Received: 29 September 2022 | Revised: 9 February 2023 | Accepted: 31 March 2023

DOI: 10.1002/ecy.4052

ARTICLE

ECOLOGY
ECOLOGICAL SOCIETY OF AMERICA

Resource modification by ecosystem engineers generates hotspots of stream community assembly and ecosystem function

Benjamin B. Tumolo[1,2] | **Lindsey K. Albertson**[1] | **Wyatt F. Cross**[1] | **Geoffrey C. Poole**[3] | **Grace Davenport**[1] | **Melinda D. Daniels**[4] | **Leonard S. Sklar**[5]

[1]Department of Ecology, Montana State University, Bozeman, Montana, USA

[2]Department of Zoology and Physiology, University of Wyoming, Laramie, Wyoming, USA

[3]Department of Land Resources and Environmental Sciences, Montana State University, Bozeman, Montana, USA

[4]Stroud Water Research Center, Avondale, Pennsylvania, USA

[5]School of Environmental Science, Simon Fraser University, Burnaby, British Columbia, Canada

Correspondence
Benjamin B. Tumolo
Email: btumolo@uwyo.edu

Funding information
Division of Environmental Biology, Grant/Award Numbers: 1556684, 1945941

Handling Editor: Daniel E. Schindler

Abstract

Ecosystem engineers can generate hotspots of ecological structure and function by facilitating the aggregation of both resources and consumers. However, nearly all examples of such engineered hotspots come from long-lived foundation species, such as marine and freshwater mussels, intertidal cordgrasses, and alpine cushion plants, with less attention given to small-bodied and short-lived animals. Insects often have rapid life cycles and high population densities and are among the most diverse and ubiquitous animals on earth. Although these taxa have the potential to generate hotspots and heterogeneity comparable to that of foundation species, few studies have examined this possibility. We conducted a mesocosm experiment to examine the degree to which a stream insect ecosystem engineer, the net-spinning caddisfly (Tricoptera:Hydropsychidae), creates hotspots by facilitating invertebrate community assembly. Our experiment used two treatments: (1) stream benthic habitat with patches of caddisfly engineers present and (2) a control treatment with no caddisflies present. We show that compared to controls, caddisflies increased local resource availability measured as particulate organic matter (POM) by 43%, ecosystem respiration (ER) by 70%, and invertebrate density, biomass, and richness by 96%, 244%, and 72%, respectively. These changes resulted in increased spatial variation of POM by 25%, invertebrate density by 76%, and ER by 29% compared to controls, indicating a strong effect of caddisflies on ecological heterogeneity. We found a positive relationship between invertebrate density and ammonium concentration in the caddisfly treatment, but no such relationship in the control, indicating that either caddisflies themselves or the invertebrate aggregations they create increased nutrient availability. When accounting for the amount of POM, caddisfly treatments increased invertebrate density by 48% and richness by 40% compared to controls, suggesting that caddisflies may also enhance the nutritional quality of resources for the invertebrate assemblage. The caddisfly treatment also increased the rate of ecosystem respiration as a function of increasing POM compared to the control. Our study demonstrates that insect ecosystem

https://doi.org/10.1002/ecy.4052

engineers can generate heterogeneity by concentrating local resources and consumers, with consequences for carbon and nutrient cycling.

KEYWORDS
detritus, facilitation, heterogeneity, Hydropsychidae, insect, positive interaction

INTRODUCTION

Environmental heterogeneity governs spatio-temporal patterns of community structure and ecosystem function (Li & Reynolds, 1995; Stein et al., 2014). Thus, understanding the causes and consequences of heterogeneity has long been a fundamental pursuit for ecologists (Bernhardt et al., 2017; Palmer et al., 1997; Winemiller et al., 2010). Traditionally, heterogeneity in ecological processes has been attributed to variation in physical conditions which can give rise to hotspots or areas with disproportionately high rates of material cycling and ecosystem processes (Bernhardt et al., 2017; Li & Reynolds, 1995; McClain et al., 2003; Palmer et al., 1997). More recently, various taxa have been recognized as an important source of heterogeneity because organisms themselves can directly alter habitats and resources with consequences for community structure and ecosystem function (Altieri et al., 2007; Jones et al., 1994; Lopez et al., 2020).

Ecosystem engineers—organisms that physically alter habitat or the availability and quality of resources—have been recognized as important sources of heterogeneity because they facilitate the aggregation of consumers with consequences for ecosystem functions (Altieri et al., 2007; Jones et al., 1994; Romero et al., 2015). Despite important progress in recognizing organisms as agents of heterogeneity, nearly all examples of such ecosystem engineered hotspots are from longer-lived foundation species, such as corals, trees, intertidal cordgrasses, and alpine cushion plants (Altieri et al., 2007; Angelini et al., 2011), with less attention given to the plethora of engineers with greater mobility, smaller-body sizes, shorter lifespans, and higher population densities. In particular, insects act as ecosystem engineers and exemplify natural history traits (e.g., high population densities, mobility, and rapid life cycles) that could generate more transient and spatially variable hotspots that constitute comparatively high levels of heterogeneity to those initiated by foundation species. A growing body of literature shows that insect engineering increases resource availability, which in turn can facilitate aggregations of consumers, sometimes with ecosystem level effects (Dangerfield et al., 1998; Hölker et al., 2015; Swanson et al., 2019). For example, termite and ant mounds can host a diversity of microbial, invertebrate, and vertebrate species that amplify carbon and nutrient turnover (Dangerfield et al., 1998; Swanson et al., 2019). However, despite their global ubiquity and potential to generate substantial heterogeneity across the landscape, we still understand little about the causes and consequences of insect-mediated hotspots compared to foundation species.

Ecological hotspots can be generated by organism-mediated habitat and resource modification that attracts consumers and subsequently alters ecosystem functions (Allen et al., 2012; Lopez et al., 2020; VanBlaricom, 1982). Within stream ecosystems in particular, ecosystem engineering activities can strongly modify detrital resources, such as those arising from mussels or fish, with community and ecosystem level consequences (Allen et al., 2012; Booth et al., 2020). The foraging of sucker fish, for instance, creates mosaics in detrital resource concentrations and macroinvertebrate consumer density (Booth et al., 2020). Additionally, stream insects control detrital resource quantity and quality by concentrating detrital material into retreat structures (Nakano et al., 2005), modifying the hydraulic environment (Hammock & Bogan, 2014; MacDonald et al., 2021), and through nutrient recycling (Halvorson et al., 2015). Therefore, examining how insect-mediated detrital modification generates hotspots in community assembly and ecosystem functions may further our understanding of how numerous, small-bodied, short-lived ecosystem engineers generate potentially widespread ecological heterogeneity in nature.

To investigate if and how insects can generate hotspots of community assembly and ecosystem function, we studied whether net-spinning caddisflies affect detrital resources, invertebrate consumers, ecosystem respiration, and nutrient concentrations. Net-spinning caddisflies are aquatic insect larvae that act as ecosystem engineers within streams by building silk catch-nets with retreats of organic material. Caddisfly silk and retreats alter habitat structure by decreasing local hyporheic exchange and within-bed velocity, which in turn can concentrate detrital resources and increase local invertebrate density and biomass (MacDonald et al., 2021; Nakano et al., 2005; Tumolo et al., 2019; Wallace, 1975). Net-spinning caddisflies have also been shown to negatively affect other benthic filter-feeding insects via interspecific competition (Diamond, 1986; Hemphill, 1988). Because ecosystem engineers are part of the community in which they live, experimental manipulation of engineer presence, other species, and food resource availability is required to understand how community assembly and ecosystem function respond to presence or absence of engineers across scales. To this end, we designed an experiment to simulate stream reaches with pre-colonized patches of caddisfly engineers or reaches with all patches isolated from caddisflies (Figure 1). We then simulated invertebrate consumer colonization in these two distinct experimental steam reaches with standardized and representative invertebrate colonist and detrital pools. By stocking artificial streams with colonists following the establishment of caddisflies, we could examine how invertebrate colonists, basal resources, and ecosystem processes respond to the presence or absence of caddisflies in any given patch and reach.

Compared to controls, we predicted that the presence of caddisflies would: (1) increase patch levels of detrital resource availability, invertebrate density, biomass, richness, and ecosystem respiration; (2) affect ecological responses at larger aggregate reach-level spatial scales measured as (i) increased standard deviation in the spatial distribution of these ecological responses, or (ii) greater overall values of these metrics, or (iii) a combination of both outcomes; (3) increase local nutrient recycling due to higher levels of colonist and engineer excretion, which is expected to increase the strength of the relationships between resource quantity and the ecological responses of: invertebrate density, biomass, richness, and ecosystem respiration at both local and aggregate scales.

METHODS

Experimental design and procedure

We conducted an experiment in outdoor recirculating flumes ($n = 12$) at the Bozeman Agricultural Research

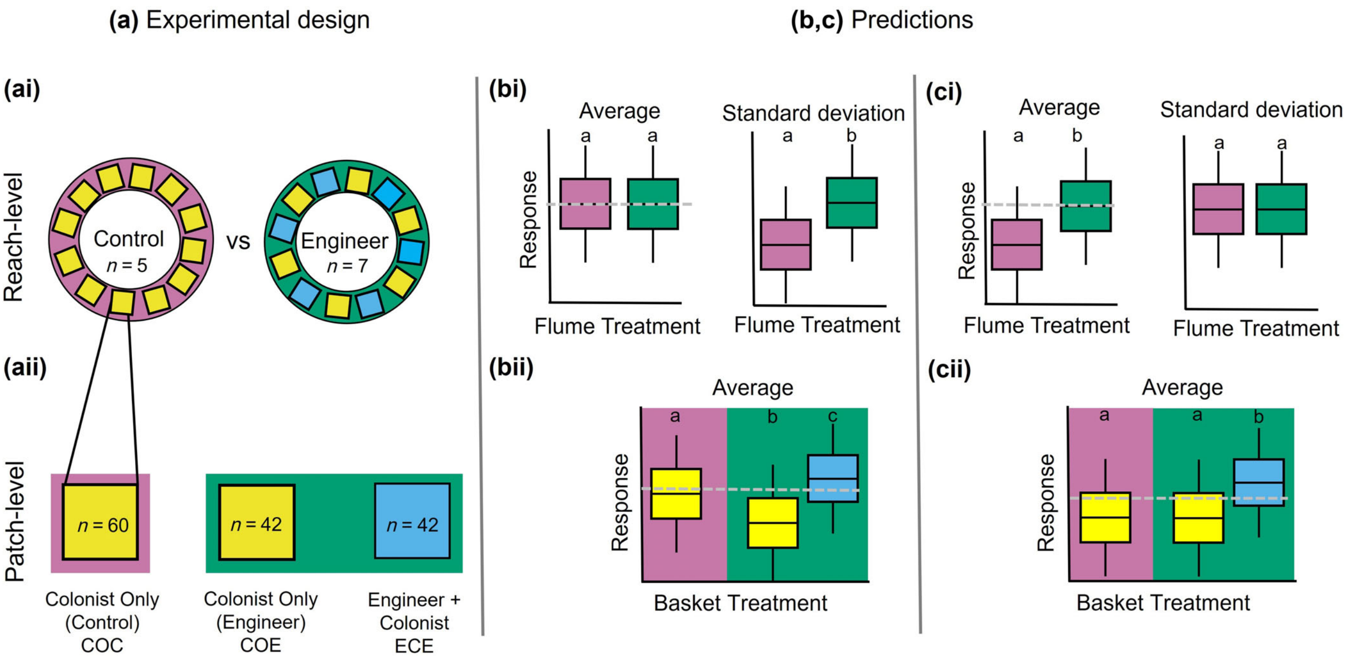

FIGURE 1 Expected patterns in experimental data indicating ecosystem engineering influences on community assembly and ecosystem function. We measured the effects of caddisfly at two levels of experimental unit (ai) reach-level, to quantify the cumulative ecological effects of engineering patches and (aii) patch-level, to quantify the direct localized effect of caddisfly silk and retreat structures. We applied this conceptual model to multiple response variables of interest measured at these patch- and reach-level. Here, we present two example predictions (b, c) that would confirm caddisfly effects on invertebrate colonist density. The dashed gray line represents even distribution of invertebrates across baskets because all flumes were initially stocked with an equal colonist pool. The effect of caddisflies would be detectable if (bi) the response variable had a higher standard deviation (S) at the reach-level in the engineer flumes relative to controls because caddisflies facilitate the aggregation of invertebrates. (bii) At the basket level, higher standard deviation at the reach-level could be represented by the response variable distributing evenly across all of the baskets in the control flumes, but disproportionately favoring ECE-engineer + colonist in engineer (ECE) baskets in the engineer treatment flumes. (ci) Alternatively, the response variable could have a higher mean in the engineer treatment at the reach-level with similar levels of standard deviation because caddisflies facilitate retention of invertebrates within experimental baskets. (cii) At the basket level this pattern would be represented by colonist only in control (COC) and colonist only in engineer (COE) treatments being indistinguishable and ECE having higher levels of response.

and Teaching Farm (hereafter BART farm) located in Bozeman, Montana, USA (45°39′36″ N 111°04′23″ W) from August 3 to 29, 2020. We implemented a hierarchical nested design in which an entire flume represented a stream reach and subdivisions within the flume represented patches within that reach (Figure 1, Appendix S1: Figure S1). We measured the effects of caddisfly engineers at two levels of experimental unit: (1) flume-level, to quantify the reach-level effects of engineering patches; and (2) patch-level, to quantify the direct localized effect of caddisfly engineering. We chose a 26-day duration for our experiment to encompass a typical colonization time frame of biofilms and invertebrates following dispersal and disturbance events (Fisher et al., 1982). Furthermore, we chose to use recirculating annular or ring-shaped flumes with a continuous bed of discrete removable sampling baskets to represent stream reaches. These experimental conditions created a scenario where invertebrate colonists and detrital resources were given equal chance to colonize all experimental patches, allowing for the comparison of patch- and reach-level effects of caddisflies. The working area in the flumes was a 0.1 m^2 annulus with a 0.56 m outer diameter and 0.09 m wide racetrack. Although the size of experimental units only represents what would be a portion of a natural river reach, this design enabled replication and a necessary level of control over the environment and species pool, while still achieving a realistic representation of patch-level abundances and habitat use of focal organisms (Cardinale, 2011; Vogel & LaBarbera, 1978).

To examine effects of caddisfly engineers at the flume-level (representing a simulated "reach-level" effect), we deployed two flume-level treatments: (1) caddisflies present (hereafter "engineer" treatment), and (2) no caddisflies present (hereafter "control" treatment). To examine effects of caddisflies at the patch-level, as well as how these effects propagated throughout flumes, we nested two patch-level treatments within the two reach-level treatments: (1) an Engineer + Colonist patch type in the Engineer reach (ECE), and (2) a Colonist Only patch type in both the engineer (COE) and control reaches (COC, Figure 1). The ECE patch treatment consisted of baskets pre-inoculated with caddisflies and later open to colonization by other invertebrates in the engineer flumes (Figure 1ai). The COE patch treatment consisted of baskets initially isolated from caddisfly colonization, but later interspersed among ECE patches. The COC patch treatment consisted of baskets always isolated from engineers within control flumes. All flumes and patch treatments received the addition of invertebrate colonists and organic matter at the beginning of the experiment. To quantify the effects of engineers, we measured reach- and patch-level community assembly metrics (invertebrate colonist density, biomass, richness), and ecosystem metrics of particulate organic matter (POM), ecosystem respiration (ER), and ammonium.

Flumes were filled with 20 L of well water from the BART farm and 0.75 g of crushed aquarium algae wafers were added for invertebrate food. To account for evaporation and sample extraction from the flumes throughout the experiment we added 1 L of spring water once a week (3 L total or 15% of starting volume). Flow in flumes was generated by aquarium pumps (Aleko multi-function pump, model number G2950) and was maintained at 4 cm s^{-1} (Appendix S1: Figure S2). The flow velocities were on the low end of natural levels for small streams inhabited by net-spinning caddisflies (3–50 cm s^{-1}, Fonseca & Hart, 1996; Gibbins et al., 2010; Minshall & Minshall, 1977). Velocities were maintained at this low level to isolate resource modification as the mechanism of facilitation conferred by caddisfly engineering as opposed to caddisfly-mediated flow refuge, which occurs at higher velocities (Nakano et al., 2005). Water temperature was maintained between 12 and 16°C, averaging 14°C (Appendix S1: Figure S1), which was comparable to conditions in nearby third-order streams during summer months where invertebrates were collected. The flume raceway included 12 patches, which consisted of strawberry baskets (10 cm^2; mesh opening = 1 cm^2) filled with 750 g (±5 g) of 22–32 mm gravels. All experimental gravels were dry and denuded of biofilm for >1 year prior to the experiment. The baskets represented discrete sampling units that retained gravel and allowed for water, organic material, and invertebrate movement.

To inoculate engineer treatments, hydropsychid caddisflies (*Hydropsyche* spp.) of consistent body size (third instar, average length = 8.95 ± 0.30 mm, $n = 20$ reference samples) were hand collected from Bridger Creek (45°42′21″ N 111°00′22″ W) over a 12-h period and used to inoculate ECE baskets. To ensure that COE baskets did not get colonized by engineers during the caddisfly stocking period COE baskets were held in isolation within control treatment flumes. The ECE treatment baskets were established by adding 20 caddisflies to each basket (2000 individuals m^{-2}) by placing them directly upstream of the target basket. Caddisfly densities of this magnitude are common throughout the USA and conservative for some streams that can contain over 10,000 hydropsychids m^{-2} (Statzner et al., 1999). Caddisflies were given 7 days to colonize and establish silk prior to stocking invertebrate colonists and organic matter. Following the caddisfly establishment period, the COE baskets were added into the engineer flumes, being careful not to agitate ECE baskets and hydropsychid retreats therein. After adding the COE baskets to the engineer flumes, we simulated invertebrate colonization while also stocking flumes with organic matter. Each flume was inoculated with an equal and representative community of stream invertebrates along with detritus from Bridger Creek following a procedure commonly used to create consistent aliquots of benthic community members and organic material in experiments (Appendix S1: Figure S3).

Sampling and processing of flumes and baskets

Flumes were sampled on August 29, 2020, 19 days after colonist stocking and 26 days after caddisfly stocking. First, we measured benthic ecosystem respiration (ER) as change in dissolved oxygen concentration (Δ mg O_2 L $^{-1}$ H $^{-1}$) in sealed 2 L dark chambers placed in a temperature and light controlled environment. ER was measured on a subset ($n = 57$) of the baskets that were carefully removed from flumes and placed intact (including invertebrates and POM) in a chamber. Our subset sample size for ER included: $n = 15$ for COC baskets, with an $n = 3$ from each of the control flumes, $n = 21$ for COE baskets, with an $n = 3$ for each of the engineer treatment flumes, and $n = 21$ for ECE baskets, with an $n = 3$ for each of the engineer flumes. All incubations were conducted between 10:00 and 17:00 in a closed cooler with recirculating chilled water (13°C) to control for light and temperature. O_2 and chamber temperatures were recorded at 1-min intervals (YSI Pro-ODO, Yellow Springs, Ohio, USA). Each incubation was terminated after O_2 changed by 0.5 mg/L or after 0.5 h. We corrected for water column metabolism by subtracting rates measured in a chamber without experimental baskets that was being run alongside (Welter et al., 2015). Our metabolism measurements were not corrected for the invertebrates present within baskets during the incubation, therefore our use of ER serves as a measure for collective biological activity that includes invertebrate and microbial contributions.

After ER was measured, all baskets ($n = 144$) were sampled for invertebrates and POM. We measured benthic invertebrates and POM in each basket by lifting it from the flume and placing it directly on a 125 μm sieve where each rock within the basket was rinsed with filtered water over the sieve and visually inspected to ensure all macroinvertebrates and POM were removed. Invertebrates and POM collected in the sieve were transferred to a Whirl-Pak and preserved with 70% ethanol. In the laboratory, invertebrates were counted, measured in length to the nearest mm, and identified to genus or Chironomidae (Diptera) were identified as Tanypodinae or non-Tanypodinae, and non-insect groups such as Oligochaeta and Hydrachnidia were not identified beyond class or order levels (Merritt & Cummins, 1996). Total invertebrate biomass in each sample was estimated as mg AFDM sample^{-1} using established taxon-specific length-mass relationships (Benke et al., 1999). Invertebrate taxon richness was estimated as the total number of unique taxa basket^{-1}, density was estimated as no. basket^{-1} and overall biomass as mg AFDM basket^{-1}. For all treatments, all Hydropsychidae individuals were excluded in the tabulation of invertebrate density, biomass, and richness to avoid artificially inflating community assembly metrics based on the initial caddisfly inoculation that was used to create experimental treatments. Total POM in each sample was quantified by drying any remaining material after all invertebrates had been removed from each invertebrate sample (55°C, for 48 h). After drying, we weighed each sample, combusted it at 500°C for 2 h, and reweighed it to determine POM ash-free dry mass (g AFDM basket^{-1}). We present results in per basket units, but measurements of invertebrate density, invertebrate biomass, and POM at the patch scale can be converted to the meter scale by multiplying by 100.

We measured ammonium (NH_4^+ mg/L) concentrations at the reach-level by taking 50-mL syringe grabs from surface water of each flume on Day 1 and 25. Nutrient samples were processed by The Environmental Analytical Lab at Montana State University using Lachat QuickChem 8500 instrumentation (Lachat Instruments, 2003). We focused our analysis of NH_4^+ on the final day of sampling because we sought to pair nutrient concentrations with measurements of invertebrate density. Paired nutrient and invertebrate data were only possible on the terminal day of the experiment because invertebrate sampling was destructive. Furthermore, preliminary analysis show that baseline ammonium levels were statistically indistinguishable between treatments on day 1 of the experiment ($p = 0.945$, 95% family wise CI = −0.624, 0.931) warranting that differences observed at the end arose from the experiment itself.

Data analysis

Patterns in caddisfly density at the conclusion of the experiment were largely consistent with our intended treatments, and so we chose to conduct the data analysis with the initial treatment categories. Our experimental design allowed caddisflies to deploy silk during the initial 7-day colonization period and also did not prevent caddisflies from migrating to other COE or ECE baskets during the entire duration of the experiment. Further, even in the case of mortality during the experiment, any silk structures created would have persisted through the experiment (Albertson & Daniels, 2016; Maguire et al., 2020; Tumolo et al., 2019). This choice for the data analysis represented a conservative assumption, given that migration or mortality of engineers during the experiment would be likely to reduce any differences among baskets originally categorized as COE, COC, and ECE. Caddisfly density in ECE patches was 2.5 ± 0.3 caddisfly basket^{-1}, range 0–8 basket^{-1}, with 86%, or 36 out of the 42 of patches in this treatment occupied by Hydropsychidae on the final day of the experiment. In comparison, caddisfly density in COE patches was low (0.52 ± 0.14 caddisfly basket^{-1}, range 0–3 basket^{-1}, with 26% or 11 out of the 42 of baskets of this treatment being occupied by Hydropsychidae), suggesting COE patches experienced minimal levels of immigration from ECE patches. We did not detect Hydropsychidae in COC treatment patches.

Reach-level analysis

Total invertebrate density and richness were analyzed using general linear mixed effect models (GLMM) with a poisson family distribution comparing the response between treatment as a fixed effect and individual flume as a random effect. Total invertebrate biomass, POM and ER were analyzed using linear mixed effect models (LMM) comparing the response across treatment as a fixed effect and individual flume as a random effect. Density and biomass and POM were natural log-transformed to meet assumptions of normality. To test if the presence of caddisflies affected the distribution of invertebrates, POM, and ecosystem function, we compared the standard deviation (S) of density, biomass, richness, POM, and ER between the treatments using separate one-way analysis of variation (ANOVA) tests. For the analysis of standard deviation, we excluded one control basket that was identified as an outlier (Cook's distance >3).

To test if the presence of caddisflies affected the relationship between POM and community and ecosystem metrics, we constructed separate GLMM and LMMs where density, biomass, richness, and ER were a function of the fixed effects of treatment × POM and the random effects of individual flume. Ammonium concentration measured on the last day of the experiment was analyzed as a function of total flume invertebrate density (including Hydropsychidae) × flume treatment using a multiple linear regression.

Patch-level analysis

Invertebrate density and richness were each analyzed using GLMMs with a Poisson family distribution comparing the response across treatment as a fixed effect and individual flume as a random effect. Invertebrate biomass, POM, and ER were analyzed using LMMs comparing the response across treatment as a fixed effect and individual flume as a random effect.

All models

When testing for the effect of caddisflies on the relationship between POM and ecological responses (density, biomass, richness, and ER), we interpreted statistically significant interaction effects (represented by differences in slope) and statistically significant differences in intercept to be biologically relevant signals of a caddisfly effect. A statistically different slope indicated that the effect of caddisflies was dependent on the quantity of POM, where the effect of caddisflies either increased or decreased with respect to other treatments as POM increased. Alternatively, in the case of no statistically significant interaction effect between treatment and POM, we concluded that treatment slopes were parallel and ran the model with treatment as an additive term instead of an interactive term. A significantly different intercept indicated that, when accounting for the amount of POM, the effect of caddisflies on a given response variable was either higher or lower with respect to other treatments.

Mixed effect models (GLMs and LMMs) accounted for the non-independence of samples taken within the same flume using a standard mixed model hierarchical design (Bolker et al., 2009; Nakagawa & Schielzeth, 2013; Zuur et al., 2009). All mixed effects models were fit with the Lme4 package (Bates et al., 2014) and tested for significance using a Kenward-Roger denominator degrees of freedom approximation (Kenward & Roger, 1997). Post hoc comparisons of least squares means and confidence intervals for response variables between treatments were calculated using the lsmeans function (Lenth & Her, 2015). Conditional *r*-squared values were calculated for LMM and GLMM using the "*r*.squaredGLMM" function (Nakagawa & Schielzeth, 2013). To account for the multiple dependent variables from the same experimental units we conducted multivariate ANOVA (MANOVA) tests at both the reach- and patch-level. The MANOVA test was highly significant at both the reach ($F_{5,50} = 3.21$, $p = 0.0136$) and patch-level ($F_{10,100} = 3.58$, $p = 0.0004$), so we proceeded with separate univariate analysis. Scripts used in this analysis are archived in Zenodo (Tumolo, 2023b).

RESULTS

Community assembly

Presence of caddisflies affected patterns and variation in community assembly at the reach-level (Figure 2,

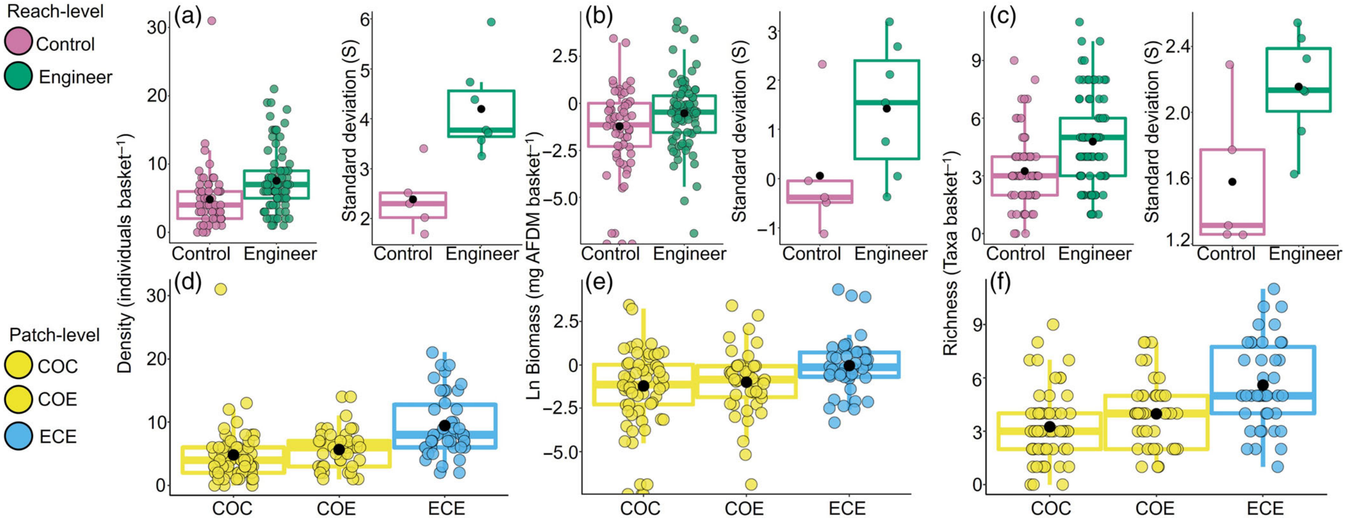

FIGURE 2 Community assembly metrics of invertebrate density (individuals basket^{-1}), biomass (mg AFDM basket^{-1}), and richness (taxa basket^{-1}) and standard deviation (S) of respective metrics as a function of flume treatment (a–c). Invertebrate density, biomass, and richness as a function of basket treatment (d–f). Box plot shows the median (horizontal line), mean (black circle) and interquartile range (IQR; vertical box bounds). Whiskers represent 1.5 × IQR, and data points are represented with circles colored based on treatment. COC, colonist only in control; COE, colonist only in engineer; ECE, ECE-engineer + colonist in engineer.

Table 1, Appendix S1: Table S1). The engineer treatment had greater density (hereafter, parameter estimate ± SE = −0.47 ± 0.15), biomass (−0.79 ± 0.40), and richness (−0.39 ± 0.12) of invertebrates relative to the control (Figure 2, Table 1, Appendix S1: Tables S2, S3, and S5–S8). Additionally, the average standard deviation in density within flumes was 76% greater in the engineer treatment compared to the control treatment (−1.81 ± 0.48, Figure 2a, Appendix S1: Table S1). The average standard deviation in biomass within flumes was 211% greater in the engineer treatment compared to the control, however this pattern was not statistically significant (−5.38 ± 4.24, Figure 2b, Appendix S1: Table S1). The average standard deviation in richness within flumes was 37% greater in engineer treatment compared to the control (−0.58 ± 0.22, Figure 2c, Appendix S1: Table S1).

Patches pre-inoculated with caddisflies (ECE) had greater density (0.69 ± 0.15), biomass (1.21 ± 0.44), and richness (0.55 ± 0.12) of invertebrates compared to patches initially isolated from caddisflies (COC and COE treatments, Figure 2, Table 1, Appendix S1: Tables S4–S8). Density, biomass, and richness were statistically indistinguishable between patches in either flume treatment that lacked initial caddisfly engineers (COC and COE, Figure 2d–f, Table 1, Appendix S1: Tables S5–S8) demonstrating that reach-level differences in average and standard deviation can be attributed to the patches that were pre-inoculated with caddisfly engineers.

Ecosystem function

Presence of caddisflies affected patterns and variation in ecosystem function at the reach-level (Figure 3, Table 1, Appendix S1: Table S1). POM (−0.25 ± 0.40) and ER (−0.05 ± 0.03) were greater in the engineer treatment compared to control (Figure 3, Table 1, Appendix S1: Tables S3, S6, and S8). Additionally, the average standard deviation in POM and ER within flumes was greater in the engineer compared to the control treatment (Figure 3, Appendix S1: Table S1). Specifically, the average standard deviation in POM within flumes was 25% greater (−0.004 ± 0.002, Appendix S1: Table S1) in the engineer compared to control treatment (Figure 3b). The average standard deviation of ER within flumes was 29% greater in the engineer compared to control treatment, however this pattern was not statistically significant (Figure 3d, Appendix S1: Table S1).

Patches pre-inoculated with caddisflies (ECE) had greater amounts of POM (0.46 ± 0.17) and ER (0.08 ± 0.04) compared to patches initially isolated from caddisflies (Table 1, Appendix S1: Tables S6 and S8). POM and ER were statistically indistinguishable between patches in either flume treatment that lacked initial caddisfly engineers (COC and COE, Figure 3e,f, Table 1, Appendix S1: Tables S6 and S8) indicating that reach-level differences in average and standard deviation of POM and ER were attributable to patches that were pre-inoculated with caddisfly engineers.

TABLE 1 Summary table of mean ± SE, and % difference, of invertebrate density (individuals basket^{-1}), biomass (mg AFDM basket^{-1}), richness (taxa basket^{-1}), particulate organic matter (g AFDM basket^{-1}), and ecosystem respiration (Δ mg O_2 L^{-1} H^{-1}) comparing (a) reach-level engineer and control treatments and (b) patch-level treatments.

Treatment	Metric	Mean ± SE	% Difference
(a) Engineer vs. control			
	Density	7.56 ± 0.59 vs. 4.82 ± 0.59	57
	Biomass	3.70 ± 1.30 vs. 1.58 ± 0.66	134
	Richness	4.79 ± 0.25 vs. 3.25 ± 0.25	47
	POM	0.033 ± 0.002 vs. 0.027 ± 0.003	22
	ER	0.157 ± 0.016 vs. 0.106 ± 0.017	48
(b) Patch-level treatments			
ECE vs. COC			
	Density	9.45 ± 0.59 vs. 4.82 ± 0.59	96
	Biomass	5.45 ± 2.45 vs. 1.58 ± 0.66	244
	Richness	5.60 ± 0.38 vs. 3.25 ± 0.25	72
	POM	0.039 ± 0.003 vs. 0.027 ± 0.003	43
	ER	0.179 ± 0.025 vs. 0.106 ± 0.017	70
COC vs. COE			
	Density	4.82 ± 0.59 vs. 5.67 ± 0.49	18
	Biomass	1.58 ± 0.66 vs. 1.96 ± 0.83	24
	Richness	3.25 ± 0.25 vs. 3.98 ± 0.29	22
	POM	0.027 ± 0.003 vs. 0.028 ± 0.008	02
	ER	0.106 ± 0.017 vs. 0.126 ± 0.015	20
ECE vs. COE			
	Density	9.45 ± 0.59 vs. 5.67 ± 0.49	67
	Biomass	5.45 ± 2.45 vs. 1.96 ± 0.83	178
	Richness	5.60 ± 0.38 vs. 3.98 ± 0.29	41
	POM	0.039 ± 0.003 vs. 0.028 ± 0.008	40
	ER	0.179 ± 0.025 vs. 0.126 ± 0.015	42

Abbreviations: COC, colonist only in control; COE, colonist only in engineer; ECE, ECE-engineer + colonist in engineer; ER, ecosystem respiration; POM, particulate organic matter.

Influence of detrital resource availability

As organic matter concentration increased, invertebrate density, biomass, richness, and ecosystem respiration increased across all treatments (Figure 4). The engineer treatment modified the relationship between POM and community and ecosystem metrics, such that engineer treatments had greater values of invertebrate density, biomass, richness, and ecosystem respiration compared to controls at both the reach- and patch- levels (Figure 4). At the reach-level the intercept for density as a function of POM in the engineer treatment was 48% greater compared to the control (−0.39 ± 0.16, Appendix S1: Tables S9 and S10). The intercept for the relationship between biomass and POM was greater in the engineer treatment; however, this relationship was not statistically significant (−0.62 ± 0.43, Figure 4b, Appendix S1: Table S11). The intercept for richness as a function of POM was 40% greater in the engineer compared to control treatment (−0.34 ± 0.13, Figure 4c, Appendix S1: Tables S9 and S10). ER showed a significant interaction effect between POM and treatment (Figure 4d, Appendix S1: Table S11) with ER having a substantially elevated and positive slope in the engineer treatment compared to the shallow negative slope of the control treatment (estimated regression equations: $Y = 2.96x \pm 0.73$ vs. $Y = -0.33X \pm 1.40$, Figure 4d, Appendix S1: Table S11).

At the patch-level, the intercept for density as a function of POM in the ECE treatment was 48% higher compared to COC treatment (−0.37 ± 0.08, Figure 4e, Appendix S1: Tables S9 and S10). The intercept for invertebrate biomass as a function of POM was higher in the ECE treatment, however this relationship was not statistically significant

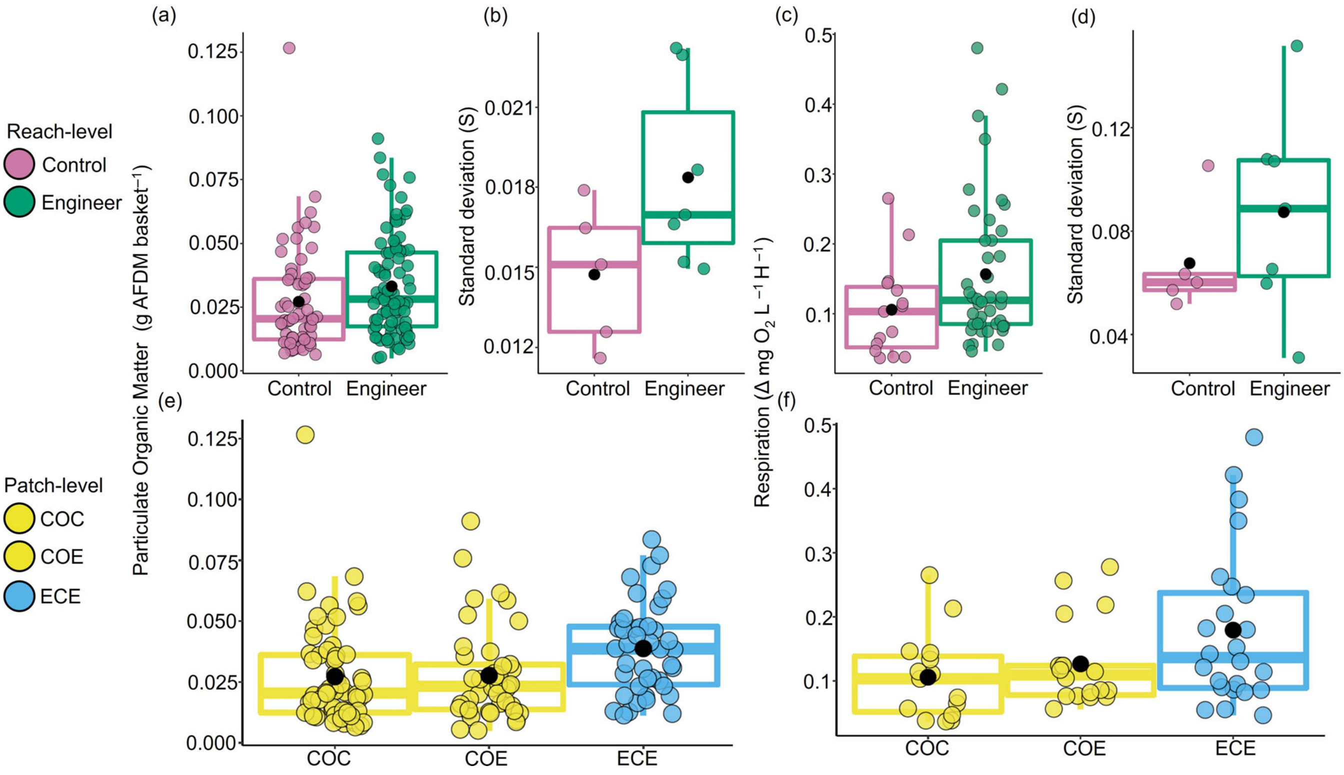

FIGURE 3 Ecosystem metrics of particulate organic matter (POM, mg AFDM basket^{-1}), and ecosystem respiration (Δ mg O_2 L^{-1} H^{-1}) and standard deviation (S) of respective metrics as a function of flume treatment (a, b). POM and ecosystem respiration as a function of basket treatment (c, d). Box plot shows the median (horizontal line), mean (black circle) and interquartile range (IQR; vertical box bounds). Whiskers represent 1.5 × IQR, and data points are represented with circles colored based on treatment. COC, colonist only in control; COE, colonist only in engineer; ECE, ECE-engineer + colonist in engineer.

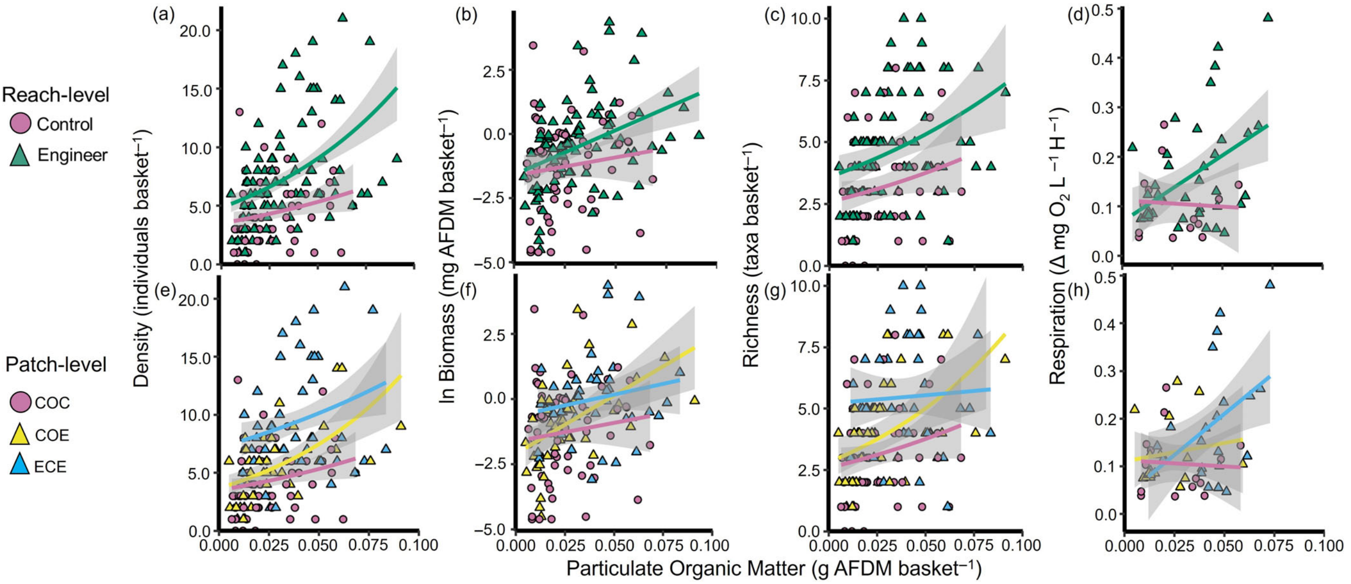

FIGURE 4 Community assembly and ecosystem metrics as a function of particulate organic matter (POM) quantity and experimental treatment. Data points are represented with circles colored based on treatment representing the measured value for a basket on the final day of sampling with line of best fit with gray shading of 95% confidence interval. COC, colonist only in control; COE, colonist only in engineer; ECE, ECE-engineer + colonist in engineer.

(0.56 ± 0.35, Figure 4f, Appendix S1: Table S11). There was a higher intercept for richness as a function of POM showing that the ECE treatment supported 29% higher levels of invertebrate richness when accounting for POM (−0.25 ± 0.10, Figure 4g, Appendix S1: Tables S9 and S10). Ecosystem respiration as a function of POM at the patch-level had an elevated slope in the ECE treatment relative to COC treatment, however this pattern was not statistically significant (−0.02 ± 0.04, Figure 4h, Appendix S1: Table S11). Patches adjacent to caddisfly patches (COE) consistently showed intermediate levels of density, biomass, richness, and ER per given POM quantity compared to engineer patches and patches isolated from engineers (Figure 4).

Nutrient response

At the reach-level ammonium concentration had a steeper more positive relationship with increasing invertebrate density in the engineer treatment compared to the shallow negative relationship of the control treatment ($Y = 0.003x \pm 0.001$ vs. $Y = -0.001x \pm 0.001$, Appendix S1: Figure S4) indicating that caddisfly-mediated invertebrate aggregations, or the caddisflies themselves, increased ammonium concentrations.

DISCUSSION

Our findings demonstrate that stream insect ecosystem engineers can generate ecological heterogeneity by aggregating both resources and consumers, with consequences for elemental cycling. Higher detrital resources, invertebrate community metrics, and ecosystem respiration associated with the presence of caddisflies aligns with previous work showing that modification of environments by ecosystem engineers can increase the abundance and diversity of other organisms, with ecosystem level consequences (Albertson et al., 2021; Romero et al., 2015). This study advances the understanding of ecosystem engineered hotspots beyond well-studied foundation species to include shorter-lived and smaller-bodied organisms.

Caddisfly-mediated facilitation through resource augmentation was likely responsible for the patterns of increased invertebrate density, biomass, and richness. Invertebrate communities responded positively to resource availability (Figure 4), and the presence of caddisflies was associated with increased local and reach-level resource concentrations (Figure 3). Additionally, supplementary analyses show that caddisflies promoted organic matter retention within experimental baskets (Appendix S1: Figure S5), offering further evidence that caddisfly silk and retreat structures aggregated detrital material. Caddisflies may have augmented resources for invertebrates through the construction of retreats, which can concentrate nutritionally rich detrital material (Mooney et al., 2014; Wallace, 1975). Additionally, caddisflies may have concentrated resources through silk-mediated detrital capture by aggregating water column and hyporheic POM within silk structures (MacDonald et al., 2021; Nakano et al., 2005). Along with altering resource availability, net-spinning caddisflies can facilitate invertebrates by providing flow refuge (Nakano et al., 2005); however, this was unlikely given the low flow conditions in our experiment. Collectively, our results show that caddisflies facilitated invertebrates by increasing organic matter food resources through a combination of retreat construction and silk-mediated detritus capture.

Given that the effects of ecosystem engineering are dependent on environmental and biotic context, it is useful to consider how experimental findings translate to natural streams where complexity in flow, substrate, and community composition might mediate patterns observed in mesocosms (Albertson et al., 2021; Jones et al., 1994). The positive effects of caddisflies on invertebrate communities found here are supported by previous research conducted under more natural field settings (Tumolo et al., 2019). However, near-bed velocity was greater under the more natural field conditions relative to the current study, and such environmental differences likely contextualize caddisfly-mediated facilitation. For example, under higher flow conditions caddisfly silk might trap fewer organic matter food resources; therefore, the role of caddisfly retreats as hydraulic refugia is expected to be more important than resource modification. Additionally, examining a larger range of flow and substrate conditions would also encompass a greater diversity of community members that would likely respond differentially to caddisfly-mediated engineering and therefore further modulate facilitation outcomes. It is clear that caddisflies can facilitate invertebrates through multiple mechanisms, and future work will benefit from characterizing the roles that environmental and biotic context play in shaping these interactions.

Caddisfly effects were dependent on spatial scale, where local effects propagated to a larger scale measured as increased heterogeneity, greater overall values of all response variables, and a combination of both outcomes (Figures 2 and 3). The finding that localized caddisfly-mediated aggregations promoted ecological heterogeneity at a larger spatial scale suggests caddisfly engineering may be an important source of patchiness within stream ecosystems. This interpretation is supported by work demonstrating that larger-bodied ecosystem engineers, including stingrays, freshwater fish, and beavers, can generate patchiness on the landscape by altering local habitat characteristics (Booth et al., 2020; VanBlaricom, 1982; Wright et al., 2003). In addition to these examples, our results join a small, but rapidly growing, body of work showing how insects can produce detectable, yet often overlooked heterogeneity in community and ecosystem processes (Hölker et al., 2015; Sileshi et al., 2010; Swanson et al., 2019).

Our finding of increases in ecological responses at a larger spatial scale suggests that caddisflies also promoted greater retention of detritus and invertebrates within the experimental baskets (Figures 2 and 3, Appendix S1: Figures S3 and S5). We suggest that caddisflies supported greater reach- and- patch-level retention of invertebrates through a combination of increased resource availability and predator refugia. In natural streams, invertebrate abundance and diversity tend to be greatest within gravel substrates of riffles (Brown & Brussock, 1991; Merrit & Cummins, 1996) and therefore we expected that stocked invertebrates would prefer the gravel matrix habitat present within baskets compared to the plastic flume sides or bottoms. However, perhaps a greater proportion of the invertebrates remained in gravels occupied by caddisflies and their silk because of the increased food resources compared to controls (Figure 3, Appendix S1: Figure S4). Additionally, caddisflies could have increased the survival and the propensity for gravel habitat selection by providing predator refugia, consistent with other studies from marine and freshwater systems (Albertson et al., 2021; Altieri et al., 2007). Our experiment included low densities of predacious invertebrates including free living caddisflies (*Rhyacophila* sp.), danceflies (Empididae) and aquatic mites (Hydrachnidia) offering support for the possibility that caddisflies increased community metrics by providing predator refugia. Furthermore, we observed variation in total invertebrate density among flumes within the engineer treatment, suggesting an unequal caddisfly effect. This finding could be attributable to differences in the spatial arrangement of engineer patches among flumes, as this was randomly assigned. Spatial arrangement of engineer patches is important to community assembly in marine systems (Crotty et al., 2018). In our experiment certain arrangements could have been more favorable to colonists resulting in greater invertebrate retention and thus a source of variation for the engineer treatment. Taken together, experimental patches pre-inoculated with caddisflies disproportionally contributed to larger-scale patterns in community assembly and ecosystem processes, underscoring the importance of localized organism-mediated habitat alterations.

The presence of caddisflies enhanced the effect of a given quantity of detrital organic matter for invertebrate colonists and ecosystem respiration (Figure 4). A possible explanation for this relationship is that caddisflies enriched the nutritional quality of detrital and autotrophic resources through excretion, consistent with other published evidence of consumer-driven nutrient recycling (Atkinson et al., 2017; Evans-White & Lamberti, 2006; Sterner, 1990). Enrichment of POM could have attracted invertebrate consumers, who further contributed their own wastes, ultimately stimulating higher growth and activity of heterotrophic microbes (Atkinson et al., 2017; Halvorson et al., 2015; Mooney et al., 2014). We observed higher concentrations of ammonium in engineer treatments compared to controls, and these higher values were explained by increased densities of invertebrates (Appendix S1: Figure S4). Enrichment of organic matter could also explain the positive relationship between POM and ER in the engineer treatment compared to the control, as increased nutrient concentrations can stimulate microbial colonization, growth, and respiration within benthic substrates (Gulis & Suberkropp, 2003; Kominoski et al., 2018). Our study did not measure the elemental compositions of resources or consumers and therefore we are unable to determine if enrichment was the causal mechanism for these observed patterns. However, the patterns we present are largely supportive of and consistent with basal resource enrichment.

The pattern of engineer-mediated community facilitation and subsequent changes to ecosystem function highlight parallels between caddisflies and the effects of foundation species observed in terrestrial, marine, and freshwater systems (Angelini et al., 2011). Foundation species have profound effects on ecosystem structure and function that are often attributed to traits that provide exceptionally stable habitats and resources for reliant community members (Altieri et al., 2007; Angelini et al., 2011). Here we show that caddisflies similarly affect communities and ecosystem functions, yet have vastly different ecologies, with shorter lifespans, and relatively small body sizes. Compared to foundation species, our results suggest that insect engineers can transform habitats with similar outcomes for community and ecosystem processes. Perhaps, larval caddisflies function as foundational species because much of their engineering effects occur from their sessile retreat structures. Yet, highly mobile organisms such as fish and birds also create stationary habitat modifications, suggesting that there is still much to learn about how different traits mediate engineering effects on the landscape (Albertson et al., 2022; Woods et al., 2021). Broadly, our findings indicate that a greater diversity of organisms and traits are likely involved in hotspot generation than is currently appreciated and suggest parallels between relatively small organism-mediated hotspots generated by semi-sessile, short-lived insects to those generated by long-lived large-bodied, and fully sessile foundation species. However, the stark differences in traits between insects and foundation species are expected to change how such hotspots scale over both time and space. Specifically, we expect that the hotspots generated by caddisflies and other insect engineers may be more transient over time and spatially variable compared those generated by foundation species. Ultimately, this work advances our understanding of the myriad ways by which organisms can control ecosystem functioning.

ACKNOWLEDGMENTS

We thank J. Long, Z. Maguire, S. Fritz, H. Oakland, L. Mohr, and M. Briggs for field assistance. We also thank E. Scholl, M. MacDonald, L. Collis, J. Sanchez, and J. Junker for constructive dialogue and M. P. Moore for statistical consult. Funding for this project was provided by the National Science Foundation (DEB 1556684 and 1945941), the Montana Water Center Student Fellowship awarded to Benjamin B. Tumolo, and the Amherst College Internship Fellowship awarded to Grace Davenport.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Tumolo, 2023a) are available in Dryad at https://doi.org/10.5061/dryad.1rn8pk0x5. Scripts (Tumolo, 2023b) are available in Zenodo at https://doi.org/10.5281/zenodo.7577242.

ORCID

Benjamin B. Tumolo https://orcid.org/0000-0001-7605-9314

Lindsey K. Albertson https://orcid.org/0000-0003-0270-6325

REFERENCES

Albertson, L. K., and M. D. Daniels. 2016. "Resilience of Aquatic Net-Spinning Caddisfly Silk Structures to Common Global Stressors." *Freshwater Biology* 61(5): 670–9.

Albertson, L. K., M. J. MacDonald, B. B. Tumolo, M. A. Briggs, Z. Maguire, S. Quinn, J. A. Sanchez-Ruiz, J. Veneros, and L. A. Burkle. 2021. "Uncovering Patterns of Freshwater Positive Interactions Using Meta-Analysis: Identifying the Roles of Common Participants, Invasive Species and Environmental Context." *Ecology Letters* 24(3): 594–607.

Albertson, L. K., L. S. Sklar, B. B. Tumolo, W. F. Cross, S. F. Collins, and H. A. Woods. 2022. "The Ghosts of Ecosystem Engineers: Legacy Effects of Biogenic Modifications." *Functional Ecology* 00: 1–21.

Allen, D. C., C. C. Vaughn, J. F. Kelly, J. T. Cooper, and M. H. Engel. 2012. "Bottom-up Biodiversity Effects Increase Resource Subsidy Flux between Ecosystems." *Ecology* 93(10): 2165–74.

Altieri, A. H., B. R. Silliman, and M. D. Bertness. 2007. "Hierarchical Organization Via a Facilitation Cascade in Intertidal Cordgrass Bed Communities." *The American Naturalist* 169(2): 195–206.

Angelini, C., A. H. Altieri, B. R. Silliman, and M. D. Bertness. 2011. "Interactions among Foundation Species and their Consequences for Community Organization, Biodiversity, and Conservation." *Bioscience* 61(10): 782–9.

Atkinson, C. L., K. A. Capps, A. T. Rugenski, and M. J. Vanni. 2017. "Consumer-Driven Nutrient Dynamics in Freshwater Ecosystems: From Individuals to Ecosystems." *Biological Reviews* 92(4): 2003–23.

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2014. "Fitting Linear Mixed-Effects Models Using lme4." *arXiv preprint* arXiv:1406.5823.

Benke, A. C., A. D. Huryn, L. A. Smock, and J. B. Wallace. 1999. "Length-Mass Relationships for Freshwater Macroinvertebrates in North America with Particular Reference to the Southeastern United States." *Journal of the North American Benthological Society* 18(3): 308–43.

Bernhardt, E. S., J. R. Blaszczak, C. D. Ficken, M. L. Fork, K. E. Kaiser, and E. C. Seybold. 2017. "Control Points in Ecosystems: Moving beyond the Hot Spot Hot Moment Concept." *Ecosystems* 20(4): 665–82.

Bolker, B. M., M. E. Brooks, C. J. Clark, S. W. Geange, J. R. Poulsen, M. H. H. Stevens, and J. S. S. White. 2009. "Generalized Linear Mixed Models: A Practical Guide for Ecology and Evolution." *Trends in Ecology & Evolution* 24(3): 127–35.

Booth, M. T., N. G. Hairston, Jr., and A. S. Flecker. 2020. "Consumer Movement Dynamics as Hidden Drivers of Stream Habitat Structure: Suckers as Ecosystem Engineers on the Night Shift." *Oikos* 129(2): 194–208.

Brown, A. V., and P. P. Brussock. 1991. "Comparisons of Benthic Invertebrates between Riffles and Pools." *Hydrobiologia* 220(2): 99–108.

Cardinale, B. J. 2011. "Biodiversity Improves Water Quality through Niche Partitioning." *Nature* 472(7341): 86–9.

Crotty, S. M., S. J. Sharp, A. C. Bersoza, K. D. Prince, K. Cronk, E. E. Johnson, and C. Angelini. 2018. "Foundation Species Patch Configuration Mediates Salt Marsh Biodiversity, Stability and Multifunctionality." *Ecology Letters* 21(11): 1681–92.

Dangerfield, J. M., T. S. McCarthy, and W. N. Ellery. 1998. "The Mound-Building Termite Macrotermes Michaelseni as an Ecosystem Engineer." *Journal of Tropical Ecology* 14(4): 507–20.

Diamond, J. M. 1986. "Effects of Larval Retreats of the Caddisfly Cheumatopsyche on Macroinvertebrate Colonization in Piedmont, USA Streams." *Oikos* 47: 13–8.

Evans-White, M. A., and G. A. Lamberti. 2006. "Stoichiometry of Consumer-Driven Nutrient Recycling across Nutrient Regimes in Streams." *Ecology Letters* 9(11): 1186–97.

Fisher, S. G., L. J. Gray, N. B. Grimm, and D. E. Busch. 1982. "Temporal Succession in a Desert Stream Ecosystem Following Flash Flooding." *Ecological Monographs* 52(1): 93–110.

Fonseca, D. M., and D. D. Hart. 1996. "Density-Dependent Dispersal of Black Fly Neonates Is Mediated by Flow." *Oikos* 75: 49–58.

Gibbins, C. N., D. Vericat, and R. J. Batalla. 2010. "Relations between Invertebrate Drift and Flow Velocity in Sand-Bed and Riffle Habitats and the Limits Imposed by Substrate Stability and Benthic Density." *Journal of the North American Benthological Society* 29(3): 945–58.

Gulis, V., and K. Suberkropp. 2003. "Leaf Litter Decomposition and Microbial Activity in Nutrient-Enriched and Unaltered

Reaches of a Headwater Stream." *Freshwater Biology* 48(1): 123–34.

Halvorson, H. M., C. Fuller, S. A. Entrekin, and M. A. Evans-White. 2015. "Dietary Influences on Production, Stoichiometry and Decomposition of Particulate Wastes from Shredders." *Freshwater Biology* 60(3): 466–78.

Hammock, B. G., and M. T. Bogan. 2014. "Black Fly Larvae Facilitate Community Recovery in a Mountain Stream." *Freshwater Biology* 59(10): 2162–71.

Hemphill, N. 1988. "Competition between Two Stream Dwelling Filter-Feeders, Hydropsyche Oslari and Simulium Virgatum." *Oecologia* 77: 73–80.

Hölker, F., M. J. Vanni, J. J. Kuiper, C. Meile, H. P. Grossart, P. Stief, et al. 2015. "Tube-Dwelling Invertebrates: Tiny Ecosystem Engineers Have Large Effects in Lake Ecosystems." *Ecological Monographs* 85(3): 333–51.

Jones, C. G., J. H. Lawton, and M. Shachak. 1994. "Organisms as Ecosystem Engineers." In *Ecosystem management* 130–47. New York: Springer.

Kenward, M. G., and J. H. Roger. 1997. "Small Sample Inference for Fixed Effects from Restricted Maximum Likelihood." *Biometrics* 53: 983–97.

Kominoski, J. S., A. D. Rosemond, J. P. Benstead, V. Gulis, and D. W. Manning. 2018. "Experimental Nitrogen and Phosphorus Additions Increase Rates of Stream Ecosystem Respiration and Carbon Loss." *Limnology and Oceanography* 63(1): 22–36.

Lachat Instruments. 2003. "Determination of Nitrate/Nitrite in Surface and Wastewaters by Flow Injection Analysis." QuickChem Method, 10-107-04-1-A.

Lenth, R. V., and M. Hervé. 2015. "lsmeans: Leastsquares Means." R Package Version, 2:20-3. http://CRAN.R-project.org/package=lsmeans.

Li, H., and J. F. Reynolds. 1995. "On Definition and Quantification of Heterogeneity." *Oikos* 73: 280–4.

Lopez, J. W., T. B. Parr, D. C. Allen, and C. C. Vaughn. 2020. "Animal Aggregations Promote Emergent Aquatic Plant Production at the Aquatic–Terrestrial Interface." *Ecology* 101: e03126.

MacDonald, M. J., L. K. Albertson, and G. C. Poole. 2021. "Ecosystem Engineering in the Streambed: Net-Spinning Caddisflies Influence Hydraulic Properties." *Ecohydrology* 14(2): e2266.

Maguire, Z., B. B. Tumolo, and L. K. Albertson. 2020. "Retreat but no Surrender: Net-Spinning Caddisfly (Hydropsychidae) Silk Has Enduring Effects on Stream Channel Hydraulics." *Hydrobiologia* 847(6): 1539–51.

McClain, M. E., E. W. Boyer, C. L. Dent, S. E. Gergel, N. B. Grimm, P. M. Groffman, et al. 2003. "Biogeochemical Hot Spots and Hot Moments at the Interface of Terrestrial and Aquatic Ecosystems." *Ecosystems* 6: 301–12.

Merritt, R. W., and K. W. Cummins. 1996. *An Introduction to the Aquatic Insects of North America*, Third ed. Dubuque: Kendall/Hunt.

Minshall, G. W., and J. N. Minshall. 1977. "Microdistribution of Benthic Invertebrates in a Rocky Mountain (USA) Stream." *Hydrobiologia* 55(3): 231–49.

Mooney, R. J., E. A. Strauss, and R. J. Haro. 2014. "Nutrient Recycling by Caddisflies Alleviates Phosphorus Limitation in Case Periphyton." *Freshwater Science* 33(4): 1086–92.

Nakagawa, S., and H. Schielzeth. 2013. "A General and Simple Method for Obtaining R2 from Generalized Linear Mixed-Effects Models." *Methods in Ecology and Evolution* 4(2): 133–42.

Nakano, D., M. Yamamoto, and T. Okino. 2005. "Ecosystem Engineering by Larvae of Net-Spinning Stream Caddisflies Creates a Habitat on the Upper Surface of Stones for Mayfly Nymphs with a Low Resistance to Flows." *Freshwater Biology* 50(9): 1492–8.

Palmer, M. A., C. C. Hakenkamp, and K. Nelson-Baker. 1997. "Ecological Heterogeneity in Streams: Why Variance Matters." *Journal of the North American Benthological Society* 16(1): 189–202.

Romero, G. Q., T. Gonçalves-Souza, C. Vieira, and J. Koricheva. 2015. "Ecosystem Engineering Effects on Species Diversity across Ecosystems: A Meta-Analysis." *Biological Reviews* 90(3): 877–90.

Sileshi, G. W., M. A. Arshad, S. Konaté, and P. O. Nkunika. 2010. "Termite-Induced Heterogeneity in African Savanna Vegetation: Mechanisms and Patterns." *Journal of Vegetation Science* 21(5): 923–37.

Statzner, B., M. F. Arens, J. Y. Champagne, R. Morel, and E. Herouin. 1999. "Silk-Producing Stream Insects and Gravel Erosion: Significant Biological Effects on Critical Shear Stress." *Water Resources Research* 35(11): 3495–506.

Stein, A., K. Gerstner, and H. Kreft. 2014. "Environmental Heterogeneity as a Universal Driver of Species Richness across Taxa, Biomes and Spatial Scales." *Ecology Letters* 17(7): 866–80.

Sterner, R. W. 1990. "The Ratio of Nitrogen to Phosphorus Resupplied by Herbivores: Zooplankton and the Algal Competitive Arena." *The American Naturalist* 136(2): 209–29.

Swanson, A. C., L. Schwendenmann, M. F. Allen, E. L. Aronson, A. ArtaviaLeón, D. Dierick, and T. J. Zelikova. 2019. "Welcome to the Atta World: A Framework for Understanding the Effects of Leaf-Cutter Ants on Ecosystem Functions." *Functional Ecology* 33: 1386–99. https://doi.org/10.1111/1365-2435.13319.

Tumolo, B. 2023a. "Resource Modification by Ecosystem Engineers Generates Hotspots of Stream Community Assembly and Ecosystem Function." Dryad, Data Set. https://doi.org/10.5061/dryad.1rn8pk0x5.

Tumolo, B. 2023b. "Resource Modification by Ecosystem Engineers Generates Hotspots of Stream Community Assembly and Ecosystem Function." Zenodo, Software. https://doi.org/10.5281/zenodo.7577242.

Tumolo, B. B., L. K. Albertson, W. F. Cross, M. D. Daniels, and L. S. Sklar. 2019. "Occupied and Abandoned Structures from Ecosystem Engineering Differentially Facilitate Stream Community Colonization." *Ecosphere* 10(5): e02734.f.

VanBlaricom, G. R. 1982. "Experimental Analyses of Structural Regulation in a Marine Sand Community Exposed to Oceanic Swell." *Ecological Monographs* 52(3): 283–305.

Vogel, S., and M. LaBarbera. 1978. "Simple Flow Tanks for Research and Teaching." *Bioscience* 28: 638–43.

Wallace, J. B. 1975. "The Larval Retreat and Food of Arctopsyche; with Phylogenetic Notes on Feeding Adaptations in Hydropsychidae Larvae (Trichoptera)." *Annals of the Entomological Society of America* 68(1): 167–73.

Welter, J. R., J. P. Benstead, W. F. Cross, J. M. Hood, A. D. Huryn, P. W. Johnson, and T. J. Williamson. 2015. "Does N2 Fixation Amplify the Temperature Dependence of Ecosystem Metabolism?" *Ecology* 96(3): 603–10.

Winemiller, K. O., A. S. Flecker, and D. J. Hoeinghaus. 2010. "Patch Dynamics and Environmental Heterogeneity in Lotic Ecosystems." *Journal of the North American Benthological Society* 29(1): 84–99.

Woods, H. A., S. Pincebourde, M. E. Dillon, and J. S. Terblanche. 2021. "Extended Phenotypes: Buffers or Amplifiers of Climate Change?" *Trends in Ecology & Evolution* 36(10): 889–98.

Wright, J. P., A. S. Flecker, and C. G. Jones. 2003. "Local Vs. Landscape Controls on Plant Species Richness in Beaver Meadows." *Ecology* 84(12): 3162–73.

Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009. *Mixed Effects Models and Extensions in Ecology with R*, Vol 574. New York: Springer.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Tumolo, Benjamin B., Lindsey K. Albertson, Wyatt F. Cross, Geoffrey C. Poole, Grace Davenport, Melinda D. Daniels, and Leonard S. Sklar. 2023. "Resource Modification by Ecosystem Engineers Generates Hotspots of Stream Community Assembly and Ecosystem Function." *Ecology* e4052. https://doi.org/10.1002/ecy.4052