

Conservation from the bottom up: forecasting effects of global change on dynamics of organic matter and management needs for river networks

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ROSEMARY MACKAY FUND ARTICLE

The Rosemary Mackay Fund was intended to promote the publication of speculative, forward-looking, and philosophical articles on any aspect of benthology. The Fund was named to honor Rosemary Mackay, the first editor of the Journal of the North American Benthological Society (now Freshwater Science). This is the last article in the series.

In this 9th article of the series, J. S. Kominoski and A. D. Rosemond argue that conserving freshwater ecosystems under global change requires attention to organic matter resources across spatial scales throughout river networks. J. S. Kominoski is a Postdoctoral Research Associate at the University of Georgia where he works on effects of global change on biodiversity and ecosystem functioning at the terrestrial–aquatic interface. A. D. Rosemond is an Associate Professor at the University of Georgia where she works on fluxes of nutrients and carbon through freshwater food webs.

Conservation from the bottom up: forecasting effects of global change on dynamics of organic matter and management needs for river networks

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Abstract. Multiple drivers of global environmental change are fundamentally altering essential basal resources, such as detritus. Metabolic processes in most aquatic ecosystems are supported by terrestrial detritus, which contributes to the production of organisms and the energetic stability of ecosystems. We suggest that conservation and management approaches to ecosystems along river networks must incorporate the organic-matter resources that support them. Understanding changes in the dynamics of detrital organic matter is particularly important because the quantity of this resource is decreasing and its qualities are being altered as a result of effects of current global changes. We summarize these effects in lotic ecosystems from reach- to network-scales and suggest future research questions aimed at adding quantitative rigor to our understanding of the interactions between dynamics of organic matter and ecological outcomes. This approach is a necessary next step to address large-scale changes in stream and river ecosystems that derive from fundamental alterations in detrital resources, which propagate through the foodweb base to higher-order consumers and emergent ecosystem properties.

Key words: biodiversity, carbon, climate, detritus, food webs, land use, DOC, POC, nutrients.

Ecosystems are changing at unprecedented rates via alterations in climate and biogeochemical cycles, changes in land use and hydrology, and reductions in biodiversity (Vitousek et al. 1997, Chapin et al. 2000, MEA 2005, IPCC 2007). Freshwater ecosystems, which comprise only 0.8% of the Earth's surface but provide critical ecosystem services to humans (Gleick 1998, Gleick and Palaniappan 2010), are particularly vulnerable to global environmental changes. Environmental changes will occur with direct effects of overexploitation on already stressed aquatic resources and indirect

effects of changes in terrestrial landscapes on aquatic ecosystem structure and functioning (Allan 2004). Declines in biodiversity in freshwater ecosystems worldwide exceed those in terrestrial ecosystems (Sala et al. 2000). Losses of consumers are not only a consequence of stressed ecosystems, but also contribute to changes in ecosystem functioning (Dudgeon et al. 2006, Poff et al. 2007, Estes et al. 2011).

Higher-order consumers are critical components of ecosystems, but we suggest that a bottom-up perspective focused on alterations in basal resources is required to achieve conservation goals for aquatic ecosystems—maintaining their biodiversity and functioning. The distribution of basal resources, primary producers and detritus (Allan and Castillo 2007), is

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the template on which aquatic ecosystem structure and functioning are based. On relatively small scales, fluxes and pools of organic matter are critical food and habitat resources for organisms and ultimately drive their production (Wallace et al. 1997). On larger scales, alterations in the availability, retention, and processing rates of detritus can affect delivery of organic matter to downstream organisms and fluxes of C to the atmosphere and oceans (Cole et al. 2007, Tranvik et al. 2009, Butman and Raymond 2011).

Why detritus?

Energy is the fundamental currency in ecology, and terrestrial primary production supports stream and riverine ecosystems through inputs of organic matter. Most C fixed by plants enters detrital foodweb pathways (Cebrian and Lartigue 2004), and many aquatic ecosystems rely on terrestrial detritus to support ecosystem functioning and foodweb structure (Vannote et al. 1980, Wetzel 1995, Wallace et al. 1997, Pace et al. 2004). Loading of terrestrial organic matter is critical to fundamental ecosystem processes and stream food webs (Wallace et al. 1999, Hall et al. 2000). Terrestrial detritus dominates metabolism in many aquatic ecosystems, rendering them net heterotrophic (Cole et al. 2000, Mulholland et al. 2001, Duarte and Prairie 2005). Detritus also provides stability and resilience to food webs via constancy and the lack of recipient control of inputs (DeAngelis et al. 1989, Wetzel 1995, Moore et al. 2004).

In this paper, we focus on the sources and fates of detrital organic matter rather than autochthonous primary production, which also is highly affected by global change (Larned 2010). Drivers of global change, primarily nutrient loading probably will increase aquatic primary production (Smith and Schindler 2009). In contrast, contributions of terrestrially derived organic matter resources to streams, rivers, reservoirs, and lakes probably will be reduced. We suggest that effects of global change on the quantity, quality, and processing rates of detrital resources are particularly important to consider because of predicted alterations and net subsequent depletion, rather than accretion, of these resources in lotic ecosystems (Fig. 1).

We will: 1) review the effects of global change on the dynamics of detrital organic matter and outline the effects of these drivers on detritus (Tables 1–3), 2) forecast the interactive effects of these drivers on the dynamics of organic matter and associated ecosystem functions (Table 4), 3) describe how forecasted effects may vary across small (reach) to large (network) scales (Fig. 2) and across latitudes and altitudes, and 4) suggest specific research topics to test assumptions

and predictions concerning causes and effects of changes in detritus-based pathways. Ideally, such research should yield quantitative information on factors affecting detrital pathways that can be used to manage aquatic systems and their surrounding watersheds. We suggest that conservation and management approaches that focus on basal resource dynamics—a bottom-up perspective—will be particularly effective at protecting aquatic ecosystems, the organisms that comprise them, and their emergent functions.

Drivers of Change in Organic-Matter Resources

Climate drivers

Climate change is expected to affect aquatic ecosystems strongly by altering the quantity, characteristics, processing, and retention of inputs of terrestrial detritus. The principle climate drivers affecting detrital dynamics in aquatic ecosystems are increases in atmospheric CO₂ and its effects on terrestrial organic matter, changes in precipitation and associated hydrologic impacts, and increases in temperature (Fig. 1, Table 1).

Elevated atmospheric CO₂ can stimulate terrestrial productivity and increase detrital inputs to aquatic systems when plant growth is not nutrient limited (Norby et al. 2010). However, increased atmospheric CO₂ decreases detrital quality by causing production of plant litter that is high in C:N:P and unpalatable secondary compounds (Rier et al. 2002, Tuchman et al. 2002, Adams et al. 2003, 2005). Leaching of water-soluble, elevated-CO₂-induced compounds can reduce negative effects on detrital quality and processing (Rier et al. 2005).

Altered patterns of precipitation will make extreme events (e.g., droughts and floods) part of flow regimes, which directly influence water quantity and indirectly influence availability (Lake 2003) and biological processing (Hutchens and Wallace 2002, Tibbets and Molles 2005, Sabo et al. 2008) of detrital resources. Drought reduces physical breakdown rates and slows biological processing (Sangiorgio et al. 2007). Higher discharge will accelerate transport and physical breakdown of organic matter (Paul et al. 2006). High-flow events can scour detritus from stream reaches. When reservoirs occur in river networks, a proportion of organic matter transported downstream will become buried in reservoirs (St. Louis et al. 2000), slowing biological processing.

Long-term temperature records show many instances of stream warming that are correlated with rising air temperatures and other drivers of global change (Kaushal et al. 2010). Recent warming also has been associated with global declines in terrestrial

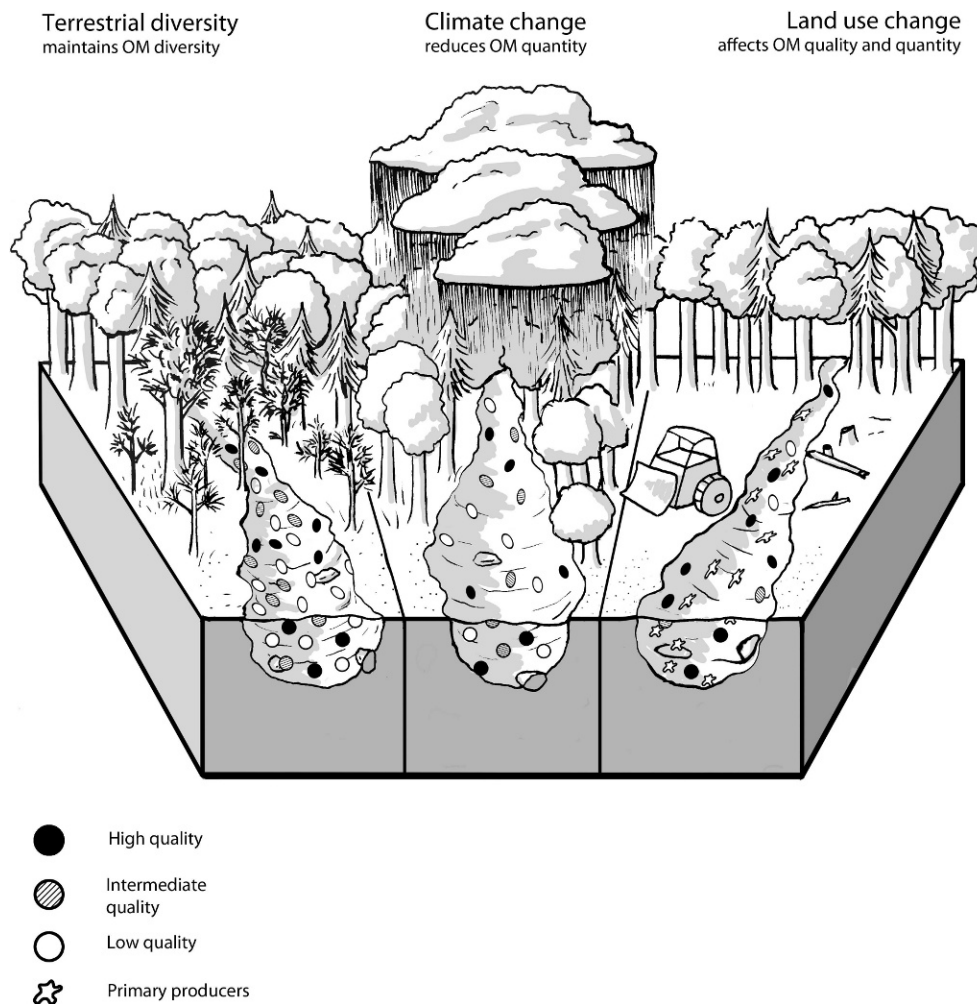


FIG. 1. Conceptual diagram of the net effects of drivers of global environmental change (biodiversity, climate, and land use) on dynamics of organic matter in riverine ecosystems. Vegetated watersheds with high terrestrial biodiversity provide a balance of low-to-high-quality organic matter (left). Climate change (altered precipitation and rising temperatures) will reduce the quantity of organic matter by increasing losses to downstream export during floods and increased processing rates (center). Land use changes will reduce inputs of terrestrial organic matter and nutrients, resulting in lower quantity of higher-quality detritus and increased autotrophic production (right). OM = organic matter. Illustration credit: © Elizabeth Nixon 2010.

net primary productivity (Zhao and Running 2010), which can reduce detrital inputs to aquatic systems. Increases in air temperature will affect the quantity and timing of terrestrial detrital inputs relative to in situ aquatic production (sensu Mulholland et al. 2009), and a tendency toward earlier leafout with warming temperatures suggests a decrease in seasonal autotrophy in light-limited systems (e.g., deciduous, forested streams; Schwartz et al. 2006). Predicted delays in litterfall associated with increased temperature (Menzel et al. 2006) will reduce light to primary producers and will shift the timing of allochthonous inputs to detritivores. Increased temperatures may promote microbial activity and nutrient sequestration (increasing detrital nutrient content) associated with

organic matter and result in greater microbial than metazoan processing (sensu Ferreira et al. 2010, Boyero et al. 2011, Ferreira and Chauvet 2011).

Land use drivers

Changes in land use have dramatic effects on detrital dynamics in aquatic ecosystems (Allan 2004). Reductions and shifts in watershed vegetation determine what forms of C serve as organic matter in stream systems. Altered riparian and upland forests and increased impervious surfaces and loss of large woody debris will reduce retention of organic matter (Entrekin et al. 2007, 2009). Land uses, such as urbanization, mining, and agriculture, differentially affect

TABLE 1. Drivers of climate change and effects on dynamics of organic matter in aquatic ecosystems. Elevated atmospheric CO₂ increases leaf biomass and alters timing (phenology) of leafout, increases C:N:P, and decreases palatability to aquatic consumers. Altered hydrology (drought and flooding) influences the quantity of detritus retained in aquatic ecosystems and the distribution of nutrients and subsequent quality of detritus (e.g., during floods). Increases in high-flow events probably will scour detritus from upstream reaches, depositing organic matter in sediments of reservoirs. Availability of water also influences the biological processing of detritus. NPP = net primary productivity.

Driver	Effects on detritus	References
Elevated atmospheric CO ₂	<i>Quantity:</i> increased productivity of C ₃ plants <i>Characteristics and quality:</i> decreased quality (increased C:N:P, phenolics) <i>Processing:</i> decreased consumer processing	Boisvenue and Running 2006 Rier et al. 2002, 2005, Tuchman et al. 2002 Rier et al. 2002, 2005, Tuchman et al. 2002, Adams et al. 2003, 2005, Wetzel and Tuchman 2005, but see Ferreira et al. 2010
Changes in precipitation, hydrology	<i>Quantity:</i> decreases with drought and increased runoff <i>Characteristics and quality:</i> nutrients decrease with drought, increase with floods <i>Processing:</i> biological activity limited by water availability, increased channel scouring and burial of detritus in reservoirs, reduced processing caused by drought	Lake 2003 Tibbets and Molles 2005 St. Louis et al. 2000, Hutchens and Wallace 2002, Lake 2003, Cole et al. 2007, Sangiorgio et al. 2007, Sabo et al. 2008
Increases in temperature	<i>Quantity:</i> reduced aquatic NPP, altered phenology, earlier leafout, delay in leaf fall <i>Characteristics and quality:</i> increased N and P uptake <i>Processing:</i> increased microbial vs metazoan contributions	Menzel et al. 2006, Schwartz et al. 2006, Mulholland et al. 2009, Zhao and Running 2010 Hall et al. 2009, Ferreira and Chauvet 2011 Bärlocher et al. 2008, Friberg et al. 2009, Ferreira et al. 2010, Boyero et al. 2011, Ferreira and Chauvet 2011

TABLE 2. Changes in land use and effects on dynamics of organic matter in aquatic ecosystems. Physical and chemical variables associated with urban streams primarily explain faster rates of processing and downstream export of organic matter. In contrast, urban runoff and wastewater effluent stimulate microbial activity, but toxins may inhibit metazoan processing of detritus. Agriculture may reduce the amount and homogenize the type of terrestrial inputs of organic matter to aquatic ecosystems. Nutrient mobilization generally results in faster detrital processing, and genetically modified crop litter has possible inhibitory consequences for detritivore consumers. Shifts in riparian vegetation resulting from landuse change affect the quantity and quality of detritus supporting aquatic food webs. DOC = dissolved organic C, POC = particulate organic C.

Driver	Effects on detritus	References
Reductions/shifts in watershed vegetation	<i>Quantity:</i> relative differences in allochthonous vs autochthonous detritus, changes in POC export <i>Characteristics and quality:</i> dependent upon riparian vegetation and in situ phytodetritus composition, changes in DOC <i>Processing:</i> altered processing depending on detrital quality <i>Characteristics and quality:</i> higher quality (lower C:N:P) because of nutrient loading from stormwater and wastewater (sewage-derived DOC and POC), but toxins reduce quality <i>Processing:</i> faster because of physiochemical and microbial processing, but metazoan processing may be reduced	Wallace et al. 1997, England and Rosemond 2004, Wipfli and Musslewhite 2004 Compton et al. 2003 Eggert and Wallace 2003, Kominoski et al. 2011 Paul and Meyer 2001, Rosi-Marshall 2004, Griffith et al. 2009
Agriculture and mining	<i>Quantity:</i> decreased inputs from watershed <i>Characteristics and quality:</i> decreased C:N:P of in situ organic matter from fertilizer enrichment, POC dominated by crop by-products, grasses, and herbs, which can vary in C:N:P <i>Processing:</i> faster processing because of nutrients, but slower because of metal toxicity and sedimentation that buries detritus and algae	Meyer et al. 2005, Walsh et al. 2005, Chadwick et al. 2006, Paul et al. 2006, Imberger et al. 2008 Tilman 1999, Imhoff et al. 2004, MEA 2005 USDA 1977, Menninger and Palmer 2007, Rosi-Marshall et al. 2007, Griffiths et al. 2009 Schofield et al. 2004, Rosi-Marshall et al. 2007, Roussel et al. 2008, Griffiths et al. 2009, Tank et al. 2010

TABLE 3. Changes in biodiversity and effects on dynamics of organic matter in aquatic ecosystems. Loss of conifers reduces the quantity and shifts the timing and characteristics of detrital inputs to aquatic ecosystems. Detrital inputs from deciduous trees occur seasonally, but coniferous and evergreen detrital inputs typically enter aquatic ecosystems year-round. Less conifer detritus means more seasonal variation in detritus that is processed faster. Increases in N-fixing and low-quality plantation species (*Eucalyptus globulus* and *Pinus* spp.) occur through increased development of agricultural land for crops and invasive riparian species (e.g., *Elaeagnus angustifolia*). Loss of terrestrial plant species worldwide will reduce genetic variation (both inter- and intraspecific), which can influence the processing of detritus in aquatic ecosystems. This genetic variation in detrital processing is primarily explained by phenotypic differences in foliar chemistry, which influences biological processes. Genetic variation also can influence the amount of terrestrial inputs to aquatic ecosystems, especially when considering that congeners can vary in their ability to stabilize stream banks (e.g., *Populus* spp).

Driver	Effects on detritus	References
Loss of conifer trees	<i>Quantity:</i> reduced total inputs, but increased proportion deciduous litter <i>Characteristics and quality:</i> altered phenology of allochthonous vs autochthonous inputs <i>Processing:</i> faster in deciduous than coniferous streams	Richardson 1992, Cramer et al. 2001, van Mantgem et al. 2009 Ellison et al. 2005 Whiles and Wallace 1997, Richardson et al. 2004, Kominoski et al. 2011
Increases in N-fixing and plantation species	<i>Quantity:</i> high quality (low C:N) for N-fixing and crop species, low quality for plantation species <i>Characteristics and quality:</i> dependent on detritus type <i>Processing:</i> faster for N-fixing and crop species, lower for plantation species	Graça et al. 2002, Griffiths et al. 2009, Follstad Shah et al. 2010 Graça et al. 2002, Griffiths et al. 2009, Follstad Shah et al. 2010 Graça et al. 2002, Griffiths et al. 2009, Follstad Shah et al. 2010
Reductions in genetic variation	<i>Quantity:</i> decreased root stability associated with certain hybrid species, causing tree losses and bank erosion <i>Characteristics and quality:</i> reduced intraspecific variation in secondary compounds <i>Processing:</i> reduced intraspecific contributions to processing, which can increase or decrease rates	Fischer et al. 2007 LeRoy et al. 2006, 2007, Bailey et al. 2009 LeRoy et al. 2006, 2007, Bailey et al. 2009

the quantity, characteristics, and processing (including retention) of detritus (Fig. 1, Table 2).

Landuse changes, such as deforestation, agricultural intensification, and urban development, reduce vegetated land cover and alter the quantity, composition, and retention of detrital inputs to streams and rivers. Deforestation has the most immediate effects on detrital dynamics in adjacent river networks, and those effects propagate to consumers and ecosystem functions. Effects of overall reductions in forest cover include lower production of higher trophic levels, less use of detrital than autochthonous resources by consumers, and less export of organic matter to downstream assemblages (Wallace et al. 1997, England and Rosemond 2004, Wipfli and Musslewhite 2004). Changes in quantity and quality of detrital inputs and processing rates will depend on the specific changes in vegetation (Eggert and Wallace 2003, Kominoski et al. 2011). Riparian and watershed deforestation are expected to increase light availability and, thus, dependence on autochthonous resources (England and Rosemond 2004).

Watershed urbanization reduces inputs of organic matter to recipient ecosystems, alters channel geomorphology, and decreases large woody debris.

These changes decrease retention of detritus (Paul and Meyer 2001, Walsh et al. 2005). Processing rates of organic matter typically are higher in urban than in forested watersheds because of excess nutrients and stimulated microbial processing (Pascoal et al. 2005, Imberger et al. 2008) but can decline because of decreases in macroinvertebrate consumers (Chadwick et al. 2006). Physical fragmentation associated with higher storm runoff in urban watersheds can increase losses of organic matter to downstream reaches (Paul et al. 2006). Inputs of organic matter in urban systems are heavily supplemented by wastewater treatment plants (WWTPs), which contribute large amounts of sewage-derived fine particulate organic matter (FPOM) that stimulates microbial processes (Griffith et al. 2009). However, such inputs can be of low quality to meta-zoan consumers if they contain contaminants (Rosi-Marshall 2004).

Agricultural landuse changes are among the most widespread globally. The doubling of world food production from 1960–2000 alone has increased use of fertilizers, water, and land area placed into cultivation (Tilman 1999, MEA 2005). In agricultural landscapes, conversion of land for food production reduces terrestrial inputs of organic matter to stream ecosystems

TABLE 4. Predicted interactive effects of drivers of global environmental change on dynamics of organic matter in aquatic ecosystems. The combination of climate, landuse, and biodiversity drivers will result in overall reductions in terrestrial detrital inputs relative to autotrophic production and in lower quantity of higher-quality detritus. Extreme hydrologic events (floods and droughts) will reduce entrainment of detrital resources, thereby further reducing organic-matter standing crops. Organic matter exported downstream will continue to be buried in sediment because of development of reservoirs, with effects on processing rates and fates of C.

Characteristic	Predicted effects
<i>Quantity and phenology</i>	<ul style="list-style-type: none"> • Declines in terrestrial inputs potentially offset locally by sewage-derived inputs • Losses to downstream export via extreme runoff, storm events and reduced retention structures • Decreased seasonal autotrophy with earlier leafout and delayed leaf fall; disproportionate storage of detritus in reservoirs
<i>Characteristics and quality</i>	<ul style="list-style-type: none"> • Shifts in quality that mirror shifts in terrestrial vegetation • Lower detrital C:N:P with increased nutrient mobilization • Shifting proportions of terrestrial detritus and autotrophic production
<i>Processing rates</i>	<ul style="list-style-type: none"> • Faster with increases in warming and runoff and increased nutrient availability • Slower with current and forecasted water scarcity and burial

(DeLong and Brusven 1994), and the magnitude of this reduction in detritus will increase with human population growth and caloric demand (Imhoff et al. 2004). Crop by-products (Griffiths et al. 2009) and litter from grasses and herbs (Menninger and Palmer 2007) enter small streams in agricultural areas, where their processing rates can be relatively rapid. Native types of organic matter may be processed more rapidly in agricultural watersheds because fertilizer runoff increases microbial activity (Paul et al. 2006), and decreases in large woody debris and streambank channelization reduce retention of organic matter (Rosi-Marshall et al. 2007).

Other effects of land use can reduce processing rates. These factors include negative effects of genetically modified crop by-products on detritivore growth rates in agricultural streams (Rosi-Marshall et al. 2007), inhibition of biological processing by acid and heavy metals in mining regions (Dangles et al. 2004, Duarte et al. 2008, Roussel et al. 2008), and general increases in sediment loading that reduce algal production and invertebrate processing of organic matter (Schofield et al. 2004, Pascoal et al. 2005).

Biodiversity drivers

Global patterns of predicted changes in terrestrial vegetation include: 1) changes in timing of litter input caused by shifts in deciduous vs conifer/evergreen species, 2) changes in plant composition via increases in N-fixing and plantation and crop plant species, and 3) reductions in the genetic diversity of riparian vegetation. Changes in the diversity and composition of terrestrial vegetation can affect recipient aquatic

ecosystems through alterations in inputs of organic matter (Fig. 1) and resultant in situ dynamics (Table 3). No general pattern linking biodiversity and ecosystem functioning has been agreed upon (Hooper et al. 2005), but the insurance (sensu Hector et al. 1999) afforded aquatic ecosystems by detrital resources with diverse traits could be lost with large-scale changes in terrestrial vegetation, including the expansion of plantation and crop plant species.

Large-scale losses of conifer species are occurring throughout North America because of pathogens, forest harvesting, and fire suppression (Ellison et al. 2005, van Mantgem et al. 2009). Models predict widespread declines in conifers in boreal regions of the northern hemisphere (Cramer et al. 2001). Loss of riparian conifers increases light availability and temperature variation in forested stream ecosystems (Ellison et al. 2005). These losses probably will lead to greater autochthony and increased breakdown rates if conifers are replaced by deciduous tree species because deciduous litter is of higher quality (Richardson et al. 2004).

Additional shifts in watershed vegetation include widespread displacement of native vegetation by crop and plantation plants and N-fixing tree species. *Pinus* and *Eucalyptus* plantations produce low-quality (low-nutrient or high-lignin) litter and have partially replaced higher-quality litter inputs of native deciduous riparian species with subsequent negative effects on stream food webs (Graça et al. 2002, Larrañaga et al. 2009). In contrast, increases in higher-quality resources, such as N-fixing deciduous trees (*Elaeagnus* spp. and *Alnus* spp.) and fertilized crops in cultivated landscapes, can increase processing rates of organic matter

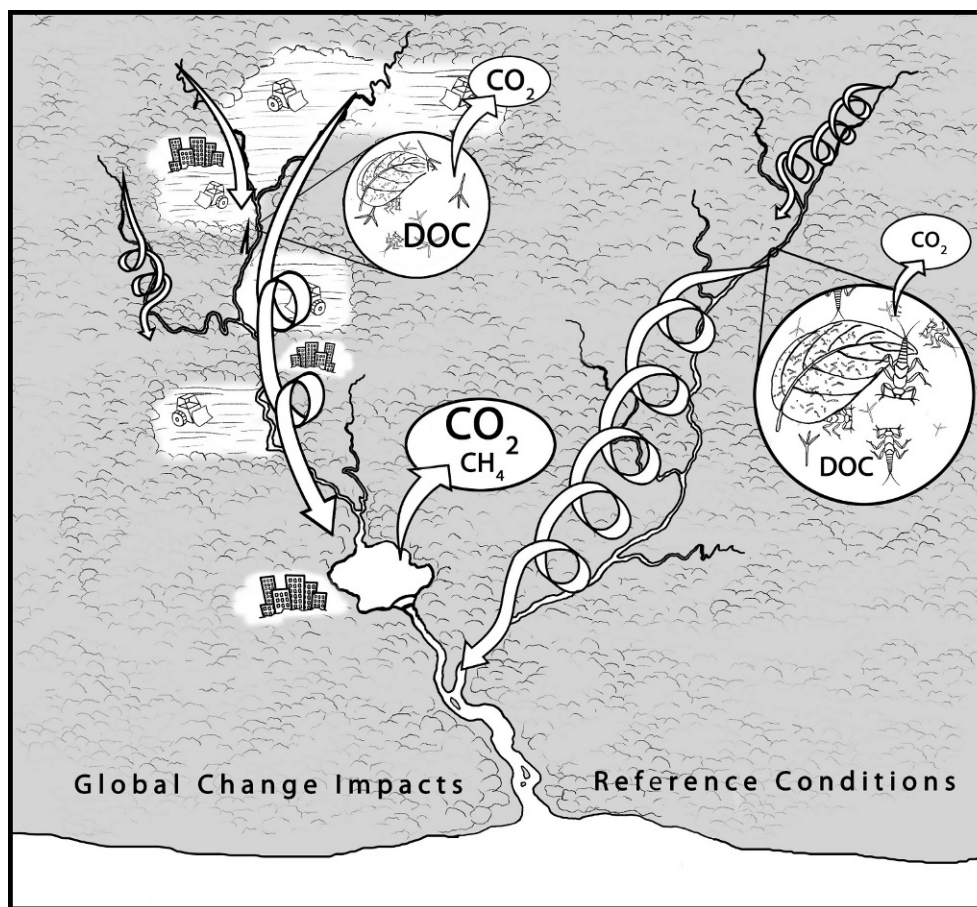


FIG. 2. Predicted interactive effects of drivers of global change on dynamics of organic matter in aquatic food webs and along river networks. Under reference conditions (right), terrestrially derived detritus is retained in situ and processed (multiple spirals in arrow indicating uptake, retention, and transformation) along river networks and supports high metazoan biomass. Drivers of global change (left) are predicted to reduce inputs and decrease retention (direct arrow) of organic matter with fewer opportunities for uptake and transformation (fewer spirals in arrow). Accumulation of particulate organic matter (POC) in reservoirs will increase reach- and network-scale losses of CO_2 and CH_4 relative to retained POC. Increased temperature and nutrient availability will promote greater microbial vs metazoan processing of organic matter (insets with leaves) and losses associated with respiration and greater leaching of dissolved organic C (DOC). Illustration credit: © Elizabeth Nixon 2010.

(Griffiths et al. 2009, Follstad Shah et al. 2010, Kominoski et al. 2011).

Increases in species invasions and declines in native and naturally hybridizing riparian tree species will reduce the genetic diversity of riparian plant species (Whitham et al. 2006). Genetic differences in C sequestration (e.g., root structure and stability; Fischer et al. 2007) and leaf phytochemistry (e.g., secondary compounds, such as tannins) among hybridizing plant species (Bailey et al. 2009) can influence the relative inputs and biological processing of organic matter in adjacent stream ecosystems (LeRoy et al. 2006, 2007, Fischer et al. 2007, Bailey et al. 2009, Axelsson et al. 2010). Genetic variation in riparian tree species (e.g., *Populus* spp.) influences the quality (C:N:P) and quantity (some species allocate more C to roots vs

leaves) of allochthonous detritus and subsequently alters rates of riparian and stream ecosystem processes (Whitham et al. 2006, Bailey et al. 2009).

Forecasting Interactive Effects of Global-Change Drivers on Detrital Resources

Drivers of global change probably will interact to change the 1) quantity and phenology, 2) characteristics and quality, and 3) processing rates of organic matter in aquatic ecosystems. Here, we integrate the forecasted effects of multiple drivers on these 3 aspects of detritus. The relative importance of these drivers will vary spatially and temporally. To make quantitative forecasts of the effects of global change, studies are needed that identify how multiple drivers

interact (additively or nonadditively) to affect these aspects of the dynamics of organic matter.

Interactive effects on quantity and phenology of organic matter

We predict overall reductions in inputs of terrestrial organic matter caused by declines in forest cover and productivity, especially in tropical rainforests of the southern hemisphere (Zhao and Running 2010) and other vegetated land areas (MEA 2005). Retention of detritus will decrease in stream reaches with increased runoff and channel scour. These reductions may be offset in some areas by increases in dissolved organic C (DOC) associated with increasing temperatures (Evans et al. 2006) and particulate organic C (POC) associated with WWTPs. Increases in autotrophic production will occur in systems with increased light availability, but decreased in-stream autotrophic production is expected throughout the northern hemisphere in systems where earlier seasonal onset and leafout and delayed leaffall of terrestrial vegetation occur (Menzel et al. 2006, Schwartz et al. 2006; but see Mulholland et al. 2009). Changes in spatiotemporal patterns of detrital resources along river networks will occur as increasing concentrations of detritus are stored in an increasing number of reservoirs (Table 4).

Changes in detrital quantity may be more important in areas directly affected by landuse changes (e.g., agricultural and urban watersheds), whereas changes in detrital phenology may be more important in areas that are less directly affected by land use (e.g., forested headwaters). For example, a late-spring freeze in southeastern USA caused defoliation in deciduous forests. The resultant increase in light availability increased stream gross primary production, nutrient uptake, and consumer biomass in a system that normally would have been shaded (Roberts et al. 2007, Mulholland et al. 2009). Detrital consumers dependent on the quantity and phenology of organic matter have life-history traits that reflect the availability and timing of inputs of organic matter (Richardson 1991, Eggert and Wallace 2003). Production of these organisms may be reduced by global environmental changes that affect the quantity and phenology of organic matter.

Interactive effects on the characteristics and quality of organic matter

We predict overall increases in detrital quality (lower C:N:P) as nutrients are mobilized worldwide. This prediction is contrary to predictions of higher C:N:P caused by increased CO₂ (Woodward et al.

2010). Increased quality may be partially balanced by other trends in high C:nutrient detrital inputs that would derive from increased cover of low-quality plantation species. POC as a by-product of agricultural crops is variable in quality and is affected by pesticides and genetic modifications of plant material that may inhibit growth and production of consumers. Lower terrestrial inputs coupled with changes in autotrophy will shift the proportions of allochthonous inputs and autotrophic production (Table 4). In addition, rapid changes in terrestrial species composition (e.g., deciduous vs coniferous/evergreen trees), particularly in high-latitude and high-elevation regions (Hickling et al. 2006, Parmesan 2006), will result in net reductions or qualitative changes in terrestrial detritus with indirect effects on aquatic food webs.

Land cover and climate changes strongly influence the characteristics and quality of organic matter in river networks. Agricultural intensification and conversion of natural forests to forest plantations (Matson et al. 1997, Vitousek et al. 1997, MEA 2005) are important regional drivers affecting inputs of organic matter. Cultivated land comprises ~50% of land area in the USA (Lubowski et al. 2006) and 24% globally (MEA 2005). Globally, forest plantations consist of *Eucalyptus globulus* (10%), *Pinus* spp. (20%), and other coniferous species (31%) (MEA 2005). Landuse effects on detrital quality probably are acute at regional scales, but larger-scale drivers, such as nutrient mobilization and elevated atmospheric CO₂, influence detrital characteristics regardless of watershed land use.

Interactive effects on processing rates of organic matter

We expect faster detrital processing rates as warming and physical abrasion associated with flashy hydrology increase. Slower breakdown rates will occur with entrainment and burial in reservoirs. These effects will be especially prominent in Asia and South America, where rates of reservoir construction are the highest in the world (MEA 2005). Contributions of consumer feeding and nutrient loading to breakdown rates can differ based on litter C quality (Royer 1999). Systems with increased nutrient loading or autotrophic (and associated phyto-detritus) production generally will have faster rates of detrital processing, but regions with current and predicted water scarcity are projected to have slower processing rates (Table 4). High-latitude and high-altitude ecosystems are experiencing faster warming than low-latitude and low-altitude ecosystems. This warming has altered permafrost and snowmelt regimes (Hassan et al. 2005). We predict that regions

with increased runoff (high latitudes and high altitudes; Milly et al. 2005) will have faster physical processing of organic matter, whereas systems in arid regions with forecasted increased water scarcity will experience slower processing rates (IPCC 2007).

The extent to which increases in temperature and nutrient mobilization affect detrital processing depends upon detrital resource quality and aquatic foodweb structure. For example, *E. globulus* litter decomposes more slowly than native plant litter in streams because it contains oils and other constituents that inhibit fungal colonization and subsequent consumption and growth by macroinvertebrate shredders (Graça et al. 2002, Larrañaga et al. 2009). In comparison, litter from heavily fertilized crops has lower C:N:P than natural riparian vegetation and is processed more rapidly than litter from unfertilized sources (Griffiths et al. 2009). Some investigators have found efficient transfer of energy from basal resources to consumers in nutrient-enriched systems (Slavik et al. 2004), whereas others have identified trophic dead ends caused by inedible resources (e.g., production of detritivorous prey that constrain gape-limited predators; Davis et al. 2010). Decomposition rates may be elevated in systems with increased temperatures and nutrients (urban, agricultural streams). However, these systems also tend to have lower densities of shredding invertebrates (Hagen et al. 2006) and other abiotic stressors that can reduce organic-matter processing rates (Paul and Meyer 2001, Walsh et al. 2005).

Scaling Effects of Global Change on Organic-Matter Resources

Changes in the quantity and phenology, characteristics and quality, and processing of detritus will affect its retention from reach-to-network scales. Thus, effects on aquatic food webs and detrital processing will vary along river networks and across continents, respectively. Within reaches, we predict that lower quantity and higher quality detritus will better support microbial than metazoan production. At network scales, we predict that reduced retention in headwaters and increased development of lowland reservoirs will alter the spatial distribution of detritus and will concentrate detrital resources in reservoir sediments, thereby increasing losses through respiration and methane production and reducing downstream export of organic matter to oceans (Fig. 2). Changes in detrital dynamics at reach and network scales will vary across continents because of differences in climate, biogeography, watershed geomorphology, and terrestrial vegetation. Scale-specific frameworks will be necessary to

evaluate and quantify the interactive effects of drivers that affect different aspects of organic matter (e.g., Royer and Minshall 2003).

Reach-scale effects of organic matter changes on freshwater consumers

At smaller spatial scales (those that occur from molecular to reach scales), effects of global change on organic matter probably will affect balances of energy flow to different consumers (inset circles, Fig. 2). Elevated nutrients stimulate microbial production associated with detritus (Suberkropp et al. 2010) and increase litter breakdown rates (Pascoal et al. 2005, Ferreira et al. 2006, Greenwood et al. 2007). Increased temperatures will stimulate microbial respiration rates (Bärlocher et al. 2008) but may inhibit metazoan feeding rates (Friberg et al. 2009, Ferreira et al. 2010, Boyero et al. 2011). In addition, increases in temperature will select for smaller body sizes among individuals, populations, and communities (Daufresne et al. 2009). Thus, microorganisms may have a selective advantage over larger organisms in warmer environments. Lower quantity and retention and higher quality of detritus coupled with increased temperatures and extreme hydrologic events that increase detrital exports will decrease organic-matter standing crops that support metazoans (Entrekin et al. 2007, 2009), shifting the relative quantity and rates of energy and nutrient flow from organic matter to microbial rather than metazoan consumers.

Increases in extreme hydrologic events (floods and droughts) and decreases in retentive structures (e.g., large woody debris) from deforestation and land clearing will reduce the amount of terrestrial detritus retained in stream ecosystems and support less metazoan secondary production (Entrekin et al. 2007, 2009). Therefore, we predict that detritus will be rapidly exported downstream during floods or will be retained outside of river margins during droughts. Reductions in quantity and quality of terrestrial detritus (e.g., via forest harvesting and crop and plantation species) will lead to declines in secondary production of metazoans, especially in food webs dominated by detritivores (Wallace et al. 1999, Graça et al. 2002, Larrañaga et al. 2009).

Network-scale effects and global C cycling

Processing and retention of organic matter and our ability to predict scaled-up effects of drivers of global change on both will depend on the type and magnitude of effects among longitudinally connected reaches within networks and on the relative strengths of local vs regional drivers. The quantity and quality of detrital inputs change in a downstream direction in

river networks (headwaters to mainstems). In many systems, these changes include a shift from coarse particulate organic matter (CPOM) in headwaters to DOC and FPOM in higher-order rivers (Vannote et al. 1980). Changes in CPOM inputs and associated microbial assemblages (fungi; Findlay et al. 2002) will have stronger effects in small, headwater reaches than in larger rivers, and changes in FPOM and DOC and associated microbial assemblages (bacteria; Findlay et al. 2002) will be more important in larger rivers than in headwaters. The extent to which upland and lowland reaches are affected by global changes will determine the cumulative effects on the larger network. For example, effects of global changes will be more predictable and scalable in river networks in which both local (e.g., land use) and regional (e.g., climate) drivers affect terrestrial inputs along the longitudinal gradient of the river network than in river networks with mostly downstream disturbances (e.g., lowland agricultural or urban land use and reservoirs), which will generate more heterogeneous detritus-processing patterns. The spatial heterogeneity of drivers and their elicited effects along longitudinal flow paths must be understood to forecast and quantify network-scale, cumulative effects of global environmental changes on detrital dynamics.

Environmental changes will reallocate detritus along river networks, thereby altering its fates in terms of evasion to the atmosphere and downstream delivery to oceans (Fig. 2). Altered hydrology (droughts and storms) will alter spiraling lengths of C and determine its rate of movement downstream. At network scales, reduced loading and standing crops of terrestrial organic matter and broad-scale alterations in hydrology will disproportionately increase storage of organic matter in reservoirs. Dams and associated reservoirs act as powerful retention structures in river networks by burying organic matter in sediments (Vörösmarty et al. 2003). Global increases in dam building (St. Louis et al. 2000) will increase the proportion of detritus stored in reservoirs (Vörösmarty et al. 2003) and will stimulate sediment respiration and methanogenesis (Tranvik et al. 2009). The flux of nutrients from rivers to oceans has increased with agricultural and industrial expansion (MEA 2005), but retention of detritus and accumulation of nutrients in reservoirs will decrease organic-matter subsidies from rivers to estuaries and coastal ecosystems. Burial of organic matter in reservoirs will decrease its availability to downstream benthic and pelagic food webs and probably will decrease secondary production of consumers (*sensu* Power et al. 1996, Wallace et al. 1997), increase microbial productivity, and increase C losses through CO₂ and CH₄

evasion (Fig. 2; Tranvik et al. 2009, Williamson et al. 2009). Decreased retention of detritus in upland reaches and increased losses of organic matter to reservoirs could increase C limitation and nutrient accrual in lower-elevation aquatic ecosystems and coastal estuaries (Taylor and Townsend 2010).

Syntheses of the effects of global change on detrital processing from reach-to-network scale will enable predictions of the effects of global change on C-cycling dynamics in inland aquatic systems across continents. Recent syntheses have improved our understanding of the importance of inland waters to the global C cycle (Battin et al. 2008, Downing et al. 2008, Tranvik et al. 2009, Butman and Raymond 2011). Estimates indicate that <50% of the total C that enters inland aquatic ecosystems is exported to the oceans, ~10% is stored within systems, and >40% is respired to the atmosphere (Cole et al. 2007). We focused on sources and fates of organic C, but terrestrially derived organic C also is transformed and processed in aquatic systems as dissolved inorganic C (DIC) that was respired in soils. These forms of C can be influenced by global change (Jones et al. 2003, Butman and Raymond 2011). Thus, our view of the fate of all terrestrially derived C ultimately must include DIC-mediated pathways. Scientists are beginning to piece together the role of inland aquatic ecosystems in the global C cycle, but environmental changes will continue to alter terrestrial subsidies of organic matter to aquatic ecosystems and the fate of that C in terms of storage, evasion, and transport. We predict that reduced inputs of terrestrial C, a greater proportion of which is retained in reservoirs and processed by microbes as temperature and nutrients increase, will reduce C export to oceans (Fig. 2).

A Bottom-Up Research and Management Agenda

Implications for management

Environmental policies in the USA (e.g., Endangered Species Act, Clean Water Reclamation Act), European Union (e.g., Water Framework Directive), and Australia (Water Act and Water Amendment Acts) focus on water scarcity, pollutants, and biotic integrity. For the most part, these policies fail to address basal resources in their guidance on conservation and management of aquatic biodiversity and ecosystem services. Protecting aquatic ecosystems requires managing watershed attributes that influence water quality, geomorphology, and hydrology (Harding et al. 1998). Broader protection of aquatic ecosystems (e.g., freshwater ecosystem reserves; Abell et al. 2007) will require attention to managing detritus and primary producers as food and habitat resources. Detrital

resources are being altered and depleted from aquatic ecosystems with predicted effects on energy flow to higher trophic levels, and recent analyses illustrate the need to consider basal resources when managing populations and ecosystems. For example, managing the effects of pesticides on salmon populations requires attention to effects of pesticides on basal resources (algal and invertebrate food resources) that ultimately affect salmon (Macneale et al. 2010). Assessment of basal food resources could be incorporated explicitly into management practices. For example, indices of detrital integrity (IDIs) could be developed as analogs to indices of biotic integrity (IBIs) with the goal of supporting and maintaining targeted levels of detritus-based biodiversity and ecosystem functioning in aquatic ecosystems.

An essential first step toward developing conservation frameworks that use a bottom-up approach is to quantify relationships among basal resources and ecological outcomes. Frameworks, such as the Ecological Limits of Hydrologic Alteration (ELOHA; Poff et al. 2010), that guide research and management promote development of quantitative relationships between specific system alterations and ecological responses. ELOHA models relationships between flow alterations and ecological outcomes. Models must be developed that address the relationships between modifications of detritus (quantity, quality, and processing rates) and ecological responses. Very few such models currently exist, but a bottom-up approach to management has been recognized as valuable and is being incorporated into programs like the European Union's RIVFUNCTION (<http://www.ecolab.ups-tlse.fr/rivfunction/>), which uses litter breakdown rates as a functional response to assess stream condition. We recommend taking steps to develop quantitative models describing the relationships between altered detrital organic matter (a fundamental basal resource in many aquatic ecosystems) and the ecosystem services it provides.

What we need to know: basic to applied research questions

Our review suggests that large changes in inputs and processing of organic matter will occur in aquatic ecosystems. However, we lack quantitative descriptions of relationships between detritus and ecological outcomes, and we have limited understanding of the primary controls and drivers of detritus-based pathways. We recommend undertaking research focused on: 1) quantifying and scaling effects of global change on detritus and 2) determining effects of global change on detritus-based foodweb pathways. In the 1st case, research should address effects of global change on detrital dynamics (process-

ing, retention, transport) and scaling these effects to river networks. In the 2nd case, research should address how the effects of global change on detritus propagate through food webs to affect multiple levels of biological organization.

Quantifying and scaling effects of global change on detritus.—1) What are the baseline inputs, standing crops, characteristics, and processing rates of detritus and DOC across a diversity of ecosystem types, especially anthropogenically dominated ecosystems? How do these baseline attributes vary temporally and spatially? 2) Can the effects of environmental changes on detritus be scaled from reaches to river networks? 3) Do multiple drivers of global change have additive or nonadditive effects on detritus? Are nonadditive effects antagonistic or synergistic? 4) What are the spatial and temporal patterns of the relative importance of terrestrially (watershed) vs aquatically (in-stream) mediated effects of global change on organic matter?

Methods to quantify standing crops of organic matter at the reach scale are labor-intensive but relatively straightforward, whereas models to estimate quantities of organic matter at the network scale are lacking. Network-scale predictive models should include hydrology, geomorphology, and watershed land cover. Researchers should use long-term, broad-scale monitoring infrastructure, e.g., the National Ecological Observatory Network (NEON) and its aquatic components (Global Lake Experimental Observatory Network [GLEON], Stream Experimental Observatory Network [STREON]), as sources of data for such models or as the basis through which to test how detrital processing varies under baseline and future global change scenarios. Coupling empirical, remotely sensed data from NEON networks with continental-scale C (and nutrient) models will enable us to understand how ecosystem stoichiometry (C:nutrients; sensu Schade et al. 2005) and trophic state (Dodds and Cole 2007) influence and are influenced by inputs and processing of organic matter at multiple spatial and temporal scales within and among river networks and across biomes. Collaborative research efforts that integrate spatial and temporal scales of dynamics of organic matter should include scalable measurements of key basal resource stocks and processing rates and modeling of both in major global river networks across biomes.

Determining effects of global change on detritus-based foodweb pathways.—1) At small spatial scales, how does production of detritus-based microbes and metazoans change in response to various, interacting drivers of global change? 2) At large spatial scales, how does the availability and quality of organic

matter support production of aquatic organisms vs CO₂ evasion? 3) How does temperature interact with variation in detrital quality and quantity to affect the relative flow of C through microbial and metazoan pathways? 4) How will the size structure of consumer communities affect C flow from detrital resources to higher trophic levels?

Research questions addressing effects of global change on C flux at reach and network scales and the relative pathways within food webs (e.g., microbial vs metazoan) are essential to meeting conservation and management objectives. A primary research need is to develop quantitative relationships between organic-matter standing crop and secondary production with data from a variety of aquatic ecosystems and along river networks. Our current understanding of the links between detritus and secondary production is limited to a small number of systems (e.g., Wallace et al. 1997). Other investigators have described the role of organic-matter snags in production of organisms from large rivers (Benke 1998) and have shown how variation in quality of organic matter affects riverine productivity (e.g., Wipfli and Musslewhite 2004, Cross et al. 2006). Investigation of wetlands have linked detritus to consumer production (e.g., Entekin et al. 2001), but comparable studies are largely lacking from lake ecosystems. Measuring and modeling how lability and stoichiometry of organic matter influence microbial and metazoan storage and flux along river networks will be critical for making predictions about the effects of global environmental change on aquatic food webs and dynamics of organic-matter processing at larger spatial scales. For example, tests of the relative importance of detrital quantity and quality to assimilation into aquatic food webs under varying levels of dissolved nutrients (N and P; Royer and Minshall 2001, Suberkropp et al. 2010) would help us predict how changes to detritus differentially influence microbial vs metazoan consumer production.

We must synthesize and use existing data on aquatic food webs and ecosystem metabolism in light of key drivers of global change—decreases in terrestrial detritus and increases in nutrients and temperatures. Interacting drivers of global environmental change probably will affect multiple levels of biological organization (Woodward et al. 2010). Decreases in terrestrial organic matter and increases in nutrient availability, water temperatures, and extreme hydrologic events will reduce the amount of secondary production supported by detritus. Body size–temperature relationships and resource–consumer stoichiometric dynamics can be used to help predict biological rates, such as metabolism and development time (Gillooly et al. 2001, 2002, 2005,

Sterner and Elser 2002). Integrating our understanding of adaptations of microbial and metazoan communities to local temperature regimes will be important for making predictions that relate community structure, nutrient availability, and climate variation to processing of organic matter from reach-to-network scales.

Conclusions

Studies linking global change, aquatic food webs, and dynamics of organic matter are needed, especially studies that scale regional drivers to reach- and network-level organic-matter dynamics (Tank et al. 2010). Our review underscores the fact that drivers of global change will influence organic matter in stream and riverine ecosystems interactively (additively and nonadditively) via altered: 1) quantity and phenology, 2) characteristics and quality, 3) and heterotrophic processing rates and autotrophic production. We predict that, in the future, food webs in stream and riverine ecosystems will have smaller organic-matter standing crops and that detrital quality will be balanced by C lability and the degree of nutrient loading to ecosystems. Systems with higher rates of C turnover will be dominated more by microbial than metazoan processes. Net reductions or qualitative changes in terrestrial vegetation and the timing and in situ retention of detrital inputs will have the largest effects on heterotrophic aquatic food webs. Changes in autotrophy and reductions in the quantity and quality of terrestrial detritus will alter production of metazoans in aquatic food webs. Future research should quantify baseline conditions in organic matter and link quantified pools and fluxes to ecological outcomes, determine the differential effects of key drivers of global change on microbes vs metazoans, and incorporate modeling to test predictions of effects of global change on detrital resources from reach-to-network scales.

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