Resource quality and stoichiometric constraints on stream ecosystem functioning

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SUMMARY

1. Resource quality and stoichiometric imbalances in carbon : nutrient ratios between consumers and resources can influence key ecosystem processes. In many streams, this has important implications for food webs that are based largely upon the utilization of terrestrial leaf-litter, which varies widely among litter types in its value as a food source for detritivores and as a substrate for microbial decomposers.

2. We measured breakdown rates and macroinvertebrate colonization of leaf-litter from a range of native and exotic plants of differing resource quality and palatability to consumers [e.g. carbon : nitrogen : phosphorus (C : N : P) ratios, lignin and cellulose content], in a field experiment. We also measured C : N : P ratios of the principal leaf-shredding invertebrates, which revealed strong stoichiometric imbalances across trophic levels: C : N and C : P ratios typically differed by at least one order of magnitude between consumers and resources, whereas N : P imbalances were less marked. Application of the threshold elemental ratio approach, which integrates animal bioenergetics and body elemental composition in examining nutrient deficiency between consumers and resources, revealed less marked C : P imbalances than those based on the simpler arithmetic differences described above.

3. Litter breakdown rates declined as nutrient imbalances widened and resource quality fell, but they were independent of whether resources were exotic or native. The principal drivers of total, microbial and invertebrate-mediated breakdown rates were lignin : N, lignin : P and fungal biomass, respectively. However, multiple regression using orthogonal predictors yielded even more efficient models of litter breakdown, as consumers responded to more than one aspect of resource quality. For example, fungal biomass and litter C : N both influenced invertebrate-mediated breakdown.

4. Large stoichiometric imbalances and changes in resource quality are likely to have serious consequences for stream ecosystem functioning, especially when riparian zones have been invaded by exotic plant species whose chemical composition differs markedly from that of the native flora. Consequently, the magnitude and direction of change in breakdown rates and, thus, resource depletion, will be driven to a large extent by the

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biochemical traits (rather than taxonomic identity *per se*) of the resident and invading flora.

Introduction

The study of elemental constraints upon consumer–resource dynamics has recently become an important focus of research in fresh waters, reflecting the increasing prominence of ecological stoichiometry as a scientific discipline (e.g. Elser *et al.*, 2000; Frost *et al.*, 2003; Cross *et al.*, 2005). Essentially, stoichiometric differences between resources and consumers can provide important insights into how the quality [most commonly assessed as carbon : nitrogen : phosphorus (C : N : P) ratios] of food and the requirements of consumers affect ecological processes (Cross *et al.*, 2005; Frost *et al.*, 2006). Basal resources in food webs vary widely in their elemental composition and resource quality (Cross *et al.*, 2005), whereas consumers often operate within more tightly-constrained limits (Sterner & Elser, 2002). Consequently, imbalances can occur when the elemental composition of the food resource does not meet the elemental requirements of the consumer (Sterner & Hessen, 1994; Sterner, 1997). This has repercussions for consumer growth, reproduction and C assimilation efficiencies, which in turn influence ecosystem processes, such as decomposition and nutrient release rates (Sterner & Elser, 2002; Cross *et al.*, 2005; Woodward, 2008).

To date, most of this research has focused on autotrophic pelagic ecosystems, whereas studies in detrital-based systems in general, and particularly in running waters, are still relatively scarce (but see Cross *et al.*, 2005; Evans-White, Stelzer & Lamberti, 2005). In many terrestrial and benthic aquatic ecosystems the majority of vascular plant material is not consumed directly by herbivores but enters the food web as dead organic matter (Cebrian, 1999) and, as such, the detrital processing represents an important, but often underestimated, component of ecosystem functioning (Moore *et al.*, 2004). Terrestrial leaf-litter is the dominant energy input to many stream communities (Wallace *et al.*, 1999; Woodward & Hildrew, 2002), where a suite of invertebrate detritivores and microbial decomposers process this allochthonous organic matter (Hieber & Gessner, 2002) and act as critical conduits for its incorporation into the higher trophic levels (Moore *et al.*, 2004; Woodward, 2008). In stream food webs based on terrestrial leaf-litter, the dominant microbial decomposers, aquatic hyphomycete fungi, play a dual role: in addition to directly degrading litter they also enhance its palatability to macroinvertebrate shredders, thereby facilitating decomposition indirectly (Suberkropp, 1992; Graça, 2001).

Although leaf-litter breakdown is clearly a key ecosystem process in streams (Webster & Benfield, 1986; Gessner, Chauvet & Dobson, 1999), relatively few studies have explicitly evaluated, simultaneously, how breakdown rates are influenced by different aspects of resource quality, as defined by chemical and structural attributes (e.g. lignin content, toughness), ratios of essential elements (e.g. C : N, C : P, N : P), or some combination of these measures (e.g. lignin : N) (e.g. Melillo, Aber & Muratore, 1982; Gessner & Chauvet, 1994; Quinn, Burrell & Parkyn, 2000; Royer & Minshall, 2001). The quality of leaf-litter as food for aquatic consumers differs considerably among plant species (Enriquez, Duarte & Sand-Jensen, 1993; Gessner & Chauvet, 1994; Tibbets & Molles, 2005) and will be determined by the composition of the riparian vegetation (Cummins *et al.*, 1989), which is itself influenced by a range of natural and anthropogenic factors, including forest succession (Benfield *et al.*, 2001), invasions of exotic species (Lecerf *et al.*, 2007a) and species replacement (e.g. forestry plantations: Graça *et al.*, 2002). Many riparian zones throughout the world now contain planted and/or non-native species and although not all non-native species become invasive, some do become naturalized and can have strong ecosystem impacts (Vitousek *et al.*, 1997; Mack *et al.*, 2000; Chapin, 2003) via the alteration of litter inputs (e.g. Graça *et al.*, 2002; Molinero & Pozo, 2006). By extension, this could have drastic consequences for the higher trophic levels that feed upon detritivores and microbial decomposers,

especially as many of these species are largely dependent upon detrital pathways for their own secondary production (Moore *et al.*, 2004; Woodward, Speirs & Hildrew, 2005b; Woodward *et al.*, 2005a).

We carried out a field experiment to determine how leaf-litter breakdown rates for a range of native and exotic riparian tree species were related to different aspects of resource quality (e.g. C : N : P and lignin content), how decomposers and detritivores responded to these differences, and to assess the potential implications of stoichiometric detritivore-detritus imbalances for stream ecosystem functioning.

Methods

Two field experiments were carried out: a pilot study (winter 2002) and the main study (winter 2003). Both were conducted at the same time of year and in the same wooded stream in SE Ireland (51°57′N, 8°06′W; 75 m a.s.l.). Mean bankfull width and mean stream depth were 5.3 and 0.2 m, respectively. The bed substrate was stony and the riparian zone was characterized by species typical of the region, including alder (*Alnus glutinosa* (L.) Gaertn.), hazel (*Corylus avellana* L.), ash (*Fraxinus excelsior* L.), oak (*Quercus robur* L.) and holly (*Ilex aquifolium* L.). Conductivity (190 μS cms^{-1}) and pH (7.29) of stream water were measured in the field and filtered water samples (Whatman GF/F, 0.7 μm average pore size, Whatman International Ltd., Maidstone, England) were analysed in the laboratory using a Lachat FIA (Lachat Instruments, Loveland, CO, U.S.A.) for ammonium (30 μg L^{-1} NH$_4$–N), nitrate (4570 μg L^{-1}NO$_3$–N), nitrite (2 μg L^{-1}NO$_2$–N) and soluble reactive phosphorus (18 μg L^{-1}PO$_4$–P). Alkalinity (77 mg CaCO$_3$ L^{-1}) was determined by titration. Mean stream temperature during the main study was 8.1 °C; this was measured every 30 min throughout the experiment using submersible data loggers.

The 2002 pilot study was used to measure the trajectory and rate of breakdown of a common native leaf type (alder) in the stream: these data were then used to assess the duration and level of replication required in the main study. Five grams of freshly-abscised air-dried leaf-litter was placed in coarse-mesh bags (10 mm mesh aperture), which were subsequently sampled after 7, 11, 14, 24 and 45 days of exposure in the stream. Four replicates were used on each date, except after 14 days when six replicates were used, as in the main study the following year.

For the main study, leaves were collected immediately after abscission from 15 different woody plant types (13 true species, plus two cultivars of sycamore [*Acer pseudoplatanus* L.]), including both native (6) and exotic (9) types that spanned a wide range of litter qualities, as defined by a suite of metrics (Table 1). After collection, leaves were air-dried to constant mass and 5 g (±0.25 g) of leaf-litter was added to experimental bags of two mesh aperture sizes (0.5 and 10 mm) to determine microbial and total breakdown rates, respectively. In addition, invertebrate-mediated breakdown (a proxy measure of detritivore feeding and, possibly, physical abrasion and fragmentation) was estimated by calculating the percent difference in mass loss between coarse-mesh and fine-mesh bags.

Six replicates of each treatment (i.e. 15 leaf types × 2 mesh sizes) were anchored to the streambed with metal bars, giving a total of 180 litter bags. The experiment was stopped after 14 days to ensure that sufficient leaf-litter of the fastest decomposing species (*Buddleja davidii* Franch.), and hence all the other leaf types, could be retrieved for weighing. Therefore, this study is focussed primarily on the initial stage of leaf-litter breakdown occurring in the stream and is not an attempt to measure the entire breakdown process for all 15 leaf types. However, as revealed by the pilot study, the exposure time used in the main experiment provided an indication of realistic process rates in a natural system.

At the end of the trial, bags were collected and immediately returned to the laboratory, where three 12-mm diameter discs were cut from leaves randomly taken from each fine-mesh bag. These discs were frozen for fungal biomass determination. Discs were not sampled from coarse-mesh bags because insufficient material was available for the most rapidly-decomposing leaf types at the end of the trial. The remaining leaf bags were immediately frozen at −20 °C. After thawing, leaf material was separated from invertebrates (using a 500 μm sieve), which were identified to the highest level of taxonomic resolution possible (usually species), assigned to functional feeding groups (see compilation in Gessner & Dobson, 1993), counted, and preserved in 70% ethanol. The sorted leaf material was oven-dried at 105 °C to constant mass and then weighed. Breakdown rates were expressed as log$_{10}$ % dry mass (DM) loss per day. In addition, exponential decay coefficients (*k*) were calculated (after Petersen & Cummins, 1974) to

Table 1 Resource quality, shredder abundance (±1 SE), fungal biomass (±1 SE) and total breakdown rate ($-k_{total}$ ± 1 SE) of 15 native and exotic woody riparian species and cultivars and C : N : P ratios of litter and the dominant invertebrate shredders

Scientific name	Common name (code)	C : N	C : P/ TER$_{C : P}$	N : P	Cellulose (% of litter DM)	Lignin (% of litter DM)	Shredder (no. g^{-1} litter DM)	Fungal biomass (mg g^{-1} litter DM)	$-k_{total}$ (day^{-1})
Litter type									
Alnus glutinosa (L.) Gaerth.	Alder (Al)	14.3	884.4	61.8	17.7 ± 0.5	14.0 ± 0.5	5.7 ± 1.1	34.0 ± 14.8	0.0841 ± 0.0087
Fraxinus excelsior L.	Ash (As)	41.8	273.3	6.5	27.8 ± 0.9	11.3 ± 0.3	9.7 ± 5.1	55.7 ± 23.7	0.0855 ± 0.0269
Fagus sylvatica L.	Beech (Be)* [n], 16th C.	55.3	2684.5	48.6	36.2 ± 2.1	27.9 ± 2.4	1.7 ± 0.7	21.6 ± 1.2	0.0045 ± 0.0015
Buddleja davidii Franch.	Butterfly-bush (Bu)* [n], 1957	19.2	336.8	17.6	16.8 ± 0.9	8.7 ± 0.3	16.9 ± 4	41.3 ± 2.3	0.2030 ± 0.0239
Corylus avellana L.	Hazel (Ha)	39.4	1136.7	28.9	21.2 ± 0.9	23.3 ± 1.3	2.7 ± 0.9	36.1 ± 6.7	0.0163 ± 0.0019
Ilex aquifolium L.	Holly (Ho)	112.7	1983.5	17.6	21.8 ± 0.6	12.8 ± 0.1	0.6 ± 0.3	10.2 ± 1.2	0.0101 ± 0.0037
Aesculus hippocastaneum L.	Horse Chestnut (Hc)* [n], 17th C	53.4	1749.8	32.7	29.3 ± 0.3	29.4 ± 0.5	2.8 ± 1.1	32.3 ± 6.4	0.0102 ± 0.0020
Hedera helix L.	Ivy (Iv)	26.6	504.2	19.0	18.5 ± 0.8	13.5 ± 0.6	0.8 ± 0.3	10.7 ± 2.7	0.0238 ± 0.0033
Prunus laurocerasus L.	Cherry Laurel (La)* [n], 1962	81.8	1738.6	21.3	29.0 ± 0.5	32.5 ± 0.8	0.6 ± 0.3	28.5 ± 8.2	0.0054 ± 0.0013
Tilia cordata x europaea L.	Lime (Li)* [p], unknown	42.5	518.5	12.5	24.2 ± 0.7	16.6 ± 0.3	1.6 ± 0.5	23.6 ± 5.6	0.0132 ± 0.0021
Quercus robur L.	Oak (Oa)	25.5	1121.8	44.0	31.1 ± 1.0	40.5 ± 0.7	1.2 ± 0.3	15.8 ± 7.3	0.0081 ± 0.0029
Acer pseudoplatanus L.	Sycamore (Sy)* [n], 17th C.	30.1	1292.1	42.9	22.0 ± 1.1	32.3 ± 1.5	3.4 ± 1.2	19.3 ± 4.4	0.0157 ± 0.0049
Acer pseudoplatanus 'Atropurpureum' Spaethii	Sycamore cultivar (c1)* [c], 20th C.	33.6	1320.5	39.3	23.8 ± 0.9	18.8 ± 0.6	1.9 ± 0.5	23.9 ± 8.6	0.0150 ± 0.0028
Acer pseudoplatanus var. corstorphinense Schwer.	Sycamore cultivar (c2)* [c], 20th C.	40.2	675.0	16.8	22.6 ± 0.5	15.7 ± 0.2	5.6 ± 2.6	32.8 ± 3.5	0.0275 ± 0.0043
Rhododendron ponticum L.	Rhododendron (Rh)* [n], 19th C.	71.8	7198.0	100.2	40.6 ± 0.8	42.3 ± 0.8	0.2 ± 0.1	19.2 ± 2.6	0.0021 ± 0.0005
Dominant shredders									
Protonemura meyeri Pictet	Stonefly nymph	7.1	338.3/ 812.0	47.1					
Gammarus duebeni Liljeborg	Freshwater shrimp	6.9	56.7/ 136.1	8.6					
Halesus radiatus Curtis	Caddis larva	6.2	525.6/ 1261.5	83.4					
Potamophylax cingulatus Stephens	Caddis larva	6.7	449.2/ 1078.2	68.8					

k-values are included here primarily to facilitate comparisons with other studies; the response variable used in statistical analyses was $\log_{10}$ % mass loss per day, which better met the assumptions of the parametric tests used (see Methods).

TER$_{C : P}$, threshold elemental ratio for dominant shredders, calculated using the multiplier of 2.4 (Frost *et al.*, 2006).

*Exotic species and first documented records in Ireland of exotic species (n, naturalized; p, planted; c, cultivar), where naturalized refers to exotics that are self-replicating components of woodland in Ireland.

facilitate comparisons with other studies, although some caution should be exercised here as only two time points were used in the current study.

The leaf discs used for ergosterol determination, as a proxy measure of fungal biomass, were freeze-dried and weighed to the nearest 0.1 mg. Lipids were then extracted with 25 mL of KOH (8 g L^{-1}) in methanol for 30 min. The extract was purified by solid-phase extraction (tC$_{18}$ Sep-Pak Vac RC cartridges; 500 mg of sorbent, Millipore-Waters Gmbh, Eschborn, Germany) and ergosterol was quantified by high performance liquid chromatography (Gessner & Schmitt, 1996). A conversion factor of 5.5 mg ergosterol per gram of fungal DM (Gessner & Chauvet, 1993) was used to calculate fungal biomass per gram of leaf-litter DM.

Resource quality was assessed using a suite of chemical measures for each leaf type. These included: (i) elemental ratios (pooled subsample from a combination of six replicates for each leaf type), determined as the initial ratios of C : P, C : N and N : P; (ii) concentrations of structural compounds, assessed as the initial percentage of lignin and cellulose and the sum of the two, lignocellulose (six replicates for each leaf type); (iii) the ratios of these two forms of structural compounds to elemental content as an integrated, composite measure (e.g. lignin : P). Stoichiometrically, C : P and C : N ratios are not exactly equivalent to lignin : P and lignin : N. The former ratios essentially reflect the potential nutrient availability in litter, but although there is always a relatively large amount of carbon in leaf-litter, the extent to which it can be used by consumers depends on the form in which it occurs (e.g. cellulose versus the more recalcitrant lignin in plant tissues). Therefore, lignin : N and lignin : P are composite measures that capture both the nutrient availability and carbon quality aspect of the litter resource. The full suite of variables is listed in the legend for Table 3. Elemental ratios were expressed as molar ratios, whereas integrated measures such as lignin : P were calculated as DM ratios. To determine nutrient concentrations, a subsample of leaf material pooled from a combination of six replicate samples was ground into a fine powder (Culatti DFH48 mill, 1 mm screen, Prolabo, Fontenay-sous-Bios, France). Carbon and nitrogen content were then determined using a Perkin Elmer Series II CHNS/O analyser (PerkinElmer Inc., Wellesley, MA, U.S.A.). Total phosphorus was quantified as phosphate in 200 mg of sample, by mixed

acid digestion (5 mL of nitric acid, 60% + 1 mL of perchloric acid, 30% + 0.5 mL of sulphuric acid, 98%) (Molinero & Pozo, 2004) at 325 °C for 15 min, and followed by spectrophotometric analysis of the digest (molybdenum blue method; Allen *et al.*, 1974). Lignin and cellulose were determined gravimetrically, using the acid-detergent fibre procedure described in Gessner (2005). Briefly, freeze-dried samples of leaf material (six replicates per leaf type) were ground to pass through a 0.5 mm screen and mixed with acid-detergent solution. Fibre was calculated as the loss of material remaining after the sample was placed in an oven for 12 h at 105 °C. Samples were then hydrolysed with 72% sulphuric acid and cellulose was determined as the loss of DM after drying for 12 h at 105 °C. Lignin was subsequently determined as the ignition loss at 550 °C for 3 h. Lignin and cellulose were expressed as percentages of leaf-litter DM.

To determine C : N : P ratios of invertebrate consumers, individuals of the dominant shredder species in the stream (Plecoptera: *Protonemura meyeri* Pictet, Amphipoda: *Gammarus duebeni* Liljeborg, Trichoptera: *Halesus radiatus* Curtis and *Potamophylax cingulatus* Stephens) were collected in the field and frozen at −20 °C within 1 h. Individual animals were gut dissected, oven-dried at 60 °C and subsequently ground to a fine powder with a mortar and pestle. To determine C : N ratios, samples were combusted in a PDZ Europa ANCA-GSL preparation model and passed through a PDZ Europa 20-20 stable isotope analyser (PDZ Europa Ltd., Sandbach, U.K.). Elemental ratios were then calculated based on the total amounts of carbon and nitrogen measured. Invertebrate P content was determined on 1–1.5 mg of sample using the same method as described for the leaf material. Elemental imbalances between consumers and resources were assessed using two commonly used methods. First, arithmetic differences were derived between animal and leaf-litter C : N : P ratios (after Sterner & Elser, 2002). This approach overestimates imbalances because invertebrate detritivores tend to conserve assimilated P more efficiently that the assimilated C, because much of the latter is respired, resulting in critical C : P threshold values that are on average more than twice as high as C : P ratios of shredder body mass (Frost *et al.*, 2006). Secondly, we used the threshold elemental ratio (TER) approach (after Sterner, 1997; Frost *et al.*, 2006). This is used to assess nutrient deficiency in

animals, with the TER being the point beyond which growth limitation switches from one element to another (Frost *et al.*, 2006). The TER approach combines animal bioenergetics with body elemental composition and thus offers a more integrated index for understanding consumer and resource elemental imbalances (Frost *et al.*, 2006). The typical TER for carbon and phosphorus ($\text{TER}_{C : P}$) has been estimated for 41 aquatic consumer taxa and was, on average, 2.4 times higher than body C : P (Frost *et al.*, 2006). We used this factor to calculate approximate $\text{TER}_{C : P}$ for our detritivorous consumers to examine imbalances between animal and leaf-litter C : P ratios.

Statistical analyses

All response variables and continuous predictors (i.e. measures of resource quality) were $\log_{10}$-transformed prior to statistical analysis, to stabilize variances and normalize the data. The response variable of leaf breakdown rates (i.e. $\log_{10}$ % mass loss day^{-1}) was analysed using a hierarchical type III mixed model ANOVA, to test for differences among leaf types (nested within exotic/native species), between exotic and native species, and between mesh sizes (coarse versus fine). Leaf species was fitted as a random factor nested within native/exotic leaf types; all other factors were fixed.

Relationships between resource quality and microbial, invertebrate-mediated, or total breakdown rate were then examined using stepwise (forward and backward selection) multiple linear regression (MLR) analysis to identify the most efficient models for describing breakdown rates. Relationships among the predictors (measures of resource quality, fungal biomass and shredder species richness and abundance) were checked for multicollinearity by regressing all predictor variables against one another and comparing variance inflation factor (VIF) values in regression models: only orthogonal variables were included in subsequent analyses. The VIF reflects the absence or presence of multicollinearity: a value greater than 10 is usually used as a cut-off and indicates strong collinearity and poorly estimated regression coefficients (Myers, 1986). The analyses described above were performed with Minitab® for Windows (version 13.32; MINITAB Inc, State College, PA, U.S.A.).

In addition to MLR, partial least-squares regression (PLS) analysis was used to determine the relative importance of the different resource quality attributes to breakdown rates. PLS extracts components from a set of variables which, as in principal components analysis, are orthogonal and so eliminates multicollinearity. In addition, PLS maximises the explained covariance between the variables. The constructed components are used to create a model for the response variable with the relative importance of the predictor variables ranked with variable importance on the projection values (Eriksson *et al.*, 1999). PLS analyses were conducted using SIMCA-P (version 11.5; Umetrics AB, Umeå, Sweden) and used the same predictor and response variables as used for MLR. Additional components were extracted until the increase in explained variance fell below 10%.

Results

Breakdown rates and resource quality

Breakdown of alder litter in the 2002 pilot study followed a rapid and exponential decay curve (Fig. 1), reflecting the high densities of shredders in the stream. Data from this more extended temporal study yielded *k*-values for this leaf type that were almost
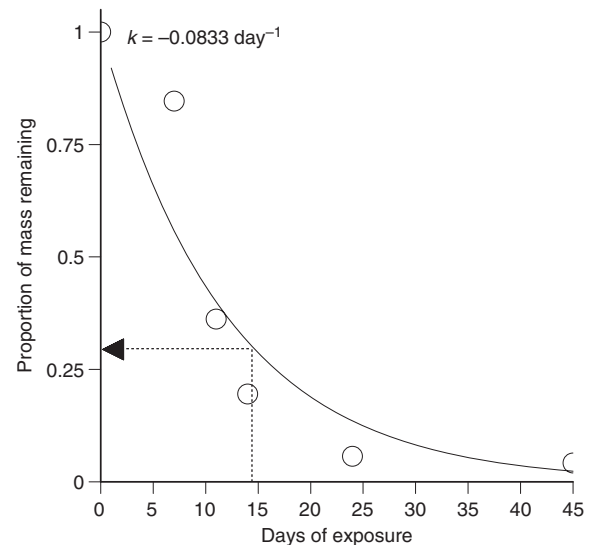

Fig. 1 Breakdown trajectory of alder litter in coarse-mesh bags over repeated sampling occasions during winter 2002. The exponential decay coefficient, $k = -0.0833$, is derived from the regression equation $y = x^{-0.0833}$. The dashed arrow highlights the predicted degree of breakdown after 14 days of exposure (i.e. the duration of the 2003 trial), and the breakdown rate observed in the main trial carried out in 2003 was almost identical (i.e. $k = 0.0841 \pm 0.0087$ SE; Table 1).

Table 2 Mixed, nested ANOVA comparing breakdown rates for 15 litter types, testing for differences among species, between exotic and native litter and between coarse and fine-mesh bags

Comparison	d.f.	F	P-value
Leaf type (native/exotic)	13	15.55	<0.001
Mesh	1	35.28	<0.001
Native/exotic	1	2.56	0.134
Mesh × native/exotic	1	3.93	0.069
Mesh × leaf type (native/exotic)	13	0.93	0.520

identical to those in the 2003 main study ($k = -0.0833$ and -0.0841, respectively). Therefore, even though we only obtained two sample points in the main study (below), we assumed exponential decay and calculated the exponent, k, to facilitate comparisons with other studies (Table 1).

In the main study, breakdown rates differed greatly among leaf types (GLM $F_{13,179} = 15.6$, $P < 0.001$), between mesh sizes (GLM $F_{1,179} = 35.3$, $P < 0.001$; coarse > fine mesh), but not between native versus exotic leaf-litter (Table 2). None of the interaction terms were statistically significant. Breakdown rates in coarse-mesh bags ranged from 0.2% to 6.6% loss per day (2.9–91.8% loss over 14 days) among the 15 leaf types, and were higher than in the fine-mesh bags, with a loss of 0.1–2.7% loss per day or 1.4–37.4% over 14 days (Fig. 2).

Resource quality differed markedly among leaf types (Table 1), and several measures were significant

predictors of breakdown rates (Table 3). The two composite measures, lignocellulose : P and lignin : N content of litter, were the best single predictors for total breakdown rates ($r^2_{adj} = 0.84$ and 0.83, respectively; Table 3). Both yielded relationships of a similar level of statistical significance and the two metrics were collinear with one another ($r = 0.86$, $P < 0.001$). The composite measure lignin : P was the best single predictor of microbial breakdown rates ($r^2_{adj} = 0.88$; Table 3). Fungal biomass and litter C : N were the two best single predictors for invertebrate-mediated breakdown rate ($r^2_{adj} = 0.61$ and 0.49, respectively; Table 3). Multiple regression models were, however, more powerful and efficient than simple linear regressions at predicting both total breakdown (lignin : N, fungal biomass and N : P; $r^2_{adj} = 0.93$; Table 3) and invertebrate-mediated breakdown rates (C : N and fungal biomass; $r^2_{adj} = 0.91$; Table 3; Fig. 3).

Although only orthogonal predictors were included in the MLR analyses, multicollinearity (e.g. VIF > 10) was evident among several measures of resource quality. C : P and lignin : P, in particular, were correlated with all other metrics except fungal biomass, shredder richness and shredder density. The PLS performed to apportion the amount of variance contributed by collinear predictors, identified 10, 9 and 3 resource quality variables as important predictors for total, microbial and invertebrate-mediated breakdown rates, respectively (Table 4). Again, metrics that included measures of P and lignin were

Table 3 Statistically significant ($P < 0.05$) equations of best-fit for SLR and for MLR analysis of breakdown rates for the 15 leaf species and cultivars

Type of breakdown and regression	Regression equation	d.f.	r^2_{adj}	F
Total				
SLR	$y = 1.32 - 1.03x_7$	1,13	0.83	69.5
SLR	$y = 2.19 - 0.79x_{12}$	1,13	0.84	76.2
MLR	$y = 1.12 + 0.36x_{13} - 0.32x_3 - 0.891x_7$	3,11	0.93	59.2
Microbial				
SLR	$y = 1.37 - 0.69x_8$	1,13	0.88	100.7
Invertebrate-mediated				
SLR	$y = -3.62 + 2.38x_{13}$	1,13	0.61	23.1
MLR	$y = -0.72 - 1.43x_1 + 1.95x_{13}$	2,12	0.91	71.7

Where multiple predictors provided better models than simple least-squares regression (SLR), only the most efficient multiple linear regression (MLR) model is shown. Predictor variables used were (C : N (x_1), C : P (x_2), N : P (x_3), % cellulose (x_4), % lignin (x_5), % lignocellulose (x_6), lignin : N (x_7), lignin : P (x_8), cellulose : N (x_9), cellulose : P (x_{10}), lignocellulose : N (x_{11}), lignocellulose : P (x_{12}), fungal biomass (mg g^{-1} litter) (x_{13}), shredder density g^{-1} litter (x_{14}) and shredder species richness (x_{15}) for the 15 leaf-types; response variable is log$_{10}$ % mass loss per day. All regressions shown were significant at $P < 0.001$.
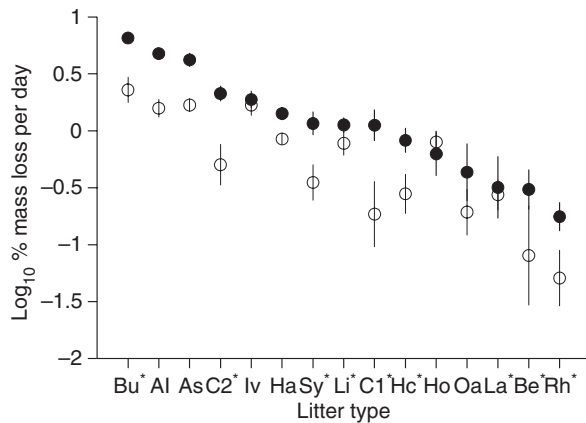
Fig. 2 Breakdown rates of the 15 leaf species and cultivars (codes correspond to those in Table 1) after 14 days of exposure in the study stream during winter 2003. Data displayed are mean values and standard errors for total (closed circles: coarse-mesh bags) and microbial-only (open circles: fine-mesh bags) breakdown rates. Leaf species are ranked left-to-right in decreasing order of total breakdown rates. '*' denotes exotic species.

important determinants of total and microbial breakdown, whereas this was not the case for breakdown mediated by invertebrates, which responded more strongly to measures of N and fungal biomass (and also shredder species richness).

Consumers

Fungal biomass differed significantly among leaf types ($F_{14,44} = 2.5$, $P = 0.018$) and was a significant predictor of invertebrate-mediated breakdown (see above). However, fungal biomass in the leaves did not correlate with any measure of resource quality. Shredder density also differed markedly among leaf types ($F_{14,75} = 6.3$, $P < 0.001$; Table 1) and reflected differences in fungal biomass and lignin : N ($\log_{10}$ shredders g^{-1} litter $= -0.69 - 0.75$ $\log_{10}$ lignin : N + 1.36 $\log_{10}$ fungal biomass g^{-1} litter; $r^2 = 0.78$, $F_{1,14} = 25.9$, $P < 0.001$). Shredder density was a significant predictor of invertebrate-mediated breakdown using SLR, but was collinear with C : N and fungal biomass, which when used together provided a more efficient model in the MLR analysis (Table 3). Shredder species richness also differed among leaf types ($F_{14,75} = 1.9$, $P = 0.045$) and was also an important predictor of invertebrate-mediated breakdown rate which increased with richness within the leaf bags ($y = -1.09 + 2.48x$; $r^2 = 0.46$, $F_{1,14} = 10.8$, $P = 0.006$).

The C : N ratios did not differ among invertebrate consumer species ($F_{3,10} = 2.7$, $P = 0.08$). However, among leaf types C : N ratios were considerably higher and more variable than they were for invertebrate consumers (Table 1; Fig. 4). Arithmetic C : N imbalances between leaf types and invertebrate detritivores spanned an order of magnitude, ranging from 8 (alder) to 107 (ivy), and breakdown rates declined as imbalances increased (e.g. $\log_{10}$ total % mass loss $= 1.56 - 0.96$ $\log_{10}$ mean C : N imbalance calculated using all shredder species; $r^2 = 0.49$, $F_{1,13} = 12.6$, $P = 0.004$). C : P ratios differed among consumers, with *Gammarus* being especially low (56.7) relative to the other consumers ($F_{3,10} = 24.2$, $P < 0.001$; *Gammarus* < *Protonemura* < *Halesus*, *Potamophylax*). This species also had a low N : P ratio ($F_{3,10} = 33.5$, $P < 0.001$; *Gammarus* < *Protonemura* < *Halesus*, *Potamophylax*), being about one order of magnitude below that of most litter types, which had N : P ratios similar to those of the other consumers. Arithmetic C : P imbalances overlapped for some consumer–resource combinations (Fig. 4). These suggested that *Gammarus* would be P-limited by all 15 leaf types, whereas, *Protonemura*, *Potamophylax* and *Halesus*, would be P-limited by 13, 13, and 11 leaf types, respectively. In comparison, imbalances calculated using the TER$_{C:P}$ approach still showed *Gammarus* to be P-limited by all 15 leaf types, whereas, *Protonemura*, *Potamophylax* and *Halesus*, were only P-limited by 10, 9 and 7 leaf types, respectively (Table 1).

Discussion

Leaf-litter breakdown rates were primarily driven by resource quality, rather than the geographical origin of the litter (i.e. native versus exotic leaves) or species identity *per se*. This suggests that it is not necessary for leaf-litter to be of a local origin for effective energy transfer to occur in stream food webs, as consumers can readily use and process exotic leaf types (cf. Graça *et al.*, 2001; Thompson & Townsend, 2003; Lecerf *et al.*, 2007a). However, microbial decomposers and invertebrate consumers did respond differentially to specific measures of resource quality: breakdown by the former was governed by the leaves' structural compounds as well as by the ratio of structural compounds to P, whereas breakdown by the latter was governed by nutrient content and the degree of microbial

Table 4 Partial least-squares (PLS) regression output for leaf breakdown rate of 15 leaf species and cultivars

Type of breakdown	Variable	VIP	Slope	Components	R^2Y
Total	Lignocellulose : P	1.18	−0.10	1	0.94
	Cellulose : P	1.18	−0.10		
	Lignin : N	1.18	−0.09		
	Lignin : P	1.17	−0.09		
	C : P	1.12	−0.09		
	Lignocellulose : N	1.11	−0.09		
	Lignocellulose	1.10	−0.09		
	% Lignin	1.05	−0.08		
	% Cellulose	1.04	−0.08		
	Cellulose : N	1.00	−0.08		
	Constant		0.28		
Microbial	Lignocellulose	1.22	−0.15	2	0.94
	Lignin : P	1.21	−0.12		
	Lignocellulose : P	1.21	−0.11		
	cellulose : P	1.19	−0.10		
	% Lignin	1.19	−0.15		
	C : P	1.11	−0.09		
	% Cellulose	1.11	−0.12		
	Lignin : N	1.10	−0.07		
	Lignocellulose : N	1.01	−0.05		
	Constant		−0.50		
Invertebrate-mediated	Fungal biomass	1.78	0.41	2	0.91
	Shredder richness	1.15	0.25		
	C : N	1.10	−0.22		
	Constant		−0.52		

Variables are listed with their regression slopes in descending VIP (variable importance to the projection) index order. Slope coefficients are not independent (unlike MLR), as the variables may be collinear. The VIP values reflect the importance of terms in the model both with respect to y and with respect to x (the projection). VIP is normalized and the average squared value is 1, so terms in the model with a VIP > 1 are important (other variables are not shown). R^2Y is the % of the variation of y explained by the model.

conditioning. Consequently, both structural and nutritional measures of resource quality contributed to determining total breakdown rates and the transfer of biomass to consumers.

The composite measure of the lignin : P content of leaves was the best single predictor of microbial breakdown rates, and multiple measures of resource quality did not improve upon this model. Similarly, in the PLS analysis, lignocellulose closely followed by lignin : P, lignocellulose : P and cellulose : P were identified as important predictors: i.e. structural compounds and P content both drove microbial activity. Lignin has been previously identified as an important determinant of microbial activity associated with decomposing leaves in streams (Gessner & Chauvet, 1994; Maharning & Bärlocher, 1996). It is intriguing that in the present study P availability appeared to be an additional important factor determining microbial

breakdown, possibly suggesting that the microbes were P-limited in our study stream. In addition to taking up P via food resources, microbial consumers can also assimilate nutrients directly from the water column for their nutritional requirements (e.g. N and P; Suberkropp, 1998) and many studies have documented positive effects of high stream nutrient concentrations on the leaf-associated microbial community and leaf breakdown (e.g. Elwood *et al.*, 1981; Ferreira, Gulis & Graça, 2006). In our study, stream soluble reactive phosphorus concentrations were two orders of magnitude lower than dissolved inorganic nitrogen (nitrate + nitrite + ammonium) concentrations, suggesting that microbial activity might have been P-limited and thus more sensitive to changes in litter P content.

Invertebrates were the main drivers of breakdown rates in the present study and differences in inverte-
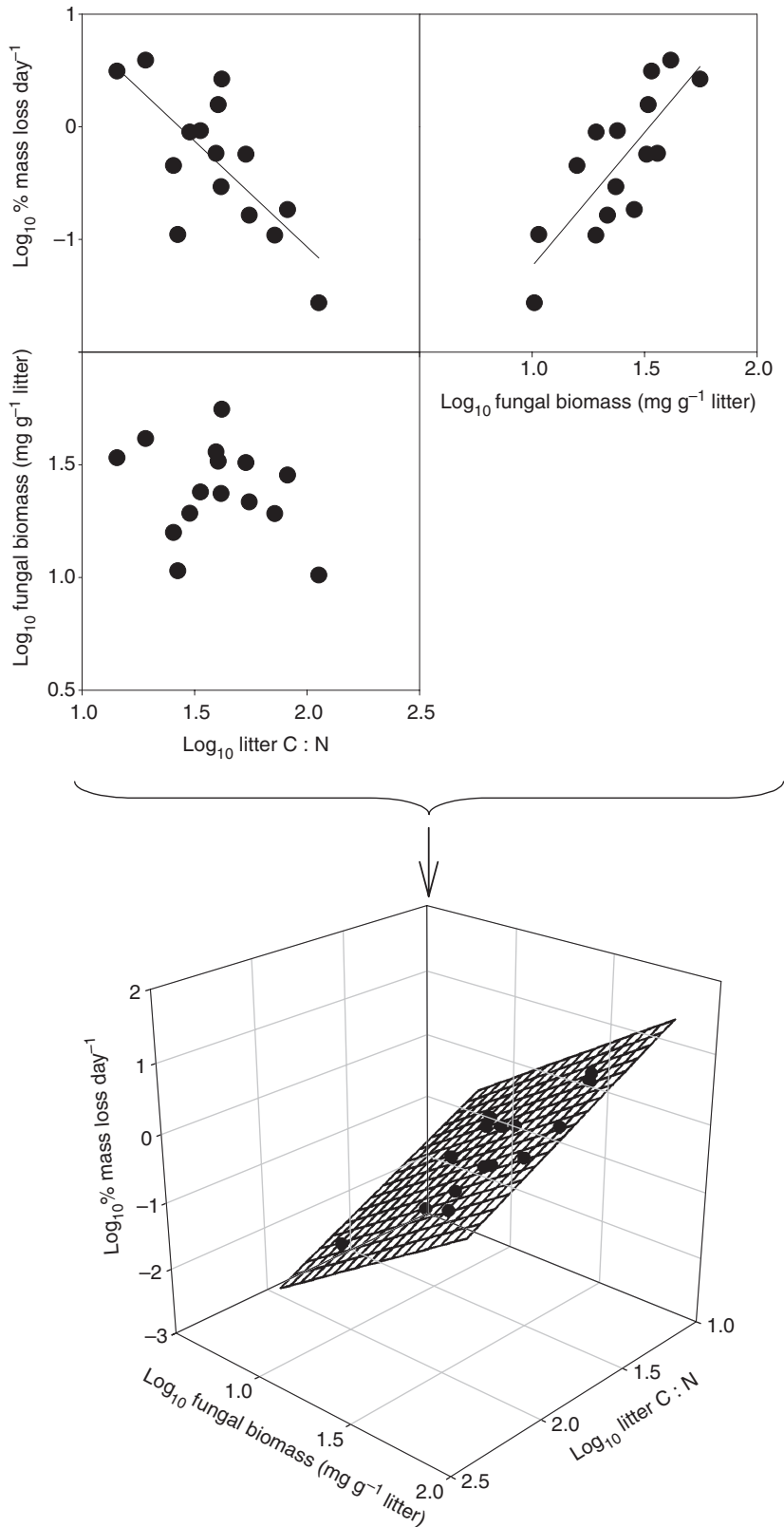
Fig. 3 Linear and planar relationships (following $\log_{10}$ transformation of axes) of daily invertebrate-mediated breakdown rates and two measures of resource quality (litter C : N and fungal biomass) for the 15 leaf species and cultivars, using predictor variables derived from best-fit multiple linear regressions. Data points represent the mean value for each leaf-type.
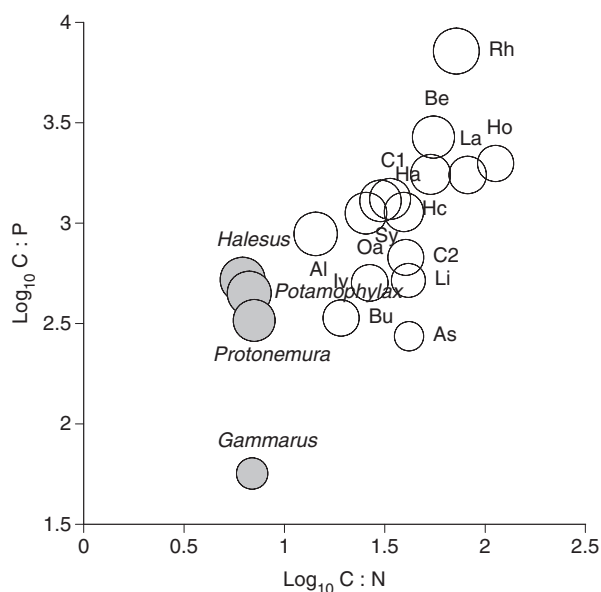
Fig. 4 C : N : P ratios in leaf-litter and consumer body tissues, illustrating stoichiometric consumer–resource imbalances among 15 leaf species and cultivars and the four dominant shredder species (grey bubbles, annotated in italics). Note axes are log-transformed, and the area of each circle is proportional to $\log_{10}$ N : P.

brate-mediated breakdown rates among leaf types were related to fungal biomass, pointing to a strong positive response of leaf-shredding detritivores to microbial conditioning (e.g. Suberkropp, 1992; Graça, 2001). Furthermore, invertebrate-mediated breakdown correlated with fungal biomass independently of other measures of resource quality; i.e. shredders responded separately to both the quality of the litter itself *and* the degree of microbial conditioning. Consumer responses to resource quality therefore may have been driven largely by a nutrient acquisition strategy of shredders, as indicated by the planar relationship between invertebrate-mediated breakdown, C : N content and fungal biomass, and the phenomenon of nutrient immobilization associated with fungal colonization (Webster & Benfield, 1986; Gessner, 1991; Quinn *et al.*, 2000).

Shredder colonization reflected the differences in breakdown rates among litter types, with both higher abundances and species richness on the better-quality resources (e.g. low lignin : N). This apparent behavioural (food choice) response from the shredder community has also been demonstrated in feeding preference laboratory trials, with individual shredder species preferring to select higher quality food items over lower quality food items (Iversen, 1974; Canhoto & Graça, 1995; Rincón & Martínez, 2006). Our findings are also consistent with at least two other field studies that have reported shredders aggregating preferentially on higher-quality litter (Haapala, Muotka & Markkola, 2001; Lecerf *et al.*, 2005). Such responses make sense from an energetic and stoichiometric viewpoint, as (assuming all else being equal) consumers should attempt to optimize growth and reproduction by feeding on high-quality food that meets their elemental requirements (Sterner & Elser, 2002; Woodward, 2008). Meeting their demand for nutrients is particularly challenging for detritivores, because their food resources differ dramatically from their body composition (Fig. 4; Cross *et al.*, 2003, 2005). Feeding on leaf-litter does, however, offer the advantage of allowing them to exploit a niche unavailable to many other taxa (Frost *et al.*, 2006). C : N imbalances between consumers and resources, although low in some cases (e.g. 2× for alder), were as high as 18× in others (holly), and may explain why shredders responded strongly to resource quality *per se* and do not necessarily favour native leaves over exotics (Parkyn & Winterbourn, 1997; Graça *et al.*, 2001). Our set of field data on a broad range of native and exotic litter types clearly supports the notion that resource quality rather than taxonomic identity *per se* is the main driver of litter breakdown.

Relatively few studies have explored stoichiometric detritivore-resource relationships in running waters. However, in a detailed analysis, Cross *et al.* (2003) found that a range of shredders had low molar C : N ratios (6.4–6.7) compared with their leaf-litter food resources (67–73) in two streams in the U.S.A. Our shredder C : N values (6.2–7.1) were very similar to these figures, suggesting very narrow constraints on tissue nitrogen content across even distantly related and geographically separated taxa, whereas our C : N values of leaf-litter were considerably more variable (14–113). In contrast to the interspecific similarities in shredder C : N values, C : P and N : P differed markedly among consumer species, reflecting taxonomic patterns reported in the few other studies carried out to date (e.g. Frost *et al.*, 2003; Evans-White *et al.*, 2005). In addition, C : P values of the insect shredders (but not the crustacean) overlapped with those of the higher quality litter, and N : P ratios for all four consumer species fell within the range of the

litter types. The ranges of C : N : P ratios we found were broadly similar to those of primary consumers in freshwaters collated from 49 literature sources (C : N, 5–9; C : P, 80–880; Cross *et al.*, 2005) and also for terrestrial riparian invertebrates (C : N, 5–7; C : P, 56–216; 9–34 N : P; Tibbets & Molles, 2005). *Gammarus duebeni*, however, was a notable exception, having unusually low C : P (56.7) and N : P (8.6) ratios. This might not be atypical for this genus: a congener found in the U.S.A., *G. pseudolimnaeus*, has C : P ratios (Evans-White *et al.*, 2005) below the range reported by Cross *et al.* (2005), and the C : P and N : P ratios of *G. duebeni* are also similar to those of other crustaceans (Frost *et al.*, 2003; Tibbets & Molles, 2005).

That litter C : N was a better predictor of invertebrate-mediated breakdown than C : P or N : P raises the question as to whether N rather than P might have been limiting for these consumers. The TER for C : P has been estimated to range from 77 to 3090 for 41 aquatic consumer taxa and was on average 2.4 times higher than body C : P; invertebrate detritivores had a higher threshold (*c.* 1000) than other functional feeding groups, reflecting the lower P content of their tissues and lower gross growth efficiencies associated with feeding on detrital carbon (Frost *et al.*, 2006). Consequently, the widespread use of consumer body elemental composition will tend to overestimate consumer–resource imbalances somewhat, and this measure should therefore be used cautiously when employed as a proxy for estimating TER. This was indeed the case in our study: for instance, *Halesus* appeared to be P-limited on 11 leaf types, but this fell to seven when using the $TER_{C : P}$ approach. The estimated $TER_{C : P}$ values (*c.* 1000) for our invertebrate detritivores were similar to those calculated by Frost *et al.* (2006), with the exception of *Gammarus*, whose lower values might represent more general differences in C : P body content between insect and crustaceans, as described above. Further studies are clearly needed to elucidate the relative importance of resource $TER_{C : N}$ versus $TER_{C : P}$ on stream consumers.

Although resource quality, rather than whether leaf-litter was native or exotic, drove breakdown rates, it would be misleading to assume that invasive riparian plants do not pose threats to stream ecosystem functioning. Certain invasive exotics, such as *Rhododendron ponticum* and cherry laurel in the British Isles, or *Eucalyptus* species in Iberia, have relatively poor quality leaf-litter and can form dense monocul-

tures along stream and river banks, a combination that could dramatically impair litter processing rates (e.g. Graça *et al.*, 2002; Lecerf *et al.*, 2007a). The litter of other riparian invaders, in contrast, may be processed more rapidly than native vegetation, as in Australia and New Zealand where high-quality willows and poplars are replacing poor-quality *Eucalyptus* and other native evergreens in many areas (Greenwood, O'Dowd & Lake, 2004). The recent expansion in Europe and parts of North America of butterfly bush (*B. davidii*) presents a similar case, given that its leaves are processed extremely rapidly (Fig. 2). This raises the question of how to view the impacts of invasions from the ecosystem perspective (Vitousek *et al.*, 1997; Chapin, 2003). The replacement of native flora can have negative, neutral or positive effects on food web fluxes, depending on the degree and direction of differences in litter chemistry of exotic versus native species. Indeed, this full range of potential outcomes was evident in our study, as revealed, for instance, by the breakdown rates of the three exotic species *B. davidii*, *Tilia cordata* and *R. ponticum*, relative to the native species. Maintaining riparian diversity in terms of litter traits relevant to detritivores and microbial decomposers provides insurance (Lecerf *et al.*, 2007b) against invader impacts, and retaining biodiversity at the base of the food web is therefore likely to be just as critical for ecosystem functioning as it is for the consumer guild.

Acknowledgments

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