Climate variability affects a vital ecosystem function: Long-term perspective on leaf decomposition in the Ogeechee River

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Abstract: Leaf-litter decomposition in stream ecosystems is an important component of the energy and nutrient cycle, representing a food source for aquatic organisms. As such, this process represents a tool for assessing long-term stream responses to disturbance that are brought about by changes in the assemblage of macroinvertebrates that colonize leaf packs. We used 5 y (2013–2017) of leaf-litter decomposition data at the Ogeechee River, Georgia, USA, following a 3-y drought period (2010–2012) to assess the effects of climatic variability, and the associated macroinvertebrate community, on the decomposition process. We predicted that climate variability, specifically drought and flood disturbances, would have an impact on the decomposition process and that stream temperature, stream discharge, and relative abundance of the shredder functional feeding group would drive these changes. Additionally, we predicted these disturbances would negatively affect macroinvertebrate abundance and richness. This study identified changes in the rate of decomposition in a post-drought year (2013) and the subsequent years that were explained by fluctuations in temperature, discharge, and potentially shredder abundance. Additionally, we detected a shift in species composition after the post-drought year into a more stable period, alluding to a lag effect in species richness. These results illustrate that we can predict an increase in decomposition rates during disturbance events, especially drought, as well as a decrease in both abundance and richness of colonizing macroinvertebrates. These findings underscore the vulnerability of key ecosystem processes to climate-driven disturbances, suggesting that shifts in decomposition dynamics and macroinvertebrate communities during drought may compromise nutrient cycling and biological integrity in freshwater systems. By linking long-term patterns to disturbance regimes, this work informs predictive frameworks for stream management under future climate scenarios and highlights the need for integrative monitoring approaches that capture both functional and biodiversity metrics.

Key words: leaf-litter decomposition, climate change, long-term data, disturbance, macroinvertebrate communities, stream function, shredder functional feeding group, Ogeechee River

Resumen: La descomposición de la hojarasca en ecosistemas fluviales es un componente importante del ciclo energético y de nutrientes, y representa una fuente de alimento para los organismos acuáticos. Por lo tanto, este proceso representa una herramienta para evaluar las respuestas a largo plazo de los arroyos a las perturbaciones provocadas por cambios en el ensamble de macroinvertebrados que colonizan los paquetes de hojas. Utilizamos 5 años (2013–2017) de datos de descomposición de hojarasca en el río Ogeechee, Georgia, EE.UU., tras un período de sequía de 3 años (2010–2012) para evaluar los efectos de la variabilidad climática y la comunidad de macroinvertebrados asociada en el proceso de descomposición. Predijimos que la variabilidad climática, específicamente las perturbaciones por sequías e inundaciones, tendría un impacto en el proceso de descomposición y que la temperatura del arroyo, el caudal y la abundancia relativa del grupo funcional de alimentación de fragmentadores impulsarían estos cambios. Además, predijimos que estas perturbaciones afectarían negativamente la abundancia y la riqueza de macroinvertebrados. Este estudio identificó cambios en la tasa de descomposición en un año posterior a la sequía (2013) y en los años subsecuentes, explicados por fluctuaciones en la temperatura, el caudal y la posible abundancia de fragmentadores. Además, detectamos un cambio en la composición de especies después del año posterior a la sequía hacia un período más estable, lo que sugiere un efecto de retardo en la riqueza de especies. Estos resultados ilustran que podemos predecir un aumento en las tasas de descomposición durante eventos de perturbación, especialmente sequías, así como una disminución tanto en la abundancia como en la riqueza de macroinvertebrados colonizadores. Estos hallazgos subrayan la vulnerabilidad de los procesos ecosistémicos clave ante perturbaciones inducidas por el clima, revelando

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que los cambios en la dinámica de descomposición y en las comunidades de macroinvertebrados durante eventos de sequía pueden comprometer el reciclaje de nutrientes y la integridad biológica de los sistemas de agua dulce. Al vincular patrones a largo plazo con regímenes de perturbación, este trabajo contribuye a marcos predictivos para la gestión de ríos en escenarios climáticos futuros y destaca la necesidad de enfoques de monitoreo integradores que consideren tanto métricas funcionales como de biodiversidad.

INTRODUCTION

The Intergovernmental Panel for Climate Change (IPCC) predicts a rise in temperatures and changes to precipitation patterns for the 21st century (IPCC 2023). In stream ecosystems, disturbances are events whose frequency, intensity, and severity lie outside predictable ranges and consequently negatively affect the ecosystem community and processes (Resh et al. 1988, Lake 2000). In Georgia, USA, climate change is expected to lead to a higher frequency of extreme disturbance events, such as drought and floods (Mulholland et al. 1997), which will lead to alterations in freshwater ecosystem hydrology, communities, and processes (Monroy et al. 2017). Additionally, because of resulting alterations in the water cycle, we can expect a higher proportion of terrestrial C (i.e., as allochthonous inputs) to be transported into inland waters through more intense erosion, deposition, and runoff (Battin et al. 2009). Plant matter represents one of the largest stores of C on the planet, part of which enters streams as allochthonous inputs (Abelho 2001, Boyero et al. 2011). Of these allochthonous inputs, conservative estimates put the amount of C that returns to the atmosphere at ~42 to 44% (Cole et al. 2007, Battin et al. 2008, 2009). Therefore, in the context of climate change, decomposition of allochthonous organic matter in streams will have strong implications for the C flux between the biosphere and atmosphere (Battin et al. 2009, Boyero et al. 2011, Monroy et al. 2017).

Long-term studies reach outside the bounds of traditional funding cycles by being designed in a multiyear context, where collecting data daily, monthly, or yearly allows researchers to account for natural variation in environmental factors (Hobbie et al. 2003). There are a small number of decomposition studies that have been conducted in such a long-term context (see Wallace et al. 1995, Benfield et al. 2001, Kelly et al. 2024). However, most leaf-decomposition experiments in streams encompass relatively short periods (1–2 y; e.g., Ferreira et al. 2006, Bruder et al. 2014, Fernández et al. 2015, Newman et al. 2015). These short-term studies yield insight into the leaf-decomposition process. Still, by design, they cannot consider the consequences of climate variability, where long-term studies can help us understand the effects of climate variability on leaf-litter decomposition dynamics (Kratz et al. 2003).

Several variables that are predicted to change with the changing climate, including freshwater macroinvertebrate communities (Boyero et al. 2011), streamwater temperature (Petersen and Cummins 1974, Boyero et al. 2011), and stream discharge (Mulholland et al. 1997, Anandhi et al. 2018), play a major role in the leaf-decomposition process. For example, decomposition mediated by macroinvertebrates in the shredder functional feeding group (FFG) has a role in transforming coarse particulate organic matter (CPOM) into fine particulate organic matter (FPOM). FPOM is, in turn, consumed by collectors and filter feeders. Boyero et al. (2011) studied the effects of climate change on the leaf-decomposition process by using a latitudinal gradient as a proxy. They found that with rising temperatures, microbially mediated decomposition increased and macroinvertebrate-mediated decomposition decreased. Although the resulting decomposition rate is expected to remain the same because of compensation by microbial activity, microbial CO_2 production is expected to increase while C retention and residence time decrease, lowering C sequestration overall (Boyero et al. 2011). However, many of the factors that may confound these results change with latitude, for example, microbial and aquatic invertebrate community structure (Irons et al. 1994, Ardón and Pringle 2008, Handa et al. 2014).

Stream discharge is also predicted to be affected by climate change, particularly in the river ecosystems of the southeastern United States (Mulholland et al. 1997, Anandhi et al. 2018). Flow rate can play an important role in leaf-litter retention, transport, fragmentation, and changes in aquatic invertebrate colonization, further lowering C residence time (Jones and Smock 1991, Mollá et al. 2017). However, Boyero et al. (2011) found no global trends for discharge and leaf-litter decomposition rates. A faster rate of decomposition in the context of climate change will have consequences for C sequestration, retention, and residence time (Jones and Smock 1991, Wallace and Webster 1996, Monroy et al. 2017). A rise in water temperatures will lead to an increase in metabolism, which in turn will accelerate the leaf-litter decomposition process (Dang et al. 2009, Boyero et al. 2011). Consequently, faster leaf decomposition will increase downstream nutrient transport, which may lead to an increase in spiraling length for the resource, resulting in a shift in secondary production at higher trophic levels, leading to changes in nutrient cycling and the food web (Boyero et al. 2011, Newman et al. 2015). On a global scale, changes in decomposition rates could have feedback implications for the climate, leading to further increases in temperature. Furthermore, assessing leaf-litter decomposition patterns in a long-term context will also show how the community of organisms associated with the process responds to environmental changes (Irons et al. 1994, Buzby and Perry 2000).

In this study, we aimed to determine how differences in environmental conditions influenced decomposition rates and the consumer communities colonizing senescing leaves in a Coastal Plain river. We asked the following question: what are the relative drivers of leaf-litter decomposition in water oak (*Quercus nigra* L.) leaves during autumn along the Ogeechee River in southeastern Georgia, USA? Our primary hypothesis was that temperature, through microbially mediated decomposition, would be the major driver of leaf-litter decomposition. Additionally, we hypothesized that other variables, such as stream discharge and the abundance of shredder macroinvertebrates, would contribute to the decomposition process, but to a lesser extent than temperature. By focusing our study on the autumn period, which is characterized by higher water temperatures and increased leaf inputs, we controlled for the confounding effects of seasonality and macroinvertebrate life history.

METHODS

In autumn 2012, the Ogeechee River, a southeastern Coastal Plain river, was at the end of a 3-y drought period (with yearly discharge of 8 m^3/s, relative to a historical mean of 37 m^3/s at the study site). Beginning that autumn, leaf-decomposition studies that deployed leaf packs were conducted at the Ogeechee River near Rocky Ford, establishing a long-term dataset that we used to examine the impact of climate on leaf-litter decomposition and the associated invertebrate communities in the river. Leaf packs of a predetermined mass were deployed annually for ~2 mo at a single location in the Ogeechee River. Leaf packs were retrieved over time, macroinvertebrates colonizing the packs were removed, and the amount of leaf material remaining was measured to determine mass loss over time. Here we present the results from 5 consecutive years (2013–2017) of leaf decomposition and colonizing macroinvertebrate data at the site. We addressed our research question through analysis of this 5-y dataset, as well as a macroinvertebrate exclusion experiment. The combination of the long-term dataset and exclusion experiment allowed us to evaluate and predict the impacts of climate variability and macroinvertebrate community on leaf-litter decomposition and to test our hypotheses about the relative contributions of stream temperature, discharge, and macroinvertebrates to decomposition rates.

Study site and environmental data

The Ogeechee River originates in the Piedmont region and flows southeasterly through the Coastal Plain of Georgia to the Atlantic Ocean. It has a mean discharge of 37 m^3/s at the study site (United States Geological Survey National Water Information System database; https://waterdata.usgs.gov/nwis/rt, accessed 2019) and remains one of the few blackwaters (tea-colored) rivers that remain unimpounded (no dam) worldwide. It has a watershed that extends 14,300 km^2 and runs for 245 km. Similar to other blackwater rivers, the Ogeechee River has low dissolved O_2 (DO) concentrations (Meyer et al. 1997). However, in contrast with other blackwater systems, it maintains a nearly neutral pH because of inputs from a large limestone spring (Meyer et al. 1997).

We conducted the study at Rocky Ford Landing on the Ogeechee River (lat 32°38′56″N, long 81°50′27″W). A United States Geological Survey gauge (#02202040; Ogeechee River at Rocky Ford Road) has recorded discharge (m^3/s) at the site since 2003 (Fig. 1A). Discharge data were obtained from the United States Geological Survey National Water Information System. This site has a maximum recorded discharge during the autumn season (since 2003) of 55.72 m^3/s. Additionally, a continuous monitoring station has recorded water chemistry parameters (temperature [°C], pH, DO [mg/L], DO_{sat} [% saturation], and specific conductance [SC; μS/cm standardized to 25°C]) from November 2012 to September 2017. In addition, we deployed Hobo® temperature loggers (Onset® Computer Corporation, Bourne, Massachusetts) for more localized temperature estimates. On each retrieval we used a YSI ProPlus multi-parameter water-quality meter (Yellow Springs Instruments, Yellow Springs, Ohio) to measure water-quality parameters (temperature, pH, SC, DO, and DO_{sat}) as a reference with which to compare the continuous monitoring data. In the case of missing data in the continuous dataset, we used our YSI ProPlus-measured values.

We assessed whether environmental variables differed across years and whether they were correlated with each other. We completed all data analyses with R statistical software (version 3.5.2; R Project for Statistical Computing, Vienna, Austria), and we only considered the years 2013 through 2017 during the autumn season. We excluded 2012 and 2018 from analysis because environmental data during these years were not collected at the same frequency as during other study years. The deployment of the monitoring station occurred after the conclusion of the 2012 data collection period; therefore, we lacked environmental data for that period. Environmental data from 2018 were collected during the spring season; thus, environmental conditions were too different and would have required introducing season as a factor for only one data-collection year to the long-term analysis. However, we included these years in the descriptive statistics for comparison. We tested the environmental variables for assumptions of normality using the Shapiro–Wilk test on the residuals and homogeneity of variance using Levene's test. Subsequently, we conducted separate 1-way analysis of variance tests and Tukey's honestly significant difference pairwise tests for temperature, discharge, DO_{sat}, DO, SC, and pH to test for yearly differences in these environmental variables. We then used the *Hmisc* package (Harrell 2019, 2025) to build a Spearman's correlation matrix to assess collinearity among environmental

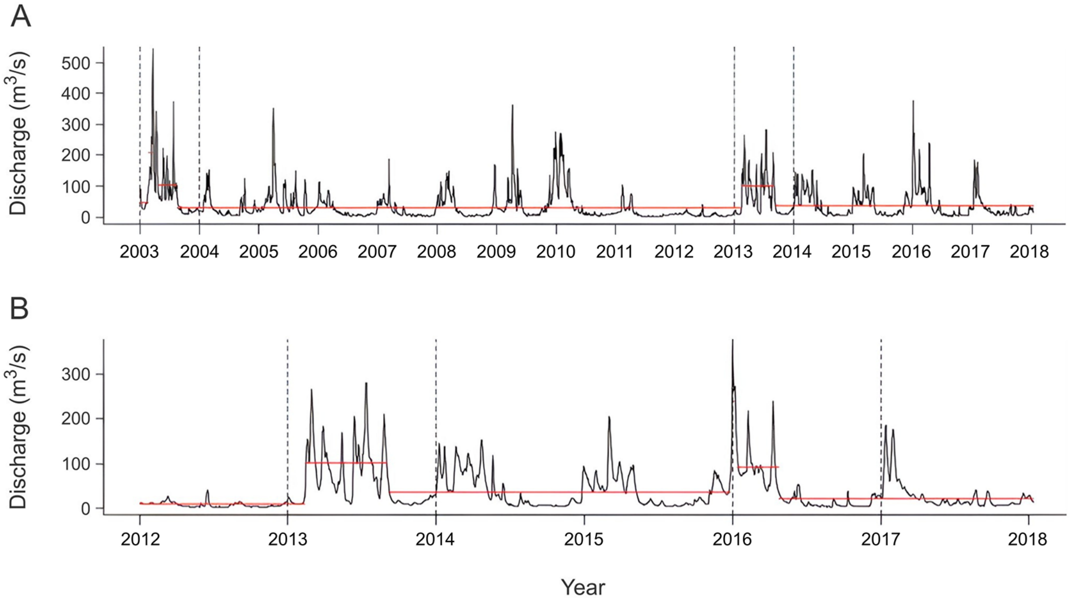

Figure 1. Historical discharge data at Rocky Ford Landing, Ogeechee River, Georgia, USA, at 2 different time scales: the full time period of 2003 to 2018, with inflection points between 2003 and 2004 and between 2013 and 2014 (A), and zoomed in to the time period of 2012 to 2018, with inflection points between 2013 and 2014 and between 2016 and 2017. Solid red lines show mean discharge over time. Dashed black vertical lines mark years in which inflection points occurred (i.e., the slope within the time series changed). Discharge data were obtained from the United States Geological Survey National Water Information System (https://waterdata.usgs.gov/nwis/rt).

variables. We assumed a ρ of ≥0.70 to indicate correlation between pairs of variables, and we dropped 1 variable from each pair of correlated variables from the analysis to account for covariation (Fernández et al. 2015). We used the *changepoint* package (Killick and Eckley 2014, Killick et al. 2024) in R to determine changes in the slope of the discharge dataset over the historical period (2003–2018) as well as at higher temporal resolution over only the study years (2012–2013).

Leaf-litter decomposition fieldwork

The source species of leaf litter for the study was water oak, a species distributed throughout the Coastal Plain from New Jersey to Texas and adapted to wetlands and stream banks (Mehring et al. 2014). Water oak is the dominant species around the Ogeechee River and is responsible for the most litter production. Total annual litter input estimates for the Ogeechee River, based on the main channel and floodplain, are ~843 g m^{-2} y^{-1}, with water oak accounting for ~30% of the inputs (Edwards and Meyer 1987, Meyer et al. 1997).

Every autumn from 2012 to 2017, we deployed 16 expandable mesh bags (~61 cm in length) filled with 15 to 20 g of water oak leaf litter in the Ogeechee River at the Rocky Ford site. We collected senesced leaves annually from various locations around the Georgia Southern University Campus in Statesboro, Georgia, and stored them in a composite mixture. These leaves were dried for at least 2 d at room temperature before being placed in coarse-mesh bags (8-mm openings) to allow macroinvertebrate colonization. We anchored the leaf packs to cinder blocks and deployed them during September and October, coinciding with peak leaf-litter accumulation (Cuffney 1988, Meyer et al. 1997). We also prepared 4 additional leaf packs to account for handling losses, totaling 20 packs/y ($n = 120$).

In autumn 2017 and spring 2018, we conducted a macroinvertebrate exclusion experiment, preparing 16 additional leaf packs (20 including handling losses) with 10 to 15 g of leaf litter in fine-mesh (500-μm openings) bags (20.32 × 30.48 cm) to reduce macroinvertebrate colonization. The absence of macroinvertebrates in fine-mesh-bag samples was visually verified in the laboratory during sample processing. This experiment allowed us to assess the contribution of macroinvertebrates to the decomposition process.

For both the long-term dataset and the exclusion experiment, we retrieved leaf packs biweekly over 4 intervals (56 d total) and stored them in 95% ethanol to halt further decomposition. In the laboratory we used 1-mm and 500-μm sieves to separate leaf packs into CPOM and FPOM. We dried all organic matter at 55°C for at least 48 h and weighed it to determine dry mass. We ground dried leaves into a fine powder and combusted 3 replicates of ~1 g each at 500°C for 1 h to obtain a mean proportion of mineral ash mass. Ash-free dry mass (AFDM) was calculated as the difference between dry mass and ash mass. We used an exponential decay model (Benfield 1996) to calculate leaf mass loss and decomposition rates.

Decomposition calculations

Litter decomposition was quantified as the proportion of litter mass loss (Benfield 1996). Original mass remaining was estimated with Eq. 1:

$$(AFDM_{\mathrm{initial}} - AFDM_{\mathrm{final}})/AFDM_{\mathrm{initial}}, \qquad \text{Eq. 1}$$

after correcting initial litter mass for humidity, ash content, and leaching losses. $AFDM_{\mathrm{initial}}$ was estimated as the mean AFDM of the leaf packs retained to estimate handling losses (Benfield 1996). Litter decomposition daily rates (k d^{-1}) were calculated by linear regression of the AFDM remaining (ln[x] transformed) over time (t, in d) (which assumes a negative exponential decay) with Eq. 2:

$$\ln(\text{fraction AFDM}) = -kt. \qquad \text{Eq. 2}$$

To account for temperature differences among years, we calculated litter decomposition as decay rate (k) by degree days (dd^{-1}) by replacing time with the sum of the accumulated mean daily temperature by the sampling day.

Macroinvertebrates

For coarse-mesh bags, we combined aquatic invertebrates from CPOM and FPOM to determine species composition (Table S1). We identified macroinvertebrates to the lowest feasible taxonomic level (usually genera for insects and order or family for non-insects) using keys from Merritt et al. (2008) and Thorp and Covich (2010). Additionally, because of a lack of resolution in the early years of the study, we grouped Chironomidae taxa (Chironominae and Orthocladinae) together, except for Tanypodinae, a known predatory subfamily. We categorized macroinvertebrates into FFGs and quantified their relative abundance (e.g., mean number of shredders/g of AFDM) for every sampling interval. We used nonparametric Kruskal–Wallis and Mann–Whitney pairwise tests to assess differences in the mean number of shredders/g of AFDM between years because these data did not meet parametric assumptions.

Assessing potential drivers of leaf-litter decomposition

To determine the effects of the exclusion experiment on leaf-litter decomposition, we conducted a 2-way analysis of covariance (ANCOVA) with decay rate (k) by days (d^{-1}) as the response variable, with treatment, season, and the interaction of treatment × season as fixed effects, and degree days as a covariate interacting with the fixed effects. Using degree days as a covariate accounts for changes in temperature over season and time. After meeting the assumption of homogeneity of the slope, we removed the interaction with the covariate from the model. The rest of the assumptions for the ANCOVA were tested and met. To determine whether the leaf-decomposition process varied over the years of study, we conducted a 1-way ANCOVA with k (d^{-1}) as the dependent variable, year as a factor, and degree days as a covariate. The same process was conducted as above, except for having only 1 fixed effect. The 1-way ANCOVA was followed by a Tukey's honestly significant difference post hoc test to determine which years were different from each other.

Using the lmer function from the *lme4* package (Bates et al. 2007, 2015) in R, we fitted several linear mixed-effects models to assess the relationship between decomposition rate by days (k d^{-1}) and temperature, discharge, pH, and shredder abundance. We scaled the data before analysis to normalize the value ranges. The fixed effects were temperature, discharge, pH, shredder abundance, and interactions between them. Year was included as a random effect. We tested the residuals posteriorly for normality with the Shapiro–Wilk test. We carried out model selection with Akaike information criterion (AIC) using a change in AIC (ΔAIC) of <2 as the threshold for selection. Significance tests for each fixed effect were performed automatically by the *lmerTest* package (Kuznetsova et al. 2017).

RESULTS

All environmental variables except temperature differed across years (Table S2). DO_{sat} differed between 2015 and 2017, which had the lowest (74.01%) and highest (91.45%) values, respectively, of all of the years (Table 1). DO exhibited a similar pattern (Table 1). Both pH and SC also differed across years (Table S2), but in contrast with DO, there were differences in these variables between multiple years. For pH, these differences were between years with more basic pH (2013 and 2016; with some values reaching 8.0) and years with more acidic pH (2015 and 2017) (Table 1). SC differed between 2013, the year with the lowest value (101 μS/cm), and 2014 and 2016, which had values ranging from 126 to 130 μS/cm. Additionally, 2015, another low-conductivity year (107.33 μS/cm), differed from 2014 (Table 1).

Discharge also changed over time (Table S2). Specifically, in 2015, mean discharge was >2× higher than in 2014, 2016, and 2017 (Table 1). Examining the historical hydrograph, we found points of change in the slope (i.e., inflection points marking the transition between increasing and decreasing discharge) coinciding with 2003 and 2013 (Fig. 1A). However, when the temporal resolution of the analysis was augmented to consider only the study period, we detected 2 periods of change (i.e., inflection points): in 2013, when discharge changed twice, and at the end of 2015 and into 2016, only to change again after spring 2016 (Fig. 1B).

Several environmental variables were strongly correlated with each other. DO_{sat} and DO were very strongly

Table 1. Environmental data (mean ± SD) by year and season from the Ogeechee River, Georgia, USA. Data from 2012 were excluded from statistical analysis but are included here for comparison. Data from the spring of 2018 are shown for comparison with the year 2017, the years we ran the exclusion experiments. CV is given for all years except 2018. Different superscript letters denote differences between study years as determined by Tukey's honestly significant difference pairwise comparisons with $p < 0.05$. DO = dissolved O_2, SC = specific conductivity. A dash (–) indicates that environmental data were not recorded during the study year.

Year	Season	Temperature (°C)	DO_{sat} (% saturation)	DO (mg/L)	SC (μS/cm)	pH	Discharge (m^3/s)
2012	Autumn	23.01 ± 2.88	–	–	–	–	5.88 ± 3.91
2013	Autumn	18.80 ± 3.31	80.46 ± 5.47^{a}	7.53 ± 1.01^{a}	100.91 ± 4.39^{a}	7.84 ± 0.38^{a}	10.71 ± 2.53^{a}
2014	Autumn	21.06 ± 3.96	81.98 ± 7.06^{a}	7.42 ± 1.26^{a}	130.31 ± 0.66^{b}	7.24 ± 0.24^{b}	6.05 ± 1.27^{b}
2015	Autumn	20.37 ± 2.50	74.01 ± 7.03^{b}	6.71 ± 0.44^{b}	107.33 ± 14.03^{c}	6.60 ± 0.17^{c}	16.10 ± 5.51^{c}
2016	Autumn	21.07 ± 3.72	81.90 ± 6.85^{a}	7.34 ± 1.13^{a}	126.01 ± 13.90^{d}	7.50 ± 0.20^{a}	6.81 ± 3.84^{b}
2017	Autumn	17.13 ± 4.99	91.45 ± 2.57^{c}	9.33 ± 0.81^{c}	110.90 ± 10.50^{c}	6.76 ± 0.47^{c}	7.37 ± 1.75^{b}
2018	Spring	19.74 ± 2.94	73.45 ± 9.45	6.64 ± 1.19	97.45 ± 11.24	7.36 ± 0.43	29.28 ± 3.69
CV		10.07	7.61	12.82	10.90	7.11	45.09

correlated ($\rho = 0.91$; Table 2). Temperature and DO_{sat} were negatively correlated ($\rho = -0.50$), as were temperature and DO ($\rho = -0.73$), with DO decreasing as temperature increased. Discharge was also negatively correlated with DO_{sat} ($\rho = -0.61$) and SC ($\rho = -0.78$). Because of this evident multicollinearity, we dropped DO, DO_{sat}, and SC from further data analyses, keeping temperature, discharge, and pH as inputs in the linear mixed-effects model analysis (see below).

The number of shredders differed between years ($H = 12.74$, $p < 0.005$), and 2013 differed from all other years, with ~10× the number of shredders relative to all other years. Additionally, 2014 differed from 2017, with 2014 having ~6× the number of shredders/g AFDM than 2017 (Table 3).

Leaf-litter decomposition in coarse-mesh and fine-mesh bags

The 2-way ANCOVA showed differences between the coarse-mesh and fine-mesh bags and between autumn and spring seasons during the exclusion experiment in 2017 and 2018 (Table S3). Regardless of the season, the coarse-mesh bags had the highest daily decomposition rates (~12% higher). When controlled for season-related temperature by using dd, all mesh sizes and seasons had similar decomposition rates (Table 3). However, although k (dd^{-1}) appears to be similar, decomposition rates appear to be higher overall during the autumn season. Furthermore, both mesh sizes had higher decomposition rates during the autumn season. Although total dd were higher in spring, dd were higher in autumn during the first 3 intervals. Overall, dd, fine-mesh bags, and spring season decreased decomposition rates. There was no interaction effect between mesh-bag size and season (Table S3).

Leaf-litter decomposition across years

Leaf-litter decomposition varied across years (1-way analysis of variance $F_{5,71} = 68.68$, $p < 0.05$; see Table S3 for results of full 1-way ANCOVA including dd as a covariate). The post hoc test identified differences between the

Table 2. Spearman's correlation matrix for environmental variables. The top half of the table (above the diagonal line) shows the correlation coefficients (ρ). The lower half of the table (below the diagonal line) shows p values. A $\rho > 0.70$ was used as a threshold to remove collinear variables. Dissolved O_2 (% saturation; DO_{sat}) was also removed because of its high correlation with DO (mg/L). Temp = stream temperature, SC = specific conductivity. Data are from the Ogeechee River, Georgia, USA (autumn only, 2013–2017).

	Temp (°C)	DO_{sat} (% sat)	DO (mg/L)	SC (μS/cm)	pH	Discharge (m^3/s)
Temp (°C)		−0.50	−0.73	0.37	0.05	0.00
DO_{sat} (% sat)	0.02		0.91	0.29	0.14	−0.61
DO (mg/L)	<0.001	<0.001		0.00	0.04	−0.41
SC (μS/cm)	0.1	0.2	>0.9		0.22	−0.78
pH	0.8	0.6	0.9	0.4		−0.38
Discharge (m^3/s)	0.9	0.004	0.07	<0.001	0.1	

Table 3. Decomposition rates (k; mean ± SD) in the Ogeechee River, Georgia, USA, by day (d^{-1}) and degree day (dd^{-1}), total dd (calculated by replacing time with the sum of the accumulated mean daily temperature by the sampling day) for the exclusion experiment (top) and comparison of decomposition rates and shredder abundances across years (bottom). The year 2012 (bottom; in italics) was excluded from the analysis but was included here for comparison. CVs shown below the lower half do not include the year 2012. Different superscript letters denote differences in decomposition rates between study years as determined by Tukey's honestly significant difference post hoc tests following 1-way analysis of covariance. AFDM = ash-free dry mass. Dashes (–) denote either unmeasured values (shredders, CV) or values identical to those shown in the adjacent row for the same season–year combination (total dd).

Year	Mesh size	Season	k (d^{-1})	k (dd^{-1})	Total dd (°C)	Shredders (no./g AFDM)
2017	Coarse	Autumn	0.0081 ± 0.0026	0.0004 ± 0.0001	959.55	–
2017	Fine	Autumn	0.0069 ± 0.0025	0.0003 ± 0.0001	–	–
2018	Coarse	Spring	0.0053 ± 0.0014	0.0003 ± 0.0001	1105.25	–
2018	Fine	Spring	0.0050 ± 0.0016	0.0003 ± 0.0001	–	–
CV			22.56	14.46	–	–
2012	*Coarse*	*Autumn*	*0.0135 ± 0.0046*	*0.0005 ± 0.0001*	*1314.59*	*0*
2013	Coarse	Autumn	0.0105 ± 0.0027^{a}	0.0005 ± 0.0001	1074.54	2.89 ± 1.89
2014	Coarse	Autumn	0.0066 ± 0.0020^{b}	0.0003 ± 0.0001	1116.71	0.50 ± 0.24
2015	Coarse	Autumn	0.0076 ± 0.0024^{c}	0.0003 ± 0.0001	1140.67	0.21 ± 0.34
2016	Coarse	Autumn	0.0068 ± 0.0022^{b}	0.0003 ± 0.0001	1180.03	0.34 ± 0.37
2017	Coarse	Autumn	0.0081 ± 0.0026^{c}	0.0004 ± 0.0001	959.55	0.09 ± 0.08
CV			19.72	23.14	–	145.98

year 2013 and every other year. Additionally, 2014 and 2016 were grouped as different from the years 2015 and 2017 (Table 3). Decomposition rates were highest in 2013 and 2017 and lowest in 2014 and 2016. The highest decomposition rate overall (2013) took 285 d to achieve 95% mass loss, almost 2× faster than the lowest decomposition rate (2014), which took 450 d to achieve 95% mass loss.

We found that leaf-litter decomposition rates were higher for coarse-mesh than fine-mesh bags, suggesting there is a relative contribution to the decomposition process by colonizing macroinvertebrates. Therefore, we added shredder abundance to the linear mixed-effects model to explain variation in decomposition rates by degree day. Using our selection criteria of $\Delta AIC < 2$, only 1 model was selected, which included discharge, temperature, and shredder abundance, as well as the interactions among them (Table 4). A test on the residuals did not show any deviations from normality ($W = 0.98$, $p = 0.3$). Temperature and discharge had a positive effect on the leaf-litter decomposition process (Table S4). Temperature was responsible for an estimated effect of 0.008, which suggests that increases in temperature would accelerate the decomposition process considerably. Taking 2014 as an example, an increase of 0.008 k (d^{-1}) would mean that it would take only 204 d to achieve 95% decomposition, 243 d faster than estimated presently. In contrast, discharge had a weak positive relationship, with an estimated coefficient of 0.0001. In the same 2014 example, an increase of 0.0001 k (d^{-1}) would mean reaching 95% decomposition 7 d faster than estimated presently. There was only marginal evidence for an effect of shredder abundance on leaf-litter decomposition rates ($p = 0.07$; Table S4), with an estimated effect of 0.0009. However, we found that 2 of the interactions (temperature × discharge, discharge × shredders), as well as the interaction between all 3 variables (temperature × discharge × shredders) explained variation in decomposition rates (Table S4). Therefore, the main effects of temperature, discharge, and shredder relative abundance must be interpreted in the context of these interactions.

DISCUSSION

The goal of this study was to assess 5 years of leaf-litter decomposition data in the Ogeechee River to determine the relative contributions of stream temperature and discharge, in conjunction with shredder abundance, to decomposition rates. We acknowledge that using leaves collected in multiple years when building leaf packs adds variation in interannual litter characteristics that may have affected our results, and we did not consider this when comparing decomposition among years. However, we do not see this as a major flaw in the study because our goal was to mimic environmental change holistically, and the characteristics of litter inputs, as well as of the stream itself, would naturally vary from year to year. Our exclusion experiment, as expected, indicated that both macroinvertebrates (i.e., shredder abundance) and seasons (spring vs autumn) contributed to differences in decomposition rates. We controlled for seasonal changes in temperature by using degree days;

Table 4. Model selection for the best-fit linear mixed-effects model of the effects of environmental and macroinvertebrate variables on leaf-litter decomposition rates (k d^{-1}), with change in Akaike information criterion (ΔAIC) < 2 as the cutoff for selection. The best-fit model was the only model selected (shown in bold).

Model	ΔAIC	df	Weight	Residuals
Temperature * discharge * shredders + (1∣year)	**0**	**10**	**0.9932**	**−814.8**
Temperature * discharge * shredders * pH + (1∣year)	10.7	18	0.0048	−820.2
Temperature * discharge * pH + (1∣year)	12.5	10	0.0019	−802.3
Temperature * discharge + (1∣year)	23	6	<0.001	−783.9
Temperature + (1∣year)	23.9	4	<0.001	−778.9
Temperature + Discharge + Shredder + pH + (1∣year)	25.6	6	<0.001	−781.3
Temperature * Shredders + (1∣year)	25.7	6	<0.001	−781.2
Temperature * Shredders * pH + (1∣year)	26.7	10	<0.001	−788.1
Discharge * Shredders * pH + (1∣year)	64.7	10	<0.001	−750.2
Discharge * Shredders + (1∣year)	76.2	6	<0.001	−730.6
Discharge * pH + (1∣year)	85.2	6	<0.001	−721.6
Shredders * pH + (1∣year)	87.8	6	<0.001	−719.1
Shredders + (1∣year)	91.1	4	<0.001	−711.7
1 + (1∣year)	99.9	3	<0.001	−700.9
pH + (1∣year)	101.1	4	<0.001	−701.7
Discharge + (1∣year)	101.4	4	<0.001	−701.4

however, we did not consider several other factors, such as the spring flood pulse (Meyer et al. 1997, Benke et al. 2000), which may explain the influence of season in our experiment. The role of macroinvertebrates in leaf decomposition has been well documented, and their contribution to the decomposition process is known to increase with increasing latitude (Wallace and Webster 1996, Graça 2001, Ferreira et al. 2006, Boyero et al. 2011, Handa et al. 2014). The contribution of macroinvertebrates to the decomposition process was evidenced further by the long-term data analysis, through which we found that temperature, discharge, and shredder abundance have positive effects on leaf-litter decomposition rates. Although we found only marginal evidence that shredder abundance explains variation in decomposition rates, we still believe that shredders are ecologically relevant for decomposition processes and important predictors of decomposition rates. Furthermore, we acknowledge that litter in coarse-mesh bags, in which macroinvertebrates are also present, is more exposed to physical abrasion than litter in fine-mesh bags, and this difference will undoubtedly increase with increases in discharge, making the interplay between drivers of decomposition complex.

Higher decomposition rates for the autumn season are well evidenced in the literature (Garden and Davies 1988, Graça et al. 2001), despite lower mean temperatures in autumn compared with summer in this region; therefore, there must be factors other than temperature, such as the macroinvertebrate assemblage and discharge, that drive the decomposition process (Ferreira et al. 2006). In the Ogeechee River, the shredder FFG is mainly composed of the genus *Nectopsyche* in the order Trichoptera (caddisflies) and the genera *Taeniopteryx* and *Pteronarcys* in the order Plecoptera (stoneflies) (Benke and Wallace 1997, Benke et al. 2001). In 2017, plecopterans were the dominant shredder group, with *Taeniopteryx* typically present from mid-September to mid-December (Stewart et al. 1976, Benke et al. 2001) and *Pteronarcys* generally emerging in the spring. However, *Pteronarcys* individuals were not observed in autumn 2017, nor were they detected in either autumn or spring surveys conducted at the same site during 2014 to 2015 (Collins 2017). Additionally, *Taeniopteryx* was absent from the Collins (2017) study, and *Nectopsyche* was found at markedly reduced densities in spring. These patterns suggest that shredder biomass during spring is low overall, potentially limiting invertebrate-mediated decomposition. In the absence of substantial shredder activity, leaf-litter breakdown during the spring may be primarily driven by microbial processes and mechanical fragmentation associated with seasonal discharge. However, the influence of macroinvertebrates on decomposition appears to vary seasonally, with their impact more pronounced during autumn when shredder abundance is higher. This seasonal contrast suggests that, regardless of the differences in degree days and discharge among the seasons, macroinvertebrate assemblages remain a key driver of decomposition dynamics, particularly when their biomass and activity levels are sufficient to exert measurable effects. This result seems consistent with a study by Boyero et al. (2011), who found that warmer temperatures increased microbial decomposition but did not accelerate overall litter breakdown because of reduced detritivore activity, highlighting the critical role of macroinvertebrates in regulating C processing in streams (see Table 3). However, our focus in the exclusion experiment was on whether shredders should be considered when modeling drivers of the long-term leaf-litter decomposition rate, and we did not consider other potential variables that could be differentially driving decomposition during the spring season.

When comparing decomposition rates between years, 2013 had the highest rate, which was likely driven by its relatively higher discharge than most years, excluding 2015 (Table 1), and the highest number of shredders (Table 3). However, this value is similar to those previously reported for water oak (Webster and Benfield 1986, McArthur et al. 1994, Newman et al. 2015). The historical hydrograph (Fig. 1A) shows a point of inflection in the slope in 2013 after a 3-y drought period. If we look at the higher resolution hydrograph for the study years (Fig. 1B), we can also find an inflection point around 2015 to 2016. These inflection points may explain the differences we found between 2014/2016 and 2015/2017. Furthermore, although it was excluded from analysis, 2012 had an even higher decomposition rate, higher temperature, and lower discharge than 2013, and there were also no shredders found during the 2012 sampling season. Thus, 2013 can be considered a post-disturbance year (Resh et al. 1988, Lake 2000, Monroy et al. 2017).

Our model showed the leaf-litter decomposition process to be dependent on temperature, discharge, shedder abundance, and the interactions between these variables. Heat drives microbial metabolism within the system, which in turn drives leaf-litter decomposition. The effect of temperature on decomposition rates has been well documented (e.g., Baldy et al. 1995, Ardón and Pringle 2008, Boyero et al. 2011, Follstad Shah et al. 2017, Amani et al. 2019), but studies have found mixed results for the effect of discharge on leaf-decomposition rates (e.g., Ferreira et al. 2006, Boyero et al. 2011, Mollá et al. 2017). The Ogeechee River, specifically, is a highly heterotrophic and slow-flowing stream where respiration exceeds primary production (Meyer et al. 1997), and we found that in this river higher rates of discharge predicted higher decomposition rates. In contrast, Collins (2017) compared leaf-litter decomposition rates in autumn 2014 and spring 2015 at the same stream and did not find any effect of discharge. At a global scale, Boyero et al. (2011) did not find any latitudinal patterns for decomposition rates related to discharge. However, Mollá et al. (2017) found that the contribution of discharge to decomposition rates varied with ecoregion and that it decreased with stream order. Although we found a discharge effect, the Ogeechee River at Rocky Ford is a mid-order stream with slow-flowing water, so we should expect minimal contribution of discharge to the decomposition process. Likewise, the marginal contribution to decomposition by shredders we found may be explained by lower shredder abundances in lower reaches (Mollá et al. 2017). Indeed, the year with the highest number of shredders also had the highest decomposition rate. However, variation in leaf-litter decomposition is driven by complex relationships and interactions among variables. Potentially, the interaction between discharge and temperature will influence decomposition through depth and temperature stratification (Harms and Fahnestock 1965), which could alter microbial activity and O_2 availability in benthic zones. For example, cooler bottom temperatures under stratified conditions may slow microbial decomposition, even when surface temperatures are elevated. The interaction between discharge and shredders may be explained by scouring effects. For example, high discharge events can dislodge leaf packs and reduce shredder colonization, thereby limiting invertebrate-mediated decomposition. Conversely, moderate discharge may enhance shredder access to leaf litter by redistributing organic matter and increasing oxygenation. The observed 3-way interaction among discharge, temperature, and shredder abundance may reflect seasonal transitions, particularly from autumn to winter, when discharge and shredder presence increase and temperatures decline (Benfield et al. 2001). During this period, decomposition may be driven by a complex interplay: cooler temperatures may suppress microbial activity, but increased shredder biomass could compensate by accelerating physical breakdown of leaf material. Correlated factors not considered in the model may also contribute to all of these interactions (Benfield et al. 2001). Conducting long-term leaf-litter decomposition experiments could reveal the underlying factors responsible for these interactions.

In complex ecological systems, it is necessary to understand the range of natural variability and how this variability affects ecosystem processes (Kratz et al. 2003). Long-term studies in stream ecosystems are essential to achieve understanding of natural variability, especially because of the predicted disturbances associated with climate change (Buzby and Perry 2000, Kratz et al. 2003, Graça and Poquet 2014, Monroy et al. 2017). Here we show how the leaf-litter decomposition process varies across multiple years, within the same season, and in the same system. Including 2012, our 6-y dataset illustrated variability in leaf-litter decomposition rates and environmental variables across the end of a drought period, a transition year (2013), and a more stable period (2014–2017). We recognize that microbial decomposition, which is mediated by temperature, is the most crucial factor in leaf-litter decomposition. Considered in the context of climate change, we can predict fluctuations in the leaf-litter decomposition rate, with an increase during drought periods likely due to a rise in temperature and, subsequently, microbial activity. However, our model suggests that additional factors, such as discharge and shredder abundance, are also important for the decomposition process. Although we found a discharge effect, data on extreme flooding events and their impact on the leaf-litter decomposition process need to be considered. Additionally, we understand the limitations of our model because of not incorporating decomposition estimates across the entire year. Thus, we do not make any assumptions about the decomposition process for the spring season or any generalizations beyond the scope of the experiment.

To our knowledge, this is the 1st study to assess leaf decomposition on a long-term (5-y) basis for a southeastern Coastal Plain river. Our 5-y study indicates that leaf-litter decomposition rates in the Ogeechee River are driven by environmental variability in temperature and discharge, alongside the presence of shredders, highlighting the ecological importance of this functional group despite ongoing biodiversity declines. Rainfall patterns in the region are predicted to become more variable with climate change; therefore, our findings underscore the need to consider these interacting factors, shedding light on how future changes in streamflow and shredder populations may alter critical ecosystem processes. This study underscores the importance of long-term data in capturing the complexity of leaf-litter decomposition. It also suggests that although temperature and discharge are key predictors, the role of shredders, despite their minimal contributions in this study, remains crucial and in need of further study. As climate change introduces more variability in rainfall patterns, our findings highlight the potential for shifts in these environmental factors to substantially affect decomposition processes, emphasizing the need to consider the dynamic interplay between temperature, discharge, and biological communities in future ecosystem management.

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