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Recovery and resilience of urban stream metabolism following Superstorm Sandy and other floods

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Abstract. Urban streams are exposed to multiple different stressors on a regular basis, with increased hydrological flashiness representing a common urban stream stressor. Stream metabolism, the coupled ecosystem functions of gross primary production (GPP) and ecosystem respiration (ER), controls numerous other ecosystem functions and integrates multiple processes occurring within streams. We examined the effect of one large (Superstorm Sandy) and multiple small and moderately sized flood events in Baltimore, Maryland, to quantify the response and recovery of urban stream GPP and ER before and after floods of different magnitudes. We also compared GPP and ER before and after Superstorm Sandy to literature values. We found that both GPP and ER decreased dramatically immediately following floods of varying magnitudes, but on average GPP was more reduced than ER (80% and 66% average reduction in GPP and ER, respectively). Both GPP and ER recovered rapidly following floods within 4–18 d, and recovery intervals did not differ significantly between GPP and ER. During the two-week recovery following Superstorm Sandy, two urban streams exhibited a range of metabolic activity equivalent to ~15% of the entire range of GPP and ER reported in a recent meta-analysis of stream metabolism. Urban streams exhibit a substantial proportion of the natural variation in metabolism found across stream ecosystems over relatively short time scales. Not only does urbanization cause increased hydrological flashiness, it appears that metabolic activity in urban streams may be less resistant, but also more resilient to floods than in other streams draining undeveloped watersheds, which have been more studied. Our results show that antecedent conditions must be accounted for when drawing conclusions about stream metabolism measurements, and the rapid recovery and resilience of urban streams should be considered in watershed management and stream restoration strategies targeting ecosystem functions and services.

Key words: disturbance; ecosystem respiration; flood; gross primary production; recovery; recurrence interval; resilience; resistance; Superstorm Sandy.

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Introduction

Urban stream ecosystems exhibit a multitude of physicochemical and biological changes in response to urban development (Walsh et al. 2005, Wenger et al. 2009, Kaushal and Belt 2012). These changes typically include geomorphic alterations such as highly incised banks and homogenous channel shape (Wolman 1967, Henshaw and Booth 2000, Vietz et al. 2016), elevated

nutrients and other chemical contaminants (Hatt et al. 2004, Carle et al. 2005), and biotic communities with decreased intolerant and increased tolerant species (Paul and Meyer 2001). These physicochemical and biological changes to urban streams are speculated to result in reductions in stream ecosystem functions such as metabolism and nutrient uptake, despite a limited amount of empirical evidence (Walsh et al. 2005, Wenger et al. 2009). In fact, a recent review found that stream nitrogen uptake rates were similar between reference and urban streams across a range of urban settings (Reisinger et al. 2016), and urban stream networks are dynamic transformers of materials and energy, particularly during baseflow (Kaushal et al. 2014*a*, *b*).

Stream metabolism is an integrative metric of stream biological activity, and it represents the fundamental ecosystem functions of gross primary production (GPP) and ecosystem respiration (ER; Odum 1956, Hoellein et al. 2013). Both GPP and ER can be simultaneously considered a driver of other ecosystem processes (e.g., metabolism controls nutrient uptake; Hall and Tank 2003) or as a dependent variable characterizing the response of different streams to extrinsic drivers (Mulholland et al. 2001, Bernot et al. 2010). The development of new technologies and modeling approaches (e.g., Grace et al. 2015, Hall et al. 2016) has allowed for rapid expansion of stream metabolism datasets and continuous records, allowing us to test the response of this fundamental ecosystem function to a range of environmental drivers.

Long-term stream metabolism datasets now show that metabolic activity within a stream varies on multiple temporal scales, including seasonal, daily, and episodic (e.g., storms, spates) scales (Acuña et al. 2004, Roberts and Mulholland 2007, Beaulieu et al. 2013). Heavily impacted stream ecosystems can vary over these different time periods. For example, highly managed agricultural ditches exhibit extreme day-to-day variability in metabolic activity over a given year, as a single agricultural ditch had a wider annual range of both GPP and ER than the entire range of all literature data on stream metabolism from a recent review (Hoellein et al. 2013, Roley et al. 2014). Therefore, this agricultural ditch appears as variable across days as across seasons, likely due to an open canopy and high nutrient conditions across seasons. Streams affected by urbanization can also exhibit high variability in metabolic parameters over a range of environmental conditions such as streamflow, day length, and nutrient status (Smith and Kaushal 2015). For example, a two-year semi-continuous record of metabolism in a suburban stream revealed that light availability, temperature, and disturbance all controlled variation in stream metabolism at different temporal scales (Beaulieu et al. 2013).

Although often considered biologically impaired due to low macroinvertebrate and vertebrate biodiversity (Moore and Palmer 2005, Walsh et al. 2005, Walters et al. 2009), urban streams can exhibit rates of ecosystem functions equivalent to, or higher than, agricultural or reference streams (Mulholland et al. 2008, Bernot et al. 2010, Reisinger et al. 2016). For example, GPP and ER in streams draining predominately urban watersheds were significantly higher than in nearby streams located within a forested state park throughout the year (Kaushal et al. 2014*a*). Similarly, streams draining a range of forested and urban watersheds, and under variable restoration strategies, all exhibited similar GPP and ER in both summer and winter (Sudduth et al. 2011). Despite the multiple physicochemical stressors present in urban streams that represent a constant "press" disturbance (sensu Lake 2000), fundamental ecosystem functions like stream metabolism and nutrient uptake (Mulholland et al. 2008, Bernot et al. 2010, Reisinger et al. 2016) may actually be more resistant to urbanization than the biodiversity of stream communities. From a practical perspective, this suggests that ecosystem functions related to urban water quality may be more resilient to disturbance in urban streams than previously appreciated, and this may be driven by high functional redundancy within microbial communities driving these ecosystem functions (Utz et al. 2016).

One of the most ubiquitous symptoms of urbanization is an increase in flow variability and magnitude, increasing the rate and magnitude of erosion, scouring, and sediment transport (Hawley and Vietz 2016). This increase in hydrologic "flashiness" is caused by a combination of impervious surfaces on the landscape and stormwater drains increasing the efficiency of runoff from the watershed to the stream (Walsh et al. 2005, Kaushal and Belt 2012, Vietz et al. 2016). High-flow events have long been recognized as a controlling factor for

stream ecosystems (Poff et al. 1997). Indeed, recovery and succession of streams following flooding has been the focus of numerous classic studies (Fisher et al. 1982, Grimm 1987). In naturally flashy streams, algal biomass and primary production recover to pre-flood levels within days to weeks (Fisher et al. 1982, Grimm 1987), and ER may be less affected by floods than GPP, leading to an increase in heterotrophy following floods (Uehlinger 2000, Uehlinger et al. 2003). Although stream ecosystems are typically thought of as highly resilient to floods (Lake 2000), increased flashiness caused by urbanization (in terms of both frequency and magnitude of flood events), coupled with multiple other stressors that impair the biological community within urban streams, may combine the pulse and press disturbances of flooding and urbanization to drastically limit the ability of urban stream metabolism to recover from flooding.

Here, we investigated the response of urban stream metabolism to flood events of various magnitudes. We quantified metabolism before and after floods and the recovery rate following the flood. We had three objectives: (1) quantify recovery rates of stream metabolism across a range of flood magnitudes, (2) establish whether recovery is controlled by flood magnitude, and (3) compare metabolic activity of urban streams during a post-flood recovery to previously measured metabolic rates from the literature. These three objectives aimed to expand our understanding of both metabolism, a key ecosystem function driving multiple processes within streams, and the response of urban streams to disturbance. These objectives are consistent with several key questions in urban stream ecology (specifically questions 1, 4, 5, and 6) identified by Wenger et al. (2009).

Methods

Study sites

We initially selected two streams located within Baltimore County and Baltimore City (Maryland, USA) that are components of the U.S. National Science Foundation-funded urban Long Term Ecological Research network Baltimore Ecosystem Study project. One stream was located near the urban core of Baltimore (Gwynns Falls at Carroll Park, hereafter the "urban site"), and the other stream was located in a more suburban area (Gwynns Falls at Gwynnbrook, hereafter the "suburban site"; Table 1). At each of these sites, we deployed dissolved oxygen (DO) and temperature sensors (miniDOT; Precision Measurement Engineering, Vista, California, USA) and photosynthetically active radiation (PAR) sensors (Odyssey PAR Recorder; Dataflow Systems Limited, Christchurch, New Zealand) programmed to log DO, temperature, and PAR every five minutes on or before 22 October 2012. We collected the sensors on or after 12 November 2012. This deployment period included Superstorm Sandy (hereafter "Sandy"), a large storm event (see *Storm events*) that affected much of the northeastern United States. Although Baltimore was less affected than areas further north, large-scale flooding did occur, allowing us to test the effect of a storm on stream metabolism and its recovery in urban streams.

In addition to these two sites, we analyzed metabolism data from four additional urban streams located within Baltimore City or County in 2015. We deployed miniDOTs which

Table 1. Characteristics of study stream watersheds (WS) and flood dates.

Site	Lat. long.	Percent developed	Percent ISC	WS area (km^2)	Flood dates
GFCP (referred to as "urban")	39°16′17.4″ N, 76°38′54.8″ W	79	28	165	29 October 2012
GFGB (referred to as "suburban")	39°26′34.6″ N, 76°47′00.3″ W	82	17	11	29 October 2012
SLB	39°22′25.7″ N, 76°47′41.5″ W	92	29	1	10 September
MBU	39°24′43.0″ N, 76°33′12.5″ W	82	23	1	18 May, 24 August, 10 September
MBD	39°24′34.6″ N, 76°33′26.1″ W	73	21	5	13 July, 24 August, 10 September
STN	39°21′22.2″ N, 76°37′49.3″ W	90	28	2	27 June, 24 August

Notes: ISC, impervious surface cover; WS area, watershed area; GFCP, Gwynns Falls at Carroll Park; GFGB, Gwynns Falls at Gwynnbrook; SLB, Scotts Level Branch; MBU, Minebank Run—Upstream; MBD, Minebank Run—Downstream; STN, Stony Run. Flood dates are from 2015 unless otherwise noted.

continuously logged DO and temperature at these four sites (beginning in April 2015), and PAR sensors at three of four sites. The site without a PAR sensor was located near a site with a PAR sensor, and we therefore used PAR from this nearby site for modeling. We quantified watershed characteristics (area, percent developed, percent impervious surface cover [ISC]) by first delineating watersheds using 30-m resolution digital elevation models from the United States Geological Survey (USGS) and then extracting land-use categories using standard methods in ArcGIS (Version 10.3.1, Esri Corporation, Redlands, California, USA). Both percent developed and percent ISC were extracted from the 2011 National Land Cover Database (NLCD; Homer et al. 2015) to provide a general representation of the land use in the watersheds of these sites (Table 1). We note that percent developed represents the sum of the four different developed land-use classifications from NLCD. These streams are representative of urban streams throughout the Baltimore area, with closed canopies, substrate ranging from sand to cobble, stormwater drain inlets, and elevated background nutrient concentrations (Kaushal et al. 2014*a*).

Storm events

On 29 October 2012, Hurricane Sandy made landfall in the northeastern United States. Although the majority of the storm surge, property loss, and economic harm occurred further north, rainfall was heaviest in eastern Maryland. For example, 16.8 cm of precipitation fell at the Baltimore-Washington Airport during the course of the storm (Blake et al. 2013), and this caused major flooding in streams throughout the Baltimore area. In less than 24 h, discharge increased from baseflow values of 0.07 and 0.83 m^3/s to 18 and 291 m^3/s for the suburban and urban streams, respectively.

For the storm events using the four additional sites, we sorted through a daily discharge and metabolism record spanning April–November 2015 to identify high-flow events with enough time at baseflow between events to allow for metabolic recovery. We only included events with at least four days of baseflow prior to the flood with relatively stable GPP and ER, coupled with enough time following the flood for GPP and ER to recover to pre-flood rates. We selected nine stream–storm events to include in addition to the Sandy data (Table 1).

We calculated the flood recurrence intervals (RIs, Eq. 1) for each of these stream–flood events (n = 11; two from Sandy and nine from 2015) using two approaches. For sites with USGS gages, we used the maximum annual flow from USGS records for every year available and produced flood RIs using the approach outlined below. For sites that did not have USGS gaging stations, we identified nearby gaging stations located on the same stream (but further downstream in the network). We used USGS data from these downstream gaging stations to estimate flood RIs for our ungaged sites, which provides a conservative estimate for site-specific flood RIs.

Flood RIs were calculated by first compiling the maximum flow for each year on record from the USGS gages. We then ranked each year by the magnitude of maximum annual flow, with the highest flow year being ranked first. We calculated RIs as

$$\text{Flood RI} = \frac{\text{N} + 1}{\text{Rank}_i} \tag{1}$$

where N is the total number of years in the USGS record, and Rank_i is the rank for year i. We then regressed $\log_{10}$-transformed flood RI vs. peak flow for each year (L/s) to provide an equation for calculating RIs for each flood event in our analysis.

Metabolism estimation

We used the single-station open-channel O_2 exchange approach to estimate stream metabolism. Our modeling approach was based upon a modification of the daytime regression approach (Atkinson et al. 2008, Grace et al. 2015) in which we modeled GPP and ER as

$$\begin{aligned}[\text{DO}]_{t+1} = {} & [\text{DO}]_t + AI_t^p - R\left(\theta^{(T_t - T_{\text{mean}})}\right) \\ & + K_{\text{DO}} \times \left(1.0241^{(T_t - T_{\text{mean}})}\right) \\ & \times \left([\text{DO}]_{\text{sat},t} - [\text{DO}]_{\text{modeled},t}\right)\end{aligned} \tag{2}$$

where t is the timestep; AI^p is the primary production term (mg $O_2 \cdot L^{-1} \cdot d^{-1}$), where A is a constant, I is surface irradiance, and p is an exponent accounting for photo-saturation; R is respiration (mg $O_2 \cdot L^{-1} \cdot d^{-1}$); θ is the temperature dependence of respiration; T_t and T_{mean} are water temperature at time t and average daily water temperature; K_{O_2} is the aeration coefficient (d^{-1}); and *sat* and *modeled* refer to [DO] at saturation

and modeled concentrations, respectively. To carry out this metabolism estimation, we used an updated version of the Bayesian single-station estimation (BASE) modeling approach (Grace et al. 2015), which has been modified based on recommendations of Song et al. (2016) to estimate daily GPP and ER. The updated BASE approach employs Eq. 2 to use direct concentration of DO rather than a stepwise approach, and uses modeled DO concentration rather than measured concentration to estimate oxygen deficiency for aeration rates. The updated BASE model (BASE v2.0) can be accessed online (https://github.com/dgiling/BASE).

Due to high levels of diel temperature fluctuation, we used BASE to simultaneously model GPP, ER, K, p, and θ. Output from BASE provides GPP and ER in volumetric units. In order to compare metabolic rates across sites and with previous literature values, we multiplied volumetric rates by mean daily stream depth to convert from volumetric to areal rates (g $O_2 \cdot m^{-2} \cdot d^{-1}$). We also calculated net ecosystem productivity (NEP; g $O_2 \cdot m^{-2} \cdot d^{-1}$) as

$$\mathrm{NEP} = \mathrm{GPP} + |\mathrm{ER}| \tag{3}$$

where |ER| is the absolute value of ER, which is traditionally expressed as a negative value. For each site, we used daily discharge coupled with an empirically derived discharge–depth relationship (unique for each site; data not shown) to estimate mean daily stream depth.

Analysis

After estimating GPP and ER for each stream before and after flood events, we calculated the percentage of reduction due to flooding as

$$\mathrm{Reduction}\,(\%) = 1 - \left(\frac{\mathrm{Rate_{post}}}{\mathrm{Rate_{pre}}}\right) \times 100\% \tag{4}$$

where $\mathrm{Rate_{post}}$ is GPP or ER on the first modelable day after the flood event, and $\mathrm{Rate_{pre}}$ is the average GPP or ER at baseflow conditions prior to the flood event. We were unable to model metabolism on the day of peak flow or often for at least one day following a flood due to the reliance of the BASE model on an assumption of constant discharge (Grace et al. 2015), which is a common assumption for whole-stream metabolism models. We also calculated recovery intervals for GPP and ER, which allowed us to compare the time it took for a site to recover to pre-flood rates while accounting for differences in base metabolic activity due to non-flood-related factors (e.g., variable canopy, water chemistry, stream size).

Metabolic recovery intervals were calculated in a multi-step approach. First, we quantified mean GPP and ER at baseflow before the flood. Next, we calculated response ratios for post-flood GPP and ER as

$$\mathrm{Rate_{RR}} = \frac{\mathrm{Rate}_i}{\mathrm{Rate_{Pre}}} \tag{5}$$

where $\mathrm{Rate_{RR}}$ is the response ratio for either GPP or ER and Rate_i is GPP or ER on day i post-flood. We applied Eq. 5 to each day post-flood until response ratios reached a plateau, suggesting a new equilibrium had been reached following the flood. After calculating response ratios for both GPP and ER on each day post-flood, we regressed response ratios vs. time since the flood event (d), providing us with a linear regression equation. The slope of the regression line represents the recovery rate. After modeling recovery trajectories from each site, we set $y = 1$ for each unique regression equation and solved for x, which equates to how much time was required following the flood for $\mathrm{Rate_{post}}$ to equal $\mathrm{Rate_{pre}}$ (alternatively, when did $\mathrm{Rate_{RR}} = 1$ based on the regression). We will refer to this length of time as the recovery interval (d). We compared recovery intervals for GPP and ER using a paired t test, and we compared seasonal differences in recovery intervals between summer (1 June–31 August; $n = 5$) and autumn (1 September–30 November; $n = 5$) flood events using independent t tests. One flood event was excluded from the seasonal analysis as it was a spring flood occurring on 18 May (Table 1).

We quantified the effect of flood magnitude on metabolic recovery using simple linear regression with recovery intervals for either GPP or ER as the response variable and flood RI as the predictor variable. This approach, coupled with the fact that recovery times are based upon response ratios and therefore account for differences in baseflow metabolic activity across space and time, allows us to isolate the effect of flood magnitude on metabolic recovery across the range of streams. Finally, to compare urban stream metabolic activity to other stream ecosystems, we compared GPP vs. ER for the suburban and

urban streams in response to Sandy to literature values of stream metabolism taken from a recent review (Hoellein et al. 2013).

Results

Response to Superstorm Sandy

Prior to Superstorm Sandy, both the suburban and urban streams were heterotrophic, with GPP averaging 0.70 and 1.80 g $O_2 \cdot m^{-2} \cdot d^{-1}$ and ER averaging 4.12 and 2.62 g $O_2 \cdot m^{-2} \cdot d^{-1}$ for the suburban and urban streams, respectively (Fig. 1). The second day following peak flow from Sandy was the first day which provided an acceptable model fit. Both the suburban and urban streams exhibited a larger reduction in GPP (84% and 92% reductions, respectively) than in ER (72% and 86% reductions, respectively), although the differences in GPP and ER reduction were modest for both sites (Fig. 1). Following Sandy, both sites exhibited a reduction in metabolic activity, suggesting a disturbance, but as time since the flood progressed, metabolic activity exhibited a post-flood recovery (Fig. 2). Both the urban and suburban streams exhibited a large amount of variation in GPP (coefficient of variation [CV] = 59.8% and 101.8%, respectively) and ER (CV = 74.8% and 40.3%, respectively) following Sandy (Figs. 2, 3). Indeed, over the two-week recovery trajectory, the

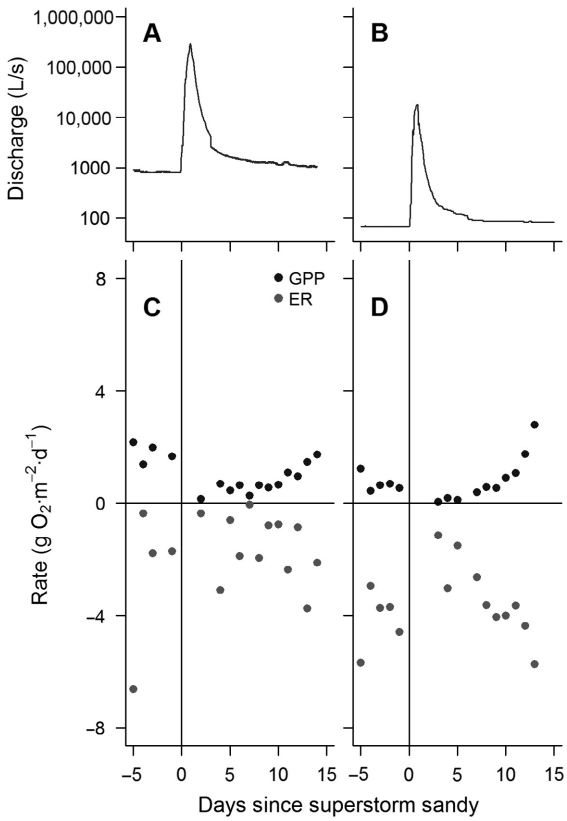

Fig. 1. Gross primary production (GPP; dark gray; C, D) and ecosystem respiration (ER; light gray; C, D) recover following Superstorm Sandy (A, B) at both the urban (A, C) and suburban (B, D) sites. Vertical lines represent the day with peak flow for Superstorm Sandy.

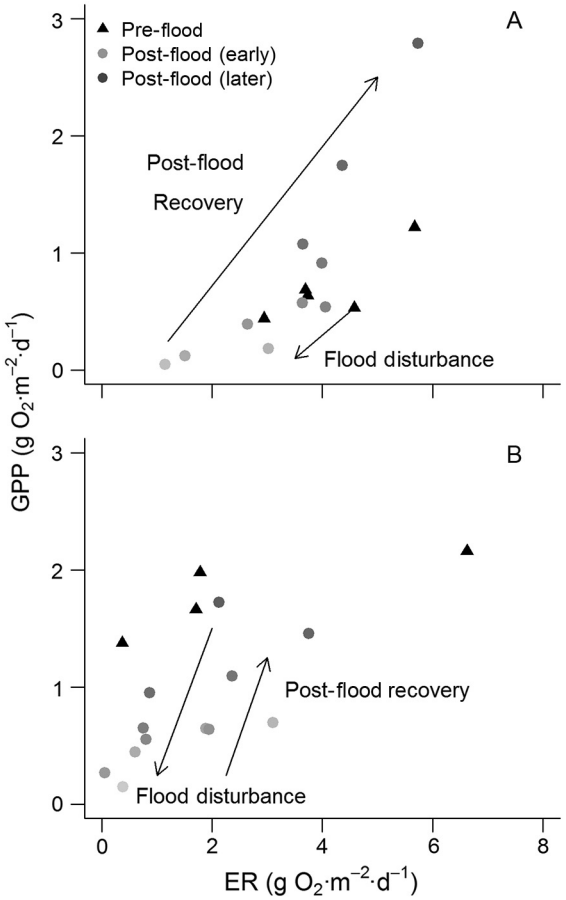

Fig. 2. Gross primary production (GPP) and ecosystem respiration (ER) decreased immediately following Superstorm Sandy, but increased to equivalent or higher rates over time. Black triangles denote pre-flood rates, whereas circles are post-flood rates, with the lightest shading immediately following Sandy and shading growing darker as metabolic rates recover.

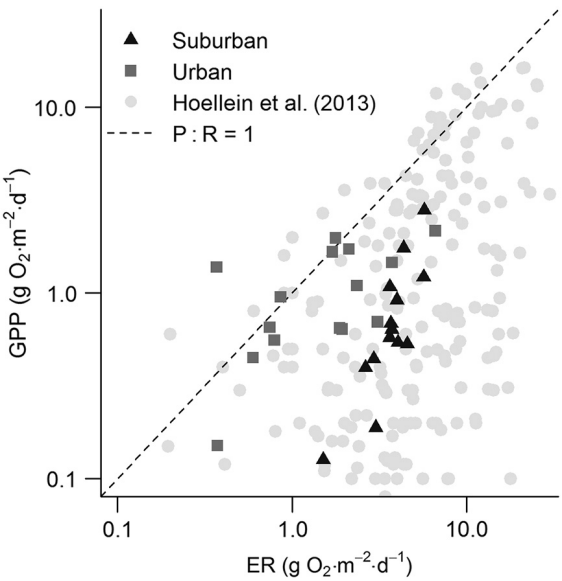

Fig. 3. Gross primary production (GPP) and ecosystem respiration (ER) from the suburban (dark gray triangles) and urban (gray squares) streams spanned a wide range of the variation present in the literature (light gray circles; from Hoellein et al. 2013). Dashed line represents GPP = ER.

range of metabolic activity in the suburban and urban streams was equal to 12% and 17% of the literature range for GPP, and 15% and 18% of the literature range for ER, respectively (Fig. 3; Hoellein et al. 2013).

Metabolic recovery across multiple flood events

Across the 11 stream–flood events, GPP showed a greater percentage of reduction on average than ER, with GPP being reduced by 79% (range 17–99%) and ER reduced by 72% (range 11–89%), but this was not statistically significant (paired *t* test; $t = 1.46$, df = 10, $P = 0.17$). Our response ratio-based regression approach for calculating recovery intervals yielded significant regressions for GPP response ratios at each stream–flood combination ($P < 0.05$, average $r^2 = 0.78$, $n = 11$; Table 2) and all but three stream–flood combinations had a significant regression for ER response ratios ($P < 0.05$, average $r^2 = 0.64$, $n = 8$; Table 2), suggesting minimal resistance (but potentially high resilience) to floods. Two stream–flood events exhibited a marginal recovery trend for ER response ratios (GFCP-10/29/2012 and MBD-7/13/2015; $P = 0.078$ and 0.070, $r^2 = 0.34$ and 0.45, respectively), and one stream–flood event did not show any relationship between ER response ratios and time since peak flow (MBU-08/24/2015; $P > 0.1$). For subsequent analyses, we used GPP ($n = 11$) and ER ($n = 10$) recovery intervals based upon significant or marginally significant ($P < 0.1$) regressions.

Recovery intervals for GPP (mean = 9.2, range = 4.3–18.2 d; Fig. 4) and ER (11.3, 6.9–15.7 d; Fig. 4) varied across the 11 stream–flood periods (Table 2). Recovery intervals for GPP and ER did not differ (paired *t* test, $t = 1.62$, df = 9, $P = 0.14$;

Table 2. Magnitude of flood events and metabolic recovery from floods in urban and suburban streams across Baltimore City and County.

			GPP				ER			
Site	Flood date	Flood RI (yr)	Percentage of reduction	*P*	r^2	Recovery interval (d)	Percentage of reduction	*P*	r^2	Recovery interval (d)
GFCP	29 October 2012	2.75	92	<0.0001	0.71	18.2	86	0.0775	0.34	15.7
GFGB	29 October 2012	1.82	84	0.0004	0.73	7.2	72	0.0005	0.79	10.3
MBU	18 May 2015	1.36	99	<0.0001	0.9	5.4	88	0.0045	0.66	6.9
STN	27 June 2015	1.81	99	<0.0001	0.93	10.1	81	0.0442	0.38	14.1
MBD	13 July 2015	3.57	53	0.0257	0.48	7.1	89	0.0702	0.45	11.2
MBD	24 August 2015	1.42	94	<0.0001	0.87	7.6	79	0.0001	0.78	13.1
MBU	24 August 2015	1.42	71	<0.0001	0.87	4.3	11	0.1324	ns	ns
STN	24 August 2015	0.97	88	<0.0001	0.85	6.9	70	<0.0001	0.83	11.2
MBD	10 September 2015	0.77	97	<0.0001	0.74	9.0	84	0.0036	0.52	8.8
MBU	10 September 2015	0.77	83	<0.0001	0.84	13.8	20	0.0002	0.73	9.9
SLB	10 September 2015	0.82	17	0.0003	0.63	11.3	50	0.0094	0.39	11.7

Notes: GPP, gross primary production; ER, ecosystem respiration; RI, recurrence interval. Site abbreviations are provided in Table 1. ns indicates no significant or marginal recovery regression ($P > 0.1$).

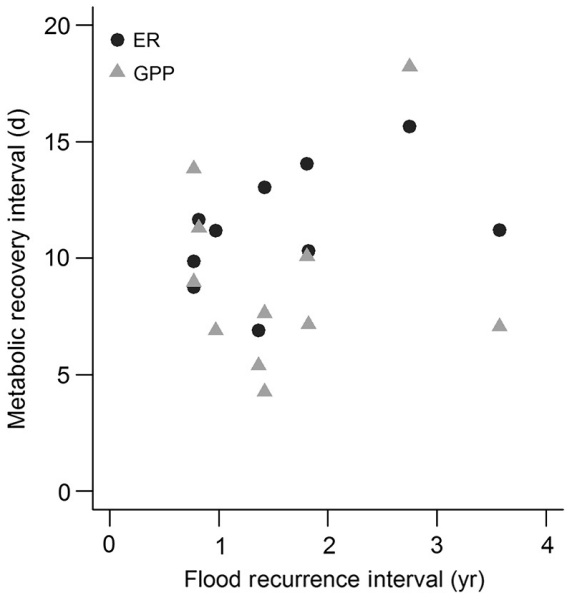

Fig. 4. Metabolic recovery intervals for gross primary production (GPP; dark gray circles) and ecosystem respiration (ER; light gray triangles) did not differ from each other and were similar across a range of flood recurrence intervals.

Fig. 4), and there was no difference in the percent reduction in GPP or ER between summer and autumn (independent t test; $t = 0.59$ and 0.40, df = 6.10 and 8.80, $P = 0.58$ and 0.70, respectively). However, there was a marginal difference in recovery intervals between summer and autumn for GPP (independent t test; $t = -2.19$, df = 5.74, $P = 0.07$), but not ER (independent t test; $t = 0.81$, df = 6.27, $P = 0.45$), with a trend for shorter recovery intervals (faster recovery) in summer. Additionally, recovery intervals of GPP and ER were not related to flood magnitude (Fig. 4).

Discussion

Extreme flow events have long been recognized as drivers of ecosystem structure and function (Poff et al. 1997), and stream ecosystems may be adapted to flashy hydrographs in areas where extreme flows are a regular occurrence (Fisher et al. 1982, Grimm 1987, Martí et al. 1997). However, urban streams are stressed by a myriad of physicochemical factors (Walsh et al. 2005, Vietz et al. 2016) in addition to the flashy hydrographs caused by urbanization. In this study, we found that both GPP and ER were diminished immediately following high flows, but both recovered in 4–18 d in these urban streams. A recovery period of approximately two weeks is similar to recovery times found for algal biomass and stream metabolism in naturally flashy desert streams (Fisher et al. 1982, Grimm 1987). The similarities between urban and desert streams in response to a major disturbance, in spite of drastically different abiotic conditions, confirm the idea that hydrological disturbances are a fundamental driver of ecosystem functioning across a range of stream types (Poff et al. 1997) and point to the need for a better understanding of disturbance ecology within urban ecosystems (Grimm et al. 2017).

The degree of reduction in GPP (17–99%) and ER (11–89%) from the 11 stream–flood events exceeded values measured in an alpine river (Uehlinger 2000), experimental alpine floods (Uehlinger et al. 2003), and a forested headwater stream (Roberts et al. 2007). In the current study, each urban stream eventually recovered to pre-flood rates despite greater reductions in metabolic activity than has been found previously (Uehlinger 2000, Roberts et al. 2007, Beaulieu et al. 2013). Although there was a slight trend for increasing metabolic recovery intervals with increased flood RIs, these were not significant. Therefore, based upon the current data, it does not appear that flood magnitude is a primary driver of either the degree of reduction or the metabolic recovery interval. The lack of a relationship, coupled with similar metabolic recovery intervals compared to desert streams (Fisher et al. 1982, Grimm 1987), suggests that stream metabolism in flashy environments may be adapted to, and therefore highly resilient to, high-flow events. The resilience that we observed is similar to previous work in a suburban stream that found that GPP was resilient to desiccation, with metabolic activity returning within three days of rewetting (Beaulieu et al. 2013).

Although resilience of stream metabolism may be a characteristic of flashy streams, the role of urban physicochemical stressors in driving both baseline metabolic activity and the ability of the stream to recover must also be considered. The multiple physicochemical stressors occurring in urban streams, collectively referred to as "the

urban stream syndrome" (Walsh et al. 2005, Wenger et al. 2009), have well-established effects on stream biodiversity (Paul and Meyer 2001, Walsh and Webb 2016), but a broader understanding of urbanization effects on stream biogeochemistry (including primary production) has been identified as a priority for research (Wenger et al. 2009). In this study, we found that metabolic activity of a set of urban streams was indistinguishable from a suite of reference, agricultural, and other urban streams (Fig. 3; Hoellein et al. 2013). This result is consistent with a recent review of nitrogen transformations in urban environments, which found no difference in process rates between urban and reference environments (Reisinger et al. 2016). Taken together, these results suggest that biogeochemical process rates may be more resistant to urbanization effects than biodiversity (Lake 2000, Utz et al. 2016).

Our results may be confounded by our comparison of floods of different magnitudes from different urban streams. We attempted to minimize these confounding effects by calculating metabolic reductions and recovery intervals by comparing post-flood to pre-flood activity from the same stream. Despite our analytical approach, physicochemical factors likely play a large role in constraining not only absolute metabolic rates, but also recovery trajectories. A larger number of floods of various sizes from the same stream are needed to clarify the effect of flood magnitude on the reduction and recovery of urban stream metabolism. As the technology for collecting and analyzing data for whole-stream metabolism continues to improve, it is likely that these data will be available soon. Nonetheless, we observed clear patterns in metabolic reductions and resiliency following floods in nearly all stream–flood events.

Reduction and recovery of stream metabolism has previously been shown to differ among seasons. For example, in a forested headwater stream, a spring storm caused a decrease in GPP and ER, whereas an autumn storm caused an increase in GPP but a decrease in ER. This seasonal difference was attributed to the storm washing leaves out of the stream in autumn and allowing light to reach benthic autotrophs (Roberts et al. 2007). A separate study found that GPP generally recovered more quickly than ER in two rivers across seasons, but that recovery rates were faster in summer than in winter for both GPP and ER (Uehlinger 2000). In contrast to these previous studies, we found no seasonal differences in recovery intervals between summer and autumn. This lack of a difference may be due to the increased frequency of storm flows in urban streams (Walsh et al. 2005, Beaulieu et al. 2013, Smith and Kaushal 2015), which could overwhelm other important drivers of metabolism which vary seasonally such as canopy cover (light), nutrient availability, and temperature.

Drastic reductions in stream metabolism following extreme flow events are not surprising. However, many of the storms we analyzed were not very extreme. In fact, of the 11 stream–flood events we analyzed, four had a RI <1 yr. We acknowledge that the discharge record used to develop our rating curves is relatively modest, but extending the discharge record for a longer period would have a minimal effect on non-extreme RIs. Urbanization increases hydrological flashiness (Walsh et al. 2005, Roy et al. 2009), and scouring events can occur in response to modest (<1.5 cm) rainfall events in urban streams (Murdock et al. 2004, Hawley and Vietz 2016, Vietz et al. 2016). It is possible that non-scouring events still disturb stream communities and reduce metabolism, suggesting that even smaller events may impact stream ecosystem function. Overall, the frequency of precipitation events coupled with the metabolic response to even small floods (Beaulieu et al. 2013, Table 2) suggests that urban stream metabolism may be in a frequent if not near-constant state of recovery.

Although metabolic activity was drastically reduced by floods, the two streams studied during Sandy were typically heterotrophic (GPP < ER) before and after Sandy. In fact, we found no significant differences in reduction in GPP and ER in response to floods, and similar recovery intervals for both metabolic rates. The similar reductions and recovery intervals between GPP and ER suggest that most of the ER recovery is driven by autotrophic respiration in urban streams (Beaulieu et al. 2013), whereas heterotrophic respiration may be less impacted by disturbance. Further study of the differential effects of storm events on autotrophic and heterotrophic processes is warranted. Additionally, these differential effects may alter other biogeochemical processes (e.g.,

denitrification) and change food web dynamics. These differential effects, as well as general metabolic responses of urban streams to flooding, merit attention by stormwater managers, as changes to the flow regime due to stormwater management will likely have different outcomes for biogeochemical and biodiversity responses within urban streams.

The balance between GPP and ER has implications for the urban carbon cycle, which is known to be altered by changes in anthropogenic inputs (e.g., wastewater treatment plant effluent, sewage leaks, organic compounds) and hydrologic connectivity (Kaushal et al. 2014*b*). Urban stream respiration may rely on higher-quality carbon during baseflow conditions than reference forested streams (Kaushal et al. 2014*a*). This higher-quality carbon also likely enters urban streams during high-flow events (either from upstream or from terrestrial sources), and may explain the apparently smaller response of ER to storms compared to GPP. Ultimately, differences in autotrophic and heterotrophic responses to storm events may be important, as headwater streams account for a disproportionately high proportion of global CO_2 emissions (Raymond et al. 2013). Given this importance, the responsiveness of GPP and ER in urban streams to even minor storm events, and the current and projected future level of urbanization occurring globally (Grimm et al. 2008, United Nations 2010, Pickett et al. 2011), there is a clear need for more research on metabolic activity in urban streams at multiple spatial and temporal scales.

Conclusions

Urban stream ecosystems are subject to hydrologically extreme events in addition to a multitude of other physicochemical stressors. Based upon our results, it appears that hydrological extremes may override other environmental stressors in controlling stream metabolic activity, but the magnitude of flooding does not affect metabolic recovery. Reduction and subsequent recovery of GPP and ER was common across a range of urban streams and flood events, suggesting both high sensitivity—higher than non-flashy stream ecosystems such as an alpine river (Uehlinger 2000, Uehlinger et al. 2003) or a forested headwater stream (Roberts et al. 2007)—and high resilience to flooding disturbance. However, the recovery intervals exhibited by these urban streams were similar to those found in naturally flashy desert streams (Fisher et al. 1982, Grimm 1987), suggesting that urban streams can adapt to floods and other disturbances in spite of myriad environmental stressors (Grimm et al. 2017). Overall, we found that urban streams can exhibit high metabolic activity despite a multitude of physicochemical stressors and that this metabolism rapidly recovers from floods, regardless of magnitude.

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