

## The metabolic regimes of flowing waters

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### Abstract

The processes and biomass that characterize any ecosystem are fundamentally constrained by the total amount of energy that is either fixed within or delivered across its boundaries. Ultimately, ecosystems may be understood and classified by their rates of total and net productivity and by the seasonal patterns of photosynthesis and respiration. Such understanding is well developed for terrestrial and lentic ecosystems but our understanding of ecosystem phenology has lagged well behind for rivers. The proliferation of reliable and inexpensive sensors for monitoring dissolved oxygen and carbon dioxide is underpinning a revolution in our understanding of the ecosystem energetics of rivers. Here, we synthesize our current understanding of the drivers and constraints on river metabolism, and set out a research agenda aimed at characterizing, classifying and modeling the current and future metabolic regimes of flowing waters.

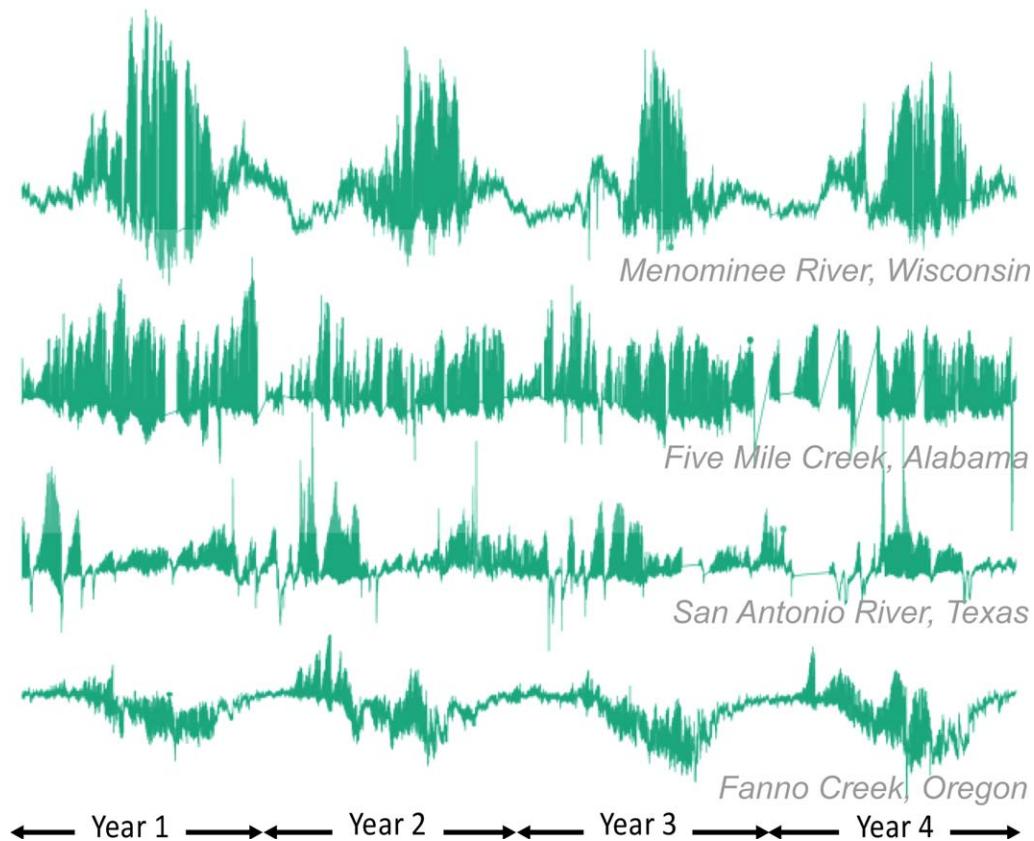
The fuel that powers almost all of Earth's ecosystems is created by organisms capable of the alchemy of photosynthesis, in which solar energy, water, and carbon dioxide are converted into reduced carbon compounds that are then used to sustain life. We measure this conversion of solar energy into organic energy as the gross primary productivity (GPP) of ecosystems. The collective dissipation of this organic energy through organismal metabolism (of both

autotrophs and heterotrophs) is measured as ecosystem respiration (ER). Together, GPP and ER are the fundamental metabolic rates of ecosystems that constrain the energy supply and energy dissipation through food chains, and the balance of these two fluxes, measured as net ecosystem production (NEP), determines whether carbon accumulates or is depleted within an ecosystem. Terrestrial ecosystems often have predictable annual cycles, with both GPP and NEP typically peaking during warmer and wetter months of the year. In many well-studied lakes productivity peaks when warming temperatures, lengthening days, and high nutrient concentrations occur in concert. The life cycles of many consumers are likely synchronized to these seasonal oscillations such that periods of peak energetic demand by consumers coincide with or follow the peak productivity of their preferred plant or prey (e.g., Lampert et al. 1986; Berger et al. 2010). As a result, ecosystem respiration tends to

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**Fig. 1.** Temporal trends in dissolved oxygen (DO shown as % of atmospheric saturation) for four contrasting U.S. rivers over a 4-yr period. High diel variation in dissolved oxygen is a proxy for high ecosystem GPP. The top trace is from the Menominee River in northern, Wisconsin, a large river with clear summer peaks and winter lows in stream metabolism. Dissolved oxygen traces for the more southern Five Mile Creek in Alabama and San Antonio River in Texas show little seasonality, with the smaller Creek having sustained high diel variation in DO and the more urban river having many alternating periods of high and low diel DO variation. The bottom trace is from Fanno Creek, a heavily shaded and frequently flooded small stream in western Oregon. Data from each of these four streams appears again (along with axes labels) in Figs. 3, 5. Here, we remove axes scores to focus on the differences in seasonality of a common signal across streams. The scale of both axes is the same for all four series.

covary with GPP. This phenology of the ecosystem, or its seasonal timing of carbon, water and energy exchange (sensu Noormets 2009) is both a cause and a consequence of the phenology of all component organisms.

The same “cause and consequence of organism phenology” argument cannot be made for river ecosystems for three reasons. First, in many rivers seasonal variation in light is uncorrelated with seasonal variation in temperature, because of the reduction in light supply due to canopy interception, sediment loads or colored organic matter. Second, in many rivers intense and frequent high flow events regularly reduce the biomass of autotrophs (algae, mosses, and macrophytes) through scouring or burial while stream drying can strand and desiccate autotrophs on the channel bed. Finally, most rivers receive energetic subsidies in the form of detritus and dissolved organic matter from their surrounding watersheds. These allochthonous inputs can match or exceed in situ GPP and thus decouple the seasonal and annual patterns of GPP and ER. For each of these reasons we expect a

reduced coherence between climate drivers and river ecosystem productivity and respiration.

Of course, the relative importance of terrestrial shading and terrestrial organic matter inputs varies with river size (Vannote et al. 1980). Just as the importance of terrestrial inputs of nutrients and organic matter to lake food webs diminishes as the ratio of lake size to watershed size increases (Tanentzap et al. 2017), we expect that the relative importance of canopy shading, allochthonous inputs, and hydrologic disturbance should decline between headwater streams and large rivers. This gradient in river size impacts the expected ecosystem phenology, with well-lit and less frequently disturbed large rivers having regular summer productivity peaks while shaded headwaters with frequent flooding are likely to have productivity peaks that are mismatched to the terrestrial growing season (Fig. 1). These predicted longitudinal patterns can be obscured for rivers with high sediment or colored organic matter inputs. Because the temporal signals of GPP and ER are so diverse across streams

and years, and so often asynchronous with terrestrial productivity and climate drivers, we propose that the term *metabolic regimes* is more appropriate than *phenology* to describe these patterns. Here, we define a metabolic regime as the characteristic temporal pattern of ecosystem GPP and ER observed for a river.

Despite the frequent mismatches in the timing of peak energy supply, thermal optima, and disturbance river ecosystems support a tremendous diversity of species (Strayer and Dudgeon 2010) and can convert enormous quantities of organic matter and inorganic nutrients into CO<sub>2</sub>, CH<sub>4</sub>, N<sub>2</sub>, and N<sub>2</sub>O gases (Cole et al. 2007; Mulholland et al. 2008; Battin et al. 2009; Raymond et al. 2013; Stanley et al. 2016). The capacity of rivers to support these critical functions depends, fundamentally, on ecosystem metabolism, defined as “the production and destruction of organic matter, and the associated fluxes of nutrients, through the gross photosynthetic and respiratory activity of organisms” (Odum 1956). Although H. T. Odum developed the general concept and made the first measurements of whole ecosystem metabolism in a river over 60 yr ago (New Hope Creek, North Carolina, Odum 1956), stream ecologists have made remarkably little progress in building our empirical understanding of stream metabolism (McDowell 2015).

It is perhaps not surprising, given the extremely dynamic nature of river metabolism, that we have uncovered no universal or even regional predictors of river productivity. Unlike terrestrial ecosystems, where rainfall and temperature explain much of the global variation in primary production (Whittaker 1962; Leith 1975; Field et al. 1998), or lentic ecosystems, in which nutrient loading and organic matter are primary drivers of productivity (Schindler 1978; Lewis et al. 2011), attempts to uncover these same patterns in streams have proven elusive (Lamberti and Steinman 1997; Bernot et al. 2010). Ironically, there is a rich history of conceptual models predicting spatial patterns of metabolism in streams and rivers beginning with the River Continuum Concept (RCC; Fig. 2) (Vannote et al. 1980). Tests of this and other models have been limited and often equivocal (e.g., Bott et al. 1985; Minshall et al. 1992; McTammany et al. 2003). A literature synthesis showed that watershed area (and thus river size) predicted the magnitude of annual GPP in relatively undisturbed watersheds, but had little predictive power for GPP in even moderately developed watersheds, or for ER across all rivers (Finlay 2011). Other syntheses at daily rather than annual timescales have found even less predictability in metabolic rates (Mulholland et al. 2001; Bernot et al. 2010; Hoellein et al. 2013).

We attribute our limited success in uncovering patterns or building predictive models of river ecosystem metabolism to the challenging combination of technological constraints and the dynamic physical environment characteristic of many rivers. In theory, the measurement of river metabolism is straightforward. An investigator simply measures changes

in the concentration of dissolved oxygen (DO) throughout a diel (24-h) cycle, using increases during daylight hours and overnight declines to calculate rates of GPP, ER, and NEP. In Odum’s initial metabolism estimates (Odum 1956, 1957) these changes were documented by collecting samples at 2–4 h intervals throughout a day followed by manual analysis of DO concentration via titration. Sampling around the clock by this method is labor intensive, and the duration of early studies was thus limited to a handful of days during the year. Later efforts were enabled by instantaneous measurements of DO with first generation environmental sensors. Because these sensors were expensive and required frequent calibration, researchers tended to deploy them for very limited periods of time. As a result, most reported rates of river ecosystem metabolism were derived from a small number of measurement days over a year (e.g., 2–12 d; synthesized by Lamberti and Steinman 1997; Finlay 2011). These brief sampling regimes are biased toward optimum field conditions for sensor deployment (e.g., sunny days with low flows). They are thus unlikely to provide accurate estimates of mean or annual metabolic rates, and are almost certainly insufficient for capturing the impacts of hydrologic disturbance or pulsed resource supply.

Fortunately, the proliferation of more rugged and less expensive environmental sensors is now allowing river scientists to overcome the traditional logistical challenges of measuring metabolism. Looking forward, we should now be able to address fundamental questions about how river ecosystems function, such as: **What controls the variation in the magnitude and timing of productivity within and among rivers? How are these controls changing in response to climate or land use change? How will resulting changes in river ecosystem productivity constrain their capacity to support freshwater biodiversity, food production, and the maintenance of water quality?** In this paper, we hope to help shape and catalyze this research frontier by summarizing our current understanding of river metabolism; proposing a series of new and fundamental research questions; and providing a series of examples demonstrating exciting new applications of continuous metabolism datasets.

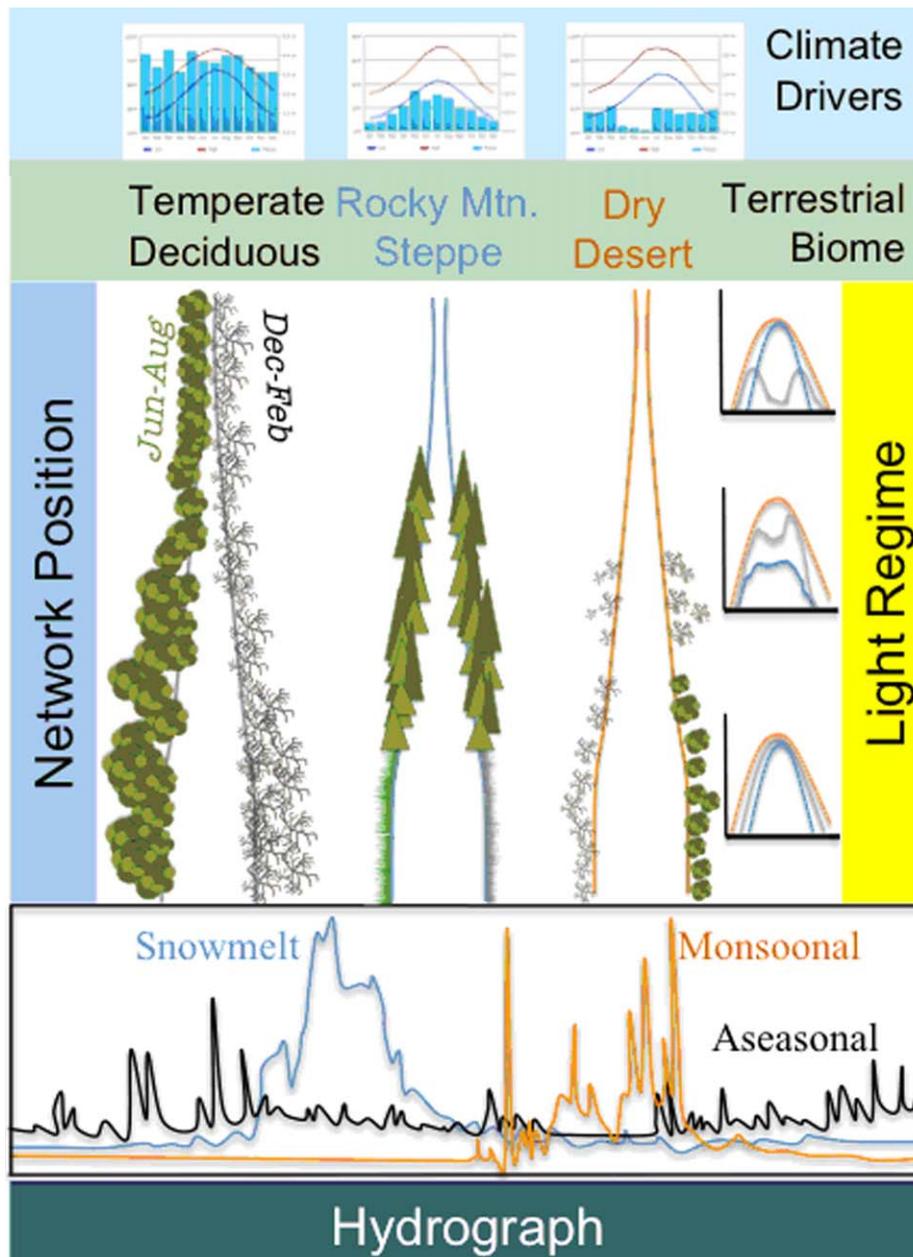
## What do we know so far?

### How we measure and model river metabolism

Stream ecosystem metabolism (in units of oxygen, g O<sub>2</sub> m<sup>-2</sup> d<sup>-1</sup>) is estimated from the daily variation in the production and consumption of oxygen by stream organisms following a simple model:

$$\frac{dDO}{dt} = \frac{GPP+ER}{z} + K(DO_{sat}-DO)$$

where  $\frac{dDO}{dt}$  is the change in dissolved oxygen concentration through time, GPP is the rate of photosynthetic O<sub>2</sub> production,

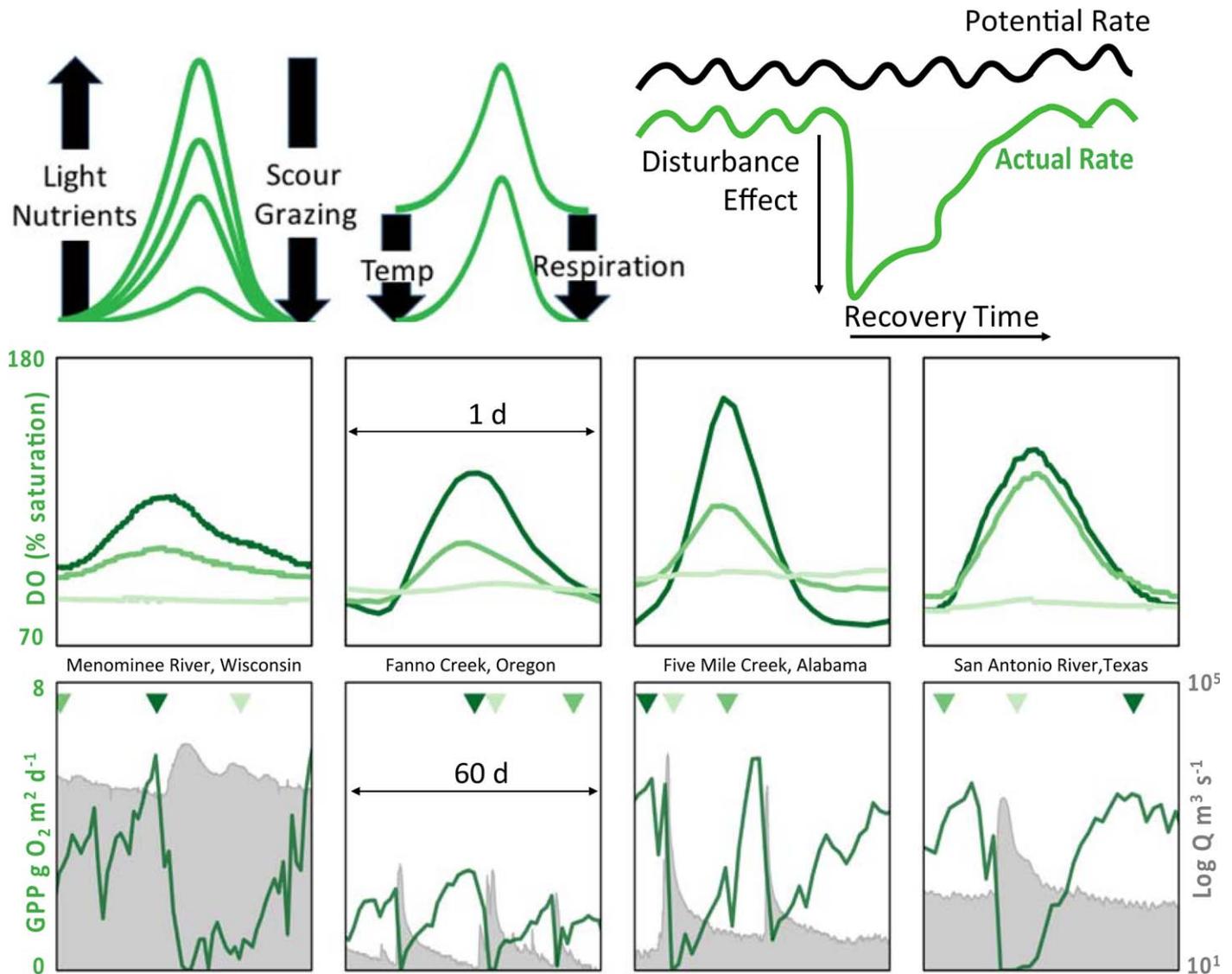


**Fig. 2.** A conceptual model depicting differences in how climate, light and hydrologic regimes vary along the river continuum and between three terrestrial biomes. The climate diagrams across the top show average monthly precipitation in blue bars with daily air temperatures shown as blue (minimum) and red (maximum) lines.

ER is the rate of oxygen consumption through both autotrophic and heterotrophic respiration and  $K(DO_{sat} - DO)$  is the net exchange of oxygen between the water column and the overlying air and is governed by a per unit time gas exchange rate  $K$ . Mean river depth ( $z$ ) converts from volumetric to areal rates. By convention, any process that lowers DO concentration in the water takes on a negative value so that ER is always a negative number. Whenever autotrophs are present, GPP will increase with light. Typically, GPP results in peak DO during the day

(Fig. 3A), except when high rates of gas exchange or flow variation obscure this pattern. Variation in the shape of this oxygen curve reflects variation in rates of GPP, ER, and  $K$  thus, with sufficient rates of GPP, it is possible to use curve fitting routines to estimate all three parameters from the oxygen data (Holtgrieve et al. 2010; Hall 2016) available for each day within a time series.

A first wave of sensor-enabled studies using this modeling approach clearly documented that light availability and



**Fig. 3.** Diel and Storm Recovery Patterns in Rivers. Figures in row A are conceptual models representing the typical variation in O<sub>2</sub> (as % saturation) at diel (A1, A2) and over storm-recovery trajectories (A3). Figures in row B show three contrasting diel curves selected from each of the four rivers shown in Fig. 1. In row C, we show 60 d of estimated rates of gross primary productivity (in green, derived from the O<sub>2</sub> data in Fig. 1) alongside the river hydrograph (gray shading). Each 60-d period encompasses at least one major flood. The color and date of the triangles shown at the top of panels in row C correspond to the dates for the diel O<sub>2</sub> curves shown in row B.

flooding are dominant and countervailing drivers of river ecosystem productivity (Uehlinger and Naegeli 1998; Houser et al. 2005; Roberts et al. 2007; Izagirre et al. 2008; Beaulieu et al. 2013; Hope et al. 2014; Hury et al. 2014; Roley et al. 2014). In contrast to lakes there is thus far limited evidence that nutrient availability controls metabolic rates in rivers (Hoellein et al. 2013; Solomon et al. 2013). In contrast, variation in stream metabolic rates can affect nutrient dynamics both within and across rivers (Hall and Tank 2003; Roberts and Mulholland 2007; Heffernan and Cohen 2010; Lupon et al. 2016). It thus seems likely that widespread nutrient pollution of rivers resulting from land

use change is having less of a direct effect on river metabolism than are the often-accompanying reductions in riparian canopy shading and increases in the frequency and severity of floods or droughts. Indeed, these alterations to river light and flow disturbance regimes are likely changing the potential for rivers to perform the critical ecosystem service of nutrient assimilation and retention (Fellows et al. 2006; Mulholland et al. 2008). Those alterations that reduce annual GPP and ER or which shift the timing of peak activity away from peak nutrient loading are likely to exacerbate nutrient pollution by reducing the potential for instream processing.

### ***The light and thermal regimes of rivers***

For terrestrial ecosystems, light and thermal regimes are controlled by latitude, topography and precipitation patterns, and thus two very basic descriptors of climate, mean annual temperature and mean annual precipitation, can explain much of the variation in GPP across terrestrial biomes (Whittaker 1962). Unfortunately, the light and thermal regimes of streams are less easily linked to these widely available environmental data. The light that penetrates from the atmosphere to river surfaces is strongly affected by both channel orientation with respect to landscape features (e.g., canyon walls or banks) and shading by terrestrial vegetation (Vannote et al. 1980; Hill and Dimick 2002; Julian et al. 2008). For small channels, the phenology of terrestrial vegetation can lead to rapid transitions in the light regime during the leaf out and litterfall periods that are particularly pronounced in temperate streams (Hill and Dimick 2002). Once light reaches the river surface there is a predictable attenuation with water depth that can be exacerbated by the reflectivity of suspended materials and light absorption by dissolved organic matter (Davies-Colley and Smith 2001; Julian et al. 2008). Light attenuates exponentially with water depth, such that benthic light availability is highest during baseflow periods and lowest during high flows. Moreover, light attenuation tends to increase in the downstream direction as larger rivers are deeper than their headwaters (Julian et al. 2008). For all these reasons, light availability varies substantially among sites as well as over time, well beyond the latitudinal variation in solar radiation that is the primary driver of variation in light regime among terrestrial ecosystems. Because of these light filtering mechanisms, periods of high light availability may not be matched to periods of high temperature or high incident solar radiation. Indeed, for many small, forested streams of the temperate zone, the highest light availability occurs in early spring before the forest canopy leafs out and late autumn after litterfall (Roberts et al. 2007).

Like the light regime, the thermal regime of rivers can deviate substantially from the temperature of the overlying atmosphere. The temperature of a river at any given time is determined by the cumulative fluxes of energy into and out of the water, including groundwater, evaporation, and sunlight (Poole and Berman 2001). In general, river temperatures will fluctuate seasonally in concert with air temperature, but the average temperature and the magnitude of diel and seasonal swings in temperature will be considerably muted in rivers relative to the overlying atmosphere. For rivers with significant rates of water and heat exchange with groundwater, or rivers below dams that receive most of their flow from reservoir depths there can be little to no correlation between air and water temperatures over time (Poole and Berman 2001; Olden and Naiman 2009). The resulting mismatches between temperature and light generate a much more diverse combination of light and thermal regimes in

river ecosystems relative to their terrestrial or lentic counterparts (e.g., Hury et al. 2014). Ecosystem respiration within rivers appears to have stronger temperature sensitivity than GPP, leading some to suggest that rivers are poised to become increasingly large sources of CO<sub>2</sub> to the atmosphere in a warming climate (Demars et al. 2011a,b).

Because terrestrial vegetation both reduces light and enhances organic matter loading to rivers, we are unlikely to see strong coherence between the productivity of rivers and the productivity of their surrounding terrestrial biome. Indeed, regions of high terrestrial primary productivity (e.g., tropical rain forests) are often associated with very low light availability for small receiving streams (Mulholland et al. 2008), while low productivity terrestrial ecosystems (e.g., deserts, tundra) can be drained by some of the most productive streams in the world (Grimm 1987). Terrestrial vegetation exerts less influence on the light regimes of larger rivers in which the attenuation of light by water depth and turbidity become dominant constraints (Vannote et al. 1980). Similarly, as rivers increase in size, their thermal regimes become increasingly insensitive to the stature and status of surrounding terrestrial vegetation. Thus, the position of any river segment within its river network is likely to be as important a determinant of its metabolic regime as the terrestrial biome which it drains. The distance along the river continuum at which terrestrial influence wanes is likely to vary considerably among different terrestrial biomes (Fig. 2). For example, riparian canopy cover is typically absent from the headwaters of desert, grassland, and alpine streams and seasonal light regimes are considerably different for small streams draining temperate deciduous vs. tropical or evergreen forests despite their similar channel widths. These interactions between geomorphology, vegetation, and channel size will drive wide variation in both the annual magnitude and the timing of primary production and ecosystem respiration.

### ***Disturbance regimes in river ecosystems***

Though much of what we have learned about annual patterns of river metabolism has come from studies of spring fed or regulated streams (Odum 1957; Roberts et al. 2007; Heffernan and Cohen 2010), a minority of rivers have such predictable flows. The potential for rivers to support high rates of GPP is maximized in slow flowing, clear water streams with stable flow and high light availability where productivity can rival that of temperate forests (Odum 1957; Heffernan and Cohen 2010; Acuña et al. 2011). In contrast, rivers with frequent bed-moving events typically have significantly lower productivity, even under similarly high light regimes (Uehlinger and Naegeli 1998; Uehlinger 2006). A rapidly growing body of literature documents the overriding importance of high-flow or desiccation-initiated disturbances of benthic primary producers in structuring the magnitude and timing of river ecosystem productivity (Acuña et al.

2004, 2005; Atkinson et al. 2008; O'Connor et al. 2012; Beaulieu et al. 2013).

Floods can regulate spatial and temporal patterns of many ecological processes in rivers including metabolism (Fig. 3). The return interval for events that lead to reductions in living biomass or organic matter stocks in rivers is much shorter than for almost any other ecosystem type (Grimm et al. 2003). In the most extreme cases forests may be harvested on decadal time scales and grasslands may burn annually, but some rivers experience dozens of biomass-reducing disturbances per year. A large flood can have multiple effects on primary producers and the macro- and microconsumers that live on or within riverbed sediments. Floods that are sufficiently powerful to mobilize bed sediments may lead to burial, scour or export of benthic producers and organic matter (Grimm and Fisher 1989; Young and Huryn 1996; Uehlinger and Naegeli 1998; Biggs et al. 1999; Uehlinger 2000; Uehlinger et al. 2002; Atkinson et al. 2008). It is literally true that “*the rolling stone gathers no moss*”<sup>1</sup>, as mobile substrates are unable to accumulate large and stable amounts of benthic biomass. Even in the absence of physical disturbance of channel sediments, the deeper and more turbid waters typical of floods decrease light availability to the channel bed (Hall et al. 2015). Research to date in small streams suggests that recovery times for both GPP and ER are expected to be longer for large floods that exceed the critical threshold for bed disturbance compared with small floods that mainly generate turbidity events (Cronin et al. 2007; O'Connor et al. 2012). It is likely, yet untested, that the mechanism through which floods impact river productivity may shift in larger rivers where a greater proportion of GPP may be performed by algae within the water column (Oliver and Merrick 2006). In these larger rivers, we may expect the light attenuation caused by flood-associated pulses of suspended sediment that raise turbidity to become the dominant disturbance impact rather than bed disturbance.

Low- and no-flow drought conditions are also strong constraints on river ecosystem productivity. The most conspicuous effect is obviously the reduction of total habitat area associated with drying (Stanley et al. 1997). Within the shrinking wetted channel area, responses to diminishing flow can be highly variable. In one case, progression of drying coupled with high light conditions were associated with growth of floating algae and extremely high rates of productivity in increasingly isolated pools (Acuña et al. 2005). Under such conditions, dissolved organic carbon can become highly concentrated. As streambed sediments are desiccated, primary production ceases in surface sediments and reestablishment may require an extended period of recovery after rewetting in some ecosystems (e.g., desert streams, Stanley

et al. 1997) or activate immediately in others (Antarctic streams, McKnight et al. 2007). There has been limited study to date of the ecosystem respiration rates of dry riverbeds, but one might expect enhanced mineralization of buried organic matter as anoxic areas of the sediments are oxygenated during drydown as well as pulses of microbial activity following rewetting of desiccated sediments (Merbt et al. 2016), analogous to the pulse of mineralization often observed when rain falls on dry soils (Fierer and Schimel 2002).

#### **Nutrient impacts on stream metabolic regimes**

When light and disturbance are not limiting, nutrient supply may limit the magnitude or influence the phenology of river metabolism (Hill et al. 2009). Common anthropogenic impacts on rivers such as the removal of riparian vegetation and flow regulation should exacerbate the sensitivity of metabolism to nutrient loading by reducing light limitation and disturbance frequency as constraints on river ecosystem productivity. There are plentiful examples of nutrient limitation *within* individual rivers (Grimm and Fisher 1986; Francoeur 2001; Tank and Dodds 2003). Experiments to measure the impact of nutrient loading on river metabolism have also documented substantial increases in GPP for a river in Alaska fertilized with phosphorus (Peterson et al. 1985) and enhanced rates of ER under N + P enrichment in heavily shaded, low nutrient streams in North Carolina (Kominoski et al. 2017). Outside of these experimental studies in well protected watersheds, we have had limited success in uncovering consistent relationships between nutrient supply and algal biomass *across* rivers (Francoeur et al. 1999; Dodds and Smith 2016). Since nutrient loading from farm or road runoff and wastewaters is often coincident with changes in organic matter and sediment loading and changes in disturbance regimes, it is perhaps not surprising that differences in these ultimate constraints (light and disturbance) override our ability to detect the additional effects of nutrient supply.

#### **Linking river “climate” with river metabolism**

Though we know that light, temperature and hydrologic disturbance (a river’s “climate”) are primary determinants of metabolic activity in rivers, and that nutrients may accelerate the metabolic response to each of these drivers, we have only limited information with which to predict how the distinct temporal dynamics of each driver interact to determine river metabolic regimes. Because of extensive historic investments in flow monitoring, we have large amounts of data available to understand fine scale variation in river flows (Poff et al. 1997, 2006) and thermal regimes (Olden and Naiman 2009; Maheu et al. 2016), but we have far less information about river light regimes (Hill 1996). We lack empirical measurements of light availability to the river surface for all but the largest rivers and a few well studied streams (Hill and Dimick 2002; Hill et al. 2011). We have even less information about the light regimes experienced by the primary

<sup>1</sup>First recorded in 1508 by Erasmus in his collection of Latin proverbs, *Adagia*.

**Table 1.** Changes in global temperatures and land cover will interact with widespread flow regulation to alter the light, thermal and flow regimes that ultimately shape the metabolic regimes of rivers. Direct effects of these global trends on the drivers of metabolism appear in black boxes while indirect effects appear as regular text.

		<i>Global Trajectories</i>		
		GLOBAL WARMING	LAND USE CHANGE	FLOW REGULATION
<i>Drivers of Metabolism</i>	LIGHT REGIME	<ul style="list-style-type: none"> <li>• Longer ice free period</li> <li>• Earlier leaf out</li> <li>• Later leaf fall</li> </ul>	<ul style="list-style-type: none"> <li>• Increased Sediment Load</li> <li>• Reduced Riparian Shading</li> </ul>	<ul style="list-style-type: none"> <li>• Reduced Sediment Load</li> <li>• Altered water depth</li> <li>• Altered riparian vegetation</li> </ul>
	THERMAL REGIME	Higher mean annual temperature	<ul style="list-style-type: none"> <li>• Reduced Riparian Shading</li> <li>• Channel incision enhances bank shading</li> </ul>	<ul style="list-style-type: none"> <li>• Hypolimnetic release alters natural thermal regime</li> <li>• Retention in shallow basins raises temperatures</li> </ul>
	FLOW REGIME	<ul style="list-style-type: none"> <li>• Increasing Drought Severity</li> <li>• Altered timing of Floods</li> <li>• Earlier, reduced snowmelt</li> </ul>	<ul style="list-style-type: none"> <li>• Stormwaters &amp; Tile Drainage Increase Flood Frequency &amp; Magnitude of Peak Flows</li> <li>• Withdrawals reduce baseflow</li> <li>• Leaks enhance baseflow</li> </ul>	<p><u>Hydropeaking increases frequency and magnitude of flood peaks</u></p> <p><u>Dams alter timing of seasonal floods and change baseflows</u></p>

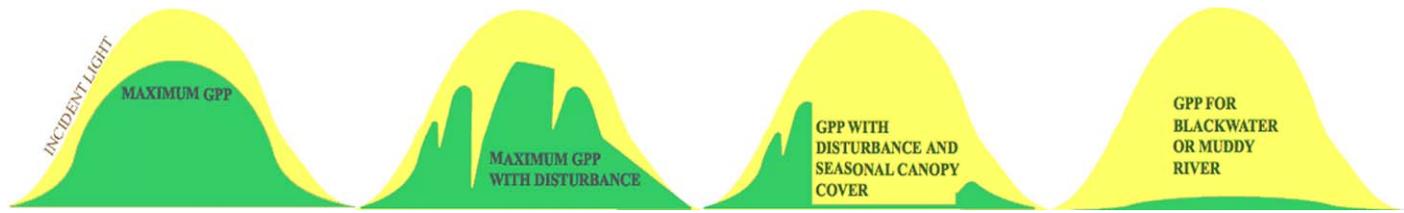
producers attached to bed sediments or transported in river flow, and thus we have limited empirical data and few models with which to estimate light availability to river autotrophs (Ochs et al. 2013). Better information on this aspect of the “climate” of rivers is sorely needed to generate mechanistic models that can predict the metabolic capacity of river ecosystems.

Such model development is essential if we want to better understand how river ecosystems are being altered by three major trajectories of change: rising global temperatures; land use change; and flow regulation (Table 1). Climate change is leading to rising temperatures and altered hydrographs for rivers globally (Oki and Kanae 2006; Grimm et al. 2013). Land use change is increasing sediment loads, nutrient inputs and flood and drought frequency for at least some portion of the channel network in every major river basin (Vorosmarty and Sahagian 2000; Vorosmarty et al. 2000; Allan 2004). The widespread construction of dams (Lehner et al. 2011; Zarfl et al. 2014) has fundamentally altered the flow regimes of many rivers (sensu Poff et al. 1997). The implications for river ecosystem energetics are difficult to predict, in part because the direct impacts of these drivers on river metabolic rates can be antagonistic (higher nutrients vs. higher disturbance frequency) and because these direct impacts may be mitigated or enhanced by the response of riparian vegetation to climate change. Periods of

high light, high nutrients, and stable flow—the “windows of opportunity” for high metabolic rates within stream ecosystems—seem likely to shift in their timing, duration and magnitude because of these competing drivers of change (e.g., Ulseth et al. 2017).

***Allochthonous carbon and river metabolism***

Further complicating efforts to measure and model river metabolism is that the energetic basis of many river food webs is not limited to in situ productivity. Streams with dense canopies of riparian vegetation, rivers carrying high particulate loads, and blackwater rivers all can support diverse and rich food webs and high rates of ecosystem respiration that are dominantly or exclusively supported by carbon derived from upslope and upstream ecosystems (Fisher and Likens 1973; Meyer et al. 1997; Wallace et al. 1997; Moore et al. 2004). At the other end of the spectrum, rivers with high water clarity and no canopy shading still receive subsidies to the autochthonous-based food web in the form of particulate detritus and dissolved organic matter from the surrounding watershed. These fixed carbon subsidies are often delivered to rivers in pulses. These may be regular and predictable (e.g., annual litterfall or snowmelt fluxes of dissolved organic matter); frequent but unpredictable (e.g., inputs of large amounts of DOM during floods; Boyer et al. 1997; Raymond and Saiers 2010); or very infrequent catastrophic events (e.g., hurricanes, ice storms, fires) that may



**Fig. 4.** A conceptual model of four possible and contrasting patterns of annual productivity that could arise for river ecosystems within the same latitude and terrestrial biome. The annual pattern of solar radiation (above any vegetation) is shown in yellow while GPP is shown in green. Maximum potential GPP is always constrained by incident light. Disturbance and the interception of light by canopy, DOC or sediment each reduce the capacity for river autotrophs to levels of productivity well below that predicted from light availability alone.

deliver large quantities of terrestrial organic matter to river ecosystems (Bernhardt et al. 2003; Earl and Blinn 2003; Dahm et al. 2015). Floods deliver, bury and remove the organic matter stored within riverbeds. The extent to which rivers store or transmit this supply of fixed OM downstream will determine the degree to which ER is tied to temporal variation in river productivity. In those river reaches where large standing stocks of organic matter accumulate, rates of ER may be decoupled from GPP, and the stored OM can support significant biological activity in rivers where primary productivity is negligible (reviewed in Webster and Meyer 1997). Differences between rivers in their capacity to store OM introduces considerable variation in the extent to which autochthonous and allochthonous energy sources support river food webs, as well as the coherence between seasonal and disturbance recovery patterns of GPP and ER.

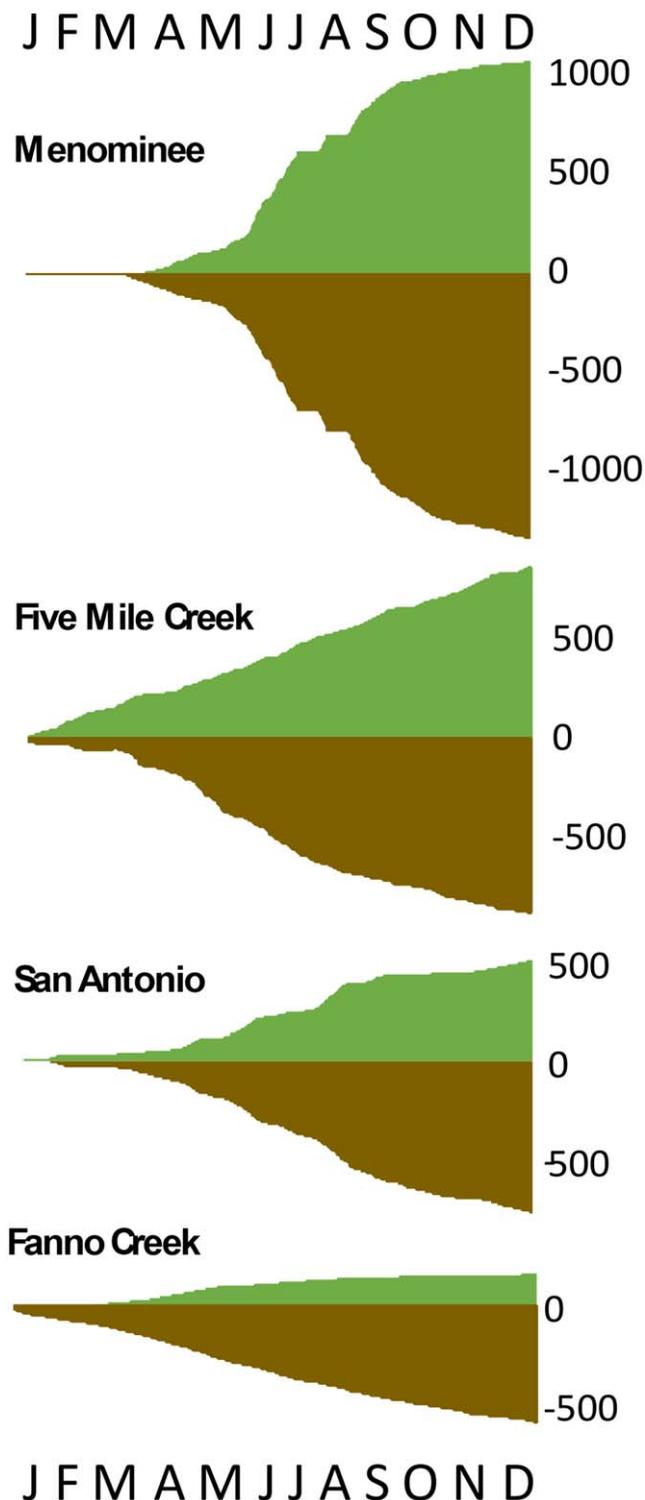
#### Annual patterns of river metabolism

As we amass a new understanding of the annual patterns of metabolism in rivers, we anticipate that there are likely to be discrete classes of river ecosystems that share a characteristic rhythm in the foundational metabolic processes of GPP and ER (e.g., Fig. 4). These “metabolic regimes” may be characterized by differences in: mean rates and their variability and skewness; the temporal structure of metabolism such as the autocorrelation and periodicity of ER and GP; the duration and timing of metabolic peaks and troughs; the post-disturbance rates of recovery; and by the variation in these characteristics among years and decades. These patterns are likely to be linked to the overlapping temporal patterns of the many factors that potentially control metabolism, and thus provide diagnostic information to determine the primary constraints on metabolism and to predict the likely energetic consequences of climate change, land use change or flow management for river ecosystems. Particularly for river ecosystems that have only short periods of peak metabolism, small shifts in the timing or magnitude of resource supply or of the peak flows, droughts or other events that constrain or reset metabolic rates may have disproportionately large impacts on river productivity at daily, seasonal, and annual time scales.

A global effort to measure, model and synthesize metabolism across many river ecosystems will reveal controls on the rates, timing and sensitivity of freshwater metabolism. Differences in metabolic regimes among rivers, and changes in these regimes over time, are likely to have wide-ranging ecological consequences. Metabolic regimes incorporate not only the amount of energy available to fuel secondary production, but also the temporal pattern of energy availability that determines which consumers are phenologically best suited to capitalize on metabolic products. Understanding ecosystem phenology and what it reveals about coupling between energetics and element cycling will open new opportunities to apply our emerging understanding of metabolic regimes as diagnostic tools for river management. Three frontier opportunities suggest themselves as particularly exciting avenues for progress:

#### **FRONTIER # 1 – linking metabolic regimes and organismal phenology**

Ecosystem rates of GPP and ER are maximized at times when and places where multiple potentially limiting resources are abundant and the biomass of primary producers is at its peak. Variation in resource supply and biomass removal thus drive considerable temporal variation in energy production across systems (Fig. 5). The study of the match or mismatch between an organism’s life history and organic matter supply has a rich history in stream ecology, where many consumers are dependent upon relatively discrete and predictable periods of either autochthonous production (e.g., spring algal blooms) or allochthonous organic matter supply (e.g., autumn litter fall). Disturbances that occur within these short periods of peak metabolic activity may have disproportionate effects on annual rates of ecosystem metabolism as well as on the productivity and identity of secondary consumers (Wootton et al. 1996; Power et al. 2008; Sponseller et al. 2010). In some rivers, changes in the identity of secondary consumers associated with intermediate levels of disturbance can lead to increased production of tertiary and higher trophic levels even as primary and secondary consumption decline (Power et al. 1996; Cross et al. 2011).



**Fig. 5.** Cumulative annual metabolism graphs for the four rivers from Fig. 1. GPP is in green, ER is in brown. Units on the y axis are in  $g\ O_2\ m^{-2}$ . Note that the southern river, Five Mile Creek has relatively uniform GPP while the northern Menominee River has high accumulation only during the summer months. The San Antonio River in Texas has alternating periods of high and very low productivity, while Fanno Creek has low GPP year-round. Rates of ER exceed GPP annually and for most daily time steps in all four streams.

However, more frequent disturbances have been shown and are predicted to favor small bodied, fast growing consumers (Gray 1981; Fisher and Gray 1983). Increased mortality and longer recovery times of larger predatory animals are proposed explanations for this trend. It is also possible, and likely, that reductions in the total energy available to consumers because of the removal of autotrophs and organic matter are in part responsible for these negative effects on higher trophic levels (as per predictions of the trophic pyramid, Elton 1927).

We suggest that simultaneous measurement and modeling of river ecosystem energetics and food web properties will be needed to predict the likely consequences of climate and land use change (Table 1) on river biodiversity and food web structure. Sabo et al. (2010) documented a negative relationship between flow variability (estimated from 16 to 20 yr of continuously measured flow data) and food chain length (FCL) for 20 U.S. rivers. In the same study, the authors concluded that there was no relationship between FCL and rates of gross primary production (Sabo et al. 2010). Since the GPP estimates used in the Sabo et al. (2010) synthesis were derived from only 1 to 20 d of midsummer (low flow) measurements they are likely highly inaccurate estimates of annual ecosystem productivity. As our measurements of river metabolism grow more similar in temporal resolution and longevity to our hydrologic records we predict we will discover strong, synergistic interactions between flow and metabolic regimes in constraining biodiversity and food web structure. There is mounting evidence that frequent high flows significantly constrain river GPP (Uehlinger 2006; Beaulieu et al. 2013, Fig. 3), and we suggest that the alterations in animal assemblages often attributed to hydrologic alteration or disturbance (Poff and Ward 1989; Sabo et al. 2009; Poff and Zimmerman 2010) may be due in part to the indirect effects of these flow alterations on ecosystem metabolism. If more comprehensive data support this prediction, it will only reinforce the importance of maintaining and restoring natural flow regimes to sustain both the disturbance and the energetic regimes that structure river food webs.

Widespread measurement of river ecosystem metabolism offers a new opportunity to confront this rich conceptual understanding with large volumes of empirical data describing the seasonal patterns of energy production and dissipation in rivers (Fig. 5). Coupling ecosystem metabolism time series with contemporaneous measurements of benthic secondary production or food web characteristics is likely to lead to new insights and re-examination of current assumptions. For example, studies of the impacts of altered flow regimes on the species composition of insect and fish communities often focus on how the life history of declining or extirpated taxa depended on natural flow regimes (Lytle and Poff 2004; Lytle et al. 2008). There has been far less consideration of how the direct impacts of flow modification on

higher trophic levels may be confounded by the indirect effects of flow on metabolism, the energetic base of these food webs. A cursory look at newly available data from just a few rivers in the United States (e.g., Fig. 3) demonstrates that high flows consistently reduce the biomass and cumulative GPP of river autotrophs. It is not just the “green,” or algal supported food web that is likely to be affected. Many river biota consume detritus delivered from the surrounding terrestrial ecosystem, with the growth and diversity of shredders and detritivores strongly tied to the standing stocks of leaf litter in small streams (Wallace et al. 1997, 1999). In soil and sediment food webs, heterotrophs rely on slow turnover of massive standing stocks of organic carbon—but in streams and rivers this “brown food web” is far more temporally dynamic due to events that can export, bury or fragment benthic organic matter standing stocks (Wallace et al. 1995). Thus, shifts in the timing of OM supply (via changes in terrestrial phenology) and removal or burial (via changes in storm magnitudes or timing) may have important implications for the wide variety of shredders and collectors that rely on these allochthonous carbon sources. The lost production that results from increasingly frequent or severe flows will certainly outlast the impact of the physical disturbance and, in some systems, may substantially alter the community of secondary consumers, with additional effects at higher trophic levels. Shifts in peak and total annual productivity resulting from global change drivers (Table 1) are likely to have important implications for the biomass and diversity of aquatic consumers that can be supported within a river, while shifts in the timing of peak productivity (Table 1) may favor new types of animals at the expense of historically dominant taxa.

## **FRONTIER # 2 - coupling energetics and element cycling**

In rivers, indeed in all ecosystems, cycling of nutrients and other elements can both depend on and influence metabolic patterns, and these reciprocal interactions operate over a wide range of time scales, within days, across seasons and through recovery from antecedent disturbances (Kirchner et al. 2004; Appling and Heffernan 2014). There is a rich history of stream ecological research that has documented strong links between metabolic phenology and the timing and magnitude of nutrient retention (Meyer 1980; Mulholland et al. 1985; Meyer et al. 1998; Roberts and Mulholland 2007). The emerging transition of stream metabolism studies from daily rates to annual regimes is part of a much wider effort to document and draw inference from hydrochemical patterns across the full span of relevant time scales, from days and storm events to seasons and decades (Kirchner et al. 2004). These efforts are greatly enabled by new technologies and approaches that can measure a rapidly

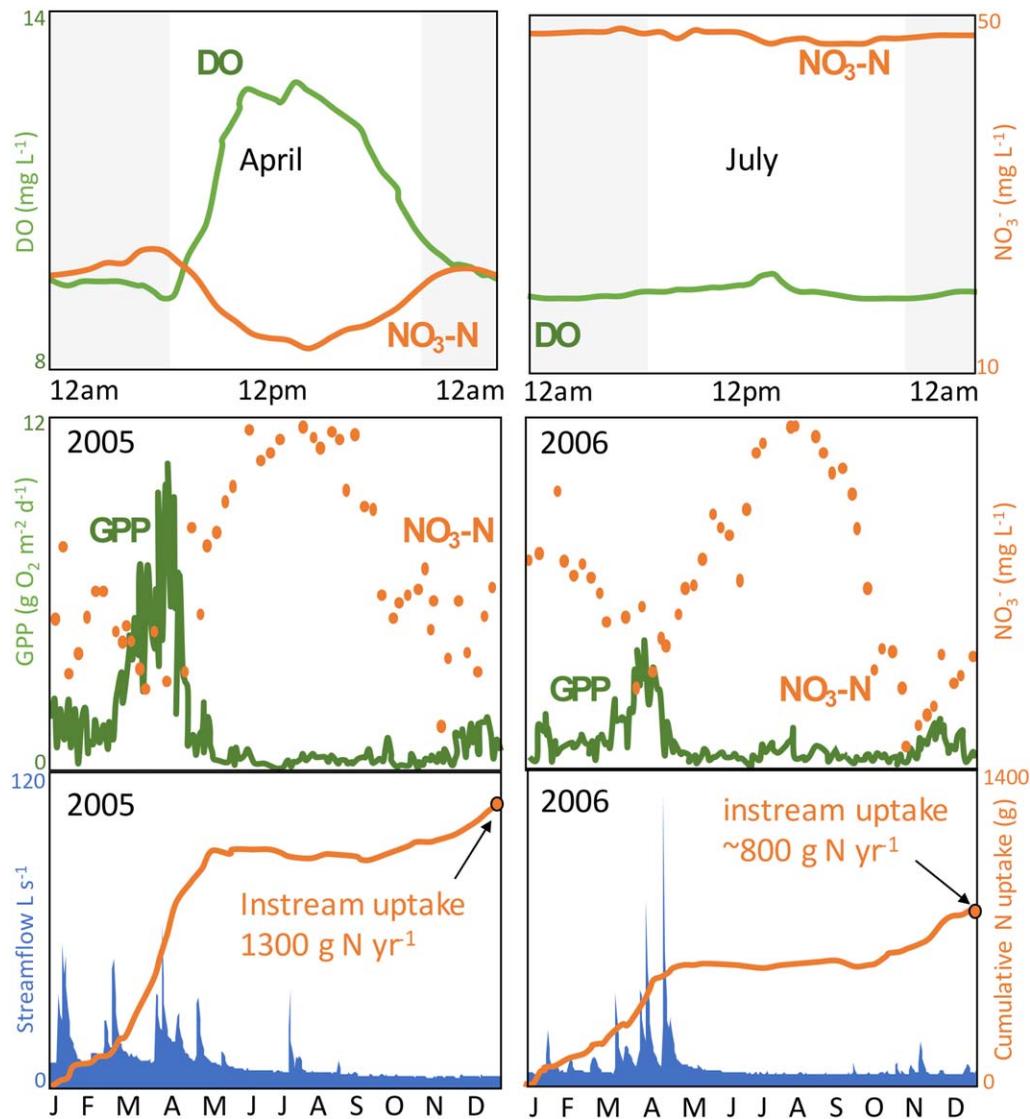
expanding portfolio of constituents continuously over long time periods (Porter et al. 2012; Pellerin et al. 2016).

Diel oscillations in a wide range of solutes are common in rivers and are linked to metabolism by both direct and indirect mechanisms (Nimick et al. 2011; Hensley and Cohen 2016). By quantifying variation in diel oscillations over time, recent empirical studies have demonstrated close coupling between instantaneous rates of metabolism and the assimilation of dissolved nutrients (e.g., Heffernan and Cohen 2010; Rode et al. 2016). While links between metabolism and nutrient cycling are also observed across rivers (e.g., Hall and Tank 2003), high-frequency continuous monitoring can illuminate relationships between metabolic processes and longer-term changes in material export. For example, in a Tennessee stream, daily GPP can drive variation in both diel  $\text{NO}_3^-$  oscillations and total uptake (Roberts and Mulholland 2007) (Fig. 6); similarly, interannual variation in springtime GPP due to storm frequency and timing accounts for much of interannual variation in watershed nutrient export (Lutz et al. 2012) (Fig. 6).

Joint high-frequency measurements of oxygen and other solutes can also illuminate the cascade of interactions between metabolism and other biogeochemical processes. In a spring-fed Florida River, variation in metabolism drives diel and seasonal variation in  $\text{NO}_3^-$  uptake, and also directly affects day-to-day variation in denitrification, which accounts for the majority of riverine  $\text{NO}_3^-$  removal (Heffernan and Cohen 2010). In the same system, metabolism affects diel variation in  $\text{PO}_4^{3-}$  concentrations, both directly through assimilatory uptake and indirectly via effects of pH on calcite saturation (de Montety et al. 2011; Cohen et al. 2013).

Riverine metabolism is obviously not the only potential cause of fine-scale variation in river chemistry; indeed, many such patterns reflect hydrologic and anthropogenic processes occurring in hillslopes, riparian zones, and upstream within river networks (Kirchner et al. 2001; Harvey 2016). For example, daily variation in evapotranspiration rates of catchment vegetation can drive diel variation in streamflow and thus the relative contribution of groundwater and shallow subsurface flowpaths, a mechanism that can drive diel variation in stream solute concentrations even in the absence of high rates of instream nutrient assimilation. Assimilation and transformation processes well upstream of a sampling location can result in temporal variation in solute concentrations which are inconsistent in their timing or magnitude with local control by in-stream processes (Pellerin et al. 2009, 2014). Relatively few studies have attempted to disentangle hydrologic and biotic drivers of diel nutrient variation using direct measurements of both processes (but *see* Aubert and Breuer 2016; Lupon et al. 2016).

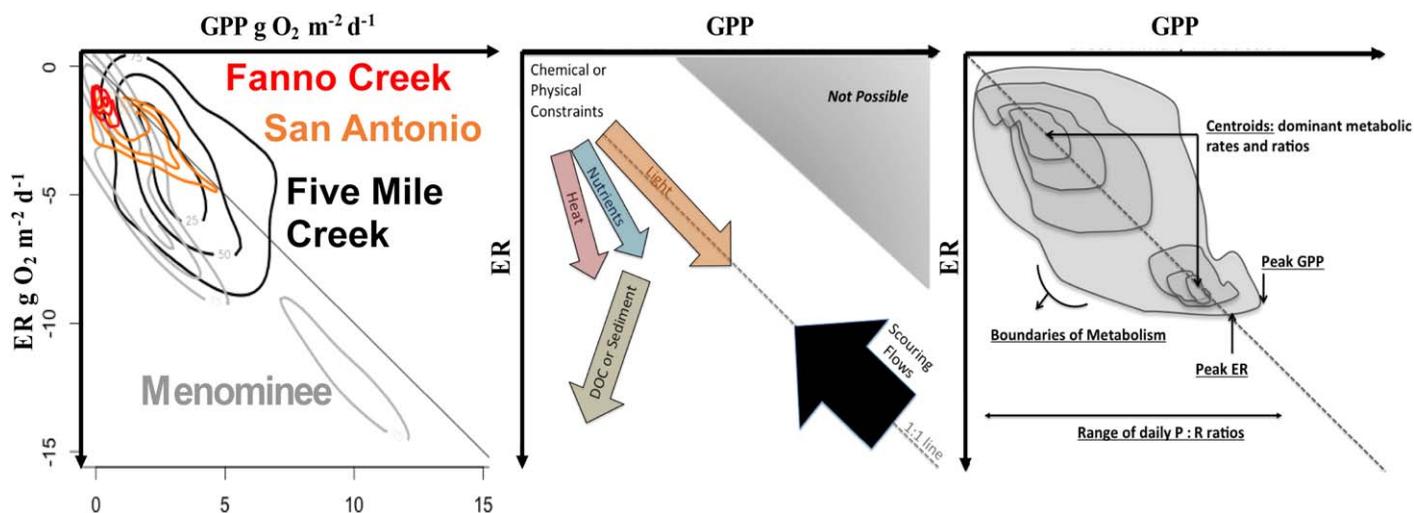
Although nutrients do not appear to drive major differences in metabolism across rivers, it is likely that nutrients do limit metabolism in rivers where nutrient supply is low,



**Fig. 6.** Data collected from Walker Branch watershed in Oak Ridge Tennessee (Roberts and Mulholland 2007; Roberts et al. 2007; Lutz et al. 2012). Upper panels during periods of the year with high GPP, diel increases in dissolved oxygen are linked to diel declines in stream nitrate concentrations while nitrate concentrations are constant (and elevated) during summer months when the forest canopy is closed. Middle panels: Seasonal variation in GPP explains the low stream nitrate concentrations during spring and fall. Lower panels: Years with larger spring algal blooms (e.g., 2005) have greater total annual instream nitrogen uptake than years in which spring storms reduce the longevity and peak productivity of spring algae (e.g., 2006).

light is abundant and disturbance is infrequent. It has been suggested that continuous daily estimates of nutrient concentrations could provide strong direct evidence for nutrient dependence of metabolism (Hall 2016). At still finer scales of diel variation, theoretical models predict that the magnitude of diel variation, relative to autotrophic demand, may depend on whether nutrients are available in sufficient supply (Appling and Heffernan 2014). High-resolution sensors are particularly valuable for testing such links between organismal physiology and ecosystem processes.

Taking full advantage of the growing capabilities of in situ sensors will require ongoing methodological and theoretical advances (Pellerin et al. 2016; Rode et al. 2016). Within rivers, the physical dynamics of transport are likely to affect covariation of solutes in ways that may both mask and influence biogeochemical processes. As one example, the footprint of processes that involve dissolved gases is likely to differ from those that lack gas phase reactants and products (Hensley and Cohen 2016). Similar challenges may arise in linking and disentangling processes that act at very different rates or in opposition (e.g., nitrification vs.



**Fig. 7.** The metabolic fingerprint is a diagnostic tool for comparing annual patterns of metabolism across rivers or across years for the same river. Panel A shows the metabolic fingerprint for 2014 GPP and ER estimates for each of the four streams shown in Fig. 1. The “fingerprint” is represented as a kernel density plot of all daily estimates of GPP and ER rates observed within each stream. The area of a river’s fingerprint (its variation along both the 1 : 1 line and ER axis) should be compressed by hydrologic disturbances and expanded by the supply of either solar energy of fixed carbon.

denitrification) within different habitat compartments (Helton et al. 2012; Gomez-Velez and Harvey 2014). Experimental approaches that take advantage of sensor capabilities may help provide estimates of whole system and compartment-specific biogeochemical processes.

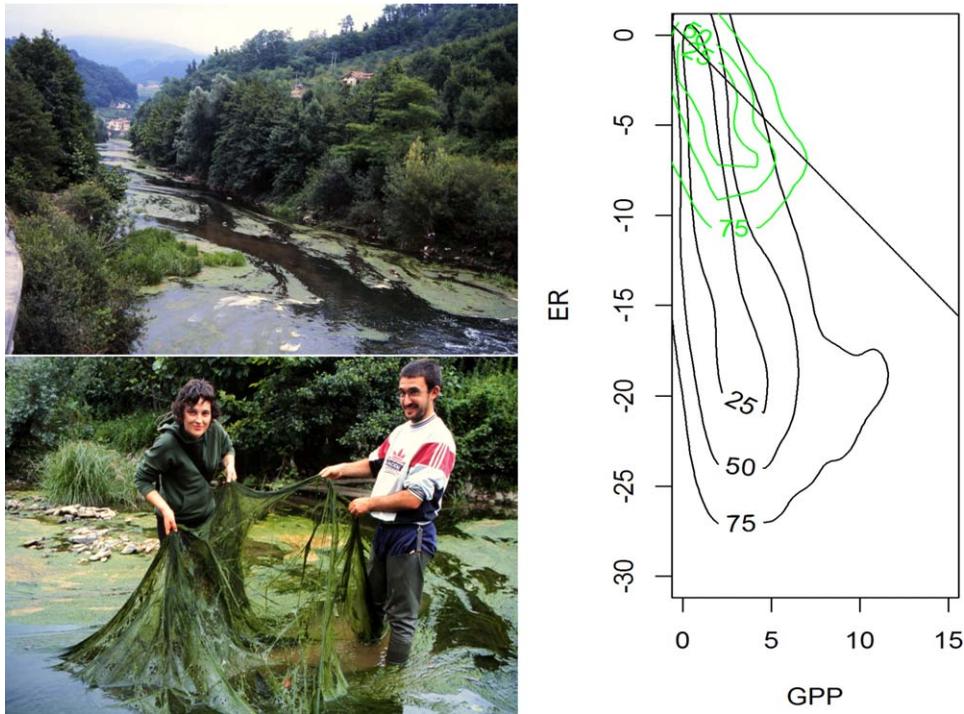
One clear need is the further development of integrative, ecosystem-level models that link metabolic, biogeochemical, and hydrologic processes within rivers. Widely used chemical loading models (i.e., Sparrow, HYDRA) couple dynamic hydrology with static assumptions about element processing within rivers. At present, river science lacks the portfolio of theoretical and modeling approaches akin to those developed by terrestrial biogeochemists and ecologists (e.g., CENTURY, Biome-BGC, P-NET) that allow for dynamic, non-equilibrium modeling of ecosystem and biogeochemical processes. Because rivers provide opportunities to observe metabolic and biogeochemical processes over comparable time scales, novel river ecosystem models offer the potential to develop and test more general theory of the interactions among element cycles and energy flow in ecological systems.

### Frontier # 3 - river metabolism for diagnosis and management

Basal metabolism constrains the “work” that ecosystems can do and we can measure this process for an entire ecosystem just as we do for an organism through monitoring its exchange of  $O_2$  or  $CO_2$  with the atmosphere. Many government agencies monitor dissolved oxygen in freshwater ecosystems to avoid or regulate low oxygen events. At no additional costs, these same data can be repurposed to provide real time, continuous measures of ecosystem function.

To take advantage of this new information, we need new diagnostic tools that are easy to explain and interpret. We propose the metabolic fingerprint as one such diagnostic tool and framework for hypothesis testing (Fig. 7). The metabolic fingerprint can be represented as the entire distribution of daily estimates of GPP and ER that are observed for a river, or the summary of those data into kernel density plots that allow easy visualization of both peak and median metabolic rates as well as variance in their ratio (Fig. 7). In Fig. 7, we show an explanatory cartoon of the fingerprint graph alongside the “fingerprints” of the four rivers presented previously in Figs. 1, 3. The highly productive Menominee River in Wisconsin occupies a much larger volume of metabolic space than does the very frequently flooded Fanno Creek in Oregon. We hypothesize that higher light and nutrient supplies will expand both the total area and the maximal rates represented by a river’s fingerprint, while hydrologic disturbance and sediment loading will constrain the metabolic fingerprint to values near the origins of both the GPP and ER axes. We suspect that as we gain annual metabolism data from an increasing number of rivers we will discover recognizable clusters of river metabolic regimes. As we develop our mechanistic understanding of how river metabolic regimes are established, maintained and disrupted, we will become better able to determine how river metabolic regimes are being altered by pollution, flow regulation or climate change as well as how effective mitigation, restoration, and preservation efforts are at returning rivers toward more natural metabolic regimes.

In addition to comparing fingerprints across streams, these same visualization tools can be used to compare across



**Fig. 8.** Two photos of the Oria River and its metabolic fingerprint before (black) and after (green) the construction of a wastewater treatment plant. Photo credits to M. Arroita and A. Elosegí.

years or among sites within the same river to examine the effects of infrastructure or restoration efforts, land use change, or hydrologic extremes. For example, the metabolic fingerprint of the Oria River in the northern Spain changed in response to the implementation of a wastewater treatment plant (WWTP) (Fig. 8). The Oria River drains a basin of 882 km<sup>2</sup> with 126,000 inhabitants in which industries had previously diverted their wastewater directly to the river. Historic water quality data collected by the monitoring station located in the upper basin (~ 333 km<sup>2</sup>) revealed that untreated sewage directly coming from houses and industries carried large amounts of both inorganic and organic pollutants, elevating ammonium in the river to concentrations as high as 2.5 mg·L<sup>-1</sup>. High loads of organic matter resulted in very high rates of stream ER that were not accompanied by similarly high rates of GPP. Although hyperoxic conditions (saturation 150%) were common during the day due to the high rates of GPP, even higher ER rates derived from organic pollution frequently resulted in hypoxia at night (saturation < 40%). In 2003, a WWTP was put into operation approximately 8 km upstream from the water quality monitoring station, and now treats the domestic sewage of 60,000 inhabitants as well as industrial sewage. The amount of inorganic and organic pollutants entering the river subsequently declined, with average ammonium concentrations falling to 0.18 mg·L<sup>-1</sup>. This improvement in water quality resulted in reduced rates of both GPP and ER, significantly changing the

distribution of metabolic rates—the “metabolic fingerprint”—of the Oria River (Fig. 8). Daily amplitudes of dissolved oxygen greatly decreased due to the reduced metabolic rates with oxygen saturation now consistently between 80% and 120%, resulting in greatly improved conditions for river biota. This case study shows just one example of how the metabolic “fingerprint” can serve as both a sensitive detector and a clear outreach tool to describe ecosystem functional responses to intervention.

### Concluding remarks

Syntheses of daily metabolism measurements from across different rivers have revealed enormous variability and had limited success in explaining this variance. We suggest that estimating GPP and ER for one or a few days provides little information about the energetics of most rivers where frequent disturbance and highly variable light regimes lead to high temporal variation in GPP and ER rates. By examining the patterns of metabolism over entire years, we can observe how the extrinsic controls of light, heat, allochthonous inputs, and disturbance together shape metabolism, and we can begin to understand and predict how these drivers have changed and are likely to change because of widespread flow regulation, climate change, land use, and eutrophication.

Land use and climate change are altering the light, thermal and disturbance regimes of rivers at both local and

global scales. Climate change has already shifted the timing, magnitude and frequency of flooding events in rivers throughout the world (Milly et al. 2002, 2005; Oki and Kanae 2006). Even in the absence of directional climate change, hydropower and water supply dams are leading to major shifts in the hydrologic regimes of most the world's rivers (Poff and Zimmerman 2010; Vörösmarty et al. 2010); while the frequency and magnitude of peak flows in smaller streams have been increased by urbanization's spreading influence (Paul and Meyer 2001; Walsh et al. 2005). All forms of land use change tend to generate increased turbidity events and accelerated bed and bank erosion (Leopold et al. 1964). Approaches to manage the stressors and protect ecosystem services of rivers are in their infancy, and we suggest that effective river conservation and management requires that we devote as much attention to the metabolic regimes of rivers as we have already invested in understanding river flow regimes.

Fortunately, we now have the technical and logistical capacity to measure dissolved gas and solute fluxes and model ecosystem metabolism at the same highly resolved time steps at which streamflow has historically been measured. If we can match these technological innovations with equally innovative theoretical breakthroughs we will enable river ecosystem science to link energetics and element cycles at the time scales at which: organisms assimilate elements (seconds to hours to days); disturbance initiates succession (weeks to months); and terrestrial and aquatic element cycles are linked (from hours to seasons). The emergent research will generate novel and sophisticated understanding of the multi-scale controls of stream metabolism, facilitating the transition from short-term, reach-scale studies toward annualized, scalable models of freshwater ecosystem energetics. In turn, these models will enable sophisticated predictions about how river food webs, biodiversity, and nutrient processing capacity are likely to change under realistic scenarios of climate and land use change.

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None declared.

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