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A CASE FOR USING LITTER BREAKDOWN TO ASSESS FUNCTIONAL STREAM INTEGRITY

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Abstract. Assessment of the condition of ecosystems is a critical prerequisite for alleviating effects of the multiple anthropogenic stresses imposed on them. For stream ecosystems, a multitude of approaches has been proposed for this purpose. However, they all rest on the assessment of structural attributes, even though it is generally recognized that adequate characterization of ecosystems requires information on both structure (pattern) and function (process). Therefore, we propose a complementary approach to stream assessment based on evaluating ecosystem-level processes. Leaf litter breakdown is a prime candidate to consider in this context. This is because of the pivotal role that allochthonous litter plays in streams, the demonstrated effects of anthropogenic perturbations on litter breakdown, and the relative ease of implementation. Leaf breakdown is governed by a variety of internal and external factors that complicate the partitioning of effects due to anthropogenic stress and natural variability (background noise), thus potentially limiting the sensitivity and robustness of litter breakdown assays. However, internal regulation factors can be controlled by standardizing assessment procedures, while variability due to external factors can be accounted for by stream classification and/or a comparative approach (e.g., downstream–upstream comparisons). Composite parameters such as ratios of breakdown rates in fine-mesh and coarse-mesh bags may further increase the power of litter breakdown assays. Analyses may also be extended to include both leaf-associated decomposer assemblages (i.e., structural measures) and processes (i.e., additional functional measures). Significant efforts are required for developing standard assessment schemes as refined as extant procedures based on structural stream attributes (e.g., structure of macroinvertebrate assemblages). These efforts are nevertheless worthwhile in view of the new dimension that is added to current assessment procedures when functional elements are incorporated.

Key words: bioassessment; decomposition; ecological integrity; ecosystem health; ecosystem-level process; environmental monitoring; functional integrity; leaf litter; river; stream.

INTRODUCTION

Streams, like other ecosystems, suffer from stresses imposed on them by human activities (e.g., Benke 1990, Zwick 1992, Allan and Flecker 1993, Dynesius and Nilsson 1994, Boon 2000). Stresses arise from environmental changes that occur at multiple scales. Relevant temporal scales range from hours to days (in the case of sudden events such as toxic spills) to decades and centuries in the case of long-term changes in land-use patterns (Harding et al. 1998) and climate (Rosenberg et al. 2000). Spatial scales include the stream channel proper, zones immediately adjacent to it, whole drainage basins, as well as much larger areas such as continents and the entire globe, through processes such as atmospheric nitrogen deposition or global warming. Societal awareness of these changes is growing, and both scientists and decision makers are seeking measures to alleviate the resulting negative effects (e.g., Convention on Biological Diversity 1992, Christensen et al. 1996, Stanford and Poole 1996, Ward 1998, Blöch 1999, Petts 1999). A critical prerequisite for such measures to be effective is assessment of the ecological state, or condition, of a stressed ecosystem. A multitude of approaches has been proposed for this purpose and a number of these are currently used by national and regional water authorities (e.g., Metcalfe-Smith 1994, Barbour et al. 1999, Norris and Thoms 1999, Jungwirth et al. 2000).

The concepts of ecological integrity and health provide a convenient framework for dealing with ecosystems affected by anthropogenic stresses. According to Karr (1991), ecological integrity (also known as biological, biotic, or ecosystem integrity) refers to a given state of a stream along a gradient of impairment that ranges from strongly impacted to pristine. More recently, the term ecological integrity has been reserved for the pristine endpoint of the impairment gradient only, whereas all other states represent different states of ecosystem health (Karr 1999). Ecosystem health thus embodies the notion of human values in the evaluation of ecosystems (Meyer 1997, Rapport et al. 1998),

whereas the concept of ecological integrity resides on a purely scientific base. The distinction between ecosystem integrity, in both its narrow and broad sense, and health is important. However, choice of one or the other concept and definition will not affect the basic arguments laid out in the present article. For the purpose of this paper, we will therefore use the word integrity in a loose sense to cover all the possibilities above, and will only differentiate them specifically when necessary.

Ecological integrity can be subdivided into two components, structural and functional integrity (Minshall 1996). From a biological point of view, structure refers to spatiotemporal patterns, particularly of biological communities and their resources, and function can be equated with ecosystem-level processes. Structural integrity may thus be defined as the qualitative and quantitative composition of biological communities and their resources under pristine conditions (to date largely hypothetical in most parts of the world; e.g., Hannah et al. 1994, Vitousek et al. 1997), or in an otherwise defined reference situation, depending on which concept of ecosystem integrity or health is used. Fish and macroinvertebrate assemblages have been the main focus for assessing structural integrity (Metcalfe-Smith 1994, Barbour et al. 1999, Norris and Hawkins 2000, Statzner et al. 2001), although a variety of alternative targets such as benthic algal communities, protozoans, and macrophytes have also been used (e.g., Barbour et al. 1999, Norris and Thoms 1999, Hill et al. 2000).

Functional integrity is a complement to structural integrity and refers to the rates, patterns, and relative importance of different ecosystem-level processes under reference conditions. Functional integrity defined in this way (i.e., in terms of ecosystem processes) is not currently considered in systematic assessments of the ecological conditions of streams (Bunn and Davies 2000). Thus the main purposes of the present paper are to provide a rationale for using ecosystem-level processes in stream assessment, to examine potentials and potential limitations for using leaf litter breakdown as an indicator process, and to provide a framework for working out the details of assessment procedures.

Ecosystem-Level Processes as a Measure of Stream Integrity

At present, official schemes for stream assessment rest almost exclusively on structural attributes of streams. This restriction is in contrast with the way ecologists view ecosystems, viz., as entities defined by both structure and function (e.g., Cummins 1974, Chapin et al. 1997). Because pattern (structure) determines process (function) and processes in turn affect patterns, both are linked. Structure and function nevertheless describe different aspects of the same entity, comparable to the two sides of a coin. Consequently, both must be considered if the integrity of an ecosystem as a whole is to be assessed (Matthews et al. 1982, Bunn and Davies 2000). Restriction to structural attributes ignores the complementary nature of pattern and process, thereby precluding comprehensive ecosystem assessment. This is the cardinal reason why, in our opinion, functional measures need to be incorporated into bioassessment schemes.

That changes in pattern do not always equate to changes in functional ecosystem attributes is not just a theoretical argument but has been demonstrated in experimental studies. Matthews et al. (1982) distinguish three possible outcomes in the response of structural and functional ecosystem attributes to stress: (1) structural changes without modification of functional parameters, (2) functional changes without alteration of community structure, and (3) changes in both structure and function. An example of the first case is provided by Nelson's (2000) study showing that macroinvertebrate community structure responded more sensitively to metal pollution than leaf breakdown in a high-altitude stream. The second case is illustrated by a study on gross primary production and community respiration (Bunn and Davies 2000). These processes clearly responded to nitrogen enrichment and increased stream water turbidity, whereas macroinvertebrate community structure, determined with an official assessment protocol, AusRivAS, failed to detect these stresses (Bunn and Davies 2000). Another example is provided by a study on periphyton in outdoor stream channels, where Rodgers et al. (1979) found primary production to be a better measure than biofilm structure for identifying experimentally induced stresses. The third case is illustrated by the study of Leland and Carter (1985). They observed that rates of algal biomass accumulation, and microbial respiration on and immobilization by decomposing litter were markedly depressed following copper additions, in line with copper-induced changes in periphyton community composition. Similarly, effects on several ecosystem processes (litter breakdown, generation and export of fine-particulate organic matter, secondary production of macroinvertebrates) corresponded to changes in standard biotic indices following experimental insecticide treatment of a stream (Wallace et al. 1996).

A number of additional arguments can be advanced in favor of using ecosystem processes in bioassessment (Bunn and Davies 2000). Like other biological variables, biologically driven processes provide an integrative measure of ecosystem integrity (Webster and Benfield 1986). Integration may work not only over time (Bunn et al. 1999), but also across organisms at different organizational levels. For example, litter decomposition in streams involves organisms ranging from bacteria and fungi to invertebrates and, in the tropics, fishes, suggesting that anthropogenic stresses on leaf breakdown can become effective through various targets and mechanisms.

A further argument is that process analyses depict a more general picture than the structure of stream biota

because processes are not critically dependent on the presence of a specific set of species. Processes are thus much less dependent on the geographical setting (e.g., Hunsaker et al. 1990, Bunn and Davies 2000). Compared to structural measures, this constitutes an advantage in practice, particularly when assessment schemes are to be standardized among geographically distinct regions possessing diverging species complements (e.g., in different regions within the United States or Australia, or countries within the European Union). Furthermore, taxonomic expertise is not normally required.

Even a cursory comparison of current approaches to bioassessment of streams and lakes illustrates how strongly tradition appears to influence ways of assessing ecosystem integrity. Bioassessment of lakes has traditionally been based on a functional ecosystem attribute (i.e., evaluation of the intensity of primary production, the most fundamental of all ecosystem processes). This approach has been extremely successful both scientifically and in terms of environmental improvement. The scientific success was due to the fact that cause (enhanced nutrient loading) and effect (e.g., increased algal production, hypolimnetic oxygen depletion, fish kill) were mechanistically linked, while success in terms of environmental policy was facilitated by effective translation of scientific understanding into political action, ultimately resulting in large-scale re-oligotrophication of lakes (e.g., Smith 1998). An instructive side issue of this re-oligotrophication success story is that planktologists commonly complain about the lack of structural criteria in the assessment of lake status, especially about the neglect of phytoplankton species composition. Clearly, stream bioassessment has gone the opposite way by focusing on structural ecosystem attributes and neglecting functional aspects.

Functional aspects of stream integrity have nevertheless been addressed indirectly (Merritt et al. 1999, Rawer-Jost et al. 2000, Statzner et al. 2001). These approaches are based on analyses of macroinvertebrate assemblages in terms of proportions of functionally defined groups, such as Cummins's (1974) functional feeding groups, and have even been included in the Rapid Bioassessment Protocols of the U.S. Environmental Protection Agency (Barbour et al. 1999). Although this functional group approach can be a useful complement to the examination of ecosystem processes, it must be borne in mind that it deduces information about ecosystem-level processes indirectly from the analysis of structural parameters. If or to what extent the information thus gained can serve as proxy for direct evaluation of ecosystem-level processes remains to be demonstrated.

Examples of Ecosystem-Level Processes in Streams

There are a variety of ecosystem-level processes that might be used in stream bioassessment (Reice and Wohlenberg 1993, Minshall 1996). Possible target processes include primary production of benthic algae (Rodgers et al. 1979, Leland and Carter 1985, Hill et al. 1997, Sabater et al. 1998, Bunn et al. 1999, Young and Huryn 1999) and macrophytes (Niemi et al. 1993), community respiration (Niemi et al. 1993, Hill et al. 1997, Bunn et al. 1999, Young and Huryn 1999), sediment respiration (Hill et al. 1998), secondary production of macroinvertebrates (Wallace et al. 1996), nitrogen fixation (Leland and Carter 1985), enzymatic transformations in epilithic biofilms (Sabater et al. 1998, Hill et al. 2000), and litter decomposition (Table 1). These processes may be driven either by diverse consortia of organisms or by rather specific groups such as the nitrifying or methanogenic bacteria. Other processes contain both biotic and abiotic components. The export of fine-particulate organic matter (Wallace et al. 1996) and the retention of dissolved nutrients are examples. In addition, purely abiotic processes, such as hydrological and geomorphological ones, or other large-scale processes involving biological elements (e.g., island dynamics) could be used in stream assessment. To date, only a rather small number of processes have even been considered for assessing stream integrity. This is in striking contrast to the immense investments made in working out metrics for examining macroinvertebrate assemblages (e.g., Rosenberg and Resh 1993, Metcalfe-Smith 1994, Barbour et al. 1999, Statzner et al. 2001). Thus it is clear that considerably more thought and empirical study must be devoted to determining which ecosystem-level processes can serve as good indicators of functional integrity.

One of the challenges is to identify the processes most useful in specific kinds of stress situations. Although comprehensive data sets are needed to make sound recommendations, ecological theory and a few data available at present already allow the pinpointing of potentially useful processes. For example, primary production of benthic algae would be expected to be an excellent indicator process in cases where light regimes of streams are altered. This could be the result of changes in riparian canopy cover (Sabater et al. 1998) or increased turbidity (Bunn and Davies 2000) accompanying intensified land use. As much as 68% of the variability in instream primary production was explained by the percent canopy cover of 15 streams whose riparian and catchment vegetation was disturbed to various degrees (Bunn and Davies 2000). The percent catchment cover by crops and pasture explained an additional 14% of the differences in instream primary production. Likewise, nutrient enrichment from both point and non-point sources (i.e., atmospheric depositions, agricultural runoff, sewage effluent), which may be exacerbated by reduced flow as a result of water abstraction, are likely to be reflected in levels of primary productivity. Stream acidification, in contrast, will not entail measurable effects if the production of epiphytic algal communities shows similar compen-

TABLE 1. Range of ratios of leaf litter breakdown coefficients at impacted (k_i) and reference (k_r) stream sites for different types of anthropogenic stresses.

Type of stress	k_i:k_r (%)	Plant species	Stream order†	Study sites	Location	Reference
A) Stream water quality						
1) Mine drainage effluent						
Copper	45–55	*Acer rubrum*	1/2	3 impacted downstream sites vs. 1 upstream reference site	VA, USA	Schultheis et al. (1997)
Zinc	18–125	*Salix* spp.		18 impacted vs. 9 reference sites	CO, USA	Niyogi et al. (2001)
Metals	22–34	*Alnus tenuifolia*	3	1 untreated and 1 treated downstream site vs. corresponding reference sites upstream	CO, USA	Gray and Ward (1983)
Coal	85‡	*Alnus glutinosa*	river	1 impacted downstream vs. 1 upstream reference site	UK	Maltby and Booth (1991)
	31–55	*Alnus glutinosa, Acer pseudoplatanus*	river	1 impacted downstream vs. 1 upstream reference site	UK	Bermingham et al. (1996)
	54–72	*Alnus serrulata*	1	2 impacted streams vs. 1 adjacent reference stream	AL, USA	Scheiring (1993)
2) Acidic precipitation	11	*Fagus sylvatica*	2	1 acidified vs. 1 adjacent reference stream	France	Dangles and Guérold (1998)
	68	*Fraxinus americana*	1	1 acidified vs. 1 reference stream	PA, USA	Kimmel et al. (1985)
3) Other chemicals						
Chlorine	57–105	*Potamogeton crispus*		1 manipulated downstream vs. 1 upstream reference site in each of 4 experimental streams	MN, USA	Newman et al. (1987)
Chlorine plus ammonia	27–136	*Potamogeton crispus*		1 downstream manipulated vs. 1 upstream reference of 7 experimental streams	MN, USA	Newman and Perry (1989)
p-Cresol	75–134	*Populus deltoides*		2 manipulated vs. 2 reference experimental stream channels	WI, USA	Stout and Cooper (1983)
Insecticide	42–49	*Acer rubrum, Rhododendron maximum*	1	2 manipulated streams vs. the same 2 streams prior to manipulation and 1 independent reference stream	NC, USA	Whiles et al. (1993)
4) Nutrients						
Nitrate	85–190	*Acer circinatum, A. macrophyllum, Alnus rubra, Pseudotsuga menziesii*		2 manipulated vs. 1 reference experimental stream channel	WA, USA	Triska and Sedell (1976)
	278–289	*Betula lenta, Robinia pseudoacacia*	1	1 impacted vs. 1 adjacent reference stream	NC, USA	Meyer and Johnson (1983)
	164–760	*Liriodendron tulipifera*	1/2	7 high-nutrient vs. 3 adjacent low-nutrient streams	AL, USA	Suberkropp and Chauvet (1995)

TABLE 1. Continued.

Type of stress	k_i:k_r (%)	Plant species	Stream order†	Study sites	Location	Reference
Phosphate	120–127	*Quercus rubra*	2	1 manipulated vs. 1 reference site in each of 2 streams	TN, USA	Elwood et al. (1981)
	207	*Alnus viridis*	1	Fertilized vs. unfertilized leaf packs in a single stream	Switzerland	Robinson and Gessner (2000)
B) Vegetation						
1) Plantation of exotic tree species						
Pine	31§	*Pinus strobus, Acer rubrum*	1	2 impacted vs. 2 reference hardwood forest streams	NC, USA	Whiles and Wallace (1997)
Eucalypt	23–59§	*Eucalyptus globulus, Alnus glutinosa*	1	2 impacted streams vs. 1 adjacent reference stream	Spain	Pozo et al. (1998)
	72‡,§	*Eucalyptus globulus, Castanea sativa*	1–5	3 impacted vs. 3 adjacent reference streams	Portugal	Abelho and Graça (1996)
Willow	800	*Salix babylonica, Eucalyptus blakelyi*	3	1 impacted stream	Australia	Pidgeon and Cairns (1981)
	186–214§	*Salix babylonica, Eucalyptus camaldulensis*	river	3 impacted vs. 3 adjacent reference sites	Australia	Schulze and Walker (1997)
2) Logging	116–494	*Cornus florida, Acer rubrum, Liriodendron tulipifera, Rhododendron maximum*	2	3 impacted streams vs. 1 adjacent reference stream	NC, USA	Benfield et al. (1991)
	142	*Acer saccharum*	2	1 impacted vs. 1 reference stream	VA, USA	Griffith and Perry (1991)
	100–284	*Cornus florida, Acer rubrum, Rhododendron maximum*	2	1 stream, before and after perturbation	NC, USA	Webster and Waide (1982)
3) Agriculture	292‡, ‖	*Chionochloa rigida* or *C. rubra*		3 impacted vs. 3 reference streams	New Zealand	Young et al. (1994)
	69–138‖	*Acer saccharum*		1 impacted vs. 1 forested reference stream	Ontario, Canada	Bird and Kaushik (1992)
	131	*Quercus alba*	2	2 impacted sites vs. 1 forested reference site upstream	MI, USA	Tuchman and King (1993)
C) Miscellaneous						
1) Highway construction	25–263¶	*Quercus alba*	3/5	4 impacted vs. 2 reference sites	TN, USA	Stout and Coburn (1989)
2) Stream regulation	197	*Alnus tenuifolia*	river	1 impacted vs. 1 adjacent reference stream	CO, USA	Short and Ward (1980)
3) Thermal pollution	139–307	*Acer saccharum, A. negundo, Cornus florida, Platanus occidentalis*	river	1 impacted vs. 1 upstream reference site	VA, USA	Paul et al. (1978)

Notes: Some of the breakdown coefficients used for calculating ratios were calculated from graphs or tabulated data in the respective papers. State abbreviations: VA, Virginia; CO, Colorado; AL, Alabama; PA, Pennsylvania; MN, Minnesota; WI, Wisconsin; NC, North Carolina; WA, Washington; TN, Tennessee; MI, Michigan.

† An empty cell indicates that the stream order cannot be inferred from the cited reference.

‡ Calculated from reported linear breakdown coefficients.

§ Breakdown of exotic species in impacted streams vs. that of native species in reference streams.

‖ Data from several seasons.

¶ Values depend on the type of investigated site and mesh size.

satory responses to lowered pH as lake phytoplankton (e.g., Schindler 1987). This prediction contrasts with the consistently observed and occasionally dramatic effect of lowered pH on leaf litter breakdown, a process that has been shown also to be affected by changes in riparian vegetation and nutrient enrichment (Table 1; Webster and Benfield 1986). Similarly, organic matter transformations by heterotrophic biofilms may be good indicators of land use alterations, such as large-scale drainage and wetland elimination, which can affect the dynamics of dissolved organic matter (Gergel et al. 1999) on which heterotrophic biofilm metabolism depends. Such organic matter transformations can be measured by means of simple enzymatic assays (e.g., Sinsabaugh et al. 1991). The retention of carbon and nutrients also will be influenced by the extent of biofilm development (Martí et al. 1997), and is likely to indicate a lack of bed-forming spates as occurs often below impoundments and water diversion devices. Finally, anaerobic processes, such as denitrification and methanogenesis, may be particularly sensitive indicators of a lack of spates and/or increased sediment load when resulting in clogging of the stream bottom.

The remainder of this paper will focus mainly on litter breakdown. This process is currently best documented by both a comprehensive set of background data and specific information on effects of anthropogenic disturbances (Anderson and Sedell 1979, Webster and Benfield 1986, Maltby 1992, Webster et al. 1995, Gessner et al. 1997, 1999, Suberkropp 1998). In addition, leaf litter and its breakdown play pivotal roles in stream food webs and energetics (Cummins et al. 1989, Gregory et al. 1991, Graça 1993, Webster et al. 1995, 1999, Wallace and Webster 1996, Wallace et al. 1997, Webster and Meyer 1997, Suberkropp 1998). The breakdown process thus suggests itself as a starting point for developing a diagnostic tool to assess functional stream integrity. However, many of the principles and arguments developed below apply to other ecosystem processes as well. Primary production in streams has also been studied to a considerable extent, sometimes in relation to anthropogenic disturbances, and is clearly another prime candidate for assessing functional integrity. Likewise, other processes may turn out to be powerful functional indicators once sufficient empirical data have been collected.

Demonstrated Effects of Anthropogenic Stress on Litter Breakdown

A prerequisite for using any type of indicator of ecosystem integrity is that it responds unequivocally to anthropogenic stresses. Such effects have been demonstrated in a number of case studies on litter breakdown in streams (Table 1; Webster and Benfield 1986). Pollution by mine drainage is among the best documented stressors affecting the process, with most pertinent investigations documenting a strong reduction in breakdown rates (Table 1), regardless of whether streams receive pretreated or untreated mine effluents (Gray and Ward 1983). For example, leaf breakdown rates were reduced by half at three sites impacted by pyrite mine drainage effluents, where stream water exhibited copper concentrations two orders of magnitude higher than at an upstream reference site (Schultheis et al. 1997). Taxonomic richness and abundance of benthic macroinvertebrates was also reduced at the impacted sites, but recovered after a treatment system was put in operation. This alleviation did not, however, translate into a similar recovery of leaf breakdown, suggesting that functional stream integrity remained impaired. In the most comprehensive study to date, Niyogi et al. (2001) likewise found a significant negative correlation between leaf breakdown rate and concentrations of dissolved zinc at 27 stream sites differing in extent and type of pollution originating from mining activities. Slower leaf breakdown also occurred downstream of a coal mine effluent carrying high metal loads (Maltby and Booth 1991, Bermingham et al. 1996) as well as in other similarly impacted systems (Table 1).

Stream acidification through atmospheric inputs and related impacts (e.g., elevated aluminum concentrations) can have similarly striking effects on litter breakdown (Table 1), especially in poorly buffered softwater streams. A particularly strong effect has been reported from a stream in the Vosges Mountains of France that drains a catchment underlain by granite and sandstone bedrock (Dangles and Guérold 1998). Even under circumneutral conditions, leaves of the dominant deciduous tree species in the area (*Fagus sylvatica*) decompose slowly (breakdown coefficient k of 0.0018/d). At pH 4.5, breakdown was virtually halted; a mass loss of only ~3% was observed eight months after exposure of leaves in the stream (k = 0.0002/d). As a result, breakdown rates were as much as nine times lower than in an adjacent circumneutral stream (average pH of 7.2; Dangles and Guérold 1998) and even >20 times lower (k = 0.0045/d) than in another softwater mountain stream in the same country (Gessner and Chauvet 1994). These results were later confirmed in a study involving seven headwater streams (Dangles and Guérold 2001), and are also consistent with a range of other studies demonstrating that decreases in stream pH are accompanied by reduced litter breakdown rates (Table 1; Webster and Benfield 1986). The broad agreement across studies addressing both point and nonpoint pollution in different regions indicates that leaf breakdown rate is an excellent indicator of functional ecosystem impairment resulting from stream water acidification and related stresses.

A variety of other published reports illustrate the utility of litter breakdown to assess the effect of anthropogenic stresses on stream integrity (Table 1; Webster and Benfield 1986). Modification of riparian vegetation is among the most obvious impacts (Vought et al. 1998, Stevens and Cummins 1999), as the composition and density of streamside vegetation affects

litter inputs to streams and, consequently, the litter breakdown process. Logging activities in the watershed, including road construction, have been shown to result in pronounced effects (Benfield et al. 2001, Abelho and Graça 1996, Pozo et al. 1998), as can unwilling replacement of natural riparian vegetation (Smock and McGregor 1988). Changes in plant species composition may result in either slower or faster breakdown of the leaf litter entering the affected streams (Table 1; Webster and Benfield 1986).

A striking example of altered breakdown rates comes from a whole-stream study involving long-term experimental application of an insecticide (Chung et al. 1993, Whiles et al. 1993, Wallace et al. 1996). Breakdown of two leaf species was greatly depressed as long as the insecticide treatment continued, whereas in nearby reference streams, interannual variation in litter breakdown rates was small. This observation, together with the similar breakdown rates in control and treated streams in the years prior to insecticide application, suggests that rates of leaf breakdown were reduced primarily because of the experimental elimination of insect fauna. This effect was not compensated for (or not fully so) by microbial activity, although leaf-degrading fungi did not appear to be affected by the insecticide (Suberkropp and Wallace 1992). In contrast, a dramatic decline of detritivorous invertebrates (shredders) at sites affected by treated sewage effluents corresponded to an increase in breakdown rates in the study by Pascoal et al. (2001). This suggests that a stimulation of microbial activity (e.g., by enhanced nutrient availability; Grattan and Suberkropp 2001) even overcompensated the decline of shredders. If breakdown rates had not been determined and functioning of the system had been deduced from changes in macroinvertebrate community structure (i.e., the abundance and relative proportion of shredders), the conclusions of this study about system functioning would have been exactly opposite to the real effect.

In the second year after the insecticide treatment was discontinued in the study by Wallace et al. (1996), breakdown rates increased greatly, such that they significantly exceeded the rates observed both before the treatment and in the reference stream. This acceleration suggests that during recovery from poisoning, leaf breakdown became impaired in a different, but similarly severe, way than during the treatment. These findings call attention to at least two points for consideration in developing bioassessment schemes based on ecosystem-level processes. First, process rates can deviate from normal by either a depression or acceleration, and second, stressors may induce secondary effects (cf. Frost et al. 1999) that can operate at different time scales than the straightforward primary effect.

Potential Limitations in Perspective

Using ecosystem-level processes for assessing the ecological integrity of streams potentially poses a number of problems. At least three objections may be raised. One criticism is that functional measures are technically difficult and/or time consuming, and therefore not cost effective (e.g., Matthews et al. 1982, Crossey and La Point 1988). Compared to some simple structural measures, the assessment of processes may indeed be more complicated and expensive (Wallace et al. 1996); however, this is not invariably so (Bruns et al. 1992, Reice and Wohlenberg 1993, Young et al. 1994, Minshall 1996). For example, manipulation of some standard leaf packs and measurement of simple integrative parameters associated with them, such as the difference in mass over a defined period, is clearly straightforward compared to the determination of structural measures involving species inventories. Species inventories not only tend to be laborious but also require specific expertise. In a comparative cost analysis, it has indeed been shown that the determination of process rates need not be more expensive than quantifying even simple parameters of biological structure, such as total macroinvertebrate density or periphyton biomass (Niemi et al. 1993). Thus criticism relating to high cost and effort does not inevitably apply to the assessment of ecosystem-level processes, but must be carefully considered in the individual case. Moreover, should time constraints, technical difficulties, and costs (within certain acceptable limits) be striking arguments if only a part of ecosystem integrity is assessed when the complementary functional component is ignored?

Another argument relates to the idea that ecosystem-level processes do not respond sensitively enough to anthropogenic stress. To some extent this issue constitutes a fundamental dilemma. This is because indicators of ecosystem integrity (both functional and structural ones) need to meet two partially incongruent requirements; they must respond to even minor changes in the environmental factor(s) of interest yet vary little in response to other variables. The underlying rationale is that false signals are avoided (i.e., indication of effects that do not exist) while real effects are detected even when they are small (Bunn and Davies 2000). This double requirement can become inextricable when generality is sought in the sense that a given metric is to indicate impairments resulting from a multitude of stress types occurring at different scales. In practice, ideal indicators will thus be difficult to find, making trade-offs among generality, sensitivity, and robustness inevitable.

The putative caveat of limited sensitivity has several other components that need to be considered separately. Low sensitivity can arise from natural variability, method-related variability, or compensatory effects within species assemblages that can occur when a stress factor affects some types of organisms involved in the process but not others. Only the last point is specific to the use of ecosystem-level processes in bioassessment, the former two affect structural indicators alike. Currently, concerns about compensatory responses are based more

on intuition than on facts from empirical work in streams. However the point is not easily refuted, and because sensitivity is critically important for any measure of ecosystem integrity, the pertinence of compensatory effects must be seriously examined. Empirical work on specific processes in specific situations is needed to provide conclusive answers.

Data from long-term experimental manipulations of lakes highlight the intricate nature of the compensatory response issue. Pelagial primary production responds sensitively to the addition of limiting nutrients, which in most lakes is phosphorus (Smith 1998), but reduction in phosphorus loading does not always result in immediate decreases in primary production. Acidification is another important stress imposed on lakes, which in contrast to the clear-cut results from nutrient loading, has not induced changes in primary production in experimental studies (e.g., Schindler 1987). Secondary production of zooplankton also remained unchanged following decreases in lake water pH, even though the zooplankton community composition changed distinctly (Frost et al. 1995). Strong compensatory effects are thus indicated. Nitrification, in contrast, completely ceased even after an initial moderate lowering of pH to a value of 5.8 (Rudd et al. 1988), and other microbial processes appeared to be affected as well (Frost et al. 1999). These contrasting outcomes from nutrient addition and acidification experiments, and the varied responses of different processes to acidification, illustrate that a given process may respond sensitively to one type of anthropogenic stress while showing virtually no response to another type, even if it is severe. Therefore, a key challenge, in view of identifying indicators of functional integrity, is to ascertain which kinds of stresses lead to predictable changes of which ecosystem-level processes under which circumstances.

In addition to compensatory effects, sensitivity of ecosystem processes is reduced by both natural and method-related variability (e.g., Webster and Benfield 1986, Young and Huryn 1999). Assays based on ecosystem processes must be able to cope with the resulting background noise, just like any other assessment tool. This challenge can be met by standardization. Possible sources of variability are differences in experimental procedures. For example, in litter breakdown assays, exposure technique (e.g., leaf bag vs. leaf pack), mesh size of leaf bags, and size and location of leaf packs in a stream (e.g., pool vs. riffle) are variables that need to be controlled. There are also differences in breakdown rates among leaf species (Petersen and Cummins 1974, Webster and Benfield 1986, Gessner and Chauvet 1994). Timing of assays in phase with natural leaf inputs is another aspect to be taken into account (Maloney and Lamberti 1995, Baldy and Gessner 1997). However, proper timing of assays is as straightforward as standardization of leaf species and experimental procedures. Consequently, none of the sources of background noise related to methodological aspects should compromise the sensitivity of litter breakdown assays in a serious way. Likewise, when accounting for methodological effects, Young and Huryn (1999) observed that landscape features affected ecosystem processes markedly, in particular the ratio of two key processes, gross primary production and community respiration.

The reduction of background noise resulting from natural variability is a greater challenge than method-related variability. Differences in litter breakdown rates, for example, may be large across streams (Hill et al. 1992, Suberkropp and Chauvet 1995, Webster et al. 1995). Stream size, geographical location, and water chemistry (e.g., ionic content, nutrient availability) are some of the potentially confounding factors. Controlling these factors is essential in those cases where appropriate reference systems are unavailable for direct comparison (e.g., comparisons before–after, upstream–downstream or, more generally speaking, between disturbed and corresponding reference sites). Stream classification thus becomes a key issue in developing assays relying on ecosystem processes, just as is the case for structural parameters (Karr 1999).

A Framework for Assessing Functional Stream Integrity Using Litter Breakdown as an Indicator Process

An important issue apart from standardization is the choice of the specific parameters that characterize the litter breakdown process. Parameters reflecting the speed of breakdown are the most obvious to consider. For example, breakdown rate coefficients (k values) calculated by regressing leaf mass remaining of standard leaf packs against time may be used. Breakdown coefficients based on an exponential decay model are the standard measure reported in the literature on litter breakdown in streams (Petersen and Cummins 1974, Suberkropp 1998); such models may, or may not, compensate for temperature effects (Cummins et al. 1989). Alternatively, the time needed to achieve 50% or 95% mass loss from standard leaf packs may be chosen (Wallace et al. 1996). Another possibility is the percent of litter mass remaining after a defined period that leaves were exposed in a stream (Maltby et al. 1995, Jonsson et al. 2001). Although there are subtle differences among these parameters, and data may need to be handled differently when parametric statistical comparisons are sought (e.g., arcsine square root transformation in the case of percent litter mass remaining), all three should give useful results. Choice of one or the other parameter will therefore depend to some extent on convenience and arbitrary conventions.

Table 2 shows an example of how metrics based on litter breakdown coefficients may be devised. The simplest case is when leaf breakdown is compared in impacted stream reaches and corresponding reference sites, or at a single site before and after an incident has occurred. The thresholds tentatively proposed in Table

TABLE 2. Framework of the breakdown rate module for assessing functional stream integrity by means of litter breakdown assays; this module can be complemented by a variety of additional modules.

Method	Assessment parameter	Criterion	Score
Comparison with reference	Ratio of breakdown coefficients at impacted (k_i) and reference (k_r) site	$k_i:k_r$ = 0.75–1.33	2
		$k_i:k_r$ = 0.5–0.75 or 1.33–2.0	1
		$k_i:k_r$ < 0.5 or >2.0	0
Absolute value	Breakdown coefficient at impacted site (k_i)	k_i = 0.01–0.03/d	2
		k_i = 0.005–0.01/d or 0.03–0.05/d	1
		k_i < 0.005/d or >0.05/d	0
Absolute value of ratio	Ratio of breakdown coefficients in coarse (k_c) and fine (k_f) mesh bags†	$k_c:k_f$ = 1.2–1.5	2
		$k_c:k_f$ = 1.5–2.0 or <1.2	1
		$k_c:k_f$ > 2.0	0

† If sizable numbers of shredders are predicted to occur in the stream.

2 are derived from information, although rather limited at present, on natural variability in both space and time. Variability at the reach scale has been examined in a few studies. For example, Fabre and Chauvet (1998) found breakdown coefficient (k values) of alder leaves to vary from 0.0204/d to 0.0365/d at seven sites in a mountain stream (their sites S4–S10). The lower and upper limits of this range correspond to 75% and 133% of the average breakdown coefficient calculated for all sites taken together. A similar range is obtained for the interannual fluctuations in breakdown rates of both maple (n = 7) and rhododendron (n = 6) leaves decomposing in an Appalachian Mountain stream, Satellite Branch (Webster et al. 1999). Thus we conclude that at the present state of knowledge, breakdown coefficients within the limits of 75–133% around the mean of a local reference system reveal no clear evidence of an impact on ecosystem functioning. This situation is given the score 2 in Table 2.

The data set collected by Jonsson et al. (2001) can be used to assess the magnitude of natural variability at a scale larger than the reach. The study comprised a total of 23 boreal streams of different size (first to seventh order), located up to 700 km apart within an ecoregion and sampled in two consecutive years. The exponential breakdown coefficients of alder leaves deduced from this study (k = 0.0079–0.0357/d) correspond to relative range limits of ~50–200% of the mean. Deviations of that magnitude, or more, are indeed regularly encountered in impacted streams (Table 1). Young et al. (1994) found ratios of breakdown coefficients between impacted and reference streams (k_i:k_r) of ~3.0 in a comparison of three streams surrounded by agricultural land with three less modified streams running through natural grassland. Similarly, rates of leaf breakdown in the six most heavily polluted streams studied by Niyogi et al. (2001) were reduced to 18–32% of the average of their nine reference systems. We thus propose as a starting point that breakdown rates outside the apparent range of natural variability at the catchment or regional scale (50–200% of the mean) may be considered indicative of severely compromised stream functioning (score 0 in Table 2).

In many situations, a reference situation is not readily available. In these cases, it would be advantageous to be able to resort to absolute target values. As an example we provide target values for alder leaves (*Alnus glutinosa* (L.) Gaertn.) calculated from litter breakdown experiments conducted in softwater upland streams in Europe (e.g., Gessner and Chauvet 1994, Canhoto and Graça 1996, Fabre and Chauvet 1998, Pozo et al. 1998, Hieber and Gessner 2002); target values for other leaf species and regions will differ from those in Table 2, often being lower (Petersen and Cummins 1974, Webster and Benfield 1986, Webster et al. 1995, 1999). Standardization of litter quality and appropriate classification of streams become especially critical when absolute values are used. To start with, stream categories could be defined following existing schemes based on morphological, chemical, and/or structural biological criteria (e.g., Rosgen 1996).

Improved sensitivity and robustness of litter breakdown assays may be achieved when ratios of breakdown rates rather than plain values are used. For examples, the ratio of breakdown coefficients in fine-mesh and coarse-mesh bags could prove powerful, because changes in the ratio would indicate a shifting balance in the contribution of microorganisms and detritivorous invertebrates (shredders), thus accounting for some of the potential compensatory responses. Similarly, ratios of breakdown coefficients of fast-decomposing and recalcitrant leaf species might be useful, if different mechanisms contribute to the breakdown of the two types of leaves and/or consideration of time scales is important in the assessment of the examined anthropogenic stress. Lastly, as suggested by Stevens and Cummins (1999), ''predictability'' of breakdown rates, rather than rates per se, might be used to indicate impairment of functional integrity.

In addition to metrics relating directly to litter mass loss, a number of other parameters associated with litter breakdown are theoretically available for assessment purposes. Some of those constitute structural measures associated with litter breakdown, and thus do not assess an ecosystem-level process per se. Examples are the abundance or biomass of shredders, various metrics

relating to litter-associated invertebrate communities (Wallace et al. 1996, Pascoal et al. 2001), or the relative importance of bacteria and fungi. On the other hand, parameters such as nitrogen and phosphorus immobilization in decomposing leaves offer possible targets for the examination of additional processes linked to litter breakdown (Leland and Carter 1985).

Conclusion

In conclusion, we propose to implement a complementary approach to assessing ecological integrity of streams consisting in the analysis of ecosystem-level processes in addition to structural biological parameters. A variety of processes hold potential for meeting this objective. Leaf litter breakdown is a good candidate process notably because of its central role in stream ecosystem functioning, relative ease of implementation, and a sizeable background database. Leaf breakdown in streams is governed by a variety of internal and external factors that may complicate separation of effects due to anthropogenic stress and natural variability, thus potentially limiting sensitivity and robustness. However many confounding factors can be controlled by standardizing assessment procedures, including the use of litter from specified reference leaf species, stream classification, and/or comparative approaches. In addition, if breakdown rates per se are not sensitive enough, one may resort to composite parameters such as ratios of breakdown coefficients in coarse-mesh and fine-mesh bags. Furthermore, analyses may be extended to a wide range of both structural and functional parameters associated with the breakdown process. Ultimately, it is desirable to include additional ecosystem-level processes besides litter breakdown into stream bioassessment, thus strengthening comprehensive assessment of these ecosystems that are persistently exposed to profound anthropogenic stresses.

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