Land use affects temporal variation in stream metabolism

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Abstract: Stream metabolism (gross primary production and ecosystem respiration) is increasingly used to assess waterway health because mean values are responsive to spatial variation in land use, but little is known about how human land use influences the temporal variability of stream metabolism. We investigated daily variation in dissolved O_2 (DO) concentrations and calculated mean and within-season variation in gross primary production (GPP) and ecosystem respiration (ER) rates at 13 stream sites across a landuse intensity gradient in the Auckland region, New Zealand, over 9 y. Based on generalized linear mixed models, mean daily GPP (0.1–12.6 g O_2 m^{-2} d^{-1}) and ER (1.8–29.6 g O_2 m^{-2} d^{-1}) and seasonal variation in stream metabolism were significantly related to landuse intensity with higher variability associated with higher values of a landuse stress score. Overall, mean daily rates and day-to-day variation in GPP and ER were greatest in summer and least in winter. We recommend summer monitoring over a minimum 5-d period to assess stream health. Our results show that human land use affects the mean and the temporal variability of DO and stream metabolism. This finding has important consequences for characterizing in-stream processes and the resilience of stream ecosystems. Only long-term temporal monitoring provides the data needed to assess fully how streams function.
Key words: ecosystem metabolism, GPP, ER, land use, variability, resistance, resilience, functional indicator, stream health, life supporting capacity

Landuse change has profound effects on the health of stream ecosystems (Allan 2004). These effects typically have been assessed on the basis of structural indicators, such as water quality or benthic invertebrate community composition, but more recently the importance and complementary value of functional indicators has gained widespread recognition (Bunn and Davies 2000, Gessner and Chauvet 2002, Feio et al. 2010, Palmer and Febria 2012). Stream metabolism, which combines gross primary production (GPP) and ecosystem respiration (ER), strongly responds to human impacts (Young and Huryn 1999, Bott et al. 2006, Gücker et al. 2009, Clapcott et al. 2010) and can be measured easily from short-term monitoring of dissolved O_2 (DO) concentrations. Hence, stream metabolism has been suggested as a functional indicator of stream ecosystem health (Fellows et al. 2006, Young et al. 2008).

Human effects influence the nature or timing of catchment- to reach-scale drivers of stream metabolism. At the catchment scale, human land use can change the hydrologic regime to a more flashy hydrology, which influences stream metabolism via an increase in the number of scouring floods (Uehlinger et al. 2003) or prolonged low flows (Young and Huryn 1996, Acuña et al. 2004).

Increased loads of nutrients and fine sediments delivered to streams can change the metabolic habitat template, leading to greater or lower metabolic rates in streams, respectively (Atkinson et al. 2008, Clapcott and Barmuta 2010). Clearance of riparian vegetation, which often is linked to catchment-scale landuse change, increases light availability and water temperature and subsequently metabolic rates at the reach scale (Fellows et al. 2006, Marcarelli et al. 2010). Reach-scale physical alteration of stream habitat by earthworks or channelization, for example, also can influence stream metabolism by altering substrate stability, habitat heterogeneity, and susceptibility to flow effects (Gelroth and Marzolf 1978). Last, the negative effects of land use on stream metabolism are likely to be further exacerbated by anthropogenic climate-change-driven changes to hydrological and temperature regimes (Marcarelli et al. 2010).

In studies of stream metabolism as a functional indicator, investigators often measure DO concentrations for short periods of time in summer to minimize variation introduced by temporal changes in natural conditions, such as the effects of flood disturbance, rain, or season (Fellows et al. 2006, Clapcott et al. 2010). The drawback of measuring metabolism for only a short and specific time period is

that doing so does not capture the pattern of temporal variation under natural and human-affected condition throughout the year, which may be an important feature of stream ecosystem functioning. Continuous DO monitoring allows estimation of the temporal variation of stream metabolism across seasons and years (e.g., Uehlinger 2006, Roberts et al. 2007), which may provide additional information for assessment of stream health.

For example, the temporal variation in stream processes could provide valuable information on the resilience of streams to human disturbance. Resilient streams recover more quickly from natural pulse disturbances, e.g., bed-moving spates, and are expected to exhibit less metabolic variation in response to such events (Uehlinger 2000). Human land use, on the other hand, is a press disturbance that inflicts ongoing stress that allows limited opportunity for the ecosystem to recover (Lake 2000). Slow and limited recovery from disturbance defines ecosystems with low resilience, and increasing variance is suggested to be a leading indicator of decreasing resilience (Scheffer et al. 2010). Human disturbance, via climate and landuse change, is suggested as the main cause for increasing variability in ecological responses and for eroding ecological resilience (Folke et al. 2004). Thus, quantifying human disturbance-driven changes in the variability of ecological responses provides a new and complementary approach to assessing ecosystem health and resilience (Fraterrigo and Rusak 2008).

We are interested in how measures of temporal variability in stream metabolism can be used to inform stream health assessment because no detailed investigations of the temporal variability in stream metabolism across a landuse gradient have been published. We hypothesize that streams draining catchments with high landuse intensity will have higher temporal variability in stream metabolic rates. Greater temporal variability in metabolism will occur because of the negative effect of landuse change on environmental factors that naturally moderate stream metabolism, such as light availability, nutrients, temperature, and flow. If predictable changes in metabolic variability are a consequence of landuse change, then our work has the potential to inform when and how stream metabolism could be applied as a functional indicator. Furthermore, if we can reliably identify changes in metabolic variability, this ability could help characterize the resilience of stream ecosystems.

METHODS
Study area and stream sites

The Auckland region is in the northern part of the North Island of New Zealand and has a warm temperate climate with an average maximum air temperature of 23.7°C in February (summer) and an average minimum air temperature of 14.5°C in July (winter). Average annual rainfall in the Auckland region is 1240 mm and falls mainly in winter, but high rainfall events can occur at any time of the year. Over 60% of the rivers in the Auckland region drain nonforested rural catchments (pasture, horticulture, rural residential), ~20% drain native forest, and ~10% drain exotic forest and urban-dominated catchments, respectively (Neale 2012). The region is home to New Zealand's largest city, Auckland, which has 1.4 million residents.

As part of the local authority's stream-monitoring network, 13 low-gradient (<5°), low-elevation (<150 m asl), 2nd- to 5th-order river sites have been sampled for a range of water-quality and biological attributes intermittently since 2003 (Neale 2012). Streams occur on soft sedimentary or volcanic ash geologies, and in-stream habitat is dominated by fine sediment and gravels. Streams range in width (0.7–16 m) and depth (0.31–2.8 m) and drain catchments with a range of land uses (Table 1).

Environmental data

Land-cover data were derived from the LCDB2 (https://lris.scinfo.org.nz/) and catchment areas from a region-wide Auckland Council light detection and ranging (LIDAR) survey in 2006–2007. Catchment land cover was used to calculate a landuse stress (LUS) score with a theoretical range of 0–300 where higher values indicate higher landuse intensity. The LUS score was calculated from the weighted contribution of urban land use (×3), agriculture and horticulture (×2), and exotic forestry (×1) to the total % land use in a catchment (Collier 2008). The LUS score is a good summary index for relating the combined effects of urban and rural land uses with stream health (Young and Collier 2009).

Dissolved O_2 (DO) concentration and water temperature were recorded at 15-min intervals at each site by permanently deployed data loggers with optical fluorescence probes (D-Opto, Zebra-Tech, New Zealand). Data loggers were calibrated monthly and only high-quality data (within 0.5 mg/L of an independent measurement) were used in our study. Other monitored variables include nutrients and *Escherichia coli* counts measured monthly at 11 sites since 2003 by standard methods (Neale 2012). Benthic macroinvertebrates have been sampled annually at 8 sites since 2007 using standard protocols (Stark et al. 2001) to calculate Macroinvertebrate Community Index scores (MCI; Stark and Maxted 2007). Stream Ecological Valuation (SEV; Storey et al. 2011) habitat descriptors measured in 2011 at all 13 sites include riparian condition (width, continuity, and age-class diversity of riparian vegetation) and % riparian shade. Stream flow has been recorded continuously at permanent stage height weirs (Table 2).

Stream metabolism

Stream metabolism was calculated from 2003 to 2011 at up to 13 sites. During each season, a period of the most stable base flow was selected and metabolism was calculated for a minimum of 3 and maximum of 6 d during a

Table 1. Catchment and site characteristics of 13 study streams in the Auckland region ordered from high-to-low landuse stress (LUS) score (see text for description).

Site	LUS score	% native forest	% urban	% pasture	% horticulture	% exotic forest	% other	Stream order	Basin area (ha)	% riparian shade	Riparian condition score
Puhinui	220.7	10.9	44.2	43.3	0.0	1.5	0.1	3	1043	0	0.20
Waitangi	193.5	3.1	0.0	88.3	8.4	0.1	0.1	3	1770	64	0.35
Ngakaroa	192.0	0.7	0.0	73.1	20.7	4.4	1.1	3	471	40	0.16
Kumeu	161.2	18.7	1.9	71.4	4.7	3.1	0.1	4	4577	6	0.30
Kaukapakapa	158.3	17.4	0.0	75.0	1.1	6.1	0.4	5	6163	74	0.50
Kaipara	150.8	13.4	1.5	56.7	4.7	23.5	0.2	5	15,621	68	0.42
Rangitopuni	147.0	17.7	0.5	62.6	1.9	16.5	0.8	5	8369	72	0.47
Wairoa	139.3	23.2	0.0	62.6	0.0	14.1	0.1	5	11,442	36	0.44
Ararimu	131.2	10.2	0.0	39.9	1.7	47.8	0.3	5	7068	80	0.68
Hoteo	130.5	23.2	0.3	53.2	0.2	22.7	0.4	5	26,832	54	0.40
Mahurangi	116.4	29.0	0.6	43.5	0.6	26.3	0.0	5	4650	74	0.81
Vaughan	113.2	39.8	3.6	45.9	0.0	10.7	0.0	2	414	20	0.29
West Hoe	0.3	99.8	0.0	0.1	0.0	0.1	0.0	2	54	94	1.00

consecutive 7-d period. For example, Fig. 1 shows an extract of continuous data that was visually assessed to select periods of relatively low and stable flow to calculate stream metabolism. Rainfall and substantial changes in flow can cause DO to be affected by factors other than reaeration and in-stream biological processes. Therefore, metabolism could not be reliably estimated on some days based on our method. Thus, sample size varied for each site, season, and year (Table S1).

Before analysis, random noise in DO data was reduced using a moving-average smoother with an interval of 5 mea-

surements. Daily metabolism values were calculated with a spreadsheet model described by Young and Collier (2009). Briefly, mean daily ER and the reaeration coefficient (k) were estimated with the nighttime regression method (Owens 1974). Only equations with $R^2 > 0.4$ were considered meaningful. k and ER were used to calculate gross photosynthetic rate over the sampling interval as:

$$GPP_t = \frac{dO}{dt} + ER - kD \qquad (Eq.1)$$

Table 2. Mean annual low flow and annual median water quality measured at 13 study streams in the Auckland region ordered from high-to-low landuse stress score during 2003–2011. MCI = macroinvertebrate community index, SRP = soluble reactive P, *E. coli* = *Escherichia coli*. – indicates no data.

| Site	Mean annual low flow (m³/s)	Mean monthly temperature (°C)	TP (mg/L)	SRP (mg/L)	TN (mg/L)	NO₂+NO₃-N (mg/L)	*E. coli* (cfu/ 100 mL)	MCI (5-y median)
Puhinui	0.014	16.79	0.06	0.02	0.94	0.61	435	43
Waitangi	0.036	15.7	0.02	0.01	2.43	1.94	465	62
Ngakaroa	0.007	14.52	0.02	0.01	3.40	2.75	280	65
Kumeu	0.02	14.81	0.06	0.02	0.80	0.32	410	63
Kaukapakapa	0.015	14.75	0.07	0.03	0.78	0.21	450	–
Kaipara	0.124	15.06	–	–	–	–	–	–
Rangitopuni	0.016	14.69	0.08	0.03	–	0.19	305	–
Wairoa	0.365	14.88	0.05	0.02	0.63	0.39	495	106
Ararimu	0.055	14.75	–	–	–	–	–	98
Hoteo	0.379	15.71	0.07	0.03	–	0.34	205	–
Mahurangi	0.075	15.55	0.04	0.01	0.42	0.13	255	–
Vaughan	0.000	15.21	0.05	0.02	0.51	0.06	885	63
West Hoe	0.002	13.27	0.02	0.01	0.13	0.01	45	125
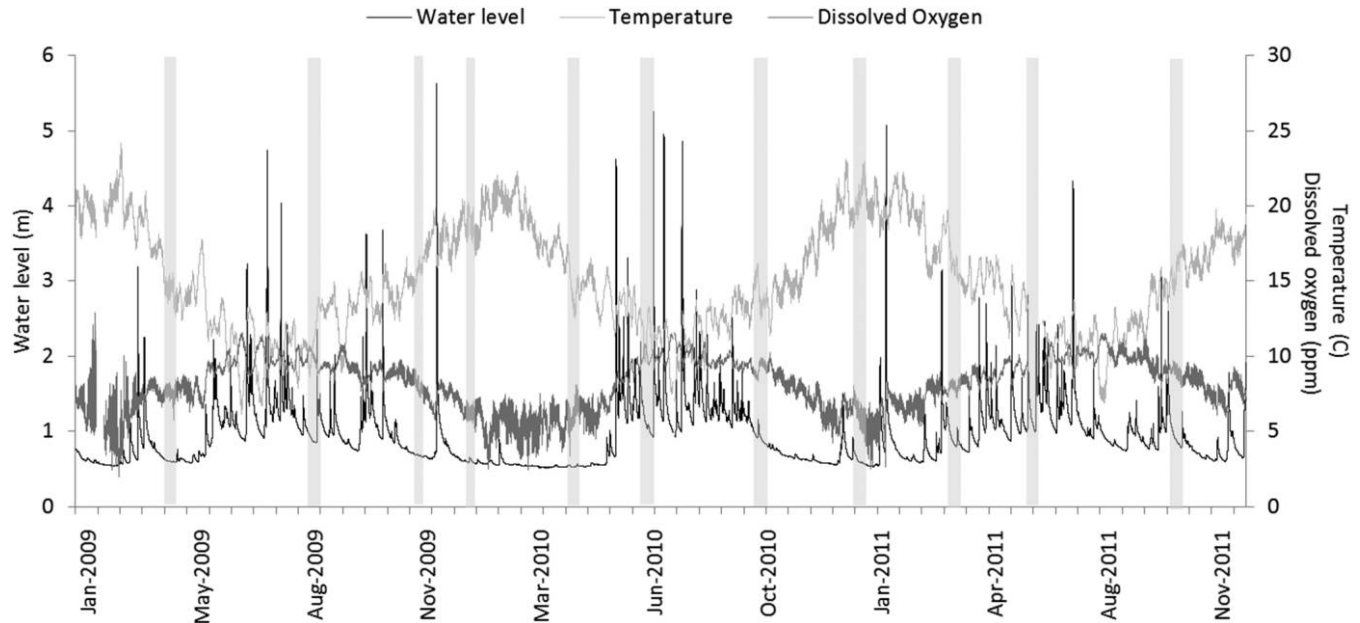
Figure 1. Daily water level, water temperature, and dissolved O$_2$ from January 2009 to December 2011 at Kaukapakapa Stream. Vertical bars show periods of ecosystem metabolism calculations.

where GPP$_t$ is the gross photosynthetic rate (g m^{-3} s^{-1}) over time interval t (s) and D is the O$_2$ deficit. To compensate for daily temperature fluctuation, ER was assumed to double with a 10°C increase in temperature (Phinney and McIntire 1965), whereas k was assumed to increase by 2.41%/°C (Kilpatrick et al. 1989). Daily GPP (g m^{-3} d^{-1}) was estimated as the integral of all temperature-corrected photosynthetic rates during daylight (Wiley et al. 1990). Areal estimates were obtained by multiplying the volume-based estimates by average reach depth (m). Average reach depth was calculated from 5 depth measurements across 5 transects within 500 m upstream of the DO logger and calibrated to a permanent stage-height gauge. Stage height was then used to estimate average reach depth for each sample time.

Statistical analyses

Measures of daily variance in DO concentrations and weekly variance and central tendency in rates of GPP and ER were calculated and explored in relation to LUS score and other stream descriptors. The relationships were initially examined with Spearman rank correlations and scatterplot matrices. Then general linear mixed models (GLMMs) were used to examine the relationship between metabolic metrics and LUS score.

For each site, the minimum, maximum, and daily ranges in DO concentration were calculated for each sampling date in 2009–2011. Daily GPP and ER were calculated for each season in all years (2003–2011) and averaged to provide mean weekly values (Table S2). Consecutive seasonal estimates of metabolism were, on average, 12 wk apart.

Hence, limited autocorrelation was assumed based on the resetting effects of high-flow events and trends observed in larger rivers (Uehlinger 2006, Dodds et al. 2013). To estimate variation at different temporal scales for each site, season was used as the topmost stratum (fixed, with 4 levels: autumn, winter, summer, spring), year was treated as random, and weeks as random nested within seasons. This design is based on the assumption that no systematic changes occurred between years, which seemed reasonable because change in medium-term climatic drivers or landuse effects was minimal during the study period. Thus, the response variable for examining variation in GPP or ER was the weekly (day-to-day) standard deviation (σ) computed for years nested within seasons. σs were analyzed by GLMM with γ errors and a log-link, which is appropriate for right-skewed data that cannot take negative values (Zuur et al. 2013). The mean daily range in DO also was computed for years nested within seasons and analyzed in the same way. LUS and season were treated as crossed fixed effects, whereas site and year were treated as crossed random effects. Significance of fixed effects was assessed with likelihood ratio tests. Results close to $p = 0.05$ were interpreted with care because of the anticonservative nature of such tests (Pinheiro and Bates 2000). The relationships among metabolic metrics and all environmental descriptors were explored with correlations, but only LUS score was used as the fixed (continuous) covariate in GLMMs because no values were missing. All GLMMs (see Appendix S1) were carried out using the *lme4* package (Bates et al. 2014) in R (version 3.3.0; R Project for Statistical Computing, Vienna, Austria).

RESULTS
DO

The daily range in DO varied greatly across sites and was related to LUS score and other environmental variables that described each site. DO ranged from 0.4 to 17.6 mg/L at 12 sites during 2009–2011. The daily range in DO data was strongly right-skewed and ranged from 0.11 to 16.70 mg/L with a median value of 1.35 mg/L. At the site with the lowest LUS score (West Hoe; Table 1), daily DO range averaged 0.3 mg/L on an annual basis (Table 3). In comparison, the site with the highest landuse effect (Puhinui) averaged daily DO ranges of 2.4 mg/L in winter and 11.5 mg/L in summer. Daily DO range was significantly correlated with environmental variables (Table 4). Daily DO range was negatively correlated with riparian condition, shade, and MCI and was positively correlated with mean annual water temperature. Daily DO range was related to LUS, but a significant LUS score × season interaction indicated that the strength of the response of DO range to LUS changed among seasons (χ^2_{3df} = 30.40, p < 0.0001). In winter, DO was not related to LUS score (χ^2_{1df} = 2.58, p = 0.11), but strong relationships occurred in summer (χ^2_{1df} = 9.11, p = 0.002) and autumn (χ^2_{1df} =8.69, p = 0.003) and a weak relationship in spring (χ^2_{1df} = 4.43, p = 0.035) (Table 5, Fig. 2A).

Stream metabolism

Very low to very high rates of stream metabolism occurred in the 13 study streams during periods of relatively stable flow. ER ranged from 0.04 to 88.7 g O_2 m^{-2} d^{-1} and GPP from <0.01 to 41.4 g O_2 m^{-2} d^{-1} at 13 sites during the 9-y study period. Data were strongly right-skewed with median values of 8.2 g O_2 m^{-2} d^{-1} (ER) and 2.6 g O_2 m^{-2} d^{-1} (GPP). Weekly estimates of GPP and ER were significantly correlated (r_s = 0.66, n = 298, p < 0.001). Bivariate plots of the mean and $\hat{\sigma}$ of weekly estimates of metabolism identified strong heteroscedasticity in both ER and GPP data (Fig. S1).

Weekly mean values and day-to-day variation in stream metabolism were related to environmental variables that described each site. Significant correlations with environmental and water-quality descriptors were evident for GPP and ER means and $\hat{\sigma}$s (Table 4). Metabolic variables were positively correlated with total N and negatively correlated with MCI, % riparian shade, and condition. GPP was correlated with mean monthly water temperature, whereas ER was correlated with *E. coli* (Table 4).

Higher day-to-day variation in GPP occurred at sites with higher LUS scores across all seasons. GPP $\hat{\sigma}$ was significantly positively related to LUS score (χ^2_{1df} = 18.1, p < 0.001) and was significantly affected by season (χ^2_{3df} = 48.4, p < 0.0001). The slopes of the relationship between GPP $\hat{\sigma}$ and LUS were parallel among seasons (i.e., no significant LUS × season interaction). GPP $\hat{\sigma}$s were consistently higher in summer than in spring, autumn, and winter (Fig. 2B). Mean GPP was significantly positively related to LUS (χ^2_{1df} = 17.51, p < 0.0001) and significantly affected by season (χ^2_{3df} = 407.9, p < 0.0001), with higher GPP in summer than in spring, autumn, and winter, and no LUS × season interaction (χ^2_{3df} = 6.300, p = 0.10) (Fig. 2C).

Landuse effects on variation in ER were more apparent in summer than in autumn or spring, and differences among sites were not evident in winter. The relationship

Table 3. Summary of daily range in dissolved O_2 (DO) at 13 study streams in the Auckland region ordered from high-to-low landuse stress score during 2009–2011, and gross primary productivity (GPP) and ecosystem respiration (ER) calculated at the same sites during 2003–2011. N = number of weeks, $\hat{\sigma}$ = standard deviation (within-week variability).

Site	Daily range in DO (mg/L)		Metabolism	GPP (g O_2 m^{-2} d^{-1})		ER (g O_2 m^{-2} d^{-1})	
	N	Mean	N	Mean	$\hat{\sigma}$	Mean	$\hat{\sigma}$
Puhinui	12	6.49	26	12.57	3.14	14.11	3.22
Waitangi	12	2.98	15	9.19	1.38	29.56	4.19
Ngakaroa	12	1.90	35	2.82	0.5	8.61	1.29
Kumeu			29	7.87	1.85	26.03	6.24
Kaukapakapa	10	0.94	29	2.9	0.97	11.11	2.91
Kaipara	12	0.97	28	2.15	0.68	10.9	3.34
Rangitopuni	11	0.74	16	0.70	0.24	7.25	2.34
Wairoa	11	1.29	22	2.70	0.58	6.01	1.21
Ararimu	11	1.09	29	2.59	0.45	12.29	1.72
Hoteo	11	1.17	25	3.78	0.72	4.44	1.06
Mahurangi	11	2.56	15	2.15	0.35	3.61	0.64
Vaughan	12	3.27	13	3.36	0.79	16.29	3.18
West Hoe	8	0.30	16	0.05	0.02	1.78	0.47

Table 4. Spearman rank correlation coefficients (r_s) of relationships between a landuse stress (LUS) score, environmental descriptors, and stream metabolism at each site. N = number of sites. DO range = daily range in dissolved O_2 concentrations (where $N = N-1$), GPP = gross primary production, ER = ecosystem respiration, $\hat{\sigma}$ = standard deviation (reflecting within-week variability), MCI = macroinvertebrate community index, $E.\ coli$ = $Escherichia\ coli$, SRP = soluble reactive P. * = $p < 0.1$, ** = $p < 0.05$, *** = $p < 0.01$.

Variable	N	LUS score	DO range	GPP mean	GPP $\hat{\sigma}$	ER mean	ER $\hat{\sigma}$
Catchment descriptors							
LUS score	13		0.29	0.59**	0.63**	0.59**	0.67**
Catchment area	13	−0.03	−0.30	−0.15	−0.07	−0.24	−0.04
Reach descriptors							
% riparian shade	13	−0.47	−0.74***	−0.73***	−0.70***	−0.48*	−0.49*
Riparian condition	13	−0.60**	−0.66**	−0.73***	−0.66**	−0.58**	−0.48*
Water quality							
MCI	8	−0.71**	−0.93***	−0.95***	−0.86***	−0.81**	−0.81**
$E.\ coli$	11	0.28	0.50	0.24	0.55*	0.69**	0.64**
Total P	11	0.03	−0.12	0.10	0.16	0.0	0.15
SRP	11		−0.24	0.12	0.17	−0.06	0.08
Total N	9	0.92***	0.33	0.72**	0.65**	0.61**	0.71**
NO_2+NO_3-N	11	0.83***	0.38	0.56*	0.46	0.41	0.37
Water temperature	13	0.18	0.71**	0.64**	0.60**	0.28	0.28

between ER $\hat{\sigma}$ and LUS differed among seasons (LUS × season interaction: χ^2_{3df} = 14.0, p = 0.003). ER $\hat{\sigma}$ was not related to LUS in winter (χ^2_{1df} = 2.6, p = 0.11) but was significantly positively related to LUS in the other seasons, most strongly in summer (Table 5, Fig. 2D). The strength of the relationship of mean ER and LUS differed among seasons (LUS × season interaction: χ^2_{3df} = 73.1, p < 0.00001), with ER significantly positively related to LUS in all seasons, with the strongest relationship in summer, the weakest in winter, and similar and intermediate relationships in spring and autumn (Table 5, Fig. 2E).

Omitting West Hoe (LUS = 0) from the analysis made no difference in the results for any response variable.

DISCUSSION
Metabolic variability as an indicator of landuse disturbance

Greater temporal variation in GPP and ER was directly related to greater landuse intensity at our 13 study sites. Previous investigators observed increasing variance associated with higher rates of stream metabolism (Roberts et al.

Table 5. Seasonal coefficients in the relationship between a landuse stress score and dissolved O_2 (DO) range, mean, and standard deviation ($\hat{\sigma}$) in ecosystem respiration (ER). A common coefficient suffices to describe the relationship with landuse stress across all seasons for gross primary production (GPP) mean (coefficient = 0.984, standard error [SE] = 0.161) and GPP $\hat{\sigma}$ (coefficient = 0.869, SE = 0.138).

| Response variable	Season	Coefficient	SE	χ^2, 1 df	p
DO range	Summer	0.639	0.164	9.107	0.002
	Autumn	0.516	0.139	8.686	0.003
	Winter	0.254	0.149	2.579	0.108
	Spring	0.476	0.204	4.425	0.035
ER mean	Summer	0.737	0.160	12.109	<0.001
	Autumn	0.420	0.141	6.651	0.010
	Winter	0.304	0.136	4.243	0.039
	Spring	0.489	0.004	7.669	0.006
ER $\hat{\sigma}$	Summer	0.696	0.207	7.956	0.005
	Autumn	0.681	0.231	6.242	0.012
	Winter	0.237	0.140	2.598	0.107
	Spring	0.389	0.146	5.703	0.017
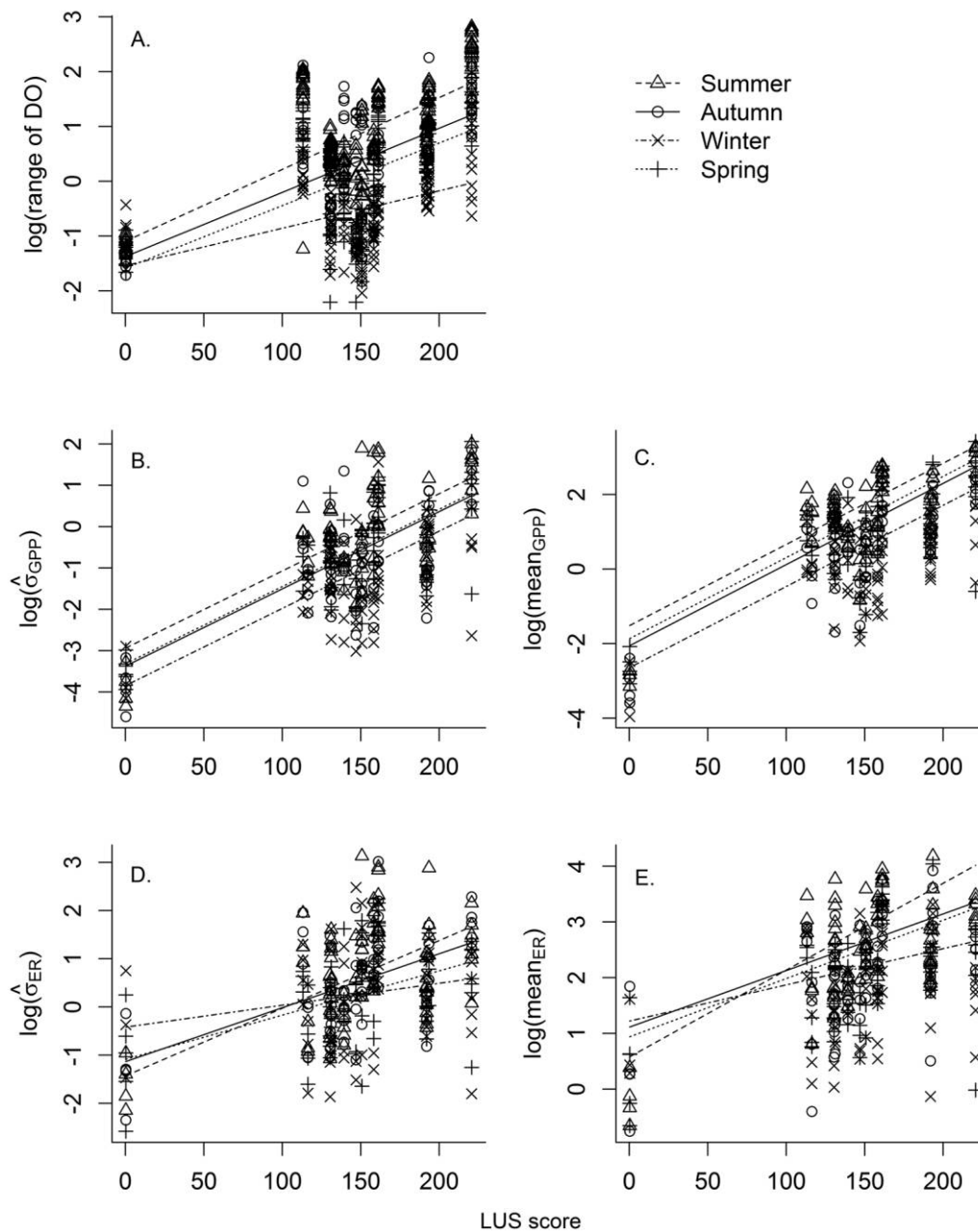
Figure 2. Fitted relationships between landuse stress (LUS) score and daily range in dissolved O_2 (DO) ($n = 133$) (A), standard deviation ($\hat{\sigma}$) of gross primary productivity (GPP) (B), mean GPP (C), standard deviation ($\hat{\sigma}$) in ecosystem respiration (ER) (D), and mean ER (E). $n = 298$ for metabolism metrics.

2007, Gerull et al. 2012) but did not compare metabolic variability across a landuse gradient. Clapcott and Barmuta (2010) observed an increase in dispersion (robust estimate of variance) and mean patch-scale GPP and net daily metabolism in small headwater streams in response to forest harvest. They attributed the short-term forestry effect to changes in catchment vegetation, canopy cover, and substrate composition. However, Clapcott and Barmuta (2010) specifically reported spatial rather than temporal variance in stream metabolism. In comparison, Houser et al. (2005)

observed a seasonal effect in the relationship between ER and catchment disturbance in headwater streams. ER decreased significantly with increasing disturbance in winter, spring, and summer, but not in autumn (Houser et al. 2005). They did not specifically test metabolic variance in response to land use, but their results showed decreased seasonal variability in ER at sites with high landuse disturbance, whereas GPP was consistently low. Houser et al. (2005) suggested that a decrease in coarse woody debris and the organic material it traps was the mechanism by

which catchment disturbance led to decreased ER, which was mediated seasonally by the availability of labile organic matter from deciduous vegetation and storm flows. In our study, both GPP and ER varied more within and among seasons at sites with higher LUS scores. Associated with higher LUS scores were higher mean N concentrations and lower riparian condition and shade values (Table 4). Increased variance associated with higher nutrients and reduced shading is not surprising because stream productivity depends on aquatic plant biomass, which can change rapidly in response to temporal fluctuations in these limiting factors (Rosemond et al. 2000, Hill et al. 2001).

Higher flow variability in unregulated rivers also is associated with increased urban land use (Poff et al. 2006) and is a major driver of temporal variability in plant biomass and stream metabolism (Uehlinger 2006). However, the effects of flow variability were not completely assessed in our study, and immediate flow effects were avoided by sampling during periods of stable flow. Even so, our results are likely to show some influence of flow history because flood events help shape the metabolic template (Biggs 1995). Our results are consistent with an early study that suggested temporal variability of community metabolism is a good indicator of eutrophication potential and general water quality (Hornberger et al. 1977).

Larger rivers are thought to have more consistent temporal patterns in metabolism than smaller rivers and streams, and very small within-week variance was observed in a 2-y study of the Mississippi and Chattahoochee Rivers (Dodds et al. 2013). In our study, mean rates and temporal variability in stream metabolism were not associated with catchment area, and highest and lowest LUS scores occurred in mid-order streams. This result suggests that the relationship between landuse effects and metabolism is likely to exist across a range of stream sizes, at least up to 5th-order streams, overriding any patterns expected based on position in the steam network (cf. Vannote et al. 1980). This result supports the application of stream metabolism as a stream-health indicator, where a predictable response to landuse gradients across a range of river sizes is ideal (e.g., Clapcott et al. 2010, Collier et al. 2013).

In our study streams, landuse effects on metabolic variability were more apparent in summer than in autumn or spring, and differences among sites were least evident in winter. For GPP, the relative difference in variability among seasons was consistent (i.e., parallel fitted slopes in Fig. 2B), but the log-link function means that the difference in absolute values increased among seasons along the landuse gradient. For example, GPP $\hat{\sigma}$s were 2.5× greater in summer than winter at the most-affected site, yet were similar at the least-affected site. These findings could indicate that temperature and light limit GPP in winter regardless of landuse status. This hypothesis is supported by the correlation between GPP ($\hat{\sigma}$s and means) and mean monthly water temperature, which was not related to LUS score. The hypothesis is further supported by results of previous studies,

for which authors have described a strong relationship between low GPP and low light levels in winter (Roberts et al. 2007, Benson et al. 2013). For ER, both relative and absolute values of variability differed among seasons. The lack of a relationship between ER and temperature and the nonsignificant effect of land use on ER in winter further suggests that seasonal variability in ER at the study sites is driven by autotrophic productivity (Beaulieu et al. 2013). Griffiths et al. (2013) also observed strong seasonality in the ecosystem metabolism of agricultural streams dominated by autotrophic productivity, which was associated with water temperature and light availability. Increased seasonal variation associated with land use has implications for ecosystem health assessment and could be used to inform targeted monitoring. Our results indicate that summer is the best time to identify landuse effects when using stream metabolism as an indicator of ecosystem health. Both GPP and ER mean values were strongly related to the landuse effect in summer, yet day-to-day variance in GPP and ER also was high in summer. Thus, obtaining a robust estimate of mean metabolic rates for stream health assessment will require multiple consecutive days of sampling. However, seasonal measurements provide information on the range of conditions to which stream organisms are subject, and greater seasonal variability is indicative of increased stress.

Metabolic variability to characterize the stream environment

Daily variations in DO show that, at times, the physicochemical properties of our study streams represent severe impairment for in-stream biota, e.g., <4 mg/L for fishes (USEPA 1986), with summer DO minima, in particular, averaging <2 mg/L at 4 of the most landuse-impacted study sites. The limiting effect of DO on organisms was suggested by a strong correlation between increasing daily DO range and the MCI metric (lower MCI values indicate a more impaired macroinvertebrate community). We suggest that DO limitation may be one pathway by which land use affects stream macroinvertebrate communities, but another pathway associated with the LUS score is increased nutrients, which together with increased sediment affects resource and habitat availability for macroinvertebrates (Allan 2004, Townsend et al. 2008). The daily variation in DO was strongly correlated with GPP but less strongly correlated with ER (GPP: r_s = 0.878, ER: r_s = 0.591, n = 132), given similar values of k, suggesting that daily variation in DO provides a good estimate of GPP (Mulholland et al. 2005) but is not a good approximation of ER in these streams.

Seasonal variation in metabolism provides insight into the limiting factors controlling stream function on an annual basis (nutrients, temperature, and riparian conditions in our study streams). The least-disturbed site (West Hoe), which showed low metabolic variation, has a dense evergreen riparian corridor that is likely to buffer the effect of

increased light and temperature in warmer months. Hence, reduced metabolic variability indicated a relatively constant in-stream environment. In contrast, sites with high seasonal variability in metabolism had high seasonal variability in physicochemical properties, such as temperature, nutrients, and probably light and organic matter inputs as indicated by poorer riparian conditions. Our findings support 2 important tenets: 1) Riparian buffers are likely to moderate the negative effects of land use on stream function (e.g., Bunn et al. 1999). 2) Calculation of stream C budgets requires, at minimum, seasonal measurements, especially in disturbed streams (e.g., Griffiths et al. 2013).

Seasonal variation in metabolism also may characterize the resilience of streams to future disturbances. In our study, stream metabolism was intentionally measured at times when flow effects would be minimal. Nevertheless, high temporal variability in metabolism was evident at sites with increased LUS scores. Stressed study streams probably are subject to even greater variability in metabolic rates at times of episodic storm events. For example, in a 2-y study of a forested headwater stream, episodic storms caused metabolic variability by initially decreasing but then stimulating ER, whereas storms depressed GPP in spring by scouring algae but increased GPP in autumn by clearing coarse benthic organic matter (Roberts et al. 2007). Resistance and resilience were not characterized in our study by measuring the temporal responses to pulse disturbances as has been done by others (Uehlinger and Naegeli 1998, O'Connor et al. 2012), but high seasonal variability in stressed streams may reflect eroded resistance and resilience to variation in other environmental controls, e.g., light and nutrients (Biggs et al. 1999). In our study, streams subject to LUS experienced high variability in stream metabolism even under baseflow conditions.

Metabolic variability and ecosystem stability

Resilience theory suggests that unstable ecosystems are more variable over time than stable ecosystems and that increased variability may indicate an impending state change (Gunderson 2000). However, no empirical evidence in our or any other published study (Capon et al. 2015) has been found to suggest that variability in river function decreases with increased disturbance beyond a certain threshold, which would be indicative of a new stable state where internal processes rather than external forces drive metabolism. Instead, we observed increasing temporal variability in stream metabolism associated with increasing LUS along a 3-fold gradient of stress equivalent to loss of 4 to 99% natural vegetation cover and an increase from 0 to 43% urban cover. If one adopts a space-for-time view, our results show that streams subject to increasing LUS become increasingly unstable, but this instability may not reflect an impending state change, possibly because of the capacity of stream ecosystems to operate far from equilibrium (O'Neill 2001).

Streams might not be subject to regime shifts as most commonly defined (Beisner et al. 2003), unless they undergo significant structural change that limits their ability to function within a defined domain, i.e., maintain homeostasis. For example, damming would change a lotic waterway to lentic water body and lead to the succession of a new biotic community with internal feedback mechanisms that would be characterized by different metabolic processes. In contrast, waterways that are naturally subject to cease-to-flow events, such as arid rivers, maintain communities that have the adaptive capacity to assimilate environmental change over a longer time frame. This statement does not mean that anthropogenic disturbance cannot affect such ecosystems, as evidenced by the effect of land use on dryland river metabolism (Fellows et al. 2009). Last, as an ecosystem-level measure, stream metabolism integrates variability observed at lower hierarchical levels (sensu Pickett et al. 1989), and may not provide an early warning tool of an impending state change (Batt et al. 2013). However, as demonstrated by the increased mean rates and metabolic variability, the streams in our study are clearly stressed by human land use, and this stress may make them vulnerable to cumulative press or pulse disturbances arising from future landuse intensification or climate change. Only long-term temporal monitoring can provide the data to assess such responses.

Conclusion

Our study showed an increase in the temporal variability of stream metabolism associated with an increase in landuse intensity, and this relationship has important consequences for characterizing the in-stream environment, assessing stream health, and ecosystem stability. Increased metabolic rates led to a higher daily range in DO concentration to the degree that the in-stream environment regularly failed to meet life-supporting capacity. Decreased riparian quality and increased nutrient concentrations were indicative of increased LUS and appear to facilitate increased temporal variability in stream metabolism. The vulnerability of landuse-stressed streams to flow pulse disturbances requires further testing because increased metabolic variability appears to typify unstable systems. Despite increased variability and potentially reduced resilience, our data did not identify a threshold of change, perhaps illustrating the adaptive capacity of lotic environments, at least on a medium time scale.

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