Received: 12 July 2020 | Revised: 15 April 2021 | Accepted: 16 April 2021

DOI: 10.1111/fwb.13728

ORIGINAL ARTICLE

Freshwater Biology WILEY

Do crayfish affect stream ecosystem response to riparian vegetation removal?

Maura P. Dudley[1] | Kelsey Solomon[1] | Seth Wenger[1] | C. Rhett Jackson[2] | Mary Freeman[3] | Katherine J. Elliott[4] | Chelcy F. Miniat[4] | Catherine M. Pringle[1]

[1]Odum School of Ecology, University of Georgia, University of Georgia, Athens, GA, U.S.A.

[2]Warnell School of Forestry and Natural Resources, University of Georgia, Athens, GA, U.S.A.

[3]Eastern Ecological Science Center, U.S. Geological Survey, Athens, GA, U.S.A.

[4]Coweeta Hydrologic Laboratory, USDA Forest Service, Southern Research Station, Otto, NC, U.S.A.

Correspondence
Maura P. Dudley, 2032 Gunstock Dr, Stone Mountain, GA 30087, U.S.A.
Email: maurapdudley@gmail.com

Present address
Maura P. Dudley, 2032 Gunstock DrStone Mountain, GA 30087, U.S.A.

Funding information
National Science Foundation, Grant/Award Number: DEB-1637522 and DEB-1440485

Abstract

1. Riparian vegetation management alters stream basal resources, but stream ecosystem responses partly depend on top-down interactions with in-stream consumers. Large-bodied omnivores can exert particularly strong influences on stream benthic environments through consumption of food resources and physical disturbance of the benthos. Trophic dynamics studies conducted within the context of reach-scale riparian vegetation manipulations can provide insights into the interactions and relative importance of top-down and bottom-up controls that determine ecosystem response to riparian change.
2. Here, we examine how top-down control by native crayfish omnivores (*Cambarus bartonii*) interacts with abiotic conditions created by reach-scale removal of riparian rhododendron (*Rhododendron maximum*) in the southern Appalachian Mountains of the U.S.A. We conducted 32-day trophic experiments by nesting five pairs of electrified (crayfish excluded) and non-electrified (crayfish access) plots within each of two 300-m stream reaches (one control and one rhododendron-removed) for 1 year pre-removal and 2 years post-removal.
3. Algal growth responded positively to the reduced canopy cover (post-rhododendron removal) only under low flow conditions combined with the absence of top-down control by crayfish. Leaf decomposition rates were reduced by *c.* 40% in the absence of crayfish, but higher inputs of rhododendron leaf litter during the summer following rhododendron removal reduced the effect of crayfish presence on decomposition. Riparian rhododendron removal also significantly increased benthic sediment and fine benthic organic matter, but crayfish exclusion did not affect these stream properties.
4. Potential long-term reductions in crayfish abundance could reduce the top-down effects of crayfish and ultimately lead to higher algal growth and reduced leaf decomposition rates in streams where rhododendron is managed through removal.

KEYWORDS

benthic, macroconsumer, rhododendron, southern Appalachian, trophic dynamics

1 | INTRODUCTION

Ecosystem processes in headwater streams are inextricably connected to the structure and species composition of adjacent riparian vegetation (Sakamaki & Richardson, 2013). Riparian management activities (e.g. complete riparian vegetation removal, alteration of burning regimes, or selective harvesting and/or removal) can alter stream ecosystem processes directly through changes to detrital inputs (e.g. quantity, quality, and timing of leaf litter inputs, Webster et al., 1990) or indirectly by altering physicochemical properties that drive these processes (e.g. disturbance-induced increases in sediment resulting in faster decomposition from abrasion, Paul & Meyer, 1996; Benfield et al., 2001; riparian harvest increases in stream water nitrate concentrations, Knoepp & Clinton, 2008). How streams respond to riparian management may depend on the type of management action, the nature of in-stream species and their relative dominance (e.g. contribution to stream food web linkages and energy flow, Hall et al., 2000; species that structure benthic habitats, Taylor et al., 2006), and how the specific management action affects trophic interactions by stream consumers (Corréa et al., 2019).

Stream macroconsumers that are large-bodied (proportionate to their habitat size) and relatively long-lived often play dominant roles in stream benthic ecosystem processes through consumption of benthic food resources, physical disturbance of the substrate, and nutrient recycling (Corréa et al., 2019; Ho & Dudgeon, 2016; Schofield et al., 2001). Macroconsumers can decrease rates of algal growth and increase leaf litter breakdown through direct consumption (Schofield et al., 2001, 2008; Yang et al., 2020) or indirectly via trophic cascades (Bush et al., 2017; Marshall et al., 2012). Non-consumptive effects may include: (1) lower benthic sediment, lower fine benthic organic matter, lower algal biomass, and higher leaf decay through bioturbation of the substrate (Cooper et al., 2016; Creed & Reed, 2004; Pringle & Blake, 1994; Ravenstel et al., 2004); (2) increased nutrient availability from excretion (Evans-White & Lamberti, 2005; Marshall et al., 2012; Hopper et al., 2020); and (3) changes in the relative competitive advantage of algal species (Creed, 1994; Ravenstel et al., 2004; Schofield et al., 2008). The dominant role of macroconsumers in stream ecosystems means that even small changes in macroconsumer populations (i.e. density or composition) following riparian management can have disproportionately large effects on stream ecosystem processes (Corréa et al., 2019; Schofield et al., 2001). Thus, the total loss of a macroconsumer can substantially alter stream ecosystems (Dangles and Guerold, 2001; Marshall et al., 2012).

While numerous studies have documented the effect of various types of reach- or catchment-scale riparian management actions on abiotic conditions and stream basal food resources, fewer studies have experimentally quantified how top-down control by in-stream consumers potentially modifies stream response to large-scale manipulations (but see Baxter et al., 2004). Furthermore, most trophic dynamics studies in natural and managed stream ecosystems have used a control-impact or space-for-time-substitution (e.g. Hall et al., 2000; Schofield et al., 2008; Wallace et al., 1982) rather than a before-after-control-impact approach. Trophic dynamics studies that simultaneously measure how both top-down and bottom-up controls change and interact over time in response to riparian management can offer powerful insights into the mechanisms by which stream ecosystems respond to disturbance.

In the southern Appalachians (ranging from Alabama to West Virginia; Yarnell, 1998), widespread mortality of American chestnut (*Castanea dentata*) and riparian eastern hemlock (*Tsuga canadensis*) has facilitated the expansion of the evergreen shrub rhododendron (*Rhododendron maximum*) (Dudley et al., 2020; Elliott & Vose, 2012; Ford et al., 2012; Pfennigwerth et al., 2018). This expansion is of concern to managers because rhododendron inhibits the recruitment of hardwood overstory species (Baker & Van Lear, 1998; Cofer et al., 2018; Elliott & Miniat, 2018). Rhododendron removal (by cutting, burning, herbicide, or a combination thereof) has been suggested as a strategy to promote hardwood tree recruitment in rhododendron-dominated riparian zones (Evans et al., 2010; Esen & Zedaker, 2004; Elliott & Miniat, 2018). Spatially distributed monitoring of summer stream temperatures in two reference streams and two rhododendron-removed streams found significant daily maximum temperature increases of 0.9–2.6°C; but these increases were patchy and did not extend downstream of the treatment reaches (Raulerson et al., 2020). These temperature increases indicated increased but spatially variable light penetration to the channel. Another study indicated that reach-scale riparian rhododendron removal alters other stream abiotic conditions, reduces benthic leaf litter standing stock quantity, and increases litter quality, but has minimal effect on algal standing stocks (Dudley, 2018). However, neither study accounts for how rhododendron removal potentially alters in-stream trophic dynamics, nor do they account for how top-down controls by any macroconsumers interact with changes to bottom-up drivers.

Here we examine how bottom-up effects of rhododendron removal interact with top-down control by native crayfish, an important macroconsumer in these streams (Huryn & Wallace, 1987; Schofield et al., 2001), to alter five properties or processes in headwater stream ecosystems in the southern Appalachian Mountains. We predict that rhododendron removal will: (1) increase benthic sediment and fine benthic organic matter (FBOM) accrual via increased sediment input to streams after riparian disturbance, while crayfish presence will decrease sediment and FBOM accrual via bioturbation; (2) accelerate algal growth via higher light and nutrient inputs, while crayfish consumption of algae and removal via bioturbation will limit algal accrual; (3) enhance the rate of leaf decomposition via higher temperatures (more open canopy) and nutrients (riparian disturbance), with crayfish further accelerating decomposition rates through consumption; and finally (4) result in increases in leaf litter quality (i.e. lower carbon:nitrogen ratios) via enhanced stream water nitrogen concentrations and microbial conditioning due to riparian disturbance, with crayfish further increasing leaf litter quality through localised nitrogen release.

2 | METHODS

2.1 | Site description

This study took place in the Nantahala Mountain Range of western North Carolina (NC), U.S.A., within the Blue Ridge Physiographic Province near the southern end of the Appalachian Mountain chain. Soils are deep sandy loams underlain by folded schist and gneiss, representing two soil orders: inceptisols and ultisols. Soil series in both riparian zones include the Cullasaja–Tuckasegee complex along the stream channel and the Edneyville–Chestnut complex on the uplands (Thomas, 1996). Average annual rainfall is 1,900 mm and air temperature is 10.8°C. The study sites drain mixed-deciduous forests with overstory canopies that include oak (*Quercus spp.*), birch (*Betula spp*), American beech (*Fagus grandifolia*), and red maple (*Acer rubrum*).

2.2 | Experimental design

We conducted our experiments within the context of a larger study aimed at quantifying the effects of reach-scale riparian rhododendron removal on headwater streams (Elliott & Miniat, 2018). In the larger study, four perennial headwater streams (second and third order) were selected within the White Oak Creek catchment (WOC, 35°20' N latitude, 83°58' W longitude), located approximately 10 km west of Franklin, NC. Stream study reaches were 300 m long and were selected to be similar with respect to catchment characteristics, rhododendron abundance, and percentage of dead eastern hemlock. For this study, we selected two of these streams (Figure 1, Table 1) in which to conduct our experiments. The *Control* reach (Kit Springs Branch) was not managed in any way for the duration of the experiment. In the *Cut+Burn* rhododendron removal treatment reach (Split White Oak Branch), rhododendron plants and leaf litter were removed by cutting stems from the stream edge to 50 m perpendicular to the stream on both sides, scattering the slashed branches on site (both in the stream and the surrounding riparian area), and burning the reach 1 year post-cut. To minimise rhododendron regrowth, a triclopyr amine herbicide (Garlon 3A®; DOW AgroSciences, U.S.A.) formulation (44.4% Triclopyr Triethylamine Salt) with an aquatic label (mixed to a ratio of 50% herbicide/50% water) was applied to freshly cut stumps and new sprouts within 24 months of the treatment and periodically thereafter as needed. Rhododendron cutting occurred March–May 2015, and the prescribed fire was implemented in March 2016 (Elliott & Miniat, 2018). The prescribed fire was hand-lit across the entire delineated stream reach (3 ha). The firing technique included backfires along the upper ridge and ignitions at 10–25 m intervals depending on slope steepness during weather conditions specified in the USDA Forest Service, Nantahala National Forest, Prescribed Burning Plan (USFS, 2011).

We quantified top-down control by the native crayfish (*Cambarus bartonii*), an important omnivorous macroconsumer in these streams, using 32-day plot-scale macroconsumer exclusion experiments nested within the reach-scale rhododendron manipulations. Experiments were conducted in mid- to late-summer for 3 years: before rhododendron removal (PreYR, 2014), post-cut (CutYR, 2015), and post-burn (BurnYR, 2016). Five pairs of copper wire frames (*c.* 0.125 m^2) were placed in five flat, shallow pools distributed along the 300-m study reach (Figure S1), which were used for all 3 years of the experiment. Pools were selected to be as similar as possible both within a stream and between study streams, and were assumed to be representative of pool habitats available to macroconsumers. One frame in each pair was electrified using a 12V fence charger (Speedrite 1,000 Unigizer) that delivered repeated pulses of electricity (pulse every 1.5–2.5 s) to the frame area. The exclusion technique, modified from Pringle and Blake (1994), has been successfully used in other headwater streams in this region to prevent the entry of macroconsumers (e.g. crayfish and fish, Schofield et al., 2008), reduce the entry of salamanders, and avoid cage artefacts, such as reduced flow and reduced invertebrate drift (Zimmerman & Vondracek, 2006). The electric exclusion technique allows the entry of smaller organisms such as aquatic insects; previous work in similar southern Appalachian streams has shown that electrified treatments did not negatively affect most insect taxa colonising substrate (e.g. chironomids, hydropsychids, baetids), with the exception of heptageniid mayflies, whose abundance was lowered by electrified treatments (Schofield, 2001). The unelectrified frame served as a control, since macroconsumers maintained access to these frames. Paired frames within each pool were placed a minimum of 7 cm apart to ensure that the electrified frame would not affect the unelectrified one, and were anchored at each corner using four similarly sized cobbles. Twice each week, fence charger batteries were replaced to ensure that electrical pulses were maintained throughout the experimental period and wire frames were cleared of any accumulated debris.

2.3 | Associated abiotic variables

Relevant stream characteristics were measured at each frame to assess potential within-pool variability (i.e. conditions between electrified and non-electrified frames within a pool) and between-pool variability (Table S1). We measured water depth at the four corners of each frame using a meter stick. We measured canopy cover over the centre of each frame using 2 (PreYR) or 4 (CutYR and BurnYR) digital photographs (Canon Powershot SD890 IS). For each photograph, we recorded cover type (rhododendron leaf or stem, non-rhododendron leaf or stem, or open) for 200 randomly distributed points using ImageJ software (Schneider et al., 2012). We calculated percent rhododendron canopy cover by dividing the points covered by rhododendron by 200, and percent total canopy cover by dividing the total number of points covered by either plant type by 200. We averaged the percentages for the two or four photographs to produce one estimate per frame. We also recorded the dominant particle size categories underneath each frame and converted our observations to a numerical value-weighted number for three of the

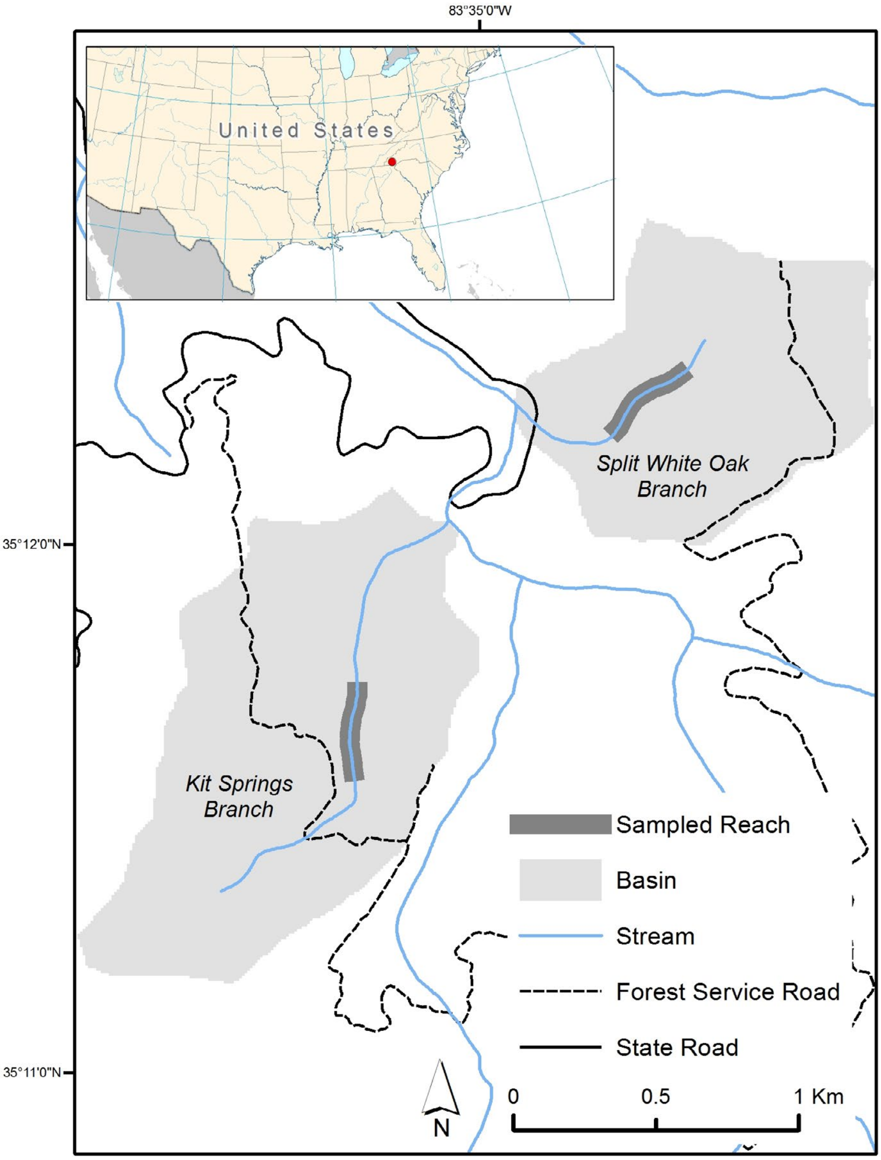

FIGURE 1 Map showing location of two study streams and the 300-m study reaches: (1) Kit Springs Branch (*Control*) and (2) Split White Oak Branch (*Cut+Burn*)

most dominant particle types present within the frame, ranked from silt/clay=1 to bedrock=7. We measured the length and width of each pool for between-pool comparisons.

We measured stage height using an Odyssey water level sensor with a 0.5 m long cable (Dataflow Systems Ltd) at the centre of each treatment reach to assess relative differences in water flow patterns between treatment reaches and between pre-treatment and post-treatment periods. Measurements were taken every 10 min throughout the study period, but gaps due to sensor malfunction were encountered.

Stream water grab samples were collected weekly during the 32-day experiments at the upstream and downstream ends of both reaches. Stream water samples were analysed for nitrate-nitrogen (NO_3-N), ammonium-nitrogen (NH_4-N), and ortho-phosphate (O-PO_4) using standard methods at Coweeta Hydrologic Laboratory (Brown et al., 2018). NO_3-N and O-PO_4 were determined using an Ion Chromatograph (ICS 4000; Thermo Scientific), and NH_4-N was determined using an Astoria 2 Analyzer (Astoria-Pacific).

2.4 | Benthic stream ecosystem properties and processes

We measured benthic sediment, FBOM, and algal accrual using unglazed white ceramic tiles (4.7 × 4.7 cm) attached to the inside of wire frames using binder clips and cable ties (five tiles in each frame; Figure S1). We began tile collection 3–5 days into the experiment and continued approximately weekly for the duration of each 32-day experiment (five tiles total). Collected tiles were carefully transferred to a plastic bag with a small amount of stream water, transported on ice, and processed within 24 hr of collection. Each tile was rinsed with deionised water and scraped with a razor blade to remove associated algae, sediment, detrital organic matter, and macroinvertebrates. Macroinvertebrates were live picked under an illuminated dissecting scope for *c.* 5 min and preserved in 70% ethanol. The remaining slurry was brought to a known volume, stirred continuously, and subsampled. Sub-samples were filtered through two pre-ashed and pre-weighed glass fibre filters (Grade F, 47mm; Sterlitech

TABLE 1 Characteristics of study stream reaches and their catchments

Stream	Treatment	Drainage area (km^2) at bottom of study reach	Elevational range of catchment (m)	Stream order (USGS Hydrography)	Elevational range at reach (m)	Average bankfull channel width (m)	Mean channel slope from LiDAR	% Forest, 2006 NLCD	Mean (± *SE*) rhododendron basal area (m^2 ha^{-1})	Mean (± *SE*) dead hemlock basal area (m^2 ha^{-1})
Kit Springs	*Control*	0.93	1,170–1,627	2	1,255–1,315	4.53	3.52%	99.6	4.61 (0.58)	7.13 (2.08)
Split White Oak	*Cut+Burn*	1.76	1,149–1,451	2	1,195–1,265	3.42	2.53%	100.0	6.02 (0.55)	10.53 (2.63)

Corporation). One filter was dried at 60°C for 1 week, weighed, ashed at 500°C for 4 hr, and reweighed to determine FBOM measured as ash-free dry mass (Steinman & Lamberti, 1996**)**. We also used the ashed-mass from these samples as a measure of inorganic benthic sediment. The second filter was frozen until chlorophyll *a* analysis was performed. Chlorophyll *a* pigments were extracted using the hot ethanol extraction method (Sartory & Grobbelaar, 1984) and analysed using a Turner Design 700 fluorometer (Turner Designs) with an optical configuration optimised for analysis of chlorophyll *a* that minimises phaeophyton interference (Welschmeyer, 1994). Benthic sediment, FBOM, and chlorophyll *a* values were converted to a per-area measure by dividing the measured value by the proportion of the total substrate area sampled. A reference sample (20 ml) was preserved with 7% formalin solution for later algae composition analyses.

We estimated leaf decomposition and leaf litter carbon:nitrogen (C:N) ratio using packs of senesced red maple leaves. We selected red maple for this study because it is a common hardwood species in the riparian areas of the study streams and could potentially experience increased recruitment after the removal of rhododendron (Baker & Van Lear, 1998). Additionally, red maple leaves are relatively fast-decomposing, allowing us to see effects over the experimental period. We added leaf packs (4.0–4.8 g ± 0.15 g) to plastic mesh bags large enough to allow the entry of crayfish (2 × 2 cm mesh size). Bags were closed with binder clips and secured to wire frames using binder clips and cable ties (4 bags per frame). We used an additional 4–10 bags to estimate handling loss and calculate initial nutrient content. We collected one leaf litter bag from each plot beginning on day 10–12 and continuing approximately weekly for the duration of the 32-day experiment (four bags total). Collected leaf litter bags were carefully placed in plastic bags with a small amount of stream water, stored on ice for transport, and processed within 24 hr. Sediment and macroinvertebrates on leaves were rinsed into a 250-μm sieve. Macroinvertebrates were then preserved in 70% ethanol, and leaves were dried to a constant weight at 60°C. Dried and ground sub-samples of leaves were placed in a desiccator for at least 24 hr, weighed, ashed at 500°C for four hours, placed in a desiccator for another 24 hr and reweighed to calculate ash-free dry mass. Leaf litter samples were pre-ground using a coffee grinder, ground to a fine powder using a ball mill (Model 8000D, Spex Sample Prep mixer/mill; Metuchen), and stored in glass vials until analysis. For all C and N analyses, a designated mass of each sample (10–20 mg) was weighed into pre-weighed tin capsules (CE Elantech Inc) and analysed on an elemental analyser (Flash EA1112 NC; Thermo Electron Corporation) using the dynamic flash combustion technique (Brown et al., 2018). Leaf C:N ratios were calculated by dividing total C by total N.

2.5 | Crayfish

During each 32-day experiment, electrified and non-electrified frames were observed approximately twice per week (5 min × 8 observations = 40 min per frame per year) and the presence of crayfish and other macroconsumers was recorded. On the last day of each experiment, baited minnow traps were set for three nights to estimate relative abundance and size of crayfish and other macroconsumers present in the vicinity of nested control and exclusion frames. We categorised captured macroconsumers into major groups (crayfish, salamanders, and fish), measured each individual (head width and body length), and released all on-site.

2.6 | Statistical analysis

Due to several larger storm events that resulted in some sloughing of accrued benthic sediment, FBOM, and chlorophyll *a* during two of the experiments, tile samples were only analysed for final accrual amounts (Day 32). We also used final leaf litter C:N ratios (Day 32) as estimates of leaf litter quality. Only PreYR and CutYR leaf litter samples were included in C:N ratio calculations due to large differences in initial C:N ratio of maple leaves used for the BurnYR. For these four benthic ecosystem response variables, we constructed linear mixed-effects models with stream identity as a random effect, and fixed effects of reach-scale rhododendron manipulation (*Cut+Burn* CutYR and BurnYR), nested plot-scale treatment (crayfish exclusion), and interactions between the two treatment types (CutYRxExclusion and BurnYRxExclusion). We also constructed linear mixed-effects models to individually test the effect of up to 11 predictor variables (benthic sediment, FBOM, chlorophyll *a*, leaf decomposition rate, nitrate, ammonium, phosphate, rhododendron canopy cover, total canopy cover, crayfish abundance, and crayfish total length) on final accrued benthic sediment, FBOM, chlorophyll *a*, and final leaf litter C:N ratio. Predictor variables were centred and standardised by standard deviation (value-mean)/*SD*). These models also included stream identity as a random effect. Models were run using the lme4 package (Bates et al., 2015) in the statistical package R (R Core Team, 2013). We calculated *p*-values using the *pnorm* function in R (Cody, 1993) with $\alpha = 0.05$.

We used hierarchical Bayesian models to calculate leaf decomposition rates while simultaneously testing: (1) reach- and plot-scale treatment effects and their interactions; and (2) the ability of the 11 predictor variables to explain variation in rates among plots. We excluded samples that were missing data from any of the 11 possible predictor variables.

The model for the rhododendron removal and crayfish exclusion treatment effects on leaf decomposition had the form:

$$\mathrm{ln}R_{i,t} = \mathrm{ln}(100) + k_i * \mathrm{days}_{i,t} + \varepsilon_{i,t},$$

$$k_i = b0 + b1 * Cut + Burn\mathrm{CutYR}_i + b2 * Cut + Burn\,\mathrm{Burn}YR_i + b3 * \mathrm{Plot}_i$$
$$b4Cut + Burn\,\mathrm{Cut}YR_i * Plot_1 + b5Cut + Burn\,\mathrm{Burn}YR_i * \mathrm{Plot}_1 + \mu_j\varepsilon_i.$$

where ln*R* is the log of the percent mass remaining in plot *i* and time *t*; *k* is the decay rate for plot *i*; days is the number of days since the initiation of the experiment when the sample was taken; treatment is *Cut+Burn* CutYR$_i$ or *Cut+Burn* BurnYR$_i$, and Plot is crayfish exclusion (treatment and plot coded as binary); *b*0, *b*1, *b*2, *b*3, *b*4, and *b*5 are parameters to be estimated; μ_j is a normally distributed random effect for stream identity(j); and $\varepsilon_{i,t}$ and ε_i are normally distributed error terms.

Predictor variable models had the form:

$$\mathrm{ln}R_{i,t} = \mathrm{ln}(100) + k_i * \mathrm{days}_{i,t} + \varepsilon_{i,t},$$

$$k_i = b0 + b1 * \mathrm{predictor} + \mu_j\varepsilon_i,$$

where ln*R* is the log of the percent mass remaining in plot *i* and time *t*; *k* is the decay rate for plot *i*; days is the number of days since the initiation of the experiment when the sample was taken; predictor is the predictor variable to be tested; *b*0 and *b*1 are parameters to be estimated; μ_j is a normally distributed random effect for stream identity(j); and $\varepsilon_{i,t}$ and ε_i are normally distributed error terms. Models were fit in JAGS (Plummer, 2017) using three packages: rjags (Plummer, 2016); runjags (Denwood, 2016); and coda (Plummer et al., 2006). Model simulations used a burn-in period of 10,000 iterations and posterior distributions were estimated with 20,000 sampling iterations. Parameter estimates were considered to be significant if the 95% confidence interval around the mean did not include 0.

3 | RESULTS

3.1 | Abiotic predictor variables

Normalised water depth time series showed similar patterns between the two stream reaches, but flow differed substantially among the 3 study years (Table 2, Figure S2). Median flow levels in PreYR were moderate and included four medium-sized and several smaller-sized peak flow events. No data were available from the *Control* stream reach in CutYR, but median flow levels in the *Cut+Burn* stream reach were *c*. 3.1× higher than PreYR median flow levels, and two large storm events occurred before the mid-point of the experiment. In contrast, BurnYR was a drier year, with lower median flow levels in both the *Control* and *Cut+Burn* stream reaches (*c*. 15.7% and *c*. 17.9% of PreYR median flow levels respectively) and two relatively large storm events around the middle of the experiment.

Mean NO_3-N concentrations in the *Cut+Burn* reach were *c*. 25%–40% of the *Control* reach throughout the study, and both streams showed comparable inter-annual changes in nitrate: similar concentrations in PreYR and BurnYR, lower in CutYR (Table 2). Within a given year, mean phosphate concentrations were similar between stream reaches, but were *c*. 60%–70% lower in both reaches during CutYR (Table 2). Ammonium concentrations were similar in both reaches in PreYR and BurnYR, but ammonium concentrations at the *Cut+Burn* reach were *c*. 50% lower than in the *Control* reach in CutYR (Table 2).

Rhododendron canopy cover was initially higher in the *Cut*+Burn reach (73.4%) than the *Control* reach (60.4%), but was significantly reduced to zero in the *Cut+Burn* reach post-treatment (Table 2, Table

TABLE 2 Mean (±*SE*) measures of potential abiotic drivers of basal resource response variables measured at the reach scale

	Control						*Cut +Burn*					
	PreYR (2014)		**CutYR (2015)**		**BurnYR (2016)**		**PreYR (2014)**		**CutYR (2015)**		**BurnYR (2016)**	
Variable	**Mean**	***SE***	**Mean**	***SE***	**Mean**	***SE***	**Mean**	***SE***	**Mean**	***SE***	**Mean**	***SE***
Normalised median flow level (cm)	5.67		No Data		0.89		0.39		1.21		0.07	
Normalised max flow level (mm)	20.22		No Data		17.00		6.54		11.46		2.82	
Nitrate (μM)	5.93	(0.35)	4.99	(0.52)	5.41	(0.15)	1.97	(0.15)	1.27	(0.19)	2.27	(0.06)
Ammonium (μM)	0.11	(0.06)	0.14	(0.03)	0.14	(0.02)	0.17	(0.05)	0.07	(0.02)	0.19	(0.03)
Phosphate (μM)	0.26	(0.02)	0.18	(0.03)	0.17	(0.03)	0.26	(0.02)	0.16	(0.03)	0.17	(0.04)
Rhododendron canopy (%)	60.38	(8.54)	43.88	(9.97)	48.26	(9.26)	73.42	(3.25)	0	(0.00)	0	(0.00)
Total canopy (%)	94.12	(0.48)	94.35	(0.66)	93.19	(0.56)	93.10	(0.92)	89.23	(1.08)	87.22	(1.84)

Note: Water flow variables represent median and maximum stage heights measured during the 32-day experimental period, which have been normalised within each stream by dividing the value at each point in time by the median stage height measured across all time points at that stream (June 2014–April 2017). Stream water nutrient concentrations (nitrate, ammonium, phosphate) were averaged for all weekly collections during the 32-day experiment. Rhododendron and total canopy represent the percent coverage of each type based on 200 random points for 2 (PreYR) or 4 (CutYR and BurnYR) digital photographs taken at the centre of each plot and averaged at the reach-scale.

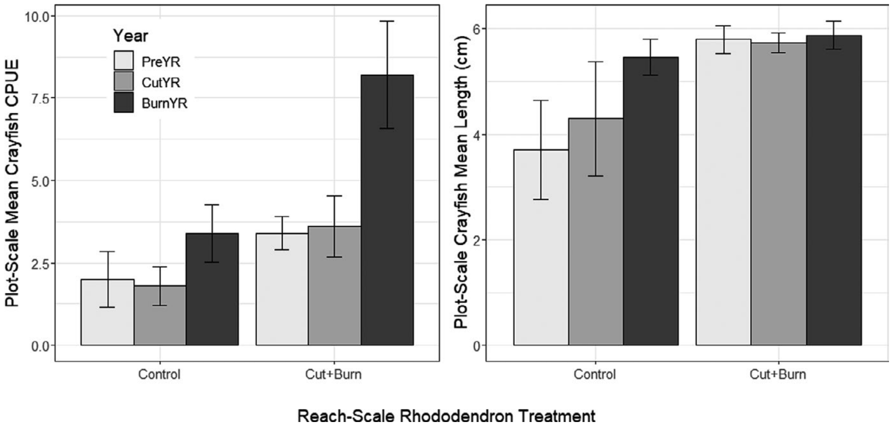

FIGURE 2 Measurements of crayfish in *Control* and *Cut+Burn* stream reaches measured at the end of each 32-day experiment. *Left panel:* mean relative crayfish catch per unit effort (CPUE, + *SE*) at location of nested experimental treatment pairs ($n = 5$). *Right panel:* mean length (± *SE*) of crayfish at location of nested experimental treatment pairs ($n = 5$)

S2, $p < 0.001$ both years). Total canopy cover was initially similar between the two sites (94.1% *Control*, 93.1% *Cut+Burn*), but also significantly declined by 5%–6% for the *Cut+Burn* reach in CutYR ($p = 0.007$) and BurnYR ($p < 0.001$).

3.2 | Crayfish

In the bi-weekly observations of the electrified plots, live crayfish were not observed within exclusion treatments across years and sites, but dead crayfish were recorded in electrified plots at least once during each 32-day experiment (Table S3). One other group of macroconsumers, salamanders, were occasionally observed within the exclusion treatments (often within the experimental leaf litter bags), but at reduced frequency relative to the control plots.

Plot-scale measurements of crayfish (conducted once at the conclusion of each experiment) using minnow traps showed crayfish abundances were generally higher in the *Cut+Burn* stream than the *Control* study reach, and the difference increased after treatment (1.7× higher in PreYR, 2× higher in CutYR, 2.4× higher in BurnYR; Figure 2, left panel). Mean crayfish lengths increased slightly in the *Control* reach over the three years but were higher and more stable in the *Cut+Burn* reach throughout the study (Figure 2, right panel). In addition to crayfish, salamanders (6 total) and one brook trout (*Salvelinus fontinalis*) were captured in plot-scale traps, but they were not abundant enough to make comparisons among streams or years.

3.3 | Stream benthic ecosystem processes

Final benthic sediment and FBOM were not affected by plot-scale crayfish exclusion in any year, but there was a significant reach-scale rhododendron removal effect on both variables during BurnYR when compared with the PreYR (Table 3, Figure 3). In BurnYR, *Cut+Burn* mean benthic sediment was 1.62× higher ($p = 0.032$, Figure S3) and mean FBOM was 5.3× higher ($p = 0.004$, Figure S4) than their

TABLE 3 Model parameter estimates (± *SE* or *SD*) for linear mixed-effects models (benthic sediment, fine benthic organic matter, chlorophyll *a*, and leaf litter C:N ratios) and Bayesian models (leaf decomposition) testing reach-scale rhododendron manipulation treatment effect (by year), plot-scale crayfish exclusion effect, and their interaction

		Benthic sediment		Fine benthic organic matter		Chlorophyll *a*		Leaf decomposition		Leaf litter C:N ratio	
Variable	Name	Estimate	*SE*	Estimate	*SE*	Estimate	*SE*	Estimate	*SD*	Estimate	*SE*
	Intercept	**25.41**	**12.05**	4.23	3.77	0.16	1.02	**3.80**	**1.40**	**62.76**	**8.54**
Reach	*Cut+Burn* CutYR	18.89	19.92	11.97	8.26	0.45	2.24	**−1.39**	**0.45**	−4.97	6.26
	Cut+Burn BurnYR	**46.30**	**21.53**	**26.29**	**9.05**	0.47	2.45	−0.33	0.71	NA	NA
Plot	Exclusion	−2.49	11.86	2.82	5.33	0.05	1.45	**−1.61**	**0.25**	1.89	3.98
Interaction	*Cut+Burn* CutYRx Excl.	27.50	25.98	4.52	11.69	0.51	3.17	**1.11**	**0.53**	10.40	7.97
	Cut+Burn BurnYR x Excl.	−34.28	28.43	−12.90	12.79	**12.62**	**3.47**	−0.02	0.75	NA	NA

Note: Significant effects are indicated in bold ($p < 0.05$).

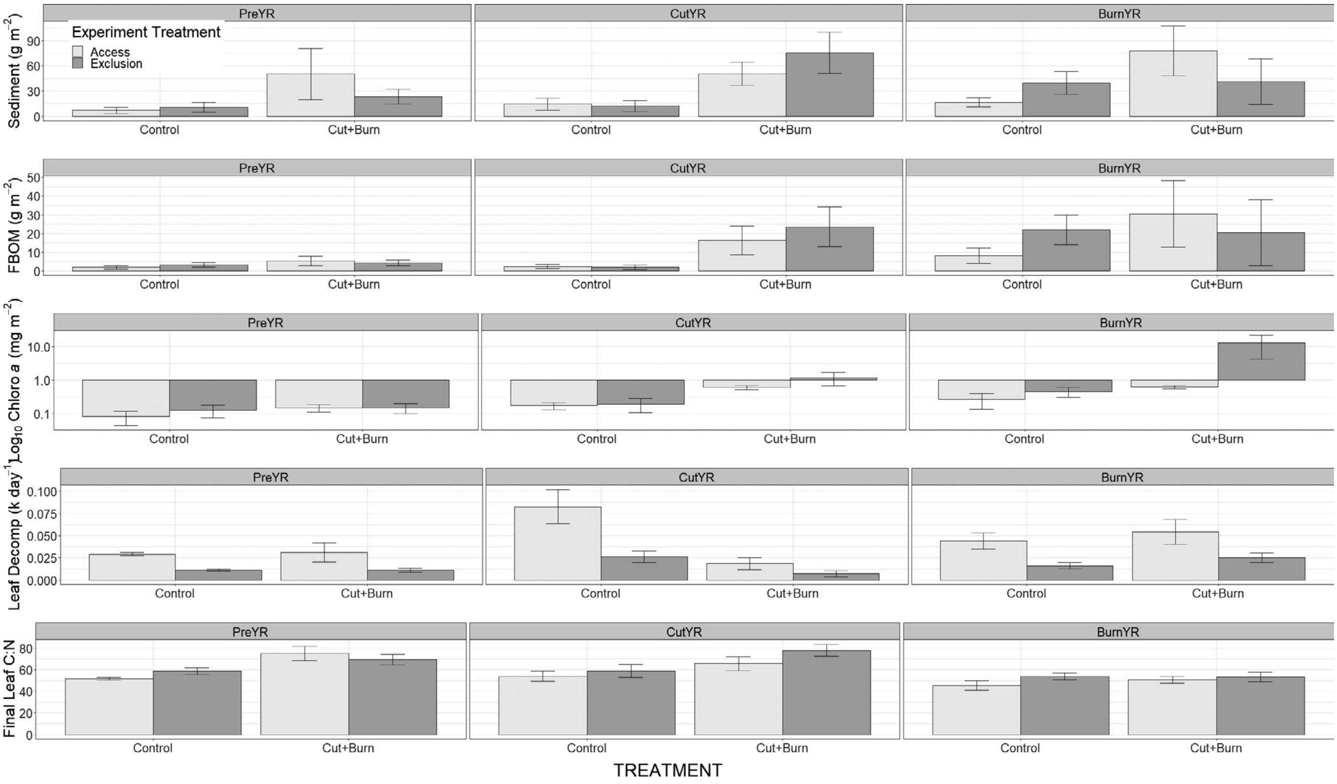

FIGURE 3 Mean (±*SE*) for five stream ecosystem response variables within crayfish access (control; light grey) and exclusion (dark grey) treatments, measured over 32-day experiments nested within whole reach treatments in each of 3 years: PreYR (left column), CutYR (middle column), and BurnYR (right column). FBOM, fine benthic organic matter

respective PreYR values at this stream. Chlorophyll *a* did not show a reach-scale rhododendron removal or plot-scale crayfish exclusion treatment response, but there was a significant interaction effect between plot-scale exclusion and reach-scale removal in BurnYR: mean chlorophyll *a* in the exclusion treatment nested within the *Cut+Burn* study reach was *c.* 21× higher than the access (control) plot in that same year ($p < 0.001$, Table 3, Figure 3, Figure S5). Rhododendron removal, crayfish exclusion, and their interaction all significantly affected leaf litter decomposition rates (Table 3, Figure 3, Figure S6). On average, leaf decomposition rates were 41.1% lower in nested crayfish exclusion treatments relative to access controls. In CutYR, leaf decomposition rates in the *Cut+Burn* study reach were only 60%

of pre-treatment rates in this stream (regardless of crayfish presence or absence). Additionally, there was an interaction between rhododendron removal in CutYR and crayfish exclusion: the effect of macroconsumer exclusion on leaf decomposition rates was reduced by 20% in the summer following rhododendron removal by cutting. Final leaf C:N ratio was not affected by rhododendron removal or crayfish exclusion (Table 3, Figure 3, Figure S7).

Two predictor variables were significantly related to final benthic sediment as a response variable: FBOM (positive, $p < 0.001$) and total canopy (negative, $p = 0.001$; Table 4). Fine benthic organic matter was positively related to benthic sediment ($p < 0.001$), and negatively related to nitrate ($p = 0.03$), phosphate ($p = 0.008$), rhododendron canopy cover ($p = 0.005$), and total canopy cover ($p < 0.001$). No potential driver was significantly related to final chlorophyll *a*. Leaf decomposition rates responded positively and significantly with increasing nitrate and rhododendron canopy cover. Final leaf litter C:N ratio was significantly and negatively related to nitrate concentrations ($p < 0.001$).

4 | DISCUSSION

By combining reach-scale rhododendron removal with nested plot-scale crayfish experiments, we simultaneously quantified bottom-up and top-down effects, and their interaction, on benthic sediment, fine benthic organic matter, chlorophyll *a*, leaf decomposition, and leaf litter C:N ratios in headwater stream ecosystems of the southern Appalachian Mountains. Benthic sediment and FBOM responses were primarily influenced by bottom-up changes resulting from *Cut+Burn* reach-scale rhododendron removal alone. However, management impacts of using this rhododendron removal method on algal growth and leaf decomposition can best be understood by also considering rhododendron's influence on crayfish and subsequent top-down control. Increased light conditions from rhododendron removal had a positive effect on algal growth when flow conditions were low, but algal consumption by crayfish mediated this effect. Nested trophic dynamics experiments enabled us to quantify the negative effect of initially higher rhododendron leaf litter inputs from the *Cut+Burn* method on crayfish contribution to leaf decomposition rates. We did not observe leaf litter quality (C:N ratio) response to riparian or crayfish manipulations in this study.

Our study offers several lines of evidence that omnivorous native crayfish (*Cambarus bartonii*) are the macroconsumers primarily responsible for top-down controls in these streams. Crayfish are abundant and ubiquitous in both study streams; we captured an average of 3.73 crayfish per trap per 3-night trapping period within or adjacent to each plot-scale pool in our nested experiment. Additionally, the electrified exclusion plots appear to be completely inaccessible to crayfish: no live crayfish were ever seen in an electrified treatment during a total of 1,200 min of observations. The influence of fish macroconsumers was likely to be negligible in these streams: only one *S. fontinalis* (brook trout) was captured at the downstream end of the Control reach in a combined 190 trap nights from this study and another reach-scale study (Dudley, 2018; Seth Wenger, personal observation, August 2018). While larval stages of aquatic species of salamanders (*Eurycea wilderae*, *Desmognathus quadramaculatus*, *Desmognathus ocoee*, and *Gyrinophilus porphyriticus*) are also abundant at these sites (Kira McEntire, personal communication, 4

TABLE 4 Model parameter estimates (±*SE* or *SD*) for linear mixed-effects models (benthic sediment, fine benthic organic matter, chlorophyll *a*, and leaf litter C:N ratios) and Bayesian models (leaf decomposition) examining the effect of up to 11 potential predictor variables on five stream ecosystem response variables. FBOM, fine benthic organic matter

	Benthic sediment		Fine benthic organic matter		Chlorophyll *a*		Leaf decomposition		Final leaf litter C:*N* Ratio (PreYR and CutYR)	
Variable	Estimate	*SE*	Estimate	*SE*	Estimate	*SE*	Estimate	*SD*	Estimate	*SE*
Sediment (g/m^2)	NA	NA	**13.47**	**1.59**	−0.91	0.79	−0.12	0.16	0.17	2.05
FBOM (g/m^2)	**28.37**	**3.56**	NA	NA	−0.50	0.75	−0.26	0.16	2.57	1.90
Chlorophyll *a* (mg/m^2)	−6.62	5.04	−1.76	2.37	NA	NA	−0.11	0.15	1.27	1.90
Leaf decomposition rate	−1.65	5.14	−0.88	2.39	0.03	0.74	NA	NA	2.02	1.87
Nitrate (μM)	NA	NA	**−5.03**	**2.33**	2.21	2.59	**0.65**	**0.25**	**−8.13**	**1.77**
Ammonium (μM)	NA	NA	−0.75	2.35	1.02	0.72	0.08	0.15	0.23	1.79
Phosphate (μM)	NA	NA	**−5.84**	**2.21**	−0.91	0.72	0.17	0.14	−0.11	1.78
Rhododendron canopy (%)	−9.38	5.18	**−6.39**	**2.29**	−1.24	0.72	**0.35**	**0.15**	−0.20	1.82
Total canopy (%)	**−16.69**	**5.13**	**−8.63**	**2.12**	−0.09	0.78	0.08	0.20	1.68	1.99
Crayfish abundance	2.96	5.60	2.25	2.53	1.18	0.72	−0.22	0.15	0.28	2.01
Crayfish total length	1.92	5.68	1.28	2.58	1.23	0.72	−0.22	0.15	−0.07	2.08

Note: Significant effects are indicated in bold ($p < 0.05$).

March 2020), electrified exclusion plots were semi-permeable to salamanders. Additionally, whereas we observed higher basal resource abundance in exclusion plots, excluding predators (such as salamanders) would probably lead to an increase in basal resources because of relaxed predation on macroinvertebrate primary consumers and associated behavioural changes on the prey (Ho & Dudgeon, 2016; Nyström et al., 2003; Pringle & Hamazaki, 1998; Trice et al., 2015).

As we predicted, higher benthic sediment and FBOM in streams after rhododendron removal (in BurnYR) may reflect the disturbance to riparian ecosystems caused by this management method. Although higher FBOM can result from in-stream production of fine organic matter (e.g. algal production, leaf litter breakdown, bacterial and fungal growth), our findings that FBOM was positively correlated with benthic sediment, and not correlated with chlorophyll *a*, suggests that it is more likely to be of terrestrial origin. Our finding that the removal of a ubiquitous shrub from riparian areas increases sediment loads is also not unexpected in light of other studies of forest vegetation management; for example, Hatten and others (2018) found that the preservation of riparian buffers in logged catchments reduced sediment loading to streams compared with historic methods (e.g. clearcutting without riparian buffers). In contrast to our prediction and the findings of some other macroconsumer studies (e.g. Pringle & Blake, 1994), we did not observe a reduction in either benthic sediment or fine benthic organic matter due to bioturbation by crayfish. Not all macroconsumers influence sediment and FBOM accumulation on benthic substrates (Ho & Dudgeon, 2016; Corréa et al., 2019), and bioturbation effects probably vary among contexts (Ho & Dudgeon, 2016) and may be overridden by effects of flow (Rice et al., 2016).

Our findings here suggest that algal response to rhododendron removal depends on both bottom-up and top-down factors: algae growth showed a significant treatment response only when light was high (*Cut+Burn* reach post-removal), flow was low (BurnYR), and crayfish were removed (plot-scale exclusion). Algae in forested headwater streams are often limited by multiple variables (e.g. Greenwood & Rosemond, 2005; Hornick et al., 1981; Rosemond, 1993; Townsend et al., 2012). Despite reduced canopy cover in the *Cut+Burn* reach during CutYR, the frequency of high-flow events over the course of the experiment probably limited algal growth via: (1) the direct limiting effect of flow as a disturbance to algal accrual (Biggs & Close, 1989; Grimm & Fisher, 1989); and (2) through its interaction with increased benthic sediment loads following rhododendron removal, increasing disturbance intensity for periphyton and limiting algal accumulation (Biggs et al., 1999). Algal growth may have been further limited in the *Cut+Burn* stream during CutYR by shading from rhododendron slash left in the stream. The presence of slash may also partially explain the lack of crayfish effect in CutYR, as it would have provided ample allochthonous food resources, and therefore delayed the switch to autochthonous food resources (i.e. algae) until the second year. In the BurnYR, when flow was lower and the presence of slash was reduced in the *Cut+Burn* stream, the effect of crayfish on algal biomass (21× higher chlorophyll *a* without crayfish) was an order of magnitude higher than the macroconsumer effect measured in other studies (e.g. 2.3× higher algal biomass with the exclusion of an omnivorous fish macroconsumer, Veach et al., 2018) or the effect of reduced canopy (e.g. *c*. 5× higher chlorophyll *a* accrual rates when canopy was thinned, Collins et al., 2016). Possibly, this large effect of crayfish exclusion may have been partly attributable to reduced densities of grazing, Heptageniid mayflies responding either to the electrified grids (Schofield, 2001) or the absence of bioturbation by crayfish (Creed & Reed, 2004).

As expected, crayfish exclusion was associated with slower litter decomposition (*c*. 40% slower when crayfish were excluded in both study reaches), confirming previous findings (Schofield et al., 2001). However, contrary to our expectation, rhododendron removal lowered rates of litter decomposition but only for CutYR. Thus, this effect is likely to be specific to the *Cut+Burn* management method. Furthermore, the effect of crayfish on accelerated litter decomposition rates was also dampened during the CutYR. Spring implementation of the rhododendron removal treatment in CutYR resulted innumerous cut rhododendron branches and their associated leaves being left as slash in the stream, and over the next few months contributed to higher summer leaf litter standing stocks at the reach-scale (Dudley, 2018). In the context of higher surrounding leaf litter, leaf decomposition in the nested experimental plots may have been affected in several ways. Microbes colonising a larger number of benthic leaves may have increased competition for streamwater ammonium (Gibson & O'Reilly, 2012), supported by the lower ammonium concentrations observed in CutYR. Lower ammonium levels may have limited fungal and bacterial colonisation on experimental leaf litter in both the crayfish exclusion and crayfish access (control) plots of the nested experiments, potentially explaining the general trend in lower leaf decomposition rates at the *Cut+Burn* treatment reach in this particular year (Gulis & Suberkropp, 2003; Tant et al., 2015). Higher ambient litter may explain the reduced crayfish effect on decomposition rates observed in the treatment stream in CutYR. In other studies where experimental leaf packs represent a significant proportion of available leaf litter in a reach (e.g. summer when autumn leaves are mostly decayed, Schofield et al., 2001, or after a flood has removed other leaf resources, Paul & Meyer, 1996), experiments can serve as *resource islands* that attract consumers and lead to higher decomposition rates. Leaves in the experimental plots in the *Cut+Burn* stream were likely to be resource islands when leaf litter in the surrounding channel was naturally low (i.e. PreYR and BurnYR), but not in CutYR when rhododendron slash was abundant.

In contrast to our fourth prediction that leaf litter C:N ratio would decrease in response to reach-scale rhododendron removal and plot-scale crayfish access, we did not observe a significant change. While the final leaf litter C:N ratio was significantly and negatively related to water nitrate concentration, ambient water concentrations of both nitrate and ammonium did not increase in response to rhododendron removal, but decreased (ammonium only) in the first year post-treatment. Thus, lower nutrient availability probably limited the potential for microbial conditioning of experimental leaf litter and subsequent reductions in C:N ratio (Manning et al., 2016). Additionally, localised exclusion of crayfish did not affect the nutrient content of experimental leaf litter as previous studies have documented with other macroconsumer species (e.g. Small et al., 2011), indicating a small effect of crayfish compared to other processes affecting leaf litter C:N ratios.

4.1 | Implications of findings

Our results show that riparian ecosystem management can interact with in-stream trophic dynamics to alter headwater stream ecosystem response to riparian changes. A limitation of our study is that we monitored only two streams, and so we cannot rule out the possibility that our findings could be idiosyncratic to these particular locations. Large-scale experiments, such as the rhododendron removal in this study, often prohibit replication. It could also be beneficial to examine the influence of macroconsumers on benthic ecosystem properties and processes in different seasons when quantity and quality of basal resources and temperatures differ (Veach et al., 2018). Nonetheless, our finding that crayfish can exert a strong influence on algal and detrital resources during summer, thereby mediating effects of riparian manipulation, appears reasonable given crayfish omnivory and abundance in low-order southern Appalachian streams. Our experiments also show that observations of static ecosystem attributes alone, such as algal standing stock, may be insufficient for understanding how any riparian manipulation influences headwater streams. In this case, algal consumption by crayfish masked the response of algal growth to the removal of rhododendron. This finding is noteworthy because algae is a high-quality resource in stream ecosystems, and even small increases can shift the balance of stream energy derived from algal versus detrital resources (Collins et al., 2016).

This and other studies on consumer response to riparian management (e.g. Corréa et al., 2019; Kaylor & Warren, 2017) demonstrate the potential for consumers to respond differently depending on the type and intensity of the riparian management action (e.g. subcanopy shrub removal, timber harvests, buffer zone widths) in the short-term versus long-term. Our results combined with findings from other studies on rhododendron removal (Dudley, 2018), and those that document the dependence of crayfish on rhododendron leaf litter (Schofield et al., 2001), suggest that rhododendron removal may lead to long-term reduction in crayfish abundance, with cascading, long-term effects on algal and detrital ecosystem processes.

ACKNOWLEDGEMENTS

This study was funded by the Coweeta Long Term Ecological Research Program, which was funded by National Science Foundation grants DEB-1637522, DEB-1440485, and by the Coweeta Hydrologic Laboratory, Southern Research Station, USDA Forest Service. Author contributions to this manuscript are conceptualisation (M.P.D., C.R.J., K.J.E., C.F.M., C.M.P.), methodology (M.P.D., S.W., M.F., C.M.P.), formal analysis (M.P.D., S.W., M.F.), investigation (M.P.D., K.S., S.W., C.R.J., K.J.E., C.F.M., C.M.P.), resources (C.R.J., K.J.E., C.F.M., C.M.P.), writing—original manuscript (M.P.D.), writing—review and editing (K.S., S.W., C.R.J., M.F., K.J.E., C.F.M., C.M.P.), visualisation (M.P.D., S.W., M.F.), supervision (C.R.J., K.J.E., C.F.M., C.M.P), project administration (M.P.D., K.S., C.R.J., K.J.E., C.F.M., C.M.P.), and funding acquisition (C.R.J., K.J.E., C.F.M., C.M.P.). Patsy Clinton assisted with site reconnaissance and orienting the team to the study area. Nantahala Ranger District staff, Nantahala National Forest, USDA Forest Service executed the treatments. Jason Love, Joel Scott, and Katie Bower provided logistical support. Cindi Brown, Carol Harper, and Sheila Gregory analysed stream and litter chemistry. Jon Skaggs assisted in making the map. The authors would also like to thank the many undergraduate students, graduate students, and technicians that assisted with the collection and processing of samples used in this study.

DATA AVAILABILITY STATEMENT

Data used in this study are available from the authors upon reasonable request.

ORCID

Maura P. Dudley https://orcid.org/0000-0001-9574-8844

REFERENCES

Baker, T. T., & Van Lear, D. H. (1998). Relations between density of rhododendron thickets and diversity of riparian forests. *Forest Ecology and Management*, *109*, 21–32. https://doi.org/10.1016/S0378-1127(98)00259-X

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1), 1–48.

Baxter, C. V., Fausch, K. D., Murakami, M., & Chapman, P. L. (2004). Fish invasion restructures stream and forest food webs by interrupting reciprocal prey subsidies. *Ecology*, *85*, 2656–2663. https://doi.org/10.1890/04-138

Benfield, E. F., Webster, J. R., Tank, J. L., & Hutchens, J. J. (2001). Long-term patterns in leaf breakdown in streams in response to watershed logging. *International Review of Hydrobiology*, *86*, 467–474. https://doi.org/10.1002/1522-2632(200107)86:4/5<467:AID-IROH467>3.0.CO;2-1

Biggs, B. J., & Close, M. E. (1989). Periphyton biomass dynamics in gravel bed rivers: The relative effects of flows and nutrients. *Freshwater Biology*, *22*, 209–231. https://doi.org/10.1111/j.1365-2427.1989.tb01096.x

Biggs, B. J., Smith, R. A., & Duncan, M. J. (1999). Velocity and sediment disturbance of periphyton in headwater streams: Biomass and metabolism. *Journal of the North American Benthological Society*, *18*, 222–241.

Brown, C., Harper, C., & Gregory, S. (2018). *Procedures for chemical analysis*. Coweeta Hydrologic Laboratory.

Bush, B. M., Hutchens, J. J., Gulis, V., & Godwin, K. S. (2017). Impact of macroconsumers on leaf breakdown and detritivores in wetlands on a southeastern US coastal plain floodplain during drought. *Wetlands*, *37*, 1169–1179. https://doi.org/10.1007/s13157-017-0949-6

Cody, W. D. (1993). Algorithm 715: SPECFUN – a portable FORTRAN package of special function routines and test drivers. *ACM Transactions on Mathematical Software*, *19*, 22–32. https://doi.org/10.1145/151271.151273

Cofer, T. M., Elliott, K. J., Bush, J. K., & Miniat, C. F. (2018). *Rhododendron maximum* impedes seed bank dynamics following eastern hemlock loss in riparian forests. *Ecosphere*, *9*(4), e02204. https://doi.org/10.1002/ecs2.2204

Collins, S. M., Sparks, J. P., Thomas, S. A., Wheatley, S. A., & Flecker, A. S. (2016). Increased light availability reduces the importance of bacterial carbon in headwater stream food webs. *Ecosystems*, *19*, 396–410. https://doi.org/10.1007/s10021-015-9940-3

Cooper, R. J., Outram, F. N., & Hiscock, K. M. (2016). Diel turbidity cycles in a headwater stream: Evidence of nocturnal bioturbation? *Journal of Soils and Sediments*, *16*, 1815–1824. https://doi.org/10.1007/s11368-016-1372-y

Corréa, E. C., de Oliveira Roque, F., Utz, R. M., de Sousa Correa, J., de Souza, F. L., & Covich, A. P. (2019). Effects of macroconsumers on benthic communities: Rapid increases in dry-season accrual of calcium in a tropical karst stream. *PLoS One*, *13*(12), e0209102. https://doi.org/10.1371/joural.pone.0209102

Creed, R. P. Jr (1994). Direct and indirect effects of crayfish grazing in a stream community. *Ecology*, *75*, 2091–2103. https://doi.org/10.2307/1941613

Creed, R. P. Jr, & Reed, J. M. (2004). Ecosystem engineering by crayfish in a headwater stream community. *Journal of the North American Benthological Society*, *23*, 224–236.

Dangles, O., & Guérold, F. (2001). Linking shredders and leaf litter processing: Insights from an acidic stream study. *International Review of Hydrobiology*, *86*, 395–406. https://doi.org/10.1002/1522-2632(200107)86:4/5<395:AID-IROH395>3.0.CO;2-1

Denwood, M. J. (2016). runjags: An R package providing interface utilities, model templates, parallel computing methods and additional distributions for MCMC models in JAGS. *Journal of Statistical Software*, *71*, 1–25.

Dudley, M. P. (2018). *Assessing the importance of a dominant understory shrub, Rhododendron maximum, to riparian forest and headwater stream ecosystems of the southern Appalachian Mountains*. PhD Thesis, University of Georgia.

Dudley, M. P., Freeman, M., Wenger, S., Jackson, C. R., & Pringle, C. M. (2020). Rethinking foundation species in a changing world: The case for *Rhododendron maximum* as an *emerging* foundation species in shifting ecosystems of the southern Appalachians. *Forest Ecology and Management*, *472*(2020), 118240.

Elliott, K. J., & Miniat, C. F. (2018). Herbaceous-layer diversity and tree seedling recruitment are enhanced following *Rhododendron maximum* shrub removal. *Forest Ecology and Management*, *430*, 403–412. https://doi.org/10.1016/j.foreco.2018.08.016

Elliott, K. J., & Vose, J. M. (2012). Age and distribution of an evergreen clonal shrub in the Coweeta Basin: *Rhododendron maximum* L. *Journal of the Torrey Botanical Society*, *139*, 149–166. https://doi.org/10.3159/TORREY-D-11-00076.1

Esen, D., & Zedaker, S. M. (2004). Control of rhododendron *(Rhododendron ponticum* and *R. flavum)* in the eastern beech *(Fagus orientalis*) forests of Turkey. *New Forests*, *27*, 69–79. https://doi.org/10.1023/A:1025072105849

Evans, D. M., Amust, W. M., Dolloff, C. A., Templeton, B. S., & Peterson, J. A. (2010). Eastern hemlock decline in riparian areas from Maine to Alabama. *Northern Journal of Applied Forestry*, *28*, 97–104.

Evans-White, M. A., & Lamberti, G. A. (2005). Grazer species effects on epilithon nutrient composition. *Freshwater Biology*, *50*, 1853–1863. https://doi.org/10.1111/j.1365-2427.2005.01452.x

Ford, C. R., Elliott, K. J., Clinton, B. D., Kloeppel, B. D., & Vose, J. M. (2012). Forest dynamics following eastern hemlock mortality in the southern Appalachians. *Oikos*, *121*, 523–536. https://doi.org/10.1111/j.1600-0706.2011.19622.x

Gibson, C. A., & O'Reilly, C. M. (2012). Organic matter stoichiometry influences nitrogen and phosphorus uptake in a headwater stream. *Freshwater Science*, *31*, 395–407. https://doi.org/10.1899/11-033.1

Greenwood, J. L., & Rosemond, A. D. (2005). Periphyton response to long-term nutrient enrichment in a shaded headwater stream. *Canadian Journal of Fisheries and Aquatic Sciences*, *62*, 2033–2045. https://doi.org/10.1139/f05-117

Grimm, N. B., & Fisher, S. G. (1989). Stability of periphyton and macroinvertebrates to disturbance by flash floods in a desert stream. *Journal of the North American Benthological Society*, *8*, 293–307. https://doi.org/10.2307/1467493

Gulis, V., & Suberkropp, K. (2003). Leaf litter decomposition and microbial activity in nutrient-enriched and unaltered reaches of a headwater stream. *Freshwater Biology*, *48*(1), 123–134. https://doi.org/10.1046/j.1365-2427.2003.00985.x

Hall, R. O., Wallace, J. B., & Eggert, S. L. (2000). Organic matter flow in stream food webs with reduced detrital resource base. *Ecology*, *81*, 3445–3463.

Hatten, J. A., Segura, C., Bladon, K. D., Hale, V. C., Ice, G. G., & Stednick, J. D. (2018). Effects of contemporary forest harvesting on suspended sediment in the Oregon Coast Range: Alsea Watershed Study revisited. *Forest Ecology and Management*, *408*, 238–248.

Ho, B. S. K., & Dudgeon, D. (2016). Are high densities of fishes and shrimp associated with top-down control of tropical benthic communities? A test in three Hong Kong streams. *Freshwater Biology*, *61*, 57–68. https://doi.org/10.1111/fwb.12678

Hopper, G. W., Gido, K. B., Pennock, C. A., Hedden, S. C., Guinnip, J. P., Fisher, M. A., … Bruckerhoff, L. A. (2020). Biomass loss and change in species dominance shift stream community excretion stoichiometry during severe drought. *Freshwater Biology*, *65*, 403–416. https://doi.org/10.1111/fwb.13433

Hornick, L. E., Webster, J. R., & Benfield, E. F. (1981). Periphyton production in an Appalachian mountain trout stream. *The American Midland Naturalist*, *106*, 22–36. https://doi.org/10.2307/2425132

Huryn, A. D., & Wallace, J. B. (1987). Production and litter processing by crayfish in an Appalachian mountain stream. *Freshwater Biology*, *18*, 277–286. https://doi.org/10.1111/j.1365-2427.1987.tb01314.x

Kaylor, M. J., & Warren, D. R. (2017). Canopy closure after four decades of postlogging riparian forest regeneration reduces cutthroat trout biomass in headwater streams through bottom-up pathways. *Canadian Journal of Fisheries and Aquatic Sciences*, *75*, 513–524.

Knoepp, J. D., & Clinton, B. D. (2008). Riparian zones in southern Appalachian headwater catchments: Carbon and nitrogen responses to forest cutting. *Forest Ecology and Management*, *258*, 2282–2293. https://doi.org/10.1016/j.foreco.2009.04.006

Manning, D. W. P., Rosemond, A. D., Gulis, V., Benstead, J. P., Kominoski, J. S., & Maerz, J. C. (2016). Convergence of detrital stoichiometry predicts thresholds of nutrient-stimulated breakdown in streams. *Ecological Applications*, *26*, 1745–1757. https://doi.org/10.1890/15-1217.1

Marshall, M. C., Binderup, A. J., Zandonà, E., Goutte, S., Bassar, R. D., El-Sabaawi, R. W., … Pringle, C. M. (2012). Effects of consumer interactions on benthic resources and ecosystem processes in a neotropical stream. *PLoS One*, *7*, e45230. https://doi.org/10.1371/journal.pone.0045230

Nyström, P., McIntosh, A. R., & Winterbourn, M. J. (2003). Top-down and bottom-up processes in grassland and forest streams. *Oecologia*, *136*, 596–608.

Paul, M. J., & Meyer, J. L. (1996). Fungal biomass of 3 leaf litter species during decay in an Appalachian stream. *Journal of the North American Benthological Society*, *15*, 421–432. https://doi.org/10.2307/1467796

Pfennigwerth, A. A., Van Nuland, M. E., Bailey, J. K., & Schweitzer, J. A. (2018). Plant-soil feedbacks mediate shrub expansion in declining forests, but only in the right light. *Journal of Ecology*, *106*, 179–194. https://doi.org/10.1111/1365-2745.12833

Plummer, M. (2016). *rjags: Bayesian Graphical Models using MCMC. R package version 4-6*. Retrieved from http://CRAN.R-project.org/package=rjags

Plummer, M. (2017). *JAGS Version 4.3.0 User Manual*.

Plummer, M., Best, N., Cowles, K., & Vines, K. (2006). CODA: Convergence diagnosis and output analysis for MCMC. *R News*, *6*, 7–11.

Pringle, C. M., & Blake, G. A. (1994). Quantitative effects of atyid shrimp (Decapoda: Atyidae) on the depositional environment in a tropical stream: Use of electricity for experimental exclusion. *Canadian Journal of Fisheries and Aquatic Science*, *51*, 1443–1450. https://doi.org/10.1139/f94-144

Pringle, C. M., & Hamazaki, T. (1998). The role of omnivory in a neotropical stream: Separating diurnal and nocturnal effects. *Ecology*, *79*, 269–280.

R Core Team. (2013). *R: A language and environment for computing*. R Foundation for Statistical Computing. Retrieved from http://www.R-project.org/

Raulerson, S., Jackson, C. R., Melear, N. D., Younger, S. E., Dudley, M., & Elliott, K. J. (2020). Do southern Appalachian Mountain summer stream temperatures respond to removal of understory rhododendron thickets? *Hydrological Processes*, *34*(13), 3045–3060. https://doi.org/10.1002/hyp.13788

Ravenstel, A. W., Lips, K. R., Pringle, C. M., Whiles, M. R., & Bixby, R. J. (2004). Neotropical tadpoles influence stream benthos: Evidence for the ecological consequences of decline in amphibian populations. *Freshwater Biology*, *49*, 274–285. https://doi.org/10.1111/j.1365-2427.2004.01184.x

Rice, S. P., Johnson, M. F., Mathers, K., Reeds, J., & Extence, C. (2016). The importance of biotic entrainment for base flow fluvial sediment transport. *Journal of Geophysical Research: Earth Surface*, *121*, 890–906. https://doi.org/10.1002/2015JF003726

Rosemond, A. D. (1993). Interactions among irradiance, nutrients, and herbivores constrain a stream algal community. *Oecologia*, *94*, 585–594. https://doi.org/10.1007/BF00566976

Sakamaki, T., & Richardson, J. S. (2013). Nonlinear variation of stream-forest linkage along a stream-size gradient: An assessment using biogeochemical proxies of in-stream fine particulate organic matter. *Journal of Applied Ecology*, *50*, 1019–1027. https://doi.org/10.1111/1365-2664.12099

Sartory, D. P., & Grobbelaar, J. U. (1984). Extraction of chlorophyll a from freshwater phytoplankton for spectrophotometric analysis. *Hydrobiologia*, *114*, 177–187. https://doi.org/10.1007/BF00031869

Schneider, C. A., Rasband, W. S., & Eliceiri, K. W. (2012). NIH Image to ImageJ: 25 years of image analysis. *Nature Methods*, *9*(7), 671–675. https://doi.org/10.1038/nmeth.2089

Schofield, K. A. (2001). *Top down interactions in southern Appalachian streams: An examination of temporal and spatial variability.* . PhD Thesis, University of Georgia.

Schofield, K. A., Pringle, C. M., Meyer, J. L., & Rosi-Marshall, E. J. (2008). Functional redundancy of stream macroconsumers despite differences in catchment land use. *Freshwater Biology*, *53*, 2587–2599. https://doi.org/10.1111/j.1365-2427.2008.02085.x

Schofield, K. A., Pringle, C. M., Meyer, J. L., & Sutherland, A. B. (2001). The importance of crayfish in the breakdown of rhododendron leaf litter. *Freshwater Biology*, *46*, 1191–1204. https://doi.org/10.1046/j.1365-2427.2001.00739.x

Small, G. E., Pringle, C. M., Pyron, M., & Duff, J. H. (2011). Role of the fish Astyanax aeneus (Characidae) as a keystone nutrient recycler in low-nutrient Neotropical streams, Costa Rica. *Ecology*, *92*, 386–397. https://doi.org/10.1890/10-0081.1

Steinman, A. D., & Lamberti, G. A. (1996). Biomass and pigments of benthic algae. In R. F. Hauer, & G. A. Lamberti (Eds.), *Methods in stream ecology*. Academic Press.

Tant, C. J., Rosemond, A. D., Helton, A. M., & First, M. R. (2015). Nutrient enrichment alters the magnitude and timing of fungal, bacterial, and detritivore contributions to litter breakdown. *Freshwater Science*, *34*, 1259–1271. https://doi.org/10.1086/683255

Taylor, B. W., Flecker, A. S., & Hall, R. O. (2006). Loss of a harvested fish species disrupts carbon flow in a diverse tropical river. *Science*, *313*, 833–836. https://doi.org/10.1126/science.1128223

Thomas, D. J. (1996). *Soil survey of Macon County, North Carolina*. USDA Natural Resources Conservation Service.

Townsend, S. A., Garcia, E. A., & Douglas, M. M. (2012). The response of benthic algal biomass to nutrient addition over a range of current speeds in an oligotrophic river. *Freshwater Sciences*, *31*, 1233–1243. https://doi.org/10.1899/11-163.1

Trice, A. E., Rosemond, A. D., & Maerz, J. C. (2015). Diet composition of two larval headwater stream salamanders and spatial distribution of prey. *Freshwater Biology*, *60*, 2424–2434. https://doi.org/10.1111/fwb.12669

USFS (2011). *Nantahala Pisgah NF Forest Plan Amendments: Prescribed fire amendment 26*. Retrieved from http://www.fs.usda.gov/Internet/FSE_DOCUMENTS/stelprdb5346291.pdf

Veach, A. M., Troia, M. J., Jumpponen, A., & Dodds, W. K. (2018). Top-down effects of a grazing, omnivorous minnow (*Campostoma anomalum*) on stream microbial communities. *Freshwater Science*, *37*(1), 121–133.

Wallace, J. B., Webster, J. R., & Cuffney, T. F. (1982). Stream detritus dynamics: Regulation by invertebrate consumers. *Oecologia*, *53*, 197–200. https://doi.org/10.1007/BF00545663

Webster, J. R., Golladay, S. W., Benfield, E. F., D'Angelo, D. J., & Peters, G. T. (1990). Effects of forest disturbance on particulate organic matter budgets of small streams. *Journal of the North American Benthological Society*, *9*, 120–140. https://doi.org/10.2307/1467446

Welschmeyer, N. A. (1994). Fluorometric analysis of chlorophyll a in the presence of chlorophyll b and pheopigments. *Limnology and Oceanography*, *39*, 1985–1992. https://doi.org/10.4319/lo.1994.39.8.1985

Yang, C., Wenger, S. J., Rugenski, A. T., Wehrtmann, I. S., Connelly, S., & Freeman, M. C. (2020). Freshwater crabs (Decapoda: Pseudothelphusidae) increase rates of leaf breakdown in a neotropical headwater stream. *Freshwater Biology*, https://doi.org/10.1111/fwb.13524

Yarnell, S. (1998). *The southern Appalachians: a history of the landscape. General Technical Report SRS-18*. United States Department of Agriculture Forest Service, Southern Research Station.

Zimmerman, J. K. H., & Vondracek, B. (2006). Effects of stream enclosures on drifting invertebrates and fish growth. *Journal of the North American Benthological Society*, *25*, 453–464.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Dudley MP, Solomon K, Wenger S, et al. Do crayfish affect stream ecosystem response to riparian vegetation removal?. *Freshwater Biology*. 2021;00:1–13. https://doi.org/10.1111/fwb.13728