Occupied and abandoned structures from ecosystem engineering differentially facilitate stream community colonization

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Abstract. Ecosystem engineers transform habitats in ways that facilitate a diversity of species; however, few investigations have isolated short-term effects of engineers from the longer-term legacy effects of their engineered structures. We investigated how initial presence of net-spinning caddisflies (Hydropsychidae) and their structures that provide and modify habitat differentially influence benthic community colonization in a headwater stream by conducting an in situ experiment that included three treatments: (1) initial engineering organism with its habitat modification structure occupied (hereafter caddisfly); (2) initial habitat modification structure alone (hereafter silk); and (3) a control with the initial absence of both engineer and habitat modification structure (hereafter control). Total invertebrate colonization density and biomass was higher in caddisfly and silk treatments compared to controls (~25% and 35%, respectively). However, finer-scale patterns of taxonomy revealed that density for one of the taxa, Chironomidae, was ~19% higher in caddisfly compared to silk treatments. Additionally, conspecific biomass was higher by an average of 50% in silk treatments compared to controls; however, no differences in *Hydropsyche* sp. biomass were detected between caddisfly treatments and controls, indicating initially abandoned silk structures elevated conspecific biomass. These findings suggest that the positive effects of the habitat modification structures that were occupied for the entirety of the experiment may outweigh any potential negative impacts from the engineer, which is known to be territorial. Importantly, these results reveal that the initial presence of the engineer itself may be important in maintaining the ecological significance of habitat modifications. Furthermore, the habitat modifications that were initially abandoned (silk) had similar positive effects on conspecific biomass compared to caddisfly treatments, suggesting legacy effects of these engineering structures may have pertinent intraspecific feedbacks of the same magnitude to that of occupied habitat modifications. Elucidating how engineers and their habitat modifications differentially facilitate organisms will allow for a clearer mechanistic understanding of the extent to which animal engineers and their actions influence aspects of community organization such as colonization.

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INTRODUCTION

Facilitation is an important process that influences broadscale patterns of community organization (Bertness and Leonard 1997, Callaway et al. 2002, Bruno et al. 2003). For example, plants in terrestrial habitats (Callaway et al. 2002), along with seaweeds and algae in marine environments (Bertness and Leonard 1997, Bracken et al. 2007), can shape spatial patterns of biodiversity through amelioration of harsh physical environments (e.g., temperature and moisture) and by acting as refugia from negative biotic interactions (e.g., grazing and predation). Often, facilitation results from ecosystem engineering activities, in which organisms maintain, modify, or create physical habitats that support beneficial conditions for other species (Jones et al. 1994, Romero et al. 2015). Ecosystem engineered habitat modifications, along with the associated effects on ecological and geomorphic processes, are ubiquitous in nature and occur at a variety of scales (Wright and Jones 2006, Sanders et al. 2014). Furthermore, engineered habitats have been shown to endure severe disturbance events and persist far beyond the life of the engineer, leading to legacy effects on community dynamics and ecosystem processes (Ólafsson and Paterson 2004, Hastings et al. 2007). Although ecosystem engineers are recognized as important facilitators that influence community structure (Hastings et al. 2007, Albertson and Allen 2015, Romero et al. 2015), we still have limited understanding of the scales over which communities are differentially affected by engineers or their habitat modifications (Hastings et al. 2007).

Despite the potentially wide-reaching consequences of ecosystem engineering, many facets of habitat engineering animals remain poorly understood (Allen et al. 2014). For example, the majority of inference surrounding community effects of animal ecosystem engineers is limited because investigations typically consider the combined effects of the engineer and its modification. This approach, albeit practical, ignores confounding, potentially negative interactions between the engineer itself and the community (Gribben et al. 2009). For example, behavioral attributes of the engineer (e.g., territoriality, Gribben et al. 2009) may offset or weaken the potentially positive effects of the additional or altered habitat. Although an engineer and its modified habitat could be largely conjunct, isolating the effects of the modification is pertinent to our broader understanding of the spatiotemporal dynamics of ecosystem engineering and could provide novel insight into ecosystem engineering consequences (Prugh and Brashares 2012). Recent research suggests that structural legacy effects of ecosystem engineered facilitation may be stronger (e.g., void of negative biotic interactions from the engineer) and occur over longer timescales than previously predicted (Jones et al. 1994, Hastings et al. 2007, Sanders et al. 2014). For example, negative behavioral (e.g., antagonism) and trophic effects (e.g., predation) of an engineer may last a matter of seconds, while the engineering structure may persist and have effects beyond the life of the engineer (Jones et al. 1994, Hastings et al. 2007, Sanders et al. 2014). Elucidating the behavioral and structural effects of ecosystem engineers, and how those may vary concurrently over space and time, will aid in better understanding and predicting the scales over which ecosystem engineers are most relevant.

Although ecosystem engineering occurs across nearly all habitats (Jones et al. 1994), the positive effects on communities are predicted to be greatest in harsh environments, for example, see support for the stress gradient hypothesis (Bertness and Callaway 1994, Crain and Bertness 2006, He and Bertness 2014). Stream ecosystems are uniquely dominated by physical disturbance events (Resh et al. 1988) and considered among the most susceptible environments to global change with increasingly altered hydrological regimes, species invasions, and frequent temperature extremes (Carpenter et al. 1992, Dodds et al. 2004, Tumolo and Flinn 2017). Given these environmental gradients and stressors, streams are fruitful model systems that can be used to better understand general patterns of ecosystem engineered facilitation (Holomuzki et al. 2010). It has been proposed that the strength of animal ecosystem engineering within streams is dependent on animal body size, density, and behavior within an abiotic context such as variation in hydrology associated with seasonal change in flow (Moore 2006). Recently, these hypotheses were tested in a meta-analysis (Albertson and

Allen 2015), which revealed that larger animals (e.g., migratory salmon) have greater influences on physical transport processes than smaller animals (e.g., insects). However, engineer traits such as biomass were highlighted as particularly important because stream insects affected sediment transport as much as 550 times more than the larger engineers when accounting for per capita biomass (Albertson and Allen 2015). Behavioral mechanisms in stream ecosystem engineering have suggested that interference competition is outweighed by facilitation, resulting in accelerated community recovery following disturbances in empirical studies (Cardinale et al. 2001, Hammock and Bogan 2014). Additionally, resilience of ecosystem engineered structures in lotic environments (e.g., beaver dams) has been shown to have strong legacy effects on ecosystem function and persist for several generations after the death of the engineer (Hastings et al. 2007). Progress has been made in investigating the intricacies of engineering effects within terrestrial, marine intertidal, and lake systems (Callaway et al. 2002, Ólafsson and Paterson 2004, Wright and Gribben 2017); however, we have only begun to understand their importance within stream ecosystems.

Here, we examine engineering effects of net-spinning caddisfly-mediated facilitation on invertebrate communities in a headwater stream. Net-spinning caddisflies (Trichoptera:Hydropsychidae) are aquatic insect larvae that act as ecosystem engineers within headwater streams by modifying the environment in several ways (Fig. 1). These animals build silk catch-nets with retreats of organic/inorganic material among streambed substrate that allow them to passively feed on items flowing through the water column. The silk nets and retreats locally ameliorate habitat by markedly decreasing local hydraulic velocity (Juras et al. 2018), thereby creating stream bed heterogeneity (Diamond 1986, Cardinale et al. 2002) and micro-flow refugia for certain taxa (Nakano et al. 2005). The silk can also act as a stabilizer of gravels and altering sediment disturbance during flood events (Statzner et al. 1999, Cardinale et al. 2004, Johnson et al. 2009, Albertson et al. 2014). Furthermore, caddisfly engineering is highly relevant to colonization dynamics following disturbance events because net-spinners are early colonizers (Hemphill 1988,

Cardinale et al. 2004, but see Hemphill and Cooper 1983). The nets also have the potential to show legacy effects following emergence, death, or downstream drift of the caddisfly itself (Albertson and Daniels 2016). For example, abandoned retreats have been shown to persist for timescales relevant to aquatic insect colonization (i.e., weeks) and withstand extended periods of drought and sediment pollution (Albertson and Daniels 2016). Concurrently, caddisflies have been shown to be highly territorial and antagonistic toward animals surrounding their retreats (Hemphill and Cooper 1983, Hemphill 1988). Thus, untangling facilitation from negative engineer traits (e.g., interference competition) has particular relevance in understanding how this engineer and its habitat modification influence community assembly following disturbance events (Cardinale et al. 2001). Collectively, these aspects of net-spinning caddisfly ecology provide an ideal system to dissect the positive and negative effects of the engineer vs. the engineered structure on stream communities over time.

We tested whether the initial presence of caddisflies and/or caddisfly silk influences characteristics of invertebrate colonization within a headwater stream. Specifically, we tested
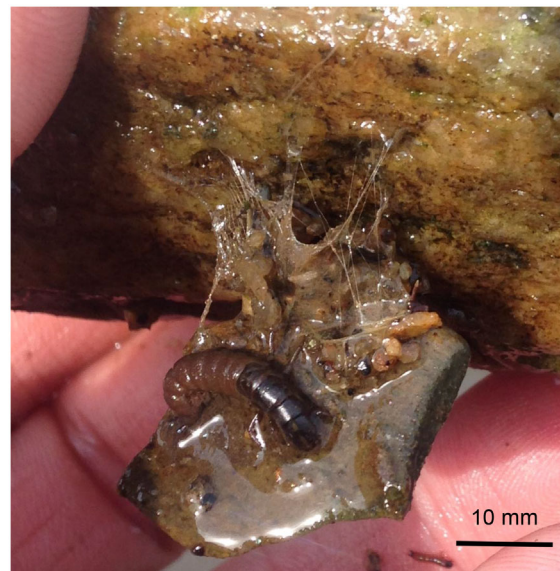

Fig. 1. A caddisfly with its retreat and silk net structure holding stream gravels together. Photo credit: Benjamin B. Tumolo.

whether the initial presence of caddisflies and their silk (hereafter caddisfly, a treatment that included both engineer and habitat modification structure) influenced macroinvertebrate colonization differently than the initial presence of caddisfly silk alone (hereafter silk, a treatment that included just the habitat modification structure) or controls with initial absence of caddisflies and silk (hereafter control). These treatments, respectively, represent (1) the presence of caddisflies prior to colonization of other invertebrates, including conspecifics, because they are early colonists (Cardinale et al. 2004), (2) caddisfly structures alone persisting through a disturbance event (Albertson and Daniels 2016), (3) and a post-disturbance scenario without early caddisfly colonization or legacy of the silk. We predicted that (1) the initial presence of caddisflies with silk and silk alone would increase invertebrate colonization rate and overall benthic density and biomass compared to controls, (2) the initial presence of caddisfly silk alone would increase invertebrate colonization rate, and overall benthic density and biomass, compared to a treatment with caddisflies initially present due to the potential negative effects (e.g., territorial interactions) of the caddisflies offsetting the positive effects of silk structures, and (3) the importance of initial silk or caddisfly presence would vary throughout the temporal duration of the experiment, if treatments converged over time when Hydropsychidae naturally colonized all treatments. Our findings provide insight into the complex ecological dynamics that control how ecosystem engineers may facilitate habitat for other organisms and the relative importance of engineering structures vs. engineer interactions.

METHODS

Experimental design

We conducted our study in the headwaters of the East Branch of White Clay Creek (hereafter WCC, 39°51′59.3″ N 75°47′09.4″ W) located in Avondale, Pennsylvania, from 25 May 2016 to 30 June 2016. The duration of the experiment (30 d) was chosen to represent aspects of the study system's flashy disturbance regimes and organismal life histories. First, macroinvertebrates in streams are known to rapidly recolonize disturbed areas within a matter of days to weeks (Fisher et al.

1982). Second, this timescale is particularly relevant to the duration over which caddisfly silk material is known to last without the engineer itself present (Appendix S1: Fig. S1; Albertson and Daniels 2016). The East Branch of WCC is classified as a third-order piedmont stream with land use predominated by forest and agriculture (Newbold et al. 1997). In our study location, median bed material grain size is approximately 35 mm, riffle width is 5 m, and shade cover is 50% (Albertson et al. 2018). Our experiment was initiated with three treatments: initial caddisflies present with their silk structures (caddisfly), initial habitat modification structure of caddisfly silk alone (silk), and a control treatment with initially no caddisflies or silk present (control). The silk treatment allowed us to test whether initial removal of engineer traits (e.g., territorial behaviors or structural maintenance) when caddisflies are absent influences the role of the habitat modification structure itself on the trajectory of overall colonization patterns. This technique has been used to isolate the effects of aquatic silk engineering structures in a previous study (Hammock and Bogan 2014). Treatments were initiated for measurement of in situ invertebrate colonization in flow-through plastic mesocosms (0.90 m long × 0.124 m wide × 0.135 m deep) with 20-mm plastic mesh secured to the upstream and downstream ends (Appendix S1: Fig. S2). Mesocosms were designed to keep gravels within the experimental units while allowing for natural water flow and invertebrate colonization. Mesocosms were carefully filled by hand with a subsurface layer of pea gravel (~5–10 mm) and then covered with a surface layer 1 grain diameter thick (median grain size of 45 mm). Surface layer gravels were quarried from WCC, while subsurface gravels were purchased. All experimental gravels were dry and denuded of biofilm prior to the experiment for >6 months. The mesocosm habitat was designed to represent an armored surface layer typical of a recently disturbed (denuded of biofilm) gravel-bedded river (Dietrich et al. 1989).

To create the experimental treatments, hydropsychid caddisflies (*Hydropsyche* spp.) of the same developmental stage (3rd–4th instar) were hand collected from WCC over a 24-h period (average length = 13.9 ± 0.11 mm, average dry weight = 5.29 ± 0.25 mg; n = 15 reference samples). Each

mesocosm of the caddisfly and silk treatments was inoculated with 134 caddisflies, equivalent to a density of 1, 290 m^{-2}. Caddisfly densities of these magnitudes are widely reported throughout the eastern United States and are conservative for WCC, which can host over 10,000 hydropsychids/m^2 (Cardinale et al. 2004, Albertson et al. 2018). Caddisfly inoculation was conducted in stream-side flume channels (Appendix S1: Fig. S2), and caddisflies were given 48 h to build silk nets (Albertson et al. 2014). Control mesocosms were also placed in neighboring but isolated stream-side flumes; however, no caddisflies were added. Flumes were kept wet during treatment initiation by pumping water from WCC through a series of settling tanks and screens, which prohibited the transport of macroinvertebrates into experimental mesocosms during initiation (Appendix S1: Fig. S2). Following the 48-h colonization period, individual caddisflies from the silk treatment were removed from nets and gravels within the mesocosm with forceps while leaving silk material intact, a method successfully used with other aquatic silk-producing insects (Hammock and Bogan 2014). Some caddisflies crawled below the surface gravels; thus, to ensure the desired treatment was accomplished, each piece of surface gravel was lifted and the subsurface layer was inspected. While we recognize that this technique potentially broke or stretched silk strands connecting adjacent gravels, thereby reducing one mechanism for invertebrate facilitation related to gravel stabilization, our study was conducted at baseflow when gravels were not mobilized by high flows. Perhaps most importantly, this technique did not interrupt the presence of silk on rock surfaces (i.e., not between gravels), where it reduces flow velocity and acts as an important facilitation pathway for benthic invertebrate taxa seeking flow refuge and optimized food delivery (Cardinale et al. 2002, Nakano et al. 2005). Following manipulation, individual mesocosms were promptly returned to the artificial channel. The caddisfly and control treatment gravels were treated identically to the silk treatment (i.e., surface gravels were briefly lifted); however, caddisflies were not removed from the caddisfly treatment and no caddisflies were present in the control. After all of the mesocosms were manipulated and treatments were

established, individual mesocosms were carefully moved and placed into WCC. One mesocosm of each treatment was placed in each of eight consecutive riffle habitats within WCC for a total of $n = 8$ for each treatment. We selected mesocosm site locations with similar physical riffle conditions (water depth, channel width, riparian vegetation) and randomized treatment position at each site to ensure a treatment was not confounded by its proximity to the left or right stream banks. Mesocosms were secured with rebar and recessed within surrounding substrates. During the experiment, detritus was removed from the upstream end of mesocosms every 24 h.

We did not maintain experimental treatments throughout the duration of the experiment by continually removing *Hydropsyche* spp. individuals from control and silk treatments. Instead, all treatments were equally exposed to natural colonization of *Hydropsyche* spp. once moved into WCC (see *Results*) with potential for treatment convergence over time. This design allowed us to address our goal of testing the effects of initial experimental treatments on total invertebrate colonization, including other hydropsychids. We chose this approach allowing for potential convergence of treatments over time for three primary reasons. First, our experiment aimed to measure the effect of initial presence of engineers or their habitat modification structures given the recognized importance of colonization history in shaping community assemblage (Cardinale et al. 2001). Second, it would be logistically challenging to exclude *Hydropsyche* spp. colonists without confounding the colonization of other taxa, which would further constrain the ecological relevance of the experimental design. Third, hydropsychids are an abundant member of headwater stream communities (Cardinale et al. 2001, 2004, Albertson et al. 2014), and being able to evaluate potential positive and/or negative feedbacks between the initial presence of this particular taxon and the final presence of this same taxon is ultimately important to advance understanding of these headwater stream ecosystems.

Sampling and processing of invertebrate colonization

Invertebrates were sampled from individual mesocosms once every 24 h for the first five days

of the experiment and then once every five days for the next 25 d for a total of 10 sampling events. During each sampling event, three randomly selected surface gravels were removed and placed on a 150-μm sieve. Rocks were sprayed with filtered water over the sieve and visually inspected to ensure all macroinvertebrates were removed. Rocks were then towel-dried and marked with a permanent marker (to avoid resampling) and placed back in the mesocosm. Invertebrates collected in the sieve were transferred to a Whirl-Pak, preserved with 70% ethanol and transported to the laboratory.

Invertebrates were enumerated, measured in length to the nearest mm, and identified to genus or lowest practical taxonomic level (Merritt and Cummins 1996, Smith 2001). Total invertebrate biomass in each sample was estimated as mg ash free dry mass (AFDM) per sample using established taxon-specific length–mass relationships (Benke et al. 1999). Invertebrate taxon richness was estimated as the total number of unique taxa per sample. All surface gravels used in the experiment were photographed, and surface area was measured to the nearest mm with ImageJ (National Institutes of Health, Bethesda, Maryland, USA). Preliminary analyses showed no significant differences in rock size among treatments; therefore, density was estimated as no. per sample and overall biomass as mg AFDM per sample. For the caddisfly treatments, all *Hydropsyche* spp. ≥13 mm length (i.e., the individuals initially added to the caddisfly treatment mesocosms) was removed from further analyses to avoid confounding our initial caddisfly inoculation with natural colonization of other taxa and/or newly colonizing individuals of this taxon. Additionally, preliminary analyses showed that three taxa (Chironomidae, *Hydropsyche* spp. and *Baetis* spp.) contributed to over 80% of the overall invertebrate density; thus, additional analyses considered the density and biomass between treatments of each of these dominant taxa separately.

Data analysis

Total invertebrate density and biomass, the dominant taxa's density and biomass, species richness and colonization rate were analyzed using linear mixed-effects models. Linear mixed-effects models comparing invertebrate density, invertebrate biomass, dominant taxa density, dominant taxa biomass, and richness across treatments included the fixed effects of treatment and day and random effects of site alone and individual mesocosm (Tank) nested within site, nested within sampling date as represented here:

$$\text{lmer}(\text{Response} \sim \text{Treatment} \times \text{Day} + (1|\text{Site/Tank}), \text{data} = \text{databasename})$$

These models accounted for the non-independence of samples taken at the same mesocosm over multiple sampling events by using a standard mixed-model repeated-measures design where mesocosm was nested within sampling date (Bolker 2008, Zuur et al. 2009). Colonization rate was calculated by fitting a linear regression to the number of invertebrates per sample colonized over the first 10 d of the experiment. Colonization rate was analyzed with a fixed effect of treatment and a random effect of site because distinction of sampling date was precluded as this metric subsumed values from the first 10 d of the experiment. Invertebrate density and biomass were calculated for the three dominant taxa. Density and biomass of the total community, as well as dominant taxa, were natural log-transformed to meet assumptions of normality. All mixed-effects models were fit with the lme4 package (Bates et al. 2014), and significance was tested using a Kenward-Roger denominator degrees of freedom approximation (Kenward and Roger 1997, Bolker et al. 2009). Post hoc comparisons of least squares means and confidence intervals for response variables between treatments were calculated using the lsmeans function (Lenth and Hervé 2015). All linear mixed-effects model analyses were conducted using R version 3.3.1 (R Development Core Team 2016).

Invertebrate community composition was compared among treatments using non-metric multi-dimensional scaling (NMDS) applied to a Bray–Curtis dissimilarity matrix based on square-root-transformed density to account for weighted contribution of rare and common taxa (Zar 1996). Non-metric multi-dimensional scaling on a Bray–Curtis dissimilarly matrix is widely practiced in community ecology as it provides robust inference to unconstrained ordination of ecological variables in multivariate space (Kruskal 1964, Faith et al. 1987, McCune et al. 2002). The NMDS ordination was conducted

using PRIMER-E v.6.2 (PRIMER-E Ltd, Ivybridge, UK; Clarke and Gorley 2006) with several random starting configurations; the lowest stress was selected after 20 trials for a 2-dimensional solution. To test for differences in invertebrate communities among treatments, we conducted an analysis of similarity (ANOSIM) using the Bray–Curtis distance matrix with 999 permutations (Oksanen et al. 2007). Taxa influencing community structure of treatments were identified using a similarity percentage analysis (SIMPER). Field experiments are expected to have high variability among sampling replicates; therefore, all analyses were tested for significance at alpha $\alpha = 0.05$ and marginal significance at $\alpha = 0.1$. Finally, because our goal was to directly compare how caddisflies and their silk habitat modification structures influence invertebrate communities, our analysis only considered invertebrates within the experimental mesocosms, and we did not compare how our experimental treatments related to ambient unmanipulated invertebrate characteristics of WCC.

Results

Throughout the experiment, a total of 20,576 invertebrates of 54 unique taxa were collected and identified from mesocosms. The three dominant taxa collected during the experiment were Chironomidae, which comprised 61.3%, *Hydropsyche* spp., which accounted for 16.4%, and the mayfly genus, *Baetis* spp., which comprised 6.7% of total individuals.

Invertebrate density showed patterns of rapid colonization across treatments, with consistently higher values recorded in caddisfly and silk treatments compared to controls ($F_{2,14} = 4.98$, $P = 0.021$; Fig. 2a, Table 1; Appendix S1: Tables S1, S2). These patterns were most evident through day 15 of the experiment, after which time invertebrate density began to converge among all treatments (Fig. 2a). Overall invertebrate density was 31% higher in caddisfly treatments than in control (83.31 ± 10.89 vs. 57.21 ± 10.90, individuals per sample, $t_{14} = 3.09$, $P = 0.008$); however, no differences were found between caddisfly treatments and silk ($P = 0.423$). Overall invertebrate density was 25% higher in silk treatments than in controls (76.34 ± 10.89 vs. 57.21 ± 10.90 individuals per

sample, $t_{14} = -2.27$, $P = 0.040$). Silk treatments showed an increase in total density after day 15 of the experiment ($F_{9, 189} = 14.26$, $P = 0.001$; Fig. 2a, Table 1; Appendix S1: Table S1). These temporal differences in total density of the silk treatment can be attributed to patterns of higher Chironomidae density observed after day 15 ($F_{9, 189} = 13.93$, $P = 0.001$, Fig. 3c, Table 1; Appendix S1: Table S2). In addition, initial caddisfly presence had a consistent positive effect by increasing Chironomidae density compared to control and silk treatments throughout the duration of the experiment, but especially up to day 15 ($F_{2,14} = 7.30$, $P = 0.07$; Fig. 3c, Table 1; Appendix S1: Tables S1, S2). Overall Chironomidae density was 37% higher in caddisfly treatments compared to controls (64.69 ± 7.47 vs. 40.68 ± 7.48 Chironomidae per sample, $t_{14} = 3.82$, $P = 0.002$) and 19% higher compared to silk (64.69 ± 7.47 vs. 52.28 ± 7.48 Chironomidae per sample, $t_{14} = 1.98$, $P = 0.068$). Furthermore, Chironomidae density was 29% higher in silk compared to control treatments with marginal statistical significance ($t_{14} = -0.20$, $P = 0.086$). No treatment effects were detected for density of *Hydropsyche* spp. and *Baetis* spp. ($P > 0.15$, Table 1; Appendix S1: Table S1).

We detected a significant difference in biomass among treatments ($F_{2,14} = 4.68$, $P = 0.023$; Fig. 2b; Appendix S1: Table S1), with a 35% increase of overall biomass in caddisfly compared to control treatments (3.39 ± 0.66 vs. 2.19 ± 0.66 mg AFDM per sample, $t_{14} = 2.56$, $P = 0.049$), and silk treatments had 45% higher overall biomass compared controls (4.01 ± 0.66 vs. 2.19 ± 0.66 mg AFDM per sample, $t_{14} = 2.56$, $P = 0.003$); however, there were no differences in overall biomass between silk and caddisfly treatments ($P = 0.3$, Table 1; Appendix S1: Table S1). When split up by the dominant three taxa initial caddisfly presence had positive effects on Chironomidae biomass relative to controls ($F_{2,14} = 7.42$, $P = 0.006$; Fig. 3f, Table 1; Appendix S1: Tables S1, S2), increasing chironomid biomass by 45% (0.76 ± 0.11 vs. 0.42 ± 0.11 Chironomidae mg AFDM per sample, $t_{14} = 3.83.56$, $P = 0.002$) and initial silk presence increased chironomid biomass by 32% compared to controls (0.63 ± 0.11 vs. 0.43 ± 0.11 Chironomidae mg AFDM per sample, $t_{14} = -2.24$, $P = 0.04$). However, no differences in Chironomidae biomass were detected between
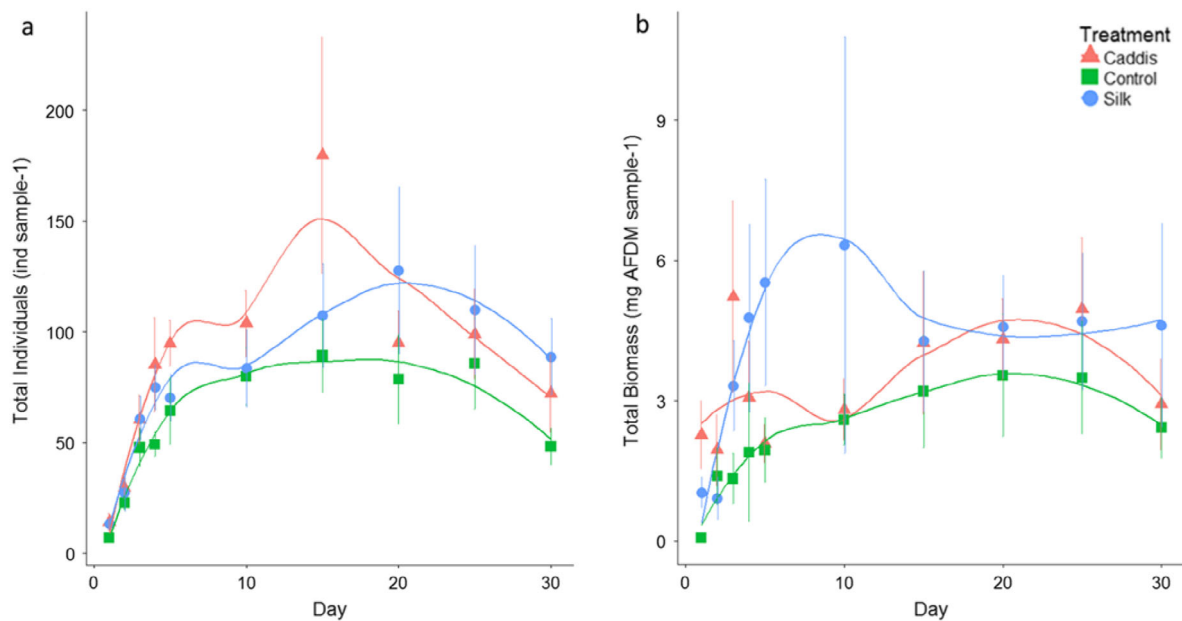
Fig. 2. Experimentally measured mean values (± standard error) with line loess fit of (a) invertebrate density (individuals per sample) and (b) invertebrate biomass (mg AFMD per sample) compared between caddisfly, silk, and control treatments samples across the ten sampling dates of the experiment.

Table 1. Summary table of treatment effects on overall invertebrate density, biomass, colonization rate, and differences in dominant invertebrate density and biomass of *Hydropsyche* sp., *Baetis* sp., and Chironomidae compared between caddisfly, silk, and control treatments across the ten sampling dates of the experiment.

	Outcome		
Metric	Caddis vs. Control	Silk vs. Control	Caddis vs. Silk
Overall density	Caddis > Control 31%	Silk > Control 25%	No difference
Overall biomass	Caddis > Control 35%	Silk > Control 45%	No difference
Richness	No difference	No difference	No difference
Colonization rate	No difference	No difference	No difference
Chironomidae density	Caddis > Control 45%	Silk > Control 32%	Caddis > Silk 19%
Baetis density	No difference	No difference	No difference
Hydropsyche density	No difference	No difference	No difference
Chironomidae biomass	Caddis > Control 45%	Silk > Control 32%	No difference
Baetis biomass	No difference	No difference	No difference
Hydropsyche biomass	No difference	Silk > Control 50%	No difference

silk and caddisfly treatments ($t_{14} = -1.60$, $P = 0.133$, Table 1; Appendix S1: Tables S1, S2). Furthermore, initial presence of silk increased *Hydropsyche* spp. biomass by 50% relative to controls (Fig. 3d, 2.87 ± 0.55 vs. 1.43 ± 0.55 *Hydropsyche* mg AFDM per sample, $t_{14} = 2.74$, $P = 0.011$); however, no differences were detected between silk and caddisfly treatments ($P = 0.2$)

or caddisfly and control treatments ($P = 0.2$). The result of greater *Hydropsyche* biomass and lower density in the silk treatment compared to the caddisfly treatment demonstrates that the same densities of larger sized individual *Hydropsyche* spp. colonized silk treatments compared to control and caddisfly treatments (Fig. 3a vs. d). Patterns in *Baetis* spp. biomass did not show any
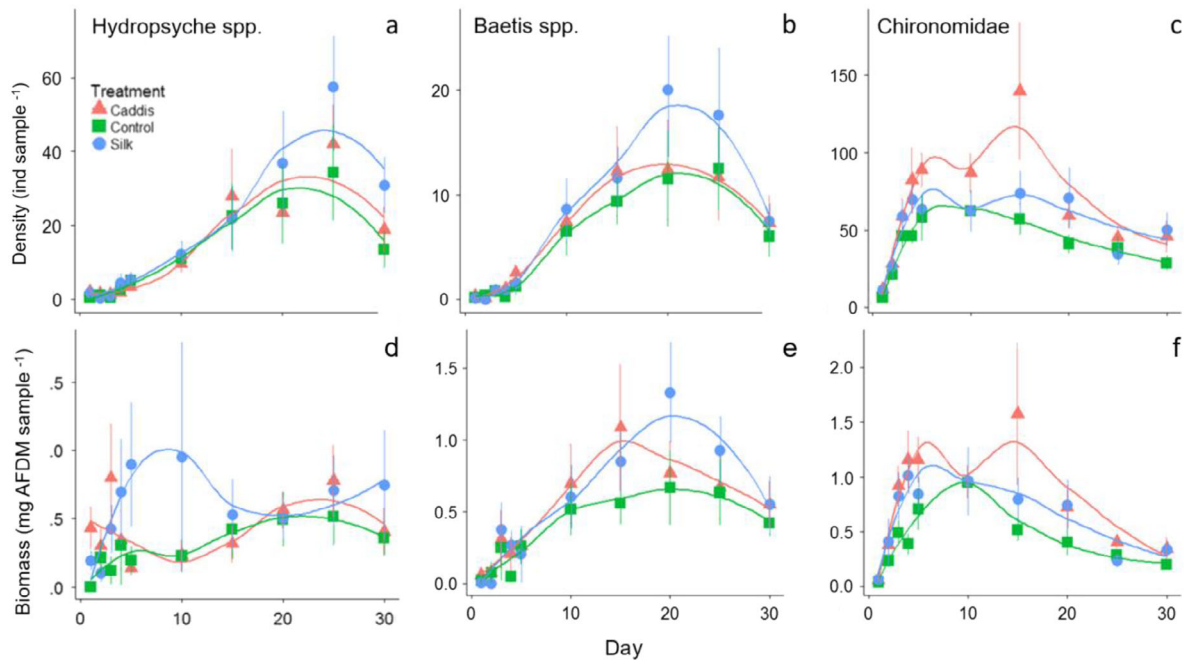
Fig. 3. Experimentally measured mean values (± standard error) with line loess fit of dominant invertebrate density (individuals per sample) and biomass (mg AFDM per sample) of *Hydropsyche* sp. (a, d), *Baetis* sp. (b, e), and Chironomidae (c, f), compared between caddisfly, silk, and control treatments across the 10 sampling dates of the experiment.

differences among treatments throughout the duration of the experiment ($F_{2,14} = 1.67$, $P = 0.222$; Fig. 3e, Table 1; Appendix S1: Table S1).

No differences were detected in richness ($P = 0.78$) or colonization rate (calculated as number of invertebrates·sample^{-1}·d^{-1}) over the first ten days of the experiment ($P = 0.26$) among treatments, suggesting there were no differences in invertebrate community composition among initial treatments throughout the experiment (Table 1; Appendix S1: Table S3). Additionally, overall invertebrate community composition pooled across time showed high overlap among treatments based on NMDS and ANOSIM analyses (Appendix S1: Fig. S3, 2D stress = 0.15, ANOSIM Global $R = -0.002$, $P > 0.9$) suggested no overall community differences among treatments. The SIMPER analysis indicated 18 taxa contributed to ~90% of the multivariate locations of communities in initial caddisfly, silk and control treatments. In all treatment comparisons, Chironomidae, *Hydropsyche* spp., *Baetis* spp., and Simuliidae explained ~52% of multivariate

locations of communities, further suggesting similar general composition among treatments.

DISCUSSION

Facilitation by habitat amelioration can influence community structure and recovery, and positive interactions are increasingly recognized as a fundamental driver of ecological organization comparable in strength to that of predation and competition. Furthermore, facilitation by habitat transformation has been documented across terrestrial, marine and freshwater environmental gradients where ecosystem engineers may serve as important targets for conservation (Crain and Bertness 2006, Romero et al. 2015). Few studies, however, have evaluated the different effects of engineers and their habitat modification structures or have considered the legacy effects of such habitat transformations on community dynamics following the loss of the engineer. Our study shows that (1) the initial presence of an ecosystem engineer (*Hydropsyche* spp.) and its abandoned structure increased aspects of

invertebrate colonization, (2) the initial presence of the engineer had variable effects on certain taxa compared to initially abandoned engineering structures, (3) positive effects of the engineer and their structure outweighed presumed negative engineer traits, and (4) initially abandoned engineered structures positively affected conspecific biomass similarly to initially occupied structures, suggesting that positive legacy effects of engineering structures occur at similar magnitudes to occupied engineering structures.

Facilitation by caddisflies

Our analysis showed that the initial presence of caddisflies and silk facilitated patterns of local invertebrate density and biomass differently during colonization. These findings were partly consistent with our prediction that caddisflies would facilitate invertebrate colonization density and biomass, namely by supporting chironomids and hydropsychids. However, our findings differed from our predictions in that abandoned ecosystem engineering structures only had greater positive effects than caddisfly presence in terms of conspecific biomass. Patterns of local aquatic invertebrate density and biomass could have implications for ecosystem function, as this group of organisms represents an important food web linkage between basal resources and higher trophic levels within and across ecosystem boundaries (Baxter et al. 2005). However, the relevance of our results to these broader scale predictions needs to be tested in future experiments and under natural field conditions. Perhaps unsurprisingly, the majority of research regarding animal engineering across a variety of ecosystems has focused on the impact of large bodied vertebrates, such as beavers and their extensive dam complexes (Naiman et al. 1988, Hastings et al. 2007) or elephants and bison clearing vegetation (Haynes 2012). In this study, we echo a growing body of work demonstrating large effects of small invertebrates (<1 cm) on local community characteristics, highlighting the significance of numerically abundant, small-bodied ecosystem engineers (Ólafsson and Paterson 2004, Benelli et al. 2018).

Previous studies have shown that caddisfly engineering increases abundances of certain invertebrates at local scales, perhaps by reducing flow velocity, increasing heterogeneity, or providing food supplements. For example, Nakano et al. (2005) showed that caddisfly retreats provide low-flow refugia and increase abundances of mayflies (*Ephemerella*). Our analysis showed that densities of Chironomidae, a family of aquatic insects with even lower flow preferences compared to those of *Ephemerella* (Armanini et al. 2011), were greater in the presence of caddisflies and silk indicating flow refuge as a possible mechanism for habitat facilitation in our study system. Indeed, these experimental findings and hypotheses are supported by hydraulic modeling demonstrating up to a 60% reduction of interstitial flow velocity in the presence of caddisfly silk structures (Juras et al. 2018). Caddisflies also stabilize surface gravels and decrease sediment disturbance by increasing critical bed shear stress (Cardinale et al. 2004, Albertson et al. 2014), which may further improve physical habitats for invertebrates by providing a refuge from scour (Brittain and Eikeland 1988). Along with the physical habitat amelioration, the silk of caddisflies and other stream insects (Diptera:Simuliidae) has also been shown to transfer water column food resources to the streambed, possibly increasing food availability to secondary producers such as invertebrates (O'Connor 1993, Hammock and Bogan 2014). Thus, we hypothesize that caddisflies facilitate invertebrate colonization through a combination of non-mutually exclusive mechanisms of physical habitat amelioration and increased food availability, which may have consequences ranging from the population to community level. These mechanisms remain to be tested and should be considered in future experiments.

We predicted that caddisflies and their silk would influence other characteristics of communities, such as colonization rate and composition; however, we found no such patterns. These findings suggest that the initial presence of caddisflies and silk did not influence the speed or composition of community assembly within a headwater stream. The underlying mechanisms, food availability or flow disturbance refuge, for caddisfly facilitation were not tested, making it difficult to evaluate why there were changes measured in density and biomass and not in composition. However, other studies have shown similar patterns of habitat modification resulting in changes in abundance with little

effect on community structure. For example, extensive habitat modification by grazing of migratory fishes has been shown to drastically alter invertebrate abundance with variable, less predictable patterns of community structure response (Flecker 1996). Perhaps our analysis shows that engineered habitat can result in more, yet functionally equivalent habitat (i.e., caddisfly retreats may provide habitat similar to that of important interstitial pore spaces within the gravel bed), leading to greater abundances but not changes in community composition.

Contrary to our predictions, we found initial presence of caddisflies had similar effects on density and biomass compared to silk treatments; however, important aspects of overall density and biomass were influenced differently by caddisfly and silk presence. Specifically, we show that initial caddisfly presence increases Chironomidae density compared to silk treatments, while initial silk presence increases body sizes of conspecific colonizers compared to initial caddisfly presence. Our results contrast with earlier work showing competitive exclusion of other stream invertebrates by hydropsychids (Hemphill and Cooper 1983, Diamond 1986, Hemphill 1988) and intense fighting between conspecifics (Englund and Olsson 1990). However, our results are congruent with other patterns observed in caddisfly and blackfly larvae colonization studies (Cardinale et al. 2002, Hammock and Bogan 2014), suggesting competition and behavioral antagonism of the caddisfly engineer can be negligible and/or offset by the positive effects of facilitative habitat modification. Furthermore, findings of conspecific legacy effects on *Hydropsyche* spp. biomass from initially abandoned engineering structures align with observations of larger instar caddisflies taking over abandoned retreats (Englund and Olsson 1990). Broadly, these results highlight the importance of untangling simultaneous effects of engineers and their habitat modifications and developing a further understanding of species interaction networks and community effects of ecosystem engineering (Prugh and Brashares 2012).

Does what you leave behind count?

Recent advances in geomorphology and ecology have recognized the importance of legacy in shaping physical landscapes and biological communities, with particular attention to the effects of land use, invasive species, and ecosystem engineering (Cuddington 2011, Ruffing et al. 2015). Our study presents evidence that experimentally abandoned engineered structures can influence colonization of community density, biomass, and conspecifics in a headwater stream for at least 30 d (Fig. 2; Appendix S1: Figs. S1, S3), suggesting that caddisfly structures may persist and continue to have positive legacy effects. Caddisflies frequently drift downstream from their retreats as a means of dispersal (Brittain and Eikeland 1988, Benke et al. 1991) and predator avoidance (Fairchild and Holomuzki 2005). If caddisfly nets remain intact during and after a drift-inducing disturbance, based on our results, community density, biomass, and conspecific biomass should experience legacy effects from caddisfly engineering. However, other aspects of invertebrate colonization that were affected by initial caddisfly presence (Chironomidae density) were affected less by initially abandoned ecosystem engineering structures. These differences in facilitation suggest the presence of the engineer with its habitat modification may be important in maintaining function of ecosystem engineered structures and consequently its positive effects on the community. Indeed, hydropsychids are known to tend their nets so as to keep them clear of suspended sediments and to alter mesh pore spacing in variable flow conditions (Runde and Hellenthal 2000), and perhaps these maintenance activities are important in regulating the extent to which caddisflies facilitate Chironomidae colonization. Furthermore, these differences in engineering effect between occupied and abandoned habitat modifications have broad implications for the way communities organized by ecosystem engineers are targeted for conservation and restoration purposes (Byers et al. 2006). For example, management strategies designed to mimic benefits of naturally occurring ecosystem engineering structures and relationships, such as beaver dam analogs, may only offer a fraction of ecological services provided by the engineer in conjunction with its habitat modification (Pollock et al. 2014). Taken together, legacy effects of caddisfly structures were shown to have a pertinent feedback; however, community effects of ecosystem engineering were greatest with the initial presence of the engineer.

Study limitations

Even given the strong evidence we detected for positive effects of initial presence of caddisfly larvae and their silk structures on benthic taxa, our findings should be interpreted with caution. Because our study was conducted within in situ mesocosms, the potential for the same patterns to develop at broader reach-scales, where colonization and dispersal dynamics occur across larger distances of natural river ecosystems is unknown (Brown and Swan 2010). Although we did not investigate how the changes to invertebrate density and biomass that we detected might influence ecosystem processes or trophic dynamics, we suspect that they could influence resource processing or availability for higher trophic levels (Graça 2001), and future work should measure how and when. Additionally, our experiment only encompassed a limited range of gravel sizes and flow conditions, when a broader range of gravel sizes and flow regimes (e.g., flooding or drought) are common in natural streams, and these physical factors are highly relevant to colonization dynamics of benthic stream invertebrates (Fisher et al. 1982). Finally, we did not maintain treatments, so the initial control and initial silk only treatments converged with the caddisfly treatments. We believe this convergence reasonably captures colonization dynamics of the entire invertebrate assemblage, including hydropsychids, but also acknowledge that this experimental approach weakens our ability to isolate effects of just silk alone. Despite these limitations, however, our conclusions remain strongly consistent with our original hypotheses and warrant further exploration.

Conclusion

Our study shows initial presence of ecosystem engineering caddisflies, and their structures have positive effects on local invertebrate density and biomass within a headwater stream ecosystem. Our results suggest potential negative behavioral (i.e., antagonism) and/or consumptive effects of the caddisfly engineer were offset by positive effects (i.e., facilitation) of the habitat modification. Additionally, our findings reveal that positive effects on local Chironomidae density associated with initial engineer presence did not occur in the initial presence of the engineers'

abandoned habitat modification structure, suggesting engineer presence may be important in maintaining facilitative habitat modifications. Finally, we detected evidence of abandoned habitat modifications increasing conspecific biomass, signifying caddisfly engineers may have intraspecific legacy effects, manifesting at equal magnitudes and temporal scales as the effects of occupied habitat modifications. Our study shows positive community-level changes resulting from ecosystem engineering, highlighting the importance of intricate animal ecologies involved in animal–environment relationships. Continued appreciation of these abiotic and biotic feedback loops and their respective legacies may further our understanding of multi-scale community dynamics (Allen et al. 2014).

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