Leaf litter diversity and shredder preferences in an Australian tropical rain-forest stream

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Abstract: Consumption of terrestrial leaf litter by stream invertebrates is an important process, but little attention has been paid to the influence of leaf diversity on the process. Tropical forests are known to have much greater diversity of plant species than their temperate counterparts, but studies of litter processing in tropical streams have not explicitly addressed this issue. This paper documents the streambed leaf litter composition and diversity of an Australian tropical rain-forest stream and the leaf preferences of consumers in the stream. We hypothesized that there would be high diversity of litter in the stream and that the shredders would have broad preferences, given that litterfall of any one species would occur over a restricted period. Leaf litter was characterized by high species diversity (81 species from one stream reach sampled on two occasions). Leaf consumers ('shredders') were associated with a relatively broad suite of leaf species (38 species) and did not indicate clear leaf preferences. However, in a laboratory feeding experiment, using the three most common shredder species and some of the most abundant leaf species in the stream, all shredder species exhibited clear preference for a single leaf species (*Endiandra bessaphila*). Preference for this and other species was affected by the conditioning age of leaves (i.e. the length of time leaves were exposed to leaching and microbial colonization), with conditioned leaves usually being preferred, and previously non-selected leaves becoming more palatable with conditioning. Thus, different successional stages were more important than the identity of leaf species in determining the distribution of shredders among the leaves.

Key Words: Australia, litter processing, shredder, species richness, stream invertebrates, Trichoptera, tropics

INTRODUCTION

Allochthonous leaf litter from riparian vegetation is typically the major source of organic material in forest streams, and is one of the major factors that determines the structure and function of biotic communities in these streams (Benfield & Webster 1985, Cummins *et al.* 1973, Kaushik & Hynes 1968, Nolen & Pearson 1993, Pearson *et al.* 1989, Petersen & Cummins 1974, Short *et al.* 1980). Once leaves enter the stream, they are subjected to a series of physical and biological processes, including 'conditioning' (the leaching of soluble materials, microbial colonization and processing), fragmentation by physical forces and invertebrate feeding (Boulton & Boon 1991, Suberkropp 1998). The organisms involved in the processing of leaves – heterotrophic bacteria, fungi and invertebrate consumers

('shredders') – are key components of the stream detrital food web and play an important role in the breakdown and transformation of organic matter, making it available to other organisms (Suberkropp 1998).

Streams are often characterized by a high level of habitat heterogeneity, which exerts a strong influence on the distribution and abundance of species, biotic interactions and the trophic structure of biological communities (Boyero 2003, Cardinale *et al.* 2002). The amount and distribution of detritus on the substratum affect heterogeneity (Murphy *et al.* 1998), and play a significant role in the distribution, species composition and total biomass of benthic invertebrates (Hearnden & Pearson 1991, Reice 1974). After leaves fall into the stream, their aggregation into leaf packs in pools and against obstacles is influenced by the flow regime, the transport and retention capacity of the stream, and the rate at which particles are processed by the biota (Dudgeon 1999). The quantity (Dudgeon 1999) and quality (Arsuffi & Suberkropp 1985) of litter on the

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stream bed may vary in space and time and contribute to the habitat heterogeneity of streams (Reice 1974). The leaf species that comprise a natural leaf pack enter the stream at different times and are likely to be subjected to different levels of microbial conditioning, invertebrate feeding and physical fragmentation, so leaf identity is also likely to influence heterogeneity, although this point has rarely been addressed (Swan & Palmer 2004 is an exception).

Most available studies on the composition of natural leaf litter accumulations have been based on streams in the northern hemisphere. In contrast with temperate streams, where most leaves enter the stream during a few weeks in autumn, tropical riparian species shed their leaves more asynchronously and some litterfall occurs year-round (Benson & Pearson 1993, Dudgeon 1999, Mathooko *et al.* 2000). Litterfall is provided by a wide diversity of tree species (Pearson *et al.* 1989), so tropical rain-forest streams are characterized by a complex mosaic of leaves (Covich 1988). The structural and chemical attributes of leaves can vary significantly among different species and have been shown to have great influence on leaf litter utilization by shredders (Anderson & Sedell 1979, Nolen & Pearson 1993, Webster & Benfield 1986). Differences among leaf species include the abundance of essential nutrients, fibre content and the presence of chemical inhibitors (Webster & Benfield 1986), which negatively affect microbial invasion and subsequent processing (Bärlocher *et al.* 1978). Leaves that differ in quality and palatability, through differences in inhibitory chemicals, microbial conditioning and/or toughness, are likely to amplify the discontinuity or non-randomness of dispersion of shredders within the stream (Wiens 1976). Tropical leaves tend to have a higher incidence and concentration of toxic compounds for protection against herbivory (Coley 1983, Covich 1988). The importance of leaf heterogeneity to habitat and resource patchiness and consequently to trophic processes, especially in the tropics, is therefore worthy of attention.

This study investigated the species diversity of stream-bed leaf litter in a low-order stream in the Australian wet tropics. Data on the species composition of leaf litter on the streambed is virtually non-existent for tropical streams. Most studies on the importance and processing of leaf litter in tropical streams have been based on leaf species that are commonly found in the riparian vegetation immediately surrounding the stream. However, the composition of leaf litter in the stream channel may not directly correspond to the riparian vegetation because of differences in the distances travelled by leaves and seasonal variation in the time of abscission (Boulton & Boon 1991). Nevertheless, we predicted that there would be high leaf diversity in the stream. The field study was followed by a series of laboratory experiments to investigate leaf preferences of several common shredder species. Leaf preference experiments have previously been based on the few dominant species in temperate zones (Anderson & Sedell 1979, Petersen & Cummins 1974, Webster & Benfield 1986) or on arbitrary selection of a few test species in the tropics (Nolen & Pearson 1993). In this study we hypothesized that, because of the likely unpredictability of litter composition due to asynchronous leaf fall and the stochastic nature of tropical storms and floods, shredders would have broad leaf preferences.

METHODS

Study site

The study site was Camp Creek (also called Little Birthday Creek; 18°58′S,146°10′E), an upland rain-forest stream in the Paluma Range National Park, north-eastern Queensland. This stream is located at about 800 m asl. in rain forest, predominately Simple Notophyll Vine Forest (Tracey 1982), which forms a closed canopy over the stream. Camp Creek has a riffle-pool geomorphology with the stream bed consisting of granite rocks and boulders, interspersed with smaller patches of gravel, sand and leaf litter.

The climate of the region is tropical and seasonal with 70% of the annual rainfall (annual mean = 2641 mm) falling during the warm wet season (December–March). Stream discharge during this period is highly variable, whereas during the cool dry season it is low and constant or steadily diminishing. Stream temperatures usually range from 11 °C to 23 °C. Litter fall occurs throughout the year but the peak of litter input to the stream occurs during the late dry season (October–November), resulting in distinct seasonal changes in the availability of food resources (Benson & Pearson 1993).

Streambed litter composition

Surveys of the stream-bed litter composition were conducted along a 50-m reach of the stream, including a riffle and a large pool. Litter was collected during the early dry season (June 2004) and late wet season (March 2005). Sampling consisted of randomly choosing and removing leaf litter leaf packs or portions of them along the study reach. Each sample unit comprised a handful of leaves (∼1 L), which were transferred directly to a white sorting tray. Forty-two sample units were collected (20 in the dry and 22 in the wet season). In riffles, sample units were usually whole leaf packs, with a size of approximately a handful of leaves. In pools, however,

leaf packs were large and the deepest part was usually hypoxic, so leaves were taken from the surface of the leaf pack.

Each leaf was carefully inspected, and the four most common shredder species in Camp Creek (Cheshire *et al.* 2005) were removed from leaves and preserved individually in labelled vials with 70% ethanol. The species were *Anisocentropus kirramus* Neboiss (Trichoptera: Calamoceratidae), *Lectrides varians* Mosley (Trichoptera: Leptoceridae), *Triplectides gonetalus* Morse & Neboiss (Trichoptera: Leptoceridae) and *Atalophlebia* sp. (Ephemeroptera: Leptophlebiidae). Only shredders that were firmly attached to leaves were included; typically, these leaves showed signs of shredding at the point of the animal's attachment. Leaves associated with shredders were placed individually in labelled paper bags, while the remaining leaves in the sample were placed in a separate bag. Samples were then taken to the laboratory for further processing. Leaves were dried at 50 °C for 48 h and were then identified to species, using Christophel & Rowett (1996), Hyland *et al.* (2003), Jackes & Cairns (2003), and the herbarium and comprehensive knowledge of one of us (BRJ). Shredders were identified to species level (verified by Dr R. St. Clair, Museum of Victoria), their body length was measured under a stereoscope and the leaf species on which they were found was recorded.

Leaf preferences

Late-instar larvae of *Anisocentropus kirramus*, *Lectrides varians* and *Triplectides gonetalus* were collected from litter packs in riffles and pools in Camp Creek and taken to the laboratory. *Anisocentropus kirramus* and *L. varians* not only feed on leaf litter, but also use leaves to construct their portable protective cases. *Triplectides gonetalus* uses hollowed-out sticks for its case. Similar-sized individuals of each species were selected. Mean body mass of late instars of these shredders is typically 1.50 mg for *A. kirramus*, 0.85 mg for *L. varians* and 2.2 mg for *T. gonetalus* (Boyero & Pearson 2006).

Prior to each experiment, larvae were kept in plastic containers (25 × 11 cm) filled with stream water and were maintained on a diet of mixed leaves (collected from the stream) that did not include any of the leaf species that were being tested. Water was filtered at 63 μm. Temperature was maintained at 20 °C and a 12:12 h light-dark photoperiod was used to mimic natural conditions.

The choice of leaf species for the experiments was based on the findings of the field study. Mature green leaves were collected from a single plant of each species in the vicinity of the stream to eliminate intraspecific variation. Although senescent leaves are commonly used in experiments of litter colonization, green leaves are

rapidly decomposed in streams (Maloney & Lamberti 1995) and have been shown to be important food sources for shredders due to their high nitrogen content, relatively soft tissue, and high availability in the streambed at certain times of the year (Kochi & Kagaya 2005, Kochi & Yanai 2006). Green leaves are sometimes colonized by shredders similarly to senescent leaves (Kochi & Yanai 2006), or even preferred over senescent leaves (Stout *et al.* 1985, Yeates & Barmuta 1999). Green leaves are a common component of the litter in Camp Creek, clearly predominant after storms and floods, and previous studies have shown that green leaves are rapidly processed by *A. kirramus* (Nolen & Pearson 1993). Thus, the use of green leaves in this experiment reflected stream conditions for at least part of the seasonal cycle.

Preference experiments were conducted in plastic pots containing 0.2 L of dechlorinated tap water and 0.2 L of water from Camp Creek. Discs of uniform venation and a diameter of approximately 20 mm were cut from leaves, oven-dried at 50 °C for 48 h and weighed to the nearest mg. One disc per leaf species was added to each container, arranged in random order, weighted down with a clean coarse sand grain and allowed to condition for 2 d before the experiment started. This short conditioning time probably only allowed leaching of soluble compounds to occur, but it allowed us to determine the response of a shredder to different leaf species without the confounding effects of colonization by microbes of differing shredder palatability (Suberkropp *et al.* 1983). The effect of conditioning was examined separately (Experiment IV, below).

After 2 d, a single shredder was introduced into each container. Treatments were replicated 4–5 times for each of the three shredder species. Containers with leaf discs but no shredders served as controls and provided estimates of weight loss resulting from leaching and microbial processing. Larvae that had died or pupated were replaced. In order to take into account weight loss due to the cutting of case pieces, the size of the cuttings was measured and their weights estimated from a linear regression of disc weight against area. Experiments were terminated after 10 d and all leaf discs were dried at 50 °C for 48 h and weighed to determine the final weight.

Weight loss due to leaching and microbial processing was determined by calculating the average difference between initial and final dry weights of control discs. Weight loss of experimental leaf discs was determined from the difference between initial and final dry weights, which was corrected by subtracting average weight loss in controls. The analysis was based on the proportion of weight loss that each leaf disc contributed to the overall weight loss (= weight loss per leaf disc divided by overall weight loss per container). This allowed the

determination of the most readily processed leaf species (highest proportion of weight loss) and made it possible to compare directly the preferences of the different shredder species.

Experiments I–III: effect of leaf species on preferences

Three separate experiments were carried out using a range of leaf species. Each experiment was conducted over 10 d. In Experiment I each container was provided with one shredder and leaf discs from nine leaf species: *Apodytes brachystylis*, *Cnesmocarpon dasyantha*, *Cryptocarya corrugata*, *Cryptocarya densiflora*, *Cryptocarya leucophylla*, *Endiandra bessaphila*, *Freycinetia excelsa*, *Macaranga subdentata* and *Sloanea* sp. Treatments and controls were replicated four times.

For Experiment II, each treatment involved one shredder and leaf discs from seven different leaf species: *Acmena smithii*, *Apodytes brachystylis*, *Blechnum* sp., *Cardwellia sublimis*, *Dysoxylum oppositifolium* and *Ripogonum album*. Because the results from Experiment I contradicted findings from previous studies (Nolen & Pearson 1993, Pearson & Connolly 2000), which suggested that *Apodytes brachystylis* was one of the most palatable leaf species, we included this leaf species in the second experiment to verify earlier findings. Treatments and controls were replicated five times.

Experiment III used the most preferred leaf species, indicated by Experiments I and II, to determine if the presence of only the most preferred species had a significant effect on selectivity and, thus, leaf processing rates. The leaf species used for this experiment were: *Acmena smithii*, *Cardwellia sublimis*, *Cryptocarya leucophylla*, *Endiandra bessaphila* and *Ripogonum album*. Treatments and controls were replicated five times.

Experiment IV: effect of leaf species and conditioning time on preferences

The effect of leaf conditioning on shredder preferences was tested using leaf discs of *Apodytes brachystylis*, *Cryptocarya leucophylla* and *Endiandra bessaphila* that were either green (no drying or conditioning) or dried and conditioned in stream water for 2, 14 or 21 d. There were thus 12 combinations of leaf species and conditioning stages (i.e. 3 leaf species × 4 conditions), which were tested with each one of the three shredder species. The 12 discs were arranged randomly in each container and a single shredder was introduced. Treatments and controls were replicated five times. The experiment was terminated after 10 d.

Statistical analysis

The variable analysed was the relative weight loss for each leaf species. Experiments I–III were analysed using a two-way ANOVA, with leaf species and shredder species as fixed factors. Experiment IV was analysed using a three-way ANOVA, with shredder species, leaf species and conditioning time as factors. In order to meet the assumptions of the statistical tests, all data, expressed as proportion that each leaf contributed to the overall processing rates, were transformed using an arcsine square-root transformation (Zar 1984), after which the assumptions were met.

RESULTS

Field study

From two seasonal samples from the 50-m study reach of Camp Creek, 2777 leaves were collected from 42 sample units. This total comprised 36 plant families, 50 genera and 81 species (Appendix 1). This count must be considered conservative as all specimens that could not be identified to (at least) family level were grouped together as unidentifiable species and were not included in this count. The distribution of leaves among taxa was skewed with >47% of all leaves comprising only five species: in decreasing abundance they were *Elaeocarpus arnhemicus* (Elaeocarpaceae), *Cryptocarya corrugata* (Lauraceae), *Syzygium endophloium* (Myrtaceae), *Flindersia pimenteliana* (Burseraceae) and *Cardwellia sublimis* (Proteaceae). Only 22 taxa contributed to greater than 1% each of the total number of leaves.

Preference Experiments I–III

Shredders showed clear leaf preferences, with breakdown rates for the most preferred leaf species significantly higher than those of all other species (Table 1, Figure 1). There were no significant differences among the processing rates of individual shredder species, so Figure 2 represents the combined results for the three species (including the combined error) used in examining processing of leaf combinations (Figure 2).

When two highly preferred species were present, as was the case in Experiment III (i.e. *Cardwellia sublimis* and *Endiandra bessaphila*), differences in breakdown rates from the most preferred to the second-most preferred species became non-significant, while differences between the two most preferred leaf species and all other species remained significant (Figure 1). The effect of leaf species was highly significant for all preference experiments, and leaf preferences were similar for all three shredder species,
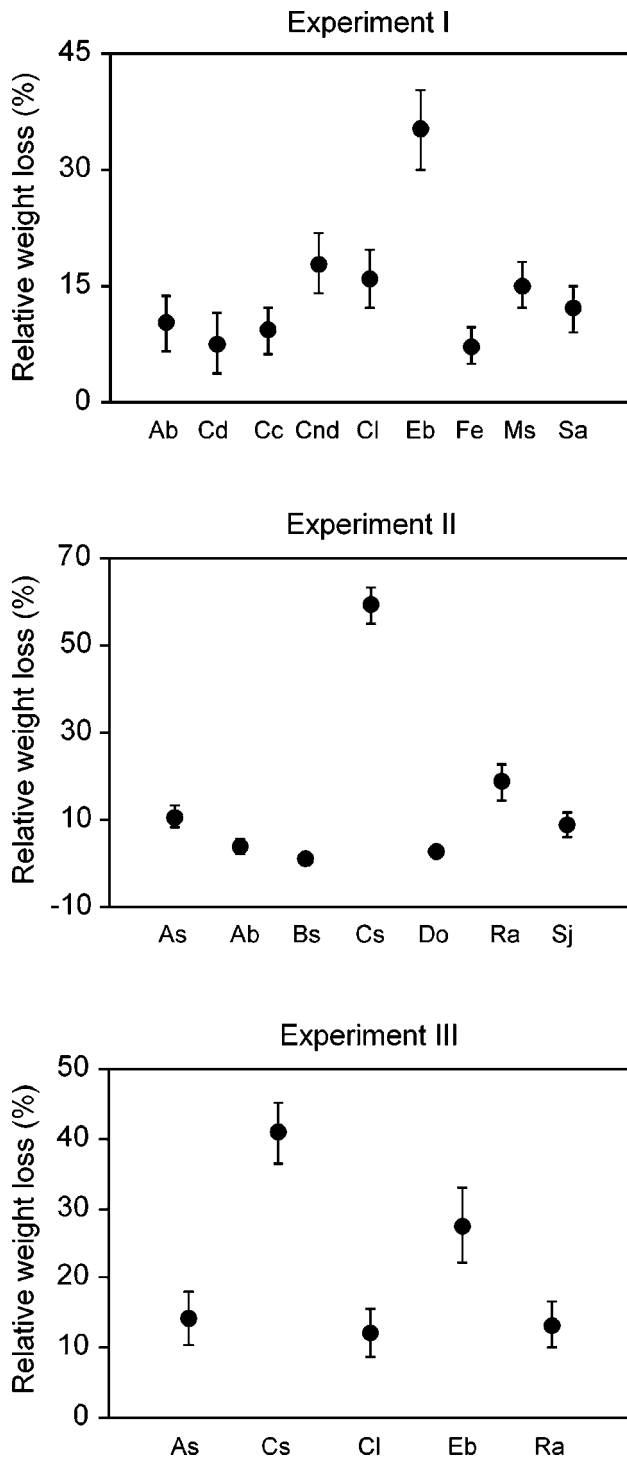
Experiment I

Experiment II

Experiment III

Figure 1. Shredder leaf preferences indicated by relative weight loss (±SE) for each leaf species, in different combinations, in Experiments I, II and III. Leaf species: Ab, *Apodytes brachystylis*; As, *Acmena smithii*; Bs, *Blechnum* sp; Cc, *Cryptocarya corrugata*; Cd, *Cryptocarya densiflora*; Cl, *Cryptocarya leucophylla*; Cnd, *Cnesmocarpon dasyantha*; Cs, *Cardwellia sublimis*; Do, *Dysoxylum oppositifolium*; Eb, *Endiandra bessaphila*; Fe, *Freycinetia excelsa*; Ms, *Macaranga subdentata*; Ra, *Ripogonum album*; Sa, *Sloanea* sp.; Sj, *Syzygium johnsonii*.

Table 1. Summary of two-way ANOVAs analysing the effect of shredder species identity, leaf species identity and the interaction between them, on leaf weight loss in Experiments I, II and III (showing degrees of freedom, F-statistic and P-values).

	Factor	df	F	P
Experiment I	Shredder sp.	2	0.68	0.512
	Leaf sp.	8	6.03	<0.001
	Shredder sp. × Leaf sp.	16	1.39	0.170
	Error	81		
Experiment II	Shredder sp.	2	0.19	0.831
	Leaf sp.	6	50.5	<0.001
	Shredder sp. × Leaf sp.	12	0.50	0.908
	Error	84		
Experiment III	Shredder sp.	2	0.14	0.866
	Leaf sp.	4	9.36	<0.001
	Shredder sp. × Leaf sp.	8	1.47	0.187
	Error	60		

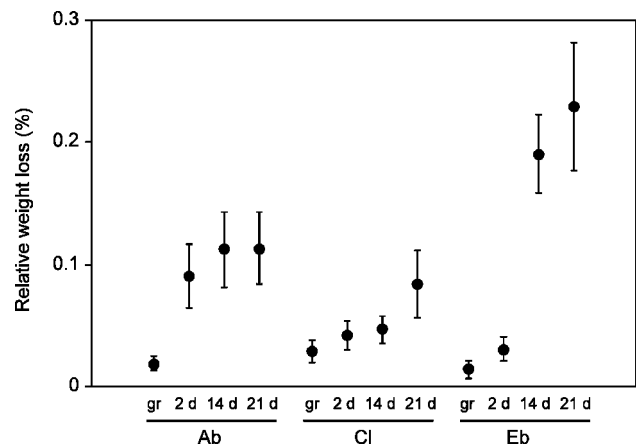**Figure 2.** Effect of leaf conditioning on shredding, indicated by relative weight loss (±SE) for the three preferred leaf species over time. Leaf species: Ab, *Apodytes brachystylis*; Cl, *Cryptocarya leucophylla*; Eb, *Endiandra bessaphila*. Conditioning: gr = green (not conditioned); 2 d, 14 d and 21 d of conditioning.

with no significant interaction effects between leaf and shredder species (Table 1).

Preference Experiment IV

Shredders exhibited clear preferences for older leaves (14–21 d of conditioning) of *Endiandra bessaphila* (Figure 2, Table 2), with less distinct but similar trends for the other two species. Preferences for leaves that had been conditioned for 14 or 21 d were not significantly different ($P = 0.095$). Unconditioned (green) leaves and leaves conditioned for 2 d were significantly different from leaves conditioned for 14 or 21 d but not from each other ($P = 0.087$).

Table 2. Summary of three-way ANOVAs analysing the effect of leaf species identity, shredder species identity, degree of leaf conditioning and interactions among them, on leaf weight loss in Experiment IV (showing degrees of freedom, F-statistic and P-values).

	df	F	P
Leaf sp.	2	3.84	0.024
Shredder sp.	2	0.91	0.404
Conditioning	3	18.0	<0.001
Leaf sp. × Shredder sp.	4	0.56	0.690
Leaf sp. × Conditioning	6	4.16	0.001
Shredder sp. × Conditioning	6	0.47	0.828
Leaf sp. × Shredder sp. × Conditioning	12	0.50	0.912
Error	144		

Endiandra bessaphila (conditioned for 14 and 21 d) was always most preferred, followed by *Apodytes brachystlis* (conditioned for 14 and 21 d). Breakdown rates for *Cryptocarya leucophylla* remained relatively low throughout the experiment, independent of conditioning stage. The leaf species, the level of conditioning, and the interaction between these factors, were all significant (Table 2). Preferences for leaf species or conditioning were similar for all three shredder species (P = 0.404). Less-preferred species such as *Apodytes brachystylis* (see Experiments I–II) became much more palatable after 14–21 d of conditioning (Figure 2), after which the processing rates for this leaf species were no longer significantly different from breakdown rates of *Endiandra bessaphila* (the most preferred species from Experiment I) with similar levels of conditioning.

General observations

Immediately following introduction into experimental containers, shredders moved between individual leaf discs until they found the most-preferred leaf species and commenced feeding. Shredders usually remained on the most-preferred leaf species until it was completely skeletonized or until the experiment was terminated. The less-preferred leaf species were largely ignored. This behaviour is evidenced by the significantly higher processing rates for the most-preferred leaf species (*Endiandra bessaphila* and *Cardwellia sublimis* in Experiments I and II respectively) compared with all remaining species. Processing rates for some of the less-preferred leaf species were very low, precluding direct comparisons among these species (e.g. in Experiment II, processing rates for *Ripogonum album* were higher than for *Acmena smithii*, while the reverse was true for Experiment III). A more reliable comparison of less-preferred species would only be possible in the absence of the most-preferred species.

In addition to having distinct feeding preferences, *Anisocentropus kirramus* and *Lectrides varians* appeared to be selective when cutting leaf discs for case construction. Both species constructed their cases from leaf species that were not preferred for feeding, possibly as a behavioural adaptation to prevent attacks from other shredders. The two species differed in their choice of leaves, with *A. kirramus* using relatively tough leaves (e.g. *Cryptocarya corrugata*, *C. leucophylla* and *Cnesmocarpon dasyantha*) and *L. varians* using much softer leaves (e.g. *Apodytes brachystylis* and *Blechnum* sp.).

DISCUSSION

The streambed litter composition of Camp Creek had high leaf diversity (81 identifiable taxa), especially when compared to streams in temperate regions – for example, Swan & Palmer (2004) list 11 species in their study of a Piedmont North American stream. Given the limited extent of the samples (spatially and temporally), this record is only a snapshot of what might be expected in this and similar streams. Variation in stream flow led to unpredictable retention and availability of litter in the stream and often to large differences in the standing crop between years (Pearson *et al.* 1989), and it is likely that differential timing of leaf-fall among species will affect litter composition through the year.

Shredders were distributed across a broad range of leaf species in the stream, with no leaf species being preferentially colonized by shredders. Given that (1) there are typically high levels of toxins and inhibitory chemicals present in most rain-forest leaf species (Covich 1988, Stout 1989), (2) most shredder species exhibit clear leaf preferences (Anderson & Sedell 1979, Mackay & Kalff 1973, Nolen & Pearson 1993), and (3) shredders are known to selectively feed on food resources of different palatability or quality (Arsuffi & Suberkropp 1985, Campbell & Fuchshuber 1995), it may have been expected that shredders would colonize a small proportion of the leaf species in Camp Creek. On the contrary, shredders actually colonized a broad range of leaf species (38 species) from several different plant families, with no apparent underlying patterns. Therefore, specific leaves may not be the primary level of patch structure capable of being detected by shredders. Arsuffi & Suberkropp (1985) demonstrated that processing rates of macro-invertebrates were affected primarily by fungal species and by degree of colonization. Leaves that were colonised by shredders in Camp Creek may have been selected on the basis of the degree of microbial colonisation, not on the identity of the leaf species themselves. Microbial colonisation and conditioning of leaves is likely to be of much greater importance in tropical systems, where higher temperatures promote greater microbial activity (Covich 1988).

However, the laboratory feeding experiments showed that shredders are able to select leaf species, at least for dried green leaves, agreeing with findings from streams in the temperate zone (Anderson & Sedell 1979, Benfield & Webster 1985, Mackay & Kalff 1973, Petersen & Cummins 1974) and in the tropics (Dobson *et al.* 2003, Nolen & Pearson 1993), which showed that leaf species is an important factor in determining leaf processing rates. Because the conditioning time was very low for Experiments I–III (2 d), the observed preferences are likely to result from characteristics of the different leaf species (i.e. nutrient levels, toxins, leaf toughness), rather than different levels of colonization by microbes.

Shredders can clearly differentiate between leaf species and feed selectively on more palatable leaves (independent of microbial colonization, given the short conditioning period), as indicated by the movement of shredders among leaf discs, until they found the preferred species, and by their remaining on that species until it was consumed or until the end of the experiment. Similar observations have been made by Arsuffi & Suberkropp (1984, 1985), Campbell & Fuchshuber (1995), and Nolen & Pearson (1993). Leaf preferences were similar for all shredder species, suggesting that preferences for different leaf species do not provide a mechanism for resource partitioning among the shredders. Shredders can also select non-palatable leaves for case building (e.g. *A. kirramus* selected tough leaves). The use of non-preferred leaves for case construction has been observed previously (Mackay & Kalff 1973), but no detailed studies exist about this aspect of leaf utilization. Nolen & Pearson (1993) and Pearson & Tobin (1989) suggested that the ability to cut case pieces, irrespective of leaf palatability, would enhance the breakdown of less-preferred leaf species.

When offered a choice between different combinations of leaf species and conditioning stage, all shredders actively sought leaves at advanced stages of conditioning, largely avoiding less conditioned or unconditioned leaves. This widely reported behaviour (Arsuffi & Suberkropp 1984, 1985; Mackay & Kalff 1973, Petersen & Cummins 1974) is most likely to result from increased microbial biomass and fungal degradative enzymes and, thus, increased leaf palatability (Suberkropp 1998). *Endiandra bessaphila*, which was the most-preferred leaf species in Experiment I, also tended to be the most processed leaf species after 1 and 14 d of conditioning. The previously non-preferred leaf species *A. brachystylis* became much more palatable after conditioning in stream water. The markedly increased processing rates for conditioned *A. brachystylis* leaves also explains the seemingly contradictory results of Experiments I–II (where *A. brachystylis* was non-preferred) and findings by Nolen & Pearson (1993) and Pearson & Connolly (2000) that *A. brachystylis* was one of the most palatable

species. If conditioned for appropriate periods of time (e.g. 6 wk for Nolen & Pearson 1993), presumably microbial colonization of the leaves is sufficient to facilitate rapid processing by macro-invertebrates. These results underline the likely significance of microbial colonization as a precursor to invertebrate shredding of less-preferred leaf species (Covich 1988). Stout (1989) suggested that this process may be of particular importance in tropical streams, which may contain micro-organisms adapted to the relatively high levels of toxins and inhibitory chemicals of the vegetation. Pearson & Connolly (2000) showed that enhanced microbial quality had direct positive impact on community abundance and on the nutritional state of *Anisocentropus kirramus.*

Breakdown rates for *C. leucophylla* were relatively low independent of conditioning stage. Differences between leaf discs conditioned for 14–21 d and those conditioned for 2 d or left unconditioned were not as pronounced as for the other leaf species. This result may be because *C. leucophylla* is a tough leaf, characterized by a persistent layer of dense hair. While *E. bessaphila* and *A. brachystylis* became increasingly soft with increasing conditioning time, *C. leucophylla* remained tough throughout the feeding experiments and may have deterred shredders from feeding.

In this study green leaves remained largely unprocessed, contrary to previous findings for streams in the same catchment as Camp Creek (Nolen & Pearson 1993) and elsewhere (Kochi & Kagaya 2005, Kochi & Yanai 2006, Maloney & Lamberti 1995, Stout *et al.* 1985, Yeates & Barmuta 1999). Boulton & Boon (1991) suggested that processing rates between oven-dried and green leaves may be significantly different due to the fact that the process of drying alters the leaf membrane and cuticle, rendering the leaves more susceptible to attack by microbes and invertebrates and enhancing the loss of soluble compounds. The higher concentrations of chemicals in some green leaves may prevent or retard microbial colonization (Arsuffi & Suberkropp 1998) but, on the other hand, green leaves may be more nutritious. Clearly there are several factors that affect processing of green leaves, yet to be elucidated for Camp Creek leaves.

This study has demonstrated the high diversity of leaf litter in a tropical stream, and that shredders colonized a substantial proportion of those leaf species, indicating their ability to feed on a broad suite of leaves. This ability is an advantage in tropical streams, where the variability of litterfall and the occurrence of wind and flow disturbances leads to unpredictable and patchy distribution of resources. The role that microbes play in these systems is likely to be of great significance, as was indicated by the results of the feeding experiment using different combinations of leaf species and levels of conditioning. Although shredders exhibit distinct

preferences for some leaves (in the absence of significant levels of microbial colonization), most likely as a result of internal physical and chemical characteristics of the different leaf species, these differences become less important with increasing conditioning of the leaves. It will be of great interest to determine the role of microbial colonization and activity on the processing of leaf litter in tropical streams.

ACKNOWLEDGEMENTS

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Appendix. Leaf litter in Camp Creek: taxonomic composition, life form of each taxon (t = tree, c = climber, f = fern, e = non-fern epiphyte), number of leaves per taxon (total and per season), relative contribution (%) of each taxon to the overall number of leaves and presence (+) of shredders associated with each taxon.

Family and species	Life form	Total count	Dry season	Wet season	%	Shredders
Apocynaceae	t	3	0	3	0.11	
Alstonia sp.						
Aquifoliaceae	t	47	25	22	1.69	+
Sphenostemon lobosporus (Muell.) L.S.Sm.						
Araliaceae	t	20	0	20	0.72	
Polyscias australiana (Muell.) Philipson						
Polyscias murrayi (Moore & Muell) Harms	t	7	3	4	0.25	+
Arecaceae	c	1	0	1	0.04	
Calamus spp.						
Balanopaceae	t	18	9	9	0.65	
Balanops australiana Muell.						
Blechnaceae	f	2	1	1	0.07	
Blechnum spp.						
Burseraceae	t	12	4	8	0.43	+
Canarium australianum Muell.						
Celastraceae	t	8	0	8	0.29	
Perrottetia arborescens (Muell.) Loes						
Elaeocarpaceae	t	20	8	12	0.72	+
Elaeocarpus angustifolius Blume						
Elaeocarpus arnhemicus Muell.	t	603	18	585	21.71	+
Elaeocarpus elliffiii Hyland & Coode	t	63	53	10	2.27	+
Elaeocarpus largiflorens White	t	41	3	38	1.48	+
Elaeocarpus ruminatus Muell.	t	18	14	4	0.65	+
Sloanea spp.	t	50	21	29	1.80	+
Euphorbiaceae	t	6	4	2	0.22	+
Drypetes acuminata Forst.						
Macaranga subdentata Benth.	t	53	14	39	1.91	+
Filicophyta	f	1	1	0	0.04	
Unidentified fern						
Grossulariaceae	t	80	2	78	2.88	+
Abrophyllum ornans (Muell.) Hook ex Benth.						
Icacinaceae	t	6	1	5	0.22	
Apodytes brachystylis Muell.						
Citronella smythii (F.Muell.) Howard	t	3	0	3	0.11	+
Lauraceae	t	4	4	0	0.14	+
Beilschmiedia collina Hyland						
Cinnamomum laubatii Muell.	t	23	14	9	0.83	
Cryptocarya corrugata White & Francis	t	321	102	219	11.56	+
Cryptocarya densiflora Blume	t	36	12	24	1.30	
Cryptocarya grandis Hyland	t	15	8	7	0.54	+
Cryptocarya hypospodia Muell.	t	5	1	4	0.18	
Cryptocarya leucophylla Hyland	t	23	6	17	0.83	+
Cryptocarya mackinnoniana Muell.	t	22	2	20	0.79	+
Endiandra bessaphila Hyland	t	78	37	41	2.81	+
Endiandra muelleri Meisn.	t	97	47	50	3.49	+
Endiandra wolfei Hyland	t	13	0	13	0.47	
Lauraceae sp.1		6	0	6	0.22	+
Litsea bindoniana Muell.	t	19	4	15	0.68	+
Litsea connorsii Hyland	t	28	9	19	1.01	+
Litsea leefeana (F.Muell.) Merr.	t	6	1	5	0.22	
Loganiaceae	t	10	2	8	0.36	+
Fagraea sp.						
Loranthaceae	e	7	2	5	0.25	
Amyema queenslandicum (Blakely) Danser						
Marattiaceae	f	2	2	0	0.07	
Marattia oreades Domin						
Meliaceae	t	10	3	7	0.36	
Synoum glandulosum ssp. *paniculosum* (Muell.) Mabb.						
Menispermaceae	c	11	5	6	0.40	
Hypserpa decumbens (Benth.) Diels						

Appendix. Continued.

Family and species	Life form	Total count	Dry season	Wet season	%	Shredders
Monimiaceae	t	24	9	15	0.86	+
Levieria acuminata (Muell.) Perkins						
Moraceae	t	2	2	0	0.07	
Ficus destruens F.Muell. ex White						
Ficus sp.	t	6	0	6	0.22	
Myrtaceae	t	1	0	1	0.04	
Syzygium canicortex Hyland						
Syzygium endophloium Hyland	t	141	21	120	5.08	+
Syzygium johnsonii (Muell.) Hyland	t	31	17	14	1.12	+
Syzygium oleosum (Muell.) B.Hyland	t	2	0	2	0.07	
Syzygium sp.1	t	9	2	7	0.32	+
Syzygium sp. 2	t	7	5	2	0.25	
Syzygium spp.	t	14	12	2	0.50	
Syzygium wesa Hyland	t	5	0	5	0.18	
Ochnaceae						
Brackenridgea nitida ssp. *australiana* (F.Muell.) Kanis	t	21	6	15	0.76	
Pandanaceae	c	35	11	24	1.26	+
Freycinetia excelsa Muell.						
Freycinetia scandens Gaudich.	c	15	3	12	0.54	
Pittosporaceae	s	1	0	1	0.04	
Pittosporum rubiginosum Cunn.						
Podocarpaceae	t	1	1	0	0.04	
Sundacarpus amarus (Blume) Page						
Polypodiaceae	f	1	0	1	0.04	
Platycerium bifurcatum (Cav.) Chr.						
Proteaceae	t	115	29	86	4.14	+
Cardwellia sublimis Muell.						
Darlingia darlingiana (Muell.) Johnson	t	2	0	2	0.07	
Gevuina bleasdalei (Muell.) Sleumer	t	26	9	17	0.94	+
Helicia lamingtoniana (F.M.Bailey) White ex L.S.Sm.	t	1	0	1	0.04	
Rhamnaceae	t	96	70	26	3.46	+
Alphitonia petriei Braid & White						
Rubiaceae	t	24	2	22	0.86	
Timonius singularis (Muell.) L.S.Sm.						
Rutaceae	t	3	2	1	0.11	+
Acronychia vestita Muell.						
Flindersia pimenteliana Muell.	t	136	16	120	4.90	+
Melicope sp.	t	2	1	1	0.07	
Sapindaceae	t	35	12	23	1.26	+
Cnesmocarpon dasyantha (Radlk.) Adema						
Sacropteryx sp.	t	1	0	1	0.04	
Sapindaceae sp. 1	t	18	8	10	0.65	+
Sapindaceae sp. 2	t	3	3	0	0.11	
Sapindaceae sp. 3	t	4	2	2	0.14	
Synima cordierorum (Muell.) Radlk.	t	1	0	1	0.04	
Synima sp.	t	9	2	7	0.32	
Sapotaceae	t	9	3	6	0.32	
Pouteria sp. 1						
Pouteria sp. 2	t	29	22	7	1.04	
Smilaceae	c	9	5	4	0.32	+
Smilaceae sp.						
Symplocaceae	t	26	6	20	0.94	
Symplocos cochinchinensis (Lour.) Moore						
Vitaceae	c	4	1	3	0.14	
Cissus hypoglauca Gray						
Xanthophyllaceae	t	69	12	57	2.48	+
Xanthophyllum octandrum (Muell.) Domin						
Unidentified sp. 1		2	0	2	0.07	
Other unidentifiable leaves		39	20	19	1.40	
Total		2777				