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More microbial activity, not abrasive flow or shredder abundance, accelerates breakdown of labile leaf litter in urban streams

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Abstract. Urban land use degrades stream ecosystems, but the nature and mechanisms of its effects on ecological processes, such as leaf breakdown, are poorly understood. Leaf litter breakdown has pivotal effects on energy and nutrient flows in stream ecosystems. Our goals were to test the effect of catchment urbanization on breakdown rates of leaves of 2 common riparian species in southeastern Australia and to identify the mechanisms responsible for changes in breakdown rates. Catchment urbanization was quantified as the percentage of catchment covered by impervious surfaces with connection to streams via stormwater sewers (effective imperviousness [EI]). *Eucalyptus obliqua* and *Pittosporum undulatum* leaf packs were placed in 6 streams that ranged from 0 to 20% EI. Packs were left for up to 69 d and, upon removal, were analyzed for mass loss, microbial activity, and abundance of associated shredding macroinvertebrates. Stream nutrient concentrations, temperature, and abrasive flow were measured as potential correlates of leaf breakdown. *Pittosporum undulatum* leaves broke down faster than those of *E. obliqua*. Breakdown rates of *P. undulatum*, but not *E. obliqua*, leaves increased as EI increased. Faster *P. undulatum* breakdown in streams with higher EI probably was caused by greater microbial activity (associated with higher temperatures and P concentrations) but not by differences in shredder abundance or abrasive flow. Elevated microbial activity in urban streams has a greater effect on leaf species with more-labile C than on leaf species with refractory C. In urban streams with large proportions of labile leaf litter, increased microbe-driven breakdown might decrease benthic organic matter availability and ultimately impair ecosystem function. Physical abrasion is not necessarily an important agent in faster breakdown, despite the increased hydrologic flashiness of urban streams. Effects of urbanization that accelerate leaf breakdown in streams could be mitigated through eradication of exotic riparian trees with leaves that are more labile than those of indigenous species and through management measures that reduce stream temperatures and nutrient concentrations.

Key words: leaf breakdown, urbanization, organic matter, ecosystem function, decomposition, effective imperviousness, fluorescein diacetate.

The degradation of stream ecosystems in urban catchments (Paul and Meyer 2001, Allan 2004) is so widespread that the term "urban stream syndrome" has been coined to describe the phenomenon (Meyer et al. 2005). The syndrome, driven primarily by stormwater runoff delivered through piped and sealed drainage systems, is typified by symptoms that include hydrologic flashiness, elevated nutrient and contaminant concentrations, and altered biotic communities. Many attributes of stream ecosystems show consistent responses to urban land use and associated

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stormwater runoff, but the reported responses of some ecosystem processes, such as leaf breakdown, have been inconsistent (Walsh et al. 2005b).

Changes to leaf breakdown rates can have major effects on stream ecosystem structure and function. Leaf litter constitutes a large proportion of organic matter in streams (Maltby 1992a), and its breakdown can contribute to the aquatic pools of dissolved and fine particulate organic C and, thus, directly and indirectly provide an energy resource to aquatic food webs (Allan 1995). Alterations to leaf litter breakdown rates can affect the timing and mass of benthic organic matter standing stocks and, thus, the seasonal feeding patterns of shredders (Gulis and Suberkropp 2003). This effect can ultimately limit shredder abundance and diversity, which can have bottom-up effects on the food web (Lepori et al. 2005). Alterations to organic matter stocks also affect nutrient export, dissolved organic C composition and availability, and habitat for microorganisms and larger biota (Jones 1997, Findlay and Sinsabaugh 1999, Paul et al. 2006).

Urban land use has been reported to affect leaf breakdown rates and mechanisms in different ways. Paul et al. (2006) observed faster breakdown in more-urban streams and attributed this difference to greater abrasive power, rather than to changes in microbial or invertebrate activity. In contrast, Chadwick et al. (2006) observed a positive correlation between breakdown rates and catchment total imperviousness (TI) between 0 and 40%, whereas breakdown and TI were negatively correlated when TI $>$ 40%. Chadwick et al. (2006) attributed this to peaks in fungal biomass, invertebrate abundance, and discharge at intermediate TI (40%), but these patterns also could be explained by large differences in the sizes of their study streams.

Urbanization also can alter leaf breakdown processes indirectly by altering the species composition of litter and increasing leaf litter input (Miller and Boulton 2005). If leaves of introduced urban trees differ in lability from those of indigenous species, then leaf breakdown mechanisms and rates are likely to change (Miller and Boulton 2005, Ryder and Miller 2005). Urbanization can alter the assemblage of riparian plants through enrichment of riparian soils (Riley and Banks 1996), drying of riparian soils following stream incision (Groffman et al. 2003), or direct deforestation and replanting. Thus, the effect of urban land use on leaf breakdown processes might be influenced by leaf species composition and by changes in environmental variables driving leaf breakdown.

Our goals were to test the effect of urban land use on breakdown rates of leaves of 2 common riparian species in southeastern Australia and to identify the mechanisms responsible for changes in breakdown rates. Two leaf species (indigenous *Eucalyptus obliqua* and locally introduced *Pittosporum undulatum*) were chosen to assess whether different leaf properties affect urban-related changes in leaf breakdown rates and mechanisms. Breakdown rates were determined across streams with varying urban stormwater impact, and 3 breakdown mechanisms—microbial activity, abrasive flow, and leaf-shredding macroinvertebrates (shredders)—were measured directly. The 4th general mechanism that contributes to leaf breakdown, leaching, was not measured because it is thought not to be strongly influenced by environmental variation (Petersen and Cummins 1974).

We define microbial activity as enzymatic and mechanical activity of fungi or bacteria that leads to chemical and structural modification of leaves (Webster and Benfield 1986, Maltby 1992b, Gessner and Ryckegem 2002). Microbial activity is influenced by water-quality variables, such as stream temperature, N, P, pH, metals, pesticides, and other organic pollutants (Maltby 1992b, Suberkropp and Chauvet 1995), all of which can be influenced strongly by urban stormwater runoff (Walsh et al. 2005b). Organic pollutants and metals might restrain microbial activity, but heightened temperatures and nutrient concentrations typical of urban streams (Walsh et al. 2005b) are likely to increase microbial activity in urban streams (Chadwick et al. 2006).

Stream abrasive power can contribute to leaf breakdown (Gessner 1999, Paul et al. 2006) and is influenced by suspended sediment concentrations and flow velocity (Campbell et al. 1992, Allan 1995, Paul et al. 2006). Urbanization is likely to change abrasive power because urban stormwater runoff alters stream hydrographs by increasing the frequency and magnitude of high flows, and it can alter sediment loads (Paul 1999). Many studies have alluded to the effects of abrasive power on leaf litter breakdown, but none has attempted to quantify it directly.

Shredders are important agents in leaf breakdown in many streams (Allan 1995). Loss of sensitive invertebrate species in streams affected by catchment urbanization is likely to reduce shredder activity in more-urban streams (Miller and Boulton 2005, Pascoal et al. 2005).

We hypothesize that: 1) urban stormwater runoff will increase microbial activity (Chadwick et al. 2006) and, in turn, leaf breakdown rates; 2) this effect will be weaker in leaves with less-labile C where lignin forms complexes with otherwise readily consumed cellulose (Melillo et al. 1984, Gessner and Chauvet 1994, Royer and Minshall 2001); and 3) urbanization will increase abrasive power of stream flow (tending to increase breakdown rates) but will reduce the abundance of

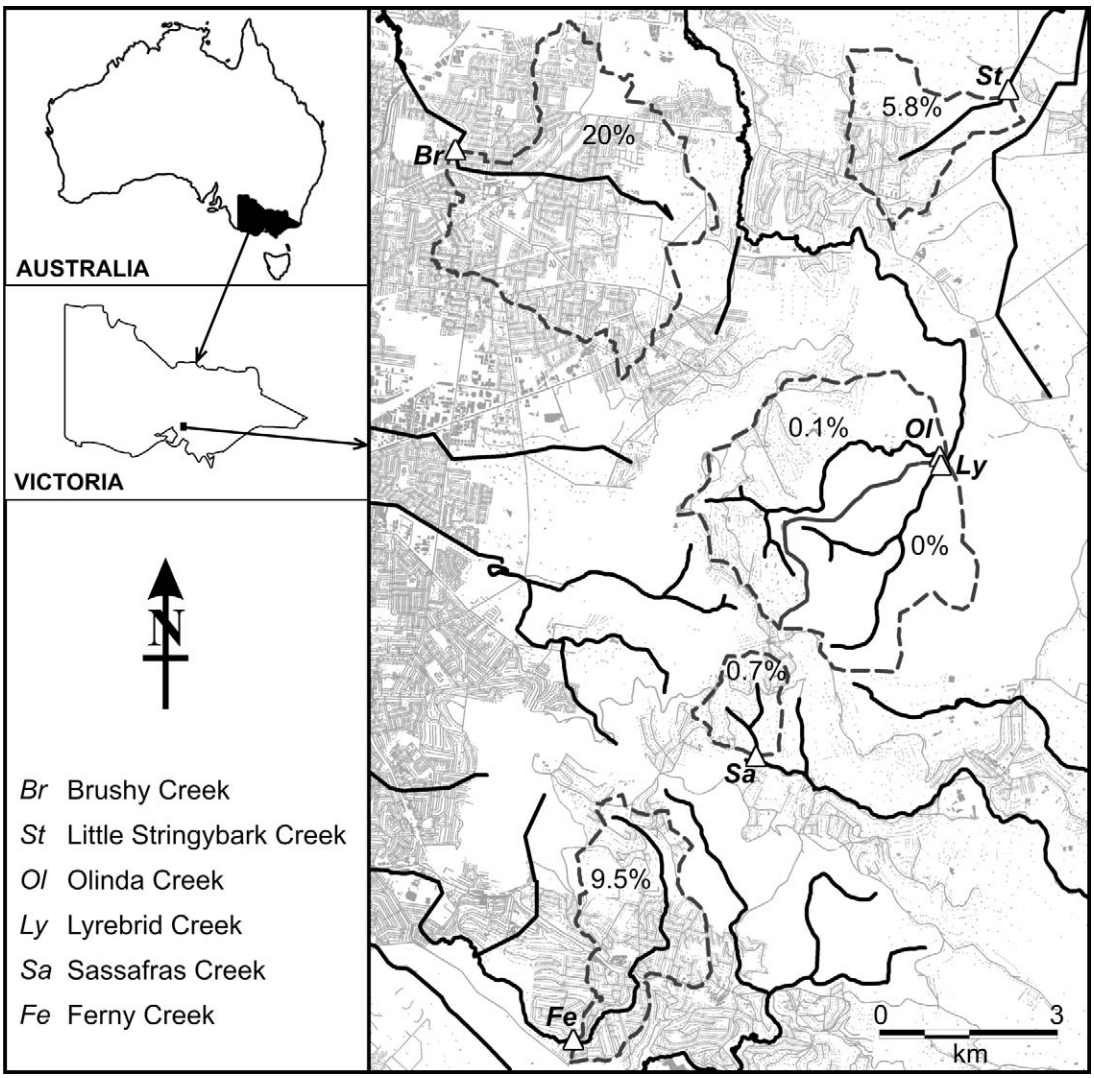

FIG. 1. Study area showing streams, catchment boundaries, and impervious surfaces. Percent effective imperviousness of each catchment (from Walsh et al. 2005a) is indicated.

shredders (tending to decrease breakdown rates) (Miller and Boulton 2005, Paul et al. 2006).

Methods

Reaches on 6 streams on the eastern fringe of metropolitan Melbourne, Victoria, Australia, were selected to encompass a range of catchment urban densities (Fig. 1). Predominant land use in all catchments was either urban or forest, with some nonintensive agriculture in the lower reaches of one catchment (St; Fig. 1). The streams were 1st- or 2nd-order (catchment size range = 2–15 km^2), and all had riparian tree cover. However, the more-urban streams tended to be more open because they were wider. More information on the study streams can be found in Hatt et al. (2004) and Walsh et al. (2005a).

Water quality and quantity

Electrical conductivity (EC), turbidity, dissolved O_2 (DO), pH, and temperature were measured on each sampling occasion with an Horiba® U-10 Water Quality Checker (Horiba Ltd., Kyoto, Japan), and water samples were collected for determination of filterable reactive P (FRP), NO_3/NO_2, and total suspended solids (TSS) by an accredited (National Association of Testing Authorities; http://www.nata.asn.au) laboratory. Nutrient samples were filtered through 0.45-μm cellulose acetate membranes and stored frozen until analyzed. Temperature was recorded hourly at each site with HOBO® H8 or Water Temp Pro loggers (Onset Computer Corporation, Pocasset, Massachusetts). Water depth was logged every 5 min at Fe, St, Sa, and Ol (Fig. 1) with Odyssey® Capacitance Water Level Probes

(Dataflow Systems Pty. Ltd., Christchurch, New Zealand) placed inside polyvinyl chloride stilling wells. Depth loggers failed at Br and Ly.

Breakdown rate

Leaves were collected from ~8 plants of each species at Fe (Fig. 1) on 1 day to minimize spatial and temporal variation in leaf nutrient status. Green leaves were collected from live branches because both tree species are evergreen and do not have a seasonal peak in litterfall, and sufficient similarly aged, abscised leaves could not be collected. Only similarly sized, mature leaves without blemishes, breached cuticles, or galls were selected. Collected leaves were sealed in humidified plastic bags and refrigerated at 4°C until deployment in the stream 12 d later.

Leaf packs consisted of 5.0 ± 0.2 g of 1 leaf species (weighed after leaves were washed with ultrapure water and blotted dry) tied together at their petioles with fishing line. Packs were tied to a snap swivel and identified with a numbered plastic tag.

Over 17–18 January 2006, 23 packs of each species were installed at each site. Three lines (198-kg breaking strain, 1- × 7-strand stainless-steel wire), each strung along the direction of flow between 2 steel pickets, were set within a pool (depth range = 25–60 cm) at each site. Packs of each species were arranged alternately along each line.

Two packs of each species were collected from each site 5, 11, 21, 31, 43, 56, and 69 d after deployment (a pilot study determined that duplicate packs were adequate to detect differences in breakdown rate between sites). Each leaf pack was positioned within a 250-μm-mesh net and removed from the wire. Material caught in the net was rinsed into a jar with 100% ethanol for macroinvertebrate analysis (see *Shredding macroinvertebrates* section). Packs were sealed in a bag and kept on ice until they were processed (within 7 h). Each leaf pack was gently rinsed over a 500-μm-mesh sieve, and the residue, which included all macroinvertebrates, was added to the appropriate macroinvertebrate sample (see *Shredding macroinvertebrates* section). Leaf packs were dried at 40°C for 40 h, weighed to the nearest 0.01 g, and milled in a blender (Waring®; Waring Laboratory, Torrington, Connecticut). Ash-free dry mass (AFDM) was determined by combusting a 0.250 ± 0.003-g subsample of milled leaves (1 h at 550°C).

Rates of AFDM loss were assessed using negative exponential and linear models with and without intercepts. The model of best fit (negative exponential with intercept) was used to calculate breakdown rates per day and per degree day (dd) (Petersen and Cummins 1974, Young 2006). Ten packs that were constructed and taken into the field but not actually deployed were processed as described already to determine a species-specific correction for the average initial organic matter content of the leaves used in the calculation of AFDM loss (Benfield 1996).

Mass-loss curves through time approached an asymptote at ~10% initial mass remaining because the leaves were held in packs with ties around the petioles (checks of packs on retrieval confirmed that no leaf had broken off at the petiole). Therefore, decay models from *P. undulatum* at 4 sites were truncated at 9% remaining.

Microbial activity

Microbial activity in leaves was estimated using a fluorescein diacetate hydrolysis technique adapted from Claret and Boulton (2003) and Battin (1997). This method measures fungal and bacterial activities, and resulting data are strongly correlated with adenosine triphosphate (ATP) and cell-density estimates of microbial biomass (Stubberfield and Shaw 1990, Gillian and Duncan 2001). Two additional leaf packs of each species were collected for microbial assay on days 5, 11, and 21. Packs were stored in plastic bags at 4°C for <20 h before being rinsed in ultrapure water to remove excess sediment. This procedure ensured minimal disturbance to surface biofilms. Every leaf in each pack was cut into ~1-cm^2 segments and homogenized. A subsample (1.0 ± 0.1 g) of each leaf was weighed into each of 3 sterile, 15-mL Falcon tubes (Becton, Dickinson and Company, Franklin Lakes, New Jersey). The tubes were then incubated at 18 to 18.5°C for 2 h.

Two milliliters of ultrapure water and 3 mL of pH 7.6 buffer (0.1-M KH_2PO_4 solution added to 850 mL of 0.1-M Na_2HPO_4 until pH 7.6 was obtained) were added to each tube. One hundred microliters of fluorescein diacetate (FDA) stock solution (0.02-g FDA + 6-mL C_3H_6O + 4-mL ultrapure water) were added to 2 of the 3 replicate tubes per leaf pack. Tubes were shaken and incubated in the dark at 18 to 18.5°C. Incubation was stopped after 25 to 35 min (when a fluorescent green color was observed) by adding 3 mL of 0.0015-M $HgCl_2$ and immediately shaking the tubes. Tubes were centrifuged at 5000 rpm for 5 min. The supernatant was filtered through a 0.45-μm cellulose nitrate membrane, frozen, and stored in the dark. Samples were later thawed and diluted 10-fold (v/v) with ultrapure water and incubated at 18 to 18.5°C for ~1.5 h before fluorometric analysis (Hitachi F-2000 fluorescence spectrophotometer, Hitachi High-Technologies [Singapore] Pte. Ltd., Singapore; 1-cm glass cuvette, emission wavelength: 512 nm, excitation wavelength: 400 nm).

TABLE 1. Macroinvertebrate taxa classified as shredders in our study.

Order	Families with shredder genera	Shredder genera	Reference[a]
Amphipoda	All	All	A
Coleoptera	Scirtidae	All	B
	Ptilodactylidae	All	C, D, E
	Chrysomelidae	All	B
	Curculionidae	All	B
	Elmidae	*Notriolus*	D, E, F
		Kingolus	D, E, F
		Coxelmis	D
Decapoda			E
	Parastacidae	All	A
Diptera	Tipulidae	All	B
Ephemoptera	Leptophlebidae	*Atalophlebia*	D, E
Isopoda	Oniscidae	All	A
Lepidoptera	Pyralidae	All	B
Plecoptera	Gripopterygidae	*Dinotoperla*	D, E
	Austroperlidae	*Acruroperla*	D, G
		Austroheptura	D, G
		Austropentura	G
Trichoptera	Conoesucidae	*Costora*	H
	Calocidae	All	E, H
	Calamoceratidae	*Anisocentropus*	E
	Leptoceridae	All	B, D, E

[a] A = Gooderham and Tsyrlin (2003), B = Merritt and Cummins (1996), C = Anderson (1982), D = Chessman (1986), E = Boulton and Lake (1992), F = McKie and Cranston (1998), G = Sephton and Hynes (1983), H = Jackson (1998).

Standard reporting formulae were used to ensure comparable results between assays under varying measurement conditions caused by lamp degeneration between analysis blocks.

$$C = F_u(\text{time}_1)/F_u(\text{time}_x),$$

$$F_a = (10CF_uv)/m, \text{and}$$

$$D = (F_a[\text{sample}] - F_a[\text{blank}])/\varepsilon t,$$

where C = standard correction factor; $F_u(\text{time}_1)$ = unadjusted standard fluorescence during analysis period 1 (intensity); $F_u(\text{time}_x)$ = unadjusted standard fluorescence during subsequent analysis periods (intensity); m = leaf dry mass (g); v = incubation volume (mL); $F_a = F_u$ adjusted for dilution, standard, m, and v; t = incubation time (min); ε = laboratory-assessed extinction coefficient of fluorescein (302.6×10^5 M^{-1} cm^{-1}); D = FDA hydrolysis (μmol g^{-1} min^{-1}); $v = 8.1$ mL (sample); and $v = 8.0$ mL (blank).

Physical abrasion

Abrasion blocks (Webb et al. 2006) were used to measure the physical abrasion power of each stream. Forty-eight blocks (50 × 50 × 25 mm) were constructed from CSR™ Hebel® Thermoblocks (autoclaved lightweight aerated concrete; CSR Limited, Chatswood, Australia) (Webb et al. 2006). Eight abrasion blocks were attached to a mesh frame, which was secured to the most-downstream steel pickets of the leaf-pack lines to enable secure attachment and adequate intrasite replication.

After 69 d, abrasion blocks were removed from the streams, covered with cloth, and tightly packed into a container to minimize abrasion during transport. In the laboratory, blocks were submerged in ultrapure water for 30 min, and each surface was gently wiped once before being rinsed with ultrapure water. The cleaned blocks were left to dry in the laboratory for 3 d (to remove excess water) and then dried in an oven at 60°C to constant mass (~3 d). Physical abrasion power in each stream was estimated as the % mass loss of abrasion blocks over 69 d.

Shredding macroinvertebrates

Macroinvertebrate samples were collected (as described in *Breakdown rate* section) from 2 leaf packs for each species at each site on day 21 and stored in 70% ethanol. Macroinvertebrates were identified and counted under a binocular dissecting microscope to either family or genus level, depending whether the whole family or only some genera were classified as shredders (Table 1). Shredder abundance was expressed as individuals (ind.)/g leaf dry mass, but results were similar if ind./leaf pack was used.

Shredders that colonize leaf packs might be a smaller proportion of the total pool of potential leaf colonizers in streams that have abundant leaf litter than in streams with little native leaf litter (Bird and Kaushik 1992). To assess if intersite patterns of shredders colonizing leaf packs matched shredder abundances in the study reaches, relative abundances of shredder taxa were calculated from qualitative riffle and edge samples collected at the 6 study sites (Walsh 2004). The family-level data from edge samples collected in autumn 2002 and from riffle samples collected in spring 2001 and autumn 2002 were combined with lowest-taxonomic-level data from edge samples collected in spring 2001.

The decision to omit or classify as shredders ambiguous taxa (i.e., unidentifiable individuals belonging to families that are not exclusively shredders) did not affect the relative abundance of shredder taxa in leaf-pack or reach-scale data sets, so they were counted as shredders. Patterns of shredder relative abundance in the reach-scale data sets were similar across habitats and seasons, so data from all 4 sample sets were combined, and reach-scale relative abun-

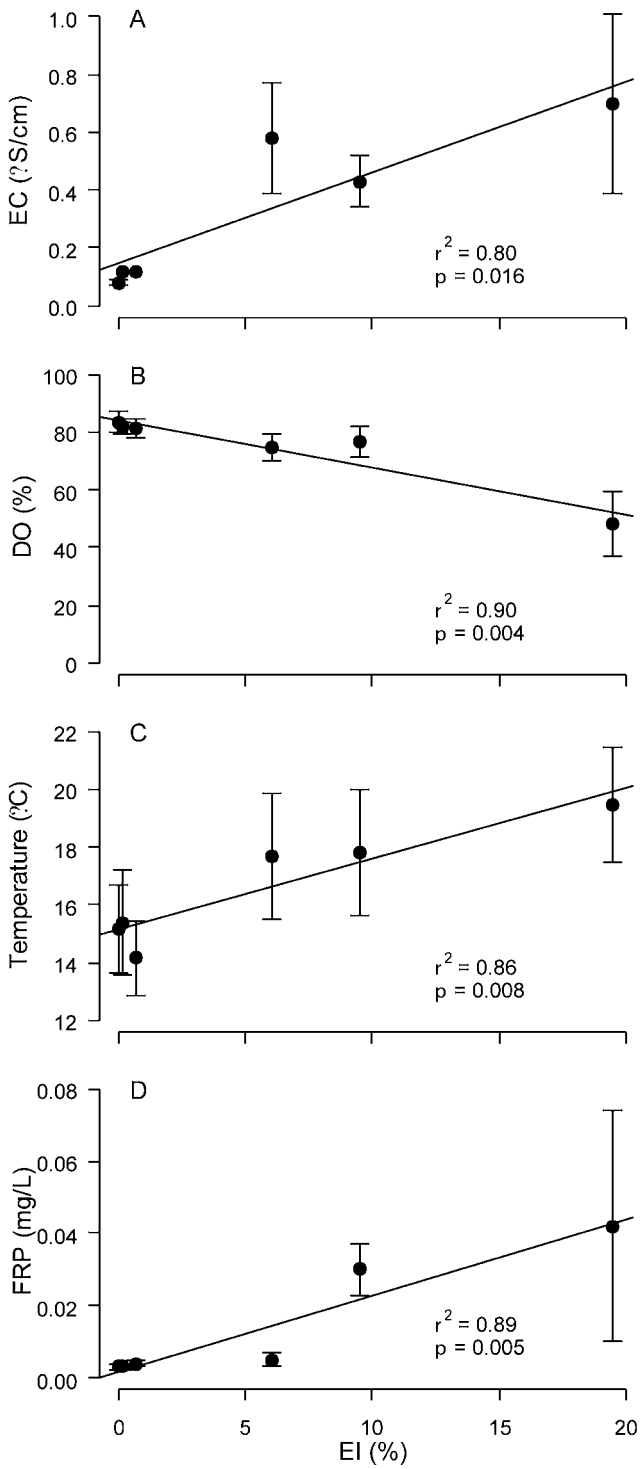

FIG. 2. Water-quality variables (mean ±1 SE) with significant relationships with catchment urbanization estimated by % effective imperviousness (EI). A.—Electrical conductivity (EC). B.—Dissolved O_2 (DO) % saturation. C.—Temperature. D.—Filterable reactive P (FRP).

dance was calculated for the combined data set. The decision to use family-level data (when families might or might not consist exclusively of shredder genera) or only the shredder genera within families (lowest-taxonomic-level data) did not affect reach-level shredder relative abundance. Therefore, relative abundance is reported on the basis of lowest-taxonomic-level data (shredder genera).

Statistical analysis

Relationships between stream variables and catchment urban land use were tested with regressions of water-quality variables, physical abrasion power, leaf species breakdown rates, microbial activity, and shredder abundances against effective imperviousness (EI = percentage of catchment covered by impervious surfaces with connection to streams via stormwater sewers; Walsh et al. 2005a). The relationship between physical abrasion power and urbanization also was tested with a 1-factor analysis of variance (ANOVA) in which urban and nonurban were defined as >6% and <1% EI, respectively. Analysis of covariance (ANCOVA) was done on the dependent variables (breakdown rates, FDA hydrolysis, and shredder abundance), with species (2 levels) as the main effect and EI as the covariate, to test if breakdown rates, microbial activity, and shredder abundance differed between leaf species and to test if difference between species changed with increasing EI. A significant species × EI interaction term indicated that the hypothesis that the 2 species had equivalent relationships with EI should be rejected. When the interaction term was not significant, the ANCOVA was repeated without the interaction term to assess the main effects on the dependent variable. Variables were transformed, where necessary, to meet the assumptions of the analyses. Significance was $p < 0.05$ for all tests.

Results

Water quality and quantity

EC, temperature, and FRP were significantly positively related to EI, and DO was significantly negatively related to EI (Fig. 2A–D). TSS, pH, and NO_3/NO_2 concentration were not significantly related to EI (TSS: $r^2 = 0.53$, $p = 0.21$; pH: $r^2 = 0.64$, $p = 0.21$; NO_3/NO_2: $r^2 = 0.23$, $p = 0.33$). Four large rain events (Fig. 3A) increased flow in all streams (Fig. 3B), but peak flows were higher and high-flow durations were shorter in streams with higher EI.

Breakdown rates

Leaves of *E. obliqua* and *P. undulatum* lost 27 to 75% and 93 to 97% mass, respectively. The r^2 values

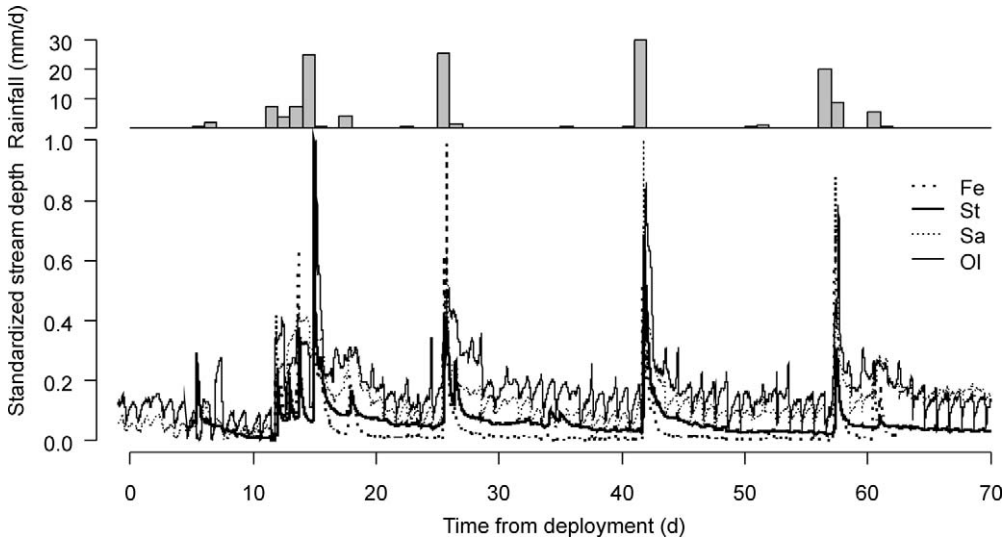

FIG. 3. Daily rainfall at Mt. Dandenong in the center of the study area (Melbourne Water: http://melbournewater.com.au/content/rivers_and_creeks/rainfall_and_river_level_data/rainfall_and_river_level_data.asp) (A) and standardized hydrographs of 4 of the study streams (see Fig. 1 for abbreviations) (B) during the 69-d leaf-pack deployment that began 17 January 2006. Depth measurements at 5-min intervals were standardized between the minimum and maximum record in each stream over the study period. Study streams are listed in the key to symbols in order of decreasing catchment effective imperviousness.

associated with mass loss over time ranged from 0.72 to 0.99 (mean across sites and species = 0.89). Breakdown rates for *E. obliqua* and *P. undulatum* ranged from 0.009 to 0.022/d and 0.031 to 0.079/d, respectively. *Pittosporum undulatum* leaves broke down faster than *E. obliqua* leaves at all sites, and this difference was more pronounced as EI increased (Fig. 4A). *Pittosporum undulatum* breakdown rates were strongly positively related to EI, whereas *E. obliqua* rates were not (species × EI interaction, $F_{1,8} = 12.15$, $p = 0.008$; Fig. 4A). Breakdown rates calculated per degree day (dd) were higher for *P. undulatum* (mean = 2.9×10^{-3}/dd) than for *E. obliqua* (mean = 8.5×10^{-4}/dd) ($F_{1,8} = 0.56$, $p = 0.82$; after removal of the nonsignificant species × EI interaction term, $F_{1,9} = 42.7$, $p < 0.001$), but EI did not significantly affect degree day breakdown rates of either species ($F_{1,9} = 0.58$, $p = 0.47$).

Breakdown mechanisms

Microbial activity ranged from 0.53 to 1.40 nmol g^{-1} min^{-1} and from 0.66 to 6.73 nmol g^{-1} min^{-1} in *E. obliqua* and *P. undulatum* leaves, respectively. On day 5, microbial activity did not differ significantly among sites for either species (*E. obliqua*: $F_{5,6} = 1.27$, $p = 0.39$; *P. undulatum*: $F_{5,6} = 2.59$, $p = 0.14$; Fig. 5A, B). On day 11, microbial activity differed between sites in both *E. obliqua* ($F_{5,6} = 6.28$, $p = 0.022$; Fig. 5A) and *P. undulatum* ($F_{5,6} = 17.15$, $p = 0.002$; Fig. 5B) leaves. On day 21, differences in microbial activity among sites could not be analyzed meaningfully because mass of *P. undulatum* remaining was <10% (excluding petiole mass) in packs at Br, and labile leaf C probably was limiting in *P. undulatum* packs at Br and Fe because of high microbial consumption prior to day 21.

On day 5, microbial activity was greater in *P. undulatum* leaves than in *E. obliqua* leaves at all sites ($F_{1,12} = 16.51$, $p = 0.002$). On day 11, microbial activity was greater in *P. undulatum* leaves than in *E. obliqua* leaves at all sites, and this difference was more pronounced as EI increased (species × EI interaction, $F_{1,8} = 29.43$, $p = 0.001$; Fig. 4B). On day 11, microbial activity was positively related to EI in both *E. obliqua* and *P. undulatum* leaves (Fig. 4B).

Physical abrasive power ranged from 2.6 to 6.6% (Fig. 4C). Physical abrasive power differed significantly among sites ($F_{5,42} = 78.37$, $p = < 0.001$), but the differences among sites were not linearly related to EI ($p = 0.28$; Fig. 4C). However, physical abrasive power was greater in nonurban (EI <1%) than in urban (EI >6%) streams ($F_{1,4} = 9.89$, $p = 0.035$). The observed differences in abrasion block mass loss are unlikely to have been experimental artifacts caused by differences in pH or temperature (Webb et al. 2006) because variability in pH (range = 6.5–7.5) and temperature (range = 15–19°C; Fig. 2C) was low during the study period (J. A. Webb, Melbourne University, personal communication).

Shredder abundance on leaf packs was highly variable (*E. obliqua*: range = 0–28 ind./g leaf dry mass,

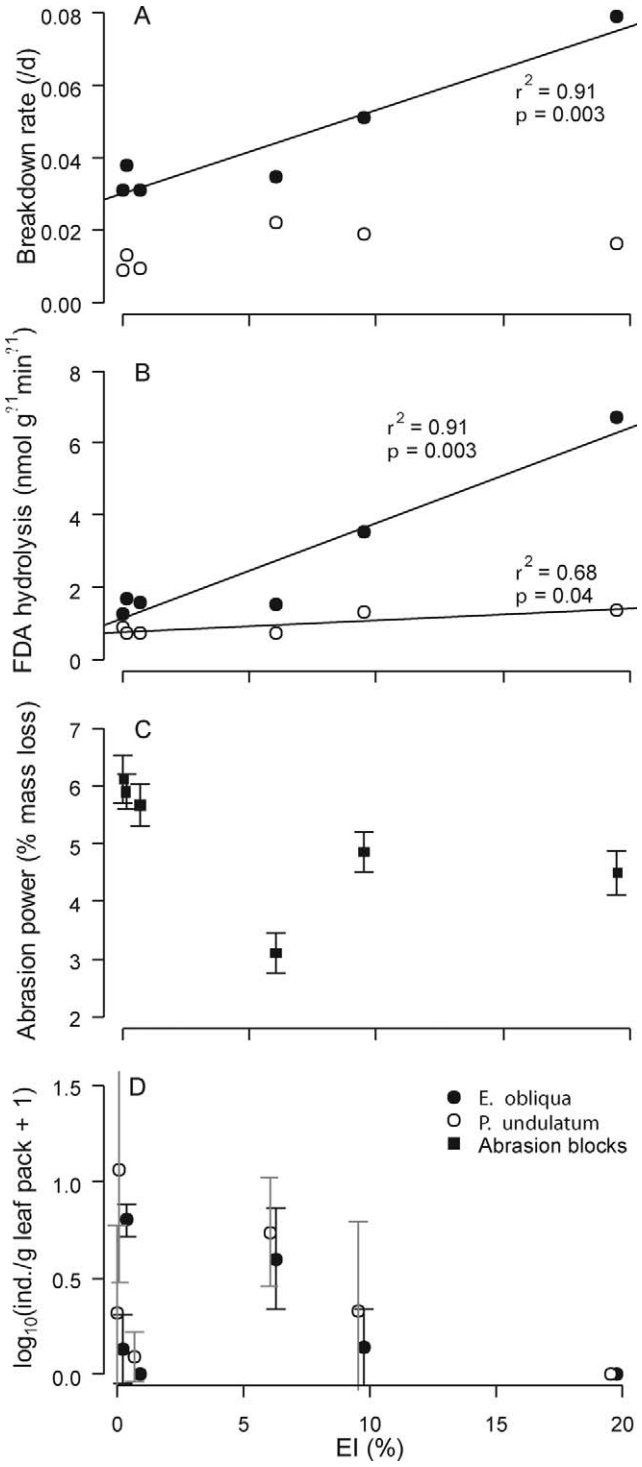

FIG. 4. Relationships of *Eucalyptus obliqua* and *Pittosporum undulatum* leaf breakdown rates (A), microbial activity in leaves estimated by fluorescein diacetate (FDA) hydrolysis (B), stream physical abrasion power estimated as mean (±1 SD) % mass loss in concrete blocks over 69 d (C), and mean (±1 SD) shredder abundance on leaf packs (D) with catchment urbanization measured as effective imperviousness (EI). Regression lines are shown for relationships that were statistically significant ($p < 0.05$).

P. undulatum: range = 0–6 ind./g leaf dry mass). Shredder abundance on leaf packs differed significantly among sites ($F_{5,12} = 6.62$, $p = 0.004$) but not between leaf species ($F_{1,12} = 1.55$, $p = 0.24$). Shredder abundance on leaf packs was not significantly related to EI in packs of either leaf species (*E. obliqua*: $p = 0.34$, *P. undulatum*: $p = 0.46$; Fig. 4D). In contrast, reach-scale relative abundance of shredders was strongly negatively correlated with EI (Fig. 6).

Discussion

How does urban land use change leaf breakdown mechanisms?

Our study tested 3 potential mechanisms for higher rates of leaf breakdown in urban compared to nonurban streams. In contrast to our a priori hypothesis, physical abrasion did not increase as EI increased. As expected, shredders are most unlikely to be a driver of increased leaf breakdown rates in urban streams because their abundance decreases as EI (our study) or other measures of urbanization (Paul 1999, Miller and Boulton 2005, Pascoal et al. 2005) increase. Thus, patterns and mechanisms of leaf breakdown in streams of eastern Melbourne indicate that increased microbial activity in urban streams is the mechanism most likely to explain observed increases in breakdown rates, particularly of leaves with more-labile C, such as those of *P. undulatum*.

The importance of a particular breakdown mechanism varied with EI, and the effects of the various breakdown mechanisms differed between the 2 leaf species. This mechanistic variation might explain the different responses to EI observed for the 2 leaf species. For example, in nonurban streams, shredders might prefer to eat *P. undulatum* leaves over *E. obliqua* leaves, which have high lignin and cellulose concentrations (Gessner 2005). Thus, in nonurban streams, the mechanism that causes *P. undulatum* leaves to break down faster than *E. obliqua* leaves might be shredder preference. However, in urban streams, where shredders are not abundant, higher microbial activity on *P. undulatum* leaves, which have low lignin and polyphenolic concentrations (Boulton 1991, Gessner 1991, 2005), than on *E. obliqua* leaves might be the mechanism underlying the faster breakdown of *P. undulatum* leaves.

The relationship between microbial activity and EI on day 11 suggests that urban land use is a strong determinant of microbial activity in leaves. However, the influence of EI on microbial activity is species specific. The increase in microbial activity in response to EI was 8× greater in *P. undulatum* than in *E. obliqua* leaves. Microbial activity in leaf litter can be strongly

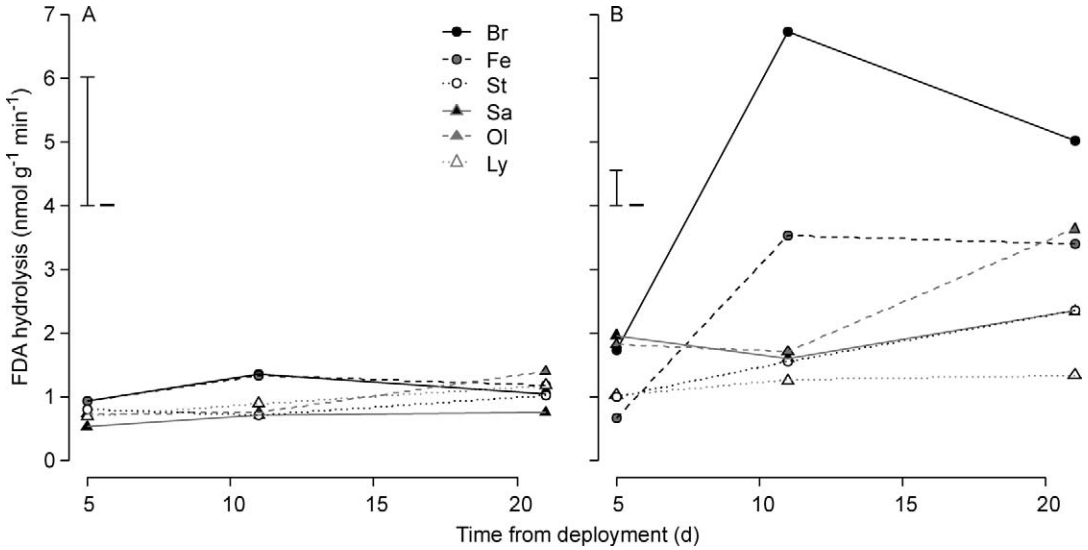

FIG. 5. Microbial activity estimated as fluorescein diacetate (FDA) hydrolysis in leaves of *Eucalyptus obliqua* (A) and *Pittosporum undulatum* (B) 5, 11, and 21 d after deployment of leaf packs in 6 streams (see Fig. 1 for abbreviations). Study streams are listed in the key to symbols in order of decreasing catchment effective imperviousness. Vertical bars indicate largest and smallest standard deviation (SD) for values plotted on each panel.

influenced by a variety of water-quality variables (Suberkropp and Chauvet 1995), but the most likely drivers for urban-related increases in microbial activity in eastern Melbourne streams are increased water temperature and P concentrations.

EI did not influence breakdown rates calculated per degree day. This absence of an effect of EI suggests that temperature (through its influence on microbial activity) might have had an important influence on breakdown rates calculated per day. FRP was strongly positively related to EI, and in the absence of urbanization, P is the nutrient most likely to limit biological productivity in these streams (Taylor et al. 2004). Thus, elevated stream temperatures and increases in bioavailable P in urban streams would be expected to increase microbial activity and should lead to a concomitant increase in the consumption of leaf C and nutrients (Webster and Benfield 1986, Gulis and Suberkropp 2003). However, stream temperature and FRP are strongly correlated in our data set, and it is not possible to isolate their individual effects using our data.

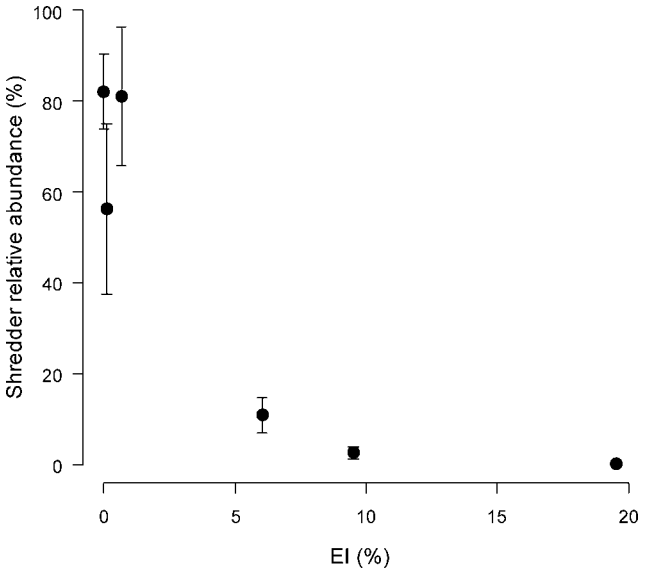

FIG. 6. Mean (±1 SD) relative abundance of shredding invertebrates in samples collected from riffles and edges of each study reach in relation to catchment urbanization measured as estimated by effective imperviousness (EI).

In our study, microbial activity increased with EI (up to 22% total imperviousness); this result is consistent with those of studies in northern Florida, USA (Chadwick et al. 2006), and Portugal (Pascoal et al. 2005), but it is different from those of a study in the Piedmont province of Georgia, USA (Paul et al. 2006), where fungal biomass did not differ significantly between forested (<1% imperviousness) and suburban streams (25–29% imperviousness) and was significantly lower in urban (40–46% imperviousness) than in forested or suburban streams. Paul et al. (2006) attributed accelerated leaf breakdown in urban streams to enhanced physical abrasion.

Authors of previous studies of leaf breakdown along urban and rural landuse gradients have postulated a positive correlation between abrasive flow and urban

landuse intensity (Benfield et al. 1977, Bird and Kaushik 1992, Tuchman and King 1993, Paul et al. 2006) but have not measured abrasion directly. Rather, they inferred abrasion from hydrological change. In our study, physical abrasive power was measured directly. Urban streams had less physical abrasive power than did nonurban streams, and this result makes abrasion unlikely to have contributed to faster leaf breakdown in our urban streams. Thus, increased hydrologic flashiness does not necessarily increase abrasive power.

Sediment loads are naturally high in streams draining the Dandenong Ranges (Hatt et al. 2004), and this underlying geology might have accentuated the abrasion observed in our nonurban streams. Urbanization increases peak flows, but it also decreases the duration of high-flow events (Fig. 3B). Thus, nonurban streams in our study might have greater physical abrasive power than urban streams because of prolonged exposure to elevated TSS during high flows. Physical abrasive power might not decrease as urbanization increases in regions where baseflow sediment concentrations are positively related to EI. Nevertheless, our study illustrates the importance of assessing abrasive power directly rather than assuming that the greater flashiness of urban hydrographs causes increased abrasion.

Interspecies differences in leaf breakdown rates

The different breakdown rates of the 2 leaf species and the difference in their responses to urban density are probably the result of varying leaf-quality variables and their response to external environmental conditions. *Eucalyptus obliqua* and *P. undulatum* leaves differ in leaf quality for microbes. Low levels of delayed microbial activity have been attributed to the lignin, N, P, polyphenol, and lipid content of *Eucalyptus* leaves (Bunn 1988, Suberkropp and Chauvet 1995, Chauvet et al. 1997, Pozo et al. 1998). Slower breakdown of *E. obliqua* also might be a result of the anatomy of its leaves, which have a thick waxy cuticle and a thick palisade cell layer that are thought to protect the internal leaf mesophyll cells from microbial attack (Boulton 1991). Moreover, lignin forms complexes with cellulose in *E. obliqua* leaves, which limits the amount of labile C available to support microbial activity regardless of the availability of other resources associated with gradients of EI (Melillo et al. 1984, Gessner and Chauvet 1994, Royer and Minshall 2001). In contrast, *P. undulatum* leaves have low lignin and polyphenol content, and microbial activity is unlikely to be C limited in these leaves. Thus, microbes on *P. undulatum* leaves should be able to respond to the increases in temperature and P associated with increasing EI (Melillo et al. 1984, Royer and Minshall 2003), whereas microbes on *E. obliqua* might not. The consequence would be species-specific differences in microbe-mediated changes in leaf breakdown rates along the EI gradient.

Management implications

The impacts of urban land use on streams are complex, but many of the effects are associated with stormwater runoff. Stormwater runoff disrupts streams by increasing the frequency and volume of high-flow events and by delivering a range of pollutants to streams from parts of the catchment that were not hydraulically connected to the stream in a pre-urban state (Walsh et al. 2005b). Our results suggest that the effects of stormwater on leaf breakdown rates (at least for leaf species with more-labile C) are consequences of its influence on streamwater quality rather than its influence on hydrology. In the P-limited streams studied here, increases in temperature or P probably drive increases in microbial breakdown of labile leaves.

A primary management action to mitigate these effects might be the reduction of the delivery of labile leaves to the streams by eradicating exotic riparian trees with leaves that are more labile than leaves of indigenous species. Riparian zones could then be replanted with indigenous species to create shade and reduce water temperature. However, conventional stormwater drainage systems connect large areas of the catchment to the stream, and these connections might allow delivery of leaf litter from parts of the catchment well beyond the riparian zone (Miller and Boulton 2005, Walsh et al. 2005b). Furthermore, although riparian forests can reduce stream temperatures in urban areas, the reduction in algal growth in shaded reaches potentially can increase nutrient concentrations (Roy et al. 2005). In general, the ecological effects of riparian zones probably are diminished in streams that are affected by stormwater runoff (Roy et al. 2005, Walsh et al. 2007).

Thus, catchment-scale actions that reduce stream temperature and nutrient concentrations are likely to be more effective tools than manipulation of riparian vegetation for returning leaf litter inputs and breakdown rates to pre-urban levels. New stormwater management practices break the direct hydraulic connections between impervious surfaces in the catchment and streams through the installation of filtration systems, wetlands, and rainwater tanks (e.g., Melbourne Water 2005). These practices are designed to reduce nutrient loads, and they moderate runoff

temperature because water is delivered to streams through subsurface flows. Widespread application of such practices is likely the most effective primary action for restoring leaf breakdown rates.

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