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Environmental drivers of the symbiotic relationship of cyanobacterium *Nostoc parmelioides* and *Cricotopus* larvae

Lily Bowen[1], Sydney Flanery[2], Nava Shapiro[1], Malcolm Wang[3]

[1]University of California, San Diego, [2]University of California, Irvine, [3]University of California, Santa Cruz

ABSTRACT

Climate change is decreasing the amount of snowmelt needed to sustain streamflow in California's Sierra Nevada mountains, warming montane streams and shifting conditions available to the organisms that live in them. The cyanobacterium *Nostoc parmelioides* forms colonies on rocks in streams, and each colony can host a single non-biting midge fly larva *Cricotopus*, a symbiosis that links algal production to montane stream food webs. We tested whether depth, canopy cover, water flow speed, and water temperature predicted *N. parmelioides* density and the percentage of colonies occupied by *Cricotopus* larvae, along Sagehen Creek in Nevada County, California. Additionally, we compared larval and colony size across three sites differing in temperature. The percentage of colonies occupied by larvae increased with colony density. Depth, flow, and canopy cover had no effect on either density or occupancy, and higher temperature only marginally decreased density. Larger larvae were found in larger colonies, and larvae were smallest at the coldest upstream site. The absence of environmental effects on occupancy suggests that *N. parmelioides* and *Cricotopus* tolerate a similar range of summer conditions, and density may be limited by factors we did not measure, such as nutrient availability. Because host density is a predictor of larval occupancy, climate-driven changes in *N. parmelioides* would affect *Cricotopus*, and the food webs they both support.

Keywords: Climate change, montane stream, *Nostoc parmelioides* density, non-biting midge fly *(Cricotopus),* host occupancy

INTRODUCTION

Climate change is altering freshwater snowmelt-driven hydrology in mountain regions worldwide, reducing overall snowpack and shortening the time it takes for snowmelt to reach stream systems at high elevations (Leathers et al. 2024). This shift is well-documented in California's Sierra Nevada mountain range, where snowmelt arrives and creates runoffs earlier in the year, and less snowmelt water remains to sustain the streamflow throughout the summer months (Halofksy 2021). Lower water volume reduces thermal mass, allowing streams to warm up quicker. These hydrologic shifts predict that water temperatures will rise as anthropogenic climate change progresses (Leathers et al. 2024).

As climate change intensity and frequency are expected to increase, invertebrate communities are vulnerable to changes in their community structure and functions in ecosystems (Herbst et al. 2019). However, the hydrologic and thermal shifts that are occurring do not affect all stream organisms

equally. Some species such as Anisoptera nymphs are relatively tolerant to a wide range of stream conditions (Stewart 2013). On the other hand, non-biting midge flies (*Cricotopus*), which are a dominant and functionally important group of insects in montane stream food webs, have shown a particular sensitivity to changing flow rates and temperatures (Leathers et al. 2024). Experimental studies of summer flow in Sierra Nevada streams have shown that free-living *Cricotopus* abundance and emergence respond strongly to reduced flow and higher temperatures, although responses vary across studies and systems (Leathers et al. 2024, Evangelista et al. 2025). The sensitivity of these non-biting midges makes them a useful group for examining how climate-driven changes in stream ecosystems may cascade through montane food webs, particularly for species of *Cricotopus* that are dependent on host algae colonies like *Nostoc parmelioides* for their development.

Nostoc parmelioides is a cyanobacterium that forms spherical colonies attached to rocks in streams and rivers (Ward et al. 1985, Dodd 1989). Colony growth and productivity are shaped by the physical conditions of the stream. The velocity of the current changes the diffusion of dissolved gases and nutrients across the colony surface, with colony morphologies changing, showing distinct photosynthetic responses to flow (Dodds 1989). Water depth and flow speed can similarly shape nutrient availability to the colony surface. Slower-moving water in deeper sections may allow nutrients to accumulate near the colony for longer, while faster flow increases the rate at which nutrients are delivered to the colony's surface (Huryn 1990, Dodds 1989). The depths at which the colonies grow may reflect a trade-off between other habitat conditions and the need for sufficient sunlight to photosynthesize (Caro Borrero et al. 2021). The shade that *N. parmelioides* receive from overhead canopy cover can restrict light availability, limiting algal biomass (Rosemond et al. 2000). Algal productivity also varies with invertebrate presence, as the grazing and colonization by *Cricotopus* influence colony structure and growth (Ward et al. 1985). Since *N. parmelioides* development is linked to various factors, the climate-change shifts that affect these conditions may impact not only the cyanobacterial colonies, but also the *Cricotopus* that depend on them.

Many *N. parmelioides* colonies host a single symbiotic midge fly larva *Cricotopus* inside their thallus, the inner body of the colony (Brock 1960). *Cricotopus* larvae occupy the host until it pupates and emerges as an adult (Ward et al. 1985). This relationship is crucial to the larva as it provides it with food and shelter through its instar developmental stages. When larvae were removed from their host colony, Dodds and Marra found that larvae failed to relocate and re-enter another *N. parmelioides,* suggesting that larvae are unlikely to survive long once they are separated from their host (Dodds and Marra 1989). The endosymbiotic midge larvae feed only on *N. parmelioides* cells and expand the diameter of the host colony while eating, which leads to higher photosynthetic rates, possibly higher light interception, and increased gas exchange (Ward et al. 1985, Dodds 1989). Adult female midge flies deliberately lay their eggs near developing *N. parmelioides* colonies, for food and shelter (Ward et al. 1985, Péry et al. 2002). As midge larva pupate, their host *N. parmelioides* colonies go through a dispersal stage where many new uninhabited colonies

form. This interaction provides benefits to both taxa, as they benefit each other's reproduction (Dodds and Marra 1989).

This symbiotic relationship has been observed in watersheds in California, Oregon, Mexico, and Spain (Brock 1960, Ward et al. 1985, Caro Borrero et al. 2021), suggesting that both these organisms provide ecological benefits to the ecosystems. As nitrogen-fixing cyanobacterium, *N. parmelioides* provides new nitrogen in nutrient-poor montane streams, which can be taken up by the surrounding microbial community, functioning as a nitrogen source for the broader stream ecosystem (Dodds 1989, Kohler et al. 2018). *Cricotopus* also supports higher trophic levels, serving as an important prey source for aquatic predators in their larval stage and for riparian predators in their adult fly stage. This links colony-level production to food webs in both the stream and surrounding terrestrial habitat (Covich et al. 1999, Nakano and Murakami 2001). This close association raises the possibility that *Cricotopus* and *N. parmelioides* have co-evolved physiological tolerances to the range of conditions within their shared habitat, which could shape how they independently respond to environmental variability (Caro Borrero et al. 2021). However, if the midge flies and cyanobacterium differ in their tolerances, they may be differentially affected by changing stream conditions, leading to variation in *Cricotopus* occupancy of *N. parmelioides*. The stability of this relationship may be at risk as climate change is altering stream conditions over time.

In the first part of this study, we tested if there was a correlation between density of *N. parmelioides* colonies and the number of *Cricotopus* that occupy them. We predicted that 1) the density and percent of occupancy would be positively correlated; as the density of colonies increases, the percent of hosts occupied by *Cricotopus* larvae will also increase, since adult females engage in selective reproduction and deposit more eggs on rocks with higher density of *N. parmelioides* (Ward et al. 1985, Péry et al. 2002). We then tested the effects of temperature, canopy cover, depth, and water flow speed on overall density of *N. parmelioides* colonies and *Cricotopus* occupancy. We predicted that 2) greater depth and flow speed will have greater densities of *N. parmelioides* due to lower temperatures at greater depths and more dissolved CO_2 at faster moving parts of the stream (Kell 1977). 3) Greater canopy cover and temperatures will lead to less density of *N. parmelioides* due to canopy cover restricting light and warmer water having less dissolved CO_2 (Kell 1977, Rosemond et al. 2000, Dodds 1989, Leathers et al. 2024, Evangelista et al. 2025). 4) Greater depth and flow speed will have a greater percentage of *N. parmelioides* colonies with a *Cricotopus* larva, because the environmental preferences of *N. parmelioides* will be reflected in *Cricotopus* larvae due to the reliance of *Cricotopus* on *N. parmelioides* for recruitment (Brock 1960). 5) Greater canopy cover and temperatures will have a lower percentage of *N. parmelioides* with a *Cricotopus* larvae, due to the reasoning of prediction 4.

In a second observational study, we asked whether temperature influences the size of *N. parmelioidies* and how larval size relates to the size of its host colony, by examining the variation in both the size of the larvae and the host colonies across upstream, middle, and downstream sites. We predicted that 6) larger larvae would be found within

larger host colonies, because they change the thallus morphology as they feed on the colony cells (Dodds 1989) and 7) larger larvae would be found in areas of the stream with colder water temperatures, as the areas supported higher midge densities in the first part of our study.

METHODS

2.1 Study Site and System

Our study area was a 1.11 km stretch of Sagehen Creek within Sagehen Creek Field Station (-120.241348, 39.432056) in Truckee, Nevada County, California. The site is located at 1,943 m above sea level in the eastern California Sierra Nevada, surrounded by mixed conifer forest in a Mediterranean climate (University of California Nature 2026). Sagehen Creek is both groundwater-fed from an aquifer and snowmelt-fed from California's Sierra Nevada mountains and leads into Stampede Reservoir, fed by the Truckee River from Lake Tahoe (Kirchner et al. 2020). The previous and current years' snowpacks correlate strongly with the seasonal low flow rates within the creek (Godsey et al. 2014). The freshwater ecosystem in Sagehen Creek is inhabited by two species of *Cricotopus* larvae (*C. fuscatus* and *C. nostocicola*) (Brock 1960). During their larval stages, which both occur during the summer months, these two species are indistinguishable from one another. There are also several aquatic predators of *Cricotopus* larva within Sagehen Creek, such as the fish *Salvelinus fontinalis* and *Cottus beldingii*, Hirudinea, Odonata nymphs, and other aquatic invertebrates (Pinder 1986). In their adult fly stage, *Cricotopus* are also a food source for predatory birds and fish.

2.2 Environmental Drivers of Colony Density and Occupancy

From July 30 to August 1, 2026, we sampled 60 locations, with a minimum of 18.5 m between each location, and sampled 3 rocks at each location. At a few locations, we were unable to access the creek at the 18.5 m mark due to heavy brush cover and instead selected the nearest accessible point. At each location, we took a canopy cover reading using a Model-A Forestry Suppliers Spherical Crown Densiometer, and a water temperature reading using a VIVOSun LCD Digital Aquarium Thermometer. Water temperature was measured daily between 3–4 PM (PST). Depth of each rock was measured by placing a meter stick at the base of the rock and recording where the water level met the meter stick. Water flow rate was calculated using water pressure force as a proxy. A bag 15 cm deep and 8 cm in diameter was attached to a spring scale and held in the water above each rock to measure the force of the flowing water. A 50 g spring scale was used for slower water, and a 250 g spring scale was used for faster water. We chose rocks large enough to place our 140 cm^2 quadrat on both sides, yet small enough to lift from the water with one arm. We selected three random rocks within our size constraints regardless of *N. parmelioides* presence. We calculated the density of *Cricotopus*-occupied and -unoccupied *N. parmelioides* by placing our quadrat on the upstream and downstream sides of rocks. All statistical analyses were done using JMP (2026 JMP® Version 18. JMP Statistical Discovery LLC, Cary, NC.). We ran several multiple regression analyses to test the effect of the four focal environmental variables on the density of *N. parmelioides* and the percent occupied by *Cricotopus* (Table 1).

Table 1. Water temperature was the only variable with a marginal effect on *N. parmelioides* density; no variable significantly predicted colony density or percent occupancy by *Cricotopus* larvae. Results of multiple regression models testing the effects of stream depth, water speed, canopy cover, and temperature on overall colony density and *Cricotopus* occupancy of *N. parmelioides* colonies.

Notes: Data was collected from July 30–August 1, 2026, along a stretch of Sagehen Creek at Sagehen Creek Field Station, Truckee, California. Depth and water speed were tested as predictors of colony density (N = 180) and percent occupancy (N = 180). Canopy cover and temperature were tested as predictors of colony density (N = 60) and percent occupancy (N = 60).

Model	Sample size	t-value	p-value
Depth & water speed on density	180		
Depth		0.23	0.815
Water speed		0.21	0.831
Depth & water speed on % occupied	180		
Depth		1.79	0.075
Water speed		0.16	0.871
Canopy cover & temperature on density	60		
Canopy cover		1.20	0.234
Temperature		1.92	0.0594
Canopy cover & temperature on % occupied	60		
Canopy cover		0.30	0.763
Temperature		1.15	0.257

2.3 Larval and Colony Size

On August 2, 2026, we conducted a second observational study to understand the effects of temperature on *N. parmelioides* and *Cricotopus* larvae size, and the correlation between the two. We measured the water temperature in Sagehen Creek from 3–4 PM (PST) at three different sites: an upstream site, a downstream site, and a site in between, to get a range of temperatures. At each of the three sites, seven rocks with *Cricotopus*-occupied *N. parmelioides* were target sampled with the same size criteria as the first study, and three *Cricotopus*-occupied *N. parmelioides* colonies were randomly sampled from each rock and measured using calipers. In the lab, *Cricotopus* larvae were removed from the *N. parmelioides* host and viewed under a dissecting microscope to measure their length. A linear regression was done comparing the *Cricotopus* larval size to the *N. parmelioides* size. We analyzed the effect of stream site (upstream, middle, downstream) on the size of *Cricotopus* larvae using a one-way ANOVA. We compared the categories pairwise using a Tukey HSD post-hoc test.

RESULTS

3.1 Density and Occupancy

As the density of *N. parmelioides* on the rock increased, the percentage that was occupied by *Cricotopus* larva increased (r^2 = 0.173, $p < 0.0001$, Fig. 1). On average, 46 percent of the *N. parmelioides* colonies were inhabited by a *Cricotopus* larva. In our first

study, the depth of rock in the creek, canopy cover, and the water flow speed did not have an effect on the density of *N. parmelioides* on the rock (Table 1). As the water temperature increased, the density of *N. parmelioides* on the rock marginally decreased (Table 1). Depth, canopy cover, water flow speed, and temperature did not affect the percentage of *N. parmelioides* occupied by a *Cricotopus* larva (Table 1).

3.2 Larval size

In our second observational study, the size of the *Cricotopus* larvae increased with the size of *N. parmelioides* colonies (N = 63, $p < 0.0001$, $r^2 = 0.579$; Fig. 2). The upstream site had a temperature of 14.8°C, the middle site had a temperature of 15.0°C, and the downstream site had a temperature of 17.8°C (Fig. 3). The larvae at the coldest upstream site were smaller in size than the larvae at the slightly warmer middle and much warmer downstream sites ($N_{upstream}$ = 21, N_{middle} = 21, $N_{downstream}$ = 21, F = 6.2009, p = 0.0036; Fig. 3).

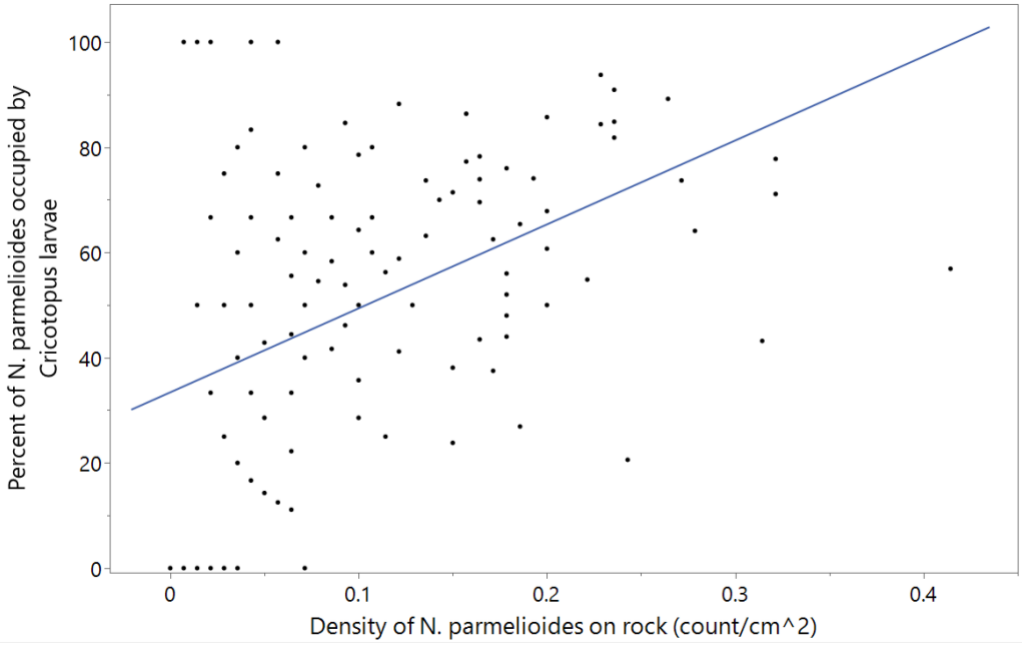


Figure 1. *Cricotopus* larvae occupy more *N. parmelioides* as the density of *N. parmelioides* increases. Data collected from July 30- August 1, 2026. Density was measured by placing a 140 cm^2 quadrat on the rock and counting all *N. parmelioides* within it. Percent occupancy was calculated by dividing the number of *N. parmelioides* with *Cricotopus* larvae by the total count of *N. parmelioides* within the quadrat. Line shows the linear regression fit (N = 180, $r^2 = 0.173$, $p < 0.0001$).

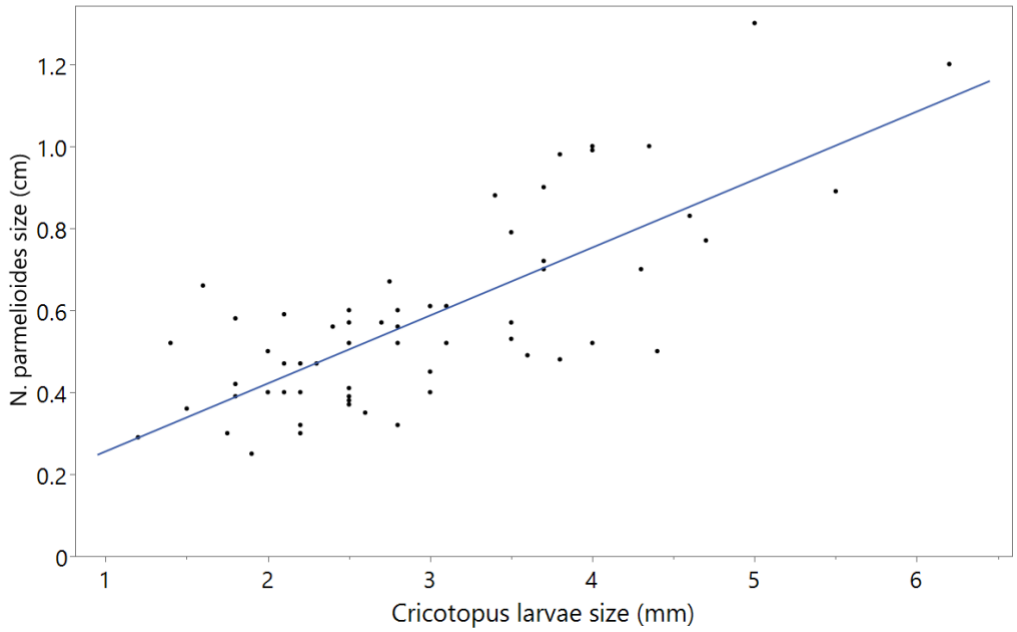


Figure 2. Larger *Cricotopus* larvae are found in larger *N. parmelioides* host colonies. Larval size and colony thallus size were measured on August 2, 2026, at three sites along Sagehen Creek, Sagehen Creek Field Station, Truckee, California: far upstream, mid-creek near the field station, and far downstream. Line shows the linear regression fit ($N = 63$, $p < 0.0001$, $r^2 = 0.579$).

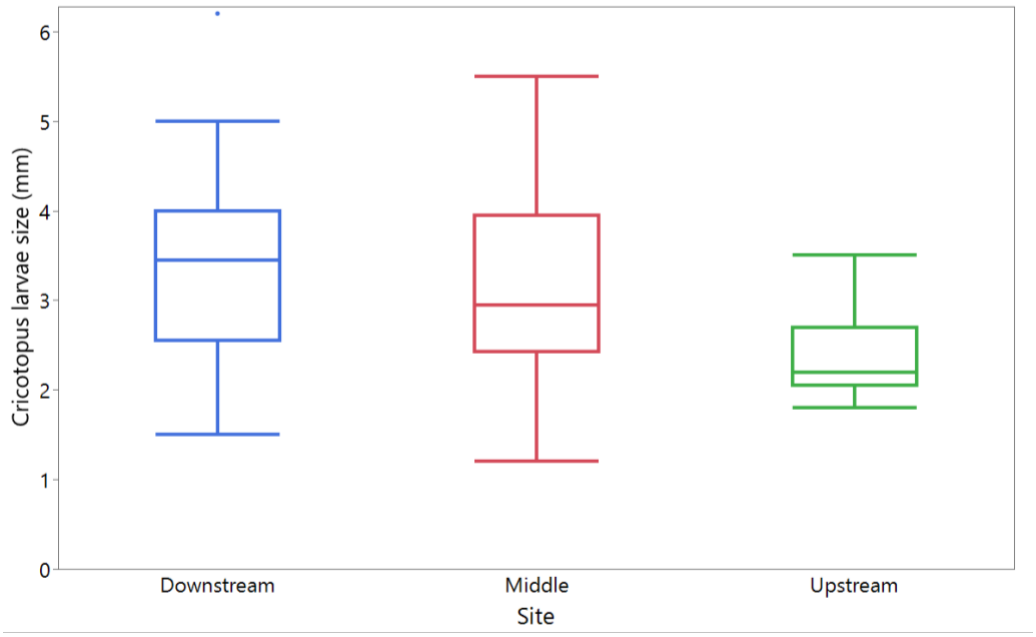


Figure 3. *Cricotopus* larvae are smaller at the upstream site than at the middle and downstream sites. Larval size was measured at three sites along Sagehen Creek, Sagehen Creek Field Station, Truckee, California, on August 2, 2026: downstream (17.8°C), middle (15.0°C), and upstream (14.8°C). Boxes show the median and interquartile range; whiskers show the full range excluding outliers, and points show outliers. Different letters indicate significant differences between zones based on a Tukey HSD post-hoc test; zones sharing a letter do not differ significantly. ($N = 63$, $F = 6.2009$, $p = 0.0036$).

DISCUSSION

In the first part of our study, we found that density of *N. parmelioides* colonies had a positive association with the percentage of *Cricotopus* occupancy, which agrees with our prediction that they would have a positive correlation. This correlation could indicate that *Cricotopus* engages in a selective reproductive strategy. *Cricotopus* adults could select rocks with a larger density of *N. parmelioides* to lay their eggs, which would then hatch and occupy more *N. parmelioides* on that rock as larvae (Ward et al. 1985). *Cricotopus* exhibit a behavior in which they deposit more eggs per egg mass given an abundance of food for their larvae to consume (Péry et al. 2002). That behavior would support this explanation as it would imply more eggs are being laid near a greater density of *N. parmelioides* colonies (Péry et al. 2002). Another potential explanation for this result is that *N. parmelioides* and *Cricotopus* larvae have adapted to a similar range of environmental conditions. The two species engage in a symbiotic relationship, which suggests that they are exerting selective pressure on each other, which in some cases causes co-evolution and thus complementary adaptations (Thompson 1999). *N. parmelioides* act as a source of food and shelter for the *Cricotopus* larva, while the larva increases photosynthetic rates and reattaches the colony to rocks once detached (Dodds 1989). These behaviors may have developed over time as the two species were experiencing selective advantages from them and could explain co-occurrence, as well as physiological adaptations to similar environmental conditions. Previous studies have speculated co-evolution between species of *Nostoc* and other aquatic macroinvertebrate larvae, which could be an explanation for the strong co-occurrence that *N. parmelioides* and *Cricotopus* exhibit (Caro Borrero et al. 2021).

There was no effect of depth, flow speed, or canopy cover on *N. parmelioides* density, which did not match our prediction that depth and flow speed would support higher density, while canopy cover would support lower density. This null effect may indicate environmental conditions affect *N. parmelioides* on a larger temporal scale, such that seasonal environmental variability affects the population of *N. parmelioides* more than environmental variability within a season. The difference between the highest and lowest stream discharge during February 2026 was 18.916 m^3/s whereas it was 1.783 m^3/s in July 2026, which implies that the stream flow speeds and depth had a greater range during the winter than the summer (US Geologic Survey 2026). The maximum depth of the stream decreases as the summer season progresses, which could indicate that the benthic algae have greater sunlight availability for photosynthesis during summer than spring (Kirchner et al. 2020). Another explanation for the lack of effect of light altering environmental drivers is that *N. parmelioides* density is limited by nutrient availability. Low concentrations of phosphorus and nitrogen are common in oligotrophic, high elevation montane streams such as Sagehen Creek (Sholz and Brahney 2022). Oligotrophic streams have greater light availability due to higher algae limitations by nitrogen and phosphorus. The lack of nutrients limits algae species richness, which minimizes attenuation of light entering the stream (Wellnitz et al. 1996). Less competition could mean that there is enough light entering the water to negate any effect of canopy cover and depth

on *N. parmelioides* density (de Nadaï-Monoury 2014).

As water temperature increased, *N. parmelioides* density marginally decreased, which matched our prediction (Table 1). This result agrees with previous studies that indicate that species of *Nostoc* generally prefer colder temperature ranges (Møller et al. 2014). Colder waters hold more dissolved CO_2, which is a requisite for photosynthesis (Kell 1977). Another possible explanation for the marginal effect of temperature could be that we did not sample areas of the stream with a broad enough temperature gradient. Species in the genus *Nostoc* are known to survive in a wide range of temperatures; we may not have sampled close enough to the edge of their temperature range, possibly due to seasonal conditions, to observe a stronger effect (Møller et al. 2014).

Depth, flow speed, canopy cover and temperature all had no effect on the percentage of *Cricotopus* larvae found in colonies of *N. parmelioides*. The absence of effect contradicted our prediction that depth and flow speed would increase *Cricotopus* occupancy whereas temperature and canopy cover would decrease *Cricotopus* occupancy. We observed that density and *Cricotopus* occupancy had a strong correlation, which could mean that the benefits that *Cricotopus* receive from *N. parmelioides* are great enough to overshadow the drawbacks of unsuitable environmental conditions. *Cricotopus* adults could prioritize rocks with *N. parmelioides* to deposit their eggs despite unsuitable environmental conditions due to the necessity of *N. parmelioides* hosts. Variability in depth, flow speed, temperature and canopy cover are typically predictors of invertebrate and algae assemblages, which were not reflected by our results (Dodds 1989, de Nadaï-Monoury 2014). Previous studies have shown that *Cricotopus* larvae exhibit a pattern of seasonal multivoltinism, which our results suggest by the lack of effect of environmental conditions on midge larvae within a season (Brock 1960, Huryn 1990). *Cricotopus* larvae tend to vacate *N. parmelioides* during winter months, which may indicate that summer months are supportive of *N. parmelioides* whereas winter conditions do not support large densities of *N. parmelioides,* as *Cricotopus* larvae and *N. parmelioides* density are strongly linked (Brock 1960, Ward et al. 1985).

In the second part of our study, we found that *Cricotopus* larvae were positively associated with the size of the *N. parmelioides* colony. This result did match our prediction, as it supports previous studies indicating that larvae expand the size of the *N. parmelioides* colony to support their growth (Brock 1960). A correlation between *N. parmelioides* size and *Cricotopus* larval size could support the idea that the morphology of the thallus of *N. parmelioides* is evolutionarily adapted to support the larva (Caro Borrero et al. 2021).

Cricotopus larvae were smaller at colder sites, which contradicted our prediction that colder temperatures would be associated with larger *Cricotopus* larvae. This finding could reflect the temperature boundary under which *Cricotopus* larvae can develop at its maximum growth rate. *N. parmelioides* at sites with a water temperature of 15.0°C and 17.8°C did not differ in size but had a greater temperature difference which could indicate the temperature gradient between 14.8°C and 15.0°C could be the threshold for temperature conditions under which *Cricotopus* larvae are developmentally

inhibited (Huryn 1990). Another possible explanation could be that other variables that we did not measure varied between sites and affected the size of *Cricotopus* larvae.

Previous studies have shown that environmental factors such as light, nutrient availability, substrate type, and anthropogenic activity contribute to freshwater benthic algae development and abundance (Dodds 1989, Wellnitz et al. 1996, Santamaria et al. 2002). Our study was designed to test for factors that we deemed variable within our study system, however the lack of effect of those factors indicates that other environmental drivers as well as seasonal variations in montane streams are a larger predictor of *Cricotopus* larvae occupying *N. parmelioides* (Brock 1960). Another interpretation could be that the lack of effect of flow speed, canopy cover, and depth on both percentage occupancy of *N. parmelioides* and density of *N. parmelioides* displays the importance of the summer months for *Cricotopus* recruitment. An area of future study could look at how these environmental conditions affect *Cricotopus* occupancy of *N. parmelioides* on a greater temporal scale, which would grant insight into the effect of seasonality on *N. parmelioides* density, as well as the difference in reproductive strategy of *Cricotopus* between seasons. Examining the environmental conditions across seasonal variation to capture a wider range of conditions would help clarify whether the lack of effects we observed reflects reproductive strategy or environmental adaptations. Our results do not agree with previous studies showing that *Cricotopus* had increased larval growth rates at colder temperatures (Huryn 1990); future studies could test how temperature, nutrient availability, and rock substrate type affect *Cricotopus* larval growth from the first instar stage, which could elucidate how environmental drivers affect recruitment and growth rate, as well as how that might change between study systems.

As climate change decreases snowpack and runoff in the California's Sierra Nevada, environmental drivers influencing *N. parmelioides* will change, affecting its density on substrate (Kirchner et al. 2020). We have shown that *N. parmelioides* density is a large predictor for *Cricotopus* larval occupancy, which indicates that changing environmental conditions that affect *N. parmelioides* will also affect *Cricotopus* recruitment as well as the greater stream food web. Our results can be used to inform assertions about montane stream health, as well as conservation action related to invertebrate and stream ecosystems. *N. parmelioides* and *Cricotopus* have a large range of environmental adaptations to summer stream conditions, and this knowledge can be used to assess and manage the stability of the stream's food web, as *Cricotopus* are a large food source for stream and riparian organisms.

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