Rivers and Soils: Parallels in Carbon and Nutrient Processing

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Ecologists usually study systems at spatial and temporal scales (e.g., from centimeters to meters and from minutes to days) that are within easy range of human perception. Critical ecological processes, however, occur over a range of spatial and temporal scales—from small and fast to big and slow. Only when the natural scale of organisms overlaps the scales easily perceived by humans are the roles of organisms readily understandable. Thus, ecologists know a great deal about the lives and roles of birds, mammals, and fishes in ecosystem processes but far less about the individual roles of the “little things that run the world” (Wilson 1987)—that is, microbes and microfauna. Most of these organisms operate at rapid paces over very short distances, far smaller than the scale at which ecologists typically measure processes to quantify the functioning of ecosystems.

The difficulties in detecting the relative roles of microbes and microfauna in ecosystem functioning can result in glaring differences in how ecologists view systems that are essentially similar. For example, both soil and stream ecosystems receive trophic inputs in the forms of leaf and root litter and living plant biomass. These inputs are processed by a variety of consumer organisms, and the end products of processing in both ecosystems are mineralized carbon and nutrients. Despite this functional similarity, terrestrial ecosystem ecologists and stream ecologists often have different views of the trophic processes involved. Terrestrial ecologists—with a perspective rooted in agronomy and soil science, from which soil ecology evolved—usually see litter decomposition in soil as a microbe-dominated process that mineralizes carbon and provides inorganic nutrients for plant uptake. Outside the small community of soil invertebrate ecologists, terrestrial decomposition is rarely treated as the product of a food web consisting of many complex interactions. By contrast, aquatic ecologists—steeped in the legacy of fishery biology, from which their discipline arose—generally view litter decomposition in a stream as a series of metabolic transformations that are mediated by specialized invertebrates interacting with microbes at each step. In this article, we show that these differing views reflect differences in the spatial and temporal scales at which the processes occur and at which ecologists measure them.

Similarities of processes

The mechanisms of leaf litter processing in stream and soil systems are remarkably similar. In general terms, the decomposition of litter can be described as the sum of the loss of mass due to leaching (i.e., the removal of soluble compounds by water), litter comminution (i.e., the conversion of large particles to small particulates, largely through the feeding activities of specialized invertebrates), and microbial catabolism (Swift et al. 1979). Litter chemistry (particularly lignin and nitrogen content) and the physical environment (moisture in soils, oxygen in aquatic systems, and temperature in both systems) affect the activities of decomposer organisms and therefore control the rates and relative importance of these three processes (Anderson 1987).

Decomposition is a cascade of processes in which the products of leaching and organismal activity become subject to further leaching, com...
minution, and catabolism (Boling et al. 1975, Swift et al. 1979, Anderson 1988). The particle size of the organic material in both soils and streams decreases as it travels "down" (i.e., down through the soil or downstream). At the same time, the carbon-to-nitrogen ratio of the organic matter usually decreases—due to microbial respiration of high-quality carbon and immobilization of nitrogen—and its recalcitrance (i.e., the resistance of its carbon to further mineralization) increases (Swift et al. 1979).

Litter entering the forest floor or a stream is "conditioned" by the leaching of soluble compounds (Peterson and Cummins 1974) and colonization by microbes (reviewed by Maltby 1992a). The litter becomes physically softer (and therefore easier for invertebrates to chew), and its carbon and nutrients begin to be mineralized by microbial activity. This period of conditioning is critical for subsequent processing by invertebrates. Stream and soil invertebrates given litter at the same state of conditioning have been observed to process it at the same rate (Merritt and Lawson 1992).

Invertebrates from a variety of taxonomic groups (such as aquatic crane flies and caddisflies, and terrestrial isopods and millipedes) that are known collectively as shredders in streams and litter comminuters in soil ingest the microbiially colonized litter and produce fine particulate organic matter (Short and Maslin 1977, Mulholland et al. 1985, Stewart and Davies 1989), which is then vulnerable to further microbial coloni- zation and further invertebrate ingestion. Shredders and comminuters derive nutrition both from the microbes and litter itself as well as from the interaction of the two, because microbes modify the physical characteristics (and, hence, the food quality) of leaf litter (reviewed by Maltby 1992b for stream systems, Luxton 1982 for soils).

Published estimates of carbon flux through invertebrate communities are difficult to compare broadly between streams and soils. The same is true even when making comparisons among soil systems and among streams. Such estimates are invariably based on estimates of animal density, which vary considerably with study design, sampling method, and extraction technique (Petersen and Luxton 1982, Webster et al. 1995). The quantitative roles of invertebrate communities in stream and soil carbon processing do, however, appear to be similar. Invertebrates may consume a significant fraction of litter entering their systems (Webster and Benfield 1986), whereas they contribute less than 10% of system respiration (Petersen and Luxton 1982).

The spatial arrangement of these processes is similar in streams and soils. A forest mor soil (i.e., characterized by the presence of thick organic horizons; Flanagan and Van Cleve 1983) and a forested stream (Vannote et al. 1980) can each be divided into three analogous regions (Figure 1). In the upper region (i.e., the headwaters in a stream and the litter layer in a soil), energy input is predominantly from leaf litter. In this region, the litter is conditioned by leaching and microbial activities, and then processed by invertebrates. Fungi are the most important microbial decomposers in this region (Parkinson 1988, Maltby 1992b).

Fine organic matter and leachates are transported "down" to the middle region.

In the middle region (i.e., the middle reaches of a stream and the sublitter regions of a forest floor and surface mineral layers of a soil), living primary producers (as opposed to detritus) provide a significant input of carbon and nutrients into food webs. In a stream, these inputs consist of macrophytes and periphyton. Algae, bacteria, and fungi embedded in a slime matrix form a "biofilm" on submerged surfaces (Lock 1981) and provide food for specialized invertebrates that scrape it from the substrate. The middle reaches of streams are typically wide and relatively shallow, and consequently have little shading from riparian vegetation; these conditions promote high rates of primary production by streamed primary producers (Minshall 1978, Vannote et al. 1980).

In soils, the inputs of the middle region consist of root litter and root exudates (Newman 1985). The "rhizosphere"—the soil surrounding roots—contains organisms that exploit exudates, both directly and indirectly. Terrestrial plants put up to

Figure 1. The litter layer of a forest soil, like the headwaters of a woodland stream, receives carbon and nutrients in the form of leaf litter from terrestrial vegetation. Additional inputs enter the middle regions of both systems in the form of root litter and exudates (in soils) and algae and macrophytes (in streams). The lower reaches of a river and the deeper mineral soil depend for carbon and nutrient input on fine particulate or dissolved material from higher in the soil profile or upstream. In both systems, as carbon moves from the upper regions to the lower regions, the particle size of the organic matter decreases and its resistance to microbial decay increases.
60–80% of their total net primary production into belowground biomass (Coleman et al. 1988), and much of that ends up as root litter. Mycorrhizae, symbiotic fungi that are associated with and receive nutrients from the roots of many plants, can also account for a significant portion—sometimes over 50% (Fogel 1988)—of carbon input into soils. Bacteria progressively increase their importance relative to fungi in carbon breakdown as the particle size of detritus decreases (Swift et al. 1979, Maltby 1992b).

The lower regions of both ecosystems (i.e., the lower reaches of a river system and the deeper mineral soil) receive little fresh input of carbon or nutrients from plants. Instead, they receive carbon and nutrients from fine particulate or dissolved material from higher in the soil profile or upstream. In these lower regions, the particulate organic matter is fine textured and recalcitrant. From these regions, dissolved organic materials may leave the system: from a soil into groundwater, from a river into the ocean. In soils, the extent of dissolved organic matter loss depends largely on the nature of the inorganic materials present. Dissolved materials pass readily through sandy soils, but clay soils resist such exports.

Differences of scale

Decomposition processes in terrestrial and aquatic systems occur at different temporal and spatial scales. In both systems, microbes and fauna consume plant litter and release products, such as nitrogenous wastes, that can then be used by other organisms. In soils, however, products are reused quickly, and the products do not usually move far before being reused. The hydrologic processes that transport carbon and nutrients from litter through the forest floor occur on a much smaller scale than transport in a stream. Invertebrates in soil eat the litter itself or its colonizing microbes and deposit fecal material a few millimeters away, at most (Seastedt 1984). Thus, the fecal material is still measured as part of the litter, and relatively little mass or nutrients appear to have been “lost” in the process of decomposition. The comminuted litter and feces largely remain in place for further microbial colonization or sampling by soil ecologists. As a result, a tight cycling of material occurs at a small spatial scale, with carbon and nutrients released from the microsite at each “turn” of the cycle. Because this cycling takes place in such a small area, dissecting it and analyzing its dynamics and the specific organisms involved in each step is difficult.

The flowing water of a stream stretches this tight cycling into a spiral (Webster and Patten 1979, Newbold 1992), because flowing water carries the products away from where they are formed to new sites for further processing. As a consequence of this stretching, ecologists have a much better understanding of the roles and interactions of specific organisms and communities within stream systems than within soils. That is, stream ecologists are better able to tie together the activities of different organisms because they occur over larger spatial scales than in soils. To a stream ecologist, invertebrate activity causes leaf litter to lose substantial amounts of mass and nutrients, whereas to a terrestrial ecologist, faunal processing usually appears to result in limited mass loss.

Another effect of stream current is the largely one-way movement of organic matter downstream. Although carbon and nutrients may be transported upstream in the form of migratory fishes (e.g., Durbin et al. 1979, Kline et al. 1990) and the upstream flight of adult insects (Müller 1974), in most streams the downstream flow of material is far greater. In soil, due to the smaller spatial scale, carbon and nutrients can more easily flow both down and up over the entire soil profile (the equivalent of the stream from headwaters to mouth). Hyphae of a single individual fungus can reach from the soil’s surface down many centimeters. Fungi actively transport carbon and nutrients among hyphae at various depths in the soil (Hart and Firestone 1991). Soil invertebrate fauna also move among soil layers in response to moisture and can move carbon and nutrients upward and downward by deposition of feces and carcasses (Anderson 1988, Parkinson 1988).

Nutrient availability in streams and soils is influenced strongly by the physical media that characterize each system. Soil organic matter contributes much to the physical structure and chemical characteristics of soils. Cations, including important nutrients such as ammonium, are retained by the cation exchange capacity of soil organic matter and thereby resist leaching and loss (Kilham 1994). Because the surface area of organic matter in soil is high relative to the quantity of water flowing through it, soil effectively retains essential plant nutrients. The large pool of nutrients stored in soil organic matter buffers soil nutrient supply and so reduces plants’ reliance on the immediate release of nutrients from decomposing litter.

Streams also have mechanisms for retaining nutrients. For example, biofilms absorb dissolved nutrients (Lock 1981). The surface areas of biofilms, however, are low relative to the volume of water flowing past, and a high proportion of nutrients is swept downstream. Therefore, the biofilm area immediately adjacent to a nutrient release site may be important in local nutrient retention and control of productivity (Pringle et al. 1988).

The different temporal scales at which soils and streams operate result in distinctly different kinds of environments. Streams provide a relatively buffered physical environment that is favorable to biological activity. Moisture is not in short supply (except in intermittent streams), and temperatures change slowly within a limited range. Soils, by contrast, are often affected by drought and are subject to more extreme temperatures, conditions that can seasonally suppress decomposition. As a result, depositional processes that occur over the course of days in streams may often take weeks or months in terrestrial systems (Merritt and Lawson 1992).

Soils and running waters also differ in their temporal responses to events that periodically reset ecosystem properties. In streams and small rivers, floods rearrange habitats, transport stored carbon and nutrients, and displace or kill many resident organisms. Nevertheless, preflow ecosystem properties and biota generally recover rapidly (Milner 1990, Yount and Niemi 1990). Larger rivers de-
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stance—and little is known about
the fate of the dissolved and particu-
late matter lost from litter.

Decomposition: a three-
dimensional process

Ecologists studying soil processes
define their system (the solum) as a
vertical column of soil that extends
from the soil surface down to the
parent material. Their perspective is
from above, looking at the soil be-
neath their feet. When leachates or
fine particulate organic matter move
down the soil profile, they are not
lost from the "system," but are still
vulnerable to further biotic uptake
and mineralization. To a terrestrial
ecologist, carbon loss is the sum of
carbon dioxide production plus any
carbon leached horizontally out of
the system. Such an observer sees
carbon and nutrients entering the
decomposition process in the form
of litter and exiting primarily as car-
dioxide and nutrient ions. Be-
cause of this focus on carbon dioxide
flux, little of which results directly
from invertebrate respiration (Petersen
and Luxtron 1982, Seastedt 1984), ter-
restrial ecologists may underestimate
the role of invertebrates in litter pro-
cessing. Moreover, the intervening
steps in decomposition are difficult
for the ecologist to discern. Conse-
quently, our knowledge of the con-
trols on decomposition in soils is
based largely on analyses of residual
experimental materials—leaf litter
decomposing in a litterbag, for in-
stance—and little is known about
the fate of the dissolved and particu-
late matter lost from litter.

Most studies of leaf-litter process-
ing in streams, by contrast, occur at
the scale of the reach, a longitudinal
section of a stream (approximately
10–100 m in length) containing a
typical range of habitats (Frisse1l et
al. 1986). Because they are working
with flowing water, stream eco-
ologists' measure of carbon loss includes
not only mineralized carbon dioxide
lost to the atmosphere (or refixed by
stream autotrophs), but also fine
particulates (and leachates) lost
downstream due to the activities of
invertebrates. Because upstream
study reaches comprise only a small
portion of the entire stream's length
from headwaters to sea, however,
stream ecologists may underestimate
the importance of microbes. In fact,
much of the carbon lost from leaf
litter in the headwaters is transported
downstream to be eventually respired
by microbes in the sediments of large
rivers, estuaries, or oceans long after
the stream ecologists have finished their observations.

The different perspectives of stream and soil ecologists are
driven by the fact that stream ecologists look at
spatially extended organic matter spirals "side-on,"
whereas soil ecologists look
at a tight spiral from the
top. A spiral, when viewed
end on, appears to be a circle
or a cycle. When viewed
from the side, it appears to
be a wave form, an oscilla-
tion. The "nutrient spiral"
of decomposition in the soils
(Figure 2), when viewed from
above, appears to be a
cycle yielding carbon diox-
ide and nutrients. From the
side, as it is viewed in
streams, it is a two-dimen-
sional oscillation of carbon
and nutrients between or-
ganic and inorganic forms. Both
are accurate views of different aspects of
decomposition, but neither by itself
provides a complete picture.

The soil ecologist is not likely to
"watch" leaves being processed in
the soil because all the action takes
place over small vertical distances
(centimeters), over long time periods
(years), and underground in the dark.
By contrast, stream ecologists may
observe decomposition in streams
over much longer horizontal dis-
tances (kilometers), shorter time pe-
riods (months), and in the daylight.
For example, stream ecologists can
easily see what is occurring in the
early stages of litter processing—
shredders ingesting leaf litter in real
time. However, the stream ecologist
fails to see the entire river (analo-
gous to a soil core) as an ecosystem.
Were it possible, it would be appropri-
ate to put an entire river in a chamber
and determine carbon dioxide flux
and nutrient regeneration.

Stream and soil ecologists can learn
much by understanding each others' perspectives. Because decompositional
processes are similar, insights that
are gained from the study of one
system may shed light on the other.
Moreover, because of the large spa-
tial scale in streams, the processing of
litter by invertebrates can be studied at
a level of detail that is difficult for soil
eralists to achieve. The longer time
periods and smaller spatial scales in soil allow soil ecologists to easily examine the process of litter conditioning, as well as to observe the fate of organic matter in the later stages of decomposition. With a better understanding of these perspectives, ecologists can learn more about the role of microbial and faunal communities in important ecosystem processes in stream and soil systems.

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