Richness and abundance of stream fish communities in a fragmented neotropical landscape

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Abstract Environmental conditions influence ecological processes that shape stream community diversity and abundance. Deforestation has the potential to limit available particulate organic matter and raise stream temperatures. The degree to which tropical stream communities are impacted by these changes is likely to differ between systems, but empirical data from tropical regions are lacking. This lack of baseline data hinders conservation policy as well as efforts to better understand biogeographic and anthropogenic impacts on species' distributions. To fill this knowledge gap, we surveyed 27 sites in six previously unstudied streams across a gradient of deforestation in northwest Ecuador and assessed the degree to which localized deforestation predicted patterns of community composition of fishes. Using general linear mixed models and AICC we found that neither forest fragmentation nor canopy closure was a significant predictor of species richness and found no difference between the species richness of fragmented and continuous sites. However, forest fragmentation was a strong predictor of abundance, occurring in 31 of 31 general linear mixed models, with higher abundance in fragmented forest than in continuous forest. Of 16 species found, eight occurred at five or more sites and one (*Pseudochalceus boehlkei*), numbered 200 out of 627 individuals. NMDS and SIMPER analysis suggested that community composition differed between fragmented and continuous sites. *P. boehlkei*, *Pseudopoecilia fria*, and *Astroblepus* cf. *fissidens* species presented in higher abundances in deforested sites, possibly suggesting a less functionally diverse community. This pattern is consistent with neotropical streams that have experienced partial deforestation but not total degradation of habitat.

Keywords Tropical ecology · Conservation biology · Stream ecology

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Introduction

Maintaining ecosystem function and preserving biodiversity requires baseline data on species composition and the roles and services the species provides (Wilson 1992). Gaps in our baseline knowledge of species diversity limit conservation efforts in many tropical systems, including freshwater streams (Bosjen and Barriga 2002). The Tropics harbor approximately half of global biodiversity (Brown 2014) and are currently experiencing rapid deforestation, which tends to fragment habitat and lead to species declines over time (Repetto 1990; Benhin 2006; Carter et al. 2017; Taubert et al. 2018).

Though the influences of deforestation on terrestrial systems have been well documented (Saunders et al. 1991; Andrieu et al. 2011; Echeverria et al. 2006), less is known about this relationship in tropical systems in general (Iwata et al. 2003), and in tropical stream community richness and structure specifically (Bosjen and Barriga 2002; Lorion and Kennedy 2009). Ecological assessments of the ways in which deforestation and habitat degradation impact tropical stream diversity and function are needed.

Streams are among the most diverse aquatic ecosystems as they are often isolated microhabitats that encourage allopatric speciation (Dijkstra et al. 2014). Lotic environments are also one of the most globally threatened ecosystems given their dependence on riparian vegetation (Gregory et al. 1991) and connectivity within a catchment (Vannote et al. 1980; Malmqvist and Rundle 2002; Friberg 2014; Carter et al. 2017). Forested stream reaches are heavily shaded (Pusey and Arthington 2003), which keeps headwaters cool (Merten et al. 2010) and prevents excessive nutrient and sediment loading (Gregory et al. 1991; Naiman et al. 2005). Pristine stream communities depend on allochthonous introductions of leaf litter and invertebrates (Pusey and Arthington 2003), which influence food web and community structure (Knight and Bottoroff 1984; Silva et al. 2014; Lorion and Kennedy 2009). Additionally, large woody debris is more common in forested reaches and provides habitat structuring, slows stream flow, and provides substrate for periphyton growth (Wang et al. 2003; Wright and Flecker 2004; Mellina and Hinch 2009). The removal of riparian vegetation opens the canopy, increasing temperature (Johnson and Jones 2000; Cole and Newton 2013) and inputs of photosynthetically active radiation (Rutherford et al. 1999), ultraviolet radiation (Kelly et al. 2003), and nutrients (Bennet et al. 2001; Naiman et al. 2005). This increases the primary productivity of streams (Bilby and Bisson 1992; Kelly et al. 2003; Ferreira et al. 2012) and has the tendency to shift food webs to the reliance of autochthonous resources (Ferreira et al. 2012).

Most efforts to research fluvial community response to habitat degradation have occurred in temperate systems (Iwata et al. 2003; Lorion and Kennedy 2009). Studies of tropical stream communities are scarcer and have produced inconsistent results (Bosjen and Barriga 2002; Iwata et al. 2003; Casatti et al. 2015; de Paula Ferreira et al. 2015). A study of streams in tropical rainforests in Borneo suggested a negative species

response to deforestation and forest regrowth (Iwata et al. 2003). Kamden et al. (1998, 1999) observed lower species abundance in deforested stream reaches of Cameroon and the larger Western African region. Conversely, Burcham (1988) found that deforestation and anthropogenic land use in Costa Rica resulted in an overall increase in both species diversity and abundance. In tropical streams in Mexico following deforestation, Lyons et al. (1995) noted a decrease in alpha diversity, while abundance increased. In instances where diversity is unaffected or even increases in the tropics, functional feeding diversity is still frequently lost (Lyons et al. 2000; Ibanez et al. 2007; Casatti et al. 2015) indicating that insectivorous species with more narrow prey preference are more vulnerable to anthropogenic disturbance than species with more diverse diets (de Paula Ferreira et al. 2015). Studies of deforestation on Andean streams have suggested decreased introductions of terrestrial invertebrates (Bosjen 2005) and that community diversity is negatively associated with large-scale habitat degradation (Iñiguez–Armijos et al. 2014). However, Bosjen and Barriga (2002) and Lorion and Kennedy (2009) found that localized deforestation had no influence on species diversity but found more abundant communities in deforested sites.

The Chocó rainforest in northwest Ecuador has experienced high rates of deforestation typical of many areas in the neotropics (Durães et al. 2013; Van der Hoek 2017). Despite the region being a globally recognized biodiversity hotspot (Conservación Internacional 2014), few surveys of the fish biota exist. Our first objective was therefore to characterize the fish species of this region, with a focus on streams in the Mache-Chindul Reserve (Fig. 1), an understudied site whose upland streams feed into the Rio Blanco, Rio Viche and Rio Cube, meaning that alterations to the fish communities of these rivers could have cascading effects to fisheries and water quality throughout the region. We then used this information to assess the separate influences of forest condition (primary forestation, secondary forestation, and selective logging), forest fragmentation (whether the site was located in a large area of continuous or an isolated forest fragment surrounded by agricultural land), and canopy closure (the proportion of visible light viewed vertically upstream and downstream at each segment) as predictor variables of fish diversity, abundance, and community structure of streams in the region. We hypothesize that deforestation will have a weak negative effect on species richness as observed by Iwata et al. (2003); a positive
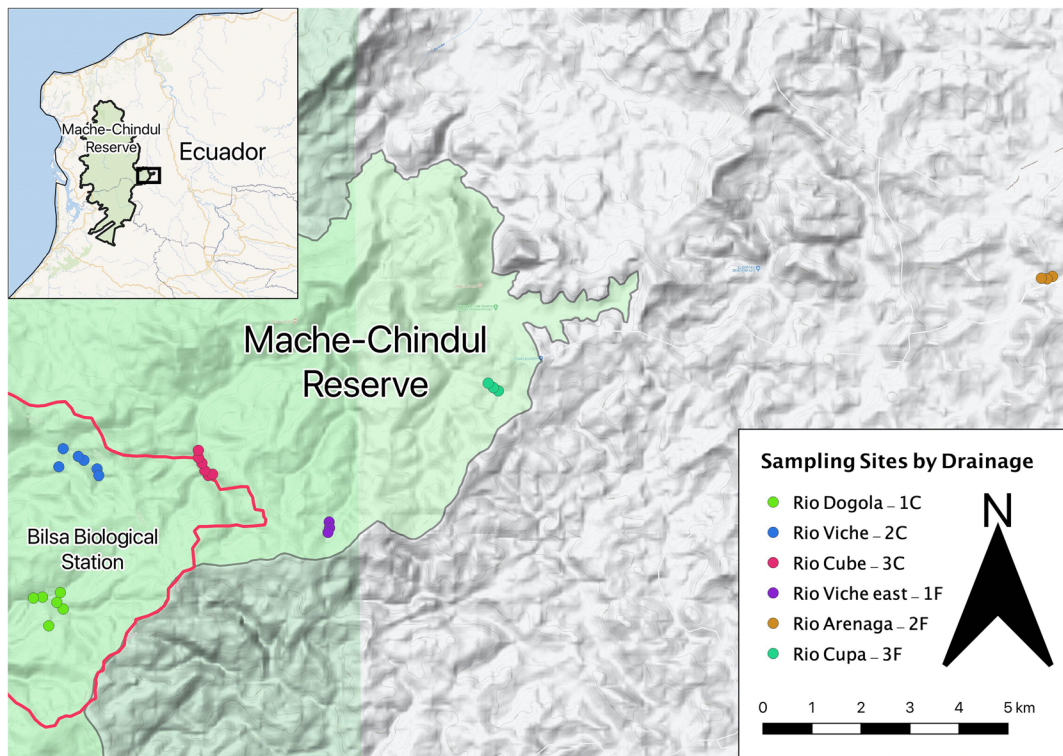
Fig. 1 Map of sampling sites coded according to drainage, whether they are continuous (C; west) or Fragmented (F; east) and position in relation to the Bilsa Biological Station and Mache-Chindul Reserve in Northwest Ecuador

relationship with abundance, potentially through increased periphyton growth as observed by Bosjen and Barriga (2002); and a negative impact on community evenness, by favoring disturbance-tolerant species over intolerant species (Iñiguez–Armijos et al. 2014). Our specific predictions were that canopy closure would be most strongly associated with overall diversity and that localized deforestation would result in an increase in fish abundance and dominance of disturbance-tolerant species and diet generalists.

Methods

Study area

The Mache-Chindul Reserve (hereafter REMACH), located in northwest Ecuador, encompasses over 115,000 ha of humid Chocó rainforest, wetlands, and streams within the Rio Esmeraldas drainage. REMACH receives an average annual rainfall of 2000–3000 mm (Durães et al. 2013). Elevations range from sea level to 800 m, and the reserve supports enormous diversity and endemism, though the

fish communities are understudied (e.g., Carrasco et al. 2013). The Chocó rainforest is one of 25 globally designated biodiversity hotspots recognized for its high degree of endemism (Conservación Internacional 2014). REMACH is affected by severe rates of deforestation (Durães et al. 2013; Van der Hoek 2017). Studies have documented the effects of deforestation for understory birds (Durães, et al. 2013), frugivorous birds (Walter et al. 2017), nocturnal birds (Walter et al. 2017), herpetofauna (Jongsma et al. 2014), avian malaria (Riveiro de Aguilar et al. 2018), euglossine bees (Botsch et al. 2017), palms (Browne and Karubian 2016), and terrestrial mammals and birds (Cook et al. 2020). No known studies of effects of deforestation on aquatic species of REMACH have been published to date. REMACH contains continuous and fragmented forest patches as well as headwaters of the Rio Esmeraldas drainage, providing a suitable venue in which to fill this knowledge gap.

Field data and sample collection

We sampled six streams within the Bilsa Biological station (BBS), a 3000-ha section of relatively

undisturbed premontane wet forest, and surrounding Mache-Chindul area, for a total of 27 sites. Sampling was conducted in June and July 2017, a transitional period between the rainy season (January – June) and dry season (August – December). All sites were located in headwaters of the Rio Viche, Rio Cube, Rio Cupa, Rio Arenaga, and Rio Dogola, which flow into Rio Quinindé. Rio Quinindé joins the Blanco river, which joins the Guayllabamba river to form the Esmeraldas river. Six sites were on a stream in continuous primary forest (1C), twelve sites were on two streams in continuous forest that had been selectively logged (2C and 3C), three sites were on a stream in fragmented forest that had been selectively logged (1F) and six sites were on two streams within fragmented forest that exhibited secondary growth (2F and 3F; Table 1).We used GPS to log the latitude and longitude of each site; five of six streams examined were found in the altitudinal range of 300–450 m (which we defined as upland streams) and the sixth (2F) was found between 150 and 200 m (which we defined as a lowland stream) in elevation. Width was comparable in all streams, ranging from an average 2–4 m and weather was consistently cloudy during the sampling period.

We sampled three segments per day moving upstream using seine nets, a 1200-V electrofisher (Alexander Samus 725G) connected to an aluminum-frame dipnet and cast nets in deeper sites. We sampled a minimum of 30 min per site and exhaustively sampled every segment. If no fish were captured after five minutes, the sampling period ended. Before processing, we anesthetized specimens with clove oil (Javahery et al. 2012). For identification, we took pictures of each morphospecies and preserved all specimens in formalin. RB identified species using the collection at the Escuela Politécnica Nacional in Quito, Ecuador.

We selected segments to reflect riffle and pool community structures and kept segments at a minimum of 100 m apart (mean: 195.06 m, range: 100.33 m–388.98 m) to maximize the distance between sampled segments in the often small forest fragments we were given permission to sample. Measurements of average depth, width, pH, density of riparian vegetation, and density of canopy closure were taken at each site. In each stream segment, we measured stream width every 5 m and depth at 2-m horizontal intervals. We took canopy photos at the center of the upstream and downstream end of each site. We made these photos binary and measured percentage of black pixel count to estimate canopy closure (Avsar and Ayyildiz 2010). To measure the density of riparian vegetation, we created a checkerboard pattern on a 20.3 × 27.9 cm piece of cardboard and counted the number of visible squares at 10 m at a height of 1.5 m above the ground in each cardinal direction. We based forest type (primary growth, secondary growth, or mixed growth) and fragmentation condition (whether the forest was part of reserved continuous forest or owned by private landowners and surrounded by agricultural processes) by speaking with REMACH resident researchers who know the land use history of our sites. To approximate stream speed, we placed a neutrally buoyant plastic water bottle in the center of flow at the top of each stream segment and timed its motion from the top to bottom of the segment.

Statistical analysis

We defined community abundance as the total abundance of fish at a site, individual abundance as the number of specimens of a species found in each site, and relative abundance as the proportion of the total abundance that a species represented at a site. We calculated Shannon and Simpson's richness of fragmented and continuous sites and made comparisons with two-sample t-tests. To determine the influences of environmental variables on fish richness and abundance we first standardized variables to have a mean of zero and scaled to have unit variance. We ran a principal components analysis on the standardized variables to characterize the environment for each site as our environmental variables were intercorrelated. We used general linear mixed models (GLMMs) and Akaike Information Criterion for small sample sizes (AICC) to test the effectiveness of each of our environmental variables as predictors of species richness, rarefied richness, and community abundance. To test for associations between environmental characteristics and abundances of individual species that occurred in at least five sites (*P. boehlkei*, *Pimelodella grisea*, *Astroblepus* cf. *fissidens*, *Chaetostoma aequinoctiale*, *Andinoacara blombergi*, *P. fria*, *Rhoadsia minor*, and *Trichomycterus* aff. *spilossoma),* we used multiple general linear mixed models with a negative binomial error structure. In cases of multiple related comparisons, we determined statistical significance with a sequential Bonferroni correction of an alpha of 0.05 (Rice 1989 and b).

Table 1 Environmental characteristics from six streams sampled in the Mache-Chindul Reserve, northwest Ecuador. Data were recorded once per 20-m segment and averaged across the segment. Streams are categorized by drainage and abbreviation as many streams were nameless

Drainage	Stream	Segments Sampled	Fragmentation	Latitude and Longitude	Forest Condition	Forest Density	Canopy Closure	Stream Time (Seconds)	Altitude (m)	Stream Width (cm)	Stream Depth (cm)
Rio Dogola	1C	6	Continuous	0.3386 −79.7288	Primary	Mean: 0.42 (0.31–0.55) SD: 0.08	Mean: 0.75 (0.69–0.85) SD:0.05	Mean: 372.54 (124.99–1200) SD: 373.4	Mean:402.61 (387.5–425.1) SD:12.64	Mean: 470.67 (203.8–641.6) SD:132.11	Mean: 31.41 (12.64–59.77) SD:15.1
Rio Viche	2C	6	Continuous	0.3646 −79.7235	Selectively Logged	Mean: 0.29 (0.14–0.46) SD: 0.11	Mean: 0.79 (0.76–0.81) SD: 0.02	Mean:304.41 (152.56–735.46) SD: 201.07	Mean:404.22 (388.1–430.7) SD:14.76	Mean:330.82 (266.4–435) SD:66.85	Mean: 14.84 (9.65–22.1) SD:4.3
Rio Cube	3C	6	Continuous	0.3642 −79.7007	Selectively Logged	Mean: 0.37 (0.23–0.53) SD: 0.12	Mean: 0.75 (0.67–0.8) SD:0.06	Mean: 241.45 (140.7–340.25) SD: 72.6	Mean:366.38 (335.2–402.5) SD:23.87	Mean: 530.26 (300–958.8) SD:216.12	Mean: 25.98 (9.78–58.33) SD:15.42
Rio Viche	1F	3	Fragmented	0.3527 −79.6778	Selectively Logged	Mean: 0.28 (0–0.58) SD:0.23	Mean: 0.81 (0.75–0.88) SD:0.06	Mean: 341.85 (205.62–441.06) SD:99.62	Mean:467.57 (455.8–479.2) SD:9.55	Mean:278.45 (192.6–392.2) SD:83.85	Mean:12.3 (7.7–16.7) SD:3.68
Rio Arenaga	2F	3	Fragmented	0.3987 −79.5461	Secondary	Mean:0.26 (0.13–0.39) SD:0.11	Mean:0.65 (0.55–0.75) SD:0.08	Mean: 314.83 (169.68–573.39) SD: 183.29	Mean: 127.58 (123.4–131.9) SD:3.45	Mean: 296.42 (234.7–329.6) SD:43.71	Mean: 11.97 (7.72–16) SD:3.38
Rio Cupa	3F	3	Fragmented	0.3786 −79.6477	Secondary	Mean:0.24 (0.13–0.34) SD:0.09	Mean:0.75 (0.59–0.83) SD:0.11	Mean: 445.7 (223.52–560.45) SD: 157.4	Mean: 325.57 (322.7–328.6) SD:2.39	Mean:277 (241.6–314.2) SD:29.67	Mean:13.52 (9.12–19.78) SD:4.55

We compared compositional differences between upland sites with ANOSIM and SIMPER analysis. We used non-metric multidimensional scaling ordination (NMDS) with Bray-Curtis dissimilarity based on presence and absence data (Fig. 2), to visualize differences in community composition. We removed site 2F from multivariate and compositional analyses as it represented the only lowland site and had a disparate community composition. We performed statistical analyses using the 'vegan' package (Oksanen et al. 2017) in R Studio (R Core Team 2013).

Results

We captured a total of 627 specimens of 16 species, representing 16 genera and 10 families (Table 2). The most abundant species, *P. boehlkei* numbered 200 individuals and was found at 71% of sites. Cyprinodontiformes represented 15.8% and 39.2% of the relative abundance of continuous and fragmented upland sites respectively. Likewise, Perciformes represented 6.3% and 5.4%, Siluriformes represented 27.5% and 16.2%, and Characiformes represented 50.4% and 39.2% of the relative abundance of continuous and fragmented upland sites respectively (Table 3). Following a sequential Bonferroni adjusted 0.05 the only

significant relationships between species occurrences and environmental variables were with *P. fria*, which was negatively associated with average depth and positively associated with canopy cover, *A. blombergi*, which was negatively associated with altitude, and *P. boehlkei*, which was positively associated with stream time (Table 4).

Average species richness was 4.4 at each site (range: 2–9), and stream systems had an average richness of seven with a range of four (1F) to 11 (2F). Continuous sites represented 10 total species, a mean Shannon diversity of 1.08 (SD = 0.33) and a mean Simpson's diversity of 2.67 (SD = 0.82). Fragmented communities represented 13 species, a mean Shannon diversity of 1.24 (SD = 0.36) and a Simpson's diversity of 3.09 (SD = 1.27). Fragmented upland communities represented 7 species, a mean Shannon diversity of 1.09 (SD = 0.2), and a mean Simpson's diversity of 2.6 (SD = 0.69). We found no difference between the average Shannon diversity (t = −1.09, p = 0.3) or Simpson's diversity (t = −0.89, P = 0.39) of continuous and fragmented sites. Similarly, we found no difference between the average Shannon diversity (t = −0.04, P = 0.97) or Simpson's diversity (t = 0.21, P = 0.84) of continuous and fragmented upland sites. According to GLMMs with AICC results, neither fragmentation nor canopy closure were significant predictors of species richness (Table 5) or rarefied richness (Table 6).

Average abundance at each site was 23.22 (SD = 13.1, range: 8–58; Table 3) and streams had an average abundance of 104.5 (SD = 26.35) with a range of 62 (2F) to 138 (3F) individuals. Our ten most important models included fragmentation and altitude (Table 7). Community abundance was significantly higher in forest fragments than in continuous forest (R = 0.63, p < 0.01). According to model averaging, fragmentation was the only significant predictive variable of community abundance over a 95% confidence interval (17.99 ± 11.32). Fragmentation was found to occur in 31 of 31 models with a model weight greater than 0.01 suggesting its importance as a predictor variable.

Limiting NMDS to 2 dimensions, we found weak stress ties of 0.167 (Fig. 2) with minimal overlap and an ANOSIM statistic of 0.312 (P = 0.002), suggesting a small but significantly different community composition between fragmented and continuous sites. SIMPER analysis revealed that 71.44% of compositional difference was driven by *P. boehlkei*, *P. fria*, and *A.* cf. *fissidens*. Linear regression suggested that
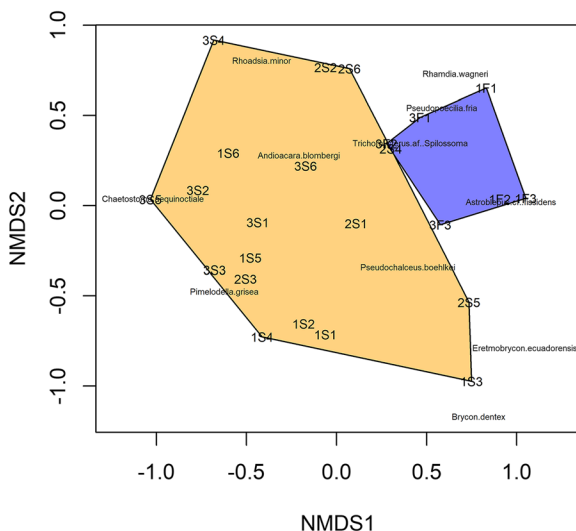

Fig. 2 Non-metric multidimensional scaling ordination (NMDS) with Bray-Curtis dissimilarity based on presence and absence data. When NMDS was limited to two dimensions, the model exhibited weak stress ties of 0.167 between fragmented communities (right; blue) and continuous communities (left; orange)

Table 2 Family, species name, IUCN Status, and total abundance of each species of freshwater fish recorded in the Mache-Chindul Reserve, northwest Ecuador

Family	Species	IUCN Status	Total Abundance
Characidae	*Pseudochalceus boehlkei*	Data Deficient	200
Poeciliidae	*Pseudopoecilia fria*	Least Concern	172
Heptapteridae	*Pimelodella grisea*	Least Concern	67
Characidae	*Rhoadsia minor*	Least Concern	58
Cichlidae	*Andinoacara blombergi*	Least Concern	44
Astroblepidae	*Astroblepus* cf. *fissidens*	Data Deficient	27
Characidae	*Brycon dentex*	Least Concern	14
Loricariidae	*Chaetostoma aequinoctiale*	Least Concern	11
Trichomycteridae	*Trichomycterus* aff. *Spilossoma*	Not Assessed	11
Characidae	*Eretmobrycon ecuadorensis*	Data Deficient	8
Heptapteridae	*Rhamdia quelen*	Not Assessed	4
Lebiasinidae	*Lebiasina bimaculata*	Not Assessed	4
Erythrinidae	*Hoplias malabaricus*	Not Assessed	3
Loricariidae	*Rineloricaria jubata*	Least Concern	2
Cichlidae	*Mesoheros festae*	Not Assessed	1
Pseudopimelodidae	*Batrochoglanis transmontanus*	Least Concern	1

fragmentation was correlated with increases in *P. fria* (R = 0.541, *P* = 0.004), *P. boehlkei* (R = 0.412, *P* = 0.026), and *A.* cf. *fissidens* (R = 0.549, *P* = 0.003) abundances.

Table 3 Abundance of each of the 16 species in continuous (C) and fragmented (F) sample sites

Species	1C	2C	3C	1F	2F	3F
Pseudochalceus boehlkei	48	52	8	27	4	61
Pimelodella grisea	22	14	29	0	2	0
Astroblepus cf. *fissidens*	2	1	1	21	0	2
Brycon dentex	14	0	0	0	0	0
Chaetostoma aequinoctiale	4	0	9	0	0	0
Andinoacara blombergi	2	15	6	0	4	15
Pseudopoecilia fria	0	28	28	40	26	50
Rhoadsia minor	0	16	21	0	13	8
Trichomycterus aff. *Spilossoma*	0	2	2	7	0	0
Eretmobrycon ecuadorensis	0	8	0	0	0	0
Hoplias malabaricus	0	0	0	0	3	0
Mesoheros festae	0	0	0	0	1	0
Rhamdia quelen	0	0	0	0	2	2
Rineloricaria jubata	0	0	0	0	2	0
Lebiasina bimaculata	0	0	0	0	4	0
Batrochoglanis transmontanus	0	0	0	0	1	0
Average Abundance	15.33	22.67	17.33	31.67	20.67	46
Total Species	6	8	8	4	11	6

Table 4 Summary of the negative binomial tests comparing associations of the eight most abundant species with average stream width, average stream depth, altitude, stream time, fragmentation, forest density, and canopy closure. Estimate, standard error, and Pr(>|z|) values are included. Values significant to sequential Bonferroni adjusted alpha values of 0.1 are designated with * and 0.05 are designated in bold

Species	Average width	Average depth	Altitude	Stream time	Fragmentation	Forest density	Canopy closure
P. boehlkei	0.0003±0.001 P=0.80	−0.0283±0.015 P=0.06	−0.0013±0.004 P=0.72	0.0024±0.001 P**<0.001**	0.666±0.439 P=0.13	−0.5517±1.216 P=0.65	−1.7244±2.423 P=0.48
P. grisea	−0.0009±0.001 P=0.53	−0.0001±0.014 P=0.99	−0.0158±0.01 P=0.11	−0.0061±0.003 P=0.03	−0.3756±3e^−7 P=1	1.043±1.84 P=0.57	−5.77±4.145 P=0.16
A. cf. fissidens	0.0039 + 0.003 P=0.23	−0.1828±0.082 P=0.02	0.0177±0.011 P=0.11	−0.0036±0.006 P=0.51	3.3684±1.525 P=0.03	6.802±3.048 P=0.03	−6.1537±5.067 P=0.22
C. aequinoctiale	−0.0026±0.003 P=0.29	0.0154±0.025 P=0.54	−0.0449±0.018 P=0.01*	−0.004±0.006 P=0.75	−20.65±580.9 P=0.99	1.43±4.504 P=0.75	2.758±9.877 P=0.78
A. blombergi	−0.0027±0.001 P=0.04	0.0058±0.014 P=0.67	−0.0172±0.006 P=0.01*	−0.0002±0.001 P=0.89	−0.7522±0.627 P=0.23	−4.2576±1.829 P=0.02	1.5732±2.982 P=0.60
P. fria	0.0006±0.002 P=0.68	−0.1374±0.046 P=**0.0025**	−0.0092±0.005 P=0.06	0.0013±0.002 P=0.38	1.3562±0.624 P=0.03	−4.8311±1.986 P=0.02*	14.3188±3.879 P **<0.001**
R. minor	−0.0027±0.002 P=0.18	−0.0619±0.033 P=0.06	−0.0283±0.012 P=0.02	−0.0022±0.002 P=0.32	−2.4463±1.33 P=0.07	−3.0292±2.899 P=0.30	−4.591±4.617 P=0.32
T. aff. Spilossoma	−0.0063±0.007 P=0.36	−0.0484±0.067 P=0.47	0.0188±0.012 P=0.10	−0.0026±0.005 P=0.61	0.1115±1.11 P=0.92	−2.5029±3.059 P=0.41	−0.9755±13.605 P=0.94

Table 5 Summary of the general linear mixed models for species richness with the importance of each variable. The number of models that contain each variable out of 35 models with a weight greater than 0.01, is also displayed

	Estimate	Number of Models	Importance
Fragmentation	0.0086	6	0.097
Average Width	0	6	0.099
Stream Time	−0.0001	6	0.142
Canopy Cover	0.7079	7	0.18
Average Depth	−0.009	13	0.337
Forest Density	−1.467	13	0.471
Altitude	−0.0057	17	0.545
Intercept	6.4761	33	1

Discussion

The freshwater fish of northwest Ecuador remain relatively poorly sampled, and the Mache Chindul Reserve (REMACH) had not had a formal survey prior to this study. Only five species (*P. fria, A. blombergi, Batrochoglanis transmontanus, Rineloricaria jubata,* and *Brycon dentex*) have been officially recorded in the reserve and its associated streams (IUCN 2019). Seven species (*P. grisea*, *P. fria*, *C. aequinoctiale*, *Mesoheros festae*, *Hoplias malabaricus*, *Lebiasina bimaculata*, and *R. quelen*) had not been previously recorded in REMACH but have been documented in past surveys of the Rio Esmeraldas drainage and other associated smaller drainages (Eigenmann 1921; Barriga 1994; Barriga 2012; IUCN 2019). Compared to coastal

Table 6 Summary of the general linear mixed models for rarefied richness with the importance of each variable obtained. The number of models that contain each variable out of 35 models with a weight greater than 0.01, is also displayed

	Estimate	Number of Models	Importance
Altitude	0	6	0.101
Average Depth	0.0007	7	0.131
Fragmentation	0.04	8	0.159
Forest Density	−0.1295	9	0.169
Canopy Cover	0.8320	12	0.311
Average Width	−0.0004	13	0.336
Stream Time	−0.0004	16	0.488
Intercept	2.5136	35	1

Table 7 The top ten GLMMs with the greatest model weight (range: 0.023–0.163)

Model	AICC	Delta AIC	Model Weight
Canopy Closure + Stream Time+Depth+Width+Altitude + Fragment	181.38	−3.949	0.163
Canopy Closure + Forest Density+Stream Time+Depth+Width+Altitude + Fragment	181.39	−3.933	0.161
Stream Time+Depth+Altitude + Fragment	182.71	−2.612	0.083
Forest Density+Stream Time+Depth+Altitude + Fragment	183.44	−1.891	0.058
Stream Time+Depth+Altitude + Fragment	183.86	−1.467	0.047
Stream Time+Depth+Width+Altitude + Fragment	184.00	−1.330	0.044
Canopy Closure + Forest Density+Stream Time+Depth+Altitude + Fragment	184.07	−1.253	0.042
Canopy Closure + Forest Density+Stream Time+Width+Altitude + Fragment	184.41	−0.912	0.036
Depth+Altitude + Fragment	184.84	−0.491	0.029
Forest Density+Stream Time+Depth+Width+Altitude + Fragment	185.33	0.000	0.023

rivers, REMACH fish diversity is relatively low but the abundance is relatively high (Barriga 2012). REMACH ichthyofaunal composition is similar to small coastal streams and other rivers in the Andean regions of Colombia, Ecuador, Peru and Venezuela (Lasso et al. 2015). Seven of the species we recorded in REMACH (*P. fria*, *C. aequinoctiale*, *P. grisea*, *B. dentex*, *B. transmontanus*, *A. blombergi*, *R. minor*, and *R. jubata*) have been evaluated by the International Union for Conservation of Nature (IUCN) as being of least conservation concern and six species (*P. boehlkei*, *M. festae*, *L. bimaculata*, *H. malabaricus*, *R. quelen*, and *P. grisea*) have not been evaluated or are data deficient. *Pimelodella grisea* populations have been identified as being on the decline (Jimenez-Prado 2016). The range and status of *T.* aff. *Spilossoma* are difficult to determine as it could not be identified to species level with certainty.

We found no difference between the species richness of fragmented and continuous forest stream sites in our study region. We observed greater abundance in fragmented sites and found fragmentation to be the most important predictor of community abundance, with higher abundances in fragmented sites vs. continuous forest sites. Additionally, we found that community composition differed between fragmented and continuous sites with greater abundances of *P. fria*, *P. boehlkei*, and *A.* cf. *fissidens* in fragmented sites. Our lowland fragment site (2F) had the most disparate community composition, with five species not found in other sites. Three species (*B. dentex*, *Eretmobrycon ecuadorensis*, and *C. aequinoctiale*) occurring in continuous forest were not found in fragmented sites, while only one species occurring in upland fragments (*Rhamdia quelen*) was not found in continuous sites. Characiformes and Siluriformes were the most diverse groups in upland continuous forest sites, with four species represented from each order. Siluriformes represented the most diverse order in fragmented upland sites with three species represented.

Our finding of no clear trend between localized deforestation and species richness is not an unusual result for tropical streams (Barriga and Bosjen 2002; Lorion and Kennedy 2009; Ilha et al. 2019). While many papers indicate decreased richness in deforested tropical streams (Kamden et al. 1998, Kamden et al. 1999; Iwata et al. 2003), these studies typically focus on lowland streams of higher stream orders. In these cases, a more significant portion of the reach has been deforested resulting in the loading of fine sediments and less habitable conditions for many species (Iñiguez–Armijos et al. 2014; Lobón-Cerviá et al. 2016), while deforestation over a smaller portion typically results in less sediment export to streams (Bosjen and Barriga 2002; Ilha et al. 2019).

The increased abundance that we recorded in deforested sites was also consistent with findings of other studies of locally deforested tropical steams (Burcham 1988; Lyons et al. 1995; Lorion and Kennedy 2009; Casatti et al. 2015; Ilha et al. 2019). Localized deforestation can free up nutrients and increase available sunlight, potentially increasing primary productivity in smaller streams (Bosjen and Barriga 2002; Ilha et al. 2019). It is also possible that nutrient and fertilizer inputs from agriculture and cattle activities upstream of our fragment sampling sites could also contribute to productivity in these sites. These increases can result in a more abundant community driven by a

few, generalist species (Burcham 1988; Casatti et al. 2015). Increased abundance is frequently driven by Poecilid fishes that are well-adapted to degraded water quality (Pusey and Arthington 2003; Casatti et al. 2009). In our case, increased abundance was primarily the result of increases in *P. boehlkei, P. fria,* and *A.* cf. *fissidens,* our three most abundant groups overall. While our design does not allow for us to comment on the diet flexibility of fishes, the observed increases in *P. fria* would support the findings of Pusey and Arthington (2003) and Casatti et al. (2009). Additionally, we recorded these species at most sample sites, supporting the hypothesis that *P. boehlkei, P. fria,* and *A.* cf. *fissidens* are generalists.

The results of our NMDS analysis suggest that community composition is significantly different between fragmented and continuous sites. Fragmentation correlated with larger relative abundances of *T.* aff. *Spilossoma, P. fria* and *A.* cf. *fissidens.* SIMPER analysis suggested that *P. boehlkei* abundance increased in fragmented sites. *C. aequinoctiale, B. dentex,* and *E. ecuadorensis* did not occur in fragmented sites. Similarly, *P. grisea* abundance tended to decrease in forest fragments. Given the shifts in community composition, fragmented sites are likely representative of an anthropogenically altered state. Although literature on REMACH species is limited, it is likely that *T.* aff. *Spilossoma, P. fria, P. boehlkei,* and *A.* cf. *fissidens* are more tolerant of deforestation than *C. aequinoctiale, B. dentex, P. grisea,* and *E. ecuadorensis.* Further analysis of species tolerance within REMACH may allow future researchers to build an Index of Biotic Integrity to determine anthropogenic influence.

Given that freshwater fish introductions are prevalent (Gozlan et al. 2010), it is worthwhile to note that we did not collect any individuals of known non-native species. In spite of the changes to abundance that we observed in forest fragments, the lack of invasive species is possibly an indication of the lack of disturbance in these sites, and potentially allows us to examine the unaltered trophic structure of these streams.

Multiple studies (Casatti et al. 2015; Lobón-Cerviá et al. 2016; Leitão et al. 2018) note that an increase in community abundance following deforestation is often associated with a loss of functional diversity. This was attributed primarily to decreased introductions of leaves and terrestrial invertebrates (Bosjen and Barriga 2002; Casatti et al. 2015) and homogenization of the streambed (Leitão et al. 2018), indicative of riparian vegetation removal. While our study suggests a similar trend, our methodology did not allow us to directly address this issue. First, we did not take substrate composition into account and did not conduct a survey of fish function. Moreover, we did not evaluate deforestation over the entire area of our catchments, which is needed to determine the degree of influence (Corbacho et al. 2003; Lobón-Cerviá et al. 2016).

The current study focused on six stream reaches and is unlikely to have recorded every species in the region. Increased sample size and larger scale sampling of the area would likely have revealed more diversity and furthered our understanding of species ranges, realized niche, and abundance within northwest Ecuador. Given that the current literature of the region is limited, this study serves as a preliminary characterization of the area's fish diversity and the impacts of deforestation.

In summation, sampling sites in forest fragments exhibited distinctive community abundance and community composition of freshwater fish relative to intact, continuous forest streams in REMACH. These findings suggest that stream communities in northwest Ecuador may respond to localized deforestation with a shift towards higher abundance of tolerant species. Additionally, though there was no observed difference in overall species richness between forested and deforested sites, certain fish species were found in lower relative abundance, and community composition observably changed. These patterns are consistent with findings of studies of tropical streams exhibiting minor deforestation, but not total habitat degradation. However, localized deforestation is not always predictive of stream function and diversity. Future surveys of REMACH should consider deforestation over the catchment and examine differences in functional diversity in association with habitat alteration. Classification of macroinvertebrates would also be useful for further studies of the aquatic environment in REMACH. Another important direction for future research is to assess how stream intermittency in our study region, which is characterized by marked seasonality, may influence diversity and abundance. The streams of the larger Mache-Chindul Reserve demonstrate impacts of human influence as compared to the relatively pristine state within the Bilsa Biological Station. The differences between these systems will allow future researchers to examine the cascading effects of anthropogenic influence throughout the region.

Authors' contributions   All authors contributed to the study conception and design. Material preparation, data collection, and analysis were performed by Samuel S Leberg, Ramiro Barriga, Alfredo Olivo and Kaushik Narasimhan. The first draft of this manuscript was written by Samuel Leberg and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Declarations

Ethics approval   This study was conducted with the approval of the Ecuadorian Ministry of the Environment (MAE –DPAE 2017–0771-O).

Consent for publication   All authors reviewed the following manuscript and have consented for its publication.

Availability of data and material   Available on Dryades upon publication.

Code availability   Available on Dryades upon publication.

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