

Keystone coleopterans? Colonization by wood-feeding elmids of experimentally immersed woods in south-eastern Australia

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Abstract. Macroinvertebrates on immersed woods in streams in montane south-eastern Australia respond to differences in wood taxa, according to a 4-month colonization study of experimentally positioned sticks. Xylophagous elmids (Coleoptera : Elmidae) strongly preferred local native *Eucalyptus* over other types of wood including non-native softer timbers (*Pinus* and *Alnus*). Where gouging elmids were abundant (in native forest streams with native riparian vegetation), immersed *Eucalyptus* wood supported high abundances of other macroinvertebrates; in their absence (in open grassland streams), *Eucalyptus* supported few other macroinvertebrates. Macroinvertebrate-gouged channels were present disproportionately on *Eucalyptus* sticks relative to other wood species. It is proposed that xylophagous elmid beetles are the principal macroinvertebrate modifiers of wood in these south-eastern Australian streams, where their gouging of channels increases surface area, thereby facilitating colonization by other macroinvertebrates and wood-decaying microorganisms and fungi.

Introduction

Terrestrial wood that enters running waters has many interacting physical and biological effects (Harmon *et al.* 1986) including the following: input of an abundant though refractory source of carbon; physical re-structuring of the stream channel, which may increase retention of organic matter; and provision of increased area of substratum that stream organisms can use for attachment, feeding, oviposition and other activities (Bilby and Likens 1980; Anderson *et al.* 1984; Lloyd *et al.* 1991; Wallace *et al.* 1995).

In temperate Australia, with evergreen *Eucalyptus* species dominating the riparian vegetation, a higher fraction of detrital input into streams may be woody material compared with the temperate Northern Hemisphere (Lake *et al.* 1985; Campbell *et al.* 1992; Thomas *et al.* 1992). *Eucalyptus* species tend to shed limbs and bark more than deciduous, leaf-shedding, Northern Hemisphere trees. Furthermore, Australian forests are argued to be more prone to natural disturbance than temperate forests overseas (Williams 1981; Lake *et al.* 1985; Harmon *et al.* 1986).

Studies of the role of inputs of terrestrial wood to lowland sections of Victorian (southern temperate Australian) streams demonstrate that artificially increasing surface complexity of wood by grooving increases macroinvertebrate abundance (O'Connor 1991, 1992). Wood often supports higher diversities and abundances of macroinvertebrates than other in-stream substrata such as macrophytes or stones (Wallace and Benke 1984; Lloyd *et al.* 1991; O'Connor 1992). In narrow channels of forested headwater streams, large woody debris is likely to be

retained for longer than in the wider channels of large rivers, allowing biological processing by wood-feeding organisms (xylophages) and other detritivores (Anderson *et al.* 1978; Bilby and Likens 1980; Dudley and Anderson 1982; Smock *et al.* 1985; O'Connor 1991; Phillips 1995). Furthermore, upstream inputs of coarse detritus, including wood, also affect higher-order rivers. Thus, processing by detritivores not only contributes particles but releases (via detritivore faeces) the nutrients and carbon locked away within the decaying wood–fungi complex to be consumed downstream by detritus feeders (Vannote *et al.* 1980; Minshall *et al.* 1985; Hax and Golladay 1993; Tank and Winterbourn 1995; Wallace and Webster 1996). In similar leaf-dominated systems in North America, survival of particulate detritus-feeding macroinvertebrates (generalist gatherers) is enhanced in the presence of leaf shredders whose re-establishment is crucial to the recovery of disturbed systems (Short and Maslin 1977; Whiles *et al.* 1993).

In Australia, little is known of the animals involved in wood processing or its importance. This study in headwater streams to the west of Canberra, Australian Capital Territory, focussed on the identity and significance of wood-associated macroinvertebrates, using an experimental framework. In particular, through manipulations of experimentally positioned wood, we addressed how wood-inhabiting communities respond to different substrate species located in streams in open grasslands, pine plantations and native eucalypt forests. This report summarizes the response of the main xylophagous taxa; the dynamics of the total community is to be discussed elsewhere.

Methods

Study area

Nine streams were studied in mountain ranges to the west and south of Canberra, Australian Capital Territory (Fig. 1) at elevations between 700 and 1100 m above sea level. Soils are nutrient poor, and valley floors are composed generally of deep (>3 m), moderately to slowly permeable, red and yellow earths with organic accumulations on the surface. Pools contain sediment accumulation over rocky substratum. Although local rainfall is similar in all months, with annual averages of 1100 mm, stream flows usually peak in September–October and are lowest in January–February (Anon. 1986; Talsma and Hallam 1982; Fraser 1988).

The nine streams were described according to riparian vegetation as 'native', 'pine' or 'open grassland', with three streams in each category (Table 1). The 'pine' streams are in exotic *Pinus radiata* (D. Don) plantations, and the remainder lie within Namadgi National Park. The six northern streams (3 'pine', 3 'native') lie within Canberra's water

catchment (Fig. 1). The pine plantations were established in the 1920s and 1930s on old grazing land and to a lesser extent on previous native forest. The native forests, dominated by eucalypts, notably *Eucalyptus viminalis* Labill. and *E. fastigata* Dean and Maiden, are now protected but were once subject to minor hardwood logging. The southern open grasslands, which include both native and introduced pasture species, are a consequence of previous stock grazing, maintained by a combination of mortality of tree seedlings in frosts and grazing by kangaroo (Anon. 1986; Fraser 1988).

During the study period, the pH and dissolved oxygen content of all streams were within the ranges previously reported (pH 6.3–7.1, and 6.0–8.8 mg dissolved oxygen L⁻¹; Talsma and Hallam 1982). Native forested streams were consistently cooler than pine and open streams (means of 11–12 v. 13–17 °C) and had lower conductivities (29–41 v. 44–73 $\mu\text{S cm}^{-1}$). Open grassland streams had slower flow (means of 0.13–0.16 v. 0.26–0.50 m s⁻¹).

Colonization study

We investigated the abundance and taxonomic composition of colonizing macroinvertebrates in a study of experimentally immersed wood of different species and in streams with different riparian vegetation. Wood species and condition reflected prevalent inputs to regional streams under field conditions. Local native eucalypts (*E. viminalis* and *E. fastigata*), an alien introduced pine (*P. radiata*), the native temperate rainforest riparian callicoma (*Callicoma seratifolia* Andrews, Cunoniaceae), and the alien introduced riparian alder (*Alnus glutinosa* Miller) were chosen. Live or recently dead sticks of these species, all with bark intact and showing no evidence of fungal or terrestrial insect attack, were collected on land. To control for appropriateness of colonization, a fifth stick type was collected by recovery *in situ* of immersed sticks, predominantly the two eucalypts or *Callicoma*. For each wood type, sticks of diameter 2.5–3.5 cm were cut to about 24.5–25.5 cm long. This range was uniform across all stick types. To kill any organisms and achieve uniform weathering, all experimental sticks were conditioned to equilibrium dry weight at constant temperature for 30 days at 25 °C. Conditioned experimental wood was weighed before immersion, but post-immersion handling (removal of macroinvertebrates, see below) caused unreliable calculation of weight loss which is not reported. Hardness was assessed by observing the depth of penetration of a pin forced into 11 replicated samples of wood of each species. Eight sticks of each conditioned but unimmersed type were tested for hardness as controls, as were some study sticks after retrieval and drying, to provide an indication of variation in hardness between each stick type and the extent of softening during the period of immersion.

Three pools were selected per stream, and two 60-cm-long metal stakes were driven into the stream bed in depositional areas where wood accumulated naturally. To each stake were attached five different stick types, each uniquely tagged, with the position being allocated randomly about the stake. Sticks were allowed to float freely in the current for four (austral summer) months commencing in November 1995.

Retrieval of sticks was by careful cutting from the stakes, with any dislodged, vagile taxa retained in a 250- μm mesh net held immediately downstream of each individual stick. Sticks (and organisms from the net) were placed individually into a plastic bag containing 70% ethanol, to kill and preserve the animals. Each stick was washed in a standardized manner into a 5-L bucket in the laboratory, with the residue washed through coarse (2000 μm) and fine (104 μm) mesh sieves. Only surface-living animals were considered, because a preliminary survey of naturally occurring immersed wood indicated that few animals occurred inside sticks, except when the wood was much softer or more pitted and grooved than in the present study. Large animals were picked from the coarse sieve, and the fine sieve residue was examined under a dissecting microscope at low power until up to 10 min had passed without detection of further animals.

Animals were preserved in 70% ethanol and identified to the lowest possible taxonomic level, usually species or genus. In some cases (Acarina, Turbellaria, some insects), animals were identified to morphospecies, to

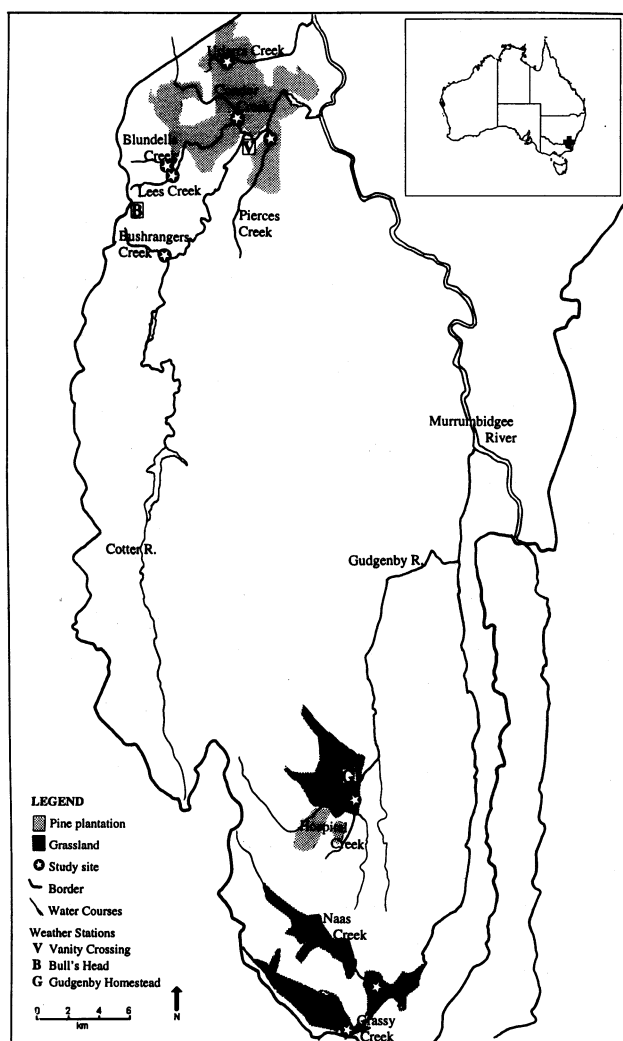


Fig. 1. Location of sites; pine plantations and grasslands shaded, remaining area native forest. Only important watercourses are plotted. Weather stations refer to data presented in Table 1 (compiled from maps and information in Anon. 1986). Border is border of Australian Capital Territory.

Table 1. Groups and characteristics of study streams, Australian Capital Territory

Altitude given to nearest 50 m. MDSMax, mean daily summer maximum; MDWMin, mean daily winter minimum. Geology: main underlying rock type about the streams, with additional rock types upstream of study area given in parentheses. Width and depth: approximate average in section studied. Compiled from observations, maps and Anon. (1976, 1986) and Fraser (1988)

Riparian vegetation	Regional temperature extremes	Stream	Latitude	Longitude	Altitude (m)	Geology	Width (m)	Depth (cm)
Pine plantation	Vanity Crossing: MDSMax: 27°C MDWMin: -2°C	Uriarra Creek	35°18'S	148°54'E	750	Sedimentary	1	>30
		Pierces Creek	35°20'S	148°56'E	700	Volcanic (Sedimentary)	2-3	<30
		Condor Creek	35°20'S	148°54'E	700	Sedimentary	1-2	>30
Native eucalypt	Bulls Head: MDSMax: 21°C MDWMin: -2°C	Lees Creek	35°22'S	148°49'E	900	Sedimentary	1-2	>30
		Blundells Creek	35°22'S	148°50'E	900	Sedimentary	1-2	>30
		Bushrangers Creek	35°25'S	148°50'E	1000	Sedimentary (Granitic)	1.0-2.5	<30
Grassland	Gudgenby Station: MDSMax: 22°C MDWMin: -5°C	Grassy Creek	35°54'S	148°59'E	1100	Granitic	1-2	<30
		Naas River	35°52'S	149°01'E	1100	Sedimentary (Granitic)	1.5-3.0	>30
		Hospital Creek	35°45'S	148°59'E	1000	Granitic	<1	>30

allow a more accurate assessment of taxon richness. Only gross levels of identification were possible for some poorly known or rarer taxa.

Spatial relationships and statistical design

Avoidance of pseudoreplication when modelling relationships between streams is difficult because streams form a continuous branching system along which clear divisions are rare (Humphrey *et al.* 1995). Although all sites in this study were independent in the sense that they were in separate catchments, clearly two spatial groups can be recognized. A northern group consisted of the six forested streams over which effectively two different forest 'treatments' had been imposed: 'pine' and 'native' (Fig. 1). Although the application of these treatments was not random, attempts to impose a division between the two groups seemed arbitrary. Because several anthropogenic factors are confounded with riparian vegetation, *P* values calculated at this level are interpreted as being descriptive of differences between riparian types rather than inferring causality. Since the three southern streams clearly constitute a geographically separate group, any grassland effects cannot be tested directly, though interactions involving other variables and 'open grassland' (as a vegetation type) were explored.

Analysis

The statistical design used for analysis of variance (ANOVA) of colonization data is summarized in Fig. 2. Data consisted of diversities and abundances of taxa. Additional variables included an estimate of the percentage of bark worm from each colonization stick, and the presence of any grooving generated on each stick during the colonization period. All data were transformed ($\ln + 1$) to correct for skewness. ANOVA was used if analysis of transformed data satisfied diagnostic plots that indicated fulfilment of assumptions of normality and constant variance. Logistic regressions were used to analyse presence-absence data, again providing that underlying assumptions were fulfilled. However, logistic regressions could not be done within the complex design of Fig. 2, so only the bottom strata effects (decay class or stick type) could be tested with confidence. Thus, significance tests from these analyses testing upper strata effects were interpreted with caution, being regarded as descriptive of differences rather than as direct tests for significant effects. For logistic analyses of the colonization stakes, the forest type and vegetation type levels were combined into one 'riparian vegetation' variable. Thus, a significance test comparing data for grassland, plantation and native streams was attained from the logistic regressions; however, the spatial confounding issues discussed earlier should be kept in mind when interpreting these analyses.

Loss of some colonization sticks was handled by substituting means corresponding to relevant combinations of characters in the ANOVAs. Because only 10 were lost (less than 5% of the sticks), such a strategy is unlikely to bias the outcome of the analyses.

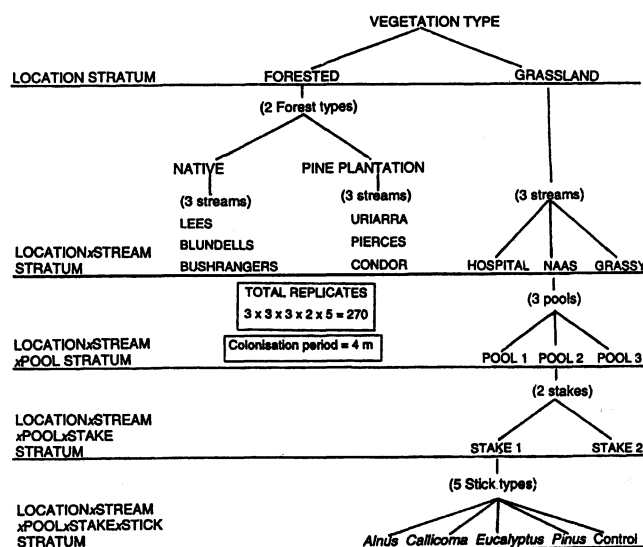


Fig. 2. Statistical design to test forest type and stick type as variables. No *P* value comparing grassland means with the other vegetation localities was calculated (see Methods). Vegetation type, streams, pools and stakes were regarded as blocked effects, though interactions involving vegetation type were tested. Placement of each stick about the stakes, and selection of stakes for individual pools, were fully randomized.

Plotted on all graphs is the least significant difference (l_{sd}, $2 \times$ s.e. of differences of means), which provides a conservative means of making multiple comparisons between means. In each case, the l_{sd} is that associated with the most complex interaction plotted. ANOVAs and logistic regressions were carried out with the GENSTAT 5 package (Lawes Agricultural Trust).

Results

Wood characteristics

Eucalyptus was the hardest wood, then *Callicoma*, *Pinus* and *Alnus* (Table 2). Wood of all four species softened by about 20% ($F_{1,68} = 17.76$; $P < 0.001$) during the 4-month colonization period. *Eucalyptus* was also the heaviest wood,

Table 2. Mass and hardness of wood

Mass analysis: $F_{4,265}=20.25$; $P<0.001$. Hardness analysis: $F_{3,68}=52.76$; $P<0.001$. Control wood was excluded from the analysis of hardness, hence lsd compares four wood species only. Hardness: depth of penetration (mm) of a pin

Stick type	Mass		Hardness	
	<i>n</i>	Mean mass (g)	<i>n</i> ^A	Mean ln(depth + 1) (ln(mm + 1))
<i>Alnus</i>	54	39.4	19	2.0
<i>Callicoma</i>	54	43.4	19	1.4
<i>Eucalyptus</i>	54	57.6	19	0.9
<i>Pinus</i>	54	37.0	19	1.7
Control	54	40.9	[20]	[1.9]
lsd		5.0		0.2

^ACounts include samples taken pre-immersion (8 per species) and post-immersion (11 per species). Although sticks softened by around 20% during immersion, multi-factor analysis indicated that there was no interaction involving stick type, hence all measurements were included in this single-factor analysis.

the others being similar in mass (Table 2). Control wood varied from as hard as *Eucalyptus* to extremely soft, and from smooth to deeply grooved, and thus was excluded from hardness analyses.

The most obvious evidence of breakdown after immersion was bark loss. *Alnus* lost most bark and *Callicoma* the least, with *Eucalyptus* and *Pinus* being intermediate (Fig. 3). The paper-thin bark of *Alnus* peeled back in substantial curls, revealing a somewhat ridged surface beneath and creating abundant interstitial spaces. *Callicoma* bark showed little visible sign of wear, and what there was appeared to result less from the action of the current than from abrasion against the stake or substratum. *Eucalyptus* bark tended to wear away in a stringy fashion, if at all, revealing a hard, smooth wood surface beneath. During immersion, the rough bark of *Pinus* softened, became quite pulpy and wore away to reveal a smooth surface beneath.

Some sticks showed surface grooves whose 1–3 mm width and depth and continuity and meandering nature

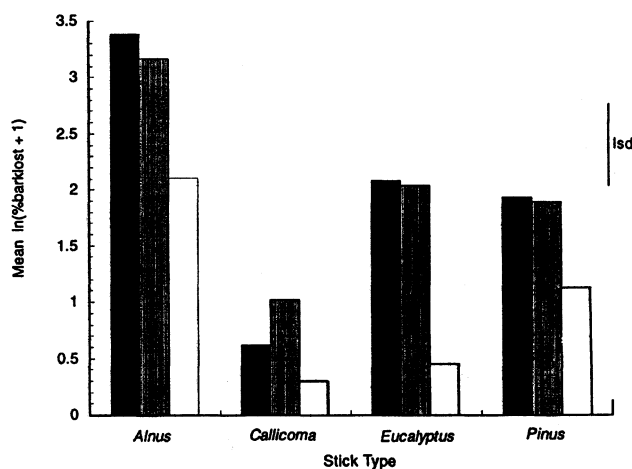


Fig. 3. Average estimated bark lost (ln %bark lost + 1) from the colonization stick species following 4-month immersion (Stick type $F_{3,146} = 33.77$, $P<0.001$, interaction not significant, but a high mean square was associated with vegetation type): lsd, least significant difference. Black columns, native eucalypt; shaded, pine plantation; white, grassland.

indicated origins in macroinvertebrate feeding. Logistic analysis on the presence–absence of these grooves indicated that they occurred most commonly on *Eucalyptus* sticks from the forested localities, especially the native streams (Table 3).

Community composition

Staked-out wood typically supported abundant and diverse assemblages of invertebrates after 4 months, with 260 sticks supporting 18 835 individuals belonging to some 150 species. The community on the experimental sticks qualitatively resembled that of the approximately 150 species found during an earlier survey of naturally occurring immersed wood of decay classes from smooth and hard to soft and punky. The common animals listed in Table 4 were also common in the earlier survey; exceptions were a few seasonal taxa as discussed below.

Table 3. Percentage of sticks showing evidence of surface grooving, by riparian vegetation and stick species
Logistic regression: riparian vegetation $F_{2,197} = 6.24$, $P = 0.002$; stick type $F_{3,197} = 6.87$, $P<0.001$; riparian × stick $F_{6,197} = 1.95$, $P = 0.075$

Riparian vegetation	Stick species				Total
	<i>Alnus</i>	<i>Callicoma</i>	<i>Eucalyptus</i>	<i>Pinus</i>	
Pine plantation	0.0	0.0	28.6	0.0	6.0
Native eucalypt	11.1	11.1	50.0	5.6	19.4
Grassland	0.0	11.1	0.0	0.0	2.9
Total	3.7	7.4	26.5	1.9	9.6

Table 4. Numbers of the most abundant macroinvertebrates (>100 individuals found) and all wood gougers

Roman numerals: probable species/generic divisions recognized from this or previous studies. Arabic numerals: probable higher-level divisions recognized from this study. All insects are juveniles. FG, feeding group; URI, Uriarra Creek; PIE, Pierces Creek; CON, Condor Creek; LEE, Lees Creek; BLU, Blundells Creek; BUS, Bushrangers Creek; HOS, Hospital Creek; NAA, Naas Creek; GRA, Grassy Creek. A, algal grazer; F, filterer; G, gatherer; N, not allocated to a feeding group (insufficient information); W, wood gouger

Taxon	FG	Pine plantation			Native eucalypt			Grassland			Total
		URI	PIE	CON	LEE	BLU	BUS	HOS	NAA	GRA	
Nematoda	N	17	261	74	38	71	59	43	286	95	944
Mollusca											
Gastropoda											
Pulmonata											
Ancyliidae											
<i>Ferrissia</i>	A ^A	3	139	10	0	0	3	8	160	25	348
Annelida											
Oligochaeta	G ^{AB}	381	1503	605	240	408	1204	1492	350	698	6881
Tardigrada	A ^A	0	65	8	0	1	4	1	10	32	121
Arthropoda											
Arachnida											
Acarina											
Oribatida I	N	0	446	0	0	0	4	6	40	242	738
Insecta											
Coleoptera											
Elmidae											
<i>Kingolus</i>	W ^{BD}	0	0	1	0	0	7	287	28	1	324
<i>Notriolus</i>	W ^{BD}	281	0	145	320	139	176	8	3	42	1114
<i>Simsonia (tasmanica)</i>	W ^{BCD}	7	0	4	69	16	2	6	0	0	104
<i>Simsonia hopsoni</i>	W ^B	0	0	0	0	0	0	3	0	0	3
Diptera											
Chironomidae											
<i>Austrobrillia longipes</i>	W ^B	0	0	0	8	0	0	0	2	0	10
<i>Cricotopus 'annuliventris'</i>	G ^B	37	1	1	61	60	5	0	1	0	166
<i>Cricotopus 'parbicinctus'</i>	G ^B	225	13	122	226	53	360	80	33	3	1115
'Grape Th' I	A ^B	34	27	43	1	1	2	6	25	8	147
<i>Harrisius</i> I	W ^B	0	0	0	0	1	0	0	0	0	1
'MOS' I	G ^B	135	23	21	208	198	435	1	5	1	1027
Orthoclaadiinae I	W ^B	1	0	0	7	1	0	1	0	0	10
Orthoclaadiinae II	W ^B	9	1	0	3	0	0	0	0	1	14
<i>Parakiefferiella</i> I	G ^B	24	8	2	104	140	12	5	9	1	305
<i>Paramerina</i> I	P ^B	24	6	2	9	26	11	50	6	9	143
<i>Paratanytarsus</i> I	G ^B	20	15	1	53	62	49	14	65	55	334
<i>Polypedilum 'near K3'</i>	G ^B	203	25	21	123	116	17	36	13	76	630
<i>Rheotanytarsus</i>	F ^B	64	11	30	96	1	46	37	7	0	292
<i>Thienemanniella</i> I	G ^B	27	13	14	272	49	82	8	38	3	506
Empididae 1	P ^{EFB}	96	9	64	121	136	183	11	6	1	627
Tanyderidae	W ^B	0	0	0	0	1	0	0	0	0	1
Tipulidae 1	W ^B	3	0	0	0	0	0	0	0	0	3
Ephemeroptera											
Baetidae II	A ^C	0	1	184	1	0	0	0	0	0	186
Leptophlebiidae											
<i>Nousia</i>	G ^B	21	39	40	13	13	10	34	4	29	203
Plecoptera											
Austroperlidae											
<i>Acruroperla atra</i>	W ^G	0	0	0	1	0	0	0	0	0	1
Trichoptera											
Calocidae											
<i>Caenota plicata</i>	W ^B	1	0	1	0	3	0	0	0	0	5
Helicophidae											
<i>Alloecella grisea</i>	G ^H	0	1	317	3	4	3	0	0	0	328
Hydrobiosidae	P ^{CF}	11	19	10	14	8	47	23	4	0	136
Leptoceridae											
<i>Triplectides ciuskus</i>	W ^{IC}	0	1	0	0	0	5	0	0	1	7
<i>Triplectides proximus</i>	W ^{IC}	0	0	0	1	2	1	0	0	0	4

Allocations based on ^AWilliams 1980; ^Bgut dissection (unpublished); ^CChessman 1986; ^DA. Glaister, personal communication; ^ECranston (unpublished); ^FMerritt and Cummins 1996; ^GSephton and Hynes 1983; ^HAnon. 1991; ^ISt Clair 1994. ^JAt least two *Notriolus* larvae and two adult species present.

Few taxa were common (Table 4), and taxonomic composition was generally patchy from stream to stream and even from stick to stick. The majority of taxa were not wood-feeding and the dynamics and responses of these taxa will be discussed elsewhere. Overall, a substantial proportion of Australia's known xylophagous fauna was found (Table 4). The dominant taxa were larval members of the family Elmidae (Coleoptera), especially *Simsonia tasmanica* (Blackburn) and *Notriolus* (Carter and Zeck) species (at least two were present — the commoner *N. quadriplagiatus* (Carter) and the rarer *N. galstonius* (Carter and Zeck) — but because of problems in distinguishing early instars they are considered together). These elmids were surface-feeding, occasionally penetrating cracks within the wood but seemingly never instigating their own tunnels. Gut dissections indicated that early instar larvae tended to consume mostly fine detritus, consuming little or no wood, whereas later instars typically had gut contents dominated by wood fibres. In contrast, adult elmids were a minor component (31 individuals from the 9 streams).

Acruroperla atra (Samal) (Plecoptera), though rare in this study, had been common in the earlier cold-weather survey. Wood-feeding Trichoptera were never locally abundant but were reasonably widespread. Three groups of gouging dipterans were found in the study: a single specimen of Tanyderidae, some Tipulidae, and the speciose chironomids, four species of which were previously unknown. None of these animals was common. Notably, no wood-gouging Ephemeroptera were found. The xylophagous fauna encountered in this geographically restricted study greatly exceeds that of neighbouring New Zealand (Anderson 1982; Tank and Winterbourn 1995).

Colonization

Abundances of macroinvertebrates on experimental woods in forested streams after the four-month colonization period were similar to those on control wood (Fig. 4a). In grassland streams, controls showed significantly higher levels of colonization than *Callicoma* and *Eucalyptus* wood (Fig. 4a). On *Callicoma* and *Pinus*, abundances of macroinvertebrates did not vary systematically between vegetation localities, with *Callicoma* supporting the lowest numbers of individuals in forested localities (Fig. 4a). *Alnus* and *Eucalyptus* supported high numbers of animals in forested localities, and low numbers (no more than *Callicoma* and less than controls) in grassland localities. Analysis of taxon richness with total abundance fitted as a covariate indicated that total taxon richness tracked the abundance pattern (Table 5).

The gouging elmid *Notriolus* (data for *N. quadriplagiatus* and *N. galstonius* pooled with small *Notriolus*) showed a strong preference for *Eucalyptus* sticks in forested localities (Fig. 4b). A high mean square associated with generally

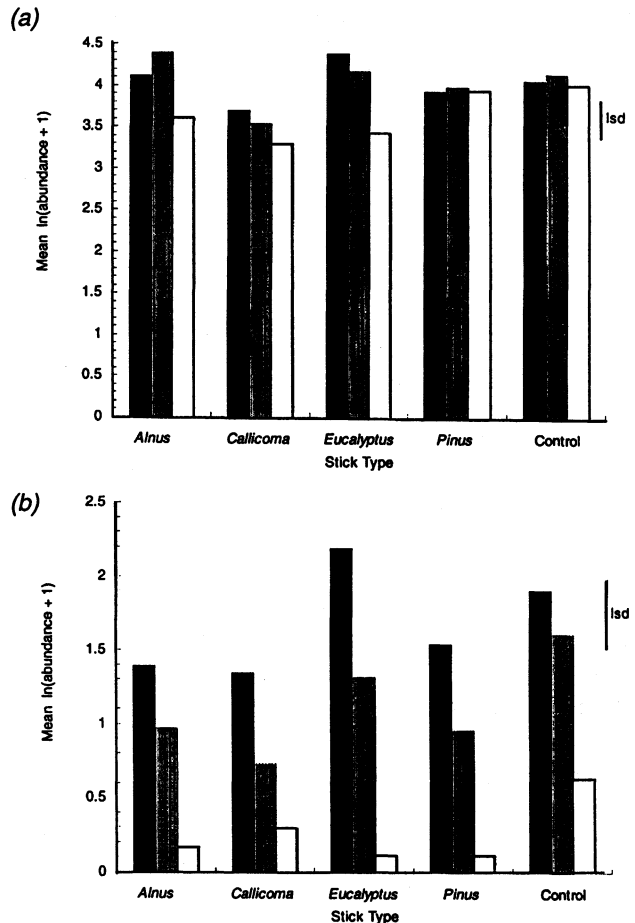


Fig. 4. Abundance means (ln abundance + 1): (a) mean total community abundance (stick $F_{4,194} = 6.56$, $P < 0.0001$; vegetation.stick $F_{4,194} = 3.52$, $P = 0.009$); (b) mean *Notriolus* (Coleoptera : Elmidae) abundance (stick $F_{4,194} = 6.99$, $P < 0.0001$; vegetation.stick $F_{4,194} = 2.38$, $P = 0.053$); lsd, least significant difference. Black columns, native eucalypt; shaded, pine plantation; white, grassland.

lower numbers in grassland streams suggested a strong locality effect. An analysis on total community abundance (*Notriolus* excluded) with *Notriolus* fitted as a covariate indicated that total community abundance covaried strongly with *Notriolus* abundance (Table 5).

Discussion

Colonization of newly immersed wood

Surface effects (especially on habitat availability) on any given substratum influence the numbers of aquatic animals that can be supported by that substratum (Dudley and Anderson 1982; Minshall 1984; Boulton and Lloyd 1991; O'Connor 1991; Phillips and Kilambi 1994; Phillips 1995). Previously exposed control wood on average had a more complex surface (sculpturing, roughness) than experimental wood. Modification of the surface area of experimental sticks during the colonization period allowed support of

Table 5. Summary of ANCOVAs on total abundance, *Notriolus* excluded (covariate: *Notriolus* abundance) and total taxon richness (covariate: total abundance)MS, mean square; *P*, probability; ns, not significant; veg, vegetation type; for, forest type; cov, covariate; res, residual; stk, stick type (see Fig. 2)

		location		location × stream			location × stream × pool		location × stream × pool × stake		location × stream × pool × stake × units				
		veg × for	cov	res	cov	res	cov	res	stk	veg × stk	veg × for × stk	cov	res		
df		1.0	1.0	1.0	5.0	1.0	17.0	1.0	26.0	4.0	4.0	4.0	1.0	192.0	
Total abundance	MS	5.1	0.0	10.7	1.1	1.9	4.5	5.4	0.9	2.2	1.3	0.2	21.9	0.3	
	<i>P</i>		ns	0.0		ns		0.0		<0.001	0.0	ns	<0.001		
Total taxon richness	MS	188.3	3.0	191.0	105.0	92.1	1.6	38.0	1.8	12.6	14.8	3.0	1382.2	6.0	
	<i>P</i>		ns	ns		<0.001		<0.001		0.1	0.0	ns	<0.001		

numbers of individuals broadly similar to numbers on control sticks (Fig. 4a). The increased surface area of immersed wood is a consequence of biological and physical modification, predominantly due to the feeding activities of wood-gouging macroinvertebrates and to physical factors such as abrasion by the current.

Macroinvertebrate modifiers in the study area included the wood-gouging elmid beetles, which, being abundant and large, have the potential to process large quantities of wood. *Notriolus* species (*N. quadriplagiatus* and *N. galstonius*) are particularly abundant. As observed by Chessman (1986), these animals chew wood in the laboratory, with feeding including the gouging of channels in the surface layer. Grooves 1–3 mm wide and deep, generated by macroinvertebrate feeding, were present disproportionately on *Eucalyptus* colonization sticks (Table 3). These grooves engendered an increase in surface area that was obvious to the naked eye, an increase that presumably is more exaggerated at the scale of a small macroinvertebrate. Such sculpturing increases the variety of niches present, differing, for example, in the degree of exposure to light and current, and in the degree of particulate detritus accumulation (Lloyd *et al.* 1991; O'Connor 1991).

Notriolus showed a strong preference for *Eucalyptus* wood, even over the soft woods, *Alnus* and *Pinus*. *Notriolus* was less abundant in grassland streams, and fewer grooves were present on *Eucalyptus* wood from those streams (Fig. 4b, Table 3). Thus, where *Notriolus* was present and generating increased surface area on *Eucalyptus* wood, the total abundance of all macroinvertebrates supported by *Eucalyptus* was high; where *Notriolus* was absent, *Eucalyptus* supported no more animals than *Callicoma*, the wood used by fewest animals overall.

At grassland localities, the low numbers of *Notriolus* larvae probably reflect the fewer colonists in the area. Many Australian elmids apparently fly rarely if at all (A. Calder, personal communication) as reported also by Brown (1987) for North American xylophagous elmids. Most elmid larvae

in the grassland streams were likely to have drifted from the forested reaches upstream.

Because *Notriolus* was less common on wood types other than *Eucalyptus*, changes in surface characteristics of these sticks may have been due more to properties of the bark and the degree to which these were affected by exposure to the physical environment. Surface area available on immersed *Alnus* was increased by bark curling to create abundant interstitial spaces and reveal a ridged wood surface beneath. In the grassland streams, *Alnus* lost little bark, its surface area was not enhanced and it supported low macroinvertebrate abundances. Differences in the amounts of bark lost by *Pinus* did not affect the numbers of organisms it supported; however, the surface area available for exploitation on *Pinus* should decline as its relatively complex bark wears away to leave a smooth wood surface. This did not occur during the colonization period, because only one *Pinus* stick lost more than 50% of its bark. The bark of *Callicoma* is smooth and wears away very slowly to reveal an equally smooth underlying wood surface; thus, it generally supported fewest animals. *Eucalyptus* bark is also smooth, and tends to wear away without creating complex interstitial spaces. Since the wood surface revealed is also smooth, it should support low numbers of animals similar to the numbers on *Callicoma*. Only in the grassland streams was this so, because, as discussed above, at the forested localities *Eucalyptus* was modified by the feeding activities of wood-gouging macroinvertebrates.

Potential functional role for xylophagous elmids

The potential role of Australian xylophagous elmids in aquatic community processes may be approached by comparison with studies of other shredding and gouging invertebrates. The North American gouging elmid *Lara avara* (LeConte) has a straight gut, limiting the residence time of ingested wood and generating large quantities of particulate faecal matter (Steedman and Anderson 1985). If Australian gouging elmids are similar, then they have the

potential to be important not only as generators of surface area but as resource enhancers and facilitators of decay.

Because oxygen concentrations diminish rapidly within waterlogged wood, decay in aquatic systems is largely a surface phenomenon (Thomas 1969; Eaton and Hale 1993) encouraged by gougers, borers and tunnellers which increase the surface area available for the action of bacterial and fungal decomposers (Aumen *et al.* 1983; Baker *et al.* 1983; Steedman and Anderson 1985; O'Connor 1991). In south-eastern Australian billabongs, river red gum (*Eucalyptus camaldulensis* Blakeley) wood is a major site of biofilm development, and can be inferred to be a site for transformations of nutrients and organic matter (Scholz and Boon 1993). The extent of the impact of gouging *Notriolus* elmids on such processes in subalpine streams is unknown, but in their absence breakdown of *Eucalyptus* wood could be impaired; this could result in concomitant under-utilization of nutrients in a manner analogous to the effects of loss of shredders in leaf-based systems (Cummins *et al.* 1973; Wallace and Webster 1996).

Although much information remains to be obtained, conceptual schemes of community succession on wood in south-eastern Australian subalpine streams can be generated from our results. The abundance and taxon richness of wood-inhabiting communities depends on the species of wood, particularly its morphology, and relates to the extent of attack by decomposers and xylophagous macroinvertebrates. Thus, *Eucalyptus* wood attacked by gougers experiences increased surface area, which has the potential to enhance decay and allow the support of increasing numbers of macroinvertebrates through time. In contrast, *Pinus* wood, once the bark has worn away, may experience much lower levels of colonization until it is very well decayed. Actual community structuring in terms of feeding groups and taxa will be discussed elsewhere, but it broadly depends on both wood species and stream type; for example, xylophages will be under-represented on non-*Eucalyptus* sticks, and grazers will be more common in streams receiving plentiful light and nutrients (McKie and Cranston, unpublished). What we propose derives from both the present study and a survey (McKie and Cranston, unpublished) of naturally occurring immersed wood that indicated that fewer gouging elmids occurred on wood, presumed to be long-immersed, from pine than from native forest streams.

If gouging elmids do play the role we envisage, they will be important as 'ecosystem-stabilizers'. Immersed wood enhances stability of aquatic ecosystems (Vannote *et al.* 1980) through the capacity of debris dams to retain detritus, because more sculptured wood creates greater drag and can cause more detritus to settle, accumulate and persist (Anderson and Sedell 1979; Harmon *et al.* 1986; Schwoerbel 1987; O'Connor 1991; Wallace *et al.* 1995).

Eastern Australian streams have been argued to be particularly prone to disturbance (Williams 1981; Lake *et al.* 1985; Bunn *et al.* 1986), but they evidently experience substantial inputs of woody material (Lake *et al.* 1985; Campbell *et al.* 1992; Thomas *et al.* 1992). This implies a role for gouging elmids as 'keystone' taxa or 'ecosystem engineers' — organisms considered to be crucial in maintaining the organization and diversity of communities without necessarily having direct trophic effects on other species (Mills *et al.* 1993; Jones *et al.* 1994). Although Wallace and Webster (1996) caution against categorization of any stream macroinvertebrate as a keystone species, we hypothesize that xylophagous elmids, a guild rather than a single species (Simberloff and Dayan 1991), appear to act as ecosystem engineers in the system we studied.

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