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Taxonomic and functional responses of macroinvertebrates to riparian forest conversion in tropical streams

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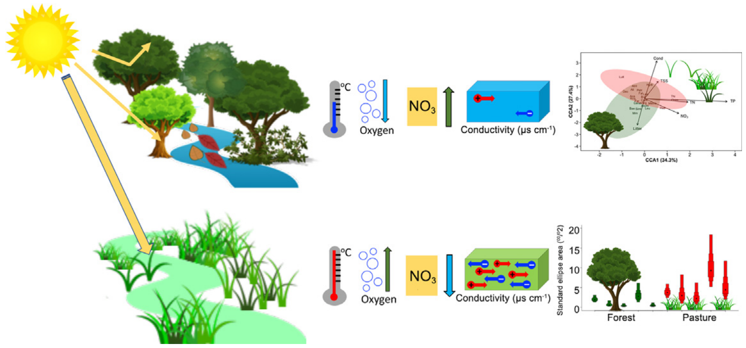
HIGHLIGHTS

- Invertebrate responses were analyzed through structural and functional approaches.
- A large proportion of taxa were common in forest and pasture streams.
- Conversion affected abundance and isotopic composition but not functional diversity.
- Functional redundancy and land management likely influenced the observed responses.

GRAPHICAL ABSTRACT



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ABSTRACT

Land use change threatens the ecological integrity of tropical rivers and streams; however, few studies have simultaneously analyzed the taxonomic and functional responses of tropical macroinvertebrates to riparian forest conversion. Here, we used community structure, functional diversity, and stable isotope analyses to assess the impacts of riparian deforestation on macroinvertebrate communities of streams in southern Mexico. Monthly sampling during the dry season was conducted in streams with riparian forest (forest streams), and in streams with pasture dominating the riparian vegetation (pasture streams). Samples were collected for water quality (physical-chemical variables, nutrient concentrations, and total suspended solids), organic matter (leaf litter abundance and algal biomass), and macroinvertebrate abundance and diversity. Higher temperature, conductivity, suspended solids, and chlorophyll *a* were detected in pasture streams, while nitrate concentrations and leaf litter biomass were greater in forest streams. Macroinvertebrate density was higher in pasture sites, while no differences in taxonomic diversity and richness were found between land uses. Functional evenness was greater in forest streams, while richness and divergence were similar between land uses, despite differences in taxonomic composition. Environmental variables were associated with taxa distribution but not with functional traits, suggesting current conditions still promote redundancy in ecological function. Isotopic analyses indicated consumers in pasture streams were enriched in ^{13}C and ^{15}N relative to forest streams, potentially reflecting the higher algal biomass documented in pasture systems. Isotopic niches were broader and more overlapped in pasture streams, indicating more generalist feeding habits. No significant losses of taxonomic or functional diversity were detected in pasture streams. However, changes in trophic ecology suggest landscape-level processes are

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altering macroinvertebrate feeding habits in streams. The changes we observed in habitat, water quality, and macroinvertebrate community were related to the removal of the riparian vegetation, suggesting the structure and function of the focal systems would benefit from riparian restoration.

1. Introduction

Riparian zones are diverse and complex habitats that link terrestrial and aquatic ecosystems and are essential in supporting aquatic communities and ecosystem function (Naiman et al., 2005). They regulate the inputs of solar radiation, nutrients, and organic matter to streams, influencing temporal and spatial patterns in freshwater population dynamics, trophic relationships, and biogeochemical processes (Burrell et al., 2014; Richardson et al. 2010; Stutter et al. 2012). Vegetation in the riparian zone contributes to the physical, chemical, and biological conditions within streams (de Oliveira-Junior et al. 2017; Morabowen et al., 2019; Randhir and Ekness 2013), and provides many ecosystem services, including recreation, nutrient retention, biodiversity conservation, and water supply (Clerici et al. 2014; Jones et al. 2010).

Global rates of deforestation have declined in recent decades; however, forests continue to be converted to other land use with subsequent effects on climate, hydrological cycle, landscape structure, and biotic communities (Broadbent et al. 2008; Hansen et al. 2013; Lambin and Meyfroidt 2011). Forest conversion is still considered one of the primary threats to the ecological integrity of lotic ecosystems, given the close relationship between the structure and function of rivers and streams and land cover (Dudgeon et al., 2006; Ramírez et al., 2008). Specifically, deforestation in the riparian zone creates a cascade of changes in rivers that begins with the modification of the physical habitat. Declines in organic matter inputs to streams reduce the aquatic habitat, and alters the quantity and lability of allochthonous and autochthonous energy in streams (Clapcott and Barmuta 2010; Halliday et al. 2016; Studinski et al. 2012; Wang and Tan 2017; Wild et al., 2019). Subsequent increases in sedimentation result from increases in runoff and soil erosion, and may alter habitat availability and the physicochemical condition of the water (Sciera et al. 2008). Additional reductions in water quality occur as water temperatures rise, turbidity increases, and dissolved oxygen and nutrient concentrations change (Deegan et al. 2011; Lenat and Crawford 1994; Molina et al. 2017; Quinn and Stroud 2002; Studinski et al. 2012). Collectively, the influence of riparian forest conversion can also have profound effects on the structure and functional attributes of aquatic communities (Bertaso et al., 2015; Iñiguez-Armijos et al. 2018; Quinn et al., 1997).

Researchers have used taxonomic and functional variables to assess the impact of land use change on aquatic organisms. For instance, anthropogenic changes in the riparian zone may alter the taxonomic composition, density, richness, and diversity, and promote the dominance of disturbance-tolerant macroinvertebrates in streams (dos Reis Oliveira et al. 2020; Encalada et al., 2010; Lorion and Kennedy 2009; Quinn et al., 1997). Shifts in organic matter, especially the relative availability of allochthonous and autochthonous resources, can also alter macroinvertebrate assemblages and trophic relationships in running waters. For instance, declines in the abundance and richness of shredders (i.e., species that shred and consume particulate organic matter), or increases in scrapers (i.e., species that scrape algae and detritus from surfaces in streams) when agricultural practices are intensified, have been observed in other studies (Iñiguez-Armijos et al. 2018; Miserendino and Masi 2010). Additionally, shifts in trophic ecology in response to riparian deforestation have also been detected using stable isotope analysis. For instance, the conversion of forest into pasture or cropland can alter the food sources of primary consumers and predators, increasing omnivory and trophic niche overlap within aquatic invertebrate communities (Castro et al., 2016; Price et al. 2019).

The impact of human activities on aquatic communities can also be examined using functional trait analysis, which assumes the ability of organisms to inhabit a site depends on their morphology, behavior, dispersal capacity, and life history (Poff et al., 2006). Species traits can be related to environmental variables (Dolédec et al. 2006; Statzner and Bêche 2010), and can be used to assess changes in functional diversity in response to environmental change (Schmera et al. 2017). In fact, some authors have argued that functional diversity assessment and other approaches that examine changes in biological traits within communities may be better indicators of changes in ecosystem function than traditional metrics such as species diversity (Gagic et al., 2015), as they may be more sensitive to anthropogenic change (Castro et al. 2018; Dolédec et al. 2006). Therefore, research combining taxonomic and functional diversity metrics may contribute to a better understanding of the changes in aquatic ecosystems resulting from human pressures (Li et al. 2019).

Establishing the impacts of land-use changes on biotic communities in tropical streams is an urgent goal, given the increasing annual deforestation rates in tropical areas (Hansen et al. 2013; Keenan et al. 2015), with conversion to agricultural activities being one of the main drivers of deforestation (Gibbs et al. 2010; Graesser et al. 2015). The primary drivers of forest conversion are diverse. In tropical Asia, industrial plantations and selective logging are major drivers, whereas conversion to cropland, including small-scale farms, drives deforestation in tropical Africa (Gaveau et al. 2016; Houghton 2012; Seymour and Harris 2019). In South America, conversion of forest to pasture is increasing, which combined to lower precipitation and increase fire frequency can accelerate forest loss (Seymour and Harris 2019). Similarly, pasture is increasing in some areas of Central America like northern Guatemala (Graesser et al. 2015). Pasture expansion can be influenced by food demand, road construction, and conservation and development policies (Graesser et al. 2015). In addition, other factors such as population growth, cultivation of illicit crops, and drug trafficking can also influence deforestation in Latin America (Armenteras et al. 2013, 2017; Tellman et al. 2020).

As with many tropical regions, rates of deforestation in Mexico have declined since the late 1990s and woody vegetation has expanded in some parts of the country; yet, the loss of forested areas continues (Bonilla-Moheno and Aide 2020; FAO and UNEP 2020; Keenan et al. 2015). Increased in pasture and decreased in forest has been documented in the south of the country and is associated with the removal of tropical moist forest (Bonilla-Moheno and Aide 2020). In this study, we compared taxonomic and functional metrics of the macroinvertebrate communities of streams in the Pichucalco River watershed that have experienced relatively limited disturbance of the riparian area (forest streams) to those that have experienced significant deforestation through conversion to pasture (pasture streams). Specifically, we compared metrics of community structure (i.e., taxonomic abundance, richness, and diversity), functional diversity (e.g., feeding habits, respiration, maximum body size), and trophic ecology (i.e., δ^{13}C and δ^{15}N) between the two types of streams. We expected riparian deforestation would result in macroinvertebrate communities with reduced taxonomic and functional diversity than streams with intact riparian zones. Moreover, we expected macroinvertebrates in pasture streams to show a more generalist feeding habits and to be isotopically enriched due to increase availability of autochthonous carbon.

2. Material and methods

2.1. Study area

The study streams were located in the northern sierra of Chiapas, in the Pichucalco River basin, a tributary of the Grijalva in southern Mexico. The region has a warm, humid climate, with mean annual precipitation exceeding 4000 mm (Station 00007193 Pichucalco, average 1981–2010, National Meteorological Service). During the dry season (February–May) the region receives an average of 786 mm of rain, while the wet season (June–January) precipitation averages approximately 3334 mm. Monthly mean temperature ranges between 21.2 °C (January) and 26.7 °C (May). Land use in the Pichucalco basin is heterogeneous, but much of the land has been converted to agricultural development: cultivated pasture (63.92%), secondary vegetation (14.54%), temporary agriculture (12.11%), tropical forest (3.82%), mountain cloud forest (1.70%), and urban area (0.29%) (INEGI 2010).

2.2. Description, characterization, and assessment of the physical habitat of streams

We sampled three streams draining forested areas and three streams running through lands converted to pasture. Forested stream reaches were located in catchments dominated by forest (55.2–70.3%). In contrast, herbaceous vegetation covered large proportions of the catchments of pasture streams (46.6–69.0%), although forested habitats were also present upstream (23.3–38.5% of the catchment area; Table S1). None of the study catchments included any urban areas, only isolated houses or buildings were observed. The riparian zones of the forest sites contained mixtures of primary and secondary forest, but scattered cocoa trees *Theobroma cacao* were found in the understory of two of the forest sites (2 and 3), indicating the habitats may have been used for agricultural development in the past. In pasture streams, herbaceous vegetation was most common in the riparian areas, but trees and shrubs were occasionally encountered.

Streams were sampled monthly during the dry season between February and May 2017 (i.e., four sampling events in each of the six study sites). The sampling was conducted in the dry season, as we expected there would be greater contrasts in processes influenced by riparian vegetation, such as allochthonous resource inputs and the growth of primary producers, between forest and pasture streams in the seasonal tropics during this time of the year (Davies et al., 2008; Ramírez et al., 2008). Moreover, higher densities of macroinvertebrates have been reported in tropical streams during the dry season when spates that can dislodge benthic substrate, reduce food resources, and increase invertebrate mortality are less common (Astudillo et al. 2014; Dudgeon 2000; Flecker and Feifarek 1994; Jacobsen et al., 2008).

All of the study streams were second- to third-order systems, and we sampled reaches with altitudes ranging from 46 to 126 m a.s.l. (Table S1). The physical habitat refers to structural attributes of streams, such as substrate type, habitat complexity, riparian vegetation structure and coverage, and anthropogenic alterations (Kaufmann et al., 1999). We applied the US Environmental Protection Agency Rapid Bioassessment Protocol (RBP) proposed by Barbour et al. (1999) to characterize and assess the physical habitat of each reach. We used the RBP to assess the following habitat parameters in each reach: epifaunal substrate/available cover, embeddedness, velocity/depth combinations, sediment deposition, channel flow status, channel alteration, frequency of riffles, bank stability, bank vegetative protection, and riparian vegetative zone width.

During each sampling event, we measured total and wet channel widths and channel depth. We also estimated the percentage of area within each 100 m reach that was covered by riffles, pools, and runs and the proportion of common inorganic substrate types using methods outlined in Barbour et al. (1999). Discharge was calculated for each site on every sampling date using the velocity-area method (Gordon et al., 2004). Percent canopy cover was estimated using a spherical concave densiometer (Forestry Suppliers Model-A) at the three sampling riffles to capture the variation along the 100 m reach. During each sampling event, we established one transect across de stream in each of the three riffle habitats we sampled in each stream. At three points in each of the transects, we used the densiometer to estimate canopy cover in the four cardinal directions (north, south, east, west). In addition to the RBP, we used the Riparian Forest Quality Index (QBR) of Munné et al. (2003) to assess the physical structure of the sites, as it specifically considers the cover of the riparian zone, the quality and structure of the cover, and the alteration of the channel.

2.3. Physicochemical variables, nutrients, and organic matter

We measured the following variables in three, fast-flowing (i.e., riffle) sites in each stream during each sampling event using a multi-parameter probe (YSI model 556): temperature, conductivity, pH, dissolved oxygen concentration, and percent oxygen saturation. We also collected water samples (one in each riffle) to estimate total phosphorus (persulfate digestion), nitrate (cadmium reduction method), total nitrogen (persulfate digestion), and suspended solids (gravimetric method), were determined via standard methods (APHA 2012).

At three points in each sampling reach, all leaf litter was collected within a 30 cm width across the entirety of the wetted channel using a Surber sampler. Samples were lightly rinsed in the laboratory, dried at 60 °C for two days, and weighed. The dry biomass of leaf litter per unit of area was estimated using the width of the wet channel to calculate area (Pozo and Elosegi 2007). We also estimated the abundance of algal resources (mg m^{-2}) in the stream using chlorophyll *a* concentration as a proxy. Briefly, we selected three flat rocks approximately 10–20 cm in length, and the top was brushed to obtain the sample. The area of the rock was calculated by covering the brushed area with aluminum foil and applying a weight-area relationship. The resulting slurry was filtered into a fiberglass filter with a 0.7 μm pore opening; chlorophyll *a* was analyzed using the ethanol-extraction method (Marker et al., 1980).

2.4. Macroinvertebrates

Macroinvertebrates were collected from three riffle habitats in each study reach on each date (one sample per riffle). In each riffle, we set a Surber sampler (0.09 m^2; 500 μm mesh) to collect animals by cleaning the larger substrate and disturbing the finer substrate in the sampler frame area for 15 min. Samples were preserved in 70% alcohol. Organisms were counted and identified to genus level, except for Hydrachnidae, Ceratopogonidae, Chironomidae, Empididae, Hidrobiidae, and Pachychilidae, which were identified to family. Taxonomic identifications were carried out using the keys of Bueno-Soria (2010), Flowers and De La Rosa (2010), Merrit et al. (2008), Ramírez (2010), and Springer (2010).

We collected additional macroinvertebrate samples in May 2017 from each site for stable isotope analyses. These samples were placed in labeled bags, transported in ice, and frozen until processing. Samples were rinsed with distilled water, dried at 60 °C for 48 h, and ground into a fine powder with a mortar and pestle. Samples were weighted in tin cups for analyses of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope ratios in the Center for Stable Isotope Analysis at the University of Georgia.

2.5. Data analysis

The model used for data analysis included two factors, a) the land use where streams were located (forest and pasture), and b) month of collection (March, April, May, June), both factors were analyzed with their respective replicates. Physicochemical parameters were compared using the ADONIS non-parametric permutation test of the "vegan" package in R (Oksanen et al., 2007; R Core Team 2015). When ADONIS reported significant differences between months, we conducted post-hoc, F-permutation tests using the "RVAideMemoire" package in R software (Hervé and Hervé 2020; R Core Team 2015). ADONIS was selected over parametric ANOVA because permutation analysis rehabilitate the loss of statistical power and preserve the effect of the factors in the experimental design under departure from normality conditions (Shapiro-Wilk) (Anderson, 2017; Gleason 2013).

We calculated density as the number of individuals per m^2 based on the area of the Surber sampler and richness (S) to compare macroinvertebrate community metrics between forest and pasture streams. We also calculated Hill's diversity and evenness (N1 and N2), called effective number of species (Chao et al. 2010; Ellison 2010; Hill 1973), using the "iNEXT" package in R (Hsieh et al. 2016). The values of these indices were presented in pirateplots using the "yarrr" package in R (Phillips, 2017) and we compared differences between land use type and month using the ADONIS non-parametric permutation test (Oksanen et al., 2007; R Core Team 2015). Community composition was also compared between forest and pasture and sampling dates using the ADONIS non-parametric permutation test of the "vegan" package in R. Additionally, a similarity percentage analysis (SIMPER) was performed to identify the taxa that contributed most to the average similarity/dissimilarity between land uses and sampling dates. This analysis was conducted with PRIMER V6+PERMANOVA (Anderson 2001).

To analyze potential relationships between species abundance and diversity and land use, sampling date, and physicochemical parameters, we used a Canonical Correspondence Analysis (CCA) based on the "vegan" package in R (Oksanen et al., 2007). We estimated the significance of variables using a R^2 goodness-of-fit permutation test using the "vegan" package. The results of the CCA were plotted with the "ggplot2" package in R (Wickham, 2016). To better visualize the CCA, we divided the results into two figures, one representing localities and months, and the other representing species.

We estimated functional diversity using three metrics: functional richness, functional evenness, and functional divergence, which are independent of one another (Mason et al. 2005; Villéger et al. 2008). Each component of functional diversity was calculated using seven attributes (feeding habits, respiration, maximum body size, body flexibility, body shape, specific adaptation to flow constraints, and mobility and attachment to the substrate) that were based on 38 modalities developed by Tomanova and Usseglio-Polatera (2007) and Tomanova et al. (2008). We gathered additional functional trait data from other studies (Baptista et al., 2006; Castro-Vargas et al. 2018; Chará-Serna et al. 2012; Floriano and Moreira 2015; Hecher and Zettel 1996; Lugo-Ortiz and McCafferty 1996; Maier, 2016; Maier and Short 2014; Merrit et al., 2008; Muñoz-Quesada and Holzenthal 1997; Parra-Trujillo 2014; Rueda Martín et al., 2011; Seagle 1982; Valente-Neto and Fonseca-Gessner 2011). Fuzzy coding was used to describe the affinity between the taxon and the modality (0, no affinity; 1, weak; 2, moderate; 3, strong) (Chevenet et al., 1994; Tomanova and Usseglio-Polatera 2007). Functional diversity indices — richness, evenness, and divergence — of the invertebrate communities (forest and pasture) per month were calculated using the "BioversityR" packages in R (Kindt and Kindt 2019) and "FD" (Laliberté et al., 2014). The values of these indices were presented in pirateplots of the "yarrr" package in R (Phillips, 2017). The functional diversity indices for each land use by month were compared using the ADONIS non-parametric permutation test of the "vegan" package in R (Oksanen et al., 2007; R Core Team 2015). When ADONIS reported significant differences between months, we conducted the post-hoc, F-permutation test based on the "RVAideMemoire" package in R (Hervé and Hervé 2020; R Core Team 2015).

To measure the magnitude of the relationship between environmental variables, species, and functional attributes of species by sites and sampling time, we used the RLQ multivariate analysis through the maximization of covariance of site and species scoring tables (L-table) as a function of the (R-table), which are scores of environmental variables by site and scores of species scores by trait (Q-table) (Dolédec et al. 1996). In addition to the description and analysis among the factors detailed above, we tested the following hypotheses from the results of the RLQ and the univariate fourth-corner analysis (Legendre et al., 1997): a) species depend on the environmental characteristics of sampling sites (Model-2), and b) the distribution of species according to their preferred sites depends on the functional attributes of these species (Model-4). The RLQ analysis was performed with the ADE-4 package in R (Dray et al., 2015). Plots were drawn with ggplot2, tidyverse, and grepel (Slowikowski et al., 2018; Wickham, 2016; Wickham et al., 2019).

To visualize the structure of the trophic web in the study streams, we plotted $\delta^{13}C$ and $\delta^{15}N$ values for consumers in an X-Y plane. The species were previously classified into trophic groups: predator, gathering collector, shredder, scraper, and filtering collector, after Merrit et al. (2008). We used the SIBER routine (Jackson et al. 2011; Parnell et al., 2008) to estimate the isotopic niche based on the standard ellipse area (SEA), size-corrected area (SEAc), and Bayesian standard ellipse area (SEAb). From the calculation of SEAb, we analyzed the percentage of isotopic niche overlap between the different trophic groups in each land use and between forest and pasture.

3. Results

3.1. Physical habitat and physicochemical variables

The study sites were dominated by fast-flowing habitats (40–80% of the total area). The substrate in forest sites was dominated by pebbles and boulders (70–85%), while pasture streams were primarily composed of pebbles and gravel (60–80%, Table S1). As expected, canopy cover was greater in the forested streams (62–76%) than in pasture streams (0–2%). The RBP and the QBR index indicated that forest sites (RBP, 0.84–0.95; QBR, 100) have better physical habitat and riparian conditions relative to pasture sites (RBP, 0.62–0.74; QBR, 25–40) (Table S1). For RBP, greatest differences were observed in categories velocity/depth combinations, bank vegetative protection, and riparian vegetative zone width.

Mean water temperature was typically greater in pasture (27.16 °C ± 2.14 SD) than in forest streams (25.72 °C ± 2.34 SD). There were significant differences in temperature between land uses ($P = .004$) and months ($P = .004$), although the interaction between factors (land use, month) was also significant ($P = .009$). Conductivity was greater in pasture sites ($P = .005$); however, there were no significant differences in pH between land use or through time (Table 1). Dissolved oxygen concentrations were significantly higher in pasture than in forest streams ($P = .01$, Table 1).

Total nitrogen concentrations were greatest in both habitat types in May ($P = .008$, Table 1) and higher values (303.31 ± 166.90 μg L^{-1}) were obtained in forested streams ($P = .004$). Temporal patterns in nitrate resembled patterns in total nitrogen, but the interaction between land use and time was significant (Table 1). Total phosphorus concentrations showed significant variation through time ($P = .005$, Table 1) but not between land use. Concentrations of suspended solids were significantly higher in pasture streams (2.89 ± 1.54 mg L^{-1}) than in forest streams (2.11 ± 0.82 mg L^{-1}) ($P = .02$, Table 1).

Peak chlorophyll *a* values were recorded in May in both stream types (forest: 146.09 ± 88.66; pasture: 225.65 ± 56.84 mg m^{-2}; Table 1). There were also significant differences in chlorophyll *a* values between land uses and between months ($P = .01$). Areal biomass of leaf litter was more than 4-fold higher in forest streams (51.55 ± 44.63 g m^{-2}) than in pasture streams (12.83 ± 11.42 g m^{-2}, Table 1).

Table 1

Monthly average ± standard deviation of physicochemical parameters, chlorophyll *a*, and leaf litter in forest and pasture streams located in the Pichucalco River watershed, Mexico. (T, water temperature; C, conductivity; DO, dissolved oxygen; TN, total nitrogen; TP, total phosphorus, TSS, total suspended solids; Chl *a*, chlorophyll *a*). Letters in superscript indicate significant differences ($P < .05$). Fe: February; Mr.: March; Ap: April; My: May.

	February	March	April	May	Average
Forest					
T (°C)	24.51 ± 1.81	25.56 ± 2.34	24.90 ± 1.39^{Mr,My}	27.92 ± 2.32	25.72 ± 2.34
C (μs cm^{-1})	409.89 ± 60.94	420.22 ± 73.25	372.11 ± 16.74	423.00 ± 60.64	406.31 ± 58.53
pH	8.80 ± 0.12	8.67 ± 0.22	8.30 ± 0.22	8.86 ± 0.27	8.66 ± 0.30
DO (mg L^{-1})	8.80 ± 0.65$^{Mr, My}$	7.19 ± 1.34$^{A, My}$	8.27 ± 0.30	7.53 ± 0.34	7.81 ± 1.88
TN (μg L^{-1})	245.22 ± 33.92^{Mr,My}	189.49 ± 82.22	205.33 ± 24.37^{My}	573.21 ± 47.43	303.31 ± 166.90
NO_3-N (μg L^{-1})	85.5 ± 18.64	58.84 ± 26.69	35.71 ± 31.16	162.05 ± 18.35^{Mr,Ap}	84.29 ± 51.79
TP (μg L^{-1})	26.48 ± 14.03	25.99 ± 15.34	32.34 ± 11.66 ^{My}	28.87 ± 31.38	33.22 ± 20.90
TSS (mg L^{-1})	1.94 ± 0.64^{Ap}	2.13 ± 0.78	1.74 ± 0.63	2.62 ± 1.01	2.11 ± 0.82
Chl *a* (mg m^{-2})	72.96 ± 29.30	58.03 ± 29.46^{My}	52.72 ± 46.61	146.09 ± 88.66	76.92 ± 56.29
Leaf litter (g m^{-2})	40.95 ± 27.96	82.37 ± 49.51	29.69 ± 18.84	72.09 ± 58.45	51.55 ± 44.63
Pasture					
T (°C)	28.66 ± 2.05	26.67 ± 0.58^{My}	24.82 ± 1.17	28.50 ± 1.75	27.16 ± 2.14
C (μs cm^{-1})	428.11 ± 54.67	453.44 ± 60.47	427.00 ± 38.36	454.89 ± 32.64	440.86 ± 47.76
pH	8.68 ± 0.10^{Ap}	8.42 ± 0.18	8.42 ± 0.16	8.73 ± 0.26	8.56 ± 0.23
DO (mg L^{-1})	9.10 ± 0.92$^{Mr, My}$	7.27 ± 0.87$^{A, My}$	8.50 ± 0.42	8.05 ± 0.51	8.31 ± 1.04
TN (μg L^{-1})	234.67 ± 36.63^{Mr,My}	172.70 ± 66.08	138.21 ± 55.38^{My}	444.39 ± 74.53	166.90 ± 133.40
NO_3-N (μg L^{-1})	14.47 ± 6.43^{Ap,My}	13.95 ± 8.49$^{Ap.My}$	18.83 ± 13.60^{My}	121.96 ± 44.50	42.30 ± 51.96
TP (μg L^{-1})	51.03 ± 12.42^{Ap,Mr,My}	29.40 ± 25.47^{Ap}	25.68 ± 5.19^{My}	42.18 ± 25.28	37.07 ± 21.00
TSS (mg L^{-1})	4.13 ± 2.37^{A}	2.08 ± 0.96	2.24 ± 0.47	3.14 ± 0.76	2.89 ± 1.54
Chl *a* (mg m^{-2})	53.00 ± 21.33$^{Ap, My}$	85.05 ± 60.27^{My}	152.07 ± 142.24	225.65 ± 104.91	128.94 ± 112.23
Leaf litter (g m^{-2})	16.89 ± 16.17	14.98 ± 10.29	7.04 ± 9.35	12.43 ± 7.36	12.83 ± 11.42

3.2. Macroinvertebrates

We collected a total of 14,852 organisms, belonging to 14 orders, 48 families, and 51 genera. Of the 59 taxa identified, 45 (75%) were present in both forest and pasture streams. Forest streams had only seven taxa that were not found in pasture streams, while eight taxa were found in pasture but not in forest streams (Table S2). Chironomidae was the most abundant group, with densities of 242.73 ± 307.26 ind m^{-2} in forest streams and 440.61 ± 491.91 ind m^{-2} in pasture streams (Table S2). Three genera of the order Ephemeroptera were also abundant in forest streams, *Baetodes* (218.79 ± 328.30 ind m^{-2}), *Thraulodes* (164.85 ± 202.75 ind m^{-2}), and *Tricorythodes* (142.73 ± 158.77 ind m^{-2}), while the most abundant genera in pasture streams were *Thraulodes* (368.03 ± 421.76 ind m^{-2}), *Fallceon* (237.78 ± 171.42 ind m^{-2}), and *Tricorythodes* (225.00 ± 250.86 ind m^{-2}, Table S2).

Total mean density of macroinvertebrates was significantly greater ($P = .011$) in pasture streams (2234.22 ± 1399.57 ind m^{-2}) than in forested systems (1369 ± 745.80 ind m^{-2}). The highest densities were observed in pasture streams in February (3111.1 ± 1345.8 ind m^{-2}) and in May in forest streams (2023.3 ± 725.4 ind m^{-2}). The lowest densities were found in February (1012.22 ± 418.2 ind m^{-2}) in forest streams (Fig. 1a).

Species richness was similar between the two land uses (forest = 17.7 ± 4.86, pasture = 19.6 ± 5.3). The greatest richness was recorded in February in pasture streams (23.6 ± 6.8), followed by forest streams in May (21.3 ± 4.7, Fig. 1b). Significant differences in richness were

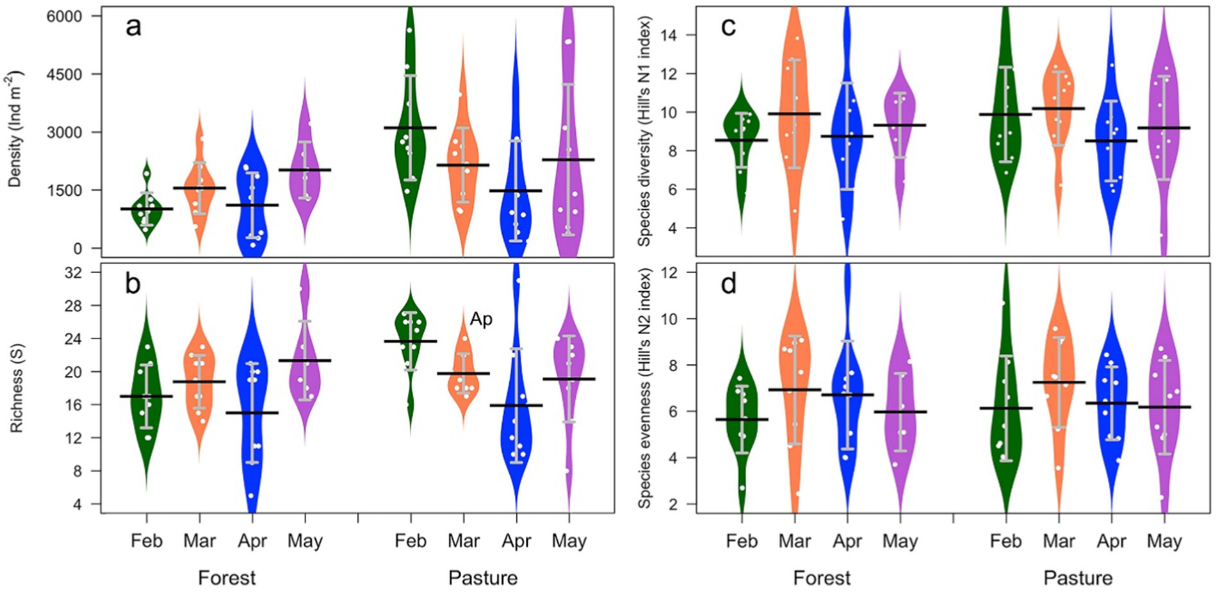

Fig. 1. Monthly density (a), species richness (b), Hill's species diversity (c) and Hill's species evenness (d) for macroinvertebrate communities at forest and pasture streams in the Pichucalco watershed in Chiapas, Mexico. Mean (horizontal black line), standard deviation (vertical gray bars), sample values (white dots) are shown. Areas correspond to kernel density shapes.

observed through time ($P = .003$), but not between land uses. There were no significant differences in Hill's species diversity between land uses (forest = 9.1 ± 2.5, pasture = 9.4 ± 2.2) or through time; the maximum was 10.1 ± 3.3 in pasture streams in March and the minimum was 8.5 ± 3.8 in forest streams in February (Fig. 1c). Likewise, there was no significant variation in Hill's evenness between land uses or among months (Fig. 1d).

There were significant differences in taxonomic structure between land use types ($P = .0001$) and among sampling dates ($P = .0001$), with a significant interaction ($P = .037$). Pairwise tests yielded significant differences between forest and pasture streams in February and March ($P < .0012$); in forest streams, there were significant differences between May and the other dates ($P < .031$), while in pasture there were differences between February and the other dates ($P < .037$). The SIMPER analysis suggested that the abundance estimates of Chironomidae, *Fallceon*, *Baetodes*, *Thraulodes*, *Tricorythodes*, *Metrichia*, *Chimarra*, *Neoelmis*, *Simulium*, *Psephenus*, and *Smicridea* contributed 57% to the differences between forest and pasture streams, and between 41 and 58% to differences between months. In forested streams, differences between May and all other months were due to greater densities of Chironomidae and *Fallceon* in May. In contrast, temporal differences in taxonomic structure in pasture streams were associated with greater densities of *Thraulodes* and Chironomidae in February.

The canonical correspondence analysis accounted for 61.7% of data variability (CCA1 = 34.3%, CCA 2 = 27.4%), indicating separation between forest and pasture streams in their physicochemical parameters. Notably, there was overlap between sites for many of the recorded taxa (Fig. 2a). Forest streams were characterized by higher biomass of leaf litter and greater nitrate concentrations (Fig. 2a), while pasture streams had higher conductivity and greater concentrations of suspended solids. *Baetodes* (Bae), *Simulium* (Siml), *Maruina* (Mrn), *Rhagovelia* (Rha), Ceratopogonidae (Ceratl), and *Leucotrichia* (Leu) were among the taxa that were strongly associated with forest sites (Fig. 2b). In contrast, *Lutrochus* (Lutl), *Thraulodes* (Thr), *Traverella* (Tra), *Metrichia* (Metl),

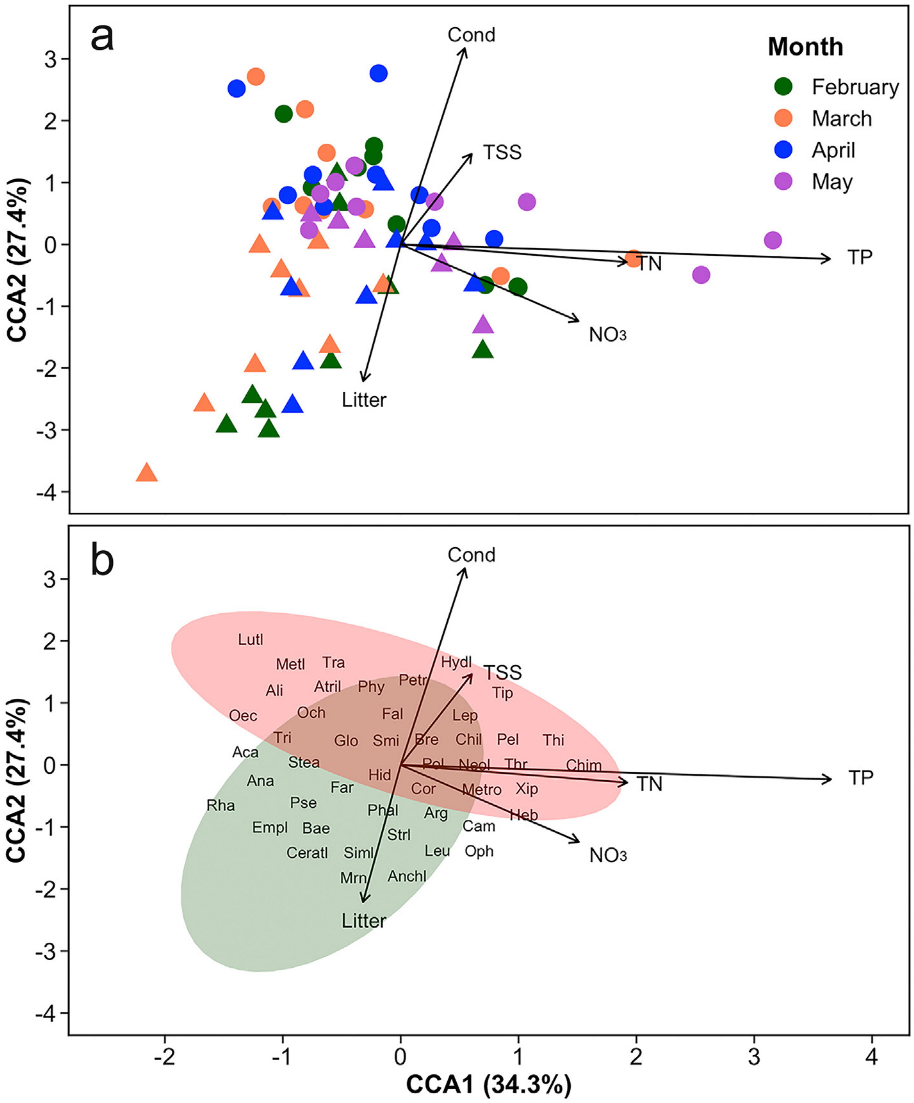

Fig. 2. Canonical correspondence analysis (CCA) plot showing a) the relation of main environmental factors (arrows) with monthly sampling points in forest (triangle) and pasture streams (circle), and b) with the macroinvertebrate composition. Ellipses are the 95% confidence interval of the canonical scores for forest (green) and pasture (red) sites. (Acronyms: Cond, conductivity; TSS, total suspended solids; TP, total phosphorus; TN, total nitrogen; NO_3, nitrate; Litter, leaf litter; Aca, Acari; Ali, *Alisotrichia*; Ana, *Anacroneuria*; Anchl, *Anchytarsus*; Arg, *Argia*; Atril, *Atrichopogon*; Bae, *Baetodes*; Bre, *Brechmorhoga*; Cam, *Camelobaetidius*; Chil, Chironomidae; Chim, *Chimarra*; Ceratl, Ceratopogonidae; Cor, *Corydalus*; Empl, Empididae; Fal, *Fallceon*; Far, *Farrodes*; Glo, *Glossosoma*; Heb, *Hebrus*; Hid, Hidrobiidae; HydL, *Hydrobius*; Lep, *Leptonema*; Leu, *Leucotrichia*; LutL, *Lutrochus*; Met, *Metrichia*; Metro, *Metrobates*; Mrn, *Maruina*; Neol, *Neoelmis*; Och, *Ochrotrichia*; Oec, *Oecetis*; Oph, *Ophiogomphus*; Pel, *Pelocoris*; Petr, *Petrophila*; Phal, *Phanocerus*; Phy, *Physa*; Rha, *Rhagovelia*; Siml, *Simulium*; Smi, *Smicridea*; Stea, *Stenelmis*; Str, *Odontomyia*; Thi, Thiaridae; Thr, *Thraulodes*; Tra, *Traverella*; Tri, *Tricorythodes*.

Alisotrichia (Ali), *Chimarra* (Chim), *Melanoides* (Thi), and *Hebrus* (Heb) were associated with pasture. Greatest overlap in taxa between forest and pasture sites was observed in May, when water levels were lowest (Fig. 2a).

There was a great deal of internal variability in functional richness over the months in both types of land uses (Fig. 3a). The greatest values were observed in May in forest streams (0.33 ± 0.23) and in February in pasture streams (0.25 ± 0.17, Fig. 3a). There were no significant differences in functional richness between land use, but there was significant temporal variation ($P = .04$, Fig. 3a). There was no significant difference in functional divergence between stream types, or thorough time. Functional divergence ranged from a minimum of 0.62 ± 0.09 in forest streams in March to a maximum of 0.65 ± 0.10 in pasture streams in April (Fig. 3b). Functional evenness was greater in forest streams (0.60 ± 0.1) than in pasture streams (0.55 ± 0.07). The greatest values were recorded in February (0.63 ± 0.08), March (0.60 ± 0.11), and April (0.60 ± 0.12, Fig. 3c). Functional evenness was significantly different between stream types ($P = .04$), but not through time.

The RLQ analysis produced similar results, and the accumulated inertia in the first two axes was 64.95 and 24.33%, respectively, for a total of 89.28%. The RLQ also suggested that there was a relationship between physicochemical parameters and forest and pasture streams. Both analyses suggested that there was greater leaf litter biomass in forested streams and greater conductivity and dissolved oxygen in pasture streams. Greater concentrations of nitrates and total nitrogen in forested systems were documented by both analyses, especially in May (Fig. 4). Greater chlorophyll *a* concentrations were associated with pasture streams. However, only leaf litter showed a significant correlation with axis 2 ($P = .048$), in which the separation between both land uses is more evident. The taxa associated with forest include *Baetodes* (Bae), *Metrobates* (Metro), *Maruina* (Mrn), *Xiphocentron* (Xip), *Odontomyia* (Strl), and *Tipula* (Tip). In contrast, Chironomidae (Chil), Empididae (Emp), *Chimarra* (Chim), *Glossosoma* (Glo), *Leptonema* (Lep), *Smicridea* (Smi), *Oecetis* (Oec), and *Lutrochus* (Lutl) were associated with pasture streams. The univariate fourth-corner analysis indicates a significant relationship between species assemblages and the environmental characteristics of sites (Model 2, $P = .003$).

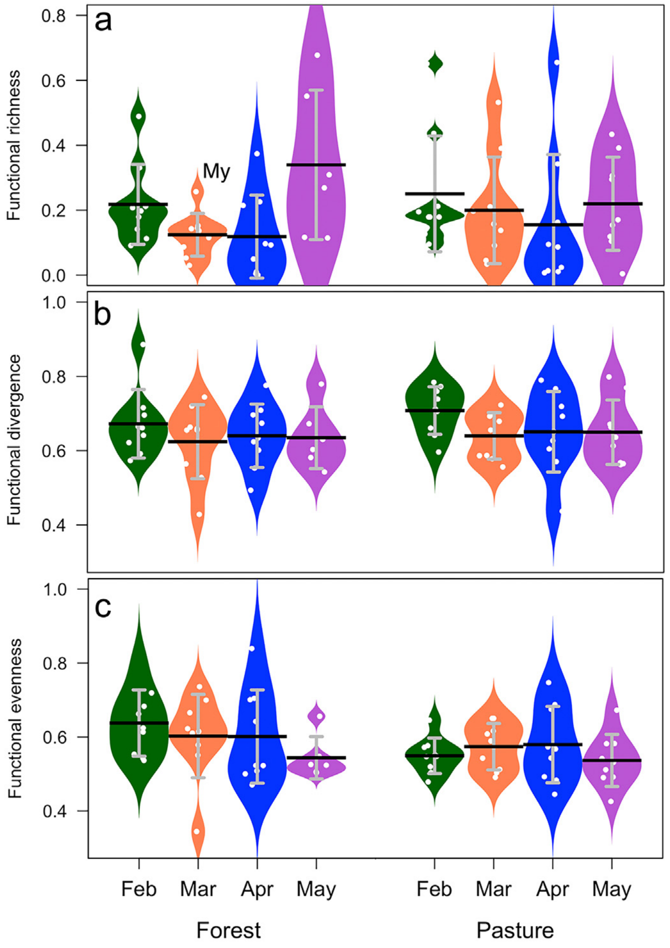

Fig. 3. Monthly functional richness (a), functional divergence (b), and functional evenness (c) for macroinvertebrate communities for forest and pasture streams in the Pichucalco watershed in Chiapas, Mexico. Mean (horizontal black line), standard deviation (vertical gray bars), and sample values (white dots) are shown. Areas correspond to kernel density shapes.

There was no significant relationship between the distribution of species and their functional attributes (fourth-corner analysis, model-4, $P = .625$). However, it was observed that organisms related to forest streams differed from those of pasture in their type of respiration (Stig and Plas), great flexibility in their body size (>45 mm), cylindrical body shape (Cyl), the presence of suction structures (SUC), and swimming traits (SWW, SWS). Functional traits that were predominantly associated with pasture included piercing feeders (PI), integumentary respiration (Teg), and larger body sizes with less size flexibility (<10 mm). Pasture-related traits also included flat organisms (Flatt), that had anal hooks (AH) and had not additional traits developed to deal with fast-flowing water (NA). The mobility of these organisms or their ability to remain fixed on substrate was also associated with pasture streams, with most species having adaptations to remain temporarily attached (TA) to substrate or were crawlers (CL) (Fig. 4).

3.3. Stable isotope analysis

The stable isotope analyses indicated that macroinvertebrates from pasture sites were more variable and were more enriched in both δ^{13}C and δ^{15}N compared to forest macroinvertebrates (Fig. 5). Of all of the invertebrates collected for analyses, δ^{13}C values were the least enriched for gathering collectors, predators and scrapers in forested streams, while the most enriched δ^{13}C values were documented in shredders, scrapers, and filtering collectors. In both types of streams, δ^{15}N values were most enriched in predators, and in general, macroinvertebrates from all trophic guilds from pastures were much more enriched in δ^{15}N that their counterparts in forested systems (Fig. 5). The greatest variability in isotopic values for macroinvertebrates within a trophic guild were documented in scrapers (Thiaridae), shredders (Tipulidae), and predators (Odonata) from pasture systems (Fig. 5).

The isotopic niches were greater for all of the functional feeding groups collected in pasture systems (Table 2; Fig. 6). In both forested and pasture streams, scrapers had the largest isotopic niches (Table 2). In both stream types, scrapers from the Thiaridae family (trumpet snails) produced broad trophic niches, and of all the taxa sampled, thiarids from pasture streams were the most enriched in both C and N (Table S3). Two families from forest streams accounted for the relatively large isotopic niche of scrapers: Leptophlebiidae (−27.14 ± 0.82 δ^{13}C and 1.08 ± 0.65 δ^{15}N) and Psephenidae (−24.86 ± 0.3082 δ^{13}C and 0.82 ± 0.14δ^{15}N), which both had relatively low δ^{15}N values (Table S3). Narrower isotopic niches were documented in forest streams, especially for shredder and filtering collector taxa (Table 2, Fig. 6). There was greater isotopic overlap in pasture streams, most likely derived from the broader isotopic niches of pasture taxa (Table 2). Comparatively, isotopic overlap was comparatively reduced in forest streams, where the greatest overlap occurred between predators and scrapers (Table 2).

4. Discussion

Land conversion of tropical forests to agriculture presents a great, but relatively understudied threat to the structure and function of

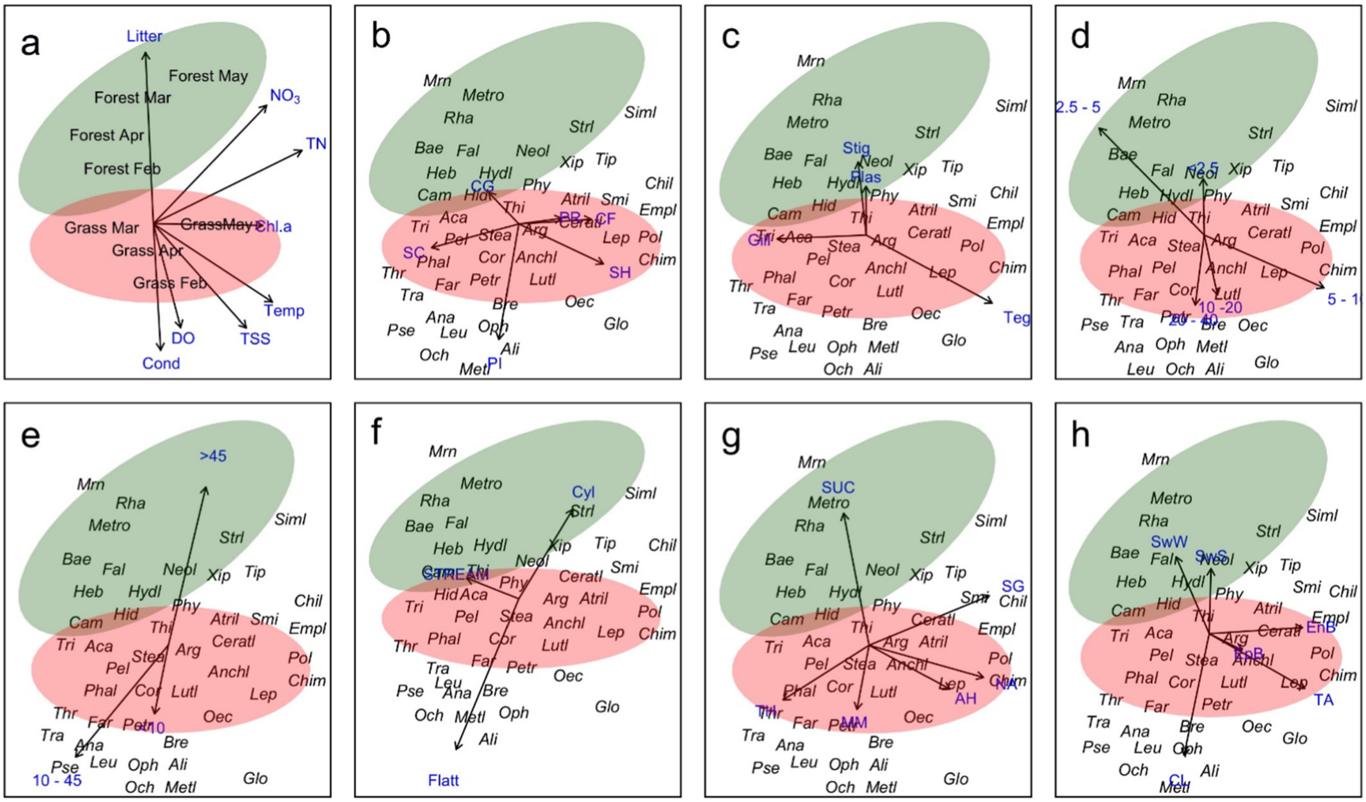

Fig. 4. First two axes of RLQ analysis showing covariation of environmental variables and the species traits (a) and covariation of species and traits categories: (b) feeding habit, (c) respiration (d), maximum body size, (e) body flexibility, (f) body form, (g) specific adaptation to flow constraints, and (h) mobility and attachment to substratum traits. Ellipses are the 95% confidence interval of the scores for forest (green) and pasture (red) sites. (Environmental variables: Cond, conductivity; DO, Dissolved oxygen concentration; TSS, total suspended solids; Temp, water temperature; Chla, benthic chlorophyll *a* concentration; TN, total nitrogen; NO3, nitrate; Litter, Leaf litter; Feeding habits: CG, collector gatherer; Pr, predator; SC, scraper; CG, collector filterer; SH, Shredder; PI, piercer; Respiration: Teg, tegument; Plas, Plastron; Stig, stigmata; Flexibility: <10, none; 10–45, low; >45, high; Body form: Flatt, flattened; STREAM, streamlined; Cyl, cylindrical; Adaptations to flow constraints: SUC, suckers; SG, silt gland; AH, anal hooks; TH, tarsal hooks; MM, mineral-material case; NA, no adaptation; Mobility and attachment to substratum: SwW, full water swimmer; SwS, Surface swimmer; EnB, Endobenthic burrower; EpB, Epibenthic burrower; TA, temporarily attached; CL, Crawler (CL). For taxa acronyms refer to Fig. 2).

freshwater macroinvertebrate communities. Here, we examined the impacts of riparian deforestation on aquatic communities in streams on southern Mexico. The results of this study suggest there is a relationship between conversion to pasture and the condition of the physical habitat, structure of the riparian area, and water quality in streams, which may affect the structure and functioning of the

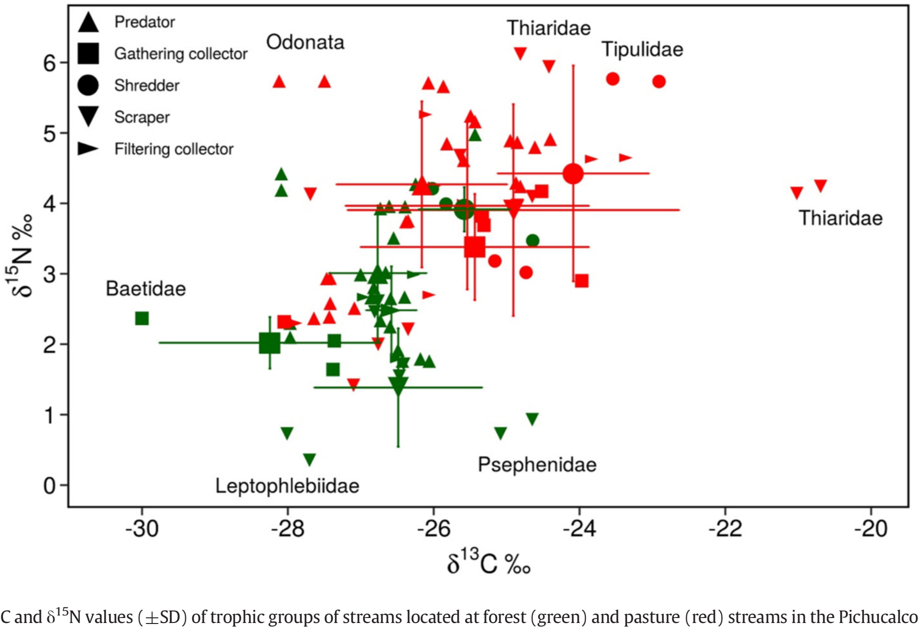

Fig. 5. Bi-plots with average δ^{13}C and δ^{15}N values (±SD) of trophic groups of streams located at forest (green) and pasture (red) streams in the Pichucalco watershed in Chiapas, Mexico.

Table 2
Total area of the convex hull (TA), standard ellipse area (SEA), small sample size corrected standard ellipse area (SEAc) and percentage overlap in SEAb between pairs of trophic groups in forest (F) and pasture (P) streams in the Pichucalco River watershed, Mexico.

Site/trophic group	TA ($\%^2$)	SEA ($\%^2$)	SEAc ($\%^2$)	SEAb overlap (%)			
Forest							
				Gathering collector	Shredder	Scraper	Filtering collector
Predator	6.38	2.03	2.13	12.53 ± 6.34	10.08 ± 6.51	28.50 ± 8.94	21.76 ± 9.31
Gathering collector	0.54	0.49	0.66		0.28 ± 1.83	13.75 ± 6.20	8.38 ± 7.27
Shredder	0.34	0.38	0.51			2.98 ± 4.85	4.70 ± 7.62
Scraper	3.88	3.04	3.55				12.90 ± 7.37
Filtering collector	0.42	0.45	0.59				
Pasture							
Predator	7.80	3.85	4.05	35.52 ± 10.38	22.28 ± 7.90	36.03 ± 10.89	49.04 ± 11.97
Gathering collector	2.88	2.94	3.93		26.89 ± 9.28	30.31 ± 10.87	40.05 ± 13.23
Shredder	1.58	1.25	1.66			22.97 ± 9.15	29.71 ± 9.24
Scraper	16.32	9.83	10.92				45.61 ± 14.12
Filtering collector	5.86	4.80	6.00				

macroinvertebrate community. Some of the changes we documented, especially related to physical habitat and water quality, were consistent with other studies conducted in tropical streams subjected to agricultural conversion (Chaves et al., 2009; Deegan et al. 2011; Neill et al. 2001; Vázquez et al. 2011). However, some of our comparisons of the macroinvertebrate communities between forest and pasture streams did not produce the expected differences in diversity metrics that have been generated in previous investigations (Encalada et al., 2010; Lorion and Kennedy 2009). Notably, the application of both taxonomic and functional trait diversity metrics in this study produced additional insights that allowed us to document differences in aquatic communities between the two types of streams that were not evident when solely examining metrics of taxonomic diversity.

In contrast to our findings, several studies have reported higher taxonomic richness and diversity in forest streams in tropical areas, relative to streams flowing through pastures (Encalada et al., 2010; Lorion and Kennedy 2009; Nessimian et al., 2008). We documented a relatively large number of taxa that were common in both pasture and forest streams (i.e., 75% of all taxa sampled), indicating that pasture streams we studied may not be as disturbed as those reported in other studies (Lorion and Kennedy 2009; Quinn et al., 1997). Groups that are thought to be sensitive to environmental change, such as Ephemeroptera, Trichoptera, and Plecoptera, still inhabit the pasture streams of Pichucalco. Alternatively, upstream conditions and land use history in the forested sites can influence site-specific species composition. The presence of forest in the catchments (Table S1) and fragments of riparian forest upstream (600-800 m) from the pasture sites may have facilitated the dispersal of some groups of organisms, such as aquatic insects, thus mitigating the effects of deforestation on macroinvertebrate communities (González-Trujillo et al. 2019; Nessimian et al., 2008). Recolonization has been proposed as a mechanism to enhance resilience to disturbance produced by land use change in tropical streams (Morabowen et al., 2019). In addition, the livestock farming conducted in the region is developed under an extensive system which may influence the physical habitat and bank condition (Chará-Serna et al., 2015; Niyogi et al. 2007), but do not involve major impacts in water quality from permanent sources of organic pollution as occur in intensive systems (Vale et al. 2019).

Species assemblages in the forested sites may have previously been subjected to historical land use, as suggested by the presence of cocoa trees in the understory of the forest sites, that shifted abiotic conditions and "filtered" sensitive species from the local species pool. Environmental filtering is a process by which the abiotic environment influences the distribution of species across a landscape (Kraft et al. 2015a) by altering processes that influence the fitness, performance, and persistence of species (Cadotte and Tucker 2017). Abiotic conditions can also filter particular traits or phenotypes from communities, and limit the ability of entire assemblages of organisms to persist under new conditions

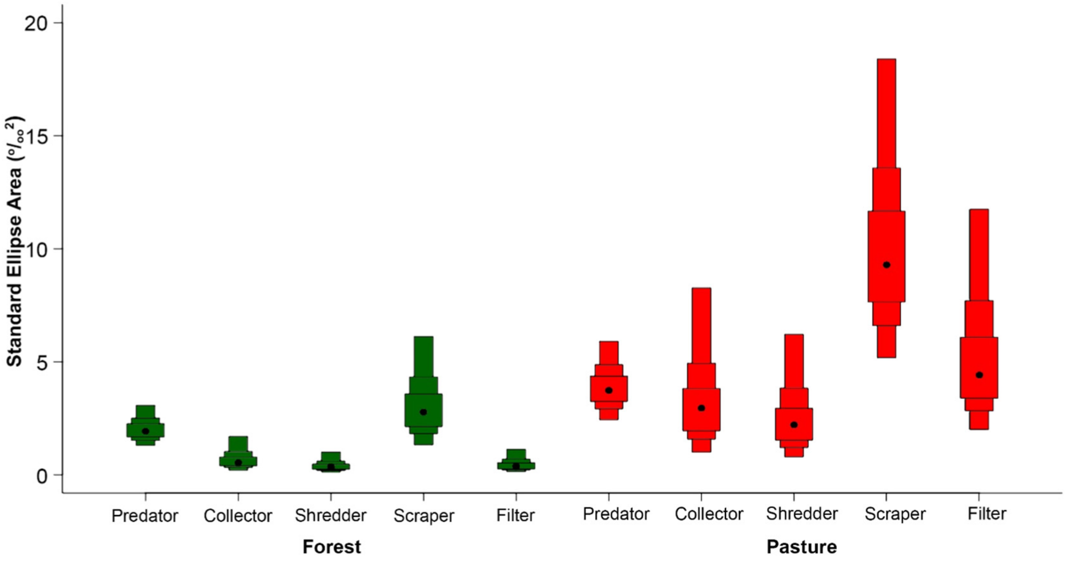

Fig. 6. Density plot of the Bayesian standard ellipse areas (SEA_B). Black dots represent the modes and boxes 50, 75 and 95% of the Bayesian credible intervals from the center to edges.

(Cadotte and Tucker 2017; Kraft et al. 2015b). For example, environmental stressors related to riparian disturbance in savanna streams of Brazil were associated to groups of traits rather than to an individual trait indicating that stressors are probably selecting a combination of traits that will influence the tolerance of macroinvertebrate taxa to a disturbed environment (Firmiano et al. 2021).

Differences in forest cover in the riparian zone can influence instream water quality and changes in allochthonous and autochthonous production. Higher water temperatures that we observed in pasture streams were most likely related to the lower canopy cover and increased solar radiation reaching the water surface (Lorion and Kennedy 2009; Quinn and Stroud 2002; Studinski et al. 2012). Greater conductivity in pasture streams documented in our work has also been reported in streams running through deforested areas converted to pasture, and may indicate higher input of solutes when the riparian forest is cleared (Deegan et al. 2011; González-Trujillo et al. 2019; Iñiguez-Armijos et al. 2018; Tanaka et al., 2016). Similarly, the higher concentrations of suspended solids we documented in pasture streams may have resulted from increased riverbank erosion due to the removal of the riparian forest and grazing activities of livestock that has been shown in other work (Nessimian et al., 2008; Shilla and Shilla 2011). Although we measured greater dissolved oxygen concentrations in pasture streams, other studies have found lower concentrations in pasture than in forest streams due to greater inputs of organic matter from aquatic grasses and higher water temperatures (Brand and Miserendino 2015; Iñiguez-Armijos et al., 2016; Neill et al., 2006; Taniwaki et al. 2019).

Higher concentrations of nitrate and total nitrogen concentrations in forest streams may be partly explained by the higher nitrogen mineralization and nitrification rates in forest versus pasture soils in the tropics (Neill et al. 1997). Livestock can represent an important source of nitrogen to streams and watersheds particularly under intensive management (Jones et al. 2019; Vidon et al. 2008), which may explain why we did not detect higher levels in our pasture streams. On the other hand, greater nitrogen uptake by autotrophic organisms may occur in pasture streams (Tank et al. 2018), as deforestation can lead to increased periphyton biomass, as more solar radiation can reach the stream (Lorion and Kennedy 2009; Vázquez et al. 2011; Wang and Tan 2017). Though we did not estimate primary productivity, the greater chlorophyll *a* concentrations we measured in pasture streams may also indicate changes in productivity in disturbed systems. In contrast to autochthonous production, we documented more allochthonous inputs in the form of leaf litter in forested streams. This pattern has also been documented in other studies (Quinn et al., 1997; Webster et al. 1990).

The influence of differences in the physicochemical environment and organic matter sources between stream types and among sampling periods on the macroinvertebrate community were analyzed using various aspects of the taxonomic and functional structure. Greater periphyton biomass in pasture streams has been shown to subsidize macroinvertebrate populations and can explain higher densities in pasture streams (Bojsen and Jacobsen 2003; Dudgeon 1994; Lorion and Kennedy 2009; Quinn et al., 1997). Differences in the taxonomic composition between forest and pasture stream communities were primarily driven by differences in the densities of chironomids and a subset of mayfly taxa. Similar to work conducted in New Zealand streams, our study documented greater densities of chironomids in sites with reduced canopy cover where periphyton biomass is greater (Quinn et al., 1997). Likewise, Iñiguez-Armijos et al. (2018), studying creeks of the Andes of Ecuador, recorded a higher abundance of Chironomidae in pasture streams and explained this finding based on the generalist nature of this group that allows them to tolerate degraded environments. Within Ephemeroptera, *Baetodes* had greater densities in forest streams, as reported by Bertaso et al. (2015), that only observed this genus at forested sites in streams of Brazil. *Baetodes* prefers habitats with high velocities and rocky substrata, as observed at the forest sites. Notably, these organisms have been previously classified as "somewhat sensitive" to habitat degradation (Buss and Salles 2007; Ríos-Touma et al. 2014) and the effects of greater sediment deposition on periphyton at disturbed sites may negatively affect this scraper (Bertaso et al. 2015).

The RLQ results indicate that species distribution in our study streams was related to environmental variables, particularly the availability of leaf litter, in agreement with the results of the CCA. Species that were more commonly found in pasture systems may be more tolerant to changing water quality or respond to changes in food resources. We documented higher densities of the genus *Fallceon* in pasture streams, likely because its greater tolerance to higher temperatures, suspended solids, and conductivity (Carlisle et al. 2007). Similarly, we collected higher densities of *Thraulodes* in pasture streams, consistent with reports of this genus inhabiting sites in good condition, but with greater conductivity (Braun et al. 2018). Greater *Tricorythodes* density in pasture streams may, in part be explained by increased tolerance to higher temperatures and conductivity, but other work has shown the genus can positively respond to increased periphyton availability (Castro-Rebolledo et al., 2014). Genera including *Chimarra* and *Glossosoma* were also more positively associated with pasture sites, and have been considered intolerant to severe environmental degradation (Torres-Olvera et al., 2018; Weir and Salice 2012), providing further evidence that the pasture sites studied here, although disturbed, are not heavily degraded. It is also notable that the differences in composition we documented between the two land uses we studied were not substantial compared when compared to findings from other work, where pasture streams were dominated by disturbance-tolerant groups such as Chironomidae, Oligochaeta, and mollusks (Lorion and Kennedy 2009; Quinn et al., 1997). In addition to disturbance levels, the effects of riparian vegetation removal on macroinvertebrate communities can vary among regions and also depends on the width of the riparian buffer, with greater impacts as the buffer becomes narrower (Dala-Corte et al. 2020) and these factors probably must be considered when examining the effects of land use conversion.

The application of functional approaches based on species traits may be more sensitive to detect the impact of human activities on animal communities (Dolédec et al. 2006; Schmera et al. 2017). Functional richness and divergence were similar between forest and pasture, but evenness was higher in forest streams, in partial agreement with the taxonomic findings. Greater evenness in forest streams in our study indicates that traits are distributed more evenly across the functional-trait space than in pasture sites, where resources may be underutilized, and increase the likelihood of invasions (Gagic et al., 2015; Schleuter et al. 2010). A lack of difference in functional richness between pasture and forest streams may indicate that the functional-trait space is used similarly in both communities (Schleuter et al. 2010). Comparable functional divergence suggests that abundance is distributed similarly across the functional-trait space in both land-use communities, indicating equal niche differentiation and competition in forest and pasture communities (Mason et al. 2005). These results are contrary to those of other studies that have documented declines in the components of functional diversity as pressure from changes in land use rises (Castro et al. 2018; Ding et al. 2017; Wang et al. 2019), suggesting we did not collect data on a temporal or spatial scale that indicated loss of richness or diversity or a reduction of the functional attributes of the macroinvertebrate communities we studied. In addition, there were no significant associations between traits and environmental conditions as indicated by the RLQ analysis, that is consistent with the results of functional diversity.

Changes in species abundance and composition but not in functional aspects may indicate high functional redundancy among communities in our pasture and forest streams. Redundancy is common in aquatic invertebrate communities (Bêche and Statzner 2009), which coupled with the high proportion of common species between pasture and forest, may result in taxa performing similar ecological functions despite differences in abundance and composition between communities (Luiza-Andrade et al., 2017). Besides redundancy, other factors may also influence the functional similarity observed between our forest and pasture streams. Bêche and Resh (2007) and Voß and Schäfer (2017) argue that functional traits are generally not measured directly but are assigned from data bases at genus or family levels. Thus, functional traits include a range of affinities between species within a given genus or family, and they are data that typically have low taxonomic resolution. This low resolution, in combination with a high percentage of common species we found in our sites, may have limited the detection of any functional changes.

Our isotopic data generated higher-resolution information about the trophic ecology of the macroinvertebrate communities in our study sites. In general, macroinvertebrates collected in pastures were enriched in ^{13}C and ^{15}N, likely reflecting increased availability of autochthonous organic matter. Although it is known that isotopic signals from autochthonous sources may be more variable than allochthonous sources (Lau et al. 2009a; Peterson and Fry 1987; Winemiller et al. 2011), some studies in tropical streams have found that algae and periphyton have higher ^{15}N and ^{13}C levels than allochthonous sources. Additionally, periphyton may be even more enriched in streams with open canopies than at forest sites (Lau et al. 2009b; March and Pringle 2003; Neres-Lima et al. 2017). Our data support those collected from similar studies where consumers were more enriched in sites with scarce riparian cover (Castro et al., 2016; Lau et al. 2009b). The presence of C4 herbaceous plants in riverbanks of pasture sites may contribute to ^{13}C enrichment; however, C4 plants represent a minor basal source in aquatic trophic webs (Castro et al., 2016). Because livestock feed on C4 plants (grasses) eventually provide enriched ^{13}C waste (Li et al. 2014). Land use intensification is directly related to ^{15}N enrichment through nitrification, N-fixation, and ammonium volatilization; consequently, pasture soils may show a higher abundance of ^{15}N than forests (Stevenson et al., 2010). Additionally, inputs from manure can increase ^{15}N concentrations, as isotopic values range from +10 to +20‰ (Bateman and Kelly 2007; Kendall and McDonnell 1998) and livestock can be a significant source of nitrogen to streams (Li et al. 2014; Vidon et al. 2008). Thus, the isotope data from pasture sites reflect changing inputs of ^{13}C and ^{15}N, as isotopic values and dispersion increase at pasture sites.

Broader and more overlapped isotopic niches were observed in pasture streams, suggesting that macroinvertebrates in this land use are characterized by generalist feeding habits. Extensive overlap between predators and primary consumers (filtering collectors) in pasture relative to forest streams, is also indicative of a greater degree of omnivory in pasture communities. Although omnivory is a common characteristic of aquatic food webs, changes in land use can favor organisms that can use a wider variety of resources (Castro et al., 2016; Price et al. 2019). In pasture streams, scrapers, particularly trumpet snails, had the broadest isotopic niches. This indicates scrapers are consuming a wide variety of algae and periphyton resources, derived from diverse and abundant communities of primary producers that positively responded to increased light availability. Similar patterns were observed by Castro et al. (2016) in pasture streams of Brazil. In contrast, forest macroinvertebrates had more compact isotopic niches, suggesting that they are more specialized in food resources. The results of isotopic analyses indicate that changes in land use in the riparian zone are altering the environmental conditions (i.e., nutrients, light, temperature), and this in turn, influences the availability of basal resources. This leads to greater ^{13}C- and ^{15}N-enrichment in pasture stream communities and favors a trend toward omnivory, indicating that changes in land use can produce cascade effects that reach multiple trophic levels (Price et al. 2019).

5. Conclusions

Tropical streams are threatened by land conversion throughout the world and much remains to be learned about how aquatic communities respond to the loss of riparian habitats. The multiple approaches used in this study allowed us to document an increase in total abundance of organisms and changes in community composition in streams without an intact riparian zone. These patterns were primarily driven by changes in the abundance of Chironomidae and some Ephemeroptera. We also documented changes in the trophic ecology that were most likely related to changes in autochthonous organic matter inputs in pasture streams. Notably, we did not observe reduced macroinvertebrate diversity or richness in pasture streams, or differences in functional diversity as have been found in previous work in tropical systems. Landscape-related processes such as recolonization facilitated by upstream riparian and catchment forest and environmental filtering from past land use likely are related to the patterns found here and they require further examination.

Riparian forest conversion in the tropics is still common, and the observed changes in water quality and sources of organic matter that we documented can be strongly linked to the loss of riparian vegetation. Therefore, the streams of Pichucalco, and similar streams in Mesoamerica, are likely to benefit from the restoration of the riparian vegetation, specifically through reforestation with native tree species and the conservation of forest remnants (Meli et al., 2017). The recovery of riparian zones can contribute to improving the physical habitat and water quality, as well as restoring key ecological processes such as organic matter dynamics and conservation of habitats and their biodiversity (Palmer et al. 2014), and this should be a continued area of study in tropical stream ecology. Furthermore, conservation planning and environmental policies devoted to protecting riparian habitats should be encouraged to retain the biodiversity and ecosystem services provided by tropical streams.

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CRediT authorship contribution statement

Andrea Espinoza-Toledo: Conceptualization, Investigation, Writing - original draft. **Manuel Mendoza-Carranza:** Conceptualization, Formal analysis, Writing - review & editing. **María M. Castillo:** Conceptualization, Investigation, Writing- review & editing, Supervision. **Everardo Barba-Macías:** Conceptualization, Writing - original draft. **Krista A. Capps:** Resources, Writing- review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2020.143972.

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