ORIGINAL ARTICLE

Aquatic biota responses to temperature in a high Andean geothermal stream

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Abstract

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- 1. The impact of global warming on mountain ecosystems is predicted to be high, and particularly in the tropical region. Geothermal streams have provided comprehensive evidence about how aquatic biodiversity changes across natural thermal gradients, but current knowledge is restricted to arctic and temperate zones. Thermal tolerances are different in tropical biological communities, resulting in high thermal sensitivity and low capacity to endure change in their thermal environments. This feature can change the response of aquatic organisms to warming, yet there is little empirical evidence to support this assumption.
- 2. In this study, we address this issue by evaluating how water temperature affects biodiversity, and the structure of primary and secondary producers of a high-elevation geothermal stream system (4,500 m above sea level) in the Bolivian Andes. We analysed multi-taxa responses to increased water temperature using benthic macroinvertebrate families, benthic algae and cyanobacteria, fishes, and macrophytes as study organisms. Different models were run to assess the response of aquatic biota to temperature. In addition, threshold indicator taxa analysis (TITAN) was used to identify changes in macroinvertebrate taxa distributions along the thermal gradient.
- 3. We found that macroinvertebrate richness decreased at 24-25°C due to the different taxon-specific responses to temperature. Threshold indicator taxa analysis identified 17 temperature thresholds for each family of macroinvertebrates. Changes in macroinvertebrate community composition were significantly associated with changes in water temperature. Similarly, changes in macrophytes were associated with temperature differences, and high macrophyte richness was found at 19–20°C. Chlorophyll-a concentration of green algae and diatoms was higher at intermediate temperatures 20-22°C, macroinvertebrates density peaked at 27°C, and fish body size reduced linearly with temperature.
- 4. Temperature increase in the geothermal stream resulted in a reduction of aquatic diversity and primary and secondary producers by simplifying the community structure to a few warm-adapted taxa and reduced body size. These patterns differed from those obtained in temperate/arctic geothermal streams, but are similar to other studies at high-elevation. In a context of increasing warming, the ecological structure of high-elevation streams might lose cold-adapted taxa, and change

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to smaller populations. Additional studies based on ecosystem functioning of geothermal streams could lead to a better understanding on how warming affects high-elevation streams.

KEYWORDS

aquatic organisms, geothermal streams, temperature, thresholds, tropical Andes

1 | INTRODUCTION

Global surface air temperature has increased by c. 1.0°C since industrial times, and it is likely to reach 1.5°C between 2030 and 2052 (IPCC, 2018). Freshwater ecosystems are highly vulnerable to climate change because water temperature and availability are climate dependent, and because their physical boundaries prevent aquatic species from tracking their thermal optima (Woodward et al., 2010). Evidence of the impact of warming on aquatic species includes changes in life history, morphology and behaviour (Brown et al., 2004; Estay et al., 2014; McCauley et al., 2015). Studies examining warming impact on freshwater communities and ecosystem function were mainly based on either experimental manipulation, spatial comparison across latitudinal and altitudinal gradients or long-term ecological surveys (Kärcher et al., 2019; Rosset et al., 2010; Sentis et al., 2017). Other studies have used geothermal streams as model ecosystems to study the impact of warming on aquatic biodiversity and function as these naturally warmed-ecosystems display a great range of temperatures within small spatial scales (O'Gorman et al., 2014; Woodward, Dybkjær, et al., 2010).

Studies on geothermal streams showed evidence of increase in both primary producers and decomposition rates at higher temperature, the latter attributed to a shift in fauna community composition and probably increased microbial activity (Friberg et al., 2009; Woodward, Dybkjær, et al., 2010). In addition, large fishes and efficient grazers dominate warmer sites, whereas small macroinvertebrates inhabit cold sites (Woodward, Dybkjær, et al., 2010). These functional shifts result in a strong top-down control of algae production in warmer sites (Friberg et al., 2009). Moreover, a recent study in 14 geothermal streams reported that increase in temperature simplified the food-web structure and shortened the pathways of energy flux between consumers and resources (O'Gorman et al., 2019). While these studies were performed in lowland subarctic and temperate zones, there is not empirical evidence for other stream types such as tropical, high-elevation systems where warming is predicted to be high (Hock et al., 2019). The tropical Andes is vulnerable to climate changes as significant trends of +0.13°C/decade (1950-2010) and +0.3°C/decade (2080-2100, RCP8.5 scenario) of surface air temperature were reported and predicted, respectively (Vuille et al., 2015, 2018).

Seasonal temperature variation is relatively low in the tropics, resulting in species showing lower thermal tolerances compared to higher latitudes, a process referred as the climate variability hypothesis (Jacobsen & Dangles, 2017; Sunday et al., 2011). Mechanistic evidence of this hypothesis was reported where stream macroinvertebrates exhibited narrower thermal tolerances and lower dispersal across elevational gradients in the tropics than those inhabiting temperate zones, resulting in higher population divergence and speciation rates (Polato et al., 2018). This feature increases the risk of extinction of aquatic species, especially those inhabiting highelevation ecosystems because of the low probability of finding alternative suitable habitats (Jacobsen & Dangles, 2017). Thus, narrow thermal tolerances might accentuate the response of aquatic biota to increasing temperature (e.g. diversity and abundance of primary and secondary producers) in high-elevation streams, but empirical evidence is needed to better predict future responses of freshwater species to warming in the tropics.

In this study, we evaluated temperature impacts on diversity, community structure and abundance of primary and secondary producers inhabiting a high-elevation geothermal stream system in the tropical Andes of Bolivia. The broad range of temperature (8-33°C) at a small spatial scale (6 km) of this ecosystem is ideal for quantifying the effect of temperature on the ecology of high-elevation streams. We hypothesised that: (1) macroinvertebrate diversity would decrease with temperature due to the lack of taxa adapted to high temperatures, and taxon-specific responses to temperature thresholds; (2) changes in macroinvertebrate community composition would be associated systematically with differences in water temperature; and (3) increased temperatures would stimulate primary and secondary producers (i.e. benthic algae and cyanobacteria biomass, macroinvertebrate density, and fish body size) up to a threshold temperature. [Correction added on 06 August 2021, after first online publication: The hypothesis number has been renumbered in sequential order in this version.]

2 | METHODS

2.1 | Study site

The study was conducted in the Juntuma geothermal stream (18°05'52"S, 69°01'47"W) located around 4,400 m above sea level (a.s.l.) in Sajama National Park (Occidental Cordillera of the Andes), Bolivia. This is a volcanic area, including both active and extinct volcanoes, such as Parinacota, Pomerape, and Sajama (Hora et al., 2007; Weide et al., 2017). Juntuma stream is a groundwater-fed, cold stream originating at 4,732 m a.s.l. The heating of the stream by the combination of a series of hot springs and heated soils begins at

about 4 km from its source. The studied stream reach was around 6 km long, covers substrates such as rocks and sand, and displayed a strong temperature gradient ranging from 8.1 to 33.3°C due to numerous hot inflows from lateral geysers along the stream (Figure 1).

2.2 | Data collection

We selected 26 sites across a temperature gradient within the study reach (Figure S1). Data collection was performed mainly during the transition wet-dry seasons in 2013 (April and August 2013), except for chlorophyll-a (Chl-a) concentration that was recorded during the wet season in 2013 (November). At 14 sites, we deployed individual temperature data loggers, recording temperature every 15 min for 6 months (continuous measurements from April to November of 2013). At all 26 sites, we measured, on a minimum of three occasions (spot sampling), water temperature and conductivity with a multiparameter probe YSI 30 (Yellow Springs, OH, U.S.A.), pH with a OAKTON portable meter (Vernon Hills, IL, U.S.A.), and dissolved oxygen concentration with an YSI 58 oximeter (Yellow Springs). We collected water samples from 12 sites encompassing the whole range of observed temperature for a further laboratory analysis of sulfates, sodium and calcium following the standard methods for the examination of water and waste water (Rice et al., 2012), and the Environmental Protection Agency methods (EPA 273.1, EPA 215.1) at the Laboratorio de Calidad Ambiental of Mayor de San Andrés University.

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At the 26 sites, Chl-a concentration of cyanobacteria, green algae, and diatoms were measured in situ with eight of nine repetitions (total of 208 recordings), and colonising different substrates rocks, sand, and sites with aquatic plants. We measured Chl-a concentration using a bbe FluoroProbe bbe-Moldaenke (Schwewntinetal, Germany, GmbH, Beutler et al., 2002; Catherine et al., 2012) coupled with a 1.5 m bbe BenthoFluor fiber-optic cable and submersible adaptor (http://enviro-analytical.com/doc bin/BenthoFluor.pdf) and a bbe BenthoTorch precursor. FluoroProbe measures Chl-a in vivo fluorescence as a proxy of biomass per surface unit, within a range of 0–3 μ g Chl-*a*/cm² and with a precision of 0.1 μ g Chl-*a*/cm². The pulse-amplitude-modulated spectrofluorimetric submersible probe excites algal Chl-a with LED light at five emission wavelengths switched alternatively: 470, 525, 570, 590, and 610 nm. Chl-a fluorescence, recorded between 690 nm and 710 nm, identifies the spectral groups as algal classes: green algae, diatoms, cyanobacteria, and cryptophytes. The final measurements recorded are indicators of biomass per surface unit (μg Chl-a/cm²).

At 23 sites we collected benthic macroinvertebrates using five quantitative Sürber samples (0.09 m²; mesh size 250 μ m) preserved in 75% alcohol. In the laboratory, samples were rinsed through sieves of different mesh sizes. No subsampling was applied. Macroinvertebrates were identified under a stereomicroscope (Wild Heerbrugg, Gais, Switzerland) to family level, according to Domínguez and Fernández (2009). *Trichomycterus* sp. was the only fish observed in the stream reach. At 10 sites, *Trichomycterus* sp. was captured in Sürber samples along a 20-m stream reach by



FIGURE 1 Juntuma stream in Sajama National Park, Bolivia. (a) Landscape view of the geothermal stream, (b) warm sites and warm water inputs from geysers into the stream, and (c) thermal image of the geothermal stream-geyser system. Temperature ranged around 10°C (blue) to 28°C (red) for the thermal image

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disturbing the stream bottom in front of a 25 cm D-framenet lasting around 20 min. We measured the body length of 96 with a ruler, and returned them to the stream immediately. No fish were damaged. At the remaining 16 sites, no fish were observed. At 23 sites, presence and absence of macrophyte taxa were recorded along 20 m of stream length for complementary analysis of macrophyte community responses to the temperature gradient. We tried to record fish and macrophyte data efficiently across the sites, but our sampling and methods were not as exhaustive or temporally replicated as other studies (e.g. O'Gorman et al., 2016; Rasmussen. et al., 2011). Thus, caution has been taken in the interpretation of these results.

2.3 | Data analysis

2.3.1 | Temperature pattern

Mean daily temperatures at 14 sites were calculated from continuous data recorded with temperature loggers. Mean daily temperatures at the 12 sites with no loggers were extrapolated based on continuous data and spot temperatures and the distance between study sites. The distances between sites were measured following the direction of the stream flow (total distance = 6.03 km). Quadratic models and generalised additive models (GAMs) were performed to estimate mean daily temperatures of the 12 unrecorded sites and the best fit was obtained with the GAM (p < 0.001, Akaike information criterion [AIC] = 137.06, Figure 2 and Table S1). The same analysis was carried out to estimate the minimum and maximum daily temperatures. We have only presented mean daily temperature as we obtained similar ecological responses with the minimum and maximum daily temperatures. GAM analyses were carried out using the mgcv R package (Wood, 2018).

2.3.2 | Temperature effects on aquatic diversity and taxon-specific responses to temperature thresholds

To quantify the effect of temperature on both macroinvertebrate and macrophyte diversity, we carried out quadratic and GAMs, and AIC values were analysed to choose the best fit. Interpretation of the occurrences of benthic macroinvertebrates were accompanied with a linear regression between Shannon diversity and temperature, and non-metric multidimensional scaling ordination performed on Hellinger-transformed data, with the vegan package in R (Oksanen et al., 2019; R Core Team, 2019). Moreover, to investigate breakpoints in specific taxa responses along the temperature gradient, we used a threshold indicator taxa analysis (TITAN) with 1,000 permutations using the R package TITAN2 (Baker & King, 2010). TITAN assesses the existence of community and single species thresholds values considering the frequency and abundance data (Baker & King, 2010). TITAN uses standardised indicator value (z-scores) to identify species-specific change, and reflects whether a species shows a greater association with the environmental gradient.

The largest z-score across all splits refers to the strongest change point along the temperature gradient. Pure and reliability indicators (>95%) indicate pure and reliable change points of taxa along the temperature gradient.

To assess how macroinvertebrate and macrophyte communities changed along the gradient, we performed Mantel tests between the community dissimilarities (Bray-Curtis and Sorensen dissimilarities for macroinvertebrates and macrophytes, respectively) and temperature differences among all pairs of sites using a Pearson's correlation analysis (Mantel, 1967). The coefficient r was calculated with 1,000 permutations. Bray-Curtis and Sorensen values of 0 indicate similar communities, and values of 1 indicate completely dissimilar communities. Mantel tests analysis were carried out because they are suitable for monotonic comparisons between the values of two distance matrices (Legendre & Fortin, 2010).

2.3.3 | Temperature effects on primary and secondary producers

To investigate how warming was associated with primary producers, we performed quadratic regressions between the periphyton biomass of the three benthic groups (i.e. diatoms, green algae and cyanobacteria) and mean temperature. For secondary producers, we carried out GAMs between the density of macroinvertebrates and mean temperature. Finally, the effect of mean temperature on fish body size was estimated using the individual measurements as a random factor in mixed linear regression models, as fish were observed only at 10 sites. The linear regression model was carried out with the Ime4 R package (Bates et al., 2015).

2.3.4 | Conductivity effects on minerals and aquatic biota

As conductivity was associated with dissolved ions in water (i.e. Na and Ca), and was strongly correlated with temperatures (Appendix Table S2, Figure S1), we analysed relationships between conductivity and macroinvertebrates richness and density, macrophytes richness, Chl-a concentrations of algae and cyanobacteria, and on fish body size. We applied generalised additive modelling to macroinvertebrates and macrophytes. Quadratic models were used for algae and linear mixed models for fish body size.

RESULTS 3 |

3.1 | Temperature gradient and environmental conditions

Mean water temperature increased from 8.1°C at the upstream site up to 33.3°C 1.8 km downstream, and then gradually cooled down after the geyser zone (Figure 2e). High variability of water



FIGURE 2 Temperature time series of representative sites of the geothermal stream (left): (a) hot site (30.7–36.45°C) (b) warm site (19.1–24.3°C), and (c) cold site (3.3–17.0°C). The colours represent the mean, maximum and minimum daily temperatures. Each point represents the mean, maximum and minimum daily temperatures recorded with individual three temperature loggers from April 26 to November 16 of 2013 (190 days, including the day zero as start day for counting). Fitted curves (right) of (d) maximum, (e) mean, and (f) minimum daily temperatures with continuous data and spot temperatures [Correction added on 06 August 2021, after first online publication: The 'warm site' value has been modified.]

temperature was observed in the colder site: average of the minimum and maximum daily temperature was 3.3 and 17.0°C, respectively (Figure 2c). In contrast, low water temperature variability was observed in the warm and hot sites: average of the minimum and maximum daily temperature ranged from 19.1 to 24.3°C, and from 30.7 to 36.5°C for the warm and hot sites respectively (Figure 2b,c). We also observed an increase in conductivity from 282 μ S/cm to 2,643 μ S/cm at 1.8 km from the beginning of the geyser zone, followed by a slow reduction to 2,240 μ S/cm, whereafter it remained constant (Figure S2). Conductivity was strongly correlated with temperature (R = 0.8, Pearson correlation), and higher conductivities were linked to high pH, and concentration of sodium and sulfates. (Table S2).

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3.2 | Temperatures effect on diversity and taxonspecific responses to temperature thresholds

We observed 34 families of macroinvertebrates, and mean daily temperature had a significant nonlinear effect on their family richness (p < 001, GCV = 0.19, deviance explained = 67.4, Figure 3a). Richness was constant (about 15 taxa) from 9 to 24°C, and then decreased from 14 taxa at 24-25°C to 8 taxa above 32.7°C. Macroinvertebrate Shannon diversity decreased linearly with mean daily temperature $(p < 0.001, F_{1.21} = 27.67, r^2 = 0.54, Figure 3b)$. Perlidae, Baetidae, and Gripopterygidae were restricted to cold sites (below 25°C), while Planariidae, Isotomidae, Dolichopodidae, and Dytiscidae occurred only at warm sites (>25°C). Simuliidae. Coenagrionidae. Tipulidae, and Hydrobiidae occurred in a narrow range of temperature (between 20 and 27°C). Chironomidae and Elmidae occurred at all sites except the warmest one (Figure 4a). Similar patterns were found when analysing relative abundance of macroinvertebrates (Figure S3). TITAN identified 17 taxa with pure and reliable tipping points along the temperature gradient (values higher than 95%), from which 16 showed a negative response to increasing mean temperature considering their frequencies and abundances, and one taxon, Ephydridae, showed a positive response (Figure 5, and Table S3).

We observed 16 taxa of aquatic macrophytes. Mean temperature was significantly related to macrophyte richness, with higher richness at intermediate mean temperatures (19–20°C, $r^2 = 0.58$, deviance explained = 62%, p < 0.001, Figure 3c). Eleocharis sp., Zannichellia sp., and Crassula sp. occurred exclusively in sites with mean temperatures above 20°C, whereas Callitriche was only present below 15°C (Figure 4b).

3.3 | Changes in community composition with temperature differences

Bray-Curtis dissimilarity of benthic macroinvertebrates was significantly correlated with temperature differences among sites (Pearson Mantel test, r = 0.59, p < 0.0001, Figure 6a), just like Sorensendissimilarity of macrophytes (Pearson Mantel test, r = 0.35, p < 0.01, Figure 6b). Threshold analysis of macroinvertebrate communities over the 17 taxa selected showed barely any patterns of community responses to the temperature gradient with a negative response at 31.8°C (See Figure S4).

3.4 | Changes in primary and secondary producers along temperature gradient

Macroinvertebrate density increased gradually from 8°C (from a minimum of 13.450 ind./m²) to a peak at 27°C (130.035 ind./m²). then it decreased sharply as mean temperatures increased, (p < 0.05, GCV = 1.02, deviance explained = 52.2%, Figure 7a). However, we found a significant relationship between mean temperature and density for only three families of macroinvertebrates: Baetidae, Chironomidae, and Elmidae (Figure 7b). Baetidae density decreased linearly with increasing mean temperature (p < 0.001, $F_{1.21} = 39.79$, $r^2 = 0.63$) while Chironomidae and Elmidae densities were highest at intermediate values of mean temperature around 27°C (p < 0.01, GCV = 1.0, deviance explained = 47.8%, *p* < 0.01, GCV = 0.9, deviance explained = 57.1%, respectively).

Our results show a hump-shaped relationship between the Chl-a concentration of diatoms and green algae with mean temperature $(r^2 = 0.25, F_{2,23} = 5.24 p < 0.01; and r^2 = 0.41, F_{2,23} = 9.77, p < 0.001$ respectively, Figure 7c). There was no significant relationship between mean temperature and cyanobacteria ($r^2 = 0.2$, $F_{2,23} = 4.48$, p = 0.10). Mean temperature had a negative effect on the mean body size of fishes ($\chi^2 = 9.6, p < 0.001$).

3.5 Conductivity effect on aquatic biota

There was no significant effect of conductivity on macrophyte richness, algal density, or macroinvertebrate density (Table S4).



FIGURE 3 Relationships between mean temperature and taxa richness of benthic macroinvertebrates (a), Shannon diversity (b), and macrophytes (c)



FIGURE 4 Occurrence across the temperature gradient of (a) benthic macroinvertebrates and (b) macrophytes. Boxplots indicate upper and lower quartile of temperature values, the line in the box represents the median, the open circles are the whiskers extending up to 1.5 times the respective quartile

However, we found a significant relationship between conductivity and macroinvertebrate richness (p > 0.01, $r^2 = 0.24$) and fish body size ($\chi^2 = 5.9$, p < 0.05). However, the relationship was weaker than with temperature. For macroinvertebrates, AIC values of 140.65 and 122.64 were obtained for conductivity and temperature, respectively. For fishes AIC values were 343.43 and 330.24 for conductivity and temperature, respectively.

DISCUSSION 4

4.1 | Temperature thresholds of diversity, community changes and individual taxa responses

In contrast to studies performed in high-latitude geothermal streams where macroinvertebrates diversity increased until 10°C (Woodward, Dybkjær, et al., 2010), we observed that macroinvertebrate diversity reduced linearly with temperature and richness declined at around 24-25°C, suggesting loss of non-adapted taxa towards the warmest sites. Dominance of few taxa in warm places was also suggested in geothermal waters of the south-temperate zones (Boothroyd, 2009). As a consequence of the temperature effect on diversity, benthic macroinvertebrate community changes were strongly associated with changes in water temperature, with no observed threshold value. In contrast, macroinvertebrates community changes (i.e. dissimilarity) peaked at 10°C of temperature differences in arctic/temperate geothermal streams (Woodward, Dybkjær, et al., 2010), and at c. 22.0°C of mean annual temperature in thermal systems with hot water inputs in Serbia (Živić et al., 2013). This difference can be attributed to the different individual taxon responses to warming between tropical and temperate zones (Polato et al., 2018). Furthermore, different macroinvertebrate responses at the species level might obscure the pattern in our study as well as the potential for intra-specific genetic variation across the thermal gradient as observed in arctic geothermal systems (Johansson et al., 2016).

Regarding individual taxon-responses to temperature, TITAN analysis detected temperature thresholds for 17 families of macroinvertebrates, especially for Elmidae, Chironomidae, Gripopterygidae, and Baetidae. For Elmidae, evidence of thermal sensitivity in natural environments is scarce and restricted to other Coleopteran families, which inhabit acidic and warm sites of 28 and 46°C

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(Boothroyd, 2009; Duggan et al., 2007). In laboratory conditions, the elmid *Hydora* sp. from a temperate spring-fed stream had the highest median lethal temperatures above 34°C and at 96 hr (Quinn et al., 1994). Similarly, Elmidae reached a critical thermal maximal of

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FIGURE 5 TITAN analysis for benthic macroinvertebrates. Change points of single taxa along the temperature gradient. The diameter of circles indicates z-score values. Filled circles indicate the thresholds values at which each single taxon declines with temperature at the left side. Empty circles indicate thresholds values at which single taxon increase with temperature at the right side. Horizontal lines represent the 5th to 95th quantile range of taxon-specific change points derived from 1,000 bootstrap replicates of the sample

behavioural response up to 39°C (Dallas & Rivers-Moore, 2012). In our study, Elmidae occurred in nearly all sites with a threshold value of 31.5°C. Chironomidae occurred in almost all sites with a threshold value of 33.2°C, while they were reported to inhabit waters from 29 to 40°C in temperate geothermal streams (Winterbourn, 1968), and hot springs at the Taupo Volcanic Zone in the North Island of New Zealand (Boothroyd, 2009). We observed Gripopterygidae in a narrow range of temperatures with a threshold value of 23.5°C. Consistently, the Plecoptera *Zelandobius furcillatus* had a relatively low mean lethal temperatures (25.5°C, 48 hr, Lethal Dose 50) in New Zealand spring-fed streams (Quinn et al., 1994), and Plecoptera were virtually absent from sites with hot water inputs in Serbia (Živić et al., 2013). Finally, Baetidae had a low threshold value (20.9°C) like the Ephemeroptera *Zephlebia dentata* that declined at 23.6°C in south-temperate geothermal streams (Boothroyd, 2009).

Stream water temperature clearly affected macroinvertebrate communities, but low oxygen concentration at high elevations limits the ability of species to sustain increased metabolic rates at high temperatures, causing a mismatch between oxygen supply and demand (Jacobsen, 2020; Madsen et al., 2015). Indeed, Ephemeroptera families of high-elevation streams in the tropics are highly sensitive to changes in water temperature, which is exacerbated by oxygen limitation (Shah et al., 2019; Verberk et al., 2016). Evidence of this in geothermal streams was observed for *Radix balthica* where increasing warming impacted their metabolic rates in long and shortterm exposures to temperature (Cloyed et al., 2019). By contrast, we observed smaller effects of conductivity on macroinvertebrate diversity compared to temperature, but high mineral concentrations in geothermal streams (Clements et al., 2011; Nimick et al., 1998)



FIGURE 6 Relationship between pairwise temperature differences and dissimilarity of macroinvertebrate (Bray-Curtis) (a) and macrophytes (Sorensen) communities (b)



FIGURE 7 Temperature effect on the density of :macroinvertebrates (a); Elmidae, Chironomidae, and Baetidae (b); benthic algae and cyanobacteria (c); and fish body size (d)

can cause osmotic stress in aquatic organisms (Hopkins et al., 2017; Velasco et al., 2019). The correlation between water temperature and conductivity was also found in temperate geothermal systems with difficulty in teasing apart their effects (Duggan et al., 2007; Gudmundsdottir et al., 2011; Velasco et al., 2019), but in laboratory conditions, Jackson and Funk, (2019) examined mayfly responses to salinity and temperature (5–25°C) and suggested that elevated salinity at cold temperatures can be less toxic than at warm temperatures.

Macrophyte richness decreased with temperature, resulting in community composition changes with temperature differences.

In contrast, higher macrophyte richness and coverage occurred in warmer sites of Icelandic geothermal streams, where macrophyte coverage increased from 12%–20% at cold sites to 22%–83% at warm sites (Rasmussen et al., 2011). Particularly, *Fontinalis antipyretica* and *Jungermannia exsertifolia* were dominant in warm and cold sites, respectively (Hannesdóttir et al., 2013), suggesting macrophyte thermal niche preferences. However, more exhaustive inventories of macrophyte taxa and coverages are needed to improve our understanding of how temperature impacts macrophytes in our study area. Moreover, macrophyte pattern along the temperature

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gradient might be linked to increases in nitrogen and phosphorous concentration along the geothermal stream (Pringle et al., 1993), although limited influence of nitrogen and phosphorus was observed in thermal systems of the arctic/temperate zones (Gudmundsdottir et al., 2011).

4.2 | Changes in primary and secondary producers along the temperature gradient

Beyond certain thresholds, the total density of macroinvertebrates declined with temperature, particularly for Chironomidae and Elmidae families. Similar to our study, Chironomid abundance and biomass decreased nonlinearly as temperature increased showing a strong reduction at around 31°C in a thermal spring system with 29.7-42.0°C of range temperature at 2,210 m a.s.l. in the Colorado Mountains, U.S.A., (Hayford et al., 1995), but reduced greatly at 10°C in subarctic thermal streams (Woodward, Dybkjær, et al., 2010). No macroinvertebrate taxon showed an increase in abundance with temperature in our study, but Ephydridae showed high abundance and frequency at 22.2°C based on threshold analysis, which is consistent with results in hot thermal spring outflows of New Zealand (Winterbourn, 1969) and Iceland (Woodward, Dybkjær, et al., 2010).

Contrary to our hypothesis, the body size of the predatory fish Trichomycterus sp. decreased with temperature increase. We attributed this pattern to the reduction of prey populations and primary producers at higher temperatures. Indeed, stomach analysis content of Trichomycterus therma showed that their diet predominantly comprised of 95% of Chironomidae and Elmidae in geothermal streams of the Bolivian Andes at around 37°C and pH 8.2 (Tarapaya River, 3,600 m a.s.l., Fernández & Miranda, 2007), indicating the consumption of thermal tolerant prey. Moreover, algae Chl-a concentration diminished at 22°C. Thus, if the increase in metabolic demand at higher temperature by the predator Tricomycterus sp. is not matched by food availability, body and population size are likely to decline or go extinct (McDonald et al., 1996), likewise for benthic macroinvertebrates. Thus, reduction in algal biomass might have resulted in smaller macroinvertebrate populations, and thus smaller fish body size at high temperature. By contrast, low oxygen supply at highelevation sites and high metabolic rates of larger organisms (i.e. basal metabolic rate increases with body mass, Brown et al., 2004) could intensify the fish body size reduction at warm sites in our study, and might explain the differences with arctic fishes where body sizes increased with temperature (O'Gorman et al., 2016). However, other ecological process (i.e. size-dependent predation, interspecific competition) might have impacted fish body size and future studies are needed. Furthermore, increasing the temporal sampling effort as used in other studies of geothermal streams (O'Gorman et al., 2016; Woodward, Dybkjær, et al., 2010) might provide a different pattern.

Increasing global warming demands that we understand and predict the responses of freshwater biota community structure and functioning in response to increasing temperature, and geothermal streams provide a natural system to address this issue. Overall, our results showed different ecological patterns than shown in arctic/ temperate geothermal streams, but patterns were relatively similar to temperate high-elevation thermal systems. Different environmental conditions linked to high-elevation and/or low thermal tolerance of tropical species, as suggested by the climate variability hypothesis, might explain our results. Our evaluation of geothermal streams has substantial implications for predicting the responses of high-elevation streams to climate change in the tropical Andes. Because space-for-time substitution studies such as ours have limitations, combining sparse-time and spatial ecological data (Damgaard, 2019) with experiments that unravel the effects of other confounding variables might help to better predict climate change effects using geothermal streams that capture the complexity of the natural environment. In a context of increasing warming in the tropical Andean region, the ecosystem structure of high-elevation streams might change to smaller populations and/or loss of coldadapted taxa. Change in precipitation patterns might exacerbate the impact by increasing drought severity as dry years are projected to increase by a factor of 4 until 2071-2100 in the Central Andes under the RCP8.5 IPCC scenario (Neukom et al., 2015). Therefore, future studies of the underlying mechanisms driving geothermal stream ecology, such as local adaptation of aquatic species, dietary shift by the predator Trichomycterus sp., metabolism, food web dynamics, and the potential effect of other factors such as conductivity will provide a more complete picture of warming impact on the ecological structure and functioning of high-elevation geothermal streams in the tropical Andes.

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CONFLICT OF INTEREST

Authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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