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Effects of increased temperature on a Trichoptera (*Hydropsychidae*) from premontane forest streams in Southern Costa Rica

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Abstract: Global warming and deforestation can significantly increase stream temperatures. This study investigated how increased stream temperatures affected a tropical caddisfly (order Trichoptera: Hydropsychidae) from first order premontane streams in southern Costa Rica. Laboratory experiments were conducted to test the effects of increased temperature on mortality and behavior of a caddisfly (*Leptonema* sp.). Forested streams and a roadside stream had mean temperatures of 20.0 and 20.7 °C and standard deviations of 0.464 and 1.43 °C, respectively. At temperatures exceeding 22.3 °C caddisfly mortality increased and retreat building decreased, with near complete mortality at temperatures exceeding 25 °C. The roadside stream exceeded 22.3 °C, 11 % of the time during the three week study period. A laboratory study revealed that caddisfly larvae were able to survive in roadside stream water and only suffered mortalities at temperatures above ~22 °C, suggesting that increased water temperature restricts this species to cooler forested streams.

Resumen: El calentamiento planetario y la deforestación pueden incrementar significativamente las temperaturas de las corrientes de agua. Este estudio investigó cómo afectaron las temperaturas de las corrientes a un tricóptero tropical (orden Trichoptera: Hydropsychidae) de arroyos de primer orden de bosque premontano en el sur de Costa Rica. Se hicieron experimentos de laboratorio para probar los efectos del incremento de la temperatura sobre la mortalidad y la conducta de un tricóptero (*Leptonema sp.*). Los arroyos en el interior del bosque y un arroyo al lado del camino tuvieron temperaturas medias de 20.0 y 20.7 °C, con desviaciones estándar de 0.464 y 1.43 °C, respectivamente. A temperaturas superiores a 22.3 °C se incrementó la mortalidad del tricóptero y se redujo la construcción de refugios, con una mortalidad casi completa a temperaturas por encima de 25 °C. El arroyo situado a la orilla del camino excedió una temperatura de 22.3 °C en 11 % del tiempo durante el periodo de estudio de tres semanas. Un estudio de laboratorio reveló que las larvas del tricóptero fueron capaces de sobrevivir en el agua de los arroyos al lado de la carretera y que sólo sufrieron mortalidad a temperaturas arriba de ~22 °C, lo que sugiere que un incremento en la temperatura del agua hace que esta especie esté restringida a corrientes más frescas ubicadas en el interior del bosque.

Resumo: O aquecimento global e a desflorestação podem aumentar significativamente as temperaturas dos cursos de água. Este estudo investigou como o aumento da temperatura do caudal afetou um insecto aquático "caddisfly" tropical (ordem Trichoptera: Hydropsychidae) a partir de córregos premontanos de primeira ordem, no sul da Costa Rica. Precederam-se a

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experiências laboratoriais para testar os efeitos do aumento da temperatura sobre a mortalidade, e o comportamento de um "caddisfly" (*Leptonema sp.*). Corregos na mata e um riacho na berma da estrada apresentaram temperaturas médias de 20,0 e 20,7 °C com um desvio-padrão de 0,464 e 1,43 °C, respectivamente. Para temperaturas superiores a 22,3 °C a mortalidade do "caddisfly" aumentou e o crescimento diminuiu, verificando-se uma mortalidade de quase total a temperaturas acima dos 25° C. O córrego na beira da estrada ultrapassou os 22.3 ℃, 11 % do tempo durante o período de estudo de três semanas. Um estudo de laboratório revelou que as larvas de "caddisfly" foram capazes de sobreviver nos córregos da beira de estrada e só sofreram mortalidade para temperaturas acima de ~ 22 °C, o que sugere que o aumento da temperatura da água restringe esta espécie aos cursos de água mais frescos sob floresta.

Key words: Aquatic habitats, Costa Rica, deforestation, global warming, streams, temperature tolerance, Trichoptera.

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Introduction

Tropical forests are being cleared at a high rate due to urbanization and agriculture (DeFries *et al.* 2010). Deforestation has far reaching implications on both terrestrial and aquatic habitats (Moore *et al.* 2005). Increases in solar radiation, sedimentation, soil erosion, and temperature on aquatic systems can occur as a result of deforestation (Iwata *et al.* 2003; Moore *et al.* 2005; Rex *et al.* 2012). Temperature is of particular importance as global warming has contributed to increasing temperatures, and is predicted to continue to increase (IPCC 2007).

Global surface temperatures have increased 0.8 °C over the past 100 years, and 0.6 °C in the last three decades (Committee on America's Climate Choices; National Research Council 2011). Species may respond to global warming via shifts in range, typically to higher latitudes or elevations (Parmesan 2006; Kannan & James 2009). Tropical systems may be more sensitive to global warming, as temperatures are more stable than in temperate areas and have been for a very long time (Janzen 1967). Tropical montane areas may even be more affected by climate change, as climate driven range shifts are more restricted (Ghalambor *et al.* 2006; Janzen 1967; Sheldon *et al.* 2011). In tropical zones there is little overlap in temperature regimes between low- and high-altitude sites, and organisms that have evolved in a more stable thermal environment are thought to have a reduced or a more narrow ability to tolerate temperature changes (Tomanek 2008), thus hindering dispersal across unsuitable habitat. Aquatic habitats within tropical montane systems are even more limited, and possibly under even greater threat from global warming.

Compared to terrestrial systems, aquatic ecosystems maintain a relatively stable temperature, thus slight temperature changes could have major effects on aquatic ecosystems. Consequently, organisms inhabiting tropical mountain streams may have reduced capacities to deal with increasing temperatures. Mobile aquatic species may be able to move upstream to higher elevations as the climate warms, however, if species are already restricted to the upper reaches of montane streams there may not be any available habitat that is higher and cooler (Domisch *et al.* 2011; Sauer *et al.* 2011). Aquatic organisms with limited dispersal ability such as some caddisfly (Trichoptera) species face an even greater threat (Collier & Smith 1998).

Increasing temperatures can directly and indirectly affect aquatic organisms. Temperature dictates phenology and distribution of stream inhabitants often to their detriment (Caissie 2006; Dingemanse & Kalkman 2008; Li *et al.* 2011; Sweeney *et al.* 1986). A two week advance in emergence for a Trichoptera and Plecoptera was observed in a first order stream where water temperature was artificially increased two degrees, as well as a shift in sex ratios for the trichopteran (Hogg & Williams 1996). Increasing water temperatures lead to increased oxygen demands (Verberk *et al.* 2011) and reductions in dissolved oxygen levels (Dodds & Whiles 2010). In highly oxygenated systems such as mountain streams slight reductions in oxygen levels can significantly impact sensitive organisms such as some species of Ephemeroptera, Plecoptera, and Trichoptera (Olson & Rueger 1968).

Caddisflies (Trichoptera) are a common insect order found in aquatic habitats worldwide (de Moor & Ivanov 2008). Trichoptera are often used as bioindicators of stream health, with many species indicative of clean water (Barbour *et al.* 1999; Rosenberg & Resh 1993). Trichoptera have been recognized as being at particular risk from climate change (Hering *et al.* 2009). Preliminary observations of streams in the rural area around Las Cruces Biological Station (LCBS) San Vito, Costa Rica revealed that caddisflies were absent or very rare in a variety of streams that flowed from or through open areas, e.g. pasture, houses, or agricultural areas. It is known that the absence of forested riparian buffers can significantly alter macrobenthic communities, resulting in reduced diversity and an elimination of the most sensitive species (Lorion & Kennedy 2009). As percent forest decreases in the riparian zone, stream temperature and variation in temperature increases (Lorion & Kennedy 2009; Rex *et al.* 2012). There has been some research conducted on the temperature tolerance of Trichoptra (Gaufin & Hern 1971; Moulton *et al.* 1993; Nebeker & Lemke 1968; Quinn *et al.* 1994) in temperate areas, however, generally not within the genus Hydropsychidae (with the exception of Dallas & Rivers-Moore 2012) nor in the tropics.

Based on our preliminary observations it was suspected that temperature might be the primary causative agent for the absence of Trichoptera in local streams experiencing anthropogenic disturbances. Thus the objective of this study was to investigate temperature tolerance of a common caddisfly (Hydropsychidae) from premontane tropical streams in Southern Costa Rica. Hydropsychids do not build mobile cases, but instead construct a retreat attached to hard structures built out of debris and small rocks (Wiggins & Currie 2008). They build silk nets to collect food and are typically omnivores/ detritivores (Wiggins & Currie 2008). As building a retreat/net is energetically costly (Mondy *et al.* 2011), and can be reduced at elevated temperatures (Philipson & Moorhouse 1974), we monitored retreat construction and mortality at various temperatures. We also monitored stream temperature in three types of watersheds, primary forest, a selectively logged primary forest, and a roadside/pasture area.

Materials and methods

Study area

This research was conducted at the Las Cruces Biological Station (LCBS) of the Organization for Tropical Studies (OTS) in Coto Brus, San Vito, Costa Rica (8° 47'7" N, 82° 57' 32" W) at an elevation of 1200 m asl (Fig. 1). The research area is characterized as a premontane tropical wet forest habitat (Holdridge *et al.* 1971) with an annual rainfall of approximately 4 m y^{-1} (OTS updated 2009 http://www.ots.ac.cr/). All research was conducted during the rainy season, in the months of June and July, 2011.

Temperature data loggers (iButtons®) were placed in three types of first order streams: primary forest, selectively logged primary forest, and a roadside/pasture stream. The streams were (1) Culvert Stream, located in a selectively logged primary forest, (2) Tributary A, a tributary to the West Java River located in the primary forest of LCBS, and (3) a small roadside stream (referred to as "Roadside Stream") located about 1 km north of the station on the road towards San Vito (Fig. 1). Culvert Stream was located in an area near the Wilson Botanical Garden and is thought to have been last logged in the 1970s and has been relatively undisturbed since then (pers. comm. R. A. Zahawi 2011).The watershed of the Roadside Stream included a house, pasture, and an asphalt road. Temperature data loggers were programmed to record temperature every two hours for 21 days (2- 23 July 2011). We also calculated water volume in each of these streams using a Global Water Flow Probe (http://www.globalw.com/) to measure water velocity across a transect. Turbidity of streams was measured using an Oakton® TN-100/T-100 Turbidimeter.

It has been shown that within the genus *Hydropsyche*, a sequence of species occupied different niches along an elevation gradient from the lowlands to mountain headwaters (Mey 2003; Statzner & Dolédec 2011). Thus it was important that the study streams selected were at a similar elevation, and similar in size (e.g. watershed, water volume, water velocity). We investigated a number of roadside/urban/pasture streams in the area, and most had few to no observable caddisflies. However, most of these streams were at lower elevations and or were larger (greater flow) than Culvert Stream. Additionally, they were far enough away from LCBS to make logistics more problematic. Thus, we present data on only one roadside stream.

Two small headwater streams within LCBS, Culvert and Culebra, were the source of our study organisms. These two streams are located within 150 m of each other in a selectively logged primary

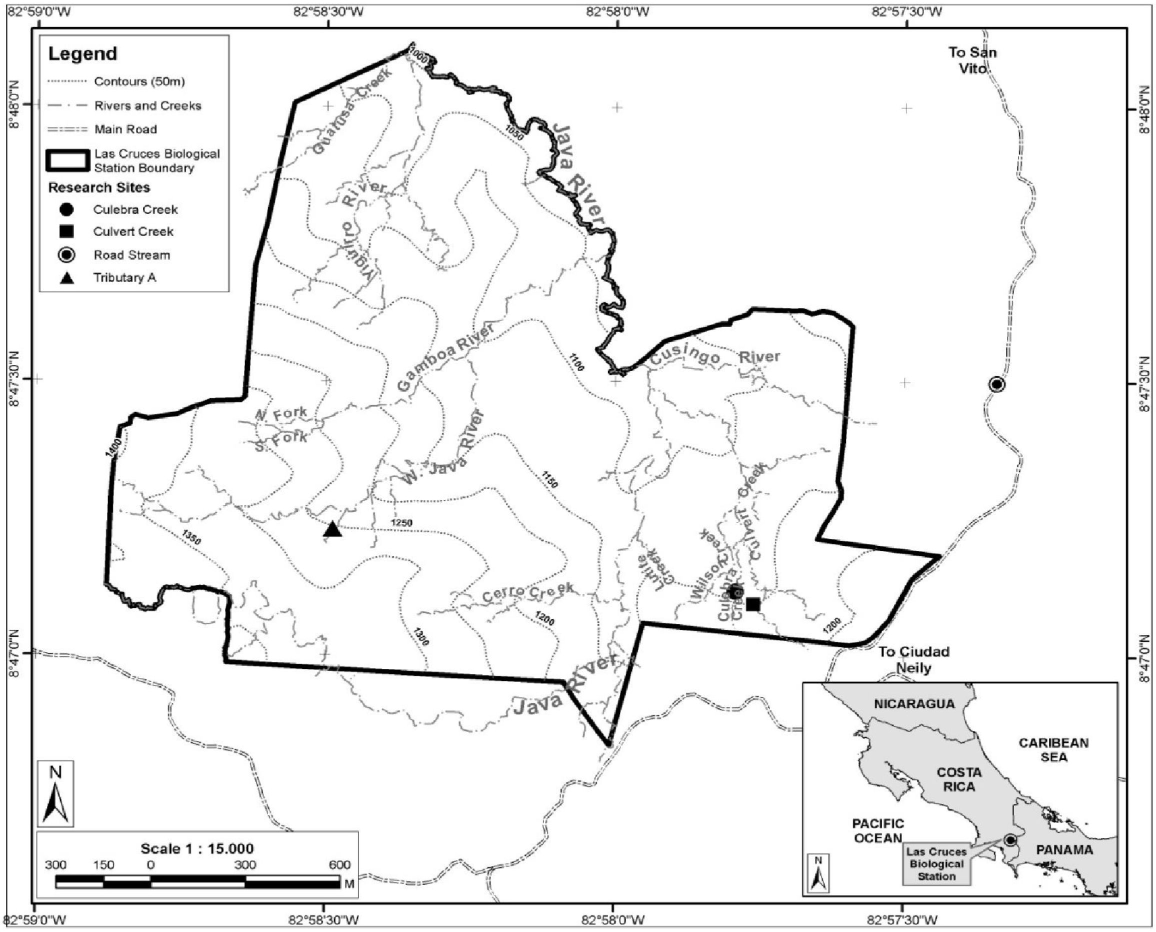

Fig 1. Study sites at and near Las Cruces Biological Station (LCBS). Map created by Mauricio Sarmiento Pancho, Organization for Tropical Studies, LCBS.

forest. Initially we only collected in Culvert Stream within the vicinity of the trail crossing; however, to prevent depletion of that site we also collected in the neighboring Culbera Stream. Consequently, as we did not initially plan on sampling within Culbera Stream, temperature data loggers were not placed in the stream. However, we have seven paired temperature measurements within 1.5 hours of each other and there was no significant difference in temperature (paired t - test: t - ratio = -1.549, P = 0.1723, mean difference = 0.0857).

Trichoptera collection

Within Culebra and Culvert Stream of LCBS there was one apparent species of Trichoptera that was dominant. In all of our sampling we saw only one other species (only two individuals). Initial collections of specimens were closely examined under a dissecting microscope to ensure that we were utilizing a single species. The dominant Trichoptera was in the family hydropsychidae and identified to the genus *Leptonema* (Springer 2010; Wiggins 1977; Wiggins & Currie 2008). The specific species is unknown.

Trichoptera specimens were collected using a modified version of the kick sampling method. Stream substrate was disturbed using one hand, while a small net was placed downstream to catch specimens carried by the current. Specimens were placed into a small plastic container along with water, small pebbles, and leaf litter, collected at the site and transported to the lab. Specimens were placed into three large aerated plastic containers filled with untreated well water and maintained at room temperature (~21 °C). Gravel and stream conditioned leaves collected at the site of capture were placed in the holding containers. They appeared to be territorial, if maintained at high densities larger individuals would attack and

Table 1. Experimental setup for the four temperature trials for Trichoptera.

Trial	Temperature treatments (°C)	Other treatments	n per treatment	Total
1	21.1,24.5	-	15	30
2	20.2, 22.0	Petri dish, plastic cups	8	32
3	15.9, 21.0, 27.3	-	20	60
4	21.5	Well water, roadside stream water	22	44

kill smaller individuals. A number of individuals pupated and some emerged as adults. Specimens were allowed to acclimate for 24 - 48 hours prior to the start of an experiment. Individuals behaving abnormally or that were damaged during collection were not used in experiments. Preliminary husbandry investigations of these Trichoptera revealed that once an individual survived the first 24 hours it was likely to survive one week, the duration of our preliminary investigations.

This species was relatively common in the two "collecting" streams. Twenty specimens were easily collected within 10-15 minutes of sampling within a five meter stretch of stream. They constructed retreats of small gravel (2 - 3 mm diameter) on hard substrates (primarily rocks) located in areas of flowing water.

Experimental trials

Four different trials were conducted to investigate temperature tolerance of the caddisfly (Table 1). In each case caddisflies were removed from the holding containers, extracted from their retreats and placed into individual plastic cups (343 ml volume) containing about 180 ml of water, enough gravel substrate to cover the bottom of the cup, and a 1 cm^2 section of a stream conditioned leaf. Individuals were randomly assigned to treatments, and their cups were placed into water baths (plastic bins, 37 cm x 74 cm x 18 cm) containing 1500 ml of water. Aeration stones were added to circulate water to maintain an even temperature within the baths. There was no water circulation within individual plastic cups within a bath, as each cup was isolated from the water bath. Warm water treatment temperatures were obtained using a submersible aquarium heater. Tempe-rature data loggers (iButton®) were placed in water baths and were programmed to record temperature every two hours. Temperature was also recorded twice a day using a portable digital temperature meter or thermometer (both calibrated in the lab). Temperature data loggers were calibrated with physical temperature measurements and temperatures adjusted accordingly for statistical analyses. Response variables measured were construction of retreats and mortality. Individuals were checked every 12 hours for the presence of a retreat, or mortality. An individual was considered dead if it was unresponsive to gentle probing with a blunt instrument. With the same blunt instrument retreats were partially destroyed every 12 hours. Experimental trials were conducted on separate days due to logistical constraints. Trial two was conducted immediately after trial one ended and the other trials were conducted four and five days after the conclusion of the previous trial. Individuals were used only once and generally after 48 hours of lab acclimation time.

The first trial consisted of two treatments, a room temperature control (21.1 °C) and a warm treatment (24.5 °C). Fifteen individuals were used for each treatment. After six hours individuals were checked for constructed retreats and mortality. After the first observation, the monitoring schedule was changed to every 12 hours for the duration of the trial (90 hours).

In trial two we had two treatments, room temperature and a cool temperature treatment. For the cool treatment instead of a plastic bin we utilized an insulated ice chest as a water bath. With periodic additions of ice and suspending frozen water bottles in the ice chest we were able to maintain a temperature of ~20.2 °C. The control treatment was at room temperature (22.0 °C). Additionally, in trial two we used two types of individual containers, Petri dishes and cups. We were concerned that perhaps the surface area of the cups did not provide enough oxygen exchange, and Petri dishes have a much greater surface area to volume ratio. For this experiment, 32 specimens were used, and randomly assigned to treatments (16 in each). This experimental trial ran for 44 hours from 10:00 on 7 July to 6:00 on 9 July 2011. This trial was ended early due to the difficulty of maintaining a consistent temperature in the cool temperature - this difficulty was rectified in subsequent trials.

Trial three had three treatments, cool (15.9 °C), room temperature (21.0 °C), and warm (27.3 °C), with 20 specimens per treatment using only the plastic cups. Trial three began at 21:00 on the 13 July and ran till 22:00 on the 16 July 2011 (73 hours).

The objective of trial four was to investigate if the absence of trichoptera in the Roadside Stream was a result of water quality factors other than temperature. The control treatment consisted of water from the Research Station the other treatment used water collected from the Roadside Stream. We also took advantage of a rainfall event to test if increased runoff and turbidity in the Roadside Stream affected Trichopteran survival. We used 22 specimens per treatment randomly assigned to one of two water baths at room temperature (21.5 °C). Water was replaced every 48 hours, and a small section of water conditioned leaf (~1 cm^2) was added to each cup. Trial four began 21 July 2011, ending 28 July 2011 (166.5 hrs). It rained 1.78 mm between 16:00 and 17:00 hours on the 26 of July 2011 (www.ots.ac.cr/meteoro). Water was collected from the Roadside Stream after the rainfall event and allowed to acclimate overnight in the lab for temperature equilibrium. On the morning of the 27th water in the Roadside treatment cups was replaced with the post rainfall water collected the previous day. Turbidity of the post rainfall Roadside Stream water was 155 NTU, while the average turbidity of the Roadside Stream excluding the rainfall sample was 8.6 NTU (SD = 10.1). Control treatment water was also replaced at the same time using Research Station water.

Statistical analyses

All data were analyzed using the statistical package JMP (V 5.0.1a: http://www.jmp.com/) or program R (http://www.r-project.org/). We examined the effect of temperature on behavior (retreat building) after 24 hours of exposure to treatment temperatures. We chose 24 hours as our endpoint for retreat building as a significant portion of the caddisflies in the higher temperature treatments did not survive to 48 hours. In addition maximum daily stream temperatures lasted for only two to three hours. We combined the results of all trials and tested the percentage of individuals that built retreats at each treatment temperature using linear regression.

We conducted a similar analysis with percent mortality after 48 hours of exposure to the treatment temperature. Due to a scheduling mistake, experiment two was only conducted for 45 hours, but for statistical analyses was treated as 48 hours.

Results

Stream characteristics

Stream flow measurements for Culvert, Culebra, and the Roadside Stream were taken once on 8 July 2011 at 9:52 a.m., 9:55 a.m., and 10:30 a.m. respectively. The average rainfall for three days prior to flow measurements was 6.6 mm per day. Water flow measurements for Tributary A were taken on 23 July 2011 at 9:39 a.m.. Summary data on stream temperature, specific conductance, turbidity, water velocity, and volume of water is presented in Table 2.

Temperature profiles of the streams varied and are presented in Fig. 2. The Roadside Stream had the greatest range of recorded temperatures and more closely followed ambient air temperature. Although there were two iButtons® placed in each of the three streams only one of the iButtons® in Tributary A and the Roadside Stream could be recovered. Therefore, data from only one of the iButtons® from the Culvert was used. Temperatures at all sites were significantly different from one another (paired T-test, all $P < 0.001$). The daily range of temperatures at each site was also significantly different among sites (ANOVA: SS = 124.2, $F_{3, 84} = 50.55$, $P < 0.0001$) (Fig. 2). Daily air temperature for 2 July - 23 July was obtained from the LCBS weather station website (www.ots.ac.cr/meteoro). The average air temperature was 19.29 °C (SD = 2.13) with a minimum and maximum temperature of 16.36 °C and 25.96 °C (Fig. 2). This air temperature range was similar to the normal range of air temperatures experienced at LCBS over the course of a year (14.14 - 27.56 °C for 2011).

The purpose of this project was not to specifically model air and stream temperature; however, simple models can provide insight into the temperature dynamics of these streams. Stream temperatures are affected by a number of variables including solar radiation (affected by vegetation, shading, etc.) groundwater input, precipitation, evaporation, wind, watershed characteristics,

Table 2. Summary data of the study streams. Temperature data is from continuous data loggers recording every two hours from 2 - 23 July 2011. Turbidity and specific conductance values were from periodic measurements. Water velocity and volume were from one measurement collected 8 July 2011. Trichoptera for experiments were collected throughout a three week period (1-19 July 2011).

	Temperature (°C)				Water flow	
Stream	Mean (± SD)	Min.-Max	Turbidity (NTU)	Sp. Cond. (µS cm^{-1})	Volume (m^3s^{-1})	Velocity (m s^{-1})
Culvert	20.3 (0.45)	19.1-21.2	3.80 (2.07)	63.8 (8.75)	0.013	0.2
Roadside	20.7 (1.4)	18.2-25.7	18.4 (38.9)	36.5 (15.4)	0.002	0.3
A	19.4 (0.51)	18.2-21.7	NA	NA	0.008	0.6

NTU: Nephelometric Turbidity Units, Sp. Cond.: specific conductance, NA: not available.

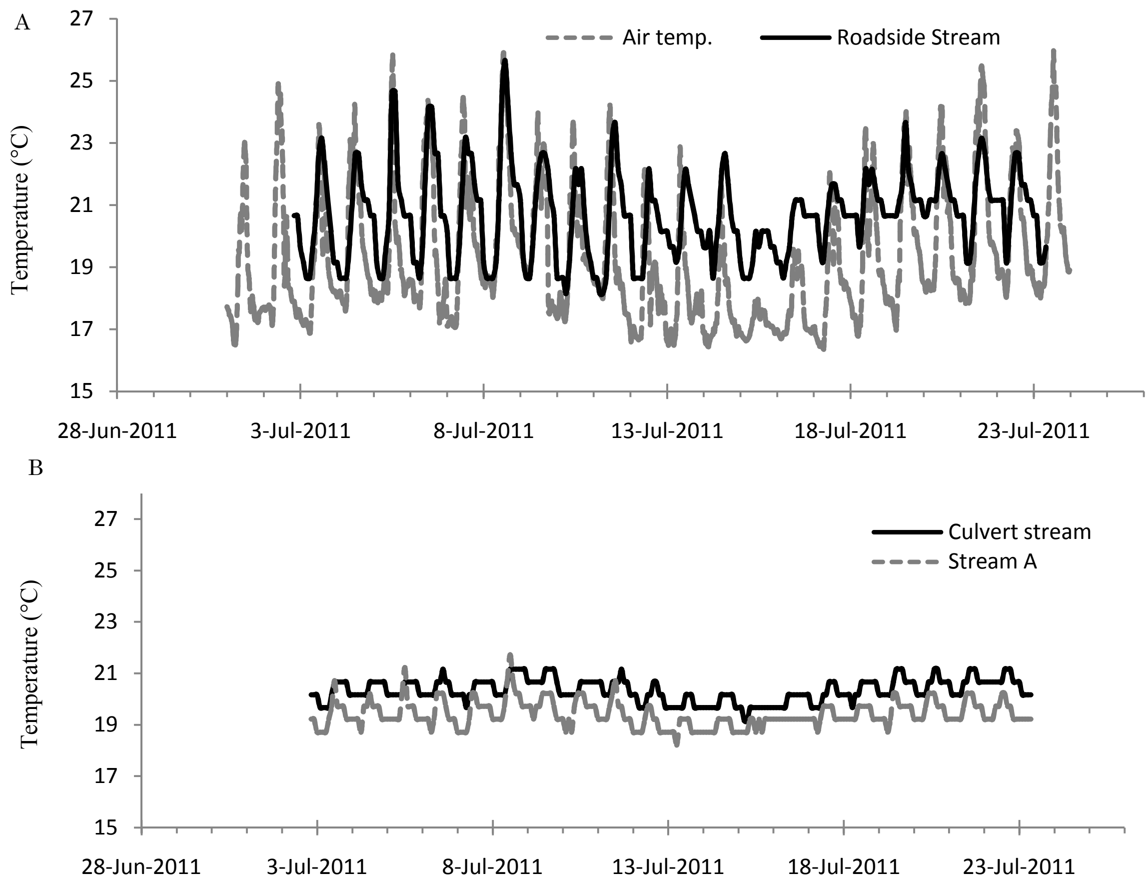

Fig. 2. Temperatures for the period of 2 July to 23 July 2011 for (A) the Roadside Stream and air, and (B) stream temperature for Culvert Stream and "Stream A".

ambient humidity levels, and air temperature (Morrill *et al.* 2005). None of these factors were quantitatively assessed other than what we could obtain (temperature, precipitation, humidity, etc.) from the weather station at LCBS. However, to keep the model simple we used only air temperature.

A cross-correlation function ("ccf" in R) was used to investigate the relationship between air and stream temperature using the two hour interval recorded by the temperature data loggers as our unit of measure. We tested lag correlations from zero to six, which equates to zero to 12 hours in two hour intervals. The maximum correlation for each stream was 0.869, 0.782, and 0.786, with a time lag of zero, two, and four hours for Tributary

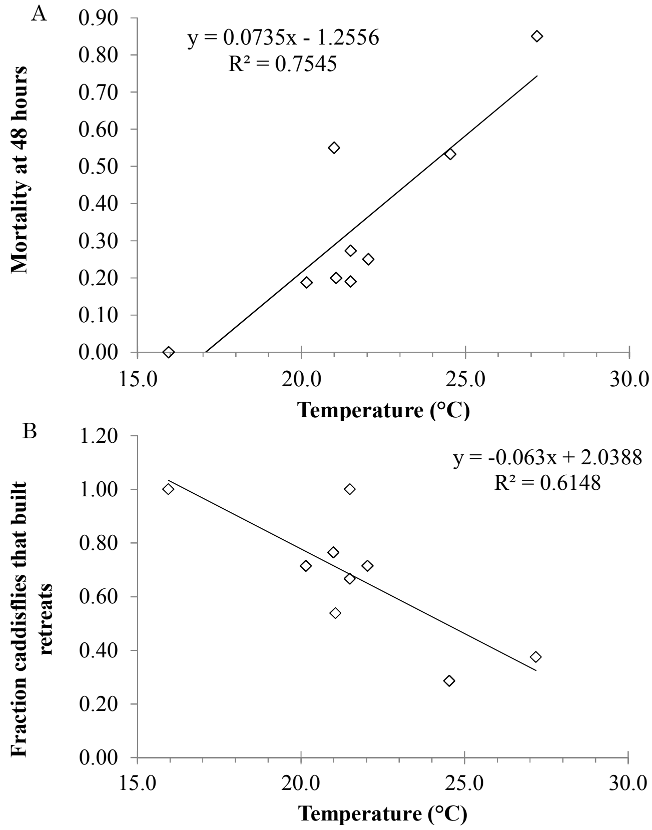

Fig. 3. (A) Mortality of Trichoptera larvae after 48 hours at various temperatures. (B) Fraction of Trichoptera that constructed retreats after 24 hours exposure to various temperatures.

A, Roadside Stream, and Culvert Stream, respectively.

Experimental results

Mortality did not differ between individuals maintained in Petri dishes compared to the plastic cups in trial two (Chi Square = 0.298, DF = 2, P = 0.836); thus these treatments were combined for subsequent statistical analyses. For the overall mortality and temperature analysis the two room temperature bins from trial four were treated as two separate temperature treatments (see trial 4 below). Mortality of Trichoptera at 48 hours was shown to be significantly affected by temperature (ANOVA: $F_{1,8}$= 20.4, P = 0.0027; Fig. 3). As water temperature increased so did mortality of Trichopterans.

Temperature had a significant effect on retreat building behavior (ANOVA: $F_{1,8}$ = 12.47, P = 0.0096). The higher the temperature the lower the percentage of caddisflies that constructed retreats (Fig. 3).

In trial four, the two room temperature water baths differed slightly in temperature (Paired T-test: t-ratio = 26.40, P < 0.0001). Bin A (21.5 ± 0.605 °C) was significantly lower than B (22.1 ± 0.593 °C) with a mean difference of 0.561. The difference was equivalent to the accuracy/precision of the iButtons® (0.5 °C). There was not a significant difference in survival of caddisflies in laboratory well water compared to the Roadside Stream water (Proportional hazard survival model: chi-square = 4.38, P = 0.223). The addition of turbid water also had no effect on survival, as none of the caddisflies in that treatment died after 12 hours exposure. At the end of the 12 hour exposure period turbidity levels dropped from 155 NTU to 32.1 NTU.

Discussion

All of our study streams were within the same general area, elevation, and climate. The primary difference among the study streams was land cover in the watershed. The Roadside Stream watershed lacked trees due to land clearing associated with the road, houses and pastures. The streams within the LCBS were heavily forested with almost complete canopy coverage over the streams, with a few canopy openings due to fallen trees. When deforestation occurs near a stream it has been shown to increase the stream temperature by 7 °C (Naiman *et al.* 2005), while experimentally shading a stream has been shown to decrease maximum temperatures 2 - 4 °C (Johnson 2004). Thus the Roadside Stream was expected to have higher and more variable water temperatures than streams in the LCBS, and our results confirmed this.

The temperatures of streams located in the primary forests and the selectively logged primary forest of the LCBS maintained relatively stable temperatures during our study period. The temperature range of the forested streams (Culvert and Stream A) was only a couple of degrees (2 - 3) whereas the Roadside Stream had a temperature range of seven degrees. Some of the temperature difference we observed may be related to stream size. The Roadside Stream was smaller than the other streams investigated, and smaller bodies of water can be subject to greater fluctuations in temperature than larger bodies of water. We believe that the increased variance and higher temperatures observed in the Roadside Stream accounts for the lack of Trichoptera. Our laboratory studies showed that increased temperatures negatively affected Trichoptera behavior (reduced retreat building) as well as increased mortality at temperatures that currently exist in streams with little to no canopy cover in the area.

Even if increased temperatures do not cause mortality, the effect on their behavior (retreat building) may indirectly affect survival. Retreats are integral to this species' survival. It serves as a shelter, without which the Trichoptera are more vulnerable to predators such as fish and decapods. Retreats also serve as a food gathering source; they contain silk webs which are used to capture algae and plant particles carried by the current. Later in development the cases/retreats house the insect during metamorphosis into a winged adult (Huryn *et al*. 2008). Case and or retreat building is energetically costly (Mondy *et al*. 2011), and if Trichoptera are unable to build retreats as a result of increased temperatures, one would expect lower survival as individuals are more exposed to predators, and their ability to feed might also be reduced without a retreat.

Having to rebuild retreats every twelve hours was an additional stress to increased temperatures, and potentially exacerbated the negative effects of increased temperature. Our design was intended to induce a stress that might be experienced at ever increasing frequencies in stream systems with reduced forest cover. This involved increasing the temperature, as well as partially destroying retreats. As forest cover declines the streams and rivers experience greater variation in flow and temperature (Lorion & Kennedy 2009; Recha *et al*. 2012; Rex *et al*. 2012). Thus it is likely that retreats might become damaged during high flow events that are more common in non-forested areas, and being able to rebuild or repair a retreat is essential.

These Trichoptera occupy high gradient streams with presumably high levels of dissolved oxygen (DO). Unfortunately, we did not have a dissolved oxygen meter or the necessary chemicals/ reagents to measure DO directly. DO levels were also a concern to us in our laboratory experiments, as individuals were placed in cups with little to no water circulation other than when they were checked every 12 hours and when water was replaced (every 48 hours). To ensure that low DO levels were not significantly affecting our results, we utilized Petri dishes as well as plastic cups in one of our trials. Petri dishes provided significantly more surface area per volume of water than the cups, if low DO levels were contributing to increased mortality, or decreased retreat building, we would have expected to observe a difference in these measures between the cups and the Petri dishes. There was no difference in trichopteran survival or retreat building between the two containers. Thus while DO levels may have contributed to reduced survival at elevated temperatures they are probably not the primary reason for the effects we observed.

We were concerned that factors other than temperature may have accounted for the absence of caddisflies in the Roadside Stream, as the stream may be exposed to a variety of anthropogenic stressors such as pollution associated with houses, agriculture, and road runoff (Brisbois *et al*. 2008; Ruiz-García *et al*. 2012; Sarriquet *et al*. 2006). Turbidity and variation in turbidity in the Roadside Stream was higher than in the forested streams, particularly after a hard rain. Trial four was to test if the Roadside Stream water quality was adequate for Trichoptera survival. We even used water collected after a short hard-rain event to investigate if there were factors present only after a pulse of runoff entered the stream that might be detrimental to Trichoptera. There was no difference in retreat building or survival of the Trichoptera between the two source of water (Roadside or Research Station water) used in our investigations. Even the turbid water collected after the rainfall event did not appear to affect retreat construction or survival. It is possible that the variation in temperature may play a part in the absence of Trichoptera in the stream. Compared to the forested sites daily temperature variation in the Roadside Stream was quite large. Thus we can conclude that the primary factor accounting for the absence of Trichoptera in the Roadside Stream was most likely temperature, whether it was the elevated temperature or the fluctuations in temperature.

Temperature is very important for many insects. It determines metabolism, and consequently how much food is required (foraging costs), as well as phenology, reproduction and behavior (Caissie 2006; Dingemanse & Kalkman 2008). Increased temperature may have other effects that were not apparent in our study. Trichoptera feeding on poor quality food are more susceptible to increased temperatures (Villanueva *et al*. 2011). We did not quantify litter fall, organic matter, phytoplankton, or any measure of stream productivity, and thus do not know if food quality differed among streams, thus we cannot rule out food quality as a reason for the absence of Trichoptera in the Roadside Stream. Higher temperatures may increase metabolism, resulting in decreased development time, and or smaller adult sizes (Gillooly *et al*. 2001), and consequently lower fecundity. Smaller adult size also means smaller wings and potentially reduced dispersal ability (Hoffsten 2004).

While we investigated the effects of temperature on Trichoptera retreat construction and mortality, we did not explore the mechanisms behind these negative effects. It is possible that the increased temperatures resulted in an increase in metabolism, and that we did not provide enough food, or that the decrease in the solubility of oxygen with increasing temperatures also contributed to the observed effects. We provided a centimeter square of stream preconditioned leaves every two days for each caddisfly, but due to logistical constraints we were not able to provide aeration or water current. We observed a number of individuals pupating, and two that subsequently emerged (after the conclusion of the experiment), thus, we believe that we were providing an adequate environment for their growth and development.

Conclusions

Stream temperatures outside of forested areas in premontane areas (~1200 m AMSL) of Costa Rica are currently at levels that cannot sustain caddisflies. With global surface temperatures expected to climb 2.5 - 4.7° higher by 2100, an increase in stream temperatures is inevitable. Thus, while land clearing and urbanization currently results in inhospitable stream environments; in the future, even the remaining forested areas are predicted to be too warm for this species of Trichoptera, and potentially other sensitive aquatic species. Their range will continue to contract and be further restricted to the dwindling higher elevation habitats.

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