

C–N mismatch in the leaf litter–shredder relationship of an Andean Patagonian stream detritivore

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Abstract. Aquatic shredders depend mostly on terrestrial leaf litter as a food resource, and differences between the C:N ratio of their food resource and their bodies may affect nutrient excretion and the composition of their feces. Laboratory experiments were used to test how the stonefly *Klapopteryx kuscheli* rebalances the high C:N ratio of its food. An experiment was designed in which *K. kuscheli* was fed 5 different leaf litters across a gradient of C:N ratios and the elemental ratios of the food, insect bodies, and feces were analyzed. *Klapopteryx kuscheli* regulated its internal elemental composition by changing its excretion of N depending on the N content of its food. An inverse relationship was found between N content of most foods and excreted NH_4^+ . However, *K. kuscheli* feces were rich in N and the insect excreted very small amounts of NH_4^+ when fed *Nothofagus pumilio*, probably because of refractory N-based compounds in the leaves of this species. Homeostatic regulation of N content by invertebrate shredders may influence N dynamics in small nutrient-poor streams.

Key words: ecological stoichiometry, leaf litter–shredder elemental mismatch, low-order streams, Plecoptera, ammonium excretion, Patagonia.

Ecological stoichiometry considers how the relative proportions of chemical elements in food sources and organisms affect the biological transformations of those elements in ecological interactions (Frost et al. 2002). Within major phylogenetic groups, animals present a relatively constant body elemental composition compared to the elemental composition of living plants or plant detritus (Sturner and Elser 2002, Evans-White et al. 2005). Imbalances occur when consumers obtain elements from their food in ratios different from those required for their growth and reproduction (Urabe et al. 2002). Primary consumers, both herbivores and detritivores, have to cope with larger differences between food and body stoichiometry than secondary consumers (i.e., organisms that feed on animal tissue) do (Sturner and Elser 2002). This circumstance forces primary consumers to increase food intake as food quality decreases or as food C:N ratios increase (Albariño and Balseiro 2001).

Regardless of food quality, primary consumers must maintain their internal homeostasis by balancing assimilation, egestion, and excretion. Despite such a compensatory strategy, benthic invertebrates fed on

poor-quality food usually attain slower growth rates than invertebrates fed high-quality food (detritivores: Albariño and Balseiro 2001, Tuchman et al. 2002; herbivores: Ledger and Winterbourn 2000, Stelzer and Lamberti 2002, Cruz-Rivera and Hay 2003), and slow growth rates may affect life-history traits (Stanko-Mishic et al. 1999, Huryn and Wallace 2000). The interplay between basal food quality and physiological strategies used by primary consumers to compensate for a stoichiometric imbalance affects nutrient cycling (Elser and Urabe 1999), population dynamics (Urabe et al. 2002), community structure (DeMott and Gulati 1999), and ecosystem processes (Hessen 1997, Sturner et al. 1997) in pelagic food webs. However, the effects of such phenomena in benthic communities are still largely unknown (Frost et al. 2002, Cross et al. 2005).

Food quality is determined by intrinsic physical and chemical characteristics that may affect consumption, assimilation, and growth of consumers (Scriber and Slansky 1981). For instance, leaf toughness and content of polyphenols and tannins characteristic of terrestrial vegetation may deter aquatic detritivores, as well as terrestrial herbivores (Ayres et al. 1997), thereby diminishing instream organic-matter decay rates (Webster and Benfield 1986, Campbell and Fuchshuber 1995). Food quality also is related to its elemental

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composition (especially N content) that may alter palatability to, consumption by, and growth of consumers (Friberg and Jacobsen 1999).

The elemental composition of leaf detritus entering aquatic systems depends on the degree of nutrient resorption by the plant before senescence of the leaves. Nutrient resorption is more important in deciduous than in evergreen plants (Perry 1994), and nutrient resorption before leaf loss may be among the most important strategies used by plants to save nutrients. The net effect of nutrient resorption is to increase the C:nutrient ratio of the litter (McGroddy et al. 2004). Detritus input from riparian vegetation makes up most of the standing stock of organic material in small temperate forested streams (Wallace et al. 2001), and invertebrate detritivores in such streams feed largely on this allochthonous material (Cummins 1996, Graça 2001). As a consequence, the elemental stoichiometry of benthic particulate organic matter in small temperate forested streams should be controlled by this allochthonous input (Frost et al. 2002).

Native forests, dominated by trees of the genus *Nothofagus*, occupy the western-most humid region of Patagonia along the Andean mountains where 4 of 7 tree species are deciduous. These deciduous trees determine autumnal organic inputs to low-order streams in the forests. The forests are mainly N-limited, and N is significantly resorbed from senescent leaves resulting in a lower N:C ratio in senescent leaves than in actively photosynthetic leaves (Diehl et al. 2003). In addition, the nutrient-poor condition of Andean headwater streams seems to be related to parent material, forest-soil biogeochemistry, and low human development (Pedrozo et al. 1993, Perakis and Hedin 2002). Inorganic dissolved N and P are exploited by autotrophs and sequestered by heterotrophic microbes growing in leaf litter and periphyton (Chadwick and Huryn 2003, Cross et al. 2003). Therefore, Andean streams with low nutrient concentrations would have low microbial activity, which may slow detritus conditioning, thereby affecting the dynamics of the pool of organic matter in the streams.

Klapopteryx kuscheli Illies (Plecoptera, Austroperliidae) is a common shredder that can contribute significantly to overall shredder biomass (up to 40% of the community biomass; Albariño 2001) in Andean Patagonian low-order forested streams (Albariño and Balseiro 2002, RA, personal observation). *Klapopteryx kuscheli* feeds and grows on a wide range of deciduous leaf litter (Albariño and Balseiro 2001), but not on periphytic algae (Albariño and Díaz Villanueva 2001). Our study is a first step toward analyzing the stoichiometric imbalances at the base of the detrital pathway that detritivores of Patagonian forested

headwaters face. We examined variability in the C:N content of *K. kuscheli* bodies and feces when larvae were fed monospecific diets of different types of leaf litter, including 4 native and 1 exotic tree species. Our goal was to determine how this plecopteran compensates for the imbalance between the C:N ratios of its food and its body. Two possible homeostatic strategies were examined. First, the insects could decrease their assimilation of the element in excess (i.e., C) and, thus, the C:N ratio of their feces should increase (assimilation hypothesis; Hessen 1997). Under this hypothesis, the difference in C:N ratios between feces and food should increase as the C:N ratio of the food increases. Second, the insects could regulate excretion rather than assimilation (excretion hypothesis; Sterner and Elser 2002). Under this hypothesis, the C:N ratio of the feces should be similar to that of the food, but the amount of excreted N should be inversely related to the C:N ratio of the food.

Methods

Field sampling and laboratory conditioning

Klapopteryx kuscheli larvae were reared experimentally on senescent leaves of 3 native deciduous trees (*Nothofagus antarctica* [Forst.] Oerst., *N. pumilio* [Poepp. et Endl.] Krasser, *N. obliqua* [Mirb.] Oerst.), 1 native deciduous shrub (*Ribes magellanicum* Poir.), and 1 exotic deciduous tree (*Alnus glutinosa* L.). Native species were selected on the basis of their ecological importance in terms of abundance and distribution in the Andean Patagonian forest and their importance in the riparian vegetation (Veblen et al. 1996), whereas *A. glutinosa* is a common ornamental species in urban and suburban areas of the city of Bariloche. We included alder for comparison because its leaves are high-quality food for detritivores (i.e., high N content, low C:N ratio, low leaf resistance, and apparent absence of chemical deterrents; Pozo 1993). Senescent leaves were picked manually from trees during autumn (2 May 2002). Only undamaged leaves were selected. Native leaves were collected from the forest, whereas *A. glutinosa* leaves were collected from trees at the Universidad del Comahue fish farm (Centro de Salmonicultura, Bariloche, Argentina). In the laboratory, leaves were placed in individual containers with stream water at 15°C for a 2-wk conditioning period (2–17 May 2002).

Stream water and *K. kuscheli* larvae were collected on 16 May 2002 from a headwater stream that is a tributary of Ñireco stream at 1000 m asl (lat 41°13'S, long 71°22'W). This unnamed 1st-order stream flows through a *Nothofagus pumilio* forest. Insects were collected with a Surber sampler. In the laboratory,

individuals of intermediate size (mean ± 1 SE body length: 17.6 ± 0.1 mm, body dry mass [DM]: 6.5 ± 0.3 mg) were selected. Individuals were acclimatized for 24 h in laboratory containers at 8°C.

Five 1.25-L containers were filled with 1 L of stream water. Each container received 10 g DM of mono-specific preconditioned leaves (a different species in each container) and 10 *K. kuscheli* larvae. Larvae were fed a monospecific diet for 30 d (17 May to 17 June 2002). Containers were aerated with an air pump and kept in a incubator at 8°C with a 12:12 light:dark photoperiod (resembling autumn field conditions). Water was renewed every 10 d. O₂ concentration was checked daily with an YSI 59B O₂ meter, and feces were removed daily. Containers also were checked daily for dead individuals and to make sure that sufficient food was available. O₂ concentration remained at saturation during the 30-d experiment, and no food shortage or insect mortality were observed.

Experimental design

Experiments were done in thirty-six 500-mL containers with 250 mL of freshly collected stream water and twenty 14-mm-diameter discs (cut with a cork borer and assumed to have identical mass) of 1 species of leaf. Each leaf species (*N. pumilio*, *N. antarctica*, *N. obliqua*, *R. magellanicum*, and *A. glutinosa*) was considered a treatment, and every treatment was replicated in 7 containers. One *K. kuscheli* larva was placed in 6 of the 7 containers in each treatment (1 container was left as a control). Larvae were assigned to leaf-species treatments based on the leaf species they had been fed during the previous 30 d (i.e., larvae acclimatized on *N. pumilio* were assigned to *N. pumilio* treatments). All containers were kept in an incubator at 8°C with a 12:12 light:dark photoperiod for 5 d (17 June–22 June 2002). Containers were inspected twice a day. Feces were collected from each container with a clean glass pipette and placed on individual precombusted glass-fiber filters (Whatman GF/C). No larvae died during the 5-d experiment.

At the end of the experiment, each larva was killed by freezing (–20°C). Insects, feces on filters, and the leaves remaining in each container (detritus) were dried at 60°C for 48 h. Dried samples of insects and detritus were ground in a precombusted glass mortar and the resulting powder was placed in tin capsules for CN analysis. Feces on filters also were placed in tin capsules. All samples were stored at –20°C until analysis. Elemental analyses (C and N) of particulate matter were done using a Thermo Finnigan Elemental Analyzer EA 1112. C and N content were expressed

atomically, and ratios were calculated for each compartment (i.e., food, body tissue, feces).

One hundred mL of water were collected from each container at the end of the experiment for analysis of dissolved N-NH₄⁺, which was used as a relative measure of excreted N. Water was filtered through glass-fiber filters (Whatman GF/F) and N-NH₄⁺ was measured with the indophenol-blue method (APHA 1985). Excreted N was the difference in water-column N-NH₄⁺ concentrations between replicates with insects and their controls within each leaf-species treatment.

Data analysis

C:N ratios of larval bodies and feces, C:N ratios of leaf litter, and excreted N-NH₄⁺ were compared among leaf-species treatments with analysis of variance (ANOVA) followed by a posteriori Tukey's tests (Zar 1996). C:N ratios of larval bodies and feces were compared to C:N ratios of leaf litter within leaf-species treatments with *t*-tests. The relationships of fecal C:N ratios and water-column N-NH₄⁺ to leaf litter C:N ratios were described with linear and exponential models. Models with the highest *R*² values were selected to describe the observed relationships. All statistical analyses were done with SigmaStat (version 2.03, SigmaStat, Richmond, California).

Results

Leaf litter C:N ratios ranged from 16 to 97 by mass (Fig. 1) and differed significantly among leaf-species treatments (ANOVA: *p* < 0.05). The native species, *N. pumilio*, and the exotic species, *A. glutinosa*, had very low ratios that did not differ (Tukey's test: *p* > 0.05; Fig. 1). All other species had C:N ratios that differed significantly (Tukey's test: *p* < 0.001 for all comparisons). *Nothofagus antarctica* and *R. magellanicum*, 2 common native species, had high ratios that differed between them (Tukey's test: *p* = 0.0101) and with the other 3 species (Tukey's test: *p* < 0.001).

Insect body C:N ratios averaged 5.55 ± 0.24 (mean ± 1 SE, all treatments pooled). Body ratios were significantly lower than leaf litter ratios in all leaf-species treatments (*t*-tests: *p* < 0.05; Fig. 1) and did not differ among leaf-species treatments (ANOVA: *p* > 0.05; Fig. 1). Fecal C:N ratios differed significantly among leaf-species treatments (ANOVA: *p* < 0.05). Fecal ratios were significantly higher in *N. antarctica* and *R. magellanicum* treatments than in *A. glutinosa*, *N. pumilio*, and *N. obliqua* treatments (Tukey's tests: *p* < 0.05; Fig. 1). Fecal ratios were significantly lower in the *N. pumilio* treatment than in any other treatment (Tukey's test, *p* < 0.05). Fecal ratios were significantly higher than leaf litter ratios in the *A. glutinosa*

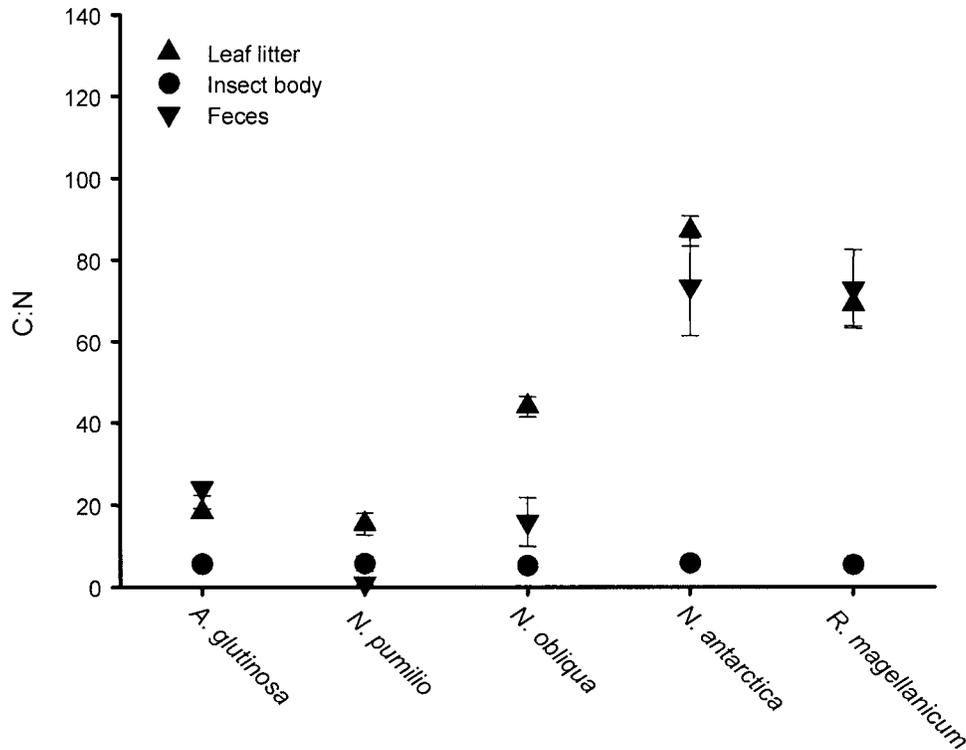


FIG. 1. Mean (± 1 SE) C:N ratios (atomic) of leaf litter, insect bodies, and feces in laboratory experiments in which *Klapopteryx kuscheli* were fed monospecific diets consisting of *Alnus glutinosa*, *Nothofagus pumilio*, *N. obliqua*, *N. antarctica*, or *Ribes magellanicum*. Error bars for body C:N ratios were smaller than the symbols.

treatment (t -test, $p < 0.05$), whereas fecal ratios did not differ from leaf litter ratios in the *N. antarctica* and *R. magellanicum* treatments (t -test: $p > 0.05$; Fig. 1). Fecal ratios were significantly lower than leaf litter ratios in the *N. pumilio* and *N. obliqua* treatments (t -tests: $p < 0.001$; Fig. 1). The C:N ratio of feces showed a general trend to increase as the C:N ratio of litter increased (Fig. 2). However, fecal C:N ratios of larvae reared on *N. pumilio* and *N. obliqua* were noticeably lower than the leaf litter ratios (Figs 1, 2) suggesting that food had ended as N-enriched egestion products (i.e., feces).

At the end of the experiment, the difference in $N-NH_4^+$ concentration between treatments and controls without larvae was analyzed as a relative measure of excreted N. As expected, the amount of $N-NH_4^+$ in the water of the experiments varied among treatments. *Klapopteryx kuscheli* fed on *A. glutinosa* excreted comparatively more $N-NH_4^+$ than those fed on any other leaves (Fig. 3). Insects fed on *N. antarctica* and *R. magellanicum* showed the lowest values of excreted $N-NH_4^+$, whereas insects fed on *N. obliqua* presented intermediate values (Fig. 3). However, the concentrations of $N-NH_4^+$ was extremely low in the treatment with *N. pumilio* (Fig. 3), indicating that the response of larvae when fed on this litter differed from their

responses to all other sources. The absolute amount of N in the feces (i.e., μMol of N in the feces produced during the 5 d) was $\sim 2 \mu\text{Mol}$ of N (for *N. antarctica*: $1 \mu\text{Mol}$ of N) in all treatments but *N. pumilio*. Thus, the different C:N ratio of feces among treatments was mainly a result of different C contents. In contrast, feces from larvae fed on *N. pumilio* had the highest N content ($65 \mu\text{Mol}$). On the other hand, the excreted $N-NH_4^+$ showed an inverse relationship with the food C:N ratio (Fig. 3). Considering all leaves but *N. pumilio*, we fitted an exponential decay model ($y = a e^{-bx}$) between the excreted $N-NH_4^+$ and the C:N of the leaf litter ($r^2 = 0.60$, $p < 0.0001$). The treatment with *N. pumilio* showed an unexpected low value of excreted $N-NH_4^+$ when compared to the C:N of the leaf litter. Therefore, it should be considered an outlier of the exponential decay model (Fig. 3).

Discussion

Detritivores are likely to encounter stoichiometric constraints on their growth and reproduction because their bodies generally contain relatively more N than terrestrially derived plant material (Elser et al. 2000, Cross et al. 2003, our study). Moreover, the C:N imbalance between leaf-litter feeders (i.e., shredders)

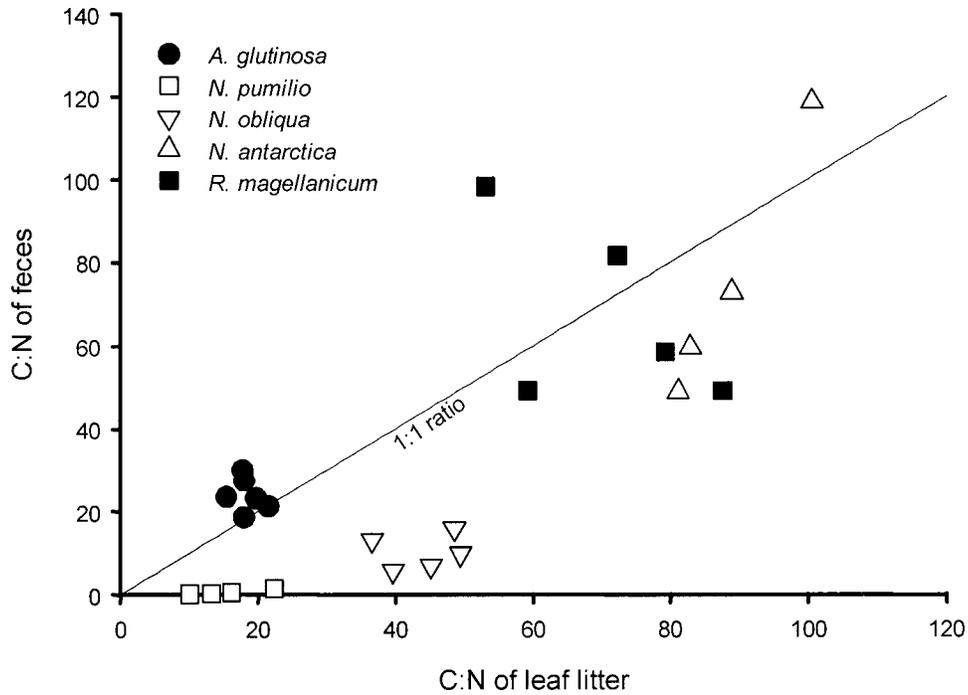


FIG. 2. Scatter plot showing the relationship between C:N ratios of leaf litter (food source) and C:N ratios of feces from *Klapopteryx kuscheli* fed monospecific diets consisting of *Alnus glutinosa*, *Nothofagus pumilio*, *N. obliqua*, *N. antarctica*, or *Ribes magellanicum*. The line shows a 1:1 relationship between detrital and fecal C:N ratios.

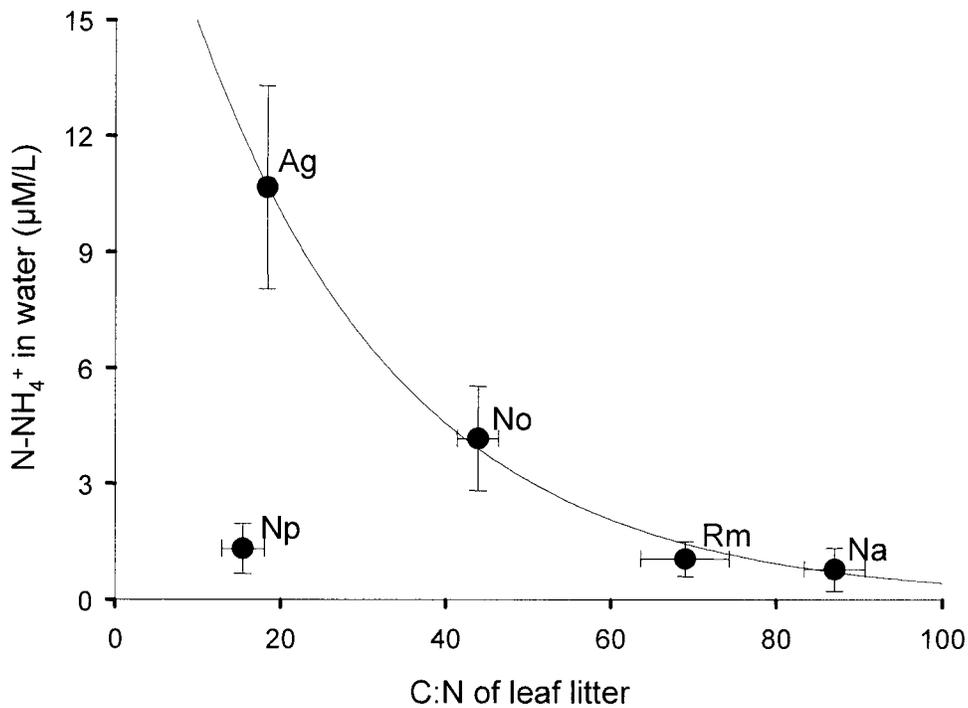


FIG. 3. Exponential regression showing the relationship between C:N ratios of leaf litter (food source) and the N-NH₄⁺ excreted by *Klapopteryx kuscheli* fed monospecific diets of each leaf species. Values for *Nothofagus pumilio* were excluded from the regression analysis. Ag = *Alnus glutinosa*, Np = *Nothofagus pumilio*, No = *N. obliqua*, Na = *N. antarctica*, Rm = *Ribes magellanicum*.

and their food resource is probably the most disproportionate among all organism–resource components in food webs (Cross et al. 2003, Evans-White et al. 2005). However, aquatic insects generally have very stable C:N (atomic) ratios of ~ 6 (Frost et al. 2003, Evans-White et al. 2005) regardless of the elemental ratios of their food. The leaf litter used as food in our study had C:N ratios that were 3 to 16 \times higher than the insect body C:N ratios. Despite the large range of C:N ratios of the native and exotic leaf litter offered to larvae, insect body C:N ratios were always lower than the C:N ratios of their food and were fairly constant (5.55 ± 0.24 ; Fig. 1), a result consistent with predictions of stoichiometric theory (Sterner and Elser 2002). This result implies that *K. kuscheli* maintains internal homeostasis and balances the elemental ratio of their diet by assimilation–egestion–excretion strategies.

Assimilation hypothesis

Hessen (1997) suggested that consumers under stoichiometric imbalance should decrease assimilation efficiency of the elements in excess. Our first hypothesis, based on Hessen's (1997) idea, predicted that the C:N ratio of feces would be higher than the C:N ratio of the food. In *N. antarctica* and *R. magellanicum* treatments, the fecal C:N ratios increased proportionally with the leaf litter C:N ratio, and no significant differences were found between fecal and leaf litter ratios (1:1 straight line in Fig. 2). To the contrary, in *A. glutinosa*, *N. pumilio*, and *N. obliqua* treatments, fecal and leaf litter C:N ratios differed significantly (Figs 1, 2). The fecal C:N ratio exceeded the leaf litter C:N ratio in the *A. glutinosa* treatment, and the leaf litter C:N ratio exceeded the fecal C:N ratio in the *N. pumilio* and *N. obliqua* treatments. Our prediction failed in 3 of 5 cases, and our results did not confirm the assimilation hypothesis.

Two factors may have contributed to this outcome. N content of the feces may have been overestimated because N content is expected to increase in feces after egestion as a consequence of microbial colonization (Anderson and Sedell 1979). However, we collected and dried feces twice a day, making this possibility negligible. The fact that feces had a lower C:N ratio than leaf litter may imply that the N-based compounds of *N. pumilio* and *N. obliqua* litter are especially difficult for *K. kuscheli* to assimilate. This explanation is probable considering the large amount of N in feces from larvae fed on *N. pumilio* (65 $\mu\text{Mol N}$).

Excretion hypothesis

Sterner and Elser (2002) suggested that insects under stoichiometric imbalance would maintain their inter-

nal balance by regulating excretion, either by increasing their release of the element in excess or by decreasing the excretion of the scarce element. In this sense, Darchambeau et al. (2003) found an increase in respiration rates (C excretion) in *Daphnia* when fed on high C:nutrient food (increase excretion of C in excess). Based on the excretion hypothesis, the C:N ratio of feces might be similar to that of the food, but if the homeostasis were based on the N excretion, the amount of excreted N would be inverse to the C:N ratio of the food. Based on Darchambeau et al. (2003) findings, it could be expected that the increase in respiration would be enough to maintain internal balance; however, consumers might display a multi-element response strategy to maintain homeostasis. Our results did show an inverse relationship between excreted N and C:N of the food indicating that this excretory mechanism appears substantial to *K. kuscheli* homeostasis.

Our results supported this second hypothesis, except when larvae were fed *N. pumilio*. *Klapopteryx kuscheli* fed on *N. pumilio* leaf litter had unexpectedly low N excretion in relation to the elemental ratio of the leaf litter, and the feces were unexpectedly rich in N. Lignin concentration in senescent leaves of deciduous South American *Nothofagus* species is lowest in *N. pumilio* (Diehl et al. 2003). Because lignin is difficult for aquatic detritivores to digest (Chapman 1998), it is possible that C content in *N. pumilio* leaves was present in relatively accessible compounds. Thus, the low lignin content in *N. pumilio* leaf litter may be indirectly related to the ability of *K. kuscheli* to digest and assimilate C-based compounds, but not N-based compounds, from this food source. Moreover, the high N-resorption strategy of *Nothofagus* deciduous species (Diehl et al. 2003) should concentrate difficult-to-assimilate refractory N-compounds in the leaf litter. On the other hand, the results obtained with *N. antarctica* leaves contrasted markedly with the results obtained with *N. obliqua* and *N. pumilio* litter, indicating large differences among these related species. *Nothofagus pumilio* forms the uppermost forest belt along the whole Andes range in Patagonia, and it is the most important leaf-litter resource in pristine low-order Patagonian streams, so further investigation to elucidate some of our results is greatly needed.

Ecological consequences

Ecological stoichiometric theory provides a useful and simplified framework within which to analyze food-source–consumer mismatches and their indirect effects on other ecosystem compartments because the great complexity of food quality can be defined by the

elemental ratio of any foodweb component. For example, the effect of *K. kuscheli* feeding on nutrient dynamics in the detrital pool would depend on whether the N is excreted as NH_4^+ or released as recalcitrant organic matter with the feces. Shredding of leaf litter contributes to fine particulate organic matter (FPOM) pools in terrestrial (Bengtsson et al. 1996) and aquatic (Cummins 1996) systems. In terms of the ecological stoichiometric theory, the interaction between food quality and internal homeostatic strategies of shredders may differentially affect the quality of FPOM available to collectors, thereby affecting the detrital pathway. However, N-enriched feces (such as those produced by *K. kuscheli* fed on *N. pumilio*) do not necessarily imply high-quality FPOM because N compounds may be recalcitrant to digestion or assimilation by collector feeders. Therefore, N availability for collector feeders might depend on further conditioning by microbes before the FPOM becomes a suitable resource.

Klapopteryx kuscheli seems to regulate the elemental balance of C and N, in part, by changing the amount of excreted N. Nutrients excreted by aquatic organisms are considered in conceptual models of nutrient spiraling (Mulholland 1996). Excreting NH_4^+ or releasing N-rich feces may have important consequences for nutrient dynamics in streams. Nutrient amendment accelerates rates of decomposition in streams with low concentrations of dissolved N and P (Robinson and Gessner 2000). *Klapopteryx kuscheli* can make up 40% of total community biomass in low-order streams (RA and Díaz Villanueva, Universidad Nacional del Comahue, Bariloche, Argentina, personal observation). Thus, the quantity and quality of N released by this shredder has the potential to affect producers and collectors, particularly because NH_4^+ is a labile molecule that is taken up rapidly by primary producers and decomposers (Kemp and Dodds 2002, Simon et al. 2004). Nutrient-based processes in Andean headwater streams are still unknown, but the oligotrophic status of these streams makes any nutrient subsidy originating from the consumer pool relevant.

Frost et al. (2002) suggested that the size of consumers might affect the way nutrients are released and cycled into the stream. For instance, nutrients excreted by small chironomids that feed within biofilms (below the boundary layer) will have different effects on dissolved N:P ratios in streams than nutrients excreted by large snails that feed on biofilms and excrete nutrients outside the boundary layer (Frost et al. 2002). However, the size of large detritivores that forage underneath substrates or within detritus accumulations may be of less importance than their microhabitat, which provides hydraulic dead zones

where nutrient dispersion is lower than in flow-exposed biofilms (Allan 1995) and where nutrient uptake probably occurs over very small spatial and temporal scales. Nutrients excreted by detritivores within the sediment probably are immobilized rapidly in the immediate surroundings because of hydraulic constraints within the stream bed. This microhabitat effect might have important implications in the dynamics of benthic detrital pools in oligotrophic systems if the homeostatic strategy of large shredders is to compensate for stoichiometric imbalances by differentially excreting elements.

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