be a significant mediator of biological response to harvesting impacts in these low gradient upland streams. The role of FPOM in affecting macroinvertebrate assemblage composition in these streams is quite different to that of organic material in larger, slash-subsidised headwater streams (Haggerty et al., 2004).

Changes in algal and macrophyte abundance appear to be related to the increased availability of light to the stream surface, associated with the loss and persistent opening of the upper forest canopy (see Davies et al., 2005). Macrophyte patches in REGEN streams were also observed to be associated with fine sediment entrapment behind instream log jams, which were more abundant in REGEN than CONTROL streams (Davies et al., 2005).

This study indicates that an ongoing legacy of forestry-induced disturbance persists in small headwater streams which received minimal specific management protection (the 1985 logging operations preceded the 1995 Tasmanian Forest Practices Act and associated year 2000 Code of Practice). The degree of change in the instream biota is related to the intensity of the original disturbance, and appears to be significantly mediated by changes in the dynamics of FPOM resulting from the disturbance.

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