BioOne COMPLETE

Stream microbial ecology

Author: Findlay, Stuart

Source: Journal of the North American Benthological Society, 29(1) : 170-181

Published By: Society for Freshwater Science

URL: https://doi.org/10.1899/09-023.1

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://complete.bioone.org/journals/Journal-of-the-North-American-Benthological-Society on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

J. N. Am. Benthol. Soc., 2010, 29(1):170–181
© 2010 by The North American Benthological Society
DOI: 10.1899/09-023.1
Published online: 5 February 2010

Stream microbial ecology

Stuart Findlay[1]
Cary Institute of Ecosystem Studies, Box AB, Millbrook, New York 12545 USA

Abstract. Microbes play numerous roles in stream ecosystems. They carry out key processes in stream nutrient cycles and are responsible for a large part of organic matter breakdown. Advances over the past 25 y in our understanding of which microbes are linked to specific processes have been rapid and fundamental, in part, because of improvements in methods. It is now clear that immobilization of inorganic nutrients and other transformations are just as important as release of nutrients during organic matter decomposition. Microbial biomass is recognized as a key portion of trophic transfer, but our understanding of the pathways of connection have changed. Information on the actual composition of microbial communities is very recent, and it is still unclear whether there are consistent biogeographic patterns in freshwater bacterial composition. One of the major areas of potential advancement is clarifying the linkage between microbial community composition and ecosystem function. Determining the strength of the connection between microbial assemblage composition and the processes they catalyze remains a technical and conceptual hurdle. Quantifying the strength of this linkage seems necessary to understand variability in both composition and function because feedbacks are likely in cases where the link is strong. The future of the field is bright, but we need to understand how microbes and the processes they carry out will respond to climate change and novel stream management approaches.

Key words: bacteria, fungi, decomposition, immobilization, trophic link, respiration.

Why microbes? Microbes play a crucial role in functioning of all ecosystems. Microbes can be an important food resource, are responsible for decomposition of organic matter (OM), and have unique capabilities for transforming nutrients (N in particular) from one form to another. The term, *microbe*, refers to a size class of organisms, rather than to a taxonomic group. More genotypic and phenotypic variability exists within microbes than among all other organisms combined. Microbes include Bacteria, Archaea, and Eukarya (Pace 2006), viruses, autotrophs, heterotrophs, parasites, and predators. Some of these organisms have macroscopic features, such as mushrooms and algal colonies, whereas others are individual cells only a fraction of a micrometer in size. Ecosystems exist where microbes are the only form of life (deep within geological formations), but even in more diverse ecosystems, microbial biomass and metabolic functioning can dominate mass and process budgets. For the purpose of reviewing the past 25 y of progress in microbial ecology, I will concentrate on the heterotrophic microbes (Bacteria, Archaea, and Fungi) that are responsible for much of the material and energy flow in streams.

[1] E-mail address: findlays@caryinstitute.org

Microorganisms collectively have tremendous capabilities for degrading organic C compounds, and they can use a wide array of electron acceptors. As autotrophs, they are capable of fixing C, and they can use sunlight or many different electron donors. One challenge is understanding how much of this observed functional variability is caused by gene expression within a taxonomic group and how much is a consequence of representation of different groups within assemblages. Microbes are unique in that detecting and measuring what they do (e.g., decay OM, immobilize NH_4^+) is easier than determining their standing stock or identity. Techniques for quantifying the net result of their metabolism (e.g., light–dark bottles, Winogradsky columns) have been in common use for well over a century, but only now are we developing a good sense of how many taxa are present in any ecosystem or whether regular patterns in taxonomic composition exist over time or across systems.

For many years, the field of microbial ecology was hampered by a lack of techniques to estimate the biomass of different microbial groups, but this limitation has been largely resolved by application of direct microscopy for estimating bacterial biomass (Findlay and Arsuffi 1989) and ergosterol assays to

Downloaded From: https://complete.bioone.org/journals/Journal-of-the-North-American-Benthological-Society on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

quantify fungi (Gessner and Chauvet 1993). Molecular techniques can provide information on microbial identity at levels of resolution ranging from deoxyribonucleic acid (DNA) sequencing at the fine scale to various fingerprinting options to measure community similarity/dissimilarity at the broad scale (Logue et al. 2008). The next frontiers are to connect presence and process by exploring the abundance and regulation of functional genes that are part of the genetic identity of microorganisms and to identify the actual mechanisms by which they acquire energy, transform elements, and alter their environment (Zak et al. 2006).

Few of the advances in methods required for measurement of microbial abundance, composition, or function have been developed in stream ecosystems. Microbial ecologists studying marine plankton probably have made the most significant improvements in methods, e.g., by perfecting the use of fluorochromes to detect and enumerate bacteria (Hobbie et al. 1977) and incorporating radiotracers to measure growth (Fuhrman and Azam 1980). Much of the recent work on developing clone libraries and taxon-specific primers (Giovannoni 2004) has been done in marine systems. Testing whether concepts of biogeography could be applied to microbes, given their capacity for wide and rapid dispersal, was done first in oceans and lakes (Horner-Devine et al. 2004, Lindström and Bergstrom 2004, Reche et al. 2005) and more recently in stream systems (Battin et al. 2004, Logue et al. 2004, Fierer et al. 2007). In addition, in many cases where microbes were used to test theories or develop concepts because of the advantages of microbes as study organisms (small samples, ubiquity, large numbers of individuals), work began in marine or lentic systems (Horner-Devine et al. 2004), perhaps because the technical problems were smaller in these systems than in streams.

I offer 2 thoughts to address why scientists working in the inherently strong discipline of stream ecology (as shown throughout this issue of *J-NABS*) have not played a more important role in advancing microbial ecology. First, the technical difficulties in diverse benthic habitats make streams a less-than-ideal test bed. However, microbial ecologists studying soil systems share many of the problems of scientists working in streams. In both systems, most bacterial cells and fungal hyphae are tightly associated with particles or surfaces. This association causes difficulties when isolating cells or extracting compounds quantitatively. Moreover, significant interference is encountered in both systems from noncellular materials, such as humics. Second, stream ecologists have a strong interest in process-derived questions, such as the balance between transport and transformation. This focus has led to a preponderance of questions that deal with the net *effect* of organisms rather than with links between organisms and processes. Perhaps stream ecologists have simply by-passed questions of microbial community structure and interactions.

Patterns in microbial composition associated with geographic distance and variation in function clearly do exist (see below), and the wealth of information on stream microbial function might encourage future research that bridges the gap between the processes that are occurring and which microbes are present (Knapp et al. 2009). In a fashion, the past emphasis on function could have made streams, with their wide diversity of habitats and rates, perfect systems in which to consider whether functional variability is associated with differences in microbial community structure. Thus, we might expect more work on these important questions to be done in streams in the near future.

Taxonomic Composition and Distribution

Taxonomic composition

The Bacteria and Archaea contain tremendous genetic diversity, and despite recent efforts, it is certain that the vast majority of variation in stream bacterial communities has yet to be quantified. Most attention has been given to the oxic, heterotrophic bacteria inhabiting leaf packs and surface sediments because of their important roles in many ecological processes (e.g., **McNamara and Leff 2004**[1], **Olapade and Leff 2004**). However, numerous cases of high concentrations of anaerobically produced metabolic products, such as methane (e.g., Jones et al. 1995) and N_2O (e.g., Beaulieu et al. 2008) have made it clear that low-O_2 habitats are reasonably common in streams. For example, bacterial anaerobic metabolism, with release of methane and use of non-O_2 electron acceptors, occurs deep within hyporheic sediments where O_2 can be depleted (Baker 2000, **Morrice et al. 2000**).

Our ability to determine taxonomic composition has grown dramatically (**Leff and Lemke 1998**), but techniques still offer very different levels of resolution. At the finest level, DNA sequencing and matching to known organisms provides the closest thing to identification of species, although the species concept transfers poorly to bacteria. At coarser levels, approaches, such as division-level probes, can be used to probe for target groups, e.g., α-, β-, and γ-

[1] Boldface indicates paper was published in *J-NABS*

Downloaded From: https://complete.bioone.org/journals/Journal-of-the-North-American-Benthological-Society on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

proteobacteria (Kirchman et al. 2004, Logue et al. 2008). Last, several finger-printing approaches (denaturing gradient gel electrophoresis [DGGE], temperature gradient gel electrophoresis [TGGE]) can be used to assess the degree of similarity among a set of samples with no information on actual taxonomic composition (Nikolcheva et al. 2003, Das et al. 2007). For instance, terminal restriction-fragment length polymorphism (tRFLP) can be used to document seasonal recurrence of certain taxa and is particularly effective at describing shifts in composition when augmented with sequencing of some bands (Hullar et al. 2006).

An important step is to link specific taxa with the functions they carry out. The prerequisite is the existence of primers to enable identification of both the taxon and the gene of interest. For example, the abundance of certain NH_4^+-oxidizing Archaea varies between 2 river systems (Herfort et al. 2009) showing, in this case, that the process might be maintained by redundant taxa.

By far, most information available on aquatic fungi is for the hyphomycetes that are responsible for leaf decomposition in wadeable streams. These fungi actually are the asexual stages of ascomycetes and basidiomycetes rather than a phylogenetically distinct group. These microorganisms produce readily visible and identifiable spores (conidia) that make feasible tracking their presence and abundance, as measured by reproductive output (e.g., Ingold 1942, Bärlocher and Kendrick 1974). Typically, their reproductive cycle begins with a period (d–wk) of hyphal growth to accumulate sufficient resources for spore production. Next, spore-containing structures are produced above the leaf surface, and spores are released to the water column. The ability to identify spores collected from water samples has made possible good surveys of hyphomycete presence. Clear community-level differences exist based on water chemistry, temperature, and other factors (Bärlocher 1992). The fruiting (sexual) stage of basidiomycetes might be significant for decay of the nonsubmerged parts of logs. Chytrid fungi are especially interesting because they can infect/kill amphibians, and thereby affect the distribution of an important top consumer (Whiles et al. 2006).

All major groups of protozoans (flagellates, ciliates, and amoeba) are abundant and can be significant grazers of other microbes in stream ecosystems (Ribblett et al. 2005). Protozoa occur at high densities ($\sim 10^6$ individuals/g sediment) and are consumed by meiofauna (**Bott and Borchardt 1999**). Protozoa can be much more abundant in accumulations of OM and fine sediments than in other habitats (Gücker and Fisher 2003). Most protozoa do not have strong abilities to hold themselves in place during high flow, so they rely on sheltered habitats and small size to keep them within the low shear-stress boundary layer. Ciliate abundances can be as high as 10^6 individuals/m^2 (Reiss and Schmid-Araya 2008), and the smaller flagellates probably reach much higher densities (Schmid et al. 2000).

Biogeography

Study of large-scale patterns in microbial communities has lagged behind similar studies of other taxonomic groups, partly because of methodological constraints but perhaps more importantly because of the idea that dispersal was so widespread that disjunct patterns were unlikely (Baas-Becking 1934). Many microbes have some form of resting stage that is protected from harsh environmental conditions (desiccation, temperature extremes) and, therefore, is capable of long-distance transport by winds, water, or in association with other organisms. However, medium- (kilometers to tens of kilometers) to large- (hundreds to thousands of kilometers) scale differences in microbial composition clearly exist (Reche et al. 2005, Crump et al. 2007, Findlay et al. 2008).

Most of these patterns probably are driven by variation in strong environmental selectors. For example, soil and stream pH affect bacterial communities (Fierer et al. 2007), and stream water chemistry has large effects on both bacterial and fungal colonizers of leaf litter (**Harrop et al. 2009**). Examples from the tundra of North America (Crump et al. 2007) and high-elevation lakes (Reche et al. 2005) indicate that dispersal limitation can cause bacterioplankton communities to differ among lakes. Perhaps the best summary of our present state of knowledge is that some strong selectors (pH, OM attributes) clearly exist, but these selectors are not universal drivers of real-world patterns in microbial composition. Dispersal limitation might be important, but when dispersal limitation is critical might not be a simple question of geographic distance.

At much finer scales, substrate quality is capable of altering relative growth rates of microbial taxa and should be manifested as differences in taxonomic composition among substrates (Findlay and Sinsabaugh 2006, Judd et al 2006). However, no consistent body of evidence indicates differentiation of microbial communities among leaf types (see Das et al. 2007), although Fazi et al. (2005) found that the quality of OM in stream microhabitats strongly influenced bacterial composition.

Downloaded From: https://complete.bioone.org/journals/Journal-of-the-North-American-Benthological-Society on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Missing linkages

What is still missing from our understanding of microbial composition and distribution is knowledge of the functional links connecting measures of which groups are present, their inherent metabolic capacity, actual expression of that capacity, and consumption or release of biomolecules in the environment. In principle, tools targeted at each of these steps are available (see table 2 in Zak et al. 2006). However, the huge array of microbes, microhabitats, and processes in stream ecosystems complicates the decision regarding which section of the complex network to tackle first. Nevertheless, stream ecologists have a large range of processes and disciplinary points of view, and enough information exists that they should be able to generate interesting and ecologically relevant hypotheses about connections between composition, activity, and ecosystem function. I suggest that we begin by proposing which processes are most probably limited by availability of the appropriate taxa based on the number of taxa known to have a certain capability. For instance, the ability to use NO_3^- as an electron acceptor is widespread, so rates of denitrification are unlikely to be controlled by absence of denitrifying bacteria. However, the ability to degrade certain complex organic molecules, such as lignin, is less common, and organisms with this ability might not always be present despite the presence of appropriate substrate.

Biomass and Production

Biomass

Stream microbes occur in or on all surfaces and voids in stream habitats, and some reasonably predictable shifts in abundance and composition occur among locations within these habitats. In low-order streams, biomass in sediments or on surfaces exceeds the planktonic microbial biomass, but the relative contribution can change with season and flow (Edwards et al. 1990). Surface benthic sediments, including OM accumulations, harbor the highest microbial biomass (100–500 mg microbial C/m^2) in most streams (Findlay et al. 2002).

The relative abundance of bacteria vs fungi is quite predictable in stream habitats. For instance, the relative abundance of fungi is much more sensitive to particle size than is bacterial abundance (Findlay et al. 2002), so bacterial biomass predominates on fine particulate OM and (generally) in deeper sediments (Findlay et al. 2002). However, even small quantities of coarse particulate OM allow fungal biomass to exceed bacterial biomass in a stream. Fungi dominate pooled microbial biomass on leaves and wood (e.g., Hieber and Gessner 2002), whereas bacteria dominate sediments and fine particles. In hyporheic sediments, which usually lack large accumulations of coarse particulate OM, the fungal contribution is small relative to bacterial biomass (**Ellis et al. 1998**, **Crenshaw et al. 2002**).

Fungal biomass makes up the largest part of heterotrophic microbial biomass in the first days to weeks of leaf litter decay (Findlay and Arsuffi 1989, **Weyers and Suberkropp 1996**). Therefore, patches of leaf litter within a stream or streams with high and sustained litter inputs can be hot spots of fungal abundance. However, fungal mass fluctuates rapidly and might be less stable (reliable) in stream ecosystems where litter inputs are periodic and litter is retained only for short periods.

Biofilms occur on stone, wood, and plant surfaces, and these highly diverse communities are responsible for significant primary production and C metabolism (Battin et al. 2008). Bacteria inhabiting epilithic biofilms can reach abundances of 10^7 cells/cm^2 of surface area, and their abundance is probably limited by the C supply or time since disturbance. Biofilms proceed through a reasonably predictable growth phase with colonization and growth of bacteria and algae (**Sobczak 1996**) leading to a thickening of the layers until basal cells become starved of O_2, C, or nutrients because of poor supply from stream water flowing past the biofilm. Biofilms are susceptible to physical disruption by high flow, scouring by sediment particles in transit, or disturbance by grazing insects. The rate of biofilm accumulation varies dramatically among streams (Hudson et al. 1992) and over time within a stream (Findlay et al. 1993). The presence or absence of a significant autotrophic component strongly influences overall biofilm growth (Haack et al. 1988) and can alter amounts and pathways of C transfer and degradation within the biofilm (**Rier et al. 2007**).

Biofilms rely on delivery of gases, OM, and inorganic nutrients from flowing stream water, and they often have physical structures, such as macropores and streamers (Battin et al. 2003), that facilitate flux from the overlying water into the core of the biofilm itself. Both algae and bacteria produce extracellular material that helps provide some structure and could help adsorb dissolved organic matter (DOM) from the overlying water (Freeman and Lock 1995, **Findlay and Sobczak 1996**, Fisher 2003,) and allow extracellular enzymes to yield energetically valuable monomers.

Downloaded From: https://complete.bioone.org/journals/Journal-of-the-North-American-Benthological-Society on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Production

Productivity is the generation of new OM over time. New OM production might be the result of conversion of inorganic C into organic C (primary production) or conversion of existing organic C into a new organism (secondary production). Stream microbes are significant primary and secondary producers. Unicellular algae and cyanobacteria account for much of the photosynthetic autotrophic production in streams (**Larned 2010**), but microbial chemosynthetic autotrophic production also can be present. Perhaps the best known example occurs during nitrification when certain bacteria oxidize NH_4^+ in the presence of O_2 to derive energy for fixation of CO_2. In addition to new production, the net result is transformation of NH_4^+ to NO_3^-, and this process has been well-studied (e.g., Kemp and Dodds 2002). Nitrifiers have low growth efficiencies, so the actual C production from this process is unlikely to be high in most streams. Moreover, heterotrophic microorganisms might outcompete nitrifiers for NH_4^+ when C supply is high (Bernhardt and Likens 2002). Other avenues of chemosynthetic primary production include oxidation of sulfide by colorless and photosynthetic bacteria, annamox, and oxidation of ferrous iron. These reactions undoubtedly occur in stream sediments or where anoxic groundwaters reenter oxic environments (Baker et al. 2000), but the contribution to whole-system primary production is probably small in most streams.

Microbial secondary production at the expense of other organic materials is almost always a major part of whole-system secondary production. For instance, fungal production on decomposing leaves can be as much as 10% of litter input (**Methvin and Suberkropp 2003**). Aside from its absolute quantitative importance, microbial secondary production often converts otherwise unavailable OM into a form that can be ingested and assimilated by macroconsumers. Perhaps the most significant of these conversions is the uptake of DOM from solution and generation of new bacterial biomass (e.g., **Wiegner et al. 2005**). DOM is almost always the largest flux of organic C through a stream segment (**Mulholland 1997**), and unless it is converted to particulate OM via secondary production, DOM is unavailable to larger consumers. In the hyporheic zone, the influx of DOM can easily make up most of the C available (Sobczak and Findlay 2002). Uptake constants for individual identifiable DOM constituents can be large enough that DOM removal and temporary retention as microbial biomass is a significant fraction of downstream transport (Kaplan and Newbold 2003). Transfer to higher trophic levels is related to efficiency of removal from the overlying water and the proportion of assimilated C respired.

A fruitful area for future research might be to determine whether various pathways of production of microbial biomass are equally important in supporting higher trophic levels, e.g.: 1) Might geochemical conditions necessary for some chemosynthetic production limit grazer access to microbial biomass? 2) Is fungal production a more stable C source than rapidly cycling bacterial biomass? When seeking answers to such questions, the heterogeneity of stream ecosystems might be a strength rather than an impediment.

Food Webs

Our understanding of the direct contribution of microbial biomass to stream food webs has changed dramatically in the past 25 y (see *Progression* below). We are now at the point of asking when, where, and why do microbes make a significant contribution to higher trophic levels rather than viewing the contribution of microbes to the food web as a yes or no dichotomy. Stream organisms with the morphological or behavioral capacity to focus their feeding on small particles can derive significant C and N from consumption of microbes (Edwards 1987). Less selective (larger?) feeders are unlikely to rely on such small particles. In either case, multiple microbial trophic transfers will have an overall negative effect on transfer of organic C to higher trophic levels. The production efficiency for microbes is *at best* ~50% (del Giorgio and Cole 1998). Therefore, more than 1 or 2 interconversions within the microbial loop will impose severe respiratory costs on the overall transfer.

Progression

The first experimental demonstration that microbes played an important part in stream food webs might (perhaps) be traced to a seminal paper by Kaushik and Hynes almost 40 y ago (1971; Fig. 1). They observed that N accumulation in decomposing leaf litter was much slower when antifungal antibiotics were added to experimental treatments, a result suggesting that fungal growth was responsible for a significant portion of increases in leaf food quality. Moreover, consumers ate only small quantities of leaf material that had been autoclaved or aged in antibiotics relative to consumption of untreated leaf discs. Their findings and other similar studies (e.g., Iversen 1973) led to the view that microbial growth on litter was an essential prerequisite to consumption by larger consumers and that the microbial biomass was

Downloaded From: https://complete.bioone.org/journals/Journal-of-the-North-American-Benthological-Society on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

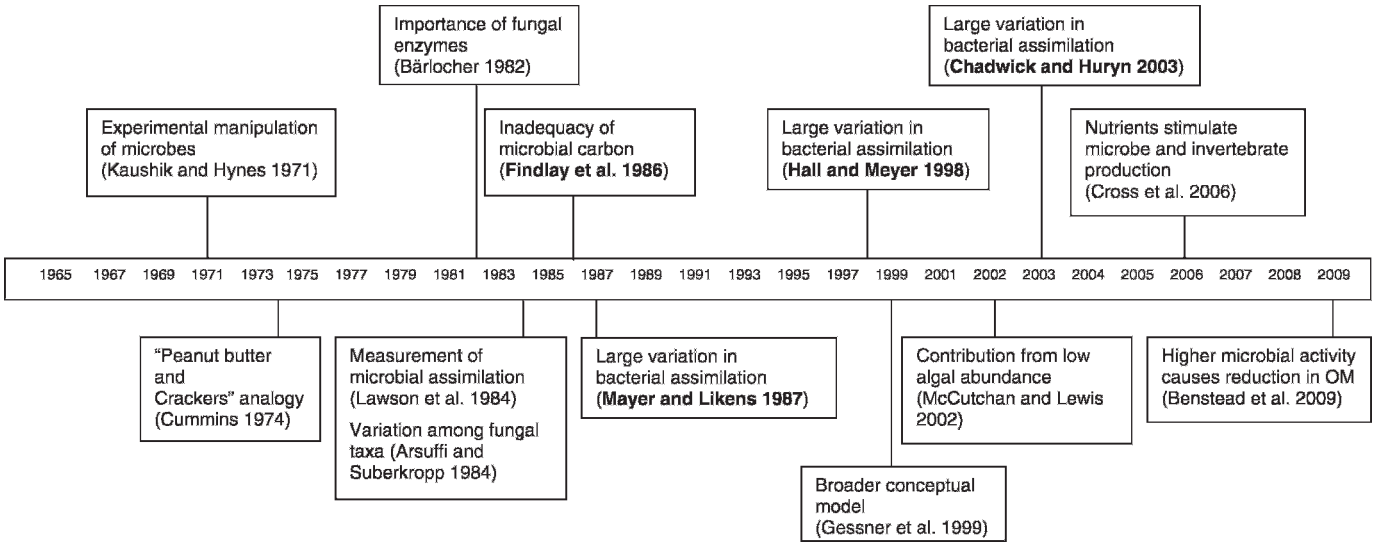


FIG. 1. Timeline of key studies aimed at quantifying the trophic linkages and interactions between stream microbes, organic matter pools, and larger consumers. Boldface indicates paper was published in *J-NABS*.

essentially the only digestible portion of leaf litter. This view was captured by Ken Cummins in his ''peanut butter and crackers'' analogy (Cummins 1974; Fig. 1), in which he suggested the microbial biomass was akin to peanut butter and the leaf substrate itself was indigestible cracker. Although probably not his intent, this effective analogy lead to a widely held paradigm that only the microbes were available to consumers and the leaf substrate contributed nothing. Numerous studies have shown associations between microbial colonization and apparent food quality (e.g., Arsuffi and Suberkropp 1984 [Fig. 1], Lawson et al. 1984 [Fig. 1], Graça et al. 2001), but answers to the question regarding the importance of microbes vs leaf material became more complex once estimates of actual microbial biomass became feasible (**Findlay et al. 1986**; Fig. 1). The quantity of bacterial and fungal biomass as C in the detritus–microbe complex is typically a only a small percentage of total leaf mass and reaches a maximum within a few weeks (e.g., **Methvin and Suberkropp 2003**). Therefore, absolute mass of substrate is so much greater than the mass of microbial C that leaf material might make the largest contribution to consumer C demand, despite the fact that the assimilation efficiency for microbial C is much greater (perhaps 5–10× higher) than assimilation efficiency for the nonliving leaf substrate. Selective feeding by larger consumers occurs at relatively large scales (i.e., one leaf vs another) and little opportunity exists to avoid consumption of the nonliving substrate. Therefore, assimilated C generally will be derived from both sources. However, smaller consumers might have finer-scale selective ability, such that they can feed on microbial biomass itself or on enriched patches on an individual leaf. Hall and Meyer (**1998**; Fig. 1) found that many smaller taxa could derive a significant portion of their C demand from bacterial biomass.

Microbes clearly play a role in altering detritus food quality, and microbes can have several important effects in addition to their contribution to consumer C needs. For example, aquatic hyphomycete fungi have differing abilities to degrade polymers present in leaf litter, and different hyphomycetes cause differential softening (predigestion?) of the detritus substrate (Arsuffi and Suberkropp 1984). Experiments in which leaf material is exposed to fungal enzymes show anticipated improvements in food quality (Bärlocher 1982; Fig. 1), a result suggesting the enzymatic effects of fungi on substrate digestibility might be as significant as their direct assimilation as microbial biomass.

In essence, our views of microbial roles in detrital food webs have changed dramatically in recent decades, although the basic observation that consumers prefer microbially conditioned leaf detritus has been confirmed numerous times. Detritus with high microbial biomass probably should be viewed as a cue for food quality rather than merely as a good source of microbial C. Stable-isotope approaches show that fairly low-biomass portions of the food web, such as benthic algae, might contribute disproportionately to higher trophic levels (**Mayer and Likens 1987**, McCutchan and Lewis 2002; Fig. 1).

The arguments presented above focus on C demands, which clearly are important for metabolic

Downloaded From: https://complete.bioone.org/journals/Journal-of-the-North-American-Benthological-Society on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

needs. However, N is frequently a limiting nutrient in consumer diets. N concentrations are much greater (perhaps 5×) in microbial biomass than in the substrate (the C concentrations are essentially the same in the 2 compartments). Thus, one could argue based on simple algebra that the proportional N contribution to consumers would be greater from microbial than from substrate biomass (Sanzone et al. 2001).

Inorganic nutrient availability can directly limit microbial growth, but recent perspectives on nutrient limitation have expanded to consider longer-term and whole-ecosystem consequences of nutrient enrichment (e.g., **Chadwick and Huryn 2003**; Fig. 1). Early researchers investigating the role of nutrients in leaf decay generally considered increased microbial activity as a positive effect (e.g., Suberkropp and Chauvet 1995). However, recent authors have asked how acceleration of microbial metabolism affects consumer secondary production over the longer-term. Results from a whole-stream fertilization experiment showed the expected stimulation of various microbial processes (Greenwood et al. 2007) and at least transient increases in invertebrate production (Cross et al. 2006; Fig. 1). However, clear signs also have been observed that the OM pools of the fertilized streams are being ''mined'' (Benstead et al. 2009; Fig. 1). Eventually, the decline in OM pools caused by faster microbial decomposition will cause decreases in heterotrophic growth, which will be followed by decreases in other processes dependent on detrital energy, such as denitrification or nutrient immobilization.

Thus, our view of microbes in detrital food webs has come full circle from an initial focus on their degradative activities (because those activities were easiest to measure) through a phase of directly tracking their transfer to consumers and now back to the larger consequences of how variation in rates and pathways of decomposition affect the whole stream ecosystem (see Gessner et al. 1999; Fig. 1).

Nutrient Cycles

Microbial growth on organic and inorganic surfaces in streams has several important effects on nutrient cycles. Microbes must assimilate inorganic N and P from the surrounding water (immobilization) because of low nutrient content of the litter. The most direct approach to quantifying immobilization is to calculate the absolute mass of N or P in a unit of decomposing litter (Caraco et al. 1998, **Gessner et al. 1998**) or to measure assimilation of added external tracer ^{15}N into microbial biomass (Sanzone et al. 2001). Increases in absolute quantity (not % composition) are evidence for incorporation of exogenous nutrients into the detrital–microbe complex. Another approach is addition of tracer levels of N or P isotopes to streams and detection of these tracer isotopes in various pools of OM. Following addition of $^{15}N\text{-}NH_4$ to several small streams, fine benthic OM and epilithon showed rapidly increasing levels of ^{15}N, a result indicating removal of exogenous N from the water column (Mulholland et al. 2008). This capacity for immobilization is widely recognized, and stream nutrient amendment studies have provided very clear evidence for greater microbial standing stocks (and hence nutrient immobilization) following addition of environmentally realistic quantities of N and P (e.g., Grattan and Suberkropp 2001, Gulis and Suberkropp 2003a, b, Cross et al. 2006, Greenwood et al. 2007). This removal of N or P from stream water can be quantitatively important, but the removal lasts only until the microbial biomass is remineralized. If net microbial growth is sustained for weeks to months of litter decay, then drawdown of inorganic nutrients can be a persistent feature and represents transformation of N and P from inorganic to organic forms. If microbial growth is neither large nor sustained, the effect of immobilization on stream nutrient export will be minimal.

Bacteria also have diverse abilities to alter the form of nutrients (particularly N) in stream ecosystems. Direct assimilation of N by stream bacteria and fungi on decomposing leaf litter has been measured or assumed to be a significant process for many decades (Cummins 1974), and at times, N-fixation by stream microbes can be a significant process (**Marcarelli et al. 2008**).

Actively metabolizing bacteria can use various forms of N as electron acceptors in the absence of O_2, and the most important of these processes certainly is denitrification. Denitrification results in permanent removal of reactive N (NO_3^-) from aquatic ecosystems. Thus, there is tremendous interest in whether this process might mitigate N loadings to streams before they cause water-quality problems in receiving waters. Numerous surveys and experiments have been designed to separate which of the 3 likely controlling factors (C supply, NO_3^- availability, and absence of O_2) drives variability in denitrification rates (**Martin et al. 2001**, **Inwood et al. 2005**, **Starry et al. 2005**, Arango et al. 2007, **Arango and Tank 2008**). NO_3^- supply frequently appears as the proximate control of denitrification capacity, a result suggesting that streams retain some capacity to consume N as more NO_3^- is loaded to streams (see Mulholland et al. 2008). This result suggests that the demand for terminal electron acceptors generally cannot be met

Downloaded From: https://complete.bioone.org/journals/Journal-of-the-North-American-Benthological-Society on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

by the available supply of O_2. Use of NO_3^- as an electron acceptor is nearly as energetically favorable as using O_2, and as NO_3^- becomes available, it probably replaces other electron acceptors with lower energy yields. Stream denitrification capacity ultimately must be affected by C availability because OM is probably the major electron donor in all stream systems. This dependence on OM shows up in several ways, e.g., detection of high denitrification rates in accumulations of OM (**Schaller et al. 2004**). Documentation of ultimate vs proximate control of denitrification rates is not straight-forward because accumulations of OM also allow depletion of O_2, forcing use of alternate electron acceptors. Stream denitrifiers rarely have the capacity to reduce annual N delivery downstream (**Martin et al. 2001**), but they certainly have their greatest effect during summer low flow when the sensitivity of downstream waters might be maximal (Royer et al. 2006)

Stream microbes have the metabolic capacity to alter other aspects of the N cycle. These processes might not cause quantitatively large alterations in N fluxes, but they have interesting and relevant effects on other elements. For instance, denitrification can be coupled to oxidation of S^{2-}, S^0 or Fe^{2+} (Burgin and Hamilton 2007). Thus, some stream habitats receiving significant quantities of these reduced species might show significant conversion of NO_3^- without requiring a source of available organic C. Bacteria also can oxidize other metals (e.g., Mn), and these processes can lead to metal deposition on surfaces. These reactions are most likely in streams carrying particularly high metal concentrations, such as acid mine drainage (Farag et al. 2007), but also could occur in localized areas receiving metal-rich ground water.

The likelihood that the physicochemical conditions allowing these various nutrient transformations will vary over short time scales in streams suggests potential research questions about the stability or resilience of these processes to change. N transformations requiring certain taxa and chemical gradients might be much more sensitive to flow alterations or landuse change than, for instance, N mineralization, which probably has high redundancy.

Future

Making microbes relevant to ecology

A significant divide exists between ecology and microbial ecology despite the huge contribution of microbial processes to important element cycles and transformations. With some notable exceptions (Long and Morin 2005, Bell et al. 2005), a broad and fruitful interchange has not occurred about how knowledge of microbes contributes to general ecological knowledge or how microbial systems might be good test cases for answering questions. In some respects, this lack of exchange is understandable. For instance, the species concept applies poorly to many microbial groups, and questions about competition become irrelevant if the players can rapidly change their genotypes and phenotypic capabilities. However, rapid response times and the possibility for multiple response variables (growth, element transformation) should make many microbes powerful cases for testing ecological principles. Moreover, looming practical issues of stream management and response to climate change would benefit from consideration of microbial processes. At the same time, these future changes in the stream physicochemical template will provide another axis of variability. I have argued throughout this overview that embracing variability in controlling factors and processes will lead to a stronger integration of microbial ecology into stream ecology.

Consideration of most stream microbial processes is not presently extensive when scientists and managers choose options for stream restoration or modification. In part, this failure to consider microbial process occurs because the practices necessary to ensure positive outcomes for larger target organisms (fishes) or processes (bank stability) are so complex and expensive that justifying consideration of additional factors is difficult. Nevertheless, it seems reasonable to assess how current practices affect the large array of microbial processes necessary for stream function. For instance, physical structures intended to add diversity to flow conditions (boulders, logs, etc.) also retain OM and, thus, provide substrate for microbial populations (Entrekin et al. 2008). Such effects could be benefits of some particular action, and if anticipated, might increase justification for necessary expenses. Moreover, some stream improvement plans could have unanticipated negative consequences on microbial process critical to restoration success. Until we understand all of the connections and trade-offs of a restoration strategy, including those related to microbes, we cannot have a useful debate about the true ecological, economic, and social costs/benefits of our management activities.

In contrast to the relatively small numbers of studies that made direct examinations of microbes as model systems, some microbial processes have been used extensively as response variables in experimental manipulations of resource diversity. For instance, many studies have addressed how mixtures of leaf species decompose relative to decomposition of individual species. Patterns often

Downloaded From: https://complete.bioone.org/journals/Journal-of-the-North-American-Benthological-Society on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

are not predictable, and both increases and decreases in decomposition rates have been reported for mixtures relative to single species of leaves (**Swan and Palmer 2004**, Kominoski et al. 2007b, Lecerf et al. 2007). Thus, we are not presently prepared to predict the effect on mass loss, food quality, or nutrient immobilization when riparian zone vegetation and, therefore, leaf inputs to streams, becomes more or less heterogeneous.

Future temperature changes will have predictable effects on rates of most microbial processes (Rowe et al. 1996, Acuña et al. 2008), but altered atmospheric composition might have the greatest and most widespread consequences. Many experiments have shown dramatic effects of elevated CO_2 levels on leaf chemical composition and, therefore, litter C content and composition (**Kominoski et al. 2007a**, **Rier et al. 2002**). In general, higher CO_2 is expected to cause higher C:N ratios, which will lead to slower decay and a potential for greater immobilization of inorganic nutrients. Litter inputs are often significant sources of C to streams, but higher atmospheric CO_2 is likely to increase the magnitude and persistence of this terrestrial–aquatic subsidy.

Stream hydrology will be significantly altered if predicted changes in amount of precipitation or its frequency lead to changes in persistence of flow or high-flow events. Inundation pattern can alter microbial communities (**Rees et al. 2006**) and in situ decomposition (Langhans et al. 2008). Consequences of climate change will be far-reaching and probably complex, but our basic understanding of streams and factors controlling their ecological functions is solid enough to make reasonable predictions about change. Moreover, the widespread availability of important techniques (hydrodynamic models and powerful tracer approaches) should enable quantification of change over the next 25 y.

I would argue that we are no longer limited by methods (although significant challenges remain), and that inclusion of microbes in discussions of stream biodiversity, resiliency, and functioning is both feasible and necessary. Microbes play a central role in many stream processes, and researchers working on emerging issues in stream ecology will need to include microbial processes explicitly in conceptual and quantitative models of stream functioning.

Acknowledgements

This manuscript was improved by comments from 2 anonymous referees and Michelle Baker. This paper is a contribution to the Cary Institute of Ecosystem Studies.

Literature Cited

ACUÑA, V., A. WOLF, U. UEHLINGER, AND K. TOCKNER. 2008. Temperature dependence of stream benthic respiration in an Alpine river network under global warming. Freshwater Biology 53:2076–2088.

ARANGO, C. P., AND J. L. TANK. 2008. Land use influences the spatiotemporal controls on nitrification and denitrification in headwater streams. Journal of the North American Benthological Society 27:90–107.

ARANGO, C. P., J. L. TANK, J. L. SCHALLER, T. V. ROYER, M. J. BERNOT, AND M. B. DAVID. 2007. Benthic organic carbon influences denitrification in streams with high nitrate concentration. Freshwater Biology 52:1210–1222.

ARSUFFI, T. L., AND K. SUBERKROPP. 1984. Leaf processing capabilities of aquatic hyphomycetes: interspecific differences and influence on shredder feeding preferences. Oikos 42:144–154.

BAAS-BECKING, L. G. M. 1934. Geobiologie, of inleiding tot de milieukunde, Serie 18/19. Van Stockum's Gravenhange, The Hague, The Netherlands.

BAKER, M. A., C. N. DAHM, AND H. M. VALETT. 2000. Anoxia, anaerobic metabolism and biogeochemistry of the stream-water ground-water interface. Pages 260–286 *in* J. B. Jones and P. J. Mulholland (editors). Streams and groundwaters. Academic Press, San Diego, California.

BÄRLOCHER, F. 1982. The contribution of fungal enzymes to the digestion of leaves by *Gammarus fossarum* (Koch) (Amphipoda). Oecologia (Berlin) 52:1–4.

BÄRLOCHER, F. 1992. The ecology of aquatic hyphomycetes. Springer-Verlag, Berlin, Germany.

BÄRLOCHER, F., AND B. KENDRICK. 1974. Dynamics of fungal populations on leaves in a stream. Journal of Ecology 62: 761–791.

BATTIN, T. J., L. A. KAPLAN, S. G. FINDLAY, C. S. HOPKINSON, E. MARTÍ, A. I. PACKMAN, J. D. NEWBOLD, AND F. SABATER. 2008. Biophysical controls on organic carbon fluxes in fluvial networks. Nature Geoscience 1:95–100.

BATTIN, T. J., L. A. KAPLAN, J. D. NEWBOLD, AND C. M. E. HANSEN. 2003. Contributions of microbial biofilms to ecosystem processes in stream mesocosms. Nature 426:439–442.

BATTIN, T. J., A. WILLE, AND R. PSENNER. 2004. Large-scale environmental controls on microbial biofilms in high-alpine streams. Biogeosciences 1:159–171.

BEAULIEU, J. J., C. P. ARANGO, S. K. HAMILTON, AND J. L. TANK. 2008. The production and emission of nitrous oxide from headwater streams in the Midwestern United States. Global Change Biology 14:878–894.

BELL, T., J. A. NEWMAN, B. W. SILVERMAN, S. L. TURNER, AND A. K. LILLEY. 2005. The contribution of species richness and composition to bacterial services. Nature 436:1157–1160.

BENSTEAD, J. P., A. D. ROSEMOND, W. F. CROSS, J. B. WALLACE, S. L. EGGERT, K. SUBERKROPP, V. GULIS, J. L. GREENWOOD, AND C. J. TANT. 2009. Nutrient enrichment alters storage and fluxes of detritus in a headwater stream ecosystem. Ecology 90:2556–2566.

BERNHARDT, E. S., AND G. E. LIKENS. 2002. Dissolved organic carbon enrichment alters nitrogen dynamics in a forest stream. Ecology 83:1689–1700.

BOTT, T. L., AND M. A. BORCHARDT. 1999. Grazing of protozoa, bacteria, and diatoms by meiofauna in lotic epibenthic communities. Journal of the North American Benthological Society 18:499–513.

BURGIN, A. J., AND S. K. HAMILTON. 2007. Have we overemphasized the role of denitrification in aquatic ecosystems? A review of nitrate removal pathways. Frontiers in Ecology and the Environment 5:89–96.

Downloaded From: https://complete.bioone.org/journals/Journal-of-the-North-American-Benthological-Society on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

CARACO, N. F., G. LAMPMAN, J. J. COLE, K. E. LIMBURG, M. L. PACE, AND D. FISCHER. 1998. Microbial assimilation of DIN in a nitrogen rich estuary: implications for food quality and isotope studies. Marine Ecology Progress Series 167:59–71.

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.

CRENSHAW, C. L., H. M. VALETT, AND J. L. TANK. 2002. Effects of coarse particulate organic matter on fungal biomass and invertebrate density in the subsurface of a headwater stream. Journal of the North American Benthological Society 21:28–42.

CROSS, W. F., J. B. WALLACE, A. D. ROSEMOND, AND S. L. EGGERT. 2006. Whole-system nutrient enrichment increases secondary production in a detritus-based ecosystem. Ecology 87:1556–1565.

CRUMP, B. C., H. E. ADAMS, J. E. HOBBIE, AND G. W. KLING. 2007. Biogeography of bacterioplankton in lakes and streams of an arctic tundra catchment. Ecology 88:1365–1378.

CUMMINS, K. 1974. Structure and function of stream ecosystems. BioScience 24:631–641.

DAS, M., T. V. ROYER, AND L. G. LEFF. 2007. Diversity of fungi, bacteria, and actinomycetes on leaves decomposing in a stream. Applied and Environmental Microbiology 73:756–767.

DEL GIORGIO, P., AND J. J. COLE. 1998. Bacterial growth efficiency in aquatic systems. Annual Review of Ecology and Systematics 29: 503–541.

EDWARDS, R. T. 1987. Sestonic bacteria as a food source for filtering invertebrates in 2 southeastern blackwater rivers. Limnology and Oceanography 32:221–234.

EDWARDS, R. T., J. L. MEYER, AND S. E. G. FINDLAY. 1990. The relative contributions of benthic and suspended bacteria to system biomass, production, and metabolism in a low gradient blackwater river. Journal of the North American Benthological Society 9:216–228.

ELLIS, B. K., J. A. STANFORD, AND J. V. WARD. 1998. Microbial assemblages and production in alluvial aquifers of the Flathead River, Montana, USA. Journal of the North American Benthological Society 17:382–402.

ENTREKIN, S. A., J. L. TANK, E. J. ROSI-MARSHALL, T. J. HOELLEIN, AND G. A. LAMBERTI. 2008. Responses in organic matter accumulation and processing to an experimental wood addition in three headwater streams. Freshwater Biology 53:1642–1657.

FARAG, A. M., D. A. NIMICK, B. A. KIMBALL, S. E. CHURCH, D. D. HARPER, AND W. G. BRUMBAUGH. 2007. Concentrations of metals in water, sediment, biofilm, benthic macroinvertebrates, and fish in the Boulder River watershed, Montana, and the role of colloids in metal uptake. Archives of Environmental Contamination and Toxicology 52:397–409.

FAZI, S., A. AMALFITANO, J. PERNTHALER, AND A. PUDDU. 2005. Bacterial communities associated with benthic organic matter in headwater stream microhabitats. Environmental Microbiology 7: 1633–1640.

FIERER, N., J. L. MORSE, S. T. BERTHRONG, E. S. BERNHARDT, AND R. B. JACKSON. 2007. Environmental controls on the landscape-scale biogeography of stream bacterial communities. Ecology 88: 2162–2173.

FINDLAY, R. H., C. YEATES, M. A. J. HULLAR, D. A. STAHL, AND L. A. KAPLAN. 2008. Biome-level biogeography of streambed microbiota. Applied and Environmental Microbiology 74:3014–3021.

FINDLAY, S. E. G., AND T. A. ARSUFFI. 1989. Microbial growth and detritus transformations during decomposition of leaf litter in a stream. Freshwater Biology 21:261–269.

FINDLAY, S., K. HOWE, AND D. FONTVIEILLE. 1993. Bacterial-algal relationships in streams of the Hubbard Brook Experimental Forest. Ecology 74:2327–2336.

FINDLAY, S., J. MEYER, AND P. J. SMITH. 1986. Incorporation of microbial biomass by *Peltoperla* sp. (Plecoptera) and *Tipula* sp. (Diptera). Journal of the North American Benthological Society 5:306–310.

FINDLAY, S., AND R. L. SINSABAUGH. 2006. Large-scale variation in subsurface stream biofilms: a cross-regional comparison of metabolic function and community similarity. Microbial Ecology 52:491–500.

FINDLAY, S., AND W. V. SOBCZAK. 1996. Variability in removal of dissolved organic carbon in hyporheic sediments. Journal of the North American Benthological Society 15:35–41.

FINDLAY, S. E. G., J. TANK, S. DYE, H. M. VALETT, P. J. MULHOLLAND, W. H. MCDOWELL, S. L. JOHNSON, S. K. HAMILTON, J. EDMONDS, W. K. DODDS, AND W. B. BOWDEN. 2002. A cross-system comparison of bacterial and fungal biomass in detritus pools of headwater streams. Microbial Ecology 43:55–66.

FISHER, H. 2003. The role of biofilms in the uptake and transformation of dissolved organic matter. Pages 285–315 *in* S. Findlay and R. L. Sinsabaugh (editors). Aquatic ecosystems. Elsevier, New York.

FREEMAN, C., AND M. A. LOCK. 1995. The biofilm polysaccharide matrix: a buffer against changing organic carbon substrate supply? Limnology and Oceanography 40:273–278.

FUHRMAN, J., AND F. AZAM. 1980. Bacterioplankton secondary production estimates for coastal waters of British Columbia, Antarctica and California. Applied and Environmental Microbiology 39:1085–1095.

GESSNER, M. O., AND E. CHAUVET. 1993. Ergosterol-to-biomass conversion factors for aquatic hyphomycetes. Applied and Environmental Microbiology 59:502–507.

GESSNER, M. O., E. CHAUVET, AND M. DOBSON. 1999. A perspective on leaf litter breakdown in streams. Oikos 85:377–384.

GESSNER, M. O., C. T. ROBINSON, AND J. V. WARD. 1998. Leaf breakdown in streams of an alpine glacial floodplain: dynamics of fungi and nutrients. Journal of the North American Benthological Society 17:403–419.

GIOVANNONI, S. 2004. Evolutionary biology – oceans of bacteria. Nature 430:515–516.

GRAÇA, 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.

GREENWOOD, J. L., A. D. ROSEMOND, J. B. WALLACE, W. F. CROSS, AND H. S. WEYERS. 2007. Nutrients stimulate leaf breakdown rates and detritivore biomass: bottom-up effects via heterotrophic pathways. Oecologia (Berlin) 151:637–649.

GÜCKER, B., AND H. FISCHER. 2003. Flagellate and ciliate distribution in sediments of a lowland river: relationships with environmental gradients and bacteria. Aquatic Microbial Ecology 31:67–76.

GULIS, V., AND K. SUBERKROPP. 2003a. Effect of inorganic nutrients on relative contributions of fungi and bacteria to carbon flow from submerged decomposing leaf litter. Microbial Ecology 45: 11–19.

GULIS, V., AND K. SUBERKROPP. 2003b. Leaf litter decomposition and microbial activity in nutrient-enriched and unaltered reaches of a headwater stream. Freshwater Biology 48:123–134.

HAACK, S. K., T. BURTON, AND K. ULRICH. 1988. Effects of whole-tree harvest on epilithic bacterial populations in headwater streams. Microbial Ecology 16:165–181.

HALL, R. O., AND J. L. MEYER. 1998. The trophic significance of bacteria in a detritus-based stream food web. Ecology 79: 1995–2012.

Downloaded From: https://complete.bioone.org/journals/Journal-of-the-North-American-Benthological-Society on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

HARROP, B. L., J. C. MARKS, AND M. E. WATWOOD. 2009. Early bacterial and fungal colonization of leaf litter in Fossil Creek, Arizona. Journal of the North American Benthological Society 28: 383–396.

HERFORT, L., J. H. KIM, M. J. L. COOLEN, B. ABBAS, S. SCHOUTEN, G. J. HERNDL, AND J. S. S. DAMSTE. 2009. Diversity of Archaea and detection of crenarchaeotal amoA genes in the rivers Rhine and Tet. Aquatic Microbial Ecology 55:189–201.

HIEBER, M., AND M. O. GESSNER. 2002. Contribution of stream detritivores, fungi and bacteria to leaf breakdown based on biomass estimates. Ecology 83:1026–1038.

HOBBIE, J. E., R. J. DALEY, AND S. JASPER. 1977. Use of nucleopore filters for counting bacteria by fluorescent microscopy. Applied and Environmental Microbiology 33:1225–1228.

HORNER-DEVINE, M. C., M. LAGE, J. B. HUGHES, AND B. J. M. BOHANNAN. 2004. A taxa-area relationship for bacteria. Nature 432:750–753.

HUDSON, J. J., J. C. ROFF, AND B. K. BURNISON. 1992. Bacterial productivity in forested and open streams in southern Ontario. Canadian Journal of Fisheries and Aquatic Sciences 49: 2412–2422.

HULLAR, M. A. J., L. A. KAPLAN, AND D. STAHL. 2006. Recurring seasonal dynamics of microbial communities in stream habitats. Applied and Environmental Microbiology 72:713–722.

INGOLD, C. T. 1942. Aquatic hyphomycetes of decaying alder leaves. Transactions of the British Mycological Society 25:339–417.

INWOOD, S. E., J. L. TANK, AND M. J. BERNOT. 2005. Patterns of denitrification associated with land use in 9 midwestern headwater streams. Journal of the North American Benthological Society 24:227–245.

IVERSEN, T. M. 1973. Decomposition of autumn-shed beech leaves in a springbrook and its significance for the fauna. Archiv für Hydrobiologie 72:305–312.

JONES, J. B., R. M. HOLMES, S. G. FISHER, N. B. GRIMM, AND D. M. GREEN. 1995. Methanogenesis in Arizona, USA, dryland streams. Biogeochemistry 31:155–173.

JUDD, K., E. B. C. CRUMP, AND G. W. KLING. 2006. Variation in dissolved organic matter controls bacterial production and community composition. Ecology 87:2068–2079.

KAPLAN, L. A., AND J. D. NEWBOLD. 2003. The role of monomers in stream ecosystem metabolism. Pages 97–120 *in* S. Findlay and R. L. Sinsabaugh (editors). Aquatic ecosystems. Elsevier, New York.

KAUSHIK, N. K., AND H. B. N. HYNES. 1971. The fate of dead leaves that fall into streams. Archiv für Hydrobiologie 68:465–515.

KEMP, M. J., AND W. K. DODDS. 2002. The influence of ammonium, nitrate, and dissolved oxygen concentrations on uptake, nitrification, and denitrification rates associated with prairie stream substrata. Limnology and Oceanography 47:1380–1393.

KIRCHMAN, D. L., A. I. DITTEL, S. E. G. FINDLAY, AND D. T. FISCHER. 2004. Changes in bacterial activity and community structure in response to dissolved organic matter in the Hudson River, New York. Aquatic Microbial Ecology 35:243–257.

KNAPP, C. W., W. K. DODDS, K. C. WILSON, J. M. O'BRIEN, AND D. W. GRAHAM. 2009. Spatial heterogeneity of denitrification genes in a highly homogenous urban stream. Environmental Science and Technology 43:4273–4279.

KOMINOSKI, J. S., P. A. MOORE, R. G. WETZEL, AND N. C. TUCHMAN. 2007a. Elevated CO_2 alters leaf-litter-derived dissolved organic carbon: effects on stream periphyton and crayfish feeding preference. Journal of the North American Benthological Society 26:663–672.

KOMINOSKI, J. S., C. M. PRINGLE, B. A. BALL, M. A. BRADFORD, D. C. COLEMAN, D. B. HALL, AND M. D. HUNTER. 2007b. Nonadditive effects of leaf litter species diversity on breakdown dynamics in a detritus-based stream. Ecology 88:1167–1176.

LANGHANS, S. D., S. D. TIEGS, M. O. GESSNER, AND K. TOCKNER. 2008. Leaf-decomposition heterogeneity across a riverine floodplain mosaic. Aquatic Sciences 70:337–346.

LARNED, S. T. 2010. A prospectus for periphyton: recent and future ecological research. Journal of the North American Benthological Society 29:182–206.

LAWSON, D. L., M. J. KLUG, AND R. W. MERRITT. 1984. The influence of the physical, chemical, and microbiological characteristics of decomposing leaves on the growth of the detritivore *Tipula abdominalis* (Diptera: Tipulidae). Canadian Journal of Zoology 62:2339–2343.

LECERF, A., G. RISNOVEANU, C. POPESCU, M. O. GESSNER, AND E. CHAUVET. 2007. Decomposition of diverse litter mixtures in streams. Ecology 88:219–227.

LEFF, L. G., AND M. J. LEMKE. 1998. Ecology of aquatic bacterial populations: lessons from applied microbiology. Journal of the North American Benthological Society 17:261–271.

LINDSTRÖM, E. S., AND A. K. BERGSTRÖM. 2004. Influence of inlet bacteria on bacterioplankton assemblage composition in lakes of different hydraulic retention time. Limnology and Oceanography 49:125–136.

LOGUE, J. B., H. BURGMANN, AND C. T. ROBINSON. 2008. Progress in the ecological genetics and biodiversity of freshwater bacteria. BioScience 58:103–113.

LOGUE, J. B., C. T. ROBINSON, C. MEIER, AND J. R. VAN DER MEER. 2004. Relationship between sediment organic matter, bacterial composition, and the ecosystem metabolism of alpine streams. Limnology and Oceanography 49:2001–2010.

LONG, Z. T., AND P. J. MORIN. 2005. Effects of organism size and community composition on ecosystem functioning. Ecology Letters 8:1271–1282.

MARCARELLI, A. M., M. A. BAKER, AND W. A. WURTSBAUGH. 2008. Is in-stream N_2 fixation an important N source for benthic communities and stream ecosystems? Journal of the North American Benthological Society 27:186–211.

MARTIN, L. A., P. J. MULHOLLAND, J. R. WEBSTER, AND H. M. VALETT. 2001. Denitrification potential in sediments of headwater streams in the southern Appalachian mountains, USA. Journal of the North American Benthological Society 20:505–519.

MAYER, M. S., AND G. E. LIKENS. 1987. The importance of algae in a shaded headwater stream as food for an abundant caddisfly (Trichoptera). Journal of the North American Benthological Society 6:262–269.

MCCUTCHAN, J. H., AND W. M. LEWIS, JR. 2002. Relative importance of carbon sources for macroinvertebrates in a Rocky Mountain stream. Limnology and Oceanography 47:742–752.

MCNAMARA, C. J., AND L. G. LEFF. 2004. Bacterial community composition in biofilms on leaves in a northeastern Ohio stream. Journal of the North American Benthological Society 23:677–685.

METHVIN, B. R., AND K. SUBERKROPP. 2003. Annual production of leaf-decaying fungi in 2 streams. Journal of the North American Benthological Society 22:554–564.

MORRICE, J. A., C. N. DAHM, H. M. VALETT, P. V. UNNIKRISHNA, AND M. E. CAMPANA. 2000. Terminal electron accepting processes in the alluvial sediments of a headwater stream. Journal of the North American Benthological Society 19:593–608.

MULHOLLAND, P. J. 1997. Dissolved organic matter concentration and flux in streams. Journal of the North American Benthological Society 16:131–141.

MULHOLLAND, P. J., A. M. HELTON, G. C. POOLE, R. O. HALL, S. K. HAMILTON, B. J. PETERSON, J. L. TANK, L. R. ASHKENAS, L. W. COOPER, C. N. DAHM, W. K. DODDS, S. E. G. FINDLAY, S. V. GREGORY, N. B. GRIMM, S. L. JOHNSON, W. H. MCDOWELL, J. L. MEYER, H. M. VALETT, J. R. WEBSTER, C. ARANGO, J. J. BEAULIEU, M.

Downloaded From: https://complete.bioone.org/journals/Journal-of-the-North-American-Benthological-Society on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

J. BERNOT, A. J. BURGIN, C. CRENSHAW, L. JOHNSON, B. R. NIEDERLEHNER, J. M. O'BRIEN, J. D. POTTER, R. W. SHEIBLEY, D. J. SOBOTA, AND S. M. THOMAS. 2008. Stream denitrification across biomes and effects of anthropogenic nitrate loading. Nature 452:202–205.

NIKOLCHEVA, L. G., A. M. COCKSHUTT, AND F. BÄRLOCHER. 2003. Diversity of freshwater fungi on decaying leaves: comparing traditional and molecular approaches. Applications in Environmental Microbiology 69:2548–2554.

PACE, N. R. 2006. Time for a change. Nature 441:289.

OLAPADE, O. A., AND L. G. LEFF. 2004. Seasonal dynamics of bacterial assemblages in epilithic biofilms in a northeastern Ohio stream. Journal of the North American Benthological Society 23: 686–700.

RECHE, I., E. PULIDO-VILLENA, R. MORAES-BAQUERO, AND E. O. CASAMAYOR. 2005. Does ecosystem size determine aquatic bacterial richness? Ecology 86:1715–1722.

REES, G. N., G. O. WATSON, D. S. BALDWIN, AND A. M. MITCHELL. 2006. Variability in sediment microbial communities in a semipermanent stream: impact of drought. Journal of the North American Benthological Society 25:370–378.

REISS, J., AND J. M. SCHMID-ARAYA. 2008. Existing in plenty: abundance, biomass and diversity of ciliates and meiofauna in small streams. Freshwater Biology 53:652–668.

RIBBLETT, S. G., M. A. PALMER, AND D. W. COATS. 2005. The importance of bacterivorous protists in the decomposition of stream leaf litter. Freshwater Biology 50:516–526.

RIER, S. T., K. A. KUEHN, AND S. N. FRANCOEUR. 2007. Algal regulation of extracellular enzyme activity in stream microbial communities associated with inert substrata and detritus. Journal of the North American Benthological Society 26:439–449.

RIER, S. T., N. C. TUCHMAN, R. G. WETZEL, AND J. A. TEERI. 2002. Elevated-CO_2-induced changes in the chemistry of quaking aspen (*Populus tremuloides* Michaux) leaf litter: subsequent mass loss and microbial response in a stream ecosystem. Journal of the North American Benthological Society 21: 16–27.

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., M. B. DAVID, AND L. E. GENTRY. 2006. Timing of riverine export of nitrate and phosphorus from agricultural watersheds in Illinois: implications for reducing nutrient loading to the Mississippi River. Environmental Science and Technology 40: 4126–4131.

SANZONE, D. M., J. L. TANK, J. L. MEYER, P. J. MULHOLLAND, AND S. E. G. FINDLAY. 2001. Microbial incorporation of nitrogen in stream detritus. Hydrobiologia 464:27–35.

SCHALLER, J. L., T. V. ROYER, M. B. DAVID, AND J. L. TANK. 2004. Denitrification associated with plants and sediments in an agricultural stream. Journal of the North American Benthological Society 23:667–676.

SCHMID, P. E., J. M. SCHMID-ARAYA, AND M. TOKESHI. 2000. Relationship between population density and body size in stream communities. Science 289:1157–1160.

SOBCZAK, W. V. 1996. Epilithic bacterial responses to variations in algal biomass and labile dissolved organic carbon during biofilm colonization. Journal of the North American Benthological Society 15:143–154.

SOBCZAK, W. V., AND S. FINDLAY. 2002. Variation in bioavailability of dissolved organic carbon among stream hyporheic flowpaths. Ecology 83:3194–3209.

STARRY, O. S., H. M. VALETT, AND M. E. SCHREIBER. 2005. Nitrification rates in a headwater stream: influences of seasonal variation in C and N supply. Journal of the North American Benthological Society 24:753–768.

SUBERKROPP, K., AND E. CHAUVET. 1995. Regulation of leaf breakdown by fungi in streams: influences of water chemistry. Ecology 76: 1433–1445.

SWAN, C. M., AND M. A. PALMER. 2004. Leaf diversity alters litter breakdown in a Piedmont stream. Journal of the North American Benthological Society 23:15–28.

WEYERS, H. S., AND K. SUBERKROPP. 1996. Fungal and bacterial production during the breakdown of yellow poplar leaves in 2 streams. Journal of the North American Benthological Society 15:408–420.

WHILES, M. R., K. R. LIPS, C. M. PRINGLE, S. S. KILHAM, R. J. BIXBY, R. BRENES, S. CONNELLY, J. C. COLON-GAUD, M. HUNTE-BROWN, A. D. HURYN, C. MONTGOMERY, AND S. PETERSON. 2006. The effects of amphibian population declines on the structure and function of Neotropical stream ecosystems. Frontiers in Ecology and the Environment 4:27–34.

WIEGNER, T. N., L. A. KAPLAN, J. D. NEWBOLD, AND P. H. OSTROM. 2005. Contribution of dissolved organic C to stream metabolism: a mesocosm study using ^{13}C-enriched tree-tissue leachate. Journal of the North American Benthological Society 24:48–67.

ZAK, D. R., C. B. BLACKWOOD, AND M. P. WALDROP. 2006. A molecular dawn for biogeochemistry. Trends in Ecology and Evolution 21:288–295.

Received: 12 February 2009
Accepted: 10 November 2009

Downloaded From: https://complete.bioone.org/journals/Journal-of-the-North-American-Benthological-Society on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use