

RESEARCH ARTICLE

Facilitation strength across environmental and beneficiary trait gradients in stream communities

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Abstract

1. Ecosystem engineers modify habitats in ways that facilitate other community members by ameliorating harsh conditions. The strength of such facilitation is predicted to be influenced by both beneficiary traits and abiotic context. One key trait of animals that could control the strength of facilitation is beneficiary body size because it should determine how beneficiaries fit within and exploit stress ameliorating habitat modifications. However, few studies have measured how beneficiary body size relates to facilitation strength along environmental gradients.
2. We examined how the strength of facilitation by net-spinning caddisflies on invertebrate communities in streams varied along an elevation gradient and based on traits of the invertebrate beneficiaries. We measured whether use of silk retreats as habitat concentrated invertebrate density and biomass compared to surrounding rock surface habitat and whether the use of retreat habitat varied across body sizes of community members along the gradient.
3. We found that retreats substantially concentrated the densities of a diversity of taxa including eight different Orders, and this effect was greatest at high elevations. Caddisfly retreats also concentrated invertebrate biomass more as elevation increased. Body size of invertebrates inhabiting retreats was lower than that of surrounding rock habitats at low elevation sites, however, body size between retreats and rocks converged at higher elevation sites. Additionally, the body size of invertebrates found in retreats varied within and across taxa. Specifically, caddisfly retreats functioned as a potential nursery for taxa with large maximal body sizes. However, the patterns of this taxon-specific nursery effect were not influenced by elevation unlike the patterns observed based on community-level body size.
4. Collectively, our results indicate that invertebrates use retreats in earlier life stages or when they are smaller in body size independent of life stage. Furthermore, our analysis suggests that facilitation strength intensifies as elevation increases within stream invertebrate communities.

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5. Further consideration of how trait variation and environmental gradients interact to determine the strength and direction of biotic interactions will be important as species ranges and environmental conditions continue to shift.

KEYWORDS

ecosystem engineering, flow refuge, habitat modification, hotspot, nursery effect positive interaction, river

1 | INTRODUCTION

Ecosystem engineering is a ubiquitous process by which organisms influence community assembly through modification of physical and resource environments (Hastings et al., 2007; Jones et al., 1994; Romero et al., 2015). Often, the modification of environments by ecosystem engineers facilitates increased density and biomass of other taxa (hereafter 'beneficiaries') by creating novel habitats and ameliorating harsh conditions (Bruno et al., 2003; Romero et al., 2015). These facilitative interactions can maintain species coexistence, structure communities and influence ecosystem function (Bruno et al., 2003; Gross, 2008; Romero et al., 2015). The strength of such interactions is predicted to be influenced by both organism traits and abiotic context; however, few studies have measured how beneficiary traits relate to facilitation strength across environmental gradients.

Functional traits of beneficiaries could be used for grouping members of the community based on how they experience stress and amelioration of stress (McGill et al., 2006; Suding et al., 2008; Tumolo et al., 2020). Body size, for example, is a functional trait that varies widely within and across species and environmental gradients (McGill et al., 2006; Woodward et al., 2005) and may affect the ability of beneficiaries to take advantage of modified habitats and resources. Body size determines the ability to fit within and exploit stress ameliorating structures (Nakano et al., 2007; Pringle, 2008; Wright & Gribben, 2017) because only organisms of certain sizes will be capable of taking refuge in or near engineered habitat structures such as burrows, crevices, and mounds that ameliorate physical stress (e.g. scouring, desiccation, temperature extremes) or provide predator refuge (Hastings et al., 2007). Positive interactions that depend on body size can change temporally throughout beneficiary life stage and over environmental gradients because of variation in resource availability and community composition (Callaway & Walker, 1997; Miriti, 2006). Consequently, taxa with large maximal body sizes may benefit more from certain positive interactions when they are small and at early stages of development (Callaway & Walker, 1997; Cameron et al., 2019; Miriti, 2006). For example, young plants experience a nursery effect when they are supported by established adult neighbours that operate as 'nurse plants' (Tewksbury & Lloyd, 2001). Therefore, focusing on beneficiaries' functional traits, such as body size along environmental gradients may uncover positive interactions that have been previously overlooked.

The ecological gradients present within stream networks make them an ideal study system for understanding how traits interact with environmental gradients to determine the strength of facilitation. Mountain streams often exhibit large changes in elevation over relatively short distances that can present a myriad of stressors to resident invertebrate communities that are expected to intensify with increasing elevation (Figure S1; Atkinson et al., 2018; Minshall et al., 1992). Higher elevation segments of stream networks typically have colder temperature regimes and shorter growing seasons that constrain the growth of invertebrates (Vannote & Sweeney, 1980). Input of allochthonous organic matter food resources is often low in unforested high elevation streams because of a limited forest canopy (McCutchan & Lewis, 2002; Minshall et al., 1992) and autochthonous production of benthic algae may be limited to short duration, ice-free times of year (Junker & Cross, 2014). Furthermore, stream channels at higher elevations tend to have steeper slopes, larger bed particles and more episodic bedload transport, which can all create more intense hydrogeomorphic conditions for invertebrates, and result in dislodgement, increased metabolic expenditure and mortality (Table S1; Effenberger et al., 2006; Halwas & Church, 2002; Montgomery & Dietrich, 1988; Schwendel et al., 2010). Collectively, the strength of positive biotic interactions that ameliorate potential stresses resulting from elevation gradients, including temperature, resource availability and bed shear stress, are expected to intensify with increasing elevation (i.e. stress gradient hypothesis, sensu Bertness & Callaway, 1994). Moreover, traits of invertebrates experiencing constraints associated with elevation should further contextualize the strength of facilitation along such an environmental gradient (Albertson et al., 2021; Silknetter et al., 2020).

We measured how the strength of positive interactions resulting from silk structures of net-spinning caddisflies is influenced by invertebrate beneficiary body size across an elevation gradient. Net-spinning caddisflies (Trichoptera: Hydropsychidae) are abundant in streams globally and act as ecosystem engineers by modifying the environment in several ways that facilitate increased invertebrate colonization creating hotspots of ecosystem function (Cardinale et al., 2001; Nakano et al., 2005; Tumolo et al., 2023). These animals build silk catch-nets with retreats of organic and inorganic material among stream substrates that allow them to passively feed on suspended detritus (Wallace, 1975). Caddisfly silk nets and retreats locally reduce hydraulic velocity (Cardinale et al., 2002; Maguire et al., 2020), creating refugia for invertebrates (Nakano et al., 2005) similar to the effects of mussels on near-bed hydraulics (Sansom et al., 2018, 2020). The silk can also

bind small gravels, reducing bed movement during high flow events (Albertson et al., 2014, 2019). Additionally, caddisfly retreats are constructed by binding together layers of wood and leaf fragments that in turn are colonized by microbial communities (Wallace, 1975) concentrating detrital and autotrophic resources for invertebrate consumers (Tumolo et al., 2023). Furthermore, retreat structures are relatively small, on the scale of 10–15 mm (Maguire et al., 2020; Wallace, 1975), and therefore should favour lower beneficiary body sizes.

Stream invertebrates that could benefit from caddisfly structures are constrained by physiological stress associated with high elevation conditions (Atkinson et al., 2018; Minshall et al., 1992; Poff et al., 2018) and demonstrate large ranges in body size spanning several orders of magnitude within and across taxa along elevation gradients (Figure S2; Huryn & Wallace, 2000; Nelson et al., 2017; Vieira et al., 2006). Invertebrate body size changes substantially throughout ontogenesis and often multiple different life stages of the same species are present in the same location because of overlapping cohorts (Huryn & Wallace, 2000; Sweeney & Vannote, 1978). Additionally, intraspecific differences in body size may be independent of age, especially in cold or more resource poor environments where growth is slow overall compared to warm, resource-rich locations (Nelson et al., 2017; Sweeney & Vannote, 1978). Thus, quantifying the strength of caddisfly facilitation for stream invertebrates at different elevations provides a model system to better understand the role of beneficiary body size in controlling the strength of facilitation along gradients. Furthermore, describing if and how caddisfly retreats provide habitat for taxa at the small end of their respective size spectrum could shed light on nursery effects within animal communities.

Here, we examined whether caddisfly retreats were inhabited by other invertebrates, and whether the potential use of retreats concentrated density and biomass of invertebrates compared to surrounding rock surface habitat. We also investigated whether the use of retreats was specific to certain taxa or body sizes of community members and how these patterns varied along an elevation gradient. In assessing the community-level use of retreats versus bare rock surfaces along the gradient we predicted that (i) density and biomass on retreats would be higher than surrounding rock habitat, and this effect would be greater at higher elevation sites because of increased facilitation strength; and (ii) body size of invertebrates on retreats would be lower than that of rocks, however, the body size on retreats and rocks would converge at higher elevations because retreats were expected favour a greater proportion of the communities in higher elevation conditions. Regarding the taxon-level use of retreats versus bare rock surfaces, we predicted that retreats would function as a nursery for taxa with large maximal body sizes as these taxa were expected to use the retreats at earlier life stages.

2 | MATERIALS AND METHODS

We collected net-spinning caddisfly retreat structures at five riffles along an elevation gradient encompassing 985 m and 70 km of river

length beginning in the headwaters of the East River and ending in the mainstem of the Gunnison River Colorado, USA, in August 2016 and 2017 (Figure S1; Table S1). The first of these two sampling periods in August 2016 was conducted to establish study sites along an elevation gradient and to determine if net-spinning caddisflies occurred throughout the gradient. The second sampling period in August 2017 was designed to collect net-spinning caddisfly retreats and associated invertebrate communities along the established gradient. Retreats and any associated beneficiary taxa were collected by hand and placed in vials. We quantified and identified density, biomass and body size of invertebrates associated with caddisfly retreat structures (hereafter retreat) and compared these measurements to those from invertebrates sampled from the nearby rock surface (hereafter rock) of the same rock from which a retreat was sampled. Additionally, at each site we measured a suite of physical habitat parameters including water temperature, grain size, channel slope, flow velocity, channel width and depth and seston concentration (Table S1). We used elevation as our gradient because it encapsulates a suite of environmental factors associated with stream invertebrate stressors (Table S1).

Each site included two consecutive riffles (a subsite) with a total of 10 randomly selected sampling locations spanning the length of riffle habitat (~20 m) for a total of $n = 20$ sampling locations at each site and for each response variable. At each sampling location, we randomly selected a rock from the stream bed representative of the site's median grain diameter (20–70 mm intermediate b -axis; Tables S1 and S2). If there was a caddisfly retreat present on the rock, the retreat and the associated caddisfly were carefully removed and placed into a vial with 70% ethanol and transported to the laboratory for processing. Median particle size (D_{50}) of each site was calculated by measuring the intermediate axis of 30 particles while walking back and forth from bank to bank within the study site using a Pebbleometer (Wildlife Supply Company; Table S2). Next, we removed invertebrates from rock surfaces by scrubbing with a wire brush and rinsing with filtered stream water into a 250 μ m sieve. The contents of the sieve were transferred to a WhirlPac®, preserved with 70% ethanol, and transported to the laboratory for further processing. If more than one retreat was present, the most subjectively intact structure was collected, and the remaining retreats were immediately removed from the rock and discarded before the rock surface was sampled. Occurrences of multiple retreats was rare, and the majority (64%) of focal rocks had one to two retreats. Furthermore, the occurrence of multiple retreats would act to increase rock values of density and biomass and therefore provide a more conservative estimate of any potential caddisfly effect.

In the laboratory, invertebrates from retreat and rock samples were counted, measured in body length to the nearest mm and identified to genus. 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 et al., 2019; Smith, 2001). Invertebrate taxa were assigned to functional feeding groups using established trait databases and references (Merritt et al., 2019; Vieira et al., 2006).

The caddisfly that built the collected retreat was removed from all analyses but was identified to genus and measured in body length to the nearest mm (Table S3). This caddisfly was easy to identify because the preservation process immobilized the caddisfly inside of the retreat structure. Rock samples with large numbers of individuals (>200) were sub-sampled using a plankton wheel until at least 100 individuals were represented in the sample fraction. Total invertebrate density in each sample was estimated as no. m⁻² scaled to the surface area of the corresponding retreat and rock size (Table S2). Diameter measurements of rocks and retreats were used to convert to surface area of m² assuming rocks and retreats had a uniform circular shape, so that densities and biomasses could be assessed across consistent aerial estimates (Table S2). Comparison of aerial surface between rocks and retreats was warranted as both surfaces were sampled from this area. Retreats were photographed and the diameter of the surface area was measured to the nearest mm with ImageJ (Table S2). Rock surface diameter was derived from measurements taken in the field using a standard ruler. Total invertebrate biomass in each sample was estimated as mg ash-free dry mass (AFDM) m⁻² using established taxon-specific length–mass relationships (Benke et al., 1999) and scaled to the aerial measures of retreat and rock size. We scaled our estimates in this way to standardize units of the retreats and rock surfaces, and to examine effect sizes of interest.

We evaluated body size across the elevation gradient on retreats and rocks as: (i) average community-level body size (i.e. community-weighted mean body size) and (ii) taxon-specific body size. Average community-level body or taxon-specific body size was estimated as mg AFDM and was calculated by dividing total biomass by total density in each sample or by dividing the total biomass by total density for each taxon respectively.

2.1 | Data analysis

We calculated log-response ratios (hereafter LRRs) for invertebrate density, biomass and community-level body size as the standardized effect size for our comparison of retreats and rocks along the elevation gradient. We calculated LRR for each retreat-rock combination using:

$$\text{LRR} = \ln\left(\frac{\text{Retreat value}}{\text{Rock value}}\right),$$

where the LRR measures the log proportional change between the retreat and rock value of interest.

The LRRs of invertebrate density, biomass and community-level body size were analysed to examine how effect sizes changed along the gradient using linear mixed-effects models. Models included the fixed effect of elevation and the random effect of riffle as a random intercept nested within site and accounted for the non-independence of consecutive riffles at the same site with a standard mixed model design where a subsite (a riffle) was nested within sampling site (Bolker, 2008; Zuur et al., 2009). To test whether the

random effect of subsite explained a significant amount of residual variation, we conducted ranova tests within the lmerTest package for all mixed effect models (Table S4). 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 & Herve, 2015). Conditional *r*-squared values were calculated using the 'r.squaredGLMM' function.

We also examined how taxon-specific body size varied between the retreat and rock habitat as a function of maximal body size present. The objective of this analysis was to test for a nursery effect, or if taxa use retreats at the small end of their respective size spectrum and if this effect intensified with increasing maximal body size. To evaluate this pattern, we calculated the LRR of body size between retreat and rock of each taxon that occurred on both habitats across all sites. Maximal body size (mg AFDM) for each co-occurring taxon was determined based on the largest individual measured within our study. LRR in taxon-specific body size was then analysed as a function of maximal body size using a simple linear regression. Maximal body sizes were log₁₀-transformed to meet assumptions of normality. The term 'nursery effect' implies that young or early development individuals were supported, however, we did not directly measure invertebrate age and instead measured body size. Often small body sizes do in fact represent younger freshwater invertebrates and offer a reasonable surrogate for developmental stage (Benke et al., 1999). Additionally, it is common for several life stages of the same species to co-occur within the same place and time making a size for age replacement an ecologically relevant measure of intraspecific body size variation. However, differences in body size can also occur independently of development because individuals of the same species may have reduced food access and thus smaller body sizes (Nelson et al., 2017; Vannote & Sweeney, 1980). Therefore, we acknowledge that our use of the term 'nursery' should be taken to mean smaller body size based on age or otherwise.

To evaluate how this body size relationship was influenced by the elevation gradient we calculated the LRR of body size between each taxon that co-occurred on retreat and rocks at a site-specific level. We then analysed LRR in taxon-specific body size as a function of both maximal body size and elevation and the interaction between these terms using multiple linear regression. All model analyses were conducted using R version 4.0.2 (R Development Core Team, 2020). To carry out field sampling we received permits from the U.S. National Park Service (permit numbers: CURE-SCI-0002 and BLCA-SCI-0001) and the U.S. Forest Service (special use permit number GUN1120). None of the research required ethical approval.

3 | RESULTS

Examination of retreats revealed high abundances of invertebrates in 19 different Genera and Families, eight different Orders and two

Phyla (Figure 1). Diptera, especially Chironomidae, was the most numerous taxon inhabiting retreats, with on average 8.4 ind. retreat⁻¹ and a maximum value of 78 ind. retreat⁻¹ (Figure 1). Most invertebrates found inhabiting retreats were classified as detritivores (70% or 14 of 20 taxa) or scrapers of biofilm (10%, or 2 of 20 taxa). Additionally, predacious invertebrates made up 20% of invertebrate taxa found on retreats represented by Ceratopogonidae, *Isoperla* spp., *Polycentropus* spp. and Hydrachnidia, and have been shown to consume Chironomidae. Furthermore, the majority of insects inhabiting retreats were in larval life stages, however, we did document occurrences of pupal Chironomidae and adult *Optioservus* spp. (Figure 1).

We found increased density and biomass on caddisfly retreat structures compared to rocks, and these effects intensified with increasing elevation and were dependent on smaller-bodied community members (Figure 2). Invertebrate density was higher on retreats compared to rocks and this effect increased with elevation ($F_{4,80.7}=12.9$, $p<0.0001$, $R^2=0.26$, Figure 2a). Biomass was lower on retreats compared to rocks at lower elevation sites and higher on retreats compared to rocks at higher elevation sites, indicating that

caddisfly effect on beneficiary biomass increased with elevation ($F_{4,64.7}=8.2$, $p<0.0001$, $R^2=0.25$, Figure 2b). Body size of invertebrates on retreats was lower than that of rocks across sites, however, this effect diminished with increasing elevation, where retreats supported a greater proportion of the body size range ($F_{4,63.7}=2.5$, $p=0.0521$, $R^2=0.11$, Figure 2c).

Caddisfly retreats functioned as a nursery for several taxa by supporting smaller body sizes of co-occurring invertebrate taxa on retreats compared to rocks (Figure 3). This nursery effect was greatest for taxa with largest maximal body sizes including *Pteronarcella* spp. and *Brachycentrus* spp., although there was no consistent linear pattern across all taxa based on maximal body size (Figure 3, $F_{1,18}=2.6$, $p=0.12$). Several co-occurring taxa were also shown to be the same size or larger on retreats compared to rocks across the body size range (Figure 3).

When comparing the slope of the body size relationship (i.e. nursery effect) across sites along the elevation gradient, we found no statistical support for differences in nursery effect as a function of elevation (Figure 4, $F_{4,47}=0.8$, $p=0.53$). The lack of support for this pattern suggests that any nursery effect did not vary along the elevation gradient as we expected based on community-level body size (Figure 2c).

4 | DISCUSSION

Our study is among the first to demonstrate that the strength of animal-mediated facilitation can be contingent on environmental context and beneficiary body size, underscoring the importance of trait variation in determining the magnitude and direction of biotic interactions along gradients. The observations of invertebrate density and biomass being concentrated within retreat structures and that the strength of this effect intensified along an environmental gradient is congruent with a collection of work showing that modification of environments by ecosystem engineers can facilitate other organisms by ameliorating harsh conditions (Albertson et al., 2021; Jones et al., 1994; Romero et al., 2015). Furthermore, the finding that caddisfly retreats supported smaller body sizes for a certain co-occurring invertebrate taxa underscores the complexity of animal-animal nursery effects and their potential roles in controlling biotic interaction sign and direction. This study therefore expands the understanding of positive biotic interactions by elucidating the roles of functional traits and environmental context in controlling facilitation strength. Continued appreciation of how variation in traits and environmental gradients interact to determine the strength of biotic interactions will be important as species ranges and environmental conditions continue to shift.

4.1 | Facilitation hotspots

The caddisfly-mediated concentration of invertebrate density and biomass documented here can create hotspots in ecosystem function

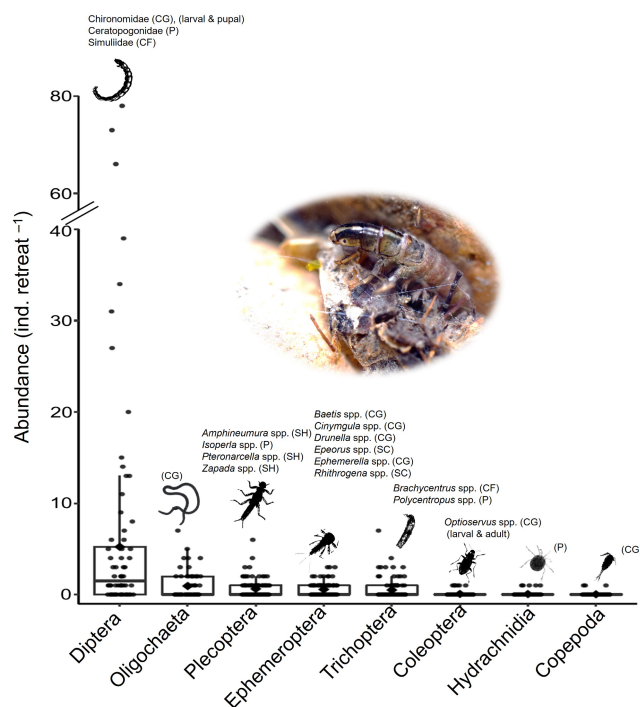


FIGURE 1 (Inset) An example of a net-spinning caddisfly (Hydropsychidae) with its retreat structure, photograph credit: M.J. MacDonald. Abundances of invertebrate taxonomic groups found in retreats ($n=100$ retreats). High abundances and a wide diversity of invertebrates were found using net-spinning caddisfly retreats, including at least 19 different Genera and Families, eight different Orders and two Phyla (Annelida and Arthropoda). Functional feeding groups are identified alongside taxa name and abbreviations are: CF, collector filterer; CG, collector gatherer; P, predator; SC, scraper; SH, shredder. For a complete list of taxa found in retreats and on rocks see Table S5. Box plots show the median (black line), mean (black diamond) and interquartile range (IQR; vertical box bounds). Whiskers represent $1.5 \times$ IQR and individual data points are represented with black circles.

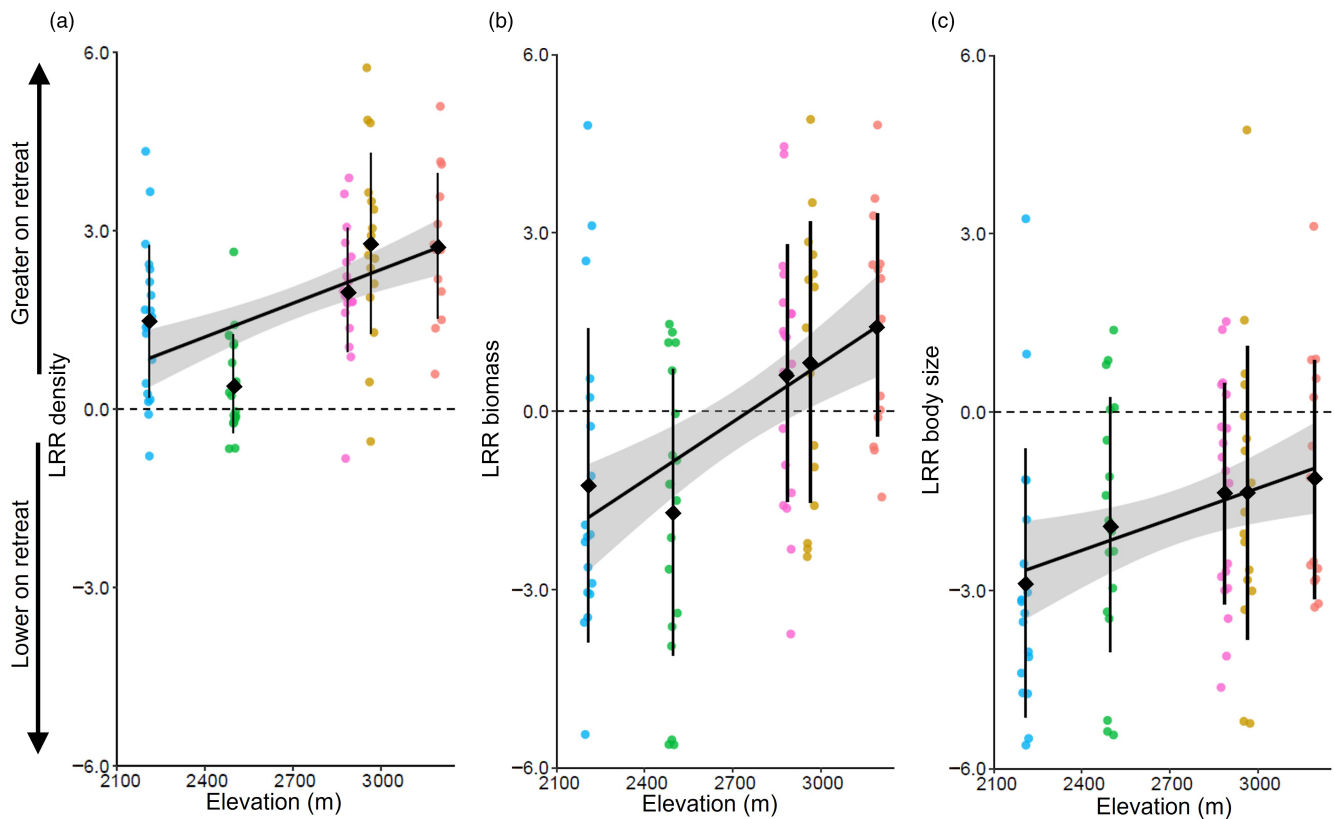


FIGURE 2 Caddisfly retreats positively affect invertebrate (a) density and (b) biomass, and the strength of these effects increased along an elevation gradient. (c) the invertebrates found in caddisfly retreats were of smaller body sizes than rocks, however, the body size on retreats relative to rocks increased along an elevation gradient. Mean values are represented by the black diamond, standard deviation is represented by vertical whiskers and individual data points are represented with coloured circles based on the location on the elevation gradient. Lines of best fit are based on the fixed effect of elevation with grey shading of 95% confidence interval shading. LRR, log-response ratio.

(Tumolo et al., 2023) and possibly concentrate prey availability for higher trophic levels. As evidenced by insects, freshwater mussels and fish, concentrations of animals and their excretion can generate hotspots of nutrient cycling, primary production and basal resource availability (Atkinson & Vaughn, 2015; Capps & Flecker, 2013; Tumolo et al., 2023). Our finding that retreats concentrated invertebrate density and biomass could also have important consequences for higher trophic levels, such as fish, which rely on invertebrates as a principal food source. Indeed, within marine systems engineer-mediated prey refugia often also attract fish predators that subsequently pressure these refuge seeking individuals (Gribben et al., 2017). Future work might investigate how the localized invertebrate concentrations measured here influence predators and ecosystem function at broader scales, as engineer-mediated aggregations have been shown to drive community dynamics and energy flux (Angelini et al., 2011; Atkinson & Vaughn, 2015; Tumolo et al., 2023).

4.2 | Role of elevational gradient

The strength of caddisfly positive effects on invertebrate communities intensified with increasing elevation (Figure 2), suggesting that the amelioration of harsh physical and resource

conditions by caddisfly retreat structures became more important to a greater proportion of the invertebrate community as environmental and resource constraints intensified within increasing elevation. If increasing elevation along this river network does in fact represent a gradient of multiple stressful environmental factors (i.e. temperature, resource availability, bed shear stress), then our findings provide support for the stress gradient hypothesis (SGH), which has rarely been tested in freshwater (Albertson et al., 2021; Silknetter et al., 2020). However, we did not design our study to test whether beneficiaries were stressed or whether the use of retreats was definitively for amelioration of stress (He & Bertness, 2014). Despite these design limitations, our conclusions remain strongly consistent with our hypotheses and with findings from terrestrial and marine environments (Bruno et al., 2003). Elevation-mediated facilitation patterns may also interact with changing temperature regimes and accompanying invertebrate species range shifts forecasted under climate change (Freeman et al., 2018; Jurgens et al., 2022). For instance, as streams temperatures increase, higher elevation streams will more closely resemble prior lower elevation conditions in both temperature and invertebrate community composition as certain species shift their distributions upward (Freeman et al., 2018; Shepard et al., 2021). Changes in species distribution

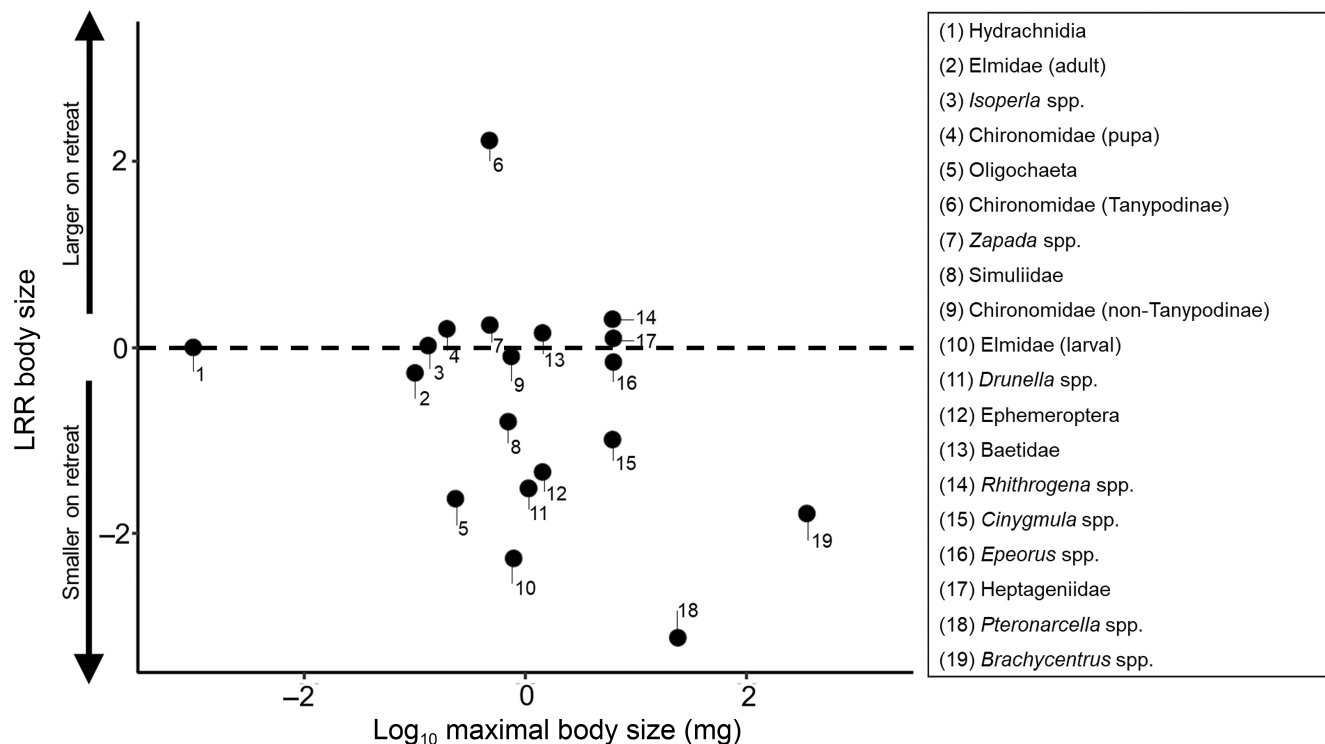


FIGURE 3 Caddisfly retreats function as a nursery for 11 of the 19 taxa that co-occurred on retreat and rock habitats (points below log-response ratio (LRR) body size of zero). These taxa use retreats in earlier life stages or at smaller body sizes. The nursery effect intensified with increasing maximal body sizes as indicated by greater distances below 0, especially for taxa with largest maximal body size (18, 19), although this was a non-significant statistical linear relationship across all taxa ($F_{1,18}=2.6$, $p=0.12$). Each point represents a taxon that co-occurred on both retreats and rock regardless of elevation site.

in response to climate change could interrupt or accentuate linkages in current positive interaction networks occurring between caddisflies and other community members (Jurgens et al., 2022; Shepard et al., 2021). Collectively, our results show that positive interactions have strong, yet overlooked, effects on freshwater community dynamics, the strength of facilitation intensifies with increasing elevation, and the magnitude and sign of species interactions is contingent on environmental and biological factors associated with ecological gradients.

4.3 | Role of body size

Small-bodied invertebrates, both within and across taxa, were likely facilitated because of their ability to fit within and exploit habitat ameliorating retreat structures. This finding is consistent with the collection of studies showing that small organisms exploit habitat modifications for refuge from predation and physiological stress across terrestrial, marine and freshwater ecosystems (Nakano et al., 2007; Pringle, 2008; Wright & Gribben, 2017). We posit that retreat structures provided flow and predation refuge, as well as increased local resource availability for invertebrates that were small enough to fit within or alongside the retreat structure. This idea is supported by the pattern of increased strength of positive effects measured at higher elevation sites that were associated with

harsher environmental conditions. Additionally, further support is provided by previous work showing that net-spinning caddisfly retreats provide flow refugia (Nakano et al., 2005) and concentrate detrital resources (MacDonald et al., 2021; Tumolo et al., 2023). We did observe that most invertebrates inhabiting retreats were detritivores, and perhaps these taxa also feed on detritus and the associated microbes growing on the retreat structure. The use of retreats as a food resource could also influence both small and large individuals since they only need to be nearby and not necessarily within the structure to feed off the material. This hypothesis would also help explain the instances when some relatively large invertebrates were found associated with retreats (Figure 3).

As elevation increased retreats supported a greater proportion of the invertebrate community body size range. This pattern could result from a number of non-mutually exclusive drivers: (1) retreats at higher elevations were more important for a greater proportion of the community size spectrum because of harsher environmental conditions; (2) invertebrate communities at higher elevation sites had smaller body sizes in general, and therefore differences in body size between rocks and retreats were less pronounced; and (3) invertebrates used retreats for different reasons depending on elevation, where retreat use at higher elevation was less dependent on small body size. Evidently, both environmental and biotic context (elevation and body size respectively) shaped the patterns of biotic interaction observed here, and future work

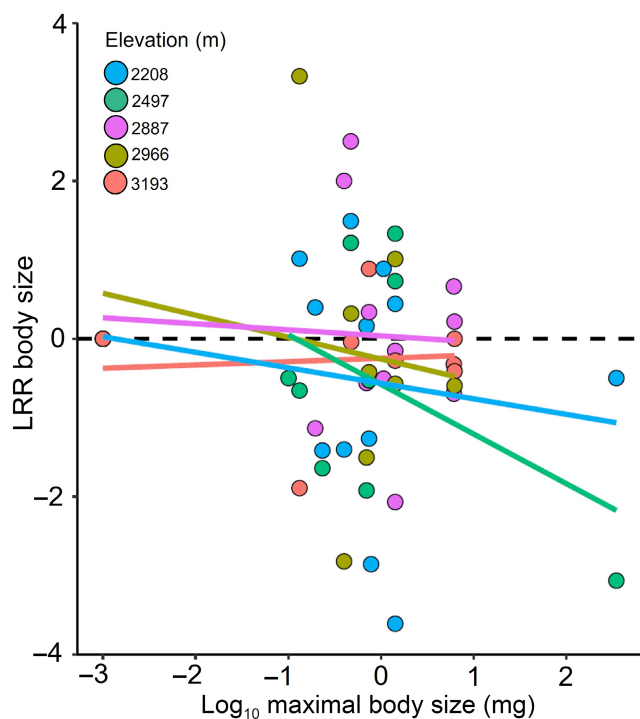


FIGURE 4 The slope of the relationship in body size between retreats and rocks (nursery effect) as a function of elevation. A negative slope can be interpreted as a signal of the nursery effect, as this slope increases to become more positive or zero it suggests a weaker nursery effect or no nursery effect. The strength of the nursery effect (increasing slope) was statistically indistinguishable along the elevation gradient ($F_{4,47}=0.8$, $p=0.53$). Each point represents a taxon that co-occurred on both retreats and rocks at a particular elevation. Lines of best fit are based on multiple linear regression fit to site level. LRR, log-response ratio.

will benefit from elucidating mechanisms underlying such interactions between environmental and functional trait gradients in nature.

4.4 | Nursery effect

There are parallels and differences between the caddisfly nursery effect observed here and well-documented nurse-plant systems in terrestrial habitats (Callaway & Walker, 1997; Miriri, 2006). Nursery effects, especially among plants, lead to temporal shifts in the strength and direction of organism interactions. Such changes in the direction and magnitude of organism interactions are of fundamental importance, as these phenomena are suggested to promote coexistence and stability within natural communities (Gross, 2008; Marcarelli et al., 2020; McCann et al., 1998). Similar to nurse plants, we document that caddisfly retreats provide habitat for certain younger, smaller-bodied, members of the community who may at larger sizes compete with caddisflies. However, unlike nurse plants, the caddisfly nursery effect encompassed a greater diversity of community members occupying multiple trophic levels,

including detritivores, grazers and predators. Thus, the beneficiaries that were facilitated in this study may eventually grow into mature forms that both compete with and prey on caddisflies or prey on other invertebrates supported by caddisfly retreats. If such predicted patterns do occur, then sign switching is far more dynamic than that previously observed within nurse-plant systems. Broadly, our findings reveal rarely documented nursery effects among animals, and highlight the need to further understand their potential role in promoting dynamic interactions and coexistence within natural communities.

5 | CONCLUSIONS

We found that functional traits of animal beneficiaries and environmental context simultaneously govern the strength of biotic interactions in stream ecosystems. Concentrations of invertebrate density and biomass on retreat structures suggest that positive interactions likely have substantial, albeit overlooked, effects on ecosystem structure and function (Albertson et al., 2021; Silknetter et al., 2020). Additionally, the finding that these effects were strongest at higher elevations underscores the urgency to better understand how climate-mediated shifts in environmental conditions and species ranges might sever or amplify linkages in current positive interaction networks. Furthermore, the finding that the strength of facilitation was dependent on body size has important implications for how positive biotic interactions affect animal populations and communities. Specifically, smaller-bodied species and younger individuals of certain large-bodied species were facilitated more strongly, which conceivably should increase their performance within communities. In conclusion, our analysis reveals that measuring functional traits of animal beneficiaries along an environmental gradient is important to uncovering the strength and direction of biotic interactions in nature.

AUTHOR CONTRIBUTIONS

Benjamin B. Tumolo, Lindsey K. Albertson, and Melinda D. Daniels designed the study, Benjamin B. Tumolo and Lindsey K. Albertson collected and analysed the data, Benjamin B. Tumolo wrote the manuscript, Lindsey K. Albertson, Melinda D. Daniels, Wyatt F. Cross and Leonard S. Sklar discussed interpretation and provided edits on previous drafts. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.3xsj3txn7> (Tumolo, 2023) Scripts used in statistical analysis are available in Zenodo <https://zenodo.org/record/8066417>.

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SUPPORTING INFORMATION

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

Figure S1: The locations, elevations, and river distance from headwaters of the sites used in this study. The study included five sites characterized as riffle habitat, beginning in the headwaters of the East River and ending in the mainstem of the Gunnison River, located from Gothic to Gunnison Colorado, USA, from 8 to 11 August 2016 and 2 to 7 August 2017.

Figure S2: Length frequency histograms of major taxonomic groups observed in the study. Histograms include both rock and retreat observations.

Table S1: Physical variables used to characterize study sites. Stream temperature was measured at each site in August 2016 with a Yellow Springs Instruments® Multiparameter Meter within the middle of the water column before 12:00 pm on the day of sample collection. Stream flow velocity was measured at each site using a SonTek FlowTracker Acoustic Doppler Velocimeter in the middle of the wetted channel at 60% depth from the water surface in August of 2016. The flow velocity measurement was an averaged reading

from a 40 second velocity reading (SON TEK, San Diego, CA, USA). Channel bankful width was measured to the nearest m by stretching a tape across the bankful width of study riffle (Johnson & Heil, 1996). Bankful depth was measured as the deepest point in the study section to the nearest cm with a stadia rod. Channel slope at each site was estimated using Google Earth to measure the change in elevation in m, over a 100m transect. Seston at each site was measured with a Wildco Fieldmaster® plankton net (20.32 cm circular opening with 153 µm mesh) in August 2017. Seston samples were collected in the middle of the channel by securing the net to a rebar post open to the direction of flow. The duration of the seston sample period was recorded to the nearest second, and a flow velocity measurement was taken directly upstream of the net following sample collection to determine the volume of water sampled. Contents of the sample were preserved and transported back the lab. In the lab, sample contents were rinsed through a nested sieve series of 1mm and 153 µm to remove coarse particulates and isolate fine particulates. The remaining material between 153 µm and 1mm was dried and combusted as a metric of Seston in mg L⁻¹ (Colon-Gaud et al., 2008).

Table S2: Average proportional area in m² ± SE of rocks and retreats measured across all sites used in this study.

Table S3: Focal caddisflies genus, size (mm ± SE) and site level density (individuals m⁻²) at each site that constructed retreats, reported as

either pooled across all sites and per site. Density was measured based on two replicates per site and each replicate consisted of three aggregate surber samples pooled together.

Table S4: Ranova results and variance of random effect testing for differences in the random effect of riffle (subsite) in the LRR of density, LRR of biomass and LRR of body size. A *p*-value less than 1 indicates that the random effect explains a significant amount of residual variation after the variation is explained by the fixed effects. Random effects with *p*-values of 1 were still included to control for non-independence.

Table S5: Taxa in retreat and rock habitat pooled across sites in this study. Presence is denoted with the number 1. Different phyla are denoted with all capital bold face font, Class and Order levels are denoted with bold face font.

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