Relations of interannual differences in stream litter breakdown with discharge: bioassessment implications

ALEX C. Y. YEUNG [iD],[1,†] JORDAN L. MUSETTA-LAMBERT [iD],[2] DAVID P. KREUTZWEISER,[3] PAUL K. SIBLEY,[2] AND JOHN S. RICHARDSON [iD][1]

[1]Department of Forest and Conservation Sciences, The University of British Columbia, Vancouver, British Columbia V6T 1Z4 Canada
[2]School of Environmental Sciences, University of Guelph, Guelph, Ontario N1G 2W1 Canada
[3]Canadian Forest Service, Natural Resources Canada, Sault Ste. Marie, Ontario P6A 2E5 Canada

Abstract. Ecosystem-level processes are increasingly used by researchers and managers as indicators of ecological integrity for bioassessment, particularly in streams. However, processes like litter breakdown integrate multiple mechanistic pathways, which can vary differentially even under natural, unimpacted conditions. In particular, weather-driven hydrologic variations may strongly influence invertebrate shredder feeding and physical abrasion, inducing high natural variability of litter breakdown rates, which may obscure the effects of anthropogenic disturbances. Yet, such variability is rarely assessed to refine benchmarks of ecological status. Here, we quantified how interannual hydrologic differences contributed to the spatio-temporal variability of litter breakdown rate and its components (fragmentation, λ_F; and dissolution and microbial decomposition, λ_m), in low-order unimpacted, perennial streams across three climatically similar regions in temperate Canada. We measured litter breakdown rates in coarse (5 or 10 mm; k_c)- and fine-mesh (0.5 mm; k_f) leaf bags during fall for 2–4 yr and used variance partitioning to disentangle the variation of k_c, λ_F, and λ_m, as explained by hydrologic indices (during and prior to leaf bag incubation), decomposer-related variables, and water chemistry. Contrary to our hypotheses, interannual hydrologic variability was unrelated to λ_F, and poorly predicted λ_m and k_c within regions. Within-region spatial (i.e., across sites in a year) and temporal (across years at a site) differences in k_c approximated or exceeded the range of natural variability suggested to characterize reference conditions by a popular bioassessment framework. Accordingly, we recommend site- and region-specific modifications of benchmarks for reference conditions that account for interannual variability, while cautioning about their potential non-stationarity under climate change. Composite parameters such as k_c/k_f and λ_F/λ_m were substantially more variable across sites, and hence are not robust assessment parameters. As the range of natural variability of litter breakdown revealed in this study can overlap with the average impacts of certain anthropogenic disturbances (e.g., nutrient enrichment) on this parameter reported by previous research, we emphasize the need to include other structural and functional indicators to ensure comprehensive stream bioassessments.

Key words: anthropogenic disturbance; bioassessment; discharge; ecological integrity; hydrologic variation; litter breakdown; microbes; reference condition; shredders; stream.

† **E-mail:** alex.yeung@alumni.ubc.ca

INTRODUCTION

The inclusion of key ecosystem-level processes that reflect ecosystem functional integrity is recommended to complement the use of structural biological attributes in bioassessment schemes, particularly in streams (Gessner and Chauvet 2002, Young et al. 2008, Clapcott et al. 2012). Litter breakdown plays a pivotal role in regulating the availability and transport of allochthonous organic matter that supports stream foodwebs and energetics (Gessner and Chauvet 2002). As litter breakdown is sensitive to environmental stressors and relatively easy to measure, it is one of the most widely used functional indicators to assess the impacts of anthropogenic disturbances in watersheds (von Schiller et al. 2017), such as forestry activities (see references in Chauvet et al. 2016), nutrient and pesticide contamination (Woodward et al. 2012, Brosed et al. 2016), flow regulation (Mollá et al. 2017), and urbanization (Chadwick et al. 2006).

However, litter breakdown rates do not respond equivalently to the same stressor type in terms of direction and/or magnitude (Ferreira et al. 2015, 2016a, Yeung et al. 2017). Concomitant changes in naturally varying abiotic factors (e.g., temperature, water chemistry, discharge) can induce high variability of litter breakdown even in undisturbed streams, potentially masking the effects associated with stressors in impacted streams. The current criteria for linking litter breakdown rates and stream integrity are partly derived from limited information on the former's natural variability across space and time. For instance, Gessner and Chauvet (2002) tentatively suggested a range of breakdown rates (i.e., 75–133% around the mean of local reference streams; 50–200% around the mean at the regional scale), and a ratio of 1.2–1.5 for breakdown rates in coarse- relative to fine-mesh bags, to indicate no impacts on ecosystem functioning. Nevertheless, these recommended criteria were established based on data from a few sites unaffected by human disturbances, and also not explicitly linked to any potential confounding factors. Moreover, the setting of these benchmarks has not incorporated the extent of interannual or regional variability of litter breakdown rates (Pozo et al. 2011). Indeed, litter breakdown studies are not commonly repeated on an annual basis (Chauvet et al. 2016). Importantly, the same assessment benchmarks may not be robust to variation between years, which could be problematic for routine monitoring and impact assessments.

Litter breakdown rates in temperate, forested headwater streams are known to differ markedly across years (Jonsson et al. 2001, Dangles et al. 2004, Kreutzweiser et al. 2010, Yeung et al. 2017). Weather-driven, year-to-year hydrologic variations can be an important top-down driver of stream litter breakdown (Graça et al. 2015), through altering decomposer communities, organic matter availability and distribution, and water chemistry (Negishi and Richardson 2006, Feller 2010, Stenroth et al. 2014). However, there is a lack of quantitative understanding about the effects of interannual variability of hydrologic regime on litter breakdown, which depend on the differential responses of key mechanistic pathways of litter breakdown. These pathways include physical abrasion (by hydraulic forces and transport of sediments), feeding of detritivorous invertebrates (shredders), microbial decomposition, and dissolution. The duration of hydrologic influences is probably not only limited to within the period of leaf bag incubation, because hydrologic patterns preceding incubation (i.e., in the preconditioning phase) can also set the conditions for the development of benthic communities and resource availability, thereby leaving legacy effects on litter breakdown (Peckarsky et al. 2015, Arroita et al. 2018).

Hydrologic effects on litter breakdown rates are expected to be mainly controlled by fragmentation (through mechanical abrasion and shredder feeding), and less by microbial decomposition and dissolution. This is because (1) shredder communities are known to vary markedly with hydrologic variability (Kreutzweiser et al. 2010, Imberger et al. 2016); (2) shredders tend to exert much greater control on breakdown than microbes (Hieber and Gessner 2002, Kreutzweiser et al. 2010, Kominoski et al. 2011, Lecerf 2017); and (3) the contribution of microbial decomposition to breakdown was shown to vary little with current velocity (Ferreira et al. 2006). Extreme hydrologic events (e.g., spates and low-flow periods) may have varying consequences on litter breakdown rates, despite the strong association of these events with the

shredder communities (Negishi and Richardson 2006, Booker et al. 2015, Patrick and Yuan 2017). For instance, spates could result in differential extent of reductions in shredder abundances and/or organic matter standing stocks, depending on the characteristics of spates (e.g., magnitude, frequency, duration) and antecedent flows (Snyder and Johnson 2006). Extended low flows could lead to altered abundance, activity and feeding patterns of shredders, and litter availability (Leberfinger et al. 2010, Jeanette and Michael 2011, Northington and Webster 2017). These responses could also be mediated by other environmental conditions, such as the timing and magnitude of litter inputs, and availability of hydraulic refuge patches (Negishi and Richardson 2006). The interplay of these processes thus regulates the responses of litter breakdown rates to hydrologic variations (Tiegs et al. 2008).

The primary goal of this study was to examine how litter breakdown rates in perennial, small forest streams varied with interannual differences in hydrologic conditions, both during and before leaf bag incubations. Multi-year measurements of litter breakdown rates were undertaken in the same sites across distinct geographic regions of similar latitude. The study was therefore a natural experiment that relied on regional disparities in weather patterns to induce differences in the extent of temporal hydrologic variation, while minimizing the potential influences of latitudinal differences between regions on the relative contributions of shredders and microbes to litter breakdown (Boyero et al. 2011). The relative roles of fragmentation and microbial decomposition and dissolution were elucidated by measuring litter breakdown rates in coarse (k_c)- and fine-mesh (k_f) leaf bags. We hypothesized that, at the site level, (1) fragmentation rate (λ_F) would tend to scale positively with the magnitude of hydraulic forces (i.e., frequency and duration of high-flow pulses), when the direct hydraulic effects on enhancing abrasion exceeds the indirect effects on reducing shredder populations; and (2) dissolution and microbial decomposition rate (λ_m) would be generally invariant along the gradient of hydraulic forces. The importance of hydrologic characteristics relative to variables associated with decomposers and water chemistry in driving the variability of

litter breakdown rates was evaluated by variance partitioning. Furthermore, the spatio-temporal variability of litter breakdown rates, as well as the ratio of breakdown rates (i.e., k_c/k_f, λ_F/λ_m), within study regions was quantified. Results would help establish regional and site-specific ranges of the natural variability of litter breakdown rates, in order to refine bioassessment benchmarks.

METHODS

Study region and site characteristics

This study was conducted in three geographically separate regions in the temperate zone of Canada. They include the University of British Columbia's Malcolm Knapp Research Forest (MKRF) in British Columbia, and the Turkey Lakes Watershed (TLW) and White River Forest Management Area (WR) in Ontario (Fig. 1). Malcolm Knapp Research Forest is located in the Pacific Maritimes ecozone approximately 60 km east of Vancouver and has a moderate oceanic climate (Köppen-Geiger climate classification *Cfb*), bordering on a warm-summer Mediterranean climate (*Csb*; Peel et al. 2007). Turkey Lakes Watershed lies on the Boreal Shield ecozone about 60 km north of Sault Ste. Marie. White River Forest is also located on the Boreal Shield, about 150 km away from TLW, and 75 km inland from the northeastern shore of
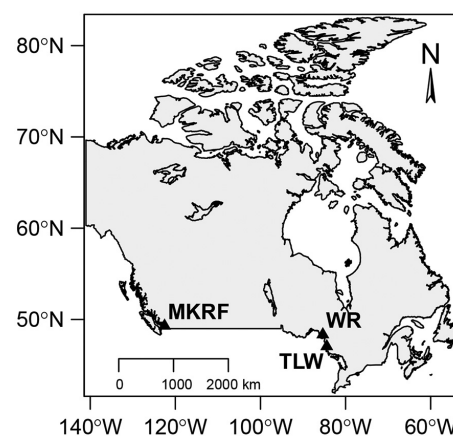

Fig. 1. Map showing the locations of study regions in British Columbia and Ontario, Canada. Abbreviations of study regions are as in Table 1.

Lake Superior. Both TLW and WR have a warm-summer humid continental climate (*Dfb*).

These study regions typically have wet early-fall and winter months. The summer months (July and August) of MKRF are generally dry, often resulting in low-flow conditions, whereas the precipitation at TLW and WR is fairly evenly distributed across seasons. The precipitation and discharge regimes of the study catchments are known to vary substantially across years (Kiffney et al. 2002, Foster et al. 2005, Kreutzweiser et al. 2009). The age of most forest stands in the study catchments, at the time of this study, ranged from around 85 yr in MKRF (Kiffney and Richardson 2010), ~20 or 140–200 yr (Creed and Band 1998) in TLW, and ~40–50 yr in WR (Musetta-Lambert et al. 2017). For additional descriptions of the study regions in terms of climate, geology, vegetation, etc., refer to Kiffney and Richardson (2010) for MKRF, Foster et al. (2005) for TLW, and Kreutzweiser et al. (2009) for WR.

Within each region, sampling was undertaken in four to five small (1st- to 3rd-order), forested streams (Appendix S1: Fig. S1a–c) over three or four consecutive (2014–2017) or near-consecutive (2009–2010, 2014) years. During the study period (early autumn) in all regions, we observed that interannual hydrologic variability did not cause complete surficial streambed drying, nor catastrophic debris flows that could remove riparian vegetation from large portions of the stream networks. Most of the study sites were minimally affected by fires and forest harvesting in catchments and in the adjacent riparian areas in the past 20 yr (Table 1). G-4 stream in MKRF was an exception, where riparian clear-cutting occurred about 10 m downstream of the site in 2015 and substantial surficial drying occurred in late September 2017; thus at G-4, only data from 2014 and 2016 were used. One TLW site (TLW34) affected by selection-based logging in its catchment 17 yr prior to the first study year included partial-harvest (at least 60% retention) riparian buffers along the study reach. Stream temperature during the incubation of leaf bags was comparable across years (MKRF, 9.2–11.4°C; TLW, 7.6–10.6°C; WR, 7.3–8.0°C). Within individual streams, the interannual difference in average daily temperature was within the range of 1.9–2.5°C in MKRF, 2.2–3.7°C in TLW, and 0.6–1.1°C in WR.

Field sampling

Litter breakdown.—Coarse (10 mm mesh size; 5 mm for WR)- and fine-mesh (0.5 mm) leaf bags were incubated along 30- to 40-m reaches of all study streams to determine litter breakdown rates. Prior to deployment, leaves of red alder (*Alnus rubra* Bong.) and speckled alder (*Alnus incana* ssp. *rugosa* (Du Roi) Clausen) had been collected at senescence, air-dried to constant mass, and stored at room temperature. Speckled alder leaves were additionally pre-leached in water for 24 h and oven-dried at 30°C for 24 h before storage. Leaves of red alder and speckled alder were used in MKRF and WR, respectively, as these deciduous tree species are commonly present in the riparian vegetation of the study streams. In TLW, leaves of foreign red alder—highly palatable to decomposers—were used in lieu of native speckled alder. Therefore, the spatio-temporal variability of breakdown rates in TLW would be influenced by fluctuations in decomposers' abundance and activities as in the other regions, and not a reduced preference for red alder (see also Boyero et al. 2011). The mesh size of leaf bags and the procedures of constructing and handling them were identical in MKRF and TLW, whereas some of them differed from those in WR (see following paragraphs).

Three coarse-mesh and three fine-mesh bags, each containing 4 ± 0.01 g of red alder leaves, were deployed in each study stream. In WR, seven coarse-mesh bags, each enclosing 10 ± 0.01 g of speckled alder leaves (4 g in 2014), and seven fine-mesh bags, each enclosing ten pre-weighed 23 mm diameter speckled alder leaf disks, were used in each stream. In WR, no fine-mesh bags were deployed in the third year of study (i.e., 2014). Placement of leaf bags in streams at all sites occurred in early autumn (mid-September to early October), which coincided with the period of natural litterfall, and were retrieved 4–6 weeks after incubation. This length of incubation period allowed for sufficient breakdown (>20% mass loss), which enabled the testing of possible differences in breakdown rates between sites and years. Each coarse-mesh bag was placed alongside a fine-mesh bag, the latter excluding the access to litter by large-bodied invertebrate shredders. Some meiobenthic decomposers (e.g., nematodes) could be present in the fine-mesh bags, but previous work has

Table 1. Catchment- and reach-scale characteristics for sites in the study regions in British Columbia and Ontario.

Region† and site	Location Lat. (N)	Location Long. (W)	W.A. (ha)	Elev. (m)	S.O.	Years since last major harv.	Extent (%) and year of harv.	Reach grad. (%)	Wetted width (m) ‡	Mid-channel depth (m) ‡	Cano. Open. (%) §
MKRF											
G-4	49°17′44″	122°35′48″	28	257	1	~85		30.6	0.97 (0.22)	0.11 (0.02)	17.0
Mike	49°16′40″	122°32′46″	30	314	1	~85		5.2	1.43 (0.12)	0.14 (0.03)	11.0 ¶
Spring	49°17′41″	122°34′2″	38	340	3	~85		8.8	2.40 (0.37)	0.15 (0.02)	8.7 ¶
Upper East	49°17′3″	122°33′43″	36	306	2	~85		57.7	1.92 (0.20)	0.15 (0.03)	7.7 ¶
TLW											
TLW34	47°3′27″	84°24′59″	68	391	2	17	61 (1997)	8.8	2.33 (0.26)	0.19 (0.04)	25.4
TLW96	47°4′39″	84°24′39″	71	362	2	140–200		3.5	1.97 (0.35)	0.14 (0.03)	26.0
TLW97	47°4′34″	84°24′59″	37	363	2	140–200		5.2	1.81 (0.31)	0.14 (0.02)	34.7
AY1-1	46°58′17″	84°17′59″	987	290	3	21	65.7 (1990); 14.1 (1993)	1.8	4.60 (0.31)	0.19 (0.03)	27.1
AY4-1	47°0′28″	84°18′41″	219	248	3	24	35.2 (1990); 0.22 (2013)	10.5	2.25 (0.33)	0.19 (0.04)	28.3
WR											
EWR4	48°45′4″	85°10′21″	655	389	2	~40–50		10.7	2.83 (0.31)	0.10 (0.01)	26.2
EWR5	48°55′11″	85°14′33″	344	355	2	~40–50		4.2	1.13 (0.15)	0.10 (0.02)	14.5
EWR6	48°44′56″	85°9′58″	787	391	2	~40–50		3.3	1.42 (0.07)	0.08 (0.01)	18.0
EWR8	48°14′3″	85°25′11″	299	450	2	~40–50		1.8	2.57 (0.20)	0.17 (0.02)	28.1
EWR9	48°15′11″	85°23′48″	45	465	1	~40–50		2.4	1.45 (0.09)	0.09 (0.01)	41.6

Notes: harv., harvest; MKRF, Malcolm Knapp Research Forest; S.O., stream order; TLW, Turkey Lakes Watershed; W.A., watershed area; WR, White River. Watershed area, stream order, and extent of forest harvesting were determined in ArcGIS using watershed delineations in Whitebox Geospatial Analysis Tools (version 3.4).

† Dominant forest vegetation in each region: (MKRF) western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), western red cedar (*Thuja plicata* Donn ex D. Don), and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco); (TLW) sugar maple (*Acer saccharum* Marsh.), with scattered stands of yellow birch (*Betula alleghaniensis* Britton); (WR) black and white spruce (*Picea mariana* (Miller) BSP and *Picea glauca* (Moench) Voss), balsam fir (*Abies balsamea* (L.) Miller), and jack pine (*Pinus banksiana* Lamb.). Riparian vegetation in each region: (MKRF) red alder (*Alnus rubra* Bong.), vine maple (*Acer circinatum* Pursh), and salmonberry (*Rubus spectabilis* Pursh); (TLW) species similar to those in forest vegetation; (WR) speckled alder (*Alnus incana* ssp. *rugosa* (Du Roi) Clausen), high bush cranberry (*Viburnum trilobum* Marshall), beaked hazel (*Corylus cornuta* Marshall), and red osier dogwood (*Cornus sericea* L.).

‡ Data are presented as mean values (±SE) measured in September/October across 2014–2017 for MKRF (2014–2016 for G-4) and TLW sites, and in 2010 for WR sites.

§ Measurements were obtained using either spherical densitometer or digital hemispherical pictures taken by fisheye lens (denoted by ¶; see Yeung et al. 2017 for details), in 2014 for MKRF and TLW and in 2010 for WR.

shown that meiofauna density is unrelated to litter breakdown inside these bags (Majdi et al. 2015).

Upon retrieval, each leaf bag was sealed in a plastic bag containing some stream water, stored on ice (whole leaf bag preserved in 5% formalin in WR), and transported to the laboratory. The leaf bags in MKRF and TLW were frozen at −20°C until later processing. Leaf materials from each bag were thawed and gently rinsed with tap water onto a 250-µm sieve to remove invertebrates and sediments from leaf surfaces. In WR, leaves removed from coarse-mesh bags were separated from invertebrates and sediments by elutriation using a 250-µm sieve (Kreutzweiser et al. 2008). Invertebrates retained on the sieves were

stored in ethanol for later enumeration. Two sets of five 9.5-mm leaf disks were randomly cut from leaves, using a cork borer, from each coarse-mesh leaf bag in MKRF and TLW. Central veins were avoided when removing leaf disks. One set was frozen at −20°C until analysis of ergosterol—a surrogate for fungal biomass in decomposing leaves (Gessner 2005). The other set of disks, as well as leaf materials from leaf bags in all regions, were oven-dried at 60°C to a constant mass and weighed to obtain dry mass (DM). Leaf materials in MKRF and TLW were further ashed at 550°C for 4 h in a muffle furnace and reweighed to determine ash-free dry mass (AFDM), by subtracting ash mass from DM. Final AFDM (DM in WR) was corrected by the

mass of leaf materials from handling losses (and leaf disks removed for fungal and AFDM determinations), prior to the calculations of k_c and k_f.

Shredders and fungal biomass.—Macroinvertebrates associated with the coarse-mesh leaf bags were counted and identified to the lowest practical taxonomic resolution (at family or genus level), except for Chironomidae in which subgroups corresponding to subfamily or tribe were identified (e.g., Orthocladiinae, Chironomini, Tanytarsini, Tanypodinae). The assignment of macroinvertebrates to shredders was based on Merritt et al. (2008). Shredder density at the site level was obtained by dividing the average shredder abundance by the average final leaf AFDM across leaf bags. The density of *Lepidostoma* and *Micrasema* caddisflies (as numerically dominant shredder taxa) and *Tipula* craneflies and *Pteronarcys* stoneflies (as large-bodied taxa with relatively high contribution to total shredder biomass) was also calculated, whose feeding possibly accounted for an appreciable proportion of shredder effects on litter breakdown (Ruesink and Srivastava 2001, Lecerf and Richardson 2011, Andrushchenko et al. 2017, Tonin et al. 2018).

The procedures of determining the ergosterol content for each set of frozen leaf disks followed Gessner (2005). Briefly, lipids were extracted from leaf disks by heating (30 min, 80°C) in 0.8% KOH–methanol, and the extract was purified by solid-phase extraction (using Sep-Pak C18 Vac RC cartridges, 500 mg, 3 cc; Waters, Milford, Massachusetts, USA) and eluted in isopropanol. Ergosterol extracts were then quantified by high-performance liquid chromatography. Fungal biomass was expressed as ergosterol mass per gram of leaf AFDM.

Stream discharge.—In MKRF, daily discharge (m^3/s) of the study streams from 2014 to 2017 was simulated using a process-based, coupled hydrology and temperature model, which was previously developed for adjacent forested catchments within the same study region (Leach and Moore 2015, 2017). This model was calibrated and evaluated against field data, and generally captured the timing of high-flow events and low-flow conditions but might underestimate peak-flow magnitude (Leach and Moore 2017). An adjustment of several model parameters was necessary to account for differences in catchment characteristics among study streams. These parameters included catchment area, mean elevation, and mean hillslope for the catchment determined from either 1- or 20-m digital elevation models. Thirty time series (=iterations) of discharge were generated for each study stream based on a generalized likelihood uncertainty estimate approach. Mean discharge specific to each date of the year was obtained by averaging across all the 30 iterations for each stream.

In TLW, discharge in study streams was modeled based on the Regional Hydro-Ecological Simulations System (RHESSys). This hydrologic model has been well calibrated based on the discharge data in a subset of gauged streams in the Batchawana River Watershed in central Ontario, and the study streams were within this Watershed (Sanford et al. 2007). The RHESSys model was evaluated to represent the timing and magnitude of observed discharge reasonably well, and monthly-to-seasonal flow metrics (e.g., duration of low-/high-flow pulses) appeared to be better estimated by the model than metrics associated with daily discharge (Sanford et al. 2007). Air temperature and precipitation data from 2014 to 2017 were obtained from nearby meteorological stations to run the simulations to generate daily discharge.

In WR, water levels were recorded every two hours from April to November during 2009–2010 and in 2014, using level-loggers (Levelogger Edge model 3001; Solinst, Georgetown, Ontario, Canada). Measurements of stream discharge were made at multiple (≥ 3) stage levels throughout each year at the approximate location of the level-loggers. Discharge (Q) was estimated using the area–velocity equation $Q = AV$, where A is the cross-sectional area of the stream, calculated by multiplying stream width by average water depth, at 6–10 points across the width of the stream, and V is average velocity, estimated with a flow meter at each point where depth was measured at 60% maximum depth (Gordon et al. 2004). Water level measurements were converted to discharge using linear rating curves established from stream discharge measurements, and discharge data were averaged for each day to give daily discharge.

Water chemistry and temperatures.—Water samples were collected during the retrieval of leaf bags (except for 2009 in WR) and analyzed by the Canadian Forest Service water chemistry

laboratory at Sault Ste. Marie, Ontario, following standardized methods (see procedures in Nicolson 1988, Hazlett et al. 2008). Water chemistry variables measured included pH, conductivity, total dissolved nitrogen, and total dissolved phosphorus (TDP). Total dissolved nitrogen and TDP were analyzed by cadmium reduction and ascorbic acid reduction of phosphomolybdic acid, respectively, following autoclave digestion. Water temperature was recorded every one or two hours during the period of leaf pack incubation, using temperature loggers (MKRF and TLW: TidbiT v2; Onset, Bourne, Massachusetts, USA; WR: Levelogger Edge model 3001; Solinst, Georgetown, Ontario, Canada). Data were averaged to yield average daily temperature for each stream during the incubation period.

Data analyses

Litter breakdown rates.—Additional samples of unleached red alder litter were leached, oven-dried, and ashed as for speckled alder litter (see *Methods: Field sampling: Litter breakdown*) to determine the percent loss in AFDM due to the initial release of water-soluble compounds. This percent of leaching correction (i.e., 20%) was applied to adjust the initial leaf litter AFDM of red alder (Pozo et al. 2011), in order to standardize the treatment of leaf litter across study regions. Additional release of solutes and dissolved organic matter from alder litter (or dissolution) could continue for a few more days after leaf bag incubation (Gessner and Konstanz 1989, McArthur and Richardson 2002). Temperature-corrected litter breakdown rate in coarse-mesh (k_c; total breakdown rate) and fine-mesh (k_f) bags was calculated as decay rate coefficients and averaged across leaf bags per site, using a first-order exponential decay model: $m_t = e^{-kt}$, where m_t is the proportion of initial leaf litter AFDM and t is the cumulative degree-days (in degrees Celsius) during the incubation period. The mean rates of litter breakdown through fragmentation (denoted as λ_F) and the combination of microbial decomposition and dissolution (λ_m) were computed following Lecerf (2017):

$$\lambda_F = k_c - \frac{k_f - k_c}{\ln(k_f) - \ln(k_c)}$$

$$k_c = \lambda_F + \lambda_m$$

All metrics of breakdown rate (k_c, k_f, λ_F, and λ_m) have the same unit (degree-day^{-1}) and are thus comparable with each other. The approach by Lecerf (2017) assumes that litter breakdown is not constant through time and that these pathways of litter breakdown are independent (e.g., the conditioning effects of microbial decomposers on fragmentation are not considered). This approach overcomes several shortcomings of previously used breakdown metrics in approximating and comparing pathway-specific litter breakdown rates.

In WR, limited variability of site-specific k_c/k_f between 2009 and 2010 was observed (range of coefficient of variation [CV]: 2–33%; Appendix S3: Table S2). Therefore, k_f at each site in this region in 2014 was calculated based on the average of k_c/k_f from these two years, allowing λ_F and λ_m to be estimated.

Hydrologic indices.—To explore the potential aspects of flow regimes both during and before leaf bag incubation, which were hypothesized to influence the spatio-temporal variability of litter breakdown rates, a group of 14 hydrologic indices was selected and calculated for each site in each year (Table 2). These hydrologic indices were initially chosen to broadly reflect magnitude, frequency, and duration of high- and low-flow events, and flashiness (Baker et al. 2004), which are representative and ecologically important components of flow regimes in perennial, runoff-driven streams (Clausen and Biggs 2000, Olden and Poff 2003, Kakouei et al. 2017, Poff 2018). Some of these indices are used as indicators of hydrologic alteration (Richter et al. 1996). The beginning of the pre-incubation period was defined to be 30 d prior to incubation to capture the effects of recent flow conditions on decomposer communities.

Median daily discharge from 1 May to 30 November (1/18 July to 30 November for WR) averaged across the three study years (excluding the fourth year in MKRF and TLW) was obtained. It was considered to be the best available long-term summer-to-fall discharge estimate normal for the study regions, as the basis for characterizing high- and low-flow events using the high.spells and low.spells functions, respectively, in the hydrostats package in R (Bond 2016). Daily discharge exceeding three times and below 25%

Table 2. Initial sets of candidate hydrologic indices, shredder-related, fungal biomass, and water chemistry variables that were expected to influence stream litter breakdown in the study regions in British Columbia and Ontario.

Notation	Variable
Hydrologic indices ($n = 14$)	
Magnitude	
BFI for incubation period, P.BFI for pre-incubation period	Base flow index: ratio of 7-d minimum flow to total discharge
Frequency of flow events†	
LF, P.LF	Low-flow period: no. of times daily discharge is below 25% of 3-yr mean of median daily discharge from summer to fall
HF, P.HF	High-flow pulse: no. of times daily discharge is above 3 times the 3-yr mean of median daily discharge from summer to fall
Duration of flow events†	
LFD, P.LFD	Low-flow duration: total no. of days of low-flow period(s)
HFD, P.HFD	High-flow duration: total no. of days of high-flow pulse(s)
Flashiness	
CV, P.CV	Variability: coefficient of variation of daily discharge
ROC, P.ROC	Rate of change: ratio of the sum of the absolute values of day-to-day changes in daily discharge to the sum of daily discharge (Richards-Baker Flashiness Index; see Baker et al. 2004)
Shredder-related variables ($n = 4$)	
SD	Shredder density
LMD	Density of *Lepidostoma* and *Micrasema* (only in MKRF) caddisflies
TPD	Density of *Tipula* craneflies and *Pteronarcys* (only in MKRF) stoneflies
STR	Shredder taxonomic richness
Fungal-related variable ($n = 1$)	
FB	Fungal biomass
Water chemistry variables ($n = 4$)	
PH	pH
CO	Conductivity
TN	Total dissolved nitrogen
TP	Total dissolved phosphorus

Note: MKRF, Malcolm Knapp Research Forest.

† Variables were adjusted by the time difference between the last day of these flow event(s) and the first day of incubation/pre-incubation period (see main text for details of calculations).

of the 3-yr mean of median daily discharge constituted high-flow and low-flow periods, respectively. Flow events of the same type were considered to be separate when they were at least 5 d apart. The frequency and duration of these flow events were first converted to percentage data by dividing each index by the number of days of incubation to standardize across sites or years for differences in study duration, and by 30 for indices for the pre-incubation period. These percentage data were then multiplied by $[(D - x + 1)/D]$, where x is the time difference between the last day of flow event(s) and the first day of incubation/pre-incubation period (in days; averaged in the case of multiple events) and D is the duration of incubation/pre-incubation period. This scaling factor incorporates the possible

effects of the timing of extreme flow events on litter breakdown rates, as it controls the time available for decomposers to re-establish, or time since community reset (Campbell et al. 2015). Adjusted by this scaling factor, more recent extreme flow events (i.e., smaller x), given the same frequency and duration, would be expected to more strongly influence decomposer (particularly shredder) communities than earlier flow events, as the former allow less time for community reset. Base flow index was computed using the IHA package in R (Law 2013). Hydrologic indices for each of the three streams at TLW (i.e., TLW34, TLW96, and TLW97), generated based on RHESSys-modeled discharge, were highly similar across the first three years of study (CV usually <10%). AY1-1 and AY4-1, without

modeled discharge, were in proximity to these three streams (~15 km away), with similar physical and biological habitat characteristics. Therefore, each hydrologic index at AY1-1 and AY4-1 for a given study year was assumed to be the average of the corresponding values at the other three study streams at TLW.

Statistical analysis.—Linear mixed-effects models (LMMs) were used to compare between k_c and k_f, and between λ_F and λ_m, averaged at the site level across study regions and years. Litter breakdown rate type and study region were the main factors, while site was a random factor nested within study region in this analysis. The magnitude of temporal variability of selected litter breakdown rates (i.e., k_c, λ_F, and λ_m) at each site was expressed as (1) the inter-year CV and (2) the relative range limits around the inter-year mean (i.e., enclosed by the minimum and maximum ratios of breakdown rates for a given year to the inter-year mean). For each year, the spatial variability of litter breakdown rates at each region was expressed as (1) inter-site CV and (2) the relative range limits around the inter-site mean (i.e., enclosed by the minimum and maximum ratios of breakdown rates at a given site to the inter-site mean). Mean values of inter-year CV (herein referred to as temporal CV) were compared among litter breakdown rates and study regions (as main factors) using a two-way ANOVA. For the analysis of inter-site CV (herein spatial CV), LMMs were fitted and included breakdown rate type and region as main factors, and year as a random factor. Linear mixed-effects models were undertaken using the lmer function in the lme4 package (Bates et al. 2017). The significance of main factors was estimated using an approximate F test based on the Kenward–Roger approach implemented using the ANOVA function in the lmerTest package (Luke 2017). For LMMs, P values were adjusted for multiple comparisons using a Holm's correction (Holm 1979). Significant main effects ($P < 0.05$) were analyzed by Tukey's honestly significant difference (HSD) post hoc tests.

To further quantify the combined spatial and temporal variability of litter breakdown rates attributable to the influences by hydrology, shredders (not for λ_m) and fungal decomposers, and water chemistry, redundancy analysis (RDA) was undertaken (Borcard et al. 2011) with the varpart function in vegan (Oksanen et al. 2017). Prior to RDA, forward selection was undertaken to select significant variables for each group of variables (Table 2) that could explain litter breakdown rate, using two stopping rules with the packfor package based on Blanchet et al. (2008). Relationships between hydrology and litter breakdown rates were further explored by a global RDA, using only forward-selected hydrologic indices. The fitted site scores on the first RDA axis (i.e., site constraints; hereinafter referred to as composite hydrologic index) were considered as a composite measure of important hydrologic indices that were strongly associated with litter breakdown. The regression coefficients from forward-selected hydrologic indices to composite hydrologic index were extracted, which were then used for calculating the composite hydrologic indices of the sites at MKRF and TLW for the fourth study year. For each region, LMMs were constructed to test for interannual differences in composite hydrologic index, with year as the main factor and site as a random factor. The significance of regression relationships between litter breakdown rate and composite hydrologic index was also tested for each region, while controlling for the random effects of site. Details about procedures for RDAs are provided in Appendix S2: Supplementary Methods.

For each region, community dissimilarity of shredders at study streams between years was visualized using non-metric multidimensional scaling (NMDS) graphs. One-way permutational multivariate analysis of variance (PERMANOVA) was performed to assess the significance of differences in shredder assemblages between years. Site-level shredder density data were used to generate the Bray-Curtis similarity matrix as the basis for PERMANOVA (999 permutations), using the adonis function in the vegan package (Oksanen et al. 2017). Within PERMANOVA, year was the main factor, and sites were used as strata to ensure that randomizations were only made within each site, given the differences in shredder assemblages among sites. Interannual differences in shredder assemblages were further assessed by pairwise PERMANOVA, and a sequential Bonferroni correction was used to adjust P values for post hoc pairwise comparisons.

Prior to all analyses, data were $\ln(x + 1)$- or arcsine-transformed as appropriate to meet assumptions of normality. All data analyses were carried out using R 3.4.1 (R Development Core Team 2017).

RESULTS

Litter breakdown rates and their spatio-temporal variability

Litter breakdown rates in coarse-mesh bags were uniformly greater than in fine-mesh bags ($F_{1,83}$: 116.3, $P < 0.001$; Appendix S3: Table S1). This was also indicated by the lower end of the range of k_c/k_f exceeding 1 for red alder (range 1.06–8.59) and speckled alder (1.32–3.09; Appendix S3: Table S2). Fragmentation rate of litter was almost always lower than dissolution and microbial decomposition rate for both litter species ($F_{1,83}$: 109.6, $P < 0.001$; Appendix S3: Table S1). λ_F/λ_m ranged from 0.03 to 1.43 for red alder and 0.14 to 0.67 for speckled alder, and λ_F was about 3–59% of k_c (Appendix S3: Table S2).

Temporal CV of litter breakdown rates was similar among breakdown rate types ($F_{2,37}$: 2.14, $P = 0.13$) and regions ($F_{2,37}$: 0.20, $P = 0.82$). Across regions, the maximum value of temporal CV was comparable between k_c (50.1%) and λ_m (47.9%) and was considerably larger for λ_F (82.4%; Table 3). Temporal CV of k_c was positively and more strongly associated with that of the corresponding λ_m (Pearson's correlation: $r = 0.88$; $P < 0.001$) than that of λ_F (Pearson's correlation: $r = 0.60$; $P < 0.05$) at each site.

Spatial CV differed significantly across breakdown rate types ($F_{2,25}$: 70.57, $P < 0.001$) and regions ($F_{2,25.5}$: 10.57, $P < 0.001$). Spatial CV of λ_F (75.0%) was the largest, followed by that of k_c (36.8%) and λ_m (24.4%; Tukey's HSD for all pairwise comparisons: $P < 0.001$). On average, spatial CV of litter breakdown rates was the largest in MKRF (58.3%; Tukey's HSD: $P < 0.01$), whereas that in TLW (40.1%) and WR (37.6%) was not significantly different from each other (Table 3). In certain years, maximum λ_F in a study region could be more than double that of the inter-site mean. Temporal CV of k_c tended to be of a smaller magnitude than spatial CV, especially in MKRF (range: 17.9–28.6% vs. 27.5–63.1%) and TLW (11.8–28.3% vs. 27.5–41.6%).

Selection of variables

Global RDAs indicated that both k_c and λ_m were strongly associated with hydrologic indices, but not λ_F (Table 4; Appendix S4: Table S1). Water chemistry was significantly related to all litter breakdown rates, and shredder-related variables related to k_c and λ_F, whereas fungal biomass was unimportant for predicting the variation of all breakdown rates. The forward-selected variable(s) from each variable set associated with litter breakdown rates were similar (Table 4). In particular, both CV of daily discharge during the incubation period (CVD) and rate of change of discharge during the pre-incubation period (P.ROC) were the selected hydrologic indices for k_c and λ_m. Coefficient of variation of daily discharge positively affected, and accounted for more variation of k_c and λ_m than did P.ROC, which negatively affected these breakdown rates (adjusted R^2 for k_c: 0.32 [CVD] vs. 0.17 [P.ROC]; λ_m: 0.43 vs. 0.19; Appendix S4: Table S1). Total shredder density and density of *Tipula* craneflies and *Pteronarcys* stoneflies were the shredder-related variables selected for, and positively related to, both k_c and λ_F. The only selected water chemistry variable was TDP, which reduced all breakdown rates at high concentrations.

Variance partitioning

Total variance explained by the forward-selected pRDA models was the highest for k_c (adjusted R^2: 0.80), followed by λ_m (0.64) and λ_F (0.53; Fig. 2), when data pooled across all regions were analyzed. Hydrologic indices appeared to explain a considerable proportion of variability of k_c and λ_m across all regions. The proportion of total explained variance of k_c attributed uniquely to hydrologic indices was 0.13, smaller than that to shredder-related variables (0.24). Hydrologic indices uniquely accounted for a much higher proportion of variance of λ_m (0.40) than water chemistry variables did (0.02). Shredder-related variables uniquely explained more variance of λ_F (0.30) than did water chemistry variables (0.15). However, within individual regions, variance partitioning of litter breakdown rates revealed considerable differences in the order of relative importance of variable sets, and in the significance of their unique effects. For instance, the proportion of variance explained by the unique effects of hydrologic indices (shredder-related

Table 3. Extent of spatio-temporal variability of in-stream total breakdown rate (k_c), fragmentation rate (λ_F), and dissolution and microbial decomposition rate (λ_m) in the study regions in British Columbia and Ontario.

Region and site	k_c		λ_F		λ_m	
	T_{CV}	Inter-year range	T_{CV}	Inter-year range	T_{CV}	Inter-year range
MKRF						
G-4	27.17	0.81–1.19	13.73	0.90–1.10	32.85	0.77–1.23
Mike	28.58	0.64–1.34	18.38	0.87–1.27	34.84	0.59–1.44
Spring	20.89	0.79–1.25	59.55	0.58–1.89	17.39	0.89–1.26
Upper East	17.87	0.84–1.19	26.63	0.79–1.37	24.18	0.84–1.36
S_{CV} (inter-site range)						
2014		47.68 (0.68–1.70)		115.48 (0.25–2.70)		24.62 (0.82–1.36)
2015		42.99 (0.64–1.48)		85.75 (0.29–1.95)		21.89 (0.82–1.24)
2016		46.78 (0.65–1.68)		101.25 (0.34–2.50)		22.70 (0.79–1.29)
2017		63.09 (0.34–1.60) †		84.93 (0.16–1.86)		41.96 (0.53–1.33)
TLW						
TLW34	23.89	0.78–1.34	53.60	0.52–1.75	10.68	0.91–1.12
TLW96	11.83	0.84–1.09	30.56	0.62–1.30	12.79	0.89–1.18
TLW97	14.31	0.80–1.11	20.68	0.84–1.30	19.06	0.77–1.23
AY1-1	22.71	0.68–1.21	58.77	0.61–1.87	26.02	0.64–1.24
AY4-1	28.27	0.83–1.42	82.38	0.15–2.10	20.52	0.80–1.29
S_{CV} (inter-site range)						
2014		34.04 (0.59–1.49)		84.45 (0.07–2.31)		22.30 (0.75–1.23)
2015		27.52 (0.81–1.49)		54.36 (0.56–1.94)		19.20 (0.84–1.33)
2016		41.58 (0.60–1.63)		68.13 (0.33–2.07)		25.98 (0.75–1.37)
2017		31.16 (0.58–1.42)		55.16 (0.19–1.70)		17.81 (0.82–1.25)
WR						
EWR4	16.50	0.82–1.14	21.04	0.81–1.23	15.74	0.82–1.10
EWR5	9.70	0.89–1.08	7.59	0.94–1.08	10.17	0.89–1.08
EWR6	34.78	0.69–1.37	55.57	0.66–1.64	29.26	0.70–1.28
EWR8	47.23	0.46–1.34	46.63	0.46–1.27	47.92	0.46–1.38
EWR9	50.10	0.51–1.51	76.42	0.48–1.88	43.68	0.52–1.37
S_{CV} (inter-site range)						
2009		29.77 (0.66–1.32)		60.65 (0.30–1.73)		17.01 (0.82–1.21)
2010		19.29 (0.80–1.27)		51.35 (0.36–1.55)		11.93 (0.84–1.16)
2014		41.31 (0.57–1.54)		63.47 (0.65–2.13)		43.34 (0.51–1.56)

Notes: T_{cv}, temporal coefficient of variation (CV; in %) of breakdown rates; S_{cv}, spatial CV of breakdown rates; MKRF, Malcolm Knapp Research Forest; TLW, Turkey Lakes Watershed; WR, White River Forest. Inter-year(site) range refers to the relative range limit around the inter-year(site) mean for a given litter breakdown rate (see main text for details of calculation).
† T_{CV} (inter-year range) becomes 28.63% (0.80–1.20) when data from Mike are excluded.

variables) ranged from 0 to 0.69 (0–0.76) for k_c and 0.04 to 0.20 for λ_m, and their significance differed across regions.

Relationships between hydrology and litter breakdown rates

Variation in both k_c and λ_m explained by forward-selected hydrologic indices did not differ significantly between linear and the polynomial form of RDAs (k_c: $P = 0.96$; λ_m: $P = 0.89$). Hence, results of linear RDAs are presented herein, and were used to generate the composite hydrologic index. Inter-year differences in the composite hydrologic index for both k_c and λ_m were

significant in MKRF and TLW, but not in WR (Fig. 3; Appendix S4: Table S2). The inter-year variation of the composite hydrologic index was not consistent among sites in WR.

When pooled across regions, an overall positive relationship between the composite hydrologic index and k_c (and λ_m) was observed (Fig. 3). However, in MKRF and TLW, significant interannual differences in the composite hydrologic index did not result in consistent shifts of k_c within sites across years (Table 5). A considerably smaller proportion of variance of k_c in these regions was explained by the composite hydrologic index alone (marginal R^2: 0.02 and 0.009,

Table 4. Results of forward selection of hydrologic indices, shredder-related, fungal biomass, and water chemistry variables on in-stream total breakdown rate (k_c), fragmentation rate (λ_F), and dissolution and microbial decomposition rate (λ_m) in the study regions in British Columbia and Ontario.

Variable set	Degrees of freedom	F	P	Variable(s) selected
k_c				
Hydrology	14, 26	4.31	<0.001	(+) CVD; (−) P.ROC
Shredder-related	4, 36	11.83	<0.001	(+) SD; (−) STR; (+) TPD; (−) LMD
Fungal biomass	1, 24	0.45	0.52	
Water chemistry	4, 31	9.24	<0.001	(−) TP
λ_F				
Hydrology	14, 26	0.74	0.74	
Shredder-related	4, 36	9.38	<0.001	(+) SD; (+) TPD
Fungal biomass	1, 24	0.21	0.65	
Water chemistry	4, 31	9.24	<0.001	(−) TP
λ_m				
Hydrology	14, 26	8.34	<0.001	(+) CVD; (−) P.ROC
Fungal biomass	1, 24	2.76	0.11	
Water chemistry	4, 31	9.70	<0.001	(−) TP

Notes: Variables selected for use in the variance partitioning analysis, and the directional effect of each variable (+, −) on litter breakdown rates are given (see Table 2 for notations of variables).

respectively) than the random effects of sites (conditional R^2: 0.81 and 0.62; variance explained by both factors), as observed for λ_m (Table 5). The composite hydrologic index in WR tended to be lower than that in the other two regions, due to more sites experiencing a greater rate of change of flows, and it was also unrelated to k_c across years.

Spatio-temporal variability of shredder assemblage structure

The NMDS ordination plots well represented data on shredder assemblage structure in all regions, given the fair stress values (stress = 0.10–0.11; Appendix S5: Fig. S1a–c). Inter-year differences significantly affected assemblage structures in MKRF (PERMANOVA $F_{2,8}$: 2.26, R^2: 0.34, $P = 0.005$, 431 permutations) and WR (PERMANOVA $F_{2,14}$: 1.38, R^2: 0.19, $P = 0.003$, 999 permutations), but not in TLW (PERMANOVA $F_{2,14}$: 0.56, R^2: 0.08, $P = 0.28$, 999 permutations). In WR, assemblage structure differed significantly between the 2nd and 3rd year (or 2010 and 2014; adjusted P: 0.033); however, no pairwise comparisons were significant in MKRF after a sequential Bonferroni correction of P values.

DISCUSSION

In this study, we reported a wide range of interannual variability of temperature-standardized litter breakdown rates in small forested streams, through multi-year repeated measurements in three geographically separate but climatically similar regions in temperate Canada. Using the approach of approximating pathway-specific contributions to litter breakdown rates in coarse-mesh bags proposed by Lecerf (2017), fragmentation was found to be consistently a less important breakdown agent than dissolution and microbial decomposition in our study regions. Contrary to our hypotheses, across regions, differences in site-level hydrologic conditions were unrelated to the interannual variability of λ_F. Furthermore, the relationships between hydrologic conditions (mainly in terms of flow flashiness) and the interannual variability of λ_m and k_c were not consistent among study sites. Overall, the temporal CV of λ_F at individual sites did not exceed that of λ_m, except for several TLW sites. While weather-driven differences in hydrologic conditions could account for some spatial variability of litter breakdown rates across study regions, their effects on breakdown rates across years within sites were inconsistent. The effects of site-level hydrologic fluctuations might be modified by unmeasured reach- and patch-scale attributes (e.g., benthic litter quality and quantity), and/or in-channel physical features (e.g., channel morphology, availability of hydraulic refugia), thereby inducing varied responses of hydraulic conditions (Turner and Stewardson 2014) and hence breakdown rates (Colas et al. 2017).
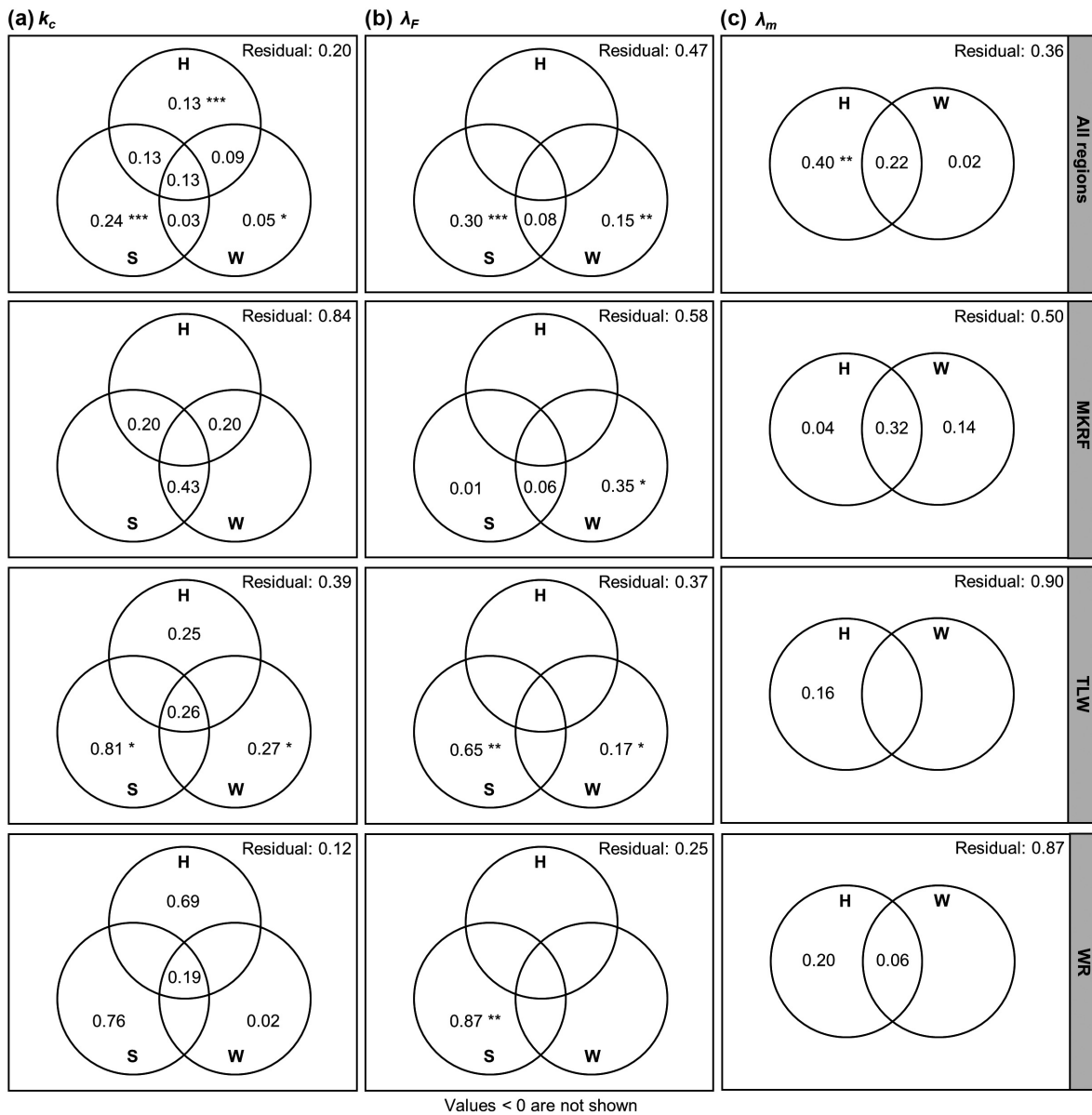
Values < 0 are not shown

Fig. 2. Results of variance partitioning for (a) total breakdown rate (k_c), (b) fragmentation rate (λ_F), and (c) dissolution and microbial decomposition rate (λ_m) across all study regions in British Columbia and Ontario, and in each of these regions, using forward-selected hydrologic (H), shredder-related (S), and/or water chemistry (W) variables as predictors (Table 2). The global redundancy analysis model involving fungal biomass is non-significant for all breakdown metrics, and hence, it is excluded from the variance partitioning analysis. Values displayed are adjusted R^2 as portion of variance explained, including the residual, unexplained variation, and negative values are not shown. The sum of variance explained by the explanatory matrices and residual variance may exceed 1 due to negative explained variances. Significance levels of the unique effects of hydrology, shredders, and water chemistry are indicated with asterisks ($^*P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$).
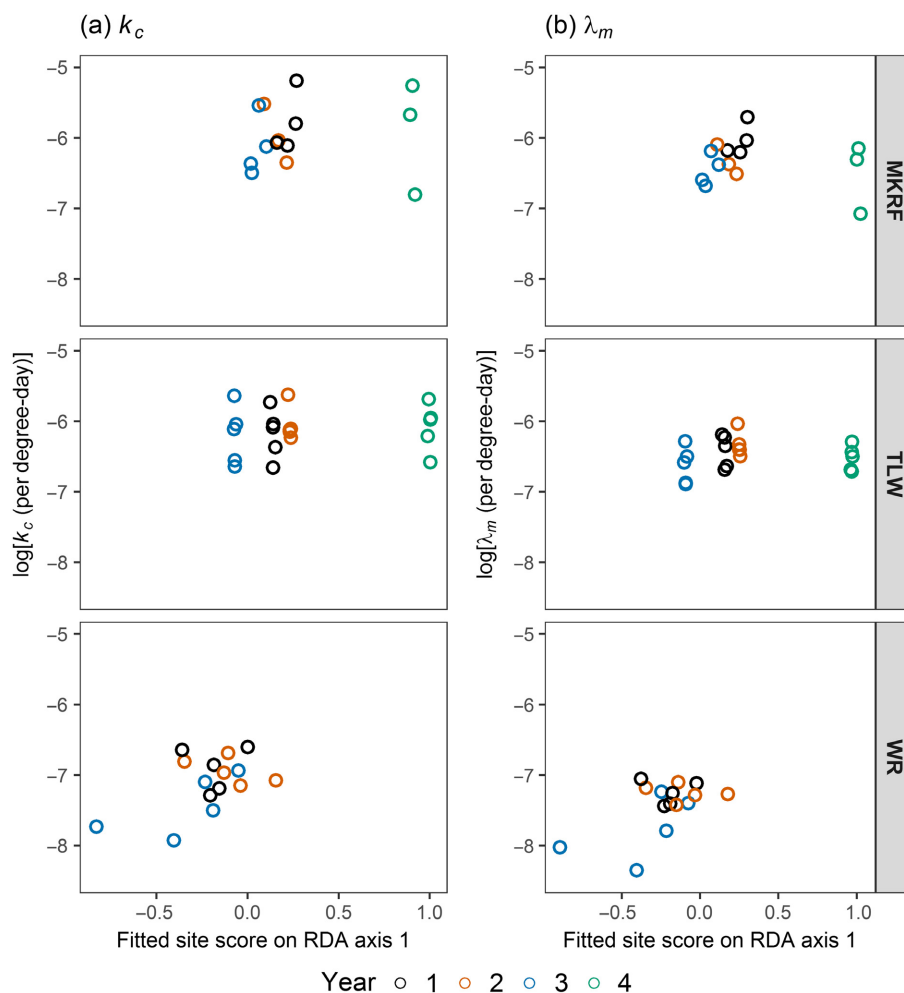
Fig. 3. Relationships between (a) total breakdown rate (k_c), (b) dissolution and microbial decomposition rate (λ_m) of leaf litter (shown on a $\log_{10}$ scale), and the corresponding fitted site scores (i.e., linear combination of selected hydrologic indices) on the first redundancy analysis (RDA) axis, generated from the global RDA across all study regions in British Columbia and Ontario. The study years are color-coded. Note that RDA axis 1 scores are not comparable between (a) and (b).

Sources of variation in litter breakdown rates

Across the study regions, λ_m represented a considerably greater proportion of k_c than λ_F. The range of percent contribution of λ_F to k_c found in this study overlapped with that in 100 temperate European streams (range: <1–70%; reanalyzed by Lecerf 2017), suggesting that the dominating role of dissolution and microbial decomposition in litter breakdown occurs over a broad geographic scale. Therefore, the observed pattern of variability of k_c was more sensitive to that of λ_m. Indeed, the forward-selected hydrologic indices and water chemistry variables

associated with k_c and λ_m were identical, whereas no hydrologic indices were significantly associated with λ_F. The significantly negative effects of TDP on k_c, λ_F, and λ_m should be interpreted with caution in the forested, nutrient-limited study sites, as phosphorus enrichment in these systems typically enhances litter breakdown rates (Ferreira et al. 2015, Rosemond et al. 2015). Considering that the direct effects of temperature on litter breakdown rates were normalized and accounted for by degree-days (Boyero et al. 2011), the rather small interannual differences in water temperature within study regions

Table 5. Results of linear mixed-effects models explaining the relationships between in-stream total breakdown rate (k_c) and dissolution and microbial decomposition rate (λ_m), and the composite hydrologic index, for each study region in British Columbia and Ontario.

Variable	Marginal R^2	Conditional R^2	Estimate	Standard error	df	F	P
k_c							
MKRF	0.02	0.81	0.00058	0.00054	1, 9.10	1.16	0.31
TLW	0.009	0.62	0.00017	0.00026	1, 14.00	0.43	0.52
WR	0.17	0.17	0.00056	0.00034	1, 12.41	2.23	0.16
λ_m							
MKRF	0.02	0.37	-0.00025	0.00038	1, 9.40	0.43	0.53
TLW	5.4×10^{-5}	0.30	-6.7×10^{-6}	0.00017	1, 14.00	0.001	0.97
WR	0.24	0.24	0.00038	0.00018	1, 12.04	3.67	0.08

Notes: MKRF, Malcolm Knapp Research Forest; TLW, Turkey Lakes Watershed; WR, White River Forest. Site was treated as a random effect for each region in regression analyses. Model fit was assessed by the marginal and conditional determination coefficients (R^2) using the rsquared.GLMM function in the MuMIn package (Nakagawa and Schielzeth 2013). The significance of regression relationships was estimated using an approximate F-test based on the Kenward–Roger approach.

(i.e., 0.6–3.7°C) likely had minor contributions to the variation in litter breakdown in our analyses.

Global RDAs and subsequent variance partitioning suggested that the variability of λ_F across sites/regions and years was negligibly related to differences in hydrologic conditions, but rather driven by shredder-related and water chemistry variables. Changes in forward-selected shredder density, density of large-bodied shredders, and TDP affected fragmentation through shredder feeding (and not mechanical abrasion). The overall effects on fragmentation by changing shredder densities in leaf bags across years did not appear to be associated with spate occurrences in the study regions. Some shredder taxa might be able to seek hydraulic refugia (e.g., leaf accumulations, hyporheic zone) for shelter during spates, and/or they could quickly colonize leaf bags post-disturbance (Whiles et al. 1993, Negishi and Richardson 2006) to maintain shredder feeding rates during the incubation period. It could be inferred that the availability of benthic refugia and litter quantity, which could drive the variations in shredder densities and assemblages (Tiegs et al. 2008) and hence litter breakdown, were not strongly influenced by site-level changes in hydrologic conditions.

Hydrologic indices reflecting flashiness during and before leaf bag incubation significantly influenced λ_m. Fungal biomass did not contribute significantly to the variability of λ_m in MKRF and TLW (unmeasured in WR), although previous studies showed strongly positive relationships between fungal biomass and litter breakdown rates (Gessner and Chauvet 1994, Lecerf and Richardson 2010). In our study, microbial decomposition and dissolution was influenced more by the degree of flow variability than by water chemistry. Similarly, in low-order streams in France, human-induced changes in flow quantity, and the intensity and frequency of extreme flow events (and geomorphological parameters) were shown to affect microbial decomposition (k_f) more strongly than water chemistry did (Colas et al. 2017). Hydrologic changes could give rise to the variability of λ_m through numerous potential pathways (unmeasured in this study), for instance, via altered microbial diversity and assemblage structure on litter (Dang et al. 2005, Judd et al. 2006, Zeglin 2015), and primary producers whose priming effects through the release of labile carbon exudates could stimulate bacterial activity (Danger et al. 2013).

Several lines of evidence suggest that variable ecological responses to flood events across watersheds could be modulated by ecological and hydromorphological parameters operating at the patch, site, and watershed scales. These variables can include current velocity, substrate composition, vegetation characteristics, and channel morphology (Tiegs et al. 2009, McMullen and Lytle 2012, Stenroth et al. 2014, Robertson et al. 2015, Colas et al. 2017). These factors might account for much of the unexplained variance of litter breakdown rates in the perennial streams of this study. For instance, site-level hydrologic indices that we examined might not be good surrogates

of hydraulic conditions (or shear stress) within and in the vicinity of leaf bags, as a similar magnitude of hydrologic variation could produce diverse, complex hydraulic responses due to the influences of channel morphology (Turner and Stewardson 2014). Hydraulic stress–discharge relationships are potentially nonlinear and spatially heterogeneous, and are operationally difficult to establish (Kakouei et al. 2017), which could limit the success in generalizing the responses of litter breakdown rates to natural hydrologic variations in perennial streams (Turner and Stewardson 2014). In contrast, hydrologic variability has clearer impacts on litter breakdown rates in drought-prone streams experiencing precipitation-induced flow intermittency (Datry et al. 2011, Dieter et al. 2011, Martínez et al. 2015), and small, perennial streams experiencing experimental flow reduction (Northington and Webster 2017). These studies demonstrated that drastic flow decreases generally slowed litter breakdown due to reduced colonization of shredders; and in the absence of surface flow, dissolution and photodegradation became the dominant mechanisms of breakdown.

Spatio-temporal variability of litter breakdown rates

The temporal variability of k_c was more strongly associated with that of λ_m at individual sites than λ_F. This was probably due to the greater contribution by λ_m to k_c, and similar temporal CV among λ_F and λ_m. In WR, the apparently greater temporal CV of λ_F might be due to the interannual differences in shredder assemblage structure and hence feeding rates. There are limited multi-year studies from which the interannual variability of either k_c or k_f at individual sites could be inferred, and their range of variability resembled that found in the present study. For example, the range of temporal CV of k_c (~26–54%) and k_f (~37–46%) in three forested reference streams in WR during 2002–2007 (Kreutzweiser et al. 2010) was comparable to that of the present study sites within the same region (i.e., ~10–50%; Table 3). Temporal CV of k_c in Satellite Branch, Coweeta Hydrologic Laboratory, USA, was 27% for rhododendron, *Rhododendron maximum* L. (6 yr; 1985–1990), and 28% for red maple, *Acer rubrum* L. (7 yr; 1985–1990, 1992; Webster et al. 1999). However, these previous studies did not explicitly quantify the sources of interannual variability of k_c, unlike the present study.

In all regions, considerable interannual differences in the across-watershed variability of litter breakdown rates were observed. In addition to hydrologic characteristics, stream temperature regime, water chemistry, and benthic litter quality and quantity are important watershed-level controls of litter breakdown via their influences on shredder feeding and microbial activity (Royer and Minshall 2003, Graça et al. 2015). Such pattern of variability could be attributed to temporally varying, climatic factors inducing watershed-specific responses of these controls (other than turbulence), which differed across years (Kreutzweiser et al. 2010).

Bioassessment implications

The selected study sites covered a range of landscape attributes, riparian vegetation characteristics, and hydrologic regimes. They were largely unaffected by recent watershed disturbances such as forest harvesting and fires, which are common in the study regions. Therefore, these sites—with efforts made to control for stream size—could be regarded as a group of objectively and realistically chosen forest streams to best approximate minimally disturbed conditions (Stoddard et al. 2006), which provided baseline (reference) conditions for evaluating the robustness of existing bioassessment benchmarks.

The range of natural variability of k_c was mostly smaller than that of λ_F, particularly in terms of spatial CV across years. Therefore, k_c is a more preferred breakdown metric to use in bioassessment, given its smaller temporal background variation and interference with disturbance effects. The variability of k_c at the regional scale indicative of no impacts suggested by Gessner and Chauvet (2002) was inferred from a study conducted in streams from 1st to 7th order in Sweden, situated in the northern temperate zone (Jonsson et al. 2001). When including only 1st- to 3rd-order streams, the range became 73–127% of the mean. Comparatively, the upper end of the corresponding range determined in the present study was higher (and also year-specific), as shown by the upper end of the inter-site range of k_c (i.e., MKRF: up to 170%; TLW: 163%; WR: 154%; see Table 3). A similar range of natural

variability of k_c was also reported in many European streams (CV: ≈ 50%; see Boyero et al. 2015). At the reach scale, the range of natural variability of k_c (i.e., 75–133% of the mean) proposed by Gessner and Chauvet (2002) encompasses that of most sites in the present study, with some exceptions in WR (range: 46–151%).

The extent of weather-driven variability of k_c obtained in this study could be used to develop site- and region-specific baseline conditions to refine the bioassessment framework based on Gessner and Chauvet (2002), depending on assessment approaches and data availability (Table 6). When pre-disturbance data are available at the site level, using the temporal CV of k_c as baseline conditions will likely have higher sensitivity to detect disturbance impacts, compared to using the spatial CV of other reference sites. This is because the temporal CV of k_c tended to be smaller than the spatial CV. Applying the baseline conditions established in the present study, previous findings of the effects of riparian/upland forest harvesting on stream litter breakdown appear to have a stronger ecological significance (in addition to statistical significance) in the same study regions. For example, the conclusions of the absence of harvesting effects on litter breakdown rates in

impacted sites in MKRF (Yeung et al. 2017) and WR (Kreutzweiser et al. 2010, Musetta-Lambert et al. 2017) are in accordance with these rates falling within the range of region-specific baseline conditions (i.e., spatial CV). Conversely, the presence of such effects in MKRF (Lecerf and Richardson 2010, in a different time frame from Yeung et al. 2017) and WR (Kreutzweiser et al. 2008) corresponds to these rates falling outside the range of baseline conditions. Nevertheless, it should be noted that the upper/lower end of natural variability of k_c in some sites (particularly in WR) approximates the mean effect sizes of other common agents of watershed disturbance, such as nutrient enrichment (Ferreira et al. 2015), and replacement of native forests by plantations and invasive plant species (Ferreira et al. 2016b). Hence, relying on litter breakdown rates as a single indicator of disturbances affecting streams might be problematic, as the possibility of interannual (hydrologic) variation obscuring putative disturbance effects in certain years cannot be excluded.

In cases where considerable hydrologic changes occurred in conjunction with particular disturbances of interest (e.g., fertilizer application), k_c (or λ_m) in impacted sites may be hydrologically adjusted to yield the expected value

Table 6. Recommended baseline conditions for assessing the functional integrity of small streams using total litter breakdown rate (k_c) in the study regions in British Columbia and Ontario.

Assessment approach	Description	Recommended range of natural variability (% of the mean of reference site(s))
1. Before–after (BA)	Sampling before and after disturbance at the same site (also applicable for sampling upstream and downstream of the impacted reach after disturbance)	Best to be site-specific; if long-term dataset is unavailable, MKRF: 60–135%; TLW: 65–145%; and WR: 50–155% (corresponding to temporal CV in this study)
2. Control–impact (CI, i.e., space-for-time substitution)	Sampling (once) after disturbance in (more than one) impacted and reference site(s)	MKRF: 60–170%; TLW: 55–165%; and WR: 55–155% (corresponding to spatial CV in this study) †
3. Before–after-control–impact (BACI), paired BACI (BACIPS), multiple BACI (MBACI), and beyond BACI (sensu Downes et al. 2002)	BACI: sampling once before and once after disturbance in a reference and an impacted site BACIPS: multiple paired samplings before and after disturbance in a reference and an impacted site MBACI: multiple samplings before and after disturbance in multiple reference and impacted sites Beyond BACI: multiple samplings before and after disturbance in multiple reference sites and one impacted site	Not necessary, as detection of impacts based on the significance of BA × CI interaction (for beyond BACI, the interaction between the times of sampling and contrast of impacted and reference sites) already takes into account the range of natural variability (see Underwood, 1992, 1994)

Notes: CV, coefficient of variation; MKRF, Malcolm Knapp Research Forest; TLW, Turkey Lakes Watershed; WR, White River Forest.

† Data from one site (i.e., Mike) in 2017 were excluded, as the inclusion of this site would have lowered the minimum of the range of variability at MKRF to 0.30 of the mean of reference sites.

under the undisturbed hydrologic condition. This is achievable only when robust relationships between k_c and the composite hydrologic index have been established for these sites prior to disturbances. Furthermore, this adjustment will not be applicable when the effects of hydrologic condition on k_c as altered by disturbances are themselves of interest in bioassessment (Chauvet et al. 2016).

The values of k_c/k_f (and λ_F/λ_m) observed in this study varied less within sites (across years) than among sites (Appendix S3: Table S2), and its range in reference sites (MKRF: 1.2–8.6; TLW: 1.1–4.4; WR: 1.3–3.1) would have been considered to reflect no impact (i.e., k_c/k_f : 1.2–1.5) to severely compromised (>2.0) stream functioning according to the criterion suggested by Gessner and Chauvet (2002). This shows that the relative contribution of fragmentation and microbial decomposition and dissolution could be highly inconsistent at least across sites in the study regions. Indeed, variable extent of consistency of k_c/k_f in reference sites across watersheds/regions has been reported in temperate (Tiegs et al. 2009, Hladyz et al. 2010) as well as tropical streams (Boyero et al. 2015). Thus, the classification of stream functional integrity solely based on the absolute values of k_c/k_f, without prior data of the study regions, could yield inaccurate results. It would be a suitable metric only when the values are known to differ significantly among impacted and reference sites (Hladyz et al. 2010).

Our study findings provide a basis for incorporating interannual variability and regional specificity to better operationalize the bioassessment framework using litter breakdown assays for temperate small streams. The apparently weak and inconsistent effects of the temporal variability of hydrologic conditions on litter breakdown rates are likely well accounted for in the recommended range of natural variability, within the gradient of hydrologic conditions encompassed in the study. However, given the relatively short span of study years and increasing occurrences of hydrologically extreme events (e.g., droughts) and changing litterfall timing anticipated under climate change (Creed et al. 2015, Coulthard et al. 2016, Imberger et al. 2016), the recommended baseline conditions for stream bioassessment should not be regarded as stationary, and this baseline may shift over time and necessitate future revisions. This also strengthens the notion of using litter breakdown rates in combination with other structural and functional measures to comprehensively assess stream ecological integrity under anthropogenic disturbances (Gessner and Chauvet 2002, Young et al. 2008, Chauvet et al. 2016).

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