Assessing the ecological quality (structure, function and biodiversity) of running waters

Literature review

by

Jenny Bergfur

Department of Environmental Assessment
Swedish University of Agricultural Sciences
Box 7050   SE 750 07 Uppsala

2005 Rapport 2005:30

Assessing the ecological quality (structure, function and biodiversity) of running waters

ISSN 1403-977X

Natural and human induced variability in stream ecosystems

Humans have for a long time been using aquatic resources to provide a number of services and functions such as supplying drinking water, fishery, and transportation and for recreational purposes. Human-induced impacts on ecosystems are at the same time increasing at an alarming rate resulting in a substantial loss of biodiversity (Vitousek et al. 1997). There is also a growing concern that not only species diversity is lost, but that ecosystem services may become lost or impaired with anthropogenic stress (Daily et al. 2000).

There is a long tradition in ecology of considering the effect of abiotic factors (ecosystem processes) on biodiversity (Loreau 2000) and for water management purposes the assessment of water quality has for a long time been based on physical, chemical or biological data. Many of the ecosystem functions such as species and habitat diversity, species interaction and mineralization of organic matter are connected to water quality and therefore a more integrated approach to water management is needed (Knoben et al. 1995).

The relationship between biodiversity and ecosystem processes has become a central issue and challenge in contemporary ecology in the last decade (Cardinale et al. 2000, Loreau 2000, Loreau et al. 2001). These interests have spurred research to determine how species loss alters the rates of ecological processes that are vital to retain inherent ecosystem functioning. Although the contribution that species diversity has per se on ecosystem function is currently debated, several studies have shown nonetheless that biological communities regulate important ecological processes such as productivity, decomposition and elemental cycling and that species loss can alter the structure and functioning of ecosystems (Naeem et al. 1994, Naeem et al. 2000, Petchey et al. 2004). Some modelling studies indicate, however, that there may be no single, general relationship between diversity and production (Cardinale et al. 2000). Likely, relationships between species diversity and ecosystem processes are complex. Jonsson (2003) and Petchey et al. (2004) recently showed that interactions between species are likely to determine what effect species loss will have on rates of ecosystem functioning.

Ecosystem function in natural and perturbed systems

A large number of methods, ranging from subtle changes at the suborganism-level to changes in population, community and ecosystem-level structure, are currently used to assess the ecological integrity of aquatic ecosystems (Johnson et al. 1993). Community-level assessment using benthic macroinvertebrates is by far the most common approach used to assess ecological quality (Cairns and Pratt 1993), and many biological metrics have been developed (Knoben et al. 1995). Although assemblage structure and composition has been successfully used in studies of impairment, there has been a recent renaissance in the use of ecosystem-level processes, such as decomposition, as a complementary approach to assessing ecological integrity. For example, Gessner and Chauvet (2002) and Dangles et al. (2004a) propose the use of leaf litter breakdown as a tool for determining the effects of human-induced change on ecosystem function. The breakdown of leaf litter from deciduous vegetation is an essential component of terrestrial and aquatic ecosystems, and a topic that has received considerable focus (Ponsard et al. 2000, Graca 2001, Royer and Minshall 2003). The importance of leaf litter as the main energy source for low order streams (Vannote et al. 1980) and to a lesser extent the littoral region of lakes (France 1995b) has been recognized for some time. The organisms that drive leaf litter breakdown processes include detritivorous macroinvertebrates (shredders), bacteria and aquatic fungi (Baldy et al. 1995, Wallace and Webster 1996, Royer and Minshall 2003). The relative importance of these three groups and the factors controlling their roles are, however, unclear (Hieber and Gessner 2002). Given the renewed focus on ecosystem function in monitoring human-induced ecological effects and the potential importance of species loss on ecosystem function and services provided, there is a current need to better understand the linkage between species diversity/composition and ecosystem function.

Allochthonous versus autochthonous driven systems

The stream ecosystem is, as all other ecosystems, dependent on a constant input of energy. The energy for running water is gained through autochthonous pathways, where solar energy supports in-stream primary production, or allochthonous pathways, where the stream ecosystem is supported by organic matter that is produced elsewhere (Fisher and Likens 1973, Giller and Malmqvist 1998).

In many headwater streams, the riparian vegetation reduces autotrophic production by reducing solar input, and the stream is often dependent on the litter input from the surrounding vegetation. As stream size increases there is a reduction in the importance of allochthonous detritus input and the significance of in-stream primary production and organic transport from upstream increases (Minshall 1967, Vannote et al. 1980).

Leaves from riparian trees are one of the most important components of allochthonous energy-input (Webster et al. 1999) and this energy input is naturally greatest in autumn when leaf abscission occurs. Therefore a seasonal shift in the relative importance of autotrophic production vs. allochthonous input can be observed in stream ecosystems (Vannote et al. 1980). More recently, terrestrial invertebrates have been recognized as an important energy source to aquatic ecosystems. Though leaves are mostly degraded by aquatic invertebrates, terrestrial invertebrates are consumed by fishes, mainly salmonids and this input to the streams is largest in the summer months in temperate zones. In tropic areas the leaf and invertebrate input is independent of season (Baxter et al. 2005). To reduce the variance in energy flow the organisms in stream ecosystems are adapted to these seasonal changes, for example: species diversity, food processing specialisation, temporal expression of functional groups and the erosional-depositional transport and storage characteristics of flowing waters are all adaptations to these temporal energy variations (Vannote et al. 1980).

CPOM breakdown

Leaching

Vascular plant or CPOM (coarse particulate organic matter) breakdown is generally thought to occur in three distinct phases, namely leaching, conditioning and fragmentation. The first phase leaching, causes an initial rapid loss of soluble and labile materials (Cummins 1974, Petersen and Cummins 1974, Webster and Benfield 1986). Most of the leaching occurs within the first 24 hours after the CPOM has entered the water (Petersen and Cummins 1974). Most studies on leaf-litter breakdown have been performed using autumn-shed leaves that have been pre-dried (Kaushik and Hynes 1971, Petersen and Cummins 1974) and most of the models concerning leaf-litter processing in streams are therefore based on results from using pre-dried leaves. However, there is a difference in the kinetics of leaching between pre-dried (air-dried) leaves and fresh leaves. Gessner & Schwoerbel (1989) found that air-dried leaves from alder (*Alder glutinosa* (L.) Gaertn.) and willow (*Salix fragilis* L.) lost 20% and 25 %, respectively, of initial air-dried mass after 24 hours of leaching. If the leaves were exposed to leaching without having been air-dried, the leaching kinetics is quite different: no significant mass loss occurred over a period of 6.5 days. The leached material enters the DOM (dissolved organic matter) pool, which also receives its input from the surrounding watershed. The DOM is then lost from the system by microbial activity (Fisher and Likens 1973).

Temperature has long been considered one of the most important factors controlling breakdown rates, irrespectively of leaf-species (Kaushik and Hynes 1971, Iversen 1975, Suberkropp et al. 1975), but Petersen and Cummins (1974) found in laboratory studies on leaf-breakdown rates that temperature had no extensive effect on the rate of leaching. Water quality and leaf composition is also considered important for the decomposition rates (Kaushik and Hynes 1971, Sampaio et al. 2001).

Microbial breakdown

After the initial leaching, microbial colonization occurs, which reaches its peak after about one or two weeks. The initial microbial colonization is mostly conducted by aquatic hyphomycetes and bacteria. During the time of microbial colonization microbial respiration takes place, which processes the plant material further (Petersen and Cummins 1974). This process is also known as microbial conditioning. The microorganisms that colonize the plant material produce hydrolysing enzymes that decompose the material and release soluble compounds and fine particles into the water (Graca 1993). This is proceeded by mechanical and invertebrate decomposition and fragmentation (Cummins 1974, Webster and Benfield 1986, Graca 1993).

The rate of conditioning is dependent on many factors. Such as; the preconditioning before the CPOM enters the water, the water temperature (Cummins 1974, Nikolcheva and Bärlocher 2005), leaf type and degree of microbial colonization (Petersen and Cummins 1974, Sampaio et al. 2001, Nikolcheva and Bärlocher 2005). The importance of preconditioning is still a matter of debate, early studies (e.g. Cummins 1974) found that in summer with temperatures above 15°C, the spores and hyphae already present on the substrate played a large role in the fungal breakdown. More recent studies have, however, hardly detected any fungal biomass, measured as ergosterol, on fresh leaves, and after placement in the stream the fungal biomass increased rapidly and peaked within a few weeks (Gessner and Chauvet 1994, Hieber and Gessner 2002). The fungal mediated breakdown has been found to be controlled by lignin (primarily) and tannin contents of the leaves, rather than the nitrogen and phosphorus content of the leaves (Gessner and Chauvet 1994). Furthermore, the external concentrations of nutrients (nitrogen and phosphorus) has been found to be an important regulator of this process (Suberkropp and Chauvet 1995, Graca et al. 2001, Grattan and Suberkropp 2001). During leaf decay the concentration of nutrients (especially nitrogen) has been found to increase, which has been attributed to the growth of microorganisms on leaves (Sampaio et al. 2001). This suggests that both internal and external factors interact to control the fungi-mediated leaf litter decomposition. Some authors have found bacterial assimilation of carbon to be almost as high as that of fungi, although fungal growth is somewhat greater than bacterial growth (Findlay and Arsuffi 1989). More recent results show that fungal mediated carbon loss greatly exceeds that of bacteria (Baldy et al. 1995, Pascoal and Cássio 2004).

Fragmentation

The fragmentation rate of CPOM is also dependent on many different factors, for example litter-quality, temperature and the number of shredders in the stream (Petersen and Cummins 1974, Oberndorfer et al. 1984, Cummins et al. 1989). Fungal breakdown is also reported to stand for a considerable part of the leaf-breakdown (Suberkropp and Klug 1980, Gessner and Chauvet 1994, Hieber and Gessner 2002) although others have found no statistically significant relationship between ergosterol content and litter disappearance, regardless of season (Graca et al. 2001). Fungal colonisation on leaves also increases palatability to shredders, which in turn increases the rate of breakdown when feeding on the microfilm on the litter (Suberkropp 1992, Gessner and Chauvet 1994). Bacteria are also part of the fragmentation. The bacteria growing on leaf surfaces is being consumed and sloughed off, removing material from the leaf in the process (Findlay and Arsuffi 1989). The microbes associated with the leaves have been described as "peanut-butter" which only occurs on nutritionally unsuitable "crackers", the leaves, and a requirement to obtaining the "peanut butter" is to consume the "cracker" (Cummins 1974). Hall and Meyer (1998) found support for this "peanut-butter cracker" theory when investigating the importance of bacteria in stream food-webs. Macroinvertebrates seemed to derive much of their carbon from the microbes in the stream rather than from the detritus itself.

Concerning the importance of macroinvertebrates (shredders) in the litter breakdown process contradicting results exist. Stockley et al. (1998) found, in his study on the contribution of invertebrates to detritial processing in the river Swale-Ouse system in the UK, that invertebrate contribution was minimal, neither Leff and McArthur (1989) found that invertebrates were the primary agent of decomposition. In a more recent study Hieber and Gessner (2002) found that shredders, fungi and bacteria all stood for a significant part of the leaf breakdown process in a temperate forest stream. But the shredders appeared to be particularly important.

Stream invertebrates that feed on leaf litter are intimately tied to the nature and timing of the litter input. Many of the aquatic invertebrates have for instance synchronized their emergence, ovipositioning and eclosion to occur just prior to leaf abscission in the autumn (Petersen and Cummins 1974, Cummins et al. 1989). Differences in decomposition rates between different seasons has been attributed to the differences in the numbers and types of invertebrates and to changes in the microbial community present in stream habitats at different seasons (Garden and Davies 1988).

Sediment composition has also been shown to influence litter breakdown rates in natural situations with varying current velocities (Reice 1974, 1977). Comparison of breakdown rates on rock, gravel, sand and silt showed that the highest breakdown rates occurred on rock sediments and this was not related to current velocity (Reice 1977). However, when current effects were eliminated, the effect of the substratum on decomposition rates was found not to be significant (Reice 1980). Abiotic factors such as current velocity might otherwise increase fragmentation rates (Stout and Coburn 1989), although these authors found indications that physical process were less important then biological processes for leaf decomposition.

Some methods commonly used to assess functional changes in stream ecosystems

Functional analysis of an ecosystem often consists of community metabolism, the energy transformation by the organisms (Teal 1957). In all ecosystems, major flows of energy occurs along detritial pathways and breakdown of vascular plants is essential to the trophic dynamics of many freshwater ecosystems processes (Cummins 1974, Petersen and Cummins 1974, Howarth and Fisher 1976, Webster and Benfield 1986, Nelson 2000). Moreover, the flow of energy is a complex interaction of physical, chemical, microbial and animal processes (Webster and Benfield 1986, Graca 2001). Since degradation rates are sensitive to physical and chemical environmental changes and relatively easy to measure (Graca 1993), measurements of breakdown rates is considered as a useful tool when investigating patterns and mechanisms driving decomposition in steams (Hieber and Gessner 2002), and when evaluating functional changes due to anthropogenic disturbance of such ecosystems (Webster and Benfield 1986). A wide range of organisms are also involved in the decomposition of leaf litter, for example: bacteria, fungi, invertebrates and, in the tropics, fishes. This suggests that anthropogenic stresses of leaf breakdown can be effective through different targets and mechanisms (Gessner and Chauvet 2002). As mentioned under the heading "CPOM breakdown", there are many factors, acting on several spatial scales, which affect litter breakdown. The many different factors controlling the rate of litter breakdown and how they interact is a major problem in interpreting the litter breakdown rates. Royer & Minshall (2003) constructed a hierarchical framework that reveals a predictable structure regarding factors regulating breakdown processes. The framework incorporates factors operating at different spatial scales: landscape/biome, basin/network, watershed, reach and patch. Incorporating these factors in the interpretation of breakdown rates is crucial if breakdown rates are to be used as a means for bioassessment.

Analyzes of functional feeding groups, FFG, (Cummins 1974, Moog 1995) is an indirect way of measuring the functional integrity of a stream. Methods such as classifying sites according to the feeding behaviour of the taxa present has been used extensively in ecological studies (Johnson 1999), although several studies have found that metrics such as ratios between functional groups were not better than measurements of community structure (Resh and Jackson 1993) and such information about ecosystem-level processes is also a deduction from structural parameters (Gessner and Chauvet 2002).

The use of different measures: decomposition, stoichiometry and stable isotopes, in understanding ecosystem processes.

Decomposition rates

Since litter breakdown is an important energy source in stream ecosystems, much effort and time has been placed on understanding the process of litter breakdown in small headwater streams (Royer and Minshall 2003). A common method is the use of leaf bags or leaf packs. One common measure of decomposition rates is the use of the k-value (Olson 1963, Petersen and Cummins 1974).

$$\boxed{W_t=W_0*e^{-kt}}$$

The exponential decay model is used to calculate the k-value, which expresses the breakdown rate as the percentage mass declining over time. The construction of methods to assess breakdown rates are also varied (Boulton and Boon 1991). One commonly used method to quantify the rate of leaf litter breakdown is the use of artificial leaf bags. The usage of different kinds of leaf bags with different sizes, shapes or mesh sizes or natural leaf packs results, in different breakdown rates (Cummins et al. 1980, Stewart and Davies 1989, Boulton and Boon 1991). The use of natural leaf pack has not gained great importance in assessing breakdown rates since it is difficult to standardise. The invertebrate composition in artificial litter bags has, however, been found to be similar to natural leaf packs, at least in the early stages of breakdown (Braioni et al. 2001).

The decomposition rates of leaves are dependent on many factors as mentioned above. Humans can however influence these factors (willingly or unwillingly) with the increase of nutrients, increased temperature due to global warming, habitat destruction such as channelling and the discharge of pollutants such as pesticides and metals. All these impacts can, however, result in different responses of decomposition rates.

Eutrophication and organic pollution.

Addition of nutrients (nitrogen, phosphorous and sewage effluents) to streams has generally been shown to increase breakdown rates (Kaushik and Hynes 1971, Iversen 1975, Howarth and Fisher 1976, Elwood et al. 1981, Meyer and Johnson 1983, Suberkropp and Chauvet 1995, Benfield et al. 2001, Grattan and Suberkropp 2001, Pascoal et al. 2001, Pascoal et al. 2003). The increase in leaf breakdown rates has been attributed to increased microbial processing (Meyer and Johnson 1983, Benfield et al. 2001, Pascoal et al. 2001). Many authors have reported increased breakdown rates as a response to increased nitrogen (N) concentrations. However, phosphorus (P) has been found to affect leaf litter differently than N. Elwood et al. (1981) found that P increase the mass loss rate in P-enriched streams, while others have found that P together with N appears to increase the decomposition rates, but alone decrease the rates (Kaushik and Hynes 1971, Howarth and Fisher 1976). It has been argued that breakdown of leaves is N-limited, but when the concentration of N is sufficient, the process becomes P-limited. High nutrient concentration might decrease breakdown rates, as shown by Pascoal and Cássio (2004). If the organic load is too high or the current velocity too low, hypoxic conditions might occur which hampers the leaf breakdown rates.

In some cases increases in N concentration in stream water has played minimal roles in regulating leaf decomposition rates (Chadwick and Huryn 2003). This finding was, however attributed to other factor such as, phosphorus limitation and acidic conditions. On the other hand, leaves grown under increased N concentration affected the leaf processing by increasing microbial activity and possibly increasing shredder biomass.

Global warming.

Leaves grown under N enrichment has been shown to stimulate leaf litter breakdown (Chadwick and Huryn 2003) and leaves grown under elevated CO_2 showed higher C:N ratios than those grown under ambient CO_2 levels (Tuchman et al. 2002, Adams et al. 2003), at least over short time scales (Rastetter et al. 1997). These leaves have higher levels of structural compounds and lower nitrogen content. The part of a leaf that appears to determine the breakdown rate is the concentration of structural compounds, e.g. lignin, this because it limits the amount of readily available carbon (Gessner and Chauvet 1994). However, in a litter breakdown study in a terrestrial environment, Taylor et al. (1989) found that the C:N ratio was the best predictor of the mass loss rate. During decomposition of leaves the organic carbon is lost and thus the C:N ratio decreases with time in the decomposing leaves (Howarth and Fisher 1976). Leaves with high C:N ratios have lower nutritional value. Such leaves support a lower bacterial production, not affecting fungi biomass though, and larval craneflies have shown a lowered consumption, lower assimilation and lower growth rates than those feeding on leaves with lower C:N ratios (Tuchman et al. 2002). Crayfish has also been shown to have a preference for leaves with lower C:N ratios (Adams et al. 2003).

Elevated CO_2 values are a result of higher atmospheric levels of CO_2 as a result of increased burning of fossil fuels (Vitousek et al. 1997). Thus anthropogenic disturbances such as eutrophication and the usage of fossil fuels could disrupt the natural decomposition processes in streams. Elevated temperatures might also be expected to affect the leaf processing rates since temperature is an important controlling factor of leaf litter breakdown, as mentioned earlier. Other factors, such as stream pH, might also be important and influence the breakdown process more than different thermal regimes (Rowe et al. 1996).

Acidification.

Low stream pH has been shown to result in low rates of decomposition (Mulholland et al. 1987, Stout and Coburn 1989, Dangles and Guerold 2001, Dangles et al. 2004a). This effect has been attributed to lower shredder biomass and lower feeding activity of the main shredder compared to less acidic streams (Dangles and Guerold 2001, Dangles et al. 2004a). Mulholland (1987) found, in a study on the effects of natural acidification on leaf litter breakdown rates, that macroinvertebrate numbers and biomass were lowest at the site with the highest pH-values, but this site had the highest decomposition rates compared to naturally acid sites. Decreased breakdown rate at the acidified sites was attributed to decreased microbial activity. Other authors (e.g. Dangles et al. 2004b), have found that in naturally acid waters the decomposition rates and the taxonomic richness were not significantly different than less acidic streams. This would indicate that organisms in naturally acidic stream are adapted to these conditions and such systems should not be exposed to liming, a measure used to alleviate the man-made acidification problems of today.

Metal pollution.

Other stressors on running waters include those of metals, which can become severely elevated as a result of mine drainage. The effects of elevated metal concentrations have been shown to have a negative impact on leaf litter breakdown rates (Niyogi et al. 2001, Carlisle and Clements 2005, Woodcock and Huryn 2005). This is suggested to be attributed to the decrease of shredders below this threshold (Niyogi et al. 2001). Elevated metal concentrations also has a negative effect on microbial activity, although microbes does not seem to be as negatively effected by metal pollution as shredders (Niyogi et al. 2001, Carlisle and Clements 2005).

In a study on metal pollution effects on breakdown rates, Nelson (2000) found no difference between metal polluted sites and control sites. The leaf packs were mostly used as algal substrates, and the algae together with FPOM (fine particulate organic matter) seemed to be the dominant food in this system and the collector-gatherers, not the shredders, were the most important predictors of metal pollution. Therefore, the algal production might have been the dominant ecosystem level function in this metal polluted system.

Stoichiometry

The balance of elements in different organisms and organic matter and their biological transformation in biological interactions in an ecosystem is considered in the theory of ecological stoichiometry (Frost et al. 2002, Sterner and Elser 2002, Cross et al. 2003). Phosphorus (P) and nitrogen (N) are two of the most important nutrients regulating biotic processes in stream ecosystems (Suberkropp and Chauvet 1995). Stoichiometry theory does not say that it is the nutrient ratios (C:N:P ratios) in the food, but that it is the nutritional requirements of an organism relative to the nutritional content of the food resource that is the basis for ecological stoichiometry . N and P may be limiting to consumers and are, if so, retained at higher efficiencies by consumers. Organisms with high body content of N and P and high growth rates, require a food source with high N and P content. If the opposite exists the organism also has low N and P requirements in the food source. These organisms are also less susceptible to stress caused by reduced quality in the food resource (Cross et al. 2003). When the requirements of a consumer with regard to nutrient ratios are not fulfilled by its food resource, an elemental imbalance occurs. This imbalance appears to be widespread and is partly created by high C:x (x can be any nutrient) ratios in the food sources available to consumers (Frost et al. 2002).

Kahlert (1998) recently reviewed literature data on freshwater periphyton and found that C:N:P ratios are a reliable tool for the assessment of the nutrient status of benthic algae, proposing an optimum ratio of 158:18:1. Experiments by Hillebrand (1999) confirmed this conjecture. Hillebrand (1999) found that cellular C:P ratios indicated P limitation and cellular C:N ratios indicated nutrient limitation in general. He also proposed that results on cellular stoichiometry could be used to evaluate nutrient situation of natural periphyton assemblages. Frost et al. (2003) studied the elemental composition of littoral invertebrates in eutrophic versus oligotrophic lakes. They found greater differences regarding the mean body content of P, N and C among taxonomic groups than among these different lake types. These results indicated that the strength of stoichiometric limitations acting on littoral food webs will depend on the taxa being considered.

In streams the autotrophic production will be governed by the supply of light, N and/or P and the benthic algae and macrophytes can serve as an important pool of elements in environments where allochthonous carbon supply is low and light availability is high (Frost et al. 2002). If there is an imbalance between allochthonous-derived material and consumers this may have consequences for the growth and production of benthic heterotrophs and important ecosystem processes such as decomposition (Frost et al. 2002).

Elser and Urabe (1999) argued that the stoichiometric perspective in stream ecology was virtually absent, although its use was widespread in pelagic studies using predominantly zooplankton. Since then some studies have been performed using the stoichiometric perspective on leaf breakdown rates.

Cross et al. (2003) studied the effect on leaf breakdown as a response to increased nutrient levels in detritus, and found that consumers dependent on leaf litter in detritus based streams were more out of balance with their food resources in relation to animals dependent on living plant tissue. They concluded that leaf-eating organisms in detritus based food-webs are more severely limited (in growth and production) than organisms living in food-webs based on living plant tissue. When nutrients were elevated artificially the consumer-resource imbalance was reduced.

In ecological stoichiometry the elemental homeostasis of organisms is a central tenet (Sterner and Elser 2002). Cross et al. (2003), however, showed that increased nutrient levels caused invertebrates to change their C:P and N:P ratios dramatically. These authors hypothesized that storage of P, or increased growth rates and greater cellular allocation of P to rRNA, was the reason for the deviation from homeostasis. Although body size was not found to be related to nutrient content, N and P content decreased with body size among collector-gatherers and collector-filterers.

Plants also have the ability to store nutrients in their cellular vacuoles; this has implications for the measurement of ecological stoichiometry. If the organisms are sampled at a time when nutrients are abundant, the C: x ratios might be different compared to the same species C: x if sampled at a time when nutrients are scarce and no nutrients are stored within the organism (Sterner and Elser 2002).

Water- and airshed properties likely have fundamental influences on stoichiometric relationships in benthic habitats. The link between the terrestrial environment and the aquatic may also influence the elemental ratios in streams, as would the shift from an allochthonous to autochthonous driven systems (Frost et al. 2002). Anthropogenic influences such as eutrophication and global warming can also alter the stoichiometry of different food sources in aquatic systems, thus causing elemental imbalances between decomposers and primary producers, and this could potentially promote ecosystem destabilization (Daufresne and Loreau 2001).

Stable isotopes

Natural-abundance isotopes ratios such as $\delta^{13}C$ and $\delta^{15}N$ can be used to evaluate origin of plant material to determine trophic relationships and food abundances in stream ecosystems. Since algae differ from terrestrial vegetation regarding these isotopes, isotopic analyses can be used to evaluate the origin of the energy in aquatic ecosystems. Stable isotopes in animals can also be used to evaluate energy flows in aquatic ecosystems since they are similar in isotopic composition to their diets (Rounick and Winterbourn 1986, Peterson and Fry 1987, France 1995a, c, 1996, Mulholland et al. 2000, Finlay 2001). Isotope tracer addition experiments may also be used; elements highly enriched in a heavy isotope are added to the environment and the response measured as changes in isotope ratios in organic matter are quantified (Hall and Meyer 1998, Mulholland et al. 2000). Stable isotopes can also be used to follow changes in ecosystems and show which processes or components are most sensitive to perturbation (Peterson and Fry 1987).

$\delta^{13}C$ and $\delta^{15}N$ denotes the ratio of $^{13}C/^{12}C$ and $^{15}N/^{14}N$, respectively, expressed as the deviation from the recognised isotopic standard. Higher $\delta^{13}C$ values (i.e. less negative) reflects enrichment in ^{13}C relative to ^{12}C, depletion in ^{13}C relative to ^{12}C is reflected reciprocally by lower (i.e. more negative) $\delta^{13}C$ values (Rounick et al. 1982, France 1995b).

The use of stable isotope analysis as a tool in discerning the origin and pathways of carbon has been examined in a literature reviews by France (1995a, 1996). He concluded that the scope for using stable carbon isotopes for this purpose is limited, due to the overlap in carbon isotope ratios between terrestrial plant detritus and algae (both lotic and lentic attached algae) in stream ecosystems. Only when carbon isotope ratios are significantly different between attached algae and forest detritus can the use of stable isotope ratios be considered as a means to evaluate carbon pathways. Such places might be rocky-shored, oligotrophic lakes without macrophytes, forest fringed estuaries and lagoons. The incorporation of $\delta^{15}N$ could, however, offer support to conclusions about allochthony or autochthony in freshwaters (France 1995c).

More recent studies have showed that stable isotopes may be useful in discerning the origin of different food sources in stream ecosystems. Finlay (2001) studied the ratio of $\delta^{13}C$ in temperate headwater streams to medium-sized rivers to analyse the energy pathways through river food webs. He found a transition from terrestrial to algal carbon sources with increases in watershed areas, which is supportive of the River Continuum Concept (Vannote et al. 1980). Consumers in small headwater streams relied primarily on terrestrial inputs as carbon sources, although algal production were important to scrapers when present. As watershed size increased (<10 km^2), consumers relied more on algal production as a carbon source, except for shredders.

Mulholland et al. (2000) found that data from natural-abundance C and N isotopes had limited value in identifying food sources to macroinvertebrates, but additional data from a ^{15}N-tracer addition experiment did, however, give more definitive information on food web relationships than the natural-abundance C and N isotope studies alone. Another value of ^{15}N tracer was that it could be used to identify if a consumer uses a food resource in a manner different from the way in which it was sampled. Since epilithon consists of many layers of living and dead algae and other forms of organic matter, the organisms feeding on the living algae would be enriched from the ^{15}N in the living material in relation to the bulk material sampled. One negative aspect of the ^{15}N-tracer approach is that the values of the isotope will lag behind in the consumers compared to the food resource.

Another approach to investigate the resource base of food webs in streams was demonstrated by Hall et al.(2001). Using secondary production estimates and gut content analysis they were able to estimate the fraction of total secondary production derived from various food sources. However, simple gut analysis might not provide reliable conclusions about energy pathways since ingestion not always implies direct assimilation of the food source (France 1998, Hall et al. 2001). Since stable isotope analysis can be used to discern the incorporation of terrestrial food sources in aquatic ecosystems, one possible use of stable isotope analysis would be to monitor the effects of riparian deforestation (Rounick et al. 1982, France 1996).

Relationship between community structure and function (e.g. functional redundancy)

Biodiversity has been placed on the political agenda in recent years as, maintaining biodiversity may be important for several reasons, for example ecological, commodity or moral reasons (Walker 1992, Daily et al. 2000). As mentioned above, the relationship between biodiversity and ecosystem processes is an area which has been given more and more attention in recent years and the integration of ecosystem functions in management schemes may give more effective means to maintain ecosystem integrity.

It has been argued that one of the best ways to maintain biodiversity in ecosystems is to preserve the integrity of ecosystem functions. One way to test the integrity of ecosystem functional integrity is to assess the ecological redundancy by assigning species to functional guilds and then the degree of redundancy could be evaluated by comparing species of similar functional guilds (Walker 1992). However, it has been suggested that the functional roles played by different species may change due to influences of local environmental conditions (Wellnitz and Poff 2001).

Walker (1992) states that “ecologically, all species are not created equal”, and that the loss of some species might lead to greater impacts on the ecosystem than the loss of other, “less important”, species. If a species is removed from a system and there is no effect on the ecosystem functions, then that species is said to be redundant; i.e. functional redundancy is when “changes in patterns occurs without any detectable changes in processes” (Bunn and Davies 2000). For the litter breakdown process the concept of functional redundancy would imply that all shredder taxa, when weighted for biomass, are equal in their quantitative effect on decomposition and any change in community assemblage would not affect litter breakdown rates.

It has been demonstrated that the effect species loss will have on ecosystem functioning can be determined by the structure of the food web and the trophic level from which a species is lost (Petchey et al. 2004). The loss of sensitive taxa might have dramatic implications for ecosystem function if the species is a dominant contributor to the ecosystem process. However, that changes in ecosystem structure does not always include changes in ecosystem function as has been demonstrated in several experimental studies (Gessner and Chauvet 2002). Carlisle and Clements (2005) found that some species seem to contribute disproportionately to litter breakdown. In their study, leaf processing was dominated by a single dominant detrivorous taxon in reference streams, but as the concentration of metals increased this species abundance decreased as did the breakdown rates, none of the other tolerant shredders seemed to compensate. Nelson (2000) investigated leaf-breakdown rates in metal polluted sites in North America and found that there were no significant differences in breakdown rates between unpolluted vs. polluted sites. However, there were structural differences in the macroinvertebrate communities and these structural differences seemed to be controlled by algal production, another ecosystem level function. Woodcock and Huryn (2005) also found structural changes in invertebrate community composition as a response to stress (increased metal concentrations and decreased nutrient concentrations) with serial replacement of more tolerant shredder taxa along the perturbation gradient. But community change was not related to changes in litter processing rates, the decrease in litter processing rates was instead attributed to the water and sediment quality, demonstrating that a variable pollution-tolerant community enables stress tolerance and preservation of ecosystem processes.

It has been found that increases in decomposition rates are more associated with shredder richness rather than shredder abundance and shredder biomass (Jonsson and Malmqvist 2000, Jonsson et al. 2001, Huryn et al. 2002). That shredder richness is more correlated with breakdown rates than shredder abundance and shredder biomass implies that ecosystem processes are sensitive to declines in biodiversity (Jonsson and Malmqvist 2000, Jonsson et al. 2001, Dangles et al. 2004b).

Can functional aspects provide a better measure of ecosystem changes than structural aspects?

The state of a freshwater system can be measured as ecological integrity. Ecological integrity can be expressed as “the maintenance of all internal and external community processes and attributes, interacting with their environment in such a way that the biotic community corresponds to the natural state of the relevant aquatic habitat, and, where the community is preserved by regulation, resilience, and resistance to environmental stress" (Moog 1995). Assessing the ecological integrity of aquatic ecosystems is an important water management issue and one that has gained increasing focus, in particular with the recent ratification of the European Water Framework Directive (European Commission 2000). Ecological integrity can be divided into structural integrity which refers to "spatiotemporal patterns, particularly of biological communities and their resources" and functional integrity which can be referred to as "the ecosystem level processes" (Gessner and Chauvet 2002).

Humans impose a broad range of changes on the environmental conditions that influences the functions in freshwater ecosystem and influences the structure of benthic communities and processes such as leaf breakdown rates (Pascoal et al. 2001, Pascoal et al. 2003). Several biomonitoring approaches, in assessing the health or integrity of streams, has been developed (Bunn and Davies 2000), but most of these rely almost exclusively on structural attributes of streams (Gessner and Chauvet 2002), and since many biomonitoring approaches are based on pattern detection they often ignore the possibility that biological processes may cause marked variation in natural community patterns (Bunn and Davies 2000). As pattern determines process and vice versa, there is a need to incorporate biological processes when developing bioassessment schemes for biomonitoring of aquatic ecosystems (Bunn and Davies 2000, Gessner and Chauvet 2002).

Especially in flowing water has the assumption that pattern (e.g. species recognition) is the most important characteristic for ecological insight been troublesome. Methods based on patterns also makes the assumption that if no anthropogenic disturbance exists, the spatial and seasonal pattern will be the same from year to year (Bunn and Davies 2000). Since stressors clearly have an impact on ecosystem processes (Cardinale et al. 2004, Gessner et al. 2004, Giller et al. 2004, Petchey et al. 2004, Vinebrooke et al. 2004), the use of functional assessment methods, such as leaf litter breakdown rates, could be a simple, powerful and low-cost tool to assess ecosystem integrity (Dangles et al. 2004a).

Gessner and Chauvet (2002) suggested that different ratios between breakdown rates from impacted and references sites (k_i:k_r) and between coarse mesh litterbags and fine mesh litterbags (k_c:k_f) could be an alternative predictor of compromised functional integrity if the sensitivity of the breakdown rates were not enough to detect effects on ecosystem functioning. In studies where the potential for leaf litter breakdown to assess water quality has been tested, it has been shown that leaf litter breakdown does detect impairment as detected with different biological indices and that it could serve as a complement to other structure based indicators (Wallace et al. 1996, Pascoal et al. 2001, Pascoal et al. 2003). In experimental removal of macroinvertebrates the leaf litter breakdown rates were found to detect disturbance, such as removal of macroinvertebrates, with decreasing processing rates (Wallace et al. 1996). The litter breakdown process also responded to the recovery of the macroinvertebrate community by increasing process rates. Pascoal et al. (2001, 2003) found a strong relationship between organic pollution and breakdown rates. However, it did not reflect improved biotic conditions as did biotic indices (Pascoal et al. 2001). However, Lepori et al. (2005) tested if restoration of degraded ecosystems, e.g. channelised streams, could improve ecosystem functioning such as CPOM retentiveness and breakdown. They found that such ecosystem functions did improve after restoration. This suggests that ecosystem functions could serve as potential indicators of ecosystem quality and restoration efforts. However, to this date there is still no index that incorporates ecosystem functioning in modern bioassessment schemes and no single index that has been suggested that is able to completely cover the processes and properties of an ecosystem (Giller et al. 2004).

References

Adams, J. A., N. C. Tuchman, and P. A. Moore. 2003. Atmospheric CO2 enrichment alters leaf detritus: impacts on foraging decisions of crayfish (Orconectes virilis). Journal of the North American Benthological Society **22**:410-422.

Baldy, V., M. O. Gessner, and E. Chauvet. 1995. Bacteria, Fungi and the Breakdown of Leaf-Litter in a Large River. Oikos **74**:93-102.

Baxter, C. V., K. D. Fausch, and W. C. Saunders. 2005. Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. Freshwater Biology **50**:201_220.

Benfield, E. F., J. R. Webster, J. L. Tank, and J. J. Hutchens. 2001. Long-term patterns in leaf breakdown in streams in response to watershed logging. International Review of Hydrobiology **86**:467-474.

Boulton, A. J., and P. I. Boon. 1991. A Review of Methodology Used to Measure Leaf Litter Decomposition in Lotic Environments - Time to Turn over an Old Leaf. Australian Journal of Marine and Freshwater Research **42**:1-43.

Braioni, M. G., B. Gumiero, and G. Salmoiraghi. 2001. Leaf bags and natural leaf packs: Two approaches to evaluate river functional characteristics. International Review of Hydrobiology **86**:439-451.

Bunn, S. E., and P. M. Davies. 2000. Biological processes in running waters and their implications for the assessment of ecological integrity. Hydrobiologia **422**:61-70.

Cairns, J. J., and J. R. Pratt. 1993. A history of biological monitoring using benthic macroinvertebrates. Pages 10-27 *in* D. M. Rosenberg and V. H. Resh, editors. Freshwater Biomonitoring and Benthic Macroinvertebrates. Chapman and Hall, New York.

Cardinale, B. J., A. R. Ives, and P. Inchausti. 2004. Effects of species diversity on the primary productivity of ecosystems: extending our spatial and temporal scales of inference. Oikos **104**:437-450.

Cardinale, B. J., K. Nelson, and M. A. Palmer. 2000. Linking species diversity to the functioning of ecosystems: on the importance of environmental context. Oikos **91**:175-183.

Carlisle, D. M., and W. H. Clements. 2005. Leaf litter breakdown, microbial respiration and shredder production in metal-polluted streams. Freshwater Biology **50**:380-390.

Chadwick, M. A., and A. D. Huryn. 2003. Effect of a whole-catchment N addition on stream detritus processing. Journal of the North American Benthological Society **22**:194-206.

Cross, W. F., J. P. Benstead, A. D. Rosemond, and J. B. Wallace. 2003. Consumer-resource stoichiometry in detritus-based streams. Ecology Letters **6**:721-732.

Cummins, K. W. 1974. Structure and Function of Stream Ecosystems. Bioscience **24**:631-641.

Cummins, K. W., G. L. Spengler, G. M. Ward, R. M. Speaker, R. W. Ovink, D. C. Mahan, and R. L. Mattingly. 1980. Processing of confined and naturally entrained leaf litter in a woodland stream ecosystem. Limnology and Oceanography **25**:952-957.

Cummins, K. W., M. A. Wilzbach, D. M. Gates, J. B. Perry, and W. B. Taliferro. 1989. Shredders and Riparian Vegetation - Leaf Litter That Falls into Streams Influences Communities of Stream Invertebrates. Bioscience **39**:24-30.

Daily, G. C., T. Soderqvist, S. Aniyar, K. Arrow, P. Dasgupta, P. R. Ehrlich, C. Folke, A. Jansson, B. O. Jansson, N. Kautsky, S. Levin, J. Lubchenco, K. G. Maler, D. Simpson, D. Starrett, D. Tilman, and B. Walker. 2000. Ecology - The value of nature and the nature of value. Science **289**:395-396.

Dangles, O., M. O. Gessner, F. Guerold, and E. Chauvet. 2004a. Impacts of stream acidification on litter breakdown: implications for assessing ecosystem functioning. Journal of Applied Ecology **41**:365-378.

Dangles, O., and F. Guerold. 2001. Linking shredders and leaf litter processing: Insights from an acidic stream study. International Review of Hydrobiology **86**:395-406.

Dangles, O., B. Malmqvist, and H. Laudon. 2004b. Naturally acid freshwater ecosystems are diverse and functional: evidence from boreal streams. Oikos **104**:149-155.

Daufresne, T., and M. Loreau. 2001. Ecological stoichiometry, primary producer-decomposer interactions, and ecosystem persistence. Ecology **82**:3069-3082.

Elser, J. J., and J. Urabe. 1999. The stoichiometry of consumer-driven nutrient recycling: Theory, observations, and consequences. Ecology **80**:735-751.

Elwood, J. W., J. D. Newbold, A. F. Trimble, and R. W. Stark. 1981. The Limiting Role of Phosphorus in a Woodland Stream Ecosystem: Effects of P Enrichment on Leaf Decomposition and Primary Producers. Ecology **62**:146–158.

European Commission. 2000. Directive 2000/60/EC of the European Parliament and of the Council - Establishing a framework for Community action in the field of water policy. Brussels, Belgium.

Findlay, S. E. G., and T. L. Arsuffi. 1989. Microbial-Growth and Detritus Transformations During Decomposition of Leaf Litter in a Stream. Freshwater Biology **21**:261-269.

Finlay, J. C. 2001. Stable-carbon-isotope ratios of river biota: Implications for energy flow in lotic food webs. Ecology **82**:1052-1064.

Fisher, S. G., and G. E. Likens. 1973. Energy flow in Bear Brook, New Hampshire: an integrative approach to stream ecosystem metabolism. Ecological Monographs **43**:421-439.

France, R. L. 1995a. Critical examination of stable isotope analysis as a means for tracing carbon pathways in stream ecosystems. Canadian Journal of Fisheries and Aquatic Sciences **52**:651-656.

France, R. L. 1995b. Differentiation between littoral and pelagic food webs in lakes using stable carbon isotopes. Limnology and Oceanography **40**:1310-1313.

France, R. L. 1995c. Source variability in delta-N-15 of autotrophs as a potential aid in measuring allochtony in freshwaters. Ecography **18**:318-320.

France, R. L. 1996. Scope for use of stable carbon isotopes in discerning the incorporation of forest detritus into aquatic foodwebs. Hydrobiologia **325**:219-222.

France, R. L. 1998. Estimating the assimilation of mangrove detritus by fiddler crabs in Laguna joyuda, Puerto Rico, using dual stable isotopes. Journal of Tropical Ecology **14**:413-425.

Frost, P. C., R. S. Stelzer, G. A. Lamberti, and J. J. Elser. 2002. Ecological stoichiometry of trophic interactions in the benthos: understanding the role of C : N : P ratios in lentic and lotic habitats. Journal of the North American Benthological Society **21**:515-528.

Frost, P. C., S. E. Tank, M. A. Turner, and J. J. Elser. 2003. Elemental composition of littoral invertebrates from oligotrophic and eutrophic Canadian lakes. Journal of the North American Benthological Society **22**:51-62.

Garden, A., and R. W. Davies. 1988. Decay-Rates of Autumn and Spring Leaf Litter in a Stream and Effects on Growth of a Detritivore. Freshwater Biology **19**:297-303.

Gessner, M. O., and E. Chauvet. 1994. Importance of Stream Microfungi in Controlling Breakdown Rates of Leaf-Litter. Ecology **75**:1807-1817.

Gessner, M. O., and E. Chauvet. 2002. A case for using litter breakdown to assess functional stream integrity. Ecological Applications **12**:498-510.

Gessner, M. O., P. Inchausti, L. Persson, D. Raffaelli, and S. Giller P. 2004. Biodiversity effects on ecosystem functioning: insights from aquatic systems. Oikos **104**:419-422.

Gessner, M. O., and J. Schwoerbel. 1989. Leachin kinetics of fresh leaf-litter with implications for the current concept of leaf-processing in streams. Archiv für Hydrobiologie **115**:81-91.

Giller, P. S., H. Hillebrand, U. G. Berninger, M. O. Gessner, S. Hawkins, P. Inchausti, C. Inglis, H. Leslie, B. Malmqvist, M. T. Monaghan, P. J. Morin, and G. O'Mullan. 2004. Biodiversity effects on ecosystem functioning: emerging issues and their experimental test in aquatic environments. Oikos **104**:423-436.

Giller, P. S., and B. Malmqvist. 1998. The biology of streams and rivers. Oxford university press inc., New York.

Graca, M. A. S. 1993. Patterns and Processes in Detritus-based Stream Systems. Limnologica **23**:107-114.

Graca, M. A. S. 2001. The role of invertebrates on leaf litter decomposition in streams - A review. International Review of Hydrobiology **86**:383-393.

Graca, M. A. S., R. C. F. Ferreira, and C. N. Coimbra. 2001. Litter processing along a stream gradient: the role of invertebrates and decomposers. Journal of the North American Benthological Society **20**:408-420.

Grattan, R. M., and K. Suberkropp. 2001. Effects of nutrient enrichment on yellow poplar leaf decomposition and fungal activity in streams. Journal of the North American Benthological Society **20**:33-43.

Hall, R. O., G. E. Likens, and H. M. Malcom. 2001. Trophic basis of invertebrate production in 2 streams at the Hubbard Brook Experimental Forest. Journal of the North American Benthological Society **20**:432-447.

Hall, R. O., and J. L. Meyer. 1998. The trophic significance of bacteria in a detritus-based stream food web. Ecology **79**:1995-2012.

Hieber, M., and M. O. Gessner. 2002. Contribution of stream detrivores, fungi, and bacteria to leaf breakdown based on biomass estimates. Ecology **83**:1026-1038.

Hillebrand, H. 1999. Effect of interactions on the structure of microphytobenthos. Dissertation. Christian-Albrechts-Universität, Kiel.

Howarth, R. W., and S. G. Fisher. 1976. Carbon, nitrogen, and phosphorus dynamics during leaf decay in nutrient-enriched stream microecosystems. Freshwater Biology **6**:221-228.

Huryn, A. D., V. M. B. Huryn, C. J. Arbuckle, and L. Tsomides. 2002. Catchment land-use, macroinvertebrates and detritus processing in headwater streams: taxonomic richness versus function. Freshwater Biology **47**:401-415.

Iversen, T. M. 1975. Disappearence of autumn shed beech leaves placed in bags in small streams. Verhandlungen der Internationalen Verinigung für Theoretishe und Angewandte Limnologie **19**:1687-1692.

Johnson, R. K. 1999. Bedömningsgrunder för miljökvalitet.Sjöar och vattendrag : bakgrundsrapport 2 : biologiska parametrar. 4921.

Johnson, R. K., T. Wiederholm, and D. M. Rosenberg. 1993. Freshwater biomonitoring using individuals organisms, populations, and species assemblages of benthic macroinvertebrates. Pages 40-158 *in* D. M. Rosenberg and V. H. Resh, editors. Freshwater Biomonitoring and Benthic Invertebrates. Chapman and Hall, New York.

Jonsson, M. 2003. Investigation of species richness effects on ecosystem functioning using stream-living macroinvertebrates as model organisms. Doctoral Dissertation. Umeå Univesity, Umeå.

Jonsson, M., and B. Malmqvist. 2000. Ecosystem process rate increases with animal speacis richness: evidence from leaf-eating, aquatic insects. Oikos **89**:519-523.

Jonsson, M., B. Malmqvist, and P. Hoffsten. 2001. Leaf litter breakdown rates in boreal streams: does shredder species richness matter? Freshwater Biology **46**:161-171.

Kahlert, M. 1998. C:N:P ratios of freshwater benthic algae. Lake Erken -- 50 years of limnological research.:105-114.

Kaushik, N. K., and H. B. N. Hynes. 1971. The fate of the dead leaves that fall into the streams. Archiv für Hydrobiologie **68**:465-515.

Knoben, R. A. E., C. Roos, and M. C. M. van Oirshot. 1995. Biological Assessment Methods for Watercourses. UN/ECE Task Force on Monitoring and Assessment:86.

Leff, L. G., and J. V. McArthur. 1989. The effect of leaf pack composition on processing: A comparison of mixed and single species packs. Hydrobiologia **182**:219-224.

Lepori, F., D. Palm, and B. Malmqvist. 2005. Effects of stream restoration on ecosystem functioning: detritus retentiveness and decomposition. Journal of Applied Ecology **42**:228-238.

Loreau, M. 2000. Biodiversity and ecosystem functioning: recent theoretical advances. Oikos **91**:3-17.

Loreau, M., S. Naeem, P. Inchausti, J. Bengtsson, J. P. Grime, A. Hector, D. U. Hooper, M. A. Huston, D. Raffaelli, B. Schmid, D. Tilman, and D. A. Wardle. 2001. Biodiversity and ecosystem functioning: Current knowledge and future challenges. Science **294**:804-808.

Meyer, J. L., and C. Johnson. 1983. The influence of elevated nitrate concentration on rate of leaf decomposition in a stream. Freshwater Biology **13**:177-183.

Minshall, G. W. 1967. Role of allochthonous detritus in the trophic structure of a woodland springbrook community. Ecology **48**:139-149.

Moog, O., editor. 1995. Fauna Aquatica Austriaca. Version 1995. - Wasserwirtschaftskataster, Bundesministerium für Land- und Forstwirtschaft, Wien, Austria.

Mulholland, P. J., A. V. Palumbo, and J. W. Elwood. 1987. Effects of acidification on leaf decomposition in streams. Journal of the North American Benthological Society **6**:147-158.

Mulholland, P. J., J. L. Tank, D. M. Sanzone, W. M. Wollheim, B. J. Peterson, J. R. Webster, and J. L. Meyer. 2000. Food resources of stream macroinvertebrates determined by natural-abundance stable C and N isotopes and a N-15 tracer addition. Journal of the North American Benthological Society **19**:145-157.

Naeem, S., D. R. Hahn, and S. G. 2000. Producer-decomposer co-dependency influences biodiversity effects. Nature **403**:762-764.

Naeem, S., L. J. Thompson, S. P. Lawler, J. H. Lawton, and R. M. Woodfin. 1994. Declining biodiversity can alter the performance of ecosystems. Nature **368**:734-737.

Nelson, S. M. 2000. Leaf pack breakdown and macroinvertebrate colonization: bioassessment tools for a high-altitude regulated system? Environmental Pollution **110**:321-329.

Nikolcheva, L. G., and F. Bärlocher. 2005. Seasonal and substrate preferences of fungi colonizing leaves in streams: traditional versus molecular evidence. Environmental Microbiology **7**:270-280.

Niyogi, D. K., W. M. J. Lewis, and D. M. McKnight. 2001. Litter breakdown in mountain streams affected by mine drainage: biotic mediation of abiotic controls. Ecological Applications **11**:506-516.

Oberndorfer, R. Y., F. A. McArthur, and J. R. Barnes. 1984. The effect of invertebrate predators on leaf litter processing in an alpine stream. Ecology **65**:1325-1331.

Olson, J. S. 1963. Energy storage and the balance of producers and decomposers in ecologicla systems. Ecology **44**:322-331.

Pascoal, C., and F. Cássio. 2004. Contribution of Fungi and Bacteria to Leaf Litter Decomposition in a Polluted River. Applied and Environmental Microbiology **70**:5266-5273.

Pascoal, C., F. Cassio, and P. Gomes. 2001. Leaf breakdown rates: A measure of water quality? International Review of Hydrobiology **86**:407-416.

Pascoal, C., M. Pinho, F. Cassio, and P. Gomes. 2003. Assessing structural and functional ecosystem condition using leaf breakdown: studies on a polluted river. Freshwater Biology **48**:2033-2044.

Petchey, O. L., A. L. Downing, G. G. Mittelbach, L. Persson, C. F. Steiner, P. H. Warren, and G. Woodward. 2004. Species loss and the structure and functioning of multitrophic aquatic systems. Oikos **104**:467-478.

Petersen, R. C., and K. W. Cummins. 1974. Leaf processing in a woodland stream. Freshwater Biology **4**:343-368.

Peterson, B. J., and B. Fry. 1987. Stable Isotopes in Ecosystem Studies. Annual Review of Ecology and Systematics **18**:293-320.

Ponsard, S., R. Arditi, and C. Jost. 2000. Assessing top-down and bottom-up control in a litter-based soil macroinvertebrate food chain. Oikos **89**:524-540.

Rastetter, E. B., G. I. Ågren, and G. R. Shaver. 1997. Responses of N-limited ecosystems to increased CO2: A balanced-nutrition, coupled-element-cycles model. Ecological Applications **7**:444-460.

Reice, S. R. 1974. Environmental patchiness and the breakdown of leaf litter in a woodland stream. Ecology **55**:1271-1282.

Reice, S. R. 1977. The role of animal associations and current velocity in sediment specific leaf litter decomposition. Oikos **29**:357-365.

Reice, S. R. 1980. The role of substratum in benthic macroinvertebrate microdistribution and litter decomposition in a woodland stream. Ecology **61**:580-590.

Resh, V. H., and J. K. Jackson. 1993. Rapid assessment Approaces to Biomonitoring Using Benthic Macroinvertebrates. Pages 195-233 *in* D. M. Rosenberg and V. H. Resh, editors. Freshwater Biomonitoring and Benthic Macroinvertebrates. Chapman 6 Hall, London.

Rounick, J. S., and M. J. Winterbourn. 1986. Stable carbon isotopes and carbon flow in Ecosystems. Bioscience **36**:171-177.

Rounick, J. S., M. J. Winterbourn, and G. L. Lyon. 1982. Differential utilization of allochtonous and autochtonous inputs by aquatic invertebrates in some New Zealand streams: a stable carbon isotope study. Oikos **39**:191-198.

Rowe, J. M., S. K. Meegan, E. S. Engstrom, S. A. Perry, and W. B. Perry. 1996. Comparison of leaf processing rates under different temperature regimes in three headwater streams. Freshwater Biology **36**:277-288.

Royer, T. V., and G. W. Minshall. 2003. Controls on leaf processing in streams from spatial-scaling and hierarchical perspectives. Journal of the North American Benthological Society **22**:352-358.

Sampaio, A., R. Cortes, and C. Leao. 2001. Invertebrate and microbial colonisation in native and exotic leaf litter species in a mountain stream. International Review of Hydrobiology **86**:527-540.

Sterner, R. W., and J. J. Elser. 2002. Ecological stoichiometry : the biology of elements from molecules to the biosphere. Princeton University Press, Princeton.

Stewart, B. A., and B. R. Davies. 1989. The Influence of Different Litter Bag Designs on the Breakdown of Leaf Material in a Small Mountain Stream. Hydrobiologia **183**:173-177.

Stockley, R. A., G. S. Oxford, and R. F. G. Ormond. 1998. Do invertebrates matter? Detrital processing in the River Swale-Ouse. Science of the Total Environment **210**:427-435.

Stout, B. M., and C. B. Coburn. 1989. Impact of highway construction on leaf processing in aquatic habitats of eastern Tennessee. Hydrobiologia **178**:233-242.

Suberkropp, K. 1992. Interactions with invertebrates. Pages 118-134 *in* F. Bärlocher, editor. The ecology of aquatic hyphomycetes. Ecological Studies Analysis and Synthesis. Springer-Verlag, Berlin Heidelberg.

Suberkropp, K., and E. Chauvet. 1995. Regulation of Leaf Breakdown by Fungi in Streams - Influences of Water Chemistry. Ecology **76**:1433-1445.

Suberkropp, K., and M. J. Klug. 1980. The maceration of deciduous leaf litter by aquatic hyphomycetes. Canadian Journal of Botany **58**:1025-1031.

Suberkropp, K., M. J. Klug, and V. J. Cummings. 1975. Community processing of leaf litter in woodland streams. Verhandlungen der Internationalen Verinigung für Theoretishe und Angewandte Limnologie **19**:1653-1658.

Taylor, B. R., D. Parkinson, and W. F. J. Parsons. 1989. Nitrogen and Lignin Content as Predictors of Litter Decay-Rates - a Microcosm Test. Ecology **70**:97-104.

Teal, J. M. 1957. Community metabolism in a temperate cold spring. Ecological Monographs **27**:283-302.

Tuchman, N. C., R. G. Wetzel, S. T. Rier, K. A. Wahtera, and J. A. Teeri. 2002. Elevated atmospheric CO2 lowers leaf litter nutritional quality for stream ecosystem food webs. Global Change Biology **8**:163-170.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The River Continuum Concept. Canadian Journal of Fisheries and Aquatic Sciences **37**:130-137.

Vinebrooke, R. D., K. L. Cottingham, J. Norberg, M. Scheffer, S. I. Dodson, S. C. Maberly, and U. Sommer. 2004. Impacts of multiple stressors on biodiversity and ecosystem functioning: the role of species co-tolerance. Oikos **104**:451-457.

Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melillo. 1997. Human domination of Earth's ecosystems. Science **277**:494-499.

Walker, B. H. 1992. Biodiversity and ecological redundancy. Conservation Biology **6**:18-23.

Wallace, J. B., J. W. Grubaugh, and M. R. Whiles. 1996. Biotic indices and stream ecosystem processes: Results from an experimental study. Ecological Applications **6**:140-151.

Wallace, J. B., and J. R. Webster. 1996. The role of macroinvertebrates in stream ecosystem function. Annual Review of Entomology **41**:115-139.

Webster, J. R., and E. F. Benfield. 1986. Vascular plant breakdown in freshwater ecosystems. Annual Review of Ecology and Systematics **17**:567-594.

Webster, J. R., E. F. Benfield, T. P. Ehrman, M. A. Schaeffer, J. L. Tank, J. J. Hutchens, and D. J. D'Angelo. 1999. What happens to allochthonous material that falls into streams? A synthesis of new and published information from Coweeta. Freshwater Biology **41**:687-705.

Wellnitz, T., and N. L. Poff. 2001. Functional redundancy in heterogeneous environments: implications for conservation. Ecology Letters **4**:177-179.

Woodcock, T. S., and A. D. Huryn. 2005. Leaf litter processing and invertebrate assemblages along a pollution gradient in a Maine (USA) headwater stream. Environmental Pollution **134**:363-375.