DEFORESTATION DEGRADES RAIN FOREST STREAM HABITAT AND BIODIVERSITY OVER TIME IN THE RAMA-KRIOL INDIGENOUS TERRITORY, SOUTHEAST NICARAGUA

By

Joel Thomas Betts

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ABSTRACT

DEFORESTATION DEGRADES RAIN FOREST STREAM HABITAT AND BIODIVERSITY OVER TIME IN THE RAMA-KRIOL INDIGENOUS TERRITORY, SOUTHEAST NICARAGUA

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In southeast Nicaragua, recent waves of illegal deforestation for cattle pasture are damaging the Indio-Maíz Biological Reserve (IMBR) and Rama-Kriol territory (RKT), with negative consequences to aquatic ecosystems and the people who rely on services they provide. Deforestation and subsequent land use are causing shifts in stream community structure that are mediated by changes in stream habitat. This study integrated temporally explicit land use information with stream habitat, macroinvertebrate, freshwater shrimp, and fish community data to assess impacts of deforestation on 15 headwater streams in southeast Nicaragua's poorly studied protected rainforests. The new calculation, *deforestation history index (DFI)*, a product of deforestation amount and time since deforestation for the catchment draining to each stream reach, was the best linear predictor of most taxa responses—better than other habitat metrics and raw forest cover at multiple scales. Stream reaches that were deforested for a longer time and to a larger extent—thus having higher values for the *DFI*—had less large wood, organic debris, macroalgae, and macrophytes; more stream bank erosion and sedimentation; degraded riparia; lower diversity and abundance of macroinvertebrates, shrimp, and fish; higher invertebrate evenness; and distinct changes in invertebrate community composition. All deforested reaches also had smaller sized game fish. New registers of fish species and insect genera were recorded for Nicaragua. As this is the first aquatic study in these watersheds of the IMBR and RKT, this region should be a high priority for further research and conservation investment before it is lost.

RESUMEN

LA DEFORESTACIÓN DEGRADA EL HABITAT Y LA BIODIVERSIDAD DE LOS RÍOS A LO LARGO DEL TIEMPO EN EL TERRITORIO INDÍGENA RAMA-KRIOL, SURESTE DE NICARAGUA

Por

Joel Thomas Betts

En el sureste de Nicaragua, las recientes actividades de deforestación ilegal para ganadería, está impactando la Reserva Biológica Indio-Maíz (RBIM) y el territorio Rama-Kriol (TRK), con consecuencias negativas para los ecosistemas acuáticos y las personas que dependen de los servicios que estos brindan. La deforestación y el uso de suelo aledaño provocan cambios en la estructura de la comunidad ecológica de los ríos, debido a cambios en su hábitat acuático. Este estudio integró la información de uso de suelo a través del tiempo de las cuencas con datos de hábitat, macroinvertebrados (MI), crustáceos y peces para evaluar los impactos de la deforestación en 15 ríos de cabecera en una zona poca estudiada del sureste de Nicaragua. Un nuevo índice, el índice de historial de deforestación (DFI), un producto que integra la cantidad y el tiempo de deforestación, calculado a nivel de la microcuenca, fue el mejor predictor lineal para la mayoría de las respuestas biológicas cuantificadas, y fue mejor que otras métricas de hábitat y cobertura forestal. Los ríos que fueron deforestados durante más tiempo y en mayor medida, tuvieron menos madera, material orgánico, macroalgas, y vegetación acuática; más erosión y sedimentación; bosque ribereño más degradado; menor diversidad y abundancia de MI, camarones y peces; mayor uniformidad de MI; y cambios distintos en la composición de la comunidad. Todos los sitios deforestados también tenían peces de menor tamaño. Se encontraron nuevos registros de peces e insectos acuáticos para Nicaragua. Esta región debería tener una alta prioridad para futuras investigaciones y esfuerzos de conservación antes de que se pierda.

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INTRODUCTION

Context of tropical deforestation

The rate of deforestation in primary rain forests is high throughout much of Latin America (Wright, 2005; Hansen et al., 2013). This is a global problem, as neotropical rainforests host a significant portion of the world's biodiversity and are critically important for global climate change mitigation (Bonan, 2008). Deforestation and subsequent conversion to pasture, agriculture, urban area, or other anthropogenic land uses threaten all components of the forest ecosystem, including aerial, canopy, terrestrial, subterranean, and aquatic organisms and ecosystems processes, as well as the people who rely on the services they provide (Foley et al., 2007).

Deforestation and stream ecosystems

Freshwater organisms and their habitat can be severely affected by deforestation and land use change. In 2003, Benstead, Douglas, & Pringle conservatively estimated that globally, each year in the humid tropics >5 x 10^5 km of stream channel are impacted by deforestation. Habitat degradation from land use change is one of the most significant threats to freshwater biodiversity and ecosystem function (Dudgeon et al., 2006; Reid et al., 2018). Inland fisheries are an important ecosystem service provided by freshwater biodiversity and are increasingly threatened by human-induced environmental change (Phang et al., 2019). Therefore, it is critical to consider the impacts of landscape changes when studying, managing, or conserving stream ecosystems (Fausch, Torgersen, Baxter, & Li, 2002; Allan 2004).

Many studies have shown that impacts to stream community structure from deforestation are caused by its effects on water quality and instream habitat (Harding, Benfield, Bolstad, Helfman, & Jones, 1998; Gergel, Turner, Miller, Melack, & Stanley, 2002; Iwata, Nakano, &

Inoue, 2003; Leitão et al., 2017; Brejão, Hoeinghaus, Pérez-Mayorga, Ferraz, & Casatti, 2018). Allan (2004) presented impacts of land use to stream habitat in six main categories as they effect stream biota: sedimentation, nutrient enrichment, contaminant pollution, hydrologic alteration, riparian clearing/canopy opening, and loss of large woody debris. The magnitude and form of these impacts to habitat depends not only on the land use type, history, and the proximity of the disturbance to the stream channel, but also on natural hydrogeological and climatic conditions. These interrelated influences of deforestation determine the specific mechanisms of impact to stream biota, and their responses differ based on the requirements and tolerance of each species.

For example, cattle ranching following deforestation in temperate regions tends to result in decreased shade and increased stream temperature, eroded banks and siltation, simplification of stream bottom habitat, and eutrophication from nutrient overload related to excrement, which together cause a loss of sensitive macroinvertebrate taxa and dominance by burrowing taxa (see Figure 1 from Strand & Merritt, 1999, 14). In general, as anthropogenic influences increase stream conditions move beyond thresholds of tolerance, and most organisms adapted to natural conditions ultimately decrease in abundance (Allan, 2004).

Many, but not all lessons learned from temperate systems apply to tropical systems (Dodds, Gido, Whiles, Daniels, & Grudzinski, 2014). In the past 15 years there has been a proliferation of studies showing how the dynamics of land use change, particularly deforestation, affect tropical stream habitat and biota. But a comprehensive review does not yet exist.

Tropical deforestation and stream habitat

The habitat impact categories from Allan (2004) (bolded below) are also relevant to tropical streams. Deforestation and associated land use causes **sedimentation** (Heartsill-Scalley & Aide, 2003; Iwata et al., 2003), which can lead to decreased bed stability (Iwata et al., 2003, Leitão et al., 2017; Macedo, Hughes, Kaufmann, & Callisto, 2018), loss of interstitial spaces (higher embeddedness) and subsequent declines in fish and invertebrate taxa richness and periphyton mass (Iwata et al., 2003). In temperate streams, Schwendel, Death, Fuller, & Joy (2010) observed declines in taxa richness and periphyton mass and increases in evenness related to decreased bed stability. Sedimentation can also result in higher rates of macroinvertebrate drift (O'Callaghan, Jocqué, & Kelly-Quinn, 2015). **Nutrient enrichment** has been related to pasture and agricultural land use (Mori, de Paula, de Barros Ferraz, Camargo, & Martinelli, 2015) and was linked to higher macroinvertebrate drift (O'Callaghan et al., 2015), and lower dissolved oxygen (Teresa, Casatti, & Cianciaruso, 2015; Tanaka, de Souza, Moschini, & de Oliveira, 2016). **Hydrologic alterations** such as bank erosion (Iwata et al., 2003, Chaves et al., 2008; Wantzen & Mol, 2013; Leitão et al., 2017), variation in depth (Leal et al., 2016), increases of bankfull width/depth ratio (Leitão et al., 2017), decreases in stream depth (Montag et al., 2019), decreases in discharge (Coe, Costa, & Soares-Filho, 2009), increases in wet-season surface flows (Chaves et al., 2008), and increased flashiness and flooding (Bradshaw, Sodhi, Peh, & Brook, 2007; Chaves et al., 2008; Recha et al, 2012; Arancibia, Bruijnzeel, Mulligan, & van Dijk, 2019) can also result from deforestation and were related in many of these cases to shifts in the biotic community.

Riparian clearing/canopy opening can cause decreases in mid-channel shade (Leal et al., 2016), higher periphyton biomass (Bojsen & Jacobsen, 2003; Lobón-cerviá, Mazzoni, & Rezende, 2016; Feijó-Lima et al., 2018), higher water temperature (Benstead et al., 2003; Fugère, Kasangaki, & Chapman, 2016; Leal et al., 2016), lower levels of benthic organic matter or leaf litter (Bojsen & Barriga, 2002; Bojsen & Jacobsen, 2003; Benstead et al., 2003; Brejão et al., 2018; Montag et al., 2019), increased aquatic vegetation (Leitão et al., 2017), and declines in terrestrial insect inputs (Chan, Zhang, & Dudgeon, 2008; da Silva Gonçalves, de Souza Braga, & Casatti, 2018; as found in Nakano, Miyasaka, & Kuhara, 1999). **Loss of instream large woody debris** results from deforestation (Heartsill-Scalley & Aide, 2003; De Paula, Gerhard, Wenger, Ferreira, Vettorazzi, Ferraz, 2011; Leal et al., 2016), and has been related to shifts in the biotic community (Wright & Flecker, 2004; Valente-Neto, Koroiva, Fonseca-Gessner, & de Oliveira Roque, 2015; Leitão et al., 2017; Brejão et al., 2018; Montag et al., 2019).

Most of these studies related these shifts in habitat to shifts in diversity, community composition, and other invertebrate and fish indicator and species responses. But since many of these habitat changes co-occur, it is challenging to connect specific changes in habitat to specific biotic responses (Gergel et al., 2002). Because of this, catchment-scale deforestation and subsequent anthropogenic land use can be used as an integrator, and therefore a strong predictor of changes to instream habitat and biota (Leal et al., 2016; Molina, Roa-Fuentes, Zeni, & Casatti, 2017).

Tropical deforestation and stream macroinvertebrates

Forested streams have consistently higher macroinvertebrate taxa richness than deforested streams in many tropical studies (Paaby, Ramirez, & Pringle, 1998; Iwata, Nakano, & Inoue, 2003; Lorion & Kennedy, 2009a; Iñiguez–Armijos, Leiva, Frede, Hampel, & Breuer, 2014; Fugère et al., 2016; Tanaka et al., 2016; Montag et al., 2019). Higher richness is often due to the maintenance of especially sensitive or specialized taxa, such as those in the orders Ephemeroptera, Plecoptera, Trichoptera, and Odonata (Siegloch, Schmitt, Spies, Petrucio, & Hernández, 2017; Brito et al., 2018). Taxa evenness/dominance has also been used to assess deforestation impact, but has shown variable results, with some studies showing no difference

(Iwata et al., 2003; Iñiguez–Armijos et al., 2014), and others showing forested sites having higher evenness (Fugère et al., 2016).

Indices of biotic integrity (IBIs) are often used to summarize the responses of sensitive taxa to disturbances, and many of these have recently been developed for tropical streams. Some efforts from Latin America include the Biological Monitoring Working Party (BMWP) Index for Colombia (Zamora, 2007), Costa Rica (Springer, Ramírez, & Hanson, 2010), Panama (Cornejo, 2010) and Cuba (Naranjo et al., 2005); the *Índice Biológico a Nivel de Familia de Invertebrados Acuaticos* for El Salvador (IBF-SV-2010: Sermeño et al., 2010); and a variety of other multi-metric indices (Helson & Williams, 2013; Chen et al., 2017). These IBIs are commonly used by neighboring countries with similar ecology, such as the BMWP index for Costa Rica in Nicaragua (González, Mateo, & Valdivia, 2013; Salvatierra, 2014). Catchment-scale deforestation and subsequent anthropogenic land uses can be strong predictors of changes in IBI indices (Ligeiro et al., 2013; Iñiguez–Armijos et al., 2014).

In addition to changes in these metrics, differences in community composition have been commonly reported. In multiple studies, the macroinvertebrate community was found to be significantly different between forested and deforested stream reaches according to multivariate techniques based on community similarity (Benstead et al., 2003; Lorion & Kennedy, 2009a; Fugère et al., 2016; Iñiguez–Armijos et al., 2014). In all these studies, forested sites were also more similar to each other than deforested sites, which were more variable in community composition. These studies show that deforestation changes the macroinvertebrate community, but not necessarily in a consistent way among sites.

These changes in community composition are driven by individual taxon responses to disturbance and subsequent trophic effects that are highly context dependent. Specific taxa responses are too contingent on study conditions and region to provide constructive background for comparative studies. But effects on important ecosystem functions can be caused by the declines in abundance of even single taxa due to deforestation, as was the case in the mountains of Ecuador where the decreases in abundance of an important leaf litter shredding genus of caddisfly at deforested sites significantly decreased large organic matter processing rates compared to forested sites (Encalada, Calles, Ferreira, Canhoto, & Graca, 2010).

Tropical deforestation and stream fish

Neotropical freshwater fishes face a variety of threats, many of which are linked to deforestation and land use change and associated habitat degradation (Pelicice et al., 2017). Multiple studies have shown that stream fish abundance, community assemblage, and trophic structure shift in response to impacts from deforestation. Deforestation in the catchments draining to streams has been linked to decreases in beta-diversity of fish, resulting in deforested sites with homogenized community structure, dominated by species adapted to deforested conditions (Bojsen & Barriga, 2002; Lorion & Kennedy, 2009b; Teresa et al., 2015; Dala-Corte et al., 2016). Studies have shown community changes are related to shifts in instream habitat. Wright and Flecker (2004) found higher abundance of most species, and especially rare species, in streams where woody debris was not removed (loss of woody debris is coincident with deforestation). Bojsen and Barriga (2002) correlated shifts in the fish community to increased sunlight and lower instream leaf abundance from loss of canopy cover.

Teresa et al. (2015) showed increases in hypoxia tolerant individuals after deforestation, which implies that shifts in water chemistry associated with deforestation also drive changes in the fish community. In Brazil, Dala-Corte et al. (2016) found that following conversion to agriculture and subsequent substrate siltation and sunlight exposure, macrophytes abounded and there was a shift from benthic and lithophilic fish towards nektonic, macrophyte-associated fish. In the same system, Leitão et al. (2017) found that deforestation was linked to declines in the functional evenness of assemblages as mediated by increases in macrophytes, and that riverscape fragmentation from road crossings from logging and agricultural roads was linked to reductions of functional diversity and evenness in streams.

Shifts in the fish communities can also result from shifts in diet related to impacts from deforestation. For example, multiple tropical studies have emphasized the importance of terrestrial arthropods from forested riparian zones in fish diets (Chan et al., 2008; da Silva Gonçalves et al., 2018). The lack of this "arthropod rain" to streams without intact riparian forest could result in shifts in the fish community. Lobón-cerviá et al. (2016) and Bojsen and Barriga (2002) showed increased dominance of periphyton in fish diet at deforested sites. They found that periphyton-feeding loricariids made up more than 50% of fish at deforested sites and were less abundant or absent at forested sites.

The importance of the history of deforestation and land use

Impacts to streams from deforestation change over time and are related to the unravelling of processes that only begin with initial deforestation and depend on the type of subsequent land uses. However, few studies have analyzed the effect of time since deforestation on stream responses. Time since deforestation and land use history could be just as or more important than the extent of forest loss for describing changes to stream habitat (Leal et al., 2016; Molina et al., 2017) and biotic responses (Brejão et al., 2018; Zeni, Pérez-Mayorga, Roa-Fuentes, Brejão, & Casatti, 2019). Brejão et al. (2018) found both time since deforestation and current extent of catchment deforestation to be important predictors of changes to the fish community in Brazil. Zeni et. al. (2019) found that fish functional diversity was reduced in streams with a longer history of deforestation. Even when reforested, there can be remnant effects from deforestation on habitat and biota that last decades (Harding et al., 1998; Iwata et al., 2003).

The context of deforestation in Southeast Nicaragua

Nicaragua is losing 1330 square kilometers of forest each year, mostly in protected reserves (Alvarez, 2016). Much of this is occurring near the Atlantic coast, as the agricultural frontier expands eastward (Jordan, 2015; Phillips, 2017). Nearly the entirety of the southern Atlantic region of Nicaragua is included in the massive Rio San Juan UNESCO Biosphere Reserve, much of which is no longer forested. Its core area, the Indio-Maíz Biological Reserve, is one of the last and largest intact regions of primary forest left in Nicaragua and hosts pristine river systems and very high biodiversity of plants, fish, and wildlife (Dans, Luna, & Jordan, 2015). Each of the limited number of published studies from Southeast Nicaragua calls for more research in these understudied and threatened systems (Fenoglio, Badino, & Bona, 2002; Organización de los Estados Americanos, 2005; Jordan, Stevens, Urquhart, Kramer, & Roe, 2010; Dans et al., 2015; Jordan, Schank, Urquhart, & Dans, 2016; Härer, Torres-Dowdall, & Meyer, 2017).

Indio-Maíz makes up the southern half of the Rama-Kriol indigenous territory, which was protected to provide space to sustain subsistence agriculture, fishing, hunting, and gathering by indigenous Rama and afro-descendant Kriol communities, on their traditional lands. The northern half of the territory is composed of the Cerro Silva and Punta Gorda National Reserves. Illegal deforestation by mestizo migrants from western Nicaragua over the last three decades has converted much of these northern reserves from primary rainforest to cattle pasture, and it is rapidly encroaching on the intact Indio-Maíz to the south (see Figure 1). Hunting and fishing by mestizo migrants have also taken their toll near the deforested areas (Jordan, Galeano, & Alonzo, 2014). In most cases of deforestation, the forest is being slashed, burned, and converted to pasture for beef and dairy cattle production. In some cases crops are also grown.

Long-term residents of the Rama-Kriol territory are alarmed by the changes in their landscape being driven by mestizo colonists invading the territory. Rama-Kriol leaders and forest rangers, along with local conservation organizations, are working to document impacts of the agricultural frontier on their resources, in order to use this information in advocacy and management. As the Rama communities rely heavily on river fish and shrimp in their diets, knowledge of the effects of illegal deforestation and fishing on river fish and shrimp populations and the river ecosystem that supports them is of utmost interest to community leaders. This is a part of the Rama-Kriol government's action plan for Indio-Maíz (Gobierno Territorial Rama y Kriol, 2018).

In many cases, streamside areas are the first to be deforested in these landscapes. Rivers and streams are entry points into the landscape, and focal points for starting new cattle ranches (unpublished data, Gobierno Territorial Rama y Kriol). This has been shown to be true with the invasion and destruction of primary forests in other parts of the world as well (Ferraro, 1994). Unlike in many areas throughout the tropics, other disturbances to these rivers from infrastructure have been minimal—there are no dams and very few road crossings in these watersheds, and in some streams in the Indio-Maíz reserve there are no human disturbances. This context not only allows for relevant conservation application of research on the impacts of deforestation on streams, but also provides a unique opportunity to document the ecological effects of deforestation for cattle ranching within a gradient ranging from pristine primary rainforest streams to streams recently deforested to those deforested much earlier.

Stream macroinvertebrates and freshwater fish are being increasingly studied in Latin America, although many gaps in research still exist (Smith & Bermingham, 2005; Ramirez & Gutiérrez-Fonseca, 2014; Pelicice et al., 2017). In Nicaragua, aquatic surveys have been scarcer, in particular along the Caribbean Coast. Species, genus, and even family presence are still being described (Maes & Salvatierra-Suarez, 2014). The most recent comprehensive list of fish species in Nicaragua was in 1982 (Villa, 1982), which was depauperate of registers from the southern Caribbean coast. Since then many updates to taxonomy and species lists in Costa Rica (Angulo Sibaja, Bussing, Garita-Alvarado, & López, 2013) and Central America (Rican, Pialek, Dragova, & Novak, 2016) have been reported, many of these taxa exist in Nicaragua.

Although Indio-Maíz is more than 3,150 square kilometers in size, and one of the best protected primary rainforests in Central America, only one formally published macroinvertebrate study (Fenoglio et al., 2002) and no formally published fish studies (not including the San Juan River, bordering the reserve to the south) exist from the rivers of the Indio-Maíz Biological Reserve. Fenoglio et al. (2002) is very limited in scope and geographic distribution. It is likely that many undescribed species exist in these rivers. In addition, the ecology and range of many aquatic species in the region are poorly described (Maes & Salvatierra-Suarez, 2014; Härer et al., 2017). There have been no studies to date that assessed the relationships between deforestation/land use, stream habitat, and stream biota in Nicaragua, and very few studies of this nature in all of Central America (Lorion & Kennedy, 2009a,b; O'Callaghan et al., 2015). Given the impending threats from deforestation and cattle ranching to this data poor region, it is a high priority area for research.

Objectives, research question, and hypotheses

The objectives of the study were (1) to describe and assess the complex impacts of deforestation to stream habitat and communities in the Rama-Kriol territory; (2) to fill knowledge gaps on distributions and ecology of aquatic species in SE Nicaragua; and (3) to provide new information and resources to scientists, conservationists, and indigenous leadership working in the region, and facilitate it’s use in conservation, advocacy, and further scientific research.

This study intended to answer the question: what are the effects of deforestation and subsequent cattle ranching on stream macroinvertebrate (including shrimp) and fish communities and their habitat in the protected areas of southeastern Nicaragua?

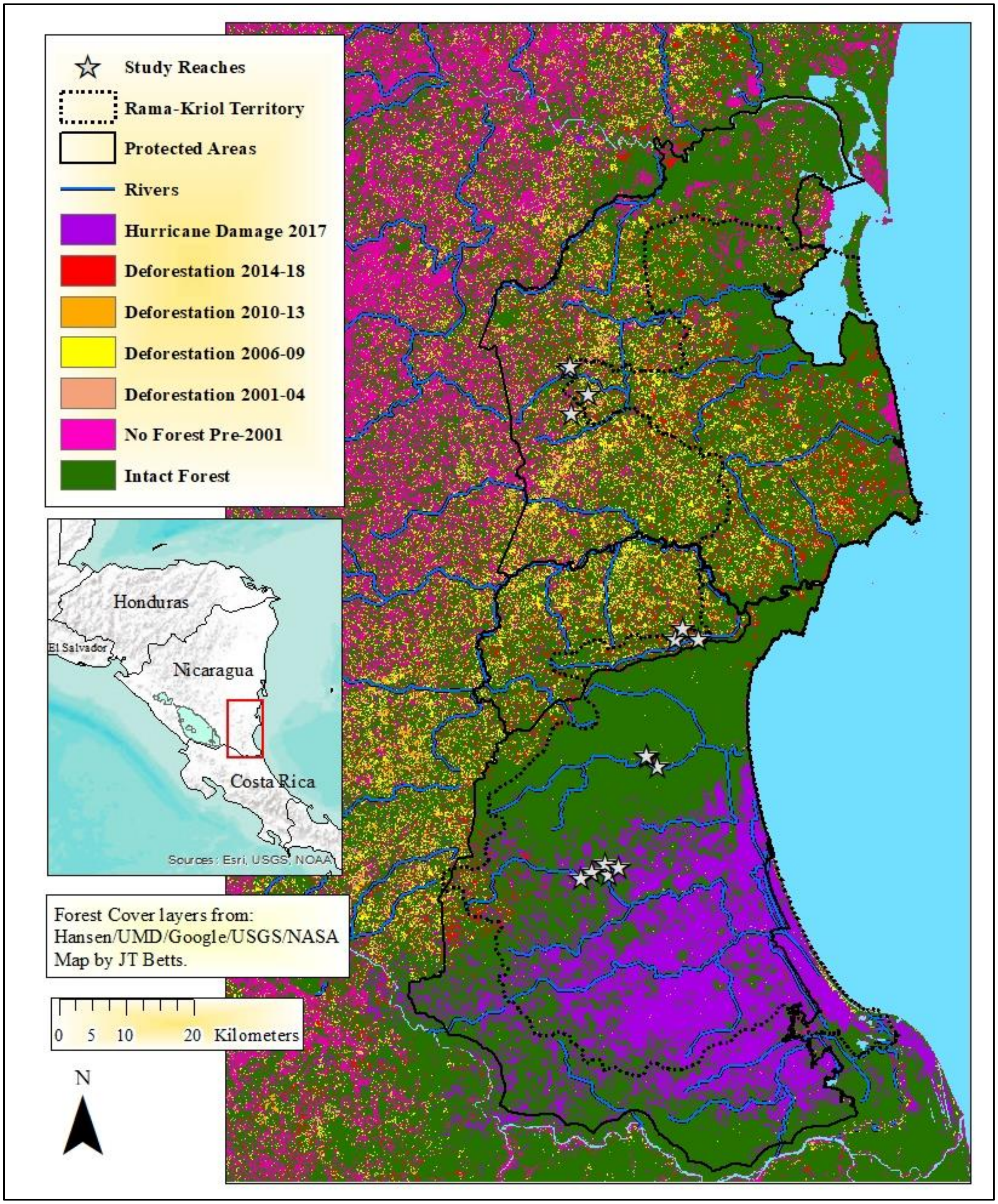
It was hypothesized that changes in stream and riparian habitat due to impacts from deforestation and cattle ranching over time within each catchment and its reach buffer would predict shifts in the stream biota. Specifically, that instream and riparian disturbances would be more evident in deforested watersheds, especially those with a longer deforestation history—including increased sedimentation, decreased stream bed and channel stability, damaged riparian condition, increased algae cover, increased temperature, decreased large wood, and decreased leaf litter, among other impacts—and that these impacts would lead to lower macroinvertebrate richness, BMWP score, diversity, evenness, and density; lower fish taxa richness, abundance, and average lengths; and differences in community composition in deforested catchments, especially those with a longer deforestation history.

METHODS

Site selection

Sampling was carried out in the Rama-Kriol territory and the national reserves of Southeast Nicaragua, including fifteen headwater stream reaches each with a distinct catchment (Figure 1). Eight stream reaches were in primary forested watersheds (Indian River, N=5 and Corn River, N=3) and seven reaches were in deforested watersheds (Pijibaye River, N=3 and Kukra River, N=4) (Figure 2). Each reach was on different streams draining to these larger rivers. Thus, reaches were considered independent, as no reach had another reach downstream of it (no catchment overlap). Each watershed represented a unique disturbance class: The Indian River watershed is primary rainforest but with some hurricane damage, the Corn River watershed is primary rainforest and without hurricane damage, the Pijibaye River watershed is recently becoming deforested, and the Kukra River watershed has been in the process of deforestation throughout the last 3 decades. An additional nine sites were planned (4 forested and 5 deforested), but Nicaragua's political uprising in April 2018 (Petriello & Joslin, 2019) cut the field season short by two months.

Data collection occurred during the dry season (February to April) of 2018, with six field trips: Kukra River (5-11 Feb.), Indian River (16-28 Feb.), Indian River (10-14 Mar.), Kukra River (21-27 Mar.), Corn River (8-16 Apr.), and Pijibaye River (17-25 Apr.). Due to the remoteness of sites, sometimes multiple days were spent traveling by boat, dugout canoe, horse, or foot before reaching the headwaters of the rivers. Selecting and sampling each stream reach took 1.5 to 2.5 days.



Forest Cover layers from: Hansen/UMD/Google/USGS/NASA
Map by JT Betts.

Figure 1: Forest cover and deforestation in the protected areas of Southeast Nicaragua. Study reaches are visualized by stars. Study reaches occur in headwater streams of Kukra, Pijibaye, Corn, and Indian River watersheds, which occur from north to south, respectively. Forest loss year data grouped in 4-5-year intervals for visualization. Hurricane damaged forest is treated as forest land cover in all analyses. No Forest Pre-2001 represents pixels without forest in 2000. See methodology for more detailed description. The heavily invaded Cerro Silva and Punta Gorda Reserves and the largely intact Indio-Maíz Reserve are from north to south, respectively, each of which overlaps with the Rama-Kriol territory.

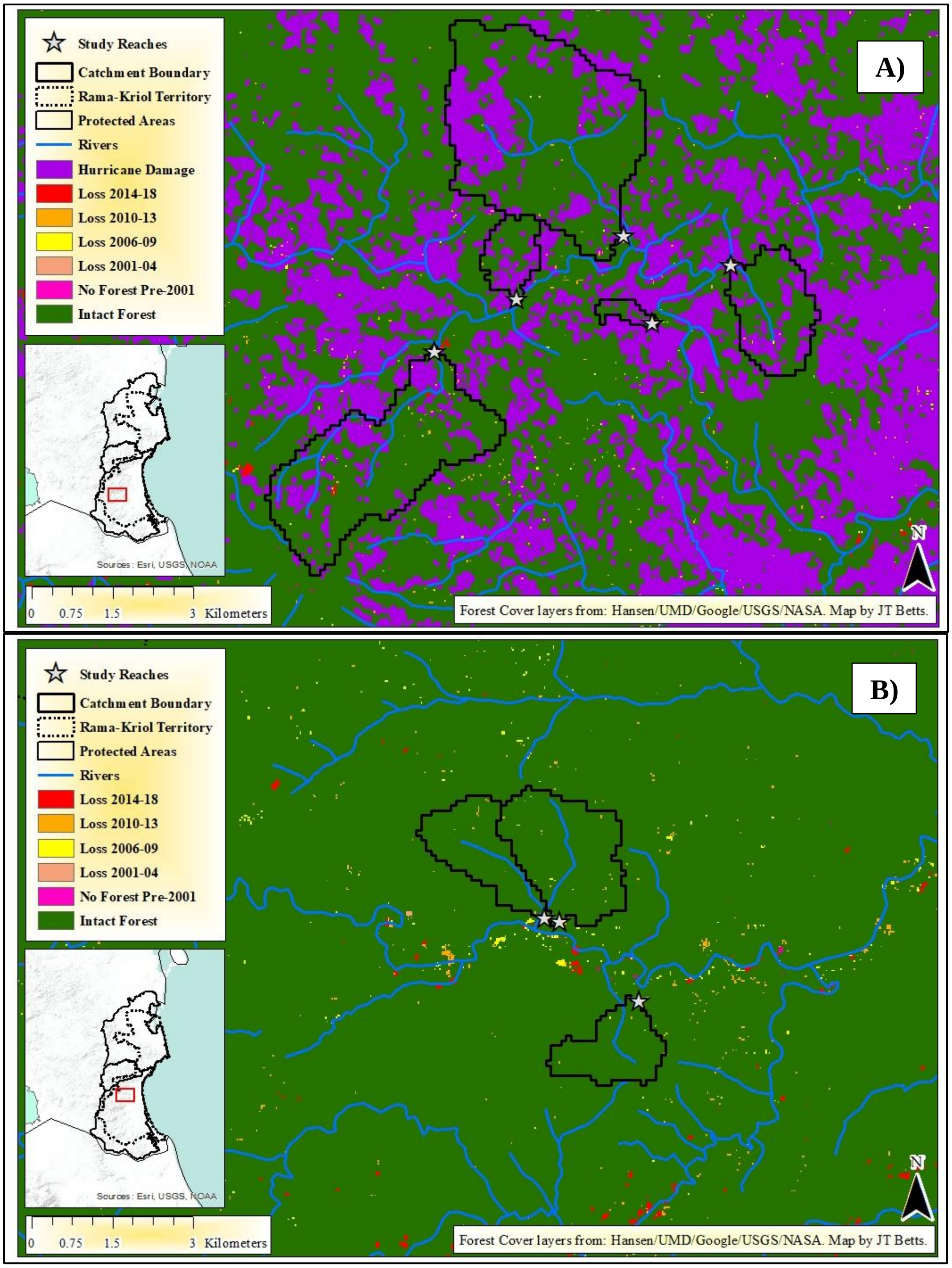
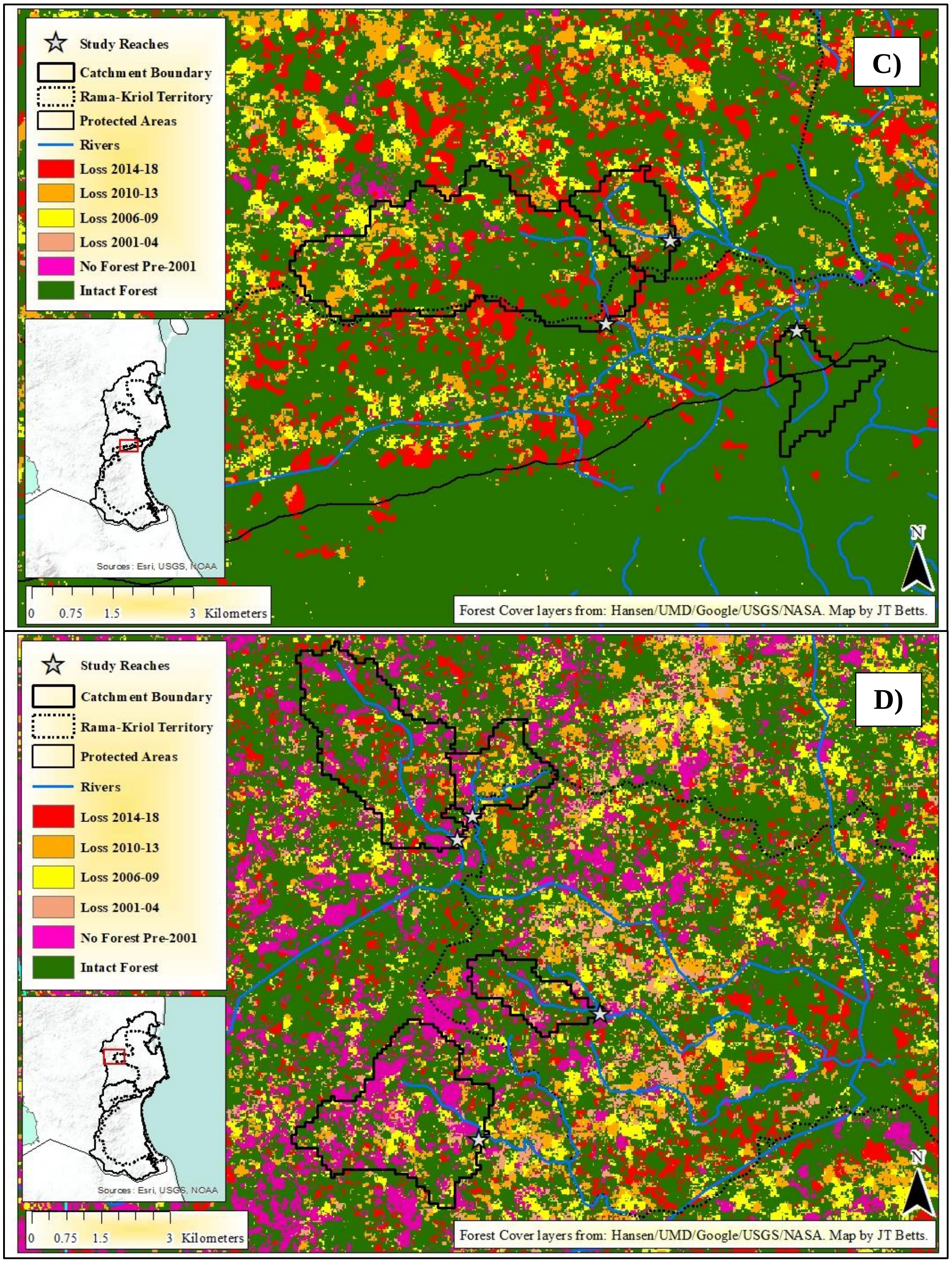


Figure 2. Forest cover and deforestation in the catchment above (draining to) each study reach (study sites). A) Five forested catchments with varying hurricane damage above sample reaches in the Indian River watershed. **B)** Three forested catchments above sample reaches in the Corn River watershed. Loss year data grouped in 4-5-year intervals for visualization, as in Figure 1. Hurricane damaged forest treated as forest land cover in all analyses. Catchment data generated in ArcMap from ASTER DEM (90M) and forest cover data from Hansen/UMD/Google/USGS/NASA (Hansen et al., 2013).

Figure 2 (cont'd)



C) Three "deforested" catchments with more recent deforestation above sample reaches in the Pijibaye River watershed. **D)** Four "deforested" catchments with older and recent deforestation above sample reaches in the Kukra River watershed.

Site set-up

Site set up and data collection used an adapted protocol based on the US EPA Ecosystem Monitoring and Assessment Program (EMAP), according to Hughes and Peck (2006) and Kaufman, Levine, Robison, Seeliger, & Peck (1999). This methodology has also been applied to tropical streams in Brazil (Leal et al., 2016; Terra, Hughes, & Araújo, 2016). In each watershed streams were selected between three and fifteen meters mean wetted width and in plane-bed or pool-riffle gradient class (Montgomery & Buffington, 1997; Lorion & Kennedy, 2009a). Streams were at remote locations, so a topographic map and local guides were consulted to estimate gradient and stream size, which were then verified upon arrival. Starting points for site selection were at least 500 meters upstream of the confluence with the larger river.

Site length was 40X mean wetted width, or 150 meters (m) for streams less than 3.75 m wide. Mean wetted width used in reach set-up was established via 10 measurements upon arrival to a proposed reach, at least 15 m apart, within the proposed sample reach. Habitat assessment and macroinvertebrate sampling occurred at eleven transects per reach, at intervals of 4X mean wetted width (Figure 3) or 15 m for streams less than 3.75 m wide. Base transects were set at the upstream edge of a riffle habitat in each stream reach. Macroinvertebrate, habitat, and riparian parameters were sampled at or between each transect, starting at the downstream-most transect A and moving upstream to transect K. Fish sampling was throughout the whole reach. Since total sampling effort for a stream reach took 10-18 hours, typically 3-5 transects were left to finish in the afternoon of the second day, after fish sampling. A GPS point was taken at each furthest downstream transect, and a track created for the sample reach distance by walking the whole stream channel from transect K to A, once all sampling was complete. All sampling was carried out under the appropriate regional and local permits.

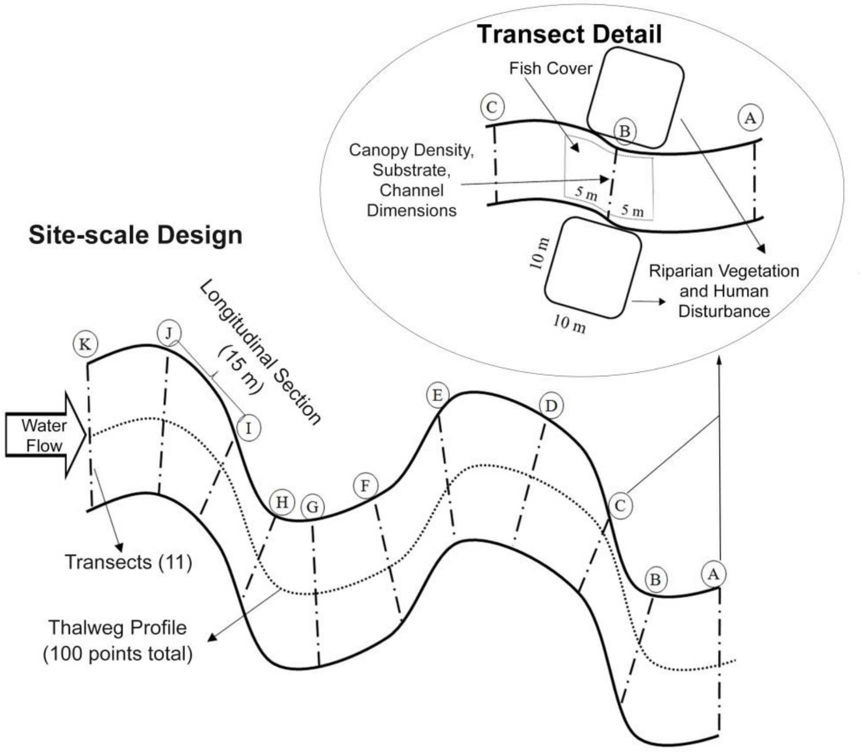


Figure 3: Transect set-up for instream habitat, riparian, and macroinvertebrate metrics. Macroinvertebrate sample locations oscillated between river right, center, and left, with one per transect. Fishing conducted throughout the reach. Example longitudinal section of 15 m shown, for an example stream of mean wetted width 3.75 m, reach length 150 m. Figure from Leal et al. (2016, Supplementary Material, 9), Figure S1.

Stream habitat sampling

Water temperature, conductivity, and pH were measured in the morning, mid-day, and late afternoon at the furthest upstream transect sampled to that point in time using Hannah Instruments' portable waterproof pH/EC/TDS Meter (High Range) (Model HI991301). At these points, turbidity was also sampled using Forestry Supplies' 120 cm transparency/turbidity tube (measured in NTU) (model 77096). The tube was filled to the top with water and allowed to drain until the disk at the bottom becomes visible, then the height of water was recorded. If the disk at the bottom of the tube was clearly visible when the tube was filled with water to the top, NTU was recorded as <5 NTU (Myre & Shaw, 2006).

At each of the eleven transects, stream wetted width was measured. Stream substrate was estimated using a standard pebble count as defined by Kaufmann, Faustini, Larsen, & Shirazi (2008). Five equidistant samples were taken at each of the 11 transects in each reach (55 samples per reach), starting one seventh of the way across the transect. Substrates were divided into eight categories using W.F. McCullough's sand-gauge (1984) to measure small substrates and a collapsible 2 meter-stick for larger substrates (Organic detritus; fines: <0.06 mm; sand: 0.06–2.0 mm; small gravel: 2.0–16 mm; Coarse gravel: >16–64; Cobble: 64-250 mm; Small Boulder: >250–1000 mm; Large boulder: >1000–4000 mm; and bedrock: >4000 mm), using the shortest substrate axis to determine substrate category. These data were summarized across each reach as geometric mean diameter (Dgm)[1] and percent of each substrate class (Kaufmann et al., 2008; Terra et al., 2016). Depth (x.x cm) was measured and percent embeddedness (Mažeika, Sullivan, Watzin, & Hession, 2004) estimated at each substrate point. Between each transect, using a collapsible two-meter stick, maximum depth (thalweg) was measured at ten consecutive points, following the deepest channel. The distance between each point was 1/100th of the calculated reach length. Each subsequent transect was set up at the 10th thalweg measurement. Thus there were two depth summary measurements, average depth (based on the 55 points, 5 evenly spread across each transect) and average thalweg depth (based on 100 points, along the reach's deepest channel).

According to EMAP protocols (Kaufmann, Levine, Robison, Seeliger, & Peck, 1999), percent cover of different habitat features in the wetted stream channel was visually estimated

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[1] Dgm will be determined as described in Kaufmann et al. (2008, 153-154): "Dgm was calculated by nominally assigning to each particle the geometric mean diameter of the upper and lower bounds of its size class (e.g., 5.66 mm for fine gravel) and then calculating the geometric mean as the antilog of the arithmetic mean of the logarithms of those frequency-weighted class midpoint values. Bedrock and fines, respectively, were assigned class midpoint values of 5660 mm and 0.0077 mm." Organic detritus does not contribute towards the Dgm.

within an area five meters upstream and five meters downstream of each of the eleven transects (Figure 3). All visual estimates were done by JT Betts, to maintain consistency. These features included periphytic macroalgae, macrophytes, large woody debris (>0.3 m diameter), small woody and leafy debris (<0.3 m diameter), live trees and roots, overhanging vegetation (within 1 meter of the water surface), boulders, and artificial structures. Proportion of stream bank actively being eroded within five meters of the transect was also estimated (see Figure 12 for example). For each reach and habitat characteristic, the percentages of the eleven transects were averaged to create a value representing the reach.

Large wood number of pieces and total volume within the bankfull channel for each reach was calculated using EMAP protocol from Kaufmann et al. (1999). Large wood was defined as woody material with diameter of at least 10 cm and length of at least 1.5 m. Wood was classified into four diameter classes (0.1 m to < 0.3 m, 0.3 m to < 0.6 m, 0.6 m to < 0.8 m, and > 0.8 m) and three length classes (1.5m to < 5.0 m, 5 m to < 15 m, and > 15 m), only counting the portion of the log that has diameter > 0.1m. Diameter and length class were visually estimated by JT Betts. The number of logs in each length-diameter category between each transect was tallied. Large wood abundance and volume was summarized into multiple reach-scale values (Kaufmann et al., 1999). For analysis, large wood volume per 100 m of stream was used. To calculate this value for each diameter and length category, a representative value was assigned ([Upper limit - lower limit]*[1/3] + lower limit) and volume of a cylinder calculated (length * $(\text{Diameter}/2)^2 * \pi$). For example, for a log in the smallest category, (length class 1.5 to <5 m and diameter class 0.1 to <0.3 m), volume was is calculated as $\{[(5-1.5) * (1/3) + 1.5] * ([(0.3-0.1) * (1/3) + 0.1] / 2)^2 * \pi\} = \{2.\bar{6} * [(0.1\bar{6}/2)]^2 * \pi\} = 0.0582\ \text{m}^3$ (Kaufmann et al., 1999; Robinson, 1998). Total volume per 100 m was calculated as the sum of volumes of all the large wood in the transect/transect length (m)*100. At two reaches in the Indian River watershed, values from a transect with a major log jam was replaced with average values from the rest of the transects at the reach, because these transects heavily biased the measurements at the log jam reaches. Large wood measures serve as useful indicators of instream habitat and cover, as well as the extent of impact from Hurricane Otto (November 2016).

Riparian condition sampling

A densiometer was used at left edge, right edge, and in each direction from the center of each transect to estimate percent shade, according to Kaufmann et al. (1999). Densiometer readings were summarized into average percent shade per reach. Riparian condition was visually estimated in 10 x 10 m plots at each transect following Kaufmann et al. (2008) with parameters as defined in Kaufmann et al. (1999) (Figure 3). Percent cover of large (>0.3 m diameter) and small (<0.3 m diameter) trees in the upper canopy (>5 m tall), and percent cover of woody and non-woody vegetation in the mid-canopy (between 0.5 m and 5 m tall) and ground layers (<0.5 m) were estimated. Values of each summary measure for all eleven transects were averaged. Presence of riparian human disturbances was recorded in 12 categories, weighted by proximity to the stream edge (presence of roads, dams, trails, pasture, crops, pipes, etc.) (Kaufmann et al., 1999). A sum was calculated that represented the riparian human disturbance index (W1_HALL). Using this information and the following formula, the riparian condition index (RCOND) was calculated (Kaufmann et al., 1999, Kaufman & Hughes, 2006, Kaufmann et al., 2008). The RCOND index is determined by riparian % cover of large trees, woody vegetation at all three canopy layers, and proximity of different human disturbances to the stream bank. The equation for the riparian condition index is as follows, from Kaufmann et al. (2008):

RCOND = {(Mean upper canopy large trees % cover) * Σ (Mean total woody veg. % cover in all three canopy layers) * [1 / (1 + W1_HALL)]} $^{1/3}$

Macroinvertebrate sampling and identification

Macroinvertebrates were sampled using a Surber Sampler (Wildco 243 µm Nitex net, sample area 0.0929 m^2=1 ft^2), at 11 locations for each reach (1 per transect), changing between river right, center, and left at each consecutive transect. Rocks were scraped clean and the sample area agitated with gloved hands until the substrate was loose within the sample area to a depth of 5 cm (2-4 minutes). The Surber sample area was not disturbed before sampling. For consistency, all macroinvertebrate samples were done by JT Betts. All samples were preserved in the field using 95% ethanol in 250 ml containers labelled inside and out. When the sample was more than three-quarters full of debris, contents were split, and an additional container was used. Samples were transported to the University of Costa Rica [exported under Law °N 28, Decree °N 3584, resolution °N 1076-22-08-2018 (SERENA) and dictate °N 31-2108-2018 (Consejo Regional), Nicaragua; and imported under Law °N 7317, Ordinary Session °N 088-SETENA, Costa Rica] (Appendix C). Lab work was carried out under supervision of Monika Springer in the Aquatic Entomology lab in the School of Biology at the University of Costa Rica.

Springer et al. (2010), Domínguez and Fernández (2009), Roldán (1988), and Merritt and Cummins (1996) were consulted for identification. JT Betts, J Román-Heracleo, P Campos, D Solano-Ulate carried out identifications, and consulted M Springer (Trichoptera, others), P Gutiérrez-Fonseca (Plecoptera, others), and W Flowers (Ephemeroptera) with unknowns. Invertebrates were identified to best taxonomic resolution possible, typically genus (see Appendix A for a full list). Identified specimens are cataloged at the University of Costa Rica Zoological Museum in the School of Biology (Contact: M Springer). Specimens were sorted in small glass vials (capped with permeable cotton) containing each distinct taxa of invertebrate found at a given reach. These vials were submerged in 90% ethanol in sealed jars for each reach (N=15) for future reference.

Shrimp sampling and identification

In pools throughout each reach four mesh pyramidal and five metal cylindrical traps were set overnight with dog food as bait. The holes of the metal traps were adjusted to 4 inches in diameter to accommodate large *Macrobrachium* shrimp (Covich, Crowl, & Heartsill-Scalley, 2006). The main purpose of the traps was to catch these freshwater shrimp, but fish captures were also recorded. Traps were set out at the end of the first day of sampling at a reach and removed the following morning. Shrimp were identified to genus and morphospecies (*Atya* [2-3 morphospecies] or *Macrobrachium* [3 morphospecies]) by JT Betts, with help from N Gonzalez-Aleman.

Fish sampling and identification

The fish community was sampled at each reach using hook and line (Montaña & Winemiller, 2010) and cast-net methods. See Bojsen and Barriga (2002) for somewhat similar mixed methods. Electrofishing was not possible due to remoteness of sites (some being >50 km from electricity or infrastructure) and the difficulty and risk of bringing expensive research equipment into Nicaragua. Consistent effort of each technique was applied, in attempt to have similar Catch per unit effort (CPUE) at each reach. Fish were sampled first thing in the morning on the second day, starting at the base transect and moving upstream. Three individuals fished with hook and line (Gamakatsu C12U size 14, 10, and 8) using worms and raw fish (*Astyanax* sp.) caught on site. Hook and line effort consisted of thorough coverage of all pools and glides in the reach (1.75-2.5 hours depending on river size). Using a cast net, one person followed behind the three hook and line anglers, attempting to cast every surface area of the stream. Due to limited sampling techniques and time, some species present at each reach could have been not captured, and inferences about the fish and shrimp communities are made with caution (Hetrick & Bromaghin, 2006).

For all fish caught, species was recorded, standard length was measured in cm, and photos taken for those that could not easily be identified in the field. Fish and shrimp were kept with a bubbler in a bucket when caught and released after measurement at the end of sampling. A few specimens were kept in 95% ethanol for identification. These are cataloged at the Zoological Museum at the University of Costa Rica. JT Betts identified fish species in the field, and A Angulo-Sibaja, J San Gil, CA Garita-Alvarado, and N Gonzalez-Aleman helped with photo and specimen ID, with reference to Bussing (1998). These efforts are the first ever recorded for these streams and can serve as an initial species list for more in-depth future investigation. Fish sampling methodology was approved via the Institutional Animal Care and Use Committee (IACUC) office at Michigan State University, AUF# 12/17-220-00.

Spatial data processing

All spatial data processing was done in ArcGIS 10.5.1. The base transect point was used along with the NASA Shuttle Radar Topography Mission (SRTM GL3) 90-meter global digital elevation model (van Zyl, 2001; Rodriguez, Morris, & Belz, 2006) to calculate the catchment area above the base transect of each reach (Brenden et al., 2006; Leal et al., 2016). The reach track was used to calculate 100-meter riparian buffers around each study reach using the *Buffer* tool (ArcGIS 10.5.1). These shapefiles were used as areas for forest cover analyses (see below).

To calculate catchments draining to the base transect at each reach, the *Hydrology* toolset in Spatial Analyst in *ArcToolbox* was used (ArcGIS 10.5.1). The DEM was used to create *fill*, *flow direction*, and *flow accumulation* raster layers, and *Snap Pour Point* was used to find cells of high accumulated flow nearest to each base transect. These pour points were used to create catchments for the whole stream network upstream of the base transect. Catchments were checked against topographic maps for accuracy (Dirección General de Cartografía de Nicaragua, 1988).

Catchment-scale forest cover parameters

Percent forest cover and forest loss for each catchment (land area contributing to each sample reach) and the 100 m buffer around each reach was calculated, using the Global Forest Change dataset (Hansen et al., 2013) (Figure 4). This is a well-known raster dataset based on NASA Landsat satellite imagery (30 m pixel resolution). Raster files "year of gross forest cover loss event (*lossyear*)" and "tree canopy cover for year 2000 (*treecover2000*)" were downloaded using the 20N, 90W extent, which includes Nicaragua. The *lossyear* raster was divided into 18 separate files representing forest loss by year (2001-2018). Using the *treecover2000* raster, which has values representing % canopy closure for each pixel on a scale of 0 (full closure) to 100 (no closure), a binary forest cover 2000 layer was created by extracting and combining all pixels with cell values ≤30 to represent deforested and ≥30 to represent forest, with the idea that if a pixel is determined as more than 30% deforested, it is considered deforested. Both above functions were done using the *Extract by Attributes* function from *Spatial Analyst Tools* in *ArcToolbox* (ArcGIS 10.5.1). To calculate forest cover in the year of sampling (2018), the sum of *lossyear* pixel values (2001-2018) was subtracted from the number of forested pixels in 2000. Percent forest cover in each catchment and reach buffer in the year of sampling, and each year prior until 2000 was calculated. This was done by using the catchment and buffer shapefiles to clip the forest cover raster files, using the *clip* function in *raster processing* in *ArcToolbox*

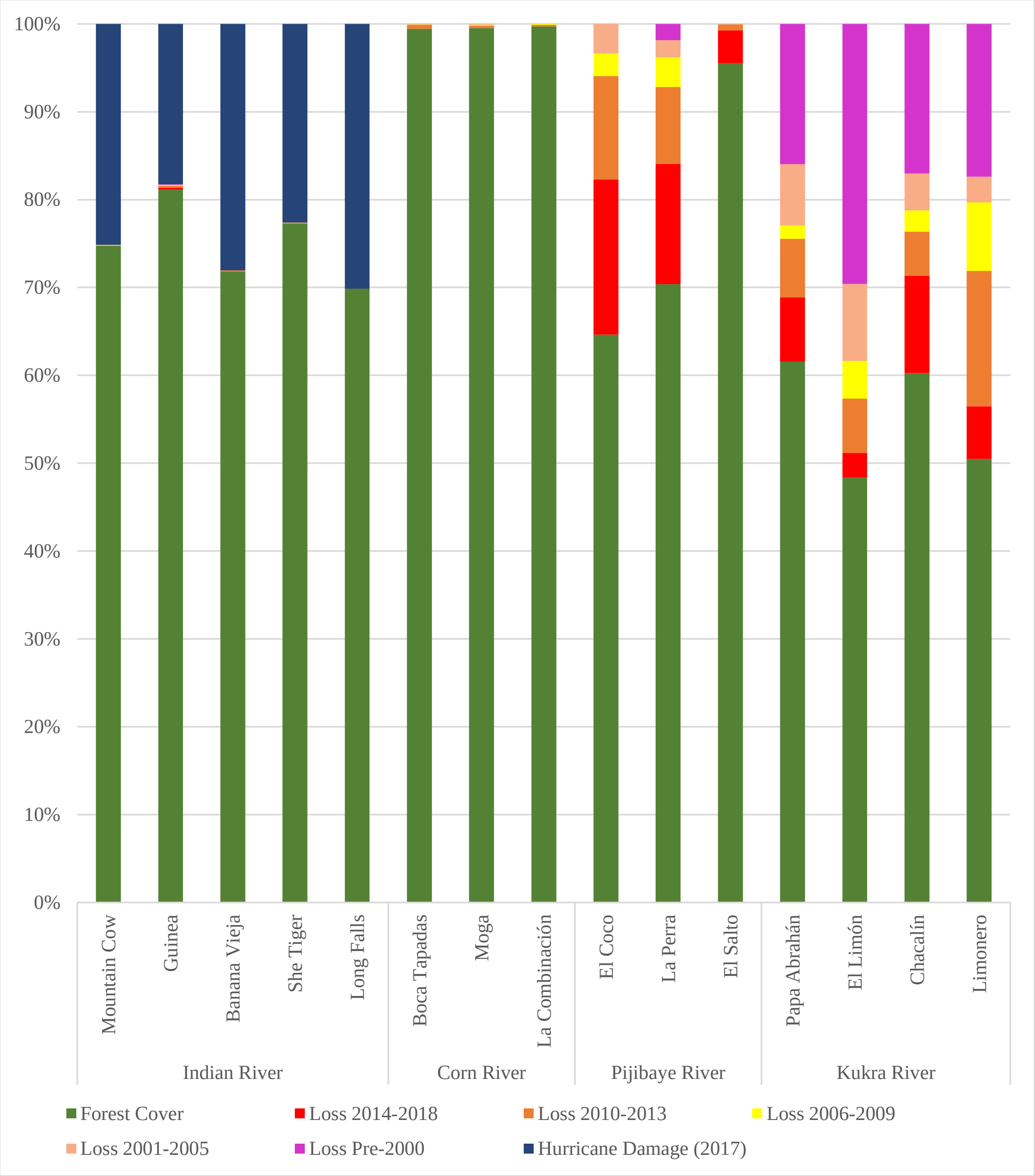
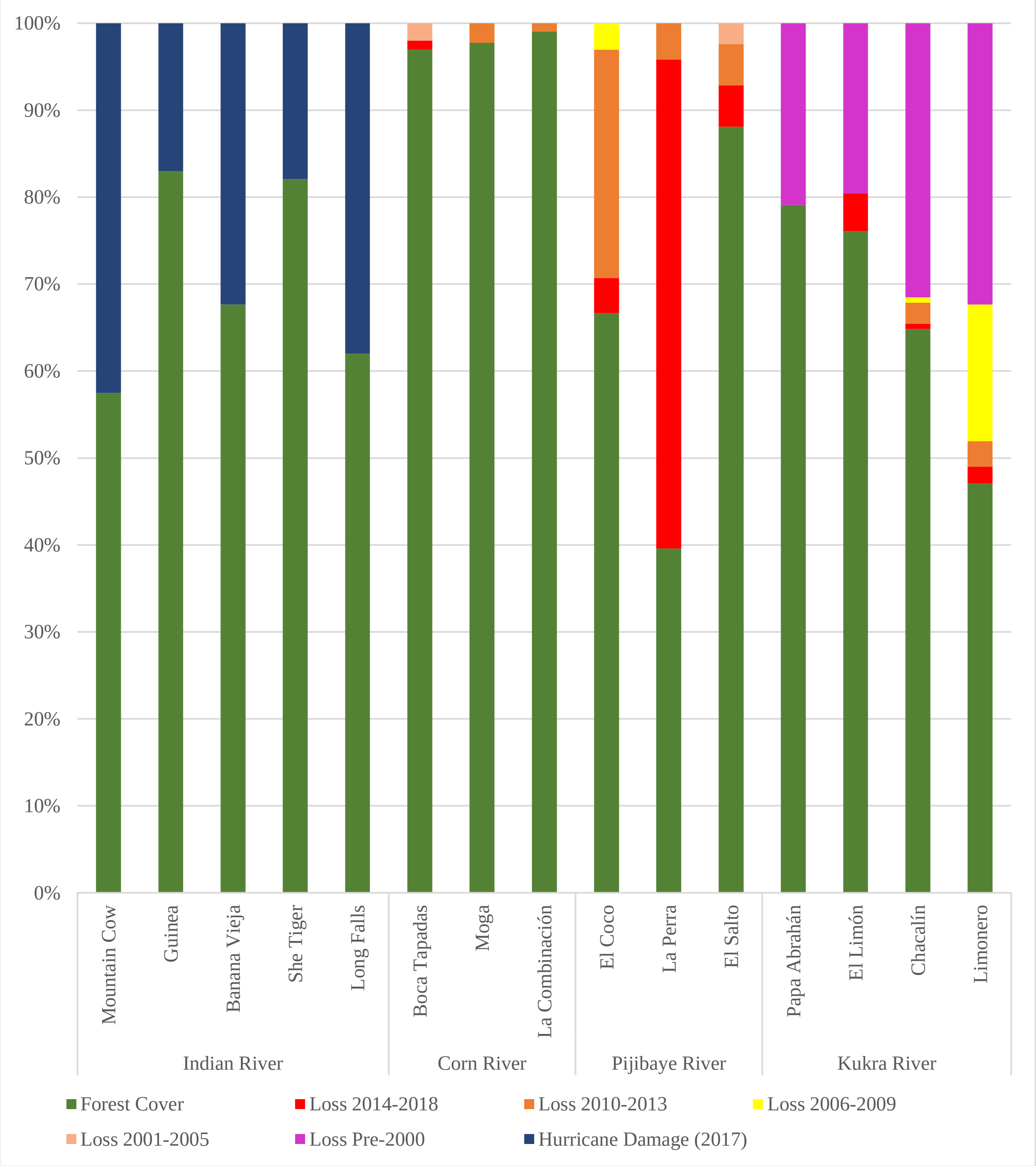


Figure 4: Forest cover in the catchment and buffer over time. A) Percent forest in catchment above (draining to) each study reach**.** Catchment data generated in ArcMap from ASTER DEM (90 m) and forest cover data from Hansen et al. (2013). Corresponds directly to areas visualized in Figure 2. Loss year data grouped in 4-5-year intervals for visualization. Hurricane damaged forest treated as forest land cover in all analyses. Loss Pre-2000 represents pixels without forest in 2000. See methodology for more detailed description. Note that Kukra River watersheds tend to be deforested much earlier than Pijibaye River watersheds.

Figure 4 (cont'd)



B) Percent forest in 100-meter buffer area around each study reach. Buffer data generated from study reach "track". Note that deforestation is higher in the buffer than the watershed for most sites.

(ArcGIS 10.5.1). These data are visualized by 4-5 year intervals of forest loss for each catchment and buffer in Figure 4 and mapped with the same intervals and color code in Figure 2.

Deforestation history index

A time-weighted index of deforestation history was developed based on the forest cover data described above from Hansen et al. (2013). To calculate the index, the area of interest (catchment or buffer) was used to clip the *lossyear* and *treecover2000* rasters, and data from the attribute table extracted into excel. For each year in the *lossyear* raster (2001-2018) for the area of interest, the number of pixels classified as deforested in a particular *lossyear* was multiplied by the number of years before present, for example 100 pixels lost in 2006 (13 years before present) would be 100 * 13 = 1300. The calculation was repeated for each year 2001-2018 and these values were summed for all years. To include forest loss before 2001, number of pixels with values ≤ 30 (at least 30% deforested) from the *treecover2000* raster for the area of interest was summed, and this value multiplied by 20 (~20 years before present) and added to the sum of multiplied values for *lossyear* 2001-2018. This total was divided by the number of pixels in the area of interest (catchment of buffer) in order to standardize comparisons. This is represented by the equation below:

$$\text{Deforestation History Index} = \{[\Sigma\ \mathit{lossyear2001} * (2019-2001), \mathit{lossyear2002} * (2019-2002) \ldots \mathit{lossyear2018} * (2019-2018)] + [\mathit{treecover2000}(\leq 30) * 20]\} / [\#\text{ of pixels in area of interest}]$$

This process created an index typically on a scale of 0-10 that portrays a time-weighted deforestation value for use in analysis. Its application is for situations in which the impacts of deforestation are accumulative over time, and recent deforestation is not the same in impact as deforestation years ago. In other words, where current percent deforestation in a study area does not fully capture its impact on a study system. This has been shown to be true for stream habitat and biota in relation to land-use history (Harding et al., 1998).

Habitat and landscape variable selection

Habitat variables were consolidated into 64 summary variables at the stream reach level. They were organized into categories of stream size, hydrology and substrate, bank disturbance, water quality, wood and debris, in-channel algae and plants, and riparian forest condition. A Pearson's correlation matrix was calculated and variables within each category with a correlation coefficient (R) of 0.6 or larger were thinned to one per category—prioritizing variables based on best judgment of ecological importance of the variable and its suitability as a representative summary measure of the category (for example, geometric mean substrate diameter was chosen over %boulder or %cobble, even though all were correlated) (Ferreira et al., 2014). Ordination techniques like PCA or PCoA were not appropriate for variable selection due to relatively low ratio of number of samples to number of habitat variables (McGarigal, Cushman, & Stafford, 2013). A few variables were kept because of their ecological importance and distinctness, even though they significantly correlated with another variable within the same category. These include small woody and leafy debris % cover and large wood volume per 100 m, which can respond differently to disturbance and interact with each other in the stream (Bilby & Likens, 1980); and mid-canopy plant % cover and the riparian condition index, which show distinct aspects of riparian habitat quality (Kaufman et al., 1999). Twenty variables were selected (see Table 1).

Four landscape predictors were selected for use in analyses. They included the deforestation history index and percent forest cover for both the catchment draining to each base transect and the 100 m buffer around the study reach.

Habitat nonparametric comparisons

Mann-Whitney U and Kruskal-Wallis tests were used to assess differences of all twenty habitat metrics between forested and deforested stream reaches, and by watershed, Pairwise comparisons were carried out using Mann-Whitney U tests. These nonparametric alternatives to T-tests and ANOVAs were selected because assumptions of normality and equal variance were not met for many comparisons, according to Shapiro-Wilk and Levene's tests. Exact p-values were used unless there were tied values—where a normal approximation was used. Tests were done using functions *wilcox.test* and *kruskal.test* from the package *stats* for R version 5.3.1 (R Core Team, 2016).

Analysis of macroinvertebrate, shrimp, and fish community response metrics

Macroinvertebrate taxa lists were organized in systematic order, as in Domínguez & Fernández (2009). Abundances were recorded for each distinct taxon based on the sum of all 11 samples for each reach. Taxa richness, and Shannon-Weiner diversity (H) and evenness (EH) indices (Jost, 2006) were calculated according using the number of distinct taxa in the reach, typically at genus level, but sometimes at family (Hydroscaphidae, for example) or higher level (Oligochaeta, for example). If a specimen was found but not identified past a coarser taxonomic level, while other taxa in the same coarse taxonomic level were identified to a finer taxonomic level, the coarse taxonomic level individual was not included as a unique taxa unless it was clearly not the same taxa (for example, trichopteran pupae that could not be identified past the order level were never included as unique taxa because other trichopterans were identified to family or genus level at the same reach).

The BMWP index for the Costa Rican Caribbean (Springer et al., 2010; Salvatierra, 2014) was calculated to generate values representing "water quality" at each reach. This index is still in the process of verification and has not yet been formally adapted to Nicaragua (Pers. comm., M Springer & T Salvatierra). Density was calculated as the total number of individual invertebrates in all Surber samples, divided by the total area of the Surber samples (11 square feet= 1.02193 square meters). Long Falls, a reach in Indian River, had only 10 transects, since one invertebrate sample was lost in transport, thus density calculations were adjusted accordingly. Diversity was calculated as Shannon' entropy (diversity, H) in terms of x (Jost, 2006):

$$\text{Shannon's entropy (diversity, H)} = \{-\textstyle\sum_{i=1}^{s}(p_i \ln p_i)\}$$

Evenness was calculated as Shannon' entropy (diversity, H) divided by the taxa richness:

$$\text{Shannon's Evenness (EH)} = \{-\textstyle\sum_{i=1}^{s}(p_i \ln p_i)\} \;/\; \text{S}$$

Where *p* is the proportion of the total number of individuals comprised by taxa *i* and *s* is the taxa richness, or total number of unique taxa identified for a given reach.

Fish taxa lists were organized taxonomically, as in Bussing (1998). Fish and Shrimp metrics were based on consistent effort of fishing the whole reach with cast net, hook and line, overnight traps, and Surber sampler (some shrimp). Cast-netting at one reach in Kukra River (Papa Abrahán Creek) was not performed due to one team member not being present with the net. This may have biased fish abundances and richness estimates to be lower for that reach, although they were in the range of other sites.

Fish in the family Cichlidae (hereafter "Cichlids") abundance was chosen instead of overall fish abundance for a variety of reasons. Sampling effort for cichlids was more comprehensive than for most other taxa, because hook and line and cast net surveys during the day were quite effective for all five species of cichlids commonly captured. Most other common taxa, such as *Rhamdia*, *Eleotris*, and *Awaous*, were more elusive. Small characidae/*Astyanax* was always present, but abundances were not recorded due to the sheer number captured in most reaches. These species of Cichlids are also important for the local fishery, thus important to this study. Cichlids also represent a range of niches, so they are vulnerable to changes in habitat (Rican et al., 2016). Fish and shrimp metrics were not standardized by stream size because these comparisons were part of subsequent regression analyses.

T-tests and ANOVAs were carried out to assess differences in means of all seven invertebrate, fish, and shrimp metrics between forested and deforested stream reaches, and by watershed. For all comparisons, assumptions of normality and equal variance were tested using Shapiro-Wilk and Levene's tests. Invertebrate density and Cichlid abundance were ln() transformed in order to meet assumptions. All models were fitted using functions t.test, anova, and tukey.test from the package *stats* for R version 5.3.1 (R Core Team, 2016). Plots were made with package *ggplot2* for R version 3.1.1 (Wickham, 2016). Invertebrate diversity (H) was not included in reporting because it is weighted by evenness and richness, and evenness and taxa richness showed clear opposite trends in our data, thus diversity was non-significant and interpretation confusing for nearly all comparisons.

ANOVAs (with subsamples nested by reach ID) were used to compare standard length of fish captured in forested and deforested reaches and by watershed. These were run for each species that had at least 5 individuals captured in both forested and deforested reaches.

Multivariate analysis of the macroinvertebrate community

Non-metric multidimensional scaling (Faith, Minchin, & Belbin, 1987) of the macroinvertebrate community was carried out using the *metaMDS* function and plots were made with function *ordiplot* from the package *vegan* for R version 2.5.4 (Oksanen et al., 2013). For NMDS, PERMANOVA, SIMPER, and Indicator Analysis, rare taxa with ≤5 individuals in the whole study were excluded from analysis (Lorion & Kennedy, 2009a). Taxa were maintained at the lowest taxonomic level possible, and unknown genera were excluded unless they could only be identified to the same coarser taxonomic level at all sites (for example, Oligochaeta). Densities were Wisconsin-standardized and square-root transformed according to the default algorithm in *metaMDS*. The community matrix was generated from invertebrate densities at each reach by taxa, using Bray-Curtis dissimilarity distances. Iterations using 2, 3, and 4-axes were attempted, and the 3-axis solution selected because it yielded a sufficiently low stress 3-axis solution (stress <0.1, R2<0.9) (Figure 8 and 9).

PERMANOVA (Anderson, 2014) and SIMPER (Warton, Wright, & Wang, 2012) analyses were carried out in PAST Statistical software Version 3.20 (Hammer, Harper & Ryan, 2001). These tests used the Bray-Curtis dissimilarity distances of square root transformed densities. To test the significance of differences in community composition between stream reach groups, PERMANOVA tests were run with reaches grouped as forested and deforested and grouped by watershed. SIMPER was used to calculate the percent contribution of each taxa to the differences in community composition between these groups.

Indicator analysis was carried out using the $Indval_{ind}^{g}$ procedure (Dufrêne & Legendre, 1997; De Cáceres & Legendre, 2009) on square root transformed invertebrate densities, to determine which taxa were significantly associated with forested and deforested reaches, as well as with each watershed. Analysis was carried out with the *multipatt* function with *IndVal.g* in package *indicspecies* R version 1.7.6 (De Cáceres & Legendre, 2009).

Linear regression analyses

Individual linear regressions were run with each of the twenty habitat variables and four landscape variables as predictors for the seven selected taxa response variables. Linear regressions were also run with the Deforestation History Index for the catchment as a predictor with each of the twenty habitat variables as a response. Models were fit using the *Regression: Linear* and *Correlate*: *Bivariate* functions in SPSS Statistics version 26.0 (IBM SPSS, 2019).

For each individual model, care was taken to see whether residuals met assumptions of normality, linearity, and homogeneity of variance. SPSS *Linear Regression* function was used to generate plots of standardized predicted versus standardized residuals to visually test for linearity and homogeneity of variance, and SPSS *Descriptive Statistics: Explore* function was used to conduct Shapiro-Wilk tests for normality of residuals (IBM SPSS, 2019). Combinations that did not meet these assumptions were not included. In one case (Periphytic Macroalgae), it was apparent that the relationship was more logarithmic than linear, so a $\log_{10}$ regression was calculated in addition to the linear regression.

RESULTS

Differences in habitat condition

Considering the 20 habitat variables retained for analysis, variables that represent bank disturbance, water quality, instream habitat, and riparian condition metrics tended to differ significantly between forested and deforested reaches, while variables for stream size, hydrology, and substrate metrics did not differ, according to non-parametric Mann-Whitney U and Kruskal-Wallis testing (Table 1 and Appendix B, Figure B.2). Notably, conductivity was significantly higher at deforested sites (Diff.=22, p=0.008), while multiple instream habitat and riparian condition metrics were significant lower, including macrophytes % cover (Diff.= -1.36, p=0.0361), instream live trees and roots % cover (Diff.= -1.360, p=0.0229), large wood volume (Diff.= -76.165, p=0.009), mid-canopy plant % cover (Diff.= -48.29, p=0.000), and the riparian condition index (Diff.= -7.514, p=0.000). Other riparian and instream metrics followed a similar pattern. For example, proportion of stream bank eroded was higher, and small woody and leafy debris % cover was lower at deforested reaches (p=0.0726 and 0.0558, respectively). More recently deforested streams had periphytic macroalgae concentrations up to 27 % cover, whereas forested streams ranged from 5 to 15 % cover, hurricane impacted streams ranged from 4-20 % cover (though one naturally erosional forested reach had <1 %), and longer deforested streams only ranged from 0 to 4 % cover (though these patterns were not significant). Turbidity, temperature, and pH appeared highly dependent on recent weather conditions and were excluded from analysis.

Large wood volume and small woody and leafy debris were highest at reaches in the Indian watershed, where there was the greatest impact from Hurricane Otto in 2017 (Figure 1 and 3). Riparian impact from the hurricane was also evidenced through upper canopy large tree

% cover (above 15M, >0.3M diameter) and % shade (densiometer) metrics, as both were significantly lower at reaches in Indian watershed than reaches in Corn watershed (P=0.036 for both metrics). All reaches in both watersheds were >99% forested, but Corn watershed was not as impacted by the hurricane. One deforested site in the Pijibaye watershed (La Perra Creek) had abnormally high large wood and leafy/woody debris levels because it was being actively deforested and cut riparian trees were left in the river.

Table 1: Nonparametric test results by habitat variable for comparison of forested (N=8) and deforested (N=7) reaches (Mann-Whitney U) and by watershed (Kruskal-Wallis)—Forested (Indian, N=5 and Corn, N=3), Recently Deforested (Pijibaye, N=3), and Longer Deforested (Kukra, N=4). A positive difference implies a higher value at deforested reaches. Exact p-values were used unless signified by red text, which implies tied values—where a normal approximation was used. Pairwise comparisons (Mann-Whitney U) are represented by the first letter of the watershed name. Letters A and B represent significance groupings between Indian (I), Corn (C), Pijibaye (P), and Kukra (K) River watersheds, respectively. P-values for pairs ≤0.1 are listed but (α = 0.05) was used for lettering. Significant p-values are bolded (α = 0.05). See methods for calculations of variables (Most values based on a reach level mean of 11 transects and associated subsamples).

	Mann-Whitney U (Forested vs. Deforested)		**Kruskal-Wallis (By Watershed)**	
Habitat Variable	**Difference**	**p-Value**	**p-Value**	**Pairwise Significance (Mann-Whitney U)**
Stream Size				
Stream Size (Reach Volume)	-235.095	0.4634	0.8757	A
Hydrology and Substrate				
% Pool	0.026	0.8168	0.497	A
% Fines	0	1	0.379	A
% Sand	-0.010	0.9536	0.684	A
Geometric Mean Substrate Size	-9.228	0.7789	0.986	A
Embeddedness in Riffles and Rapids	5	0.3519	0.202	A (IC=0.072)
Standard Deviation Embeddedness	-0.335	0.9551	0.132	A (CK=0.05714)
Bank Disturbance				
Proportion of Stream Bank Eroded	0.177	0.0726	0.080	A (IC=0.072)
Water Quality				
Conductivity (µS)	22	**0.0321**	**0.008**	A,B,B,B (IC=**0.036**,IP=**0.036**,IK=**0.016**,CP=0.077)
Instream Habitat				
Periphytic Macroalgae % Cover	-3.190	0.1642	0.166	A (IK=0.085,CK=0.057)
Macrophytes % Cover	-1.36	**0.0361**	**0.0233**	A,AB,AB,B (IC=0.099,IK=**0.015**)
Instream Live Trees and Roots % Cover	-1.360	**0.0229**	0.108	AB,A,AB,B (CK=**0.050**)
Overhanging Vegetation % Cover	-2.471	0.1015	0.119	A,AB,AB,B (IK=**0.027**)
Small Woody and Leafy Debris % Cover	-8.726	0.0558	0.078	A,AB,AB,B (IK=**0.032**)

Table 1 (cont’d)

Large Wood Volume per 100 m	-76.165	**0.009**	0.051	A,AB,AB,B (IK=**0.032**, CK=0.057)
Habitat Complexity	-11.365	0.281	0.697	A
Riparian Condition				
Upper Canopy Large Trees % Cover	0.855	1	**0.0378**	A,B,AB,AB (IC=**0.036**,CP=0.10)
Mid-Canopy Plant % Cover	-48.29	**0.000**	**0.0197**	A,AB,B,B (IP=**0.036**,IK=**0.032**,CK=0.05714,CP=0.1)
% Shade (Densiometer)	-0.024	0.8617	0.0587	A,B,AB,AB (IC=**0.036**,CP=0.077)
Riparian Condition Index	-7.514	**0.000**	**0.009**	A,AB,B,B (IP=**0.036**,IK=**0.016**,CP=0.1,CK=0.057)

Deforestation history as a predictor of stream habitat

The deforestation history index for the catchment draining to each reach was a significant predictor of bank disturbance, instream habitat, and riparian condition metrics. Proportion of stream bank eroded increased as time-weighted % of catchment deforested increased ($R^2=0.392$, p=0.012) (Table 2, Figure 10). As the index value increased (more deforestation for a longer time), instream small woody and leafy debris % cover decreased ($R^2 =0.436$, p=0.007), large wood volume decreased ($R^2 =0.425$, p=0.008), and macrophytes % cover decreased ($R^2 =0.416$, p=0.009). Overhanging vegetation % cover, instream live trees and roots % cover, and periphytic macroalgae % cover also decreased (R^2 0.238, p=0.065; R^2 0.222, p=0.076; & $R^2 =0.210$, p=0.086, respectively).

Table 2: Single regression comparisons of the deforestation history index at the watershed scale (X) as predictors of habitat responses (Y). Pearson's R, R^2, and p are listed. Bolded items are significant ($p \leq 0.05$). Habitat variables are listed in order of significance. Although regressions were run on all 20 habitat predictors, only habitat predictors with a p-value ≤0.1 were included. Italicized items did not meet assumptions of normality of residuals (Shapiro-Wilk $p<0.05$).

Deforestation History Index (Catchment) Predictor				
Habitat Response	**Transformation**	**R**	**R^2**	**p**
Mid-Canopy Riparian Plant % Cover	ArcSIN	**-0.678**	**0.460**	**0.005**
Small Woody and Leafy Debris % Cover	ArcSIN	**-0.660**	**0.436**	**0.007**
Large Wood Volume per 100 m	ln	**-0.652**	**0.425**	**0.008**
Macrophytes % Cover	ArcSIN	**-0.645**	**0.416**	**0.009**
Proportion of Stream Bank Eroded	ArcSIN	**0.626**	**0.392**	**0.012**
Riparian Condition Index	ln	**-0.591**	**0.349**	**0.020**
Overhanging Vegetation % Cover	ArcSIN	*-0.488*	*0.238*	*0.065*
Instream Live Trees and Roots % Cover	ArcSIN	-0.471	0.222	0.076
Periphytic Macroalgae % Cover	ArcSIN	-0.458	0.210	0.086

Macroinvertebrates, fish, and shrimp summary

Among all sites, 107 distinct aquatic insect taxa and 15 other distinct invertebrate taxa were captured and identified. Of the insect taxa, 92 were identified to the genus and 15 to the subfamily or family. Other invertebrates varied more in taxonomic resolution (see Appendix A, Table A.1 for a full list with reach coordinates). Site level taxa richness ranged from 37 at El Limón in the Kukra watershed, to 71 at El Coco in the Pijibaye watershed. Three species of *Macrobrachium* shrimp and at least two species of *Atya* shrimp were captured, as well as at least one species of freshwater crab (Pseudothelphusidae). Twenty distinct fish taxa were captured in our study reaches, and 11 more in other surveys. All but Characidae/*Astyanax* spp. and *Rhamdia* spp. were identified to species (see Appendix A, Table A.2 for a full list with reach coordinates). All insect, other invertebrate, and crustacean specimens are preserved in the University of Costa Rica Zoological Museum in the School of Biology (Contact: M Springer), and photos of fish are with author JT Betts.

Differences in macroinvertebrate, shrimp, and fish community response metrics

In comparing mean taxa richness, density, BMWP score, and Shannon's evenness of the macroinvertebrate community, only evenness differed significantly between forested and deforested stream reaches, being lower at forested reaches (df=10.32, T=2.25, p=0.047). But there were significant differences for each metric when compared by watershed (Table 3, Figure 5, $p \leq 0.05$). Pairwise comparisons showed that longer deforested sites (Kukra watershed, N=4) tended to have lower taxa richness, density, and BMWP score, and a higher evenness than forested sites (Indian watershed, N=5 and Corn watershed, N=3) and more recently deforested sites (Pijibaye watershed, N=3) (Table 3, Figure 5). Reaches in Corn watershed (forested) had by far the lowest evenness, as there were particularly high densities (dominance) of two subfamilies of Chironomidae, and relatively low abundances of rarer taxa. Taxa richness, BMWP score, and density (LN) were negatively correlated with evenness ($R^2=0.174$, p=0.122; $R^2=0.347$, p=0.021;

and R^2=0.281, p=0.042, respectively) (see Appendix B, Table B.1 for a list of correlations and p values between taxa response variables).

Considering mean fish taxa richness, Cichlid fish abundance, and shrimp abundance, only shrimp abundance differed significantly between forested and deforested sites, being higher at forested sites (df=12.00, T=-2.64, p=0.022). Cichlid abundance differed significantly when compared by watershed in separate ANOVA tests by metric (df=3, F=5.22, p=0.017). Tukey pairwise comparisons showed that longer deforested sites (Kukra, N=4) tended to have lower fish taxa richness, cichlid abundance, and shrimp abundance than forested (Indian, N=5 and Corn, N=3) and more recently deforested sites (Pijibaye, N=3) (see Table 3 and Figure 6), although these comparisons were only significant for cichlid abundance between Indian and Kukra (p=0.046) and Pijibaye and Kukra (p=0.020) watersheds.

Table 3: T-test and ANOVA and Tukey post-hoc pairwise comparisons for macroinvertebrate community summary statistics comparing means of deforested (N=7) and forested reaches (N=8), and means for all four watersheds—forested (Indian, N=5 and Corn, N=3), recently deforested (Pijibaye, N=3), and longer deforested (Kukra, N=4). Positive T-value implies higher value at deforested reaches. Significant p-values bolded (α = 0.05). Macroinvertebrate community statistics based on sum of eleven Surber samples (0.092903 M^2). Tukey post-hoc tests were run on pairwise comparisons of summary statistics for each watershed pair. Letters represent significance groupings between Indian, Corn, Pijibaye, and Kukra River watersheds, respectively. P-values for pairs ≤0.1 are listed but (α = 0.05) was used for lettering. Pairwise comparisons represented by the first letter of the watershed name.

	T-Tests Forested vs. Deforested			**ANOVA by Watershed**			
	df	**T**	**p**	**df**	**F**	**p**	**Pairwise Significance (Tukey)**
Macroinvertebrate Community							
Invert. Taxa Richness	10.03	-1.37	0.20	3	4.27	**0.031**	AB,AB,A,B (IK=0.065,CK=0.099,PK=0.043)
Invert. Density (ln)	7.82	-1.17	0.28	3	6.03	**0.011**	AB,A,A,B (IC=0.086,CK=0.024,PK=0.016)
BMWP Score	12.32	-1.89	0.083	3	4.17	**0.034**	AB,A,AB,B (CK=0.023)
Invert. Evenness (EH)	10.32	2.25	**0.047**	3	7.10	**0.006**	A,B,AB,A (IC=0.037,CP=0.076,CK=0.0038)
Fish and Shrimp Community							
Fish Taxa Richness	12.15	-1.03	0.321	3	1.09	0.39	A
Cichlid Abundance (ln)	9.06	-1.24	0.248	3	5.22	**0.017**	A,AB,A,B (IK=0.046,CK=0.080,PK=0.020)
Shrimp Abundance	12.00	-2.64	**0.022**	3	3.06	0.074	A (IK=0.097,CK=0.098)

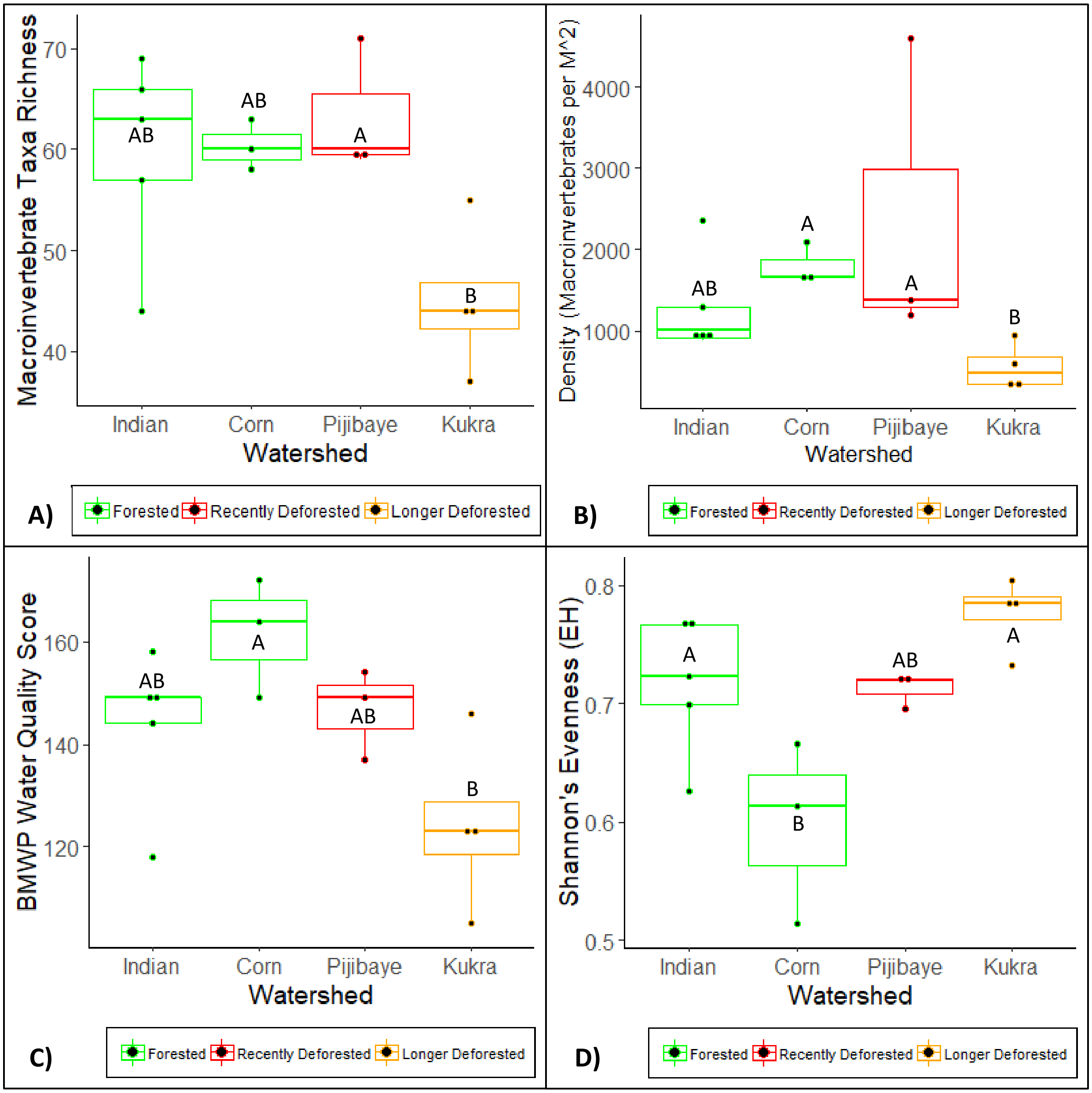


Figure 5: Macroinvertebrate community summary statistics for two forested watersheds and a recently and less recently deforested watershed. A) Macroinvertebrate Taxa Richness (mostly genus level). **B)** Macroinvertebrates per m^2. Statistics run on ln of density, to meet normality assumptions. Raw density is displayed. **C)** Biological Monitoring Working Party water quality score adapted for Costa Rica. Represents taxa richness, weighted by family sensitivity to pollution. **D)** Shannon's Evenness (EH). Reach values represented by points. Community statistics based on sum of eleven Surber samples (0.092903 m^2) subsamples. T-tests were carried out lumping forested and deforested reaches. ANOVA and Tukey Pairwise tests were run between each watershed—letters represent significance groupings of watersheds ($\alpha = 0.05$). No letters implies no significance.

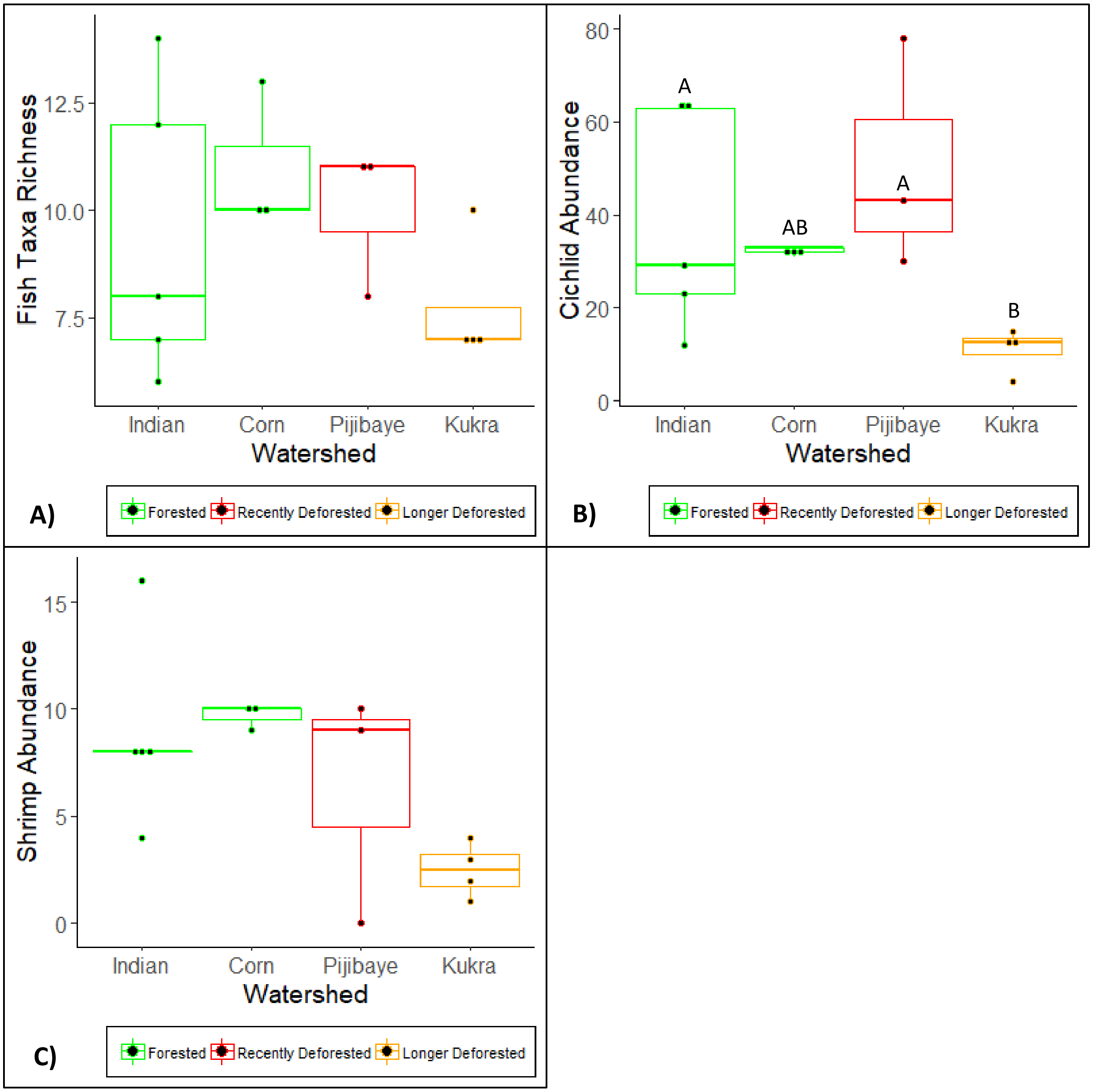


Figure 6: Fish and shrimp community summary statistics for two forested watersheds and a recently and less recently deforested watershed. A) Number of fish taxa caught in each reach. **B)** Total number of fishes in the family Cichlidae caught in each reach. Statistics run on ln of abundance, but raw abundance is displayed. **C)** Total number of shrimp (genera *Atya* and *Macrobrachium*) caught in each reach. When lumped by forested and deforested, forested sites had significantly more shrimp than deforested sites (T=-2.64, p=0.022). Reach values represented by points. Community statistics based on consistent effort of fishing the whole reach with cast net, hook and line, overnight traps, and Surber sampler. T-tests were carried out comparing forested to deforested reaches. ANOVA and Tukey Pairwise tests were run between each watershed—letters represent significance groupings of watersheds ($\alpha = 0.05$). No letters implies no significance.

Differences in fish length

The four common fish species that are important for local subsistence tended to be significantly larger at forested sites than deforested sites. These species are relatively larger and can easily be caught by hook or spear. ANOVAs with subsamples by reach showed significantly higher standard length at forested stream reaches than deforested reaches for *Brycon guatemalensis* (df=1, F=2.096, p=0.025), *Cribroheros alfari* (df=1, F=5.923, p=0.016), *Parachromis dovii* (df=1, F=63.029, p=0.000), and *Tomocichla tuba* (df=1, F=19.364, p=0.000) (Table 4, Figure 7). Other locally important subsistence species such as *Gobiomorus dormitor* and *Rhamdia* sp. were not present in high enough abundances at any reach to detect trends in size. These trends were not present for other species, most of which were only caught on very small hooks (Size 14) or by cast net in our surveys (these fishing techniques are not utilized in most communities). *Roeboides bouchelli* and *Amatitlania nigrofasciata* were notably more common at deforested reaches, while *Amatitlania septemfasciata* was abundant at forested reaches and absent in deforested reaches. Uncommon species *Bramocharax bransfordii*, *Neetroplus nematopus*, *Eleotris pisonis*, *Sicydium altum*, *Phallichthys amates*, and *Priapichthys annectens* were only found in forested reaches. No species were completely unique to deforested reaches (Table 4, Figure 7).

Table 4: ANOVA results for fish standard lengths by species comparing two forested, a recently deforested, and longer deforested watershed**.** Community statistics based on consistent effort of fishing the whole reach with cast net, hook and line, and overnight traps. ANOVA on fish length for each species (with individual fish lengths as subsamples for each reach). Comparisons between forested and deforested reaches and by watershed. Tukey Pairwise tests were run between each watershed are visualized by letters in Figure 7. Only fish that had at least 5 individuals in both forested and deforested sites were included in statistical analysis. Mean standard length and sum of captured individuals from all reaches within each watershed is included for all species. *Astyanax* spp. were highly abundant in all but one reach, so counting and measuring was limited to 20 individuals per reach, thus it is not included here. I=Indian, C=Corn, P=Pijibaye, and K=Kukra. n.d. signifies that the fish were not measured, although individuals were recorded in the watershed. P signifies "Present", where number captured was not recorded.

		Mean Length				**# Captured**				**ANOVA (Length) Forested vs. Deforested**			**ANOVA (Length) by Watershed**		
Family	**Taxa**	**I**	**C**	**P**	**K**	**I**	**C**	**P**	**K**	**df**	**F**	**p**	**df**	**F**	**p**
Characidae	*Astyanax* spp.	NA (Multiple Species)				NA				-	-	-	-	-	-
	Bramocharax bransfordii	-	6.2	-	-	0	1	0	0	-	-	-	-	-	-
	Brycon guatemalensis	14.4	10.4	9.9	8.5	43	2	10	1	1	2.096	**0.025**	3	2.096	0.113
	Roeboides bouchelli	6.7	-	6.5	6.2	4	0	41	12	-	-	-	-	-	-
Heptapteridae	*Rhamdia* sp.	20.6	16.6	-	12.2	2	2	0	10	-	-	-	-	-	-
Poeciliidae	*Alfaro cultratus*	n.d.	5.6	4.1	-	P	1	1	0	-	-	-	-	-	-
	Phallichthys amates	n.d.	-	-	-	P	0	0	0	-	-	-	-	-	-
	Poecilia gillii	5.8	6.5	5.9	7.2	P	29	54	6	1	2.169	0.145	3	2.361	0.077
	Priapichthys annectens	4.4	-	-	-	P	0	0	0	-	-	-	-	-	-
Mugilidae	*Agonostomus monticola*	7.2	8.7	8.3	8.5	25	6	21	10	1	3.389	0.072	3	2.028	0.122
Cichlidae	*Amatitlania nigrofasciata*	5.0	5.9	5.5	5.0	8	3	66	18	1	0.249	0.619	3	2.031	0.116
	Amatitlania septemfasciata	5.4	7.4	-	-	40	32	0	0	-	-	-	-	-	-
	Cribroheros alfari	6.1	9.7	6.4	7.3	86	44	53	4	1	5.923	**0.016**	3	31.874	**<0.001**
	Neetroplus nematopus	6.3	-	-	-	11	0	0	0	-	-	-	-	-	-
	Parachromis dovii	14.6	10.9	6.7	8.6	31	18	25	6	1	63.029	**<0.001**	3	25.930	**<0.001**
	Tomocichla tuba	11.2	-	7.2	7.3	17	0	7	17	1	19.364	**<0.001**	3	9.687	**<0.001**
Gobiidae	*Awaous banana*	8.5	n.d.	10.6	18.5	1	2	2	1	-	-	-	-	-	-
	Sicydium altum	9.3	-	-	-	2	0	0	0	-	-	-	-	-	-

Table 4 (cont'd)

Eleotridae	*Eleotris pisonis*	-	12.7	-	-	0	1	0	0	-	-	-	-	-	-
	Gobiomorus dormitor	16.0	14.2	17.0	11.2	3	6	5	2	1	0.098	0.765	3	1.444	0.320

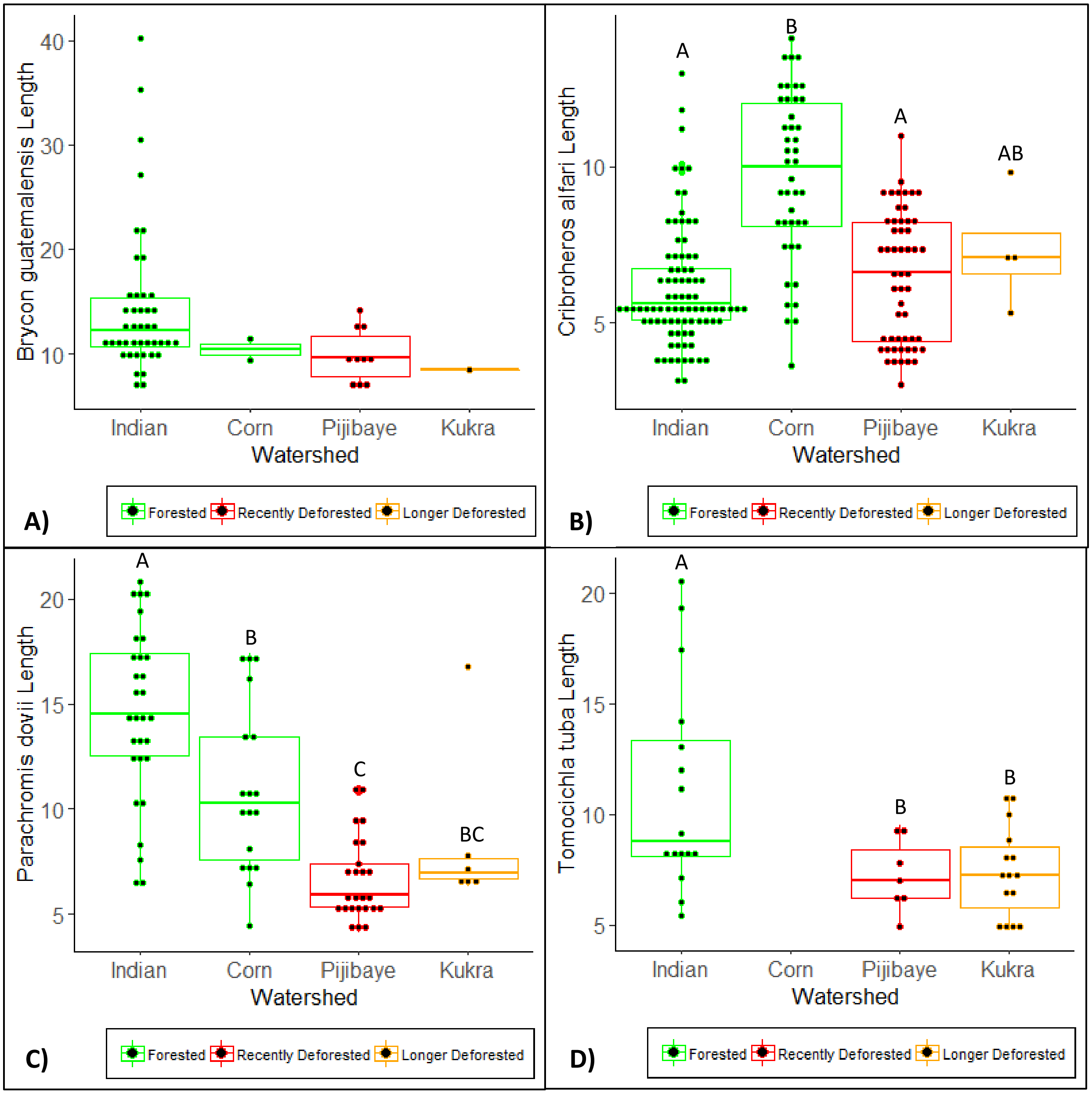


Figure 7: Fish standard lengths by species for two forested, and a recently deforested and less recently deforested watershed. The four species that are important to the local fishery and relatively high abundance in our study are highlighted: **A)** *Brycon guatemalensis* **B)** *Cribroheros alfari* **C)** *Parachromis dovii* **D)** *Tomocichla tuba*. For all four species, deforested reaches tend towards lower average lengths. When *Brycon guatemalensis* was lumped by forested and deforested, forested sites were significantly higher than deforested sites (F=2.096, p=0.025). Individual fish lengths represented by points. Community statistics based on consistent effort of fishing the whole reach with cast net, hook and line, and overnight traps (see methods). ANOVAs (with reaches nested) were carried out, categorized by forested and deforested and by watershed, with Tukey pairwise tests run between each watershed—letters represent significance groupings of watersheds (α = 0.05) (Table 4).

Changes in macroinvertebrate community structure

Non-metric multidimensional scaling of the macroinvertebrate community matrix (Wisconsin standardized and square root transformed densities) using a Bray-Curtis dissimilarity distance yielded a low stress 3 axis solution (stress <0.0945, R^2=0.929) (Figure 8). Ordinations of axis 1 and 2, 1 and 3, and 2 and 3 all showed a similar pattern of sites displayed, so axes 1 and 2 were visualized (Figure 9) (see Appendix B, Figure B.1 for other axes displays). PERMANOVA analysis of the community matrix showed that stream reaches cluster significantly by forested (Indian, N=5 and Corn, N=3) and deforested (Pijibaye, N=3 and Kukra, N=4) groupings (F=1.88, p=0.0317). Reaches clustered with much higher significance when analyzed by watershed (F=2.445, p=0.0001), which suggests that deforestation history is an important contributor to structuring the macroinvertebrate community. Forested reaches cluster together on both axes, with the exception that Guinea Creek (GU), a relatively erosional site in Indian watershed, is an outlier on axis 1. Recently deforested reaches (Pijibaye) cluster with forested reaches (Indian and Corn) on axis 1, but with longer deforested reaches (Kukra) on axis 2. When the deforestation index was fit as a gradient on the NMDS plot, it appears that both axis 1 and 2 capture the differences in the macroinvertebrate community that could be attributed to impacts from deforestation history (See Figure 9.C.) The placement of taxa on these plots aligns well with indicator analysis results described below and could be useful to help determine associations of taxa with streams degraded by deforestation.

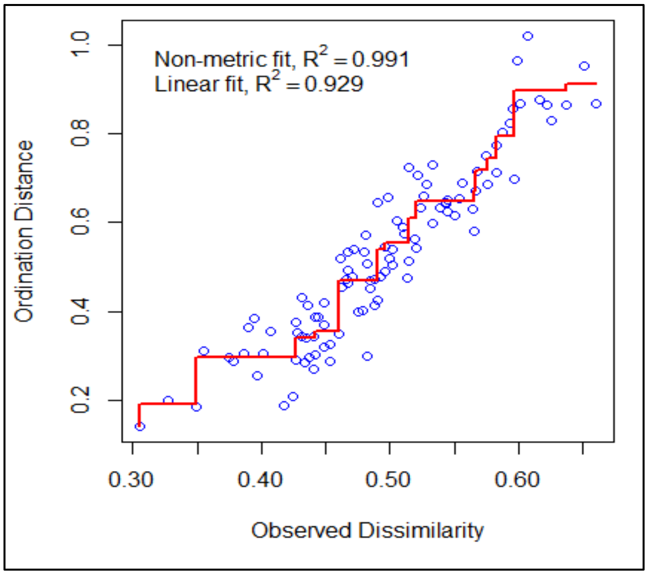


Figure 8: Stress plot for non-metric multidimensional scaling analysis of macroinvertebrate community matrix (taxa densities by reach). 3 axis solution used; stress level is 0.0945. With stress <0.1 and linear fit R^2 >0.9, the model is an excellent fit.

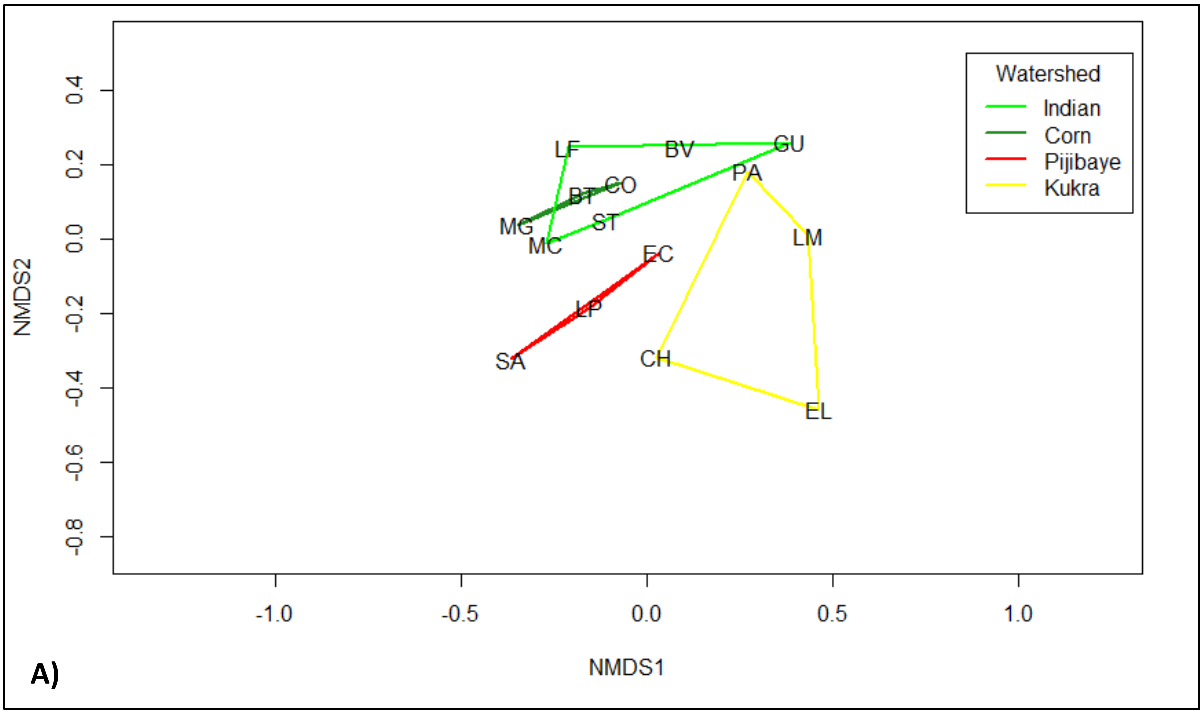
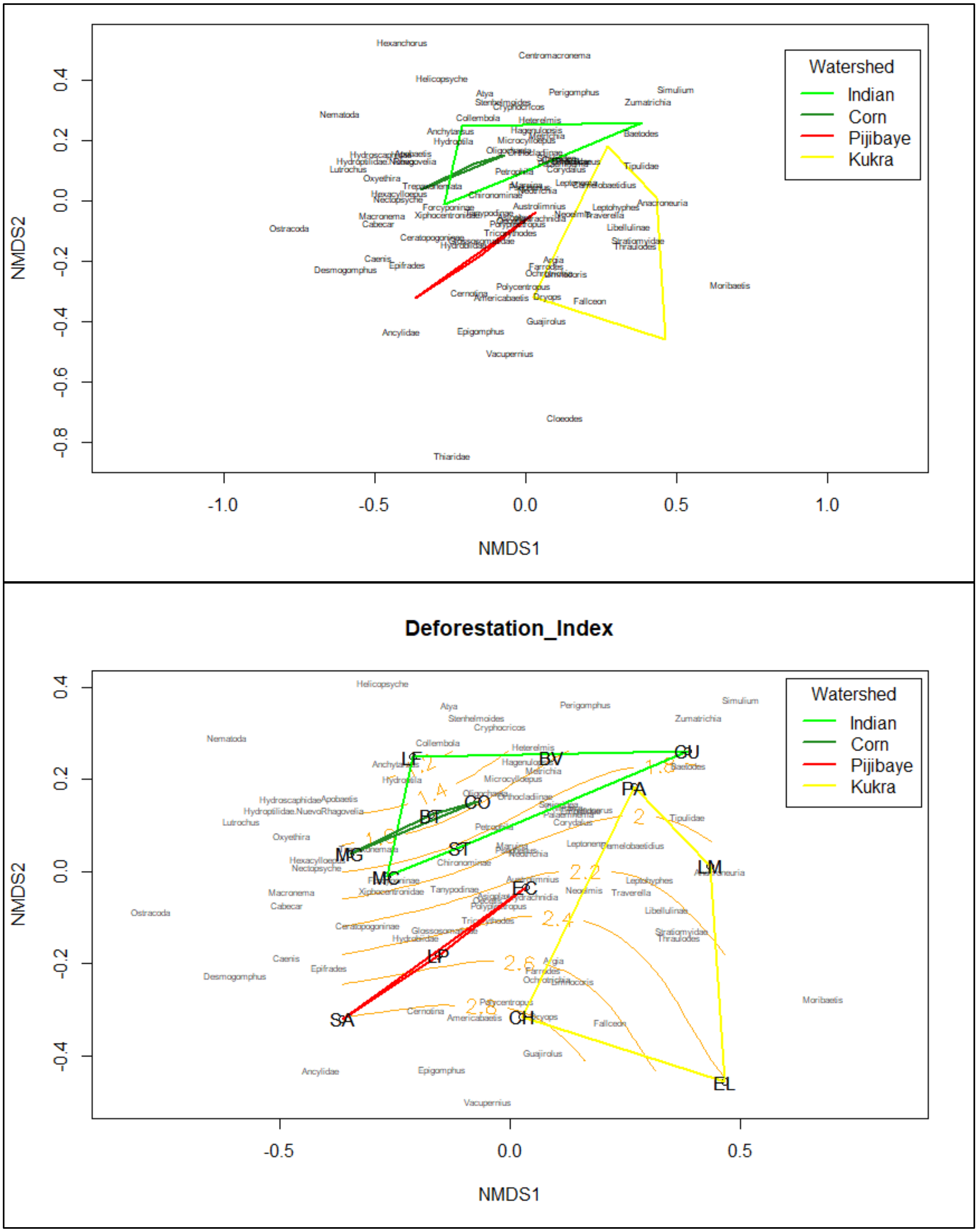


Figure 9: Non-metric multidimensional scaling ordination plots of macroinvertebrate community matrix (taxa densities by reach). **A)** Ordination plot with reaches visualized. Axis 1 and 2 represented (plots with axis three group similarly). Polygons show watershed groupings. According to PERMANOVA, reaches group significantly as forested (Indian, N=5 and Corn, N=3) and deforested (Pijibaye, N=3 and Kukra, N=4) (F=1.88, p=0.0317). Reaches group with higher significance by watershed (F=2.445, p=0.0001).

Figure 9 (cont'd)



B) Ordination plot with taxa visualized. **C)** Ordination plots A and B with the Deforestation History Index gradient visualized. Plot C could be used to infer taxa that are sensitive to the impacts of deforestation over time, aligning results to indicator analysis or SIMPER.

Taxa-specific responses

From the indicator analysis, four mayfly genera (Order Ephemeroptera) in two families were significant indicators ($\alpha<0.1$) of deforested conditions, while eight taxa from eight distinct families were indicators ($\alpha<0.1$) of forested conditions (Table 5). When broken down by watershed, only *Moribaetis* remained as a significant indicator of longer deforested conditions (Kukra), while recently deforested (Pijibaye), and each forested (Indian and Corn) watershed had a diverse assemblage of indicator taxa. The lack of indicators for Kukra can be attributed to depressed abundances of all taxa in these stream reaches.

The NMDS plot (Figure 9.B.) displays strong trends. Taxa that indicate deforested reaches tend to be located positive on axis 1 and negative on axis 2 (towards the bottom right), and taxa that indicate forested reaches tend to be located negative on axis 1 and positive on axis 2 (towards the top left). SIMPER showed some similar results to indicator analysis but was more heavily weighted by density. Therefore SIMPER was less clear to interpret than indicator analysis. For example, Chironominae had the highest percent contribution to the differences between watersheds (6.425 %) and does show up as a significant indicator for Corn watershed. The next three highest contributions according to SIMPER—*Microcylloepus*, Orthocladiinae, and *Smicridea*—account for 4.239 %, 4.125 %, and 3.116 % of the difference between watersheds, but do not show up as significant indicators of any watershed in the indicator analysis.

Table 5: Indicator analysis and SIMPER results for key taxa (mostly genus level), showing taxa that were identified by Indicator Analysis as indicators ($p<0.1$) for forested and deforested reaches, as well as by watershed. Significant p-values bolded ($\alpha = 0.05$). For these taxa, SIMPER percent contribution to the Bray-Curtis dissimilarity between categories is also recorded. Percent contributions are heavily weighted by dominant taxa. All analyses were based on the square-root of reach level densities of macroinvertebrates, based on sum of eleven Surber samples (0.092903 m^2). Mean densities (individuals per m^2) are also recorded for each category. Low BMWP values are "tolerant" taxa and high values are "sensitive" taxa. Functional Feeding Group designations based on family level assignments from Ramírez and Gutiérrez-Fonseca (2014).

Indication Category	**Taxa**	**BMWP Score**	**Functional Feeding Group**	**Indicator Value**	**Indicator Sig. (p)**	**SIMPER % Contrib.**	**Mean Invertebrate Density (per m^2)**			
							For.	**Def.**		
Forested	*Cryphocricos*	4	Pr	0.846	**0.017**	1.678	15.9	4.47	-	-
	Oligochaeta	1	NA	0.844	**0.019**	3.410	92.2	17.6	-	-
	Palaemnema	7	Pr	0.780	**0.023**	1.547	30.6	13.6	-	-
	Leucotrichini Gen. undet.	6	Generally Pc-Hb, Sc, CG	0.791	**0.029**	1.289	12.6	0	-	-
	Lutrochus	7	Sh-Dt, Hb	0.738	0.053	0.576	1.5	0.14	-	-
	Nematoda	1	NA	0.768	0.073	1.981	33.5	0.28	-	-
	Helicopsyche	5	Sc	0.707	0.077	0.555	1.76	0	-	-
Deforested	*Moribaetis*	5	CG	0.845	**0.008**	0.782	0	2.8	-	-
	Fallceon	5	CG	0.805	0.051	0.857	2.35	6.15	-	-
	Vacupernius	5	Generally CG, few Ft	0.776	0.079	2.190	1.83	30.1	-	-
	Leptohyphes	5	Generally CG, few Ft	0.815	0.093	2.803	22.5	82.2	-	-
							I	**C**	**P**	**K**
Indian	Leucotrichini Gen undet.	6	Generally Pc-Hb, Sc, CG	0.830	**0.034**	1.157	19.8	0.652	0	0
	Camelobaetidius	5	CG	0.645	**0.041**	0.895	12.3	1.96	3.26	3.42
	Hexacylloepus	5	Generally CG, Sc, Sh-Hb	0.707	0.068	0.578	1.98	0	1.63	0
	Metrichia	6	Generally Pc-Hb, Sc, CG	0.676	0.086	1.477	18.1	3.26	4.89	6.12
Corn	*Atya*	NA	Ft	0.942	**0.008**	0.550	0	4.24	0	0.245
	Chironominae	2	Generally CG, Ft	0.643	**0.013**	6.425	141	730	353	54.6
	Macronema	5	Generally Ft. Some Pr & Sc	0.755	**0.034**	1.96	10.4	3.26	0.245	1.96
	Palaemnema	7	Pr	0.586	**0.048**	1.367	26.6	37.2	10.8	15.7
	Ceratopogoninae	NA	Generally Pr, few CG	0.684	0.070	1.553	2.07	23.8	14	1.22
	Collembola	NA	NA	0.672	0.089	0.338	0.196	1.3	0	0.245

Table 5 (cont'd)

Pijibaye	*Tricorythodes*	5	Generally CG, few Ft	0.681	**0.001**	3.013	44.5	39.1	211	16.4
	Argia	4	Pr	0.693	**0.004**	1.254	4.54	8.48	46	4.65
	Limnocoris	4	Pr	0.789	**0.006**	1.385	1.96	0.326	25.1	4.16
	Ancylidae	NA	Sc	0.859	**0.007**	1.035	1.17	0.326	14	0.979
	Vacupernius	5	Generally CG, few Ft	0.851	**0.014**	2.204	2.94	0	63.3	5.14
	Oecetis	8	Pr, Facultative Sh-Hb.	0.693	**0.022**	0.852	3.13	0.652	8.48	1.71
	Tanypodinae	2	Pr	0.650	**0.036**	1.164	5.42	10.4	22.5	0.979
	Epigomphus	7	Pr	0.709	0.057	0.587	0.822	0.979	3.59	0.489
	Psephenus	7	Sc	0.594	0.063	2.555	53.3	78.3	116	15.7
	Petrophila	5	Sc, Facultative Sh-Hb	0.640	0.075	2.041	35.8	8.81	52.8	6.36
	Leptohyphes	5	Generally CG, few Ft	0.666	0.080	2.755	33.1	4.89	133	44
Kukra	*Moribaetis*	5	CG	0.768	**0.046**	0.670	0	0	3.26	2.45

Deforestation history and habitat as predictors of the stream community

The deforestation history index for the catchment draining to each reach was the best predictor of all invertebrate taxa responses except evenness, when compared to 3 other landscape-scale and 20 habitat-level predictors in a series of linear regressions (See Table 6 & Figure 11 for R, R^2, and p values). As the index value increased, invertebrate taxa richness, BMWP score, and invertebrate density (ln transformed) all decreased significantly ($R^2=0.484$, $p=0.004$; $R^2=0.445$, $p=0.007$; & $R^2=0.393$, $p=0.012$, respectively). In the case of macroinvertebrate community evenness the relationship was the opposite—as the index increased, evenness increased. The deforestation index for the 100 m buffer around the reach was the strongest landscape predictor (+) ($R^2=0.323$, $p=0.027$), followed by % Forest Cover in the catchment (-) ($R^2=0.272$, $p=0.046$), and the deforestation history index for the catchment (+) ($R^2=0.258$, $p=0.053$).

Invertebrate taxa richness was also significantly predicted by % fines (+) ($R^2=0.335$, $p=0.024$), small woody and leafy debris % cover (+) ($R^2=0.303$, $p=0.034$), and large wood volume (+) ($R^2=0.291$, $p=0.038$) (Table 6). BMWP score was significantly predicted by embeddedness in riffles and rapids (-) ($R^2=0.428$, $p=0.008$), the riparian condition index (+) ($R^2=0.365$, $p=0.017$), proportion of stream bank eroded (-) ($R^2=0.321$, $p=0.027$), periphytic macroalgae % cover (+) ($R^2=0.278$, $p=0.043$), and habitat complexity (+) ($R^2=0.265$, $p=0.049$) (Table 6). Density had no significant habitat predictors. Evenness was significantly predicted by large wood volume (-) ($R^2=0.265$, $p=0.050$). The residuals of linear regressions with periphytic macroalgae % cover as a predictor were clearly more logarithmic than linear, and this variable became a strong positive predictor of invertebrate taxa richness, BMWP score, and invertebrate density (ln transformed) when a logarithmic fit to the regression was employed ($R^2>0.4$, $p<0.01$). Other predictors ($p<0.1$) are listed in Table 6.

The deforestation history index for the catchment draining to each reach and for the 100 m buffer around each reach were significant negative predictors of cichlid abundance (ln transformed) (Catchment: $R^2=0.430$, $p=0.008$; Buffer: $R^2=0.523$, $p=0.002$) and shrimp abundance (Catchment: $R^2=0.342$, $p=0.022$; Buffer: $R^2=0.303$, $p=0.034$). The deforestation history index for the catchment was also a negative predictor for fish taxa richness, though not significant ($R^2=0.199$, $p=0.095$). These landscape scale metrics better predicted fish and shrimp response metrics than nearly all 20 habitat predictors, when compared in a series of linear regressions (Table 7 & Figure 11). Fish taxa richness was predicted by the standard deviation of embeddedness (-) ($R^2=0.472$, $p=0.005$). Cichlid abundance had no significant habitat predictors. Shrimp abundance was significantly predicted by embeddedness in riffles and rapids (-) ($R^2=0.483$, $p=0.004$), standard deviation of embeddedness (-) ($R^2=0.280$, $p=0.042$), and mid-canopy riparian plant % cover (+) ($R^2=0.264$, $p=0.050$). Other predictors ($p<0.1$) are listed in Table 7.

Table 6: Single regression comparisons of landscape and habitat variables (X) as predictors of macroinvertebrate taxa responses (Y). Pearson's R, R^2, and p are listed. Bolded items are significant ($p \leq 0.05$). Landscape parameters are shown above and habitat parameters below, in order of significance. Although regressions were run on all 20 habitat predictors, only habitat predictors with a p-value ≤ 0.1 were included. All regressions were linear, except for periphytic macroalgae, which was a better fit under a logarithmic relationship. Italicized items did not meet assumptions of normality of residuals or were influenced by an outlier (Shapiro-Wilk $p<0.05$). The deforestation history index for each study catchment was the best predictor at the landscape scale (except for with evenness, where the index at the buffer scale was better). It also predicted better than all but one of the 20 other habitat variables for each macroinvertebrate taxa summary response.

	Invert. Taxa Richness		**BMWP Score**		**Density (ln)**		**Evenness (EH)**	
				Landscape Predictors				
R	Deforestation History Index (Catchment)	**-0.696**	Deforestation History Index (Catchment)	**-0.667**	Deforestation History Index (Catchment)	**-0.627**	Deforestation History Index (100 m Buffer)	**0.568**
R^2		**0.484**		**0.445**		**0.393**		**0.323**
P		**0.004**		**0.007**		**0.012**		**0.027**
R	% Forest Cover Catchment	**0.544**	% Forest Cover Catchment	**0.56**	% Forest Cover Catchment	0.438	% Forest Cover Catchment	***-0.522***
R^2		**0.296**		**0.314**		0.191		***0.272***
P		**0.036**		**0.030**		0.103		***0.046***
R	Deforestation History Index (100 m Buffer)	**-0.517**	Deforestation History Index (100 m Buffer)	-0.478	Deforestation History Index (100 m Buffer)	-0.422	Deforestation History Index (Catchment)	0.508
R^2		**0.267**		0.229		0.178		0.258
P		**0.048**		0.071		0.118		0.053
R	% Forest Cover 100 m Buffer	0.267	% Forest Cover 100 m Buffer	0.243	% Forest Cover 100 m Buffer	0.128	% Forest Cover 100 m Buffer	-0.394
R^2		0.071		0.059		0.016		0.155
P		0.337		0.383		0.649		0.146
				Habitat Predictors				
R	% Fines	**0.579**	Embeddedness in Riffles and Rapids	**-0.654**	Periphytic Macroalgae % Cover	0.510	Large Wood Per Transect Per 100 m	***-0.515***
R^2		**0.335**		**0.428**		0.260		***0.265***
P		**0.024**		**0.008**		0.052		***0.050***
R	Small Woody & Leafy Debris % Cover	**0.55**	Riparian Condition Index	**0.604**	Embeddedness in Riffles and Rapids	-0.486	Small Woody & Leafy Debris % Cover	*-0.481*
R^2		**0.303**		**0.365**		0.236		*0.231*
P		**0.034**		**0.017**		0.066		*0.070*
R	Large Wood Volume Per 100m	**0.539**	Proportion of Stream Bank Eroded	**-0.567**	% Sand	-0.458		
R^2		**0.291**		**0.321**		0.210		
P		**0.038**		**0.027**		0.086		
R	Instream Live Trees and Roots % Cover	0.486	Periphytic Macroalgae % Cover	**0.527**				
R^2		0.236		**0.278**				
P		0.066		**0.043**				
R	Proportion of Stream Bank Eroded	-0.470	Habitat Complexity	**0.515**				
R^2		0.221		**0.265**				
P		0.077		**0.049**				

Table 6 (cont'd)

R			Small Woody & Leafy Debris % Cover	0.506				
R^2				0.256				
P				0.054				
R			Large Wood Volume Per 100 m	0.460				
R^2				0.212				
P				0.084				
R	Periphytic Macroalgae % Cover (Logarithmic)	**0.659**	Periphytic Macroalgae % Cover (Logarithmic)	**0.750**	Periphytic Macroalgae % Cover (Logarithmic)	**0.697**	Periphytic Macroalgae % Cover (Logarithmic)	-0.497
R^2		**0.434**		**0.563**		**0.486**		0.247
P		**0.008**		**0.001**		**0.004**		0.059

Table 7: Single regression comparisons of landscape and habitat variables (X) as predictors of fish and shrimp responses (Y). Pearson’s R, R^2, and p are listed. Bolded items are significant ($p \leq 0.05$). Landscape parameters are shown above and habitat parameters below, in order of significance. Although regressions were run on all 20 habitat predictors, only habitat predictors with a p-value ≤0.1 were included. All regressions were linear, except for periphytic macroalgae for shrimp abundance, which was a better fit under a logarithmic relationship. Italicized items did not meet assumptions of normality of residuals or were influenced by an outlier (Shapiro-Wilk $p<0.05$). The deforestation history index for each study catchment was the best predictor at the landscape scale (except for with evenness, where the index at the buffer scale was better). It also predicted better than all but one of the 20 other habitat variables for each macroinvertebrate taxa summary response.

	Fish Taxa Richness		Cichlid Abundance (ln)		Shrimp Abundance	
			Landscape Predictors			
R	Deforestation History Index (Catchment)	-0.446	Deforestation History Index (Buffer)	**-0.723**	Deforestation History Index (Catchment)	**-0.585**
R^2		0.199		**0.523**		**0.342**
P		0.095		**0.002**		**0.022**
R	% Forest Cover Catchment	0.416	Deforestation History Index (Catchment)	**-0.656**	Deforestation History Index (Buffer)	**-0.55**
R^2		0.173		**0.430**		**0.303**
P		0.123		**0.008**		**0.034**
R	Deforestation History Index (Buffer)	-0.371	% Forest Cover Catchment	**0.567**	% Forest Cover Catchment	0.502
R^2		0.138		**0.321**		0.252
P		0.173		**0.027**		0.057
R	% Forest Cover Buffer	0.187	% Forest Cover Buffer	*0.284*	% Forest Cover Buffer	0.316
R^2		0.035		*0.080*		0.100
P		0.504		*0.305*		0.252
			Habitat Predictors			
R	Standard Deviation of Embeddedness	**-0.687**	Periphytic Macroalgae % Cover (Linear)	0.497	Embeddedness in Riffles and Rapids	**-0.695**
R^2		**0.472**		0.247		**0.483**
P		**0.005**		0.060		**0.004**
R	Stream Size (Reach Volume)	0.497	% Shade (Densiometer)	-0.491	Standard Deviation of Embeddedness	**-0.529**
R^2		0.247		0.241		**0.280**
P		0.060		0.063		**0.042**
R					Mid-Canopy Riparian Plant % Cover	**0.514**
R^2						**0.264**
P						**0.050**
R					Riparian Condition Index	0.496
R^2						0.246
P						0.060
R					Proportion of Stream Bank Eroded	-0.478
R^2						0.228
P						0.072

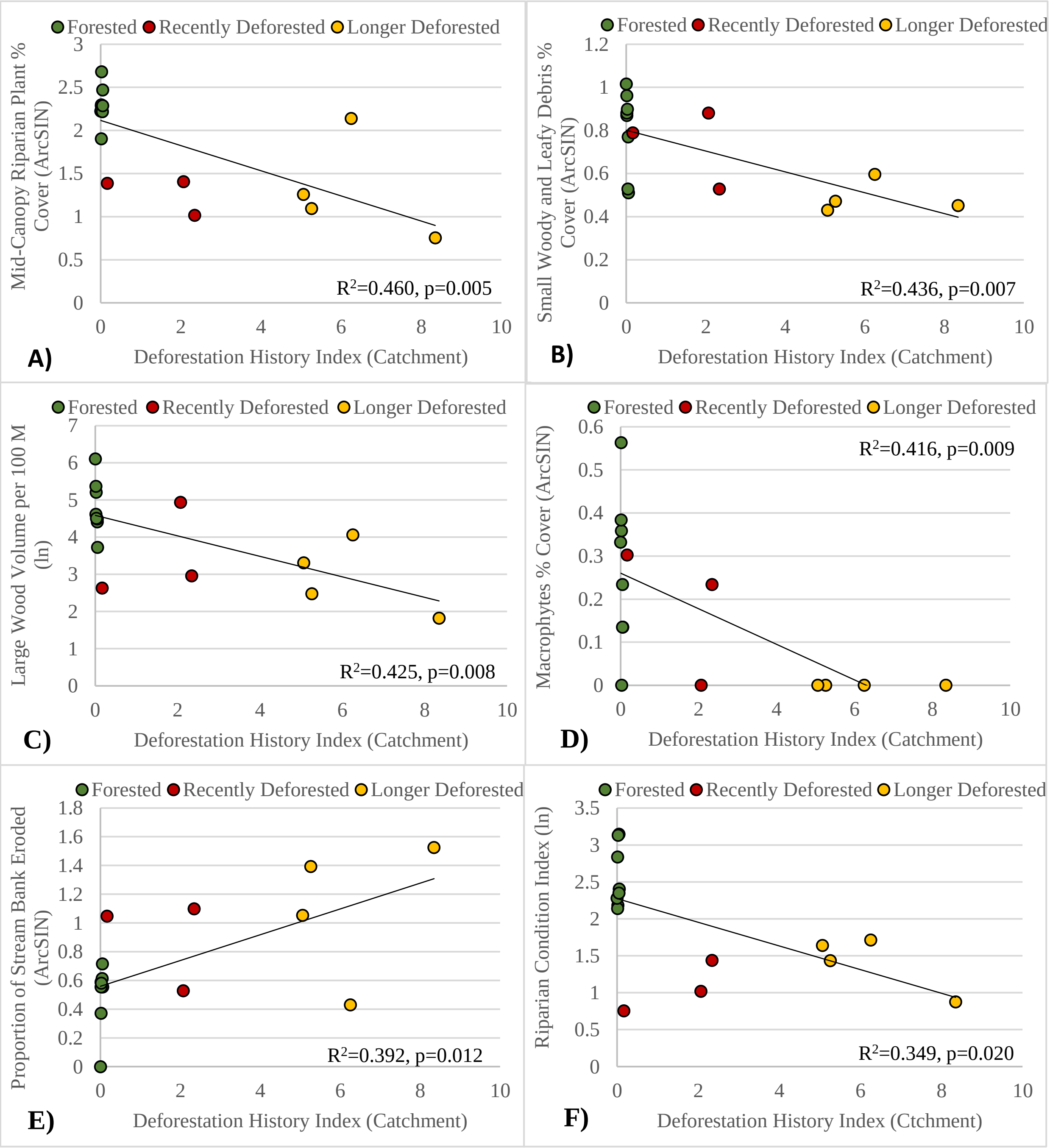
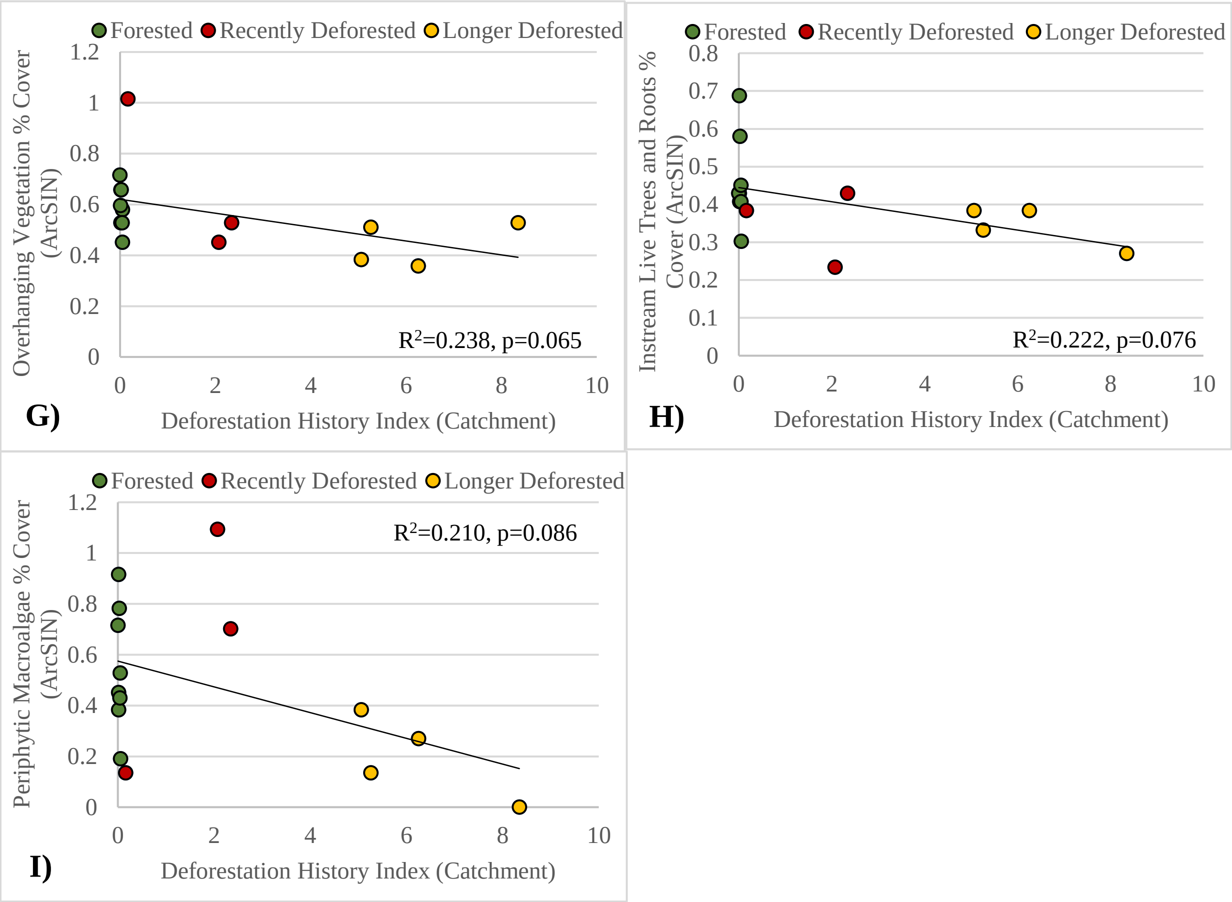


Figure 10: Single linear regression comparisons of the deforestation history index at the catchment scale (X) as a predictor of habitat responses (Y). A) ArcSIN transformed mid canopy riparian plant % cover, **B)** ArcSIN transformed small woody and leafy debris % cover, **C)** Natural log transformed large wood volume per 100 M **D)** ArcSIN transformed macrophytes % cover, **E)** ArcSIN transformed proportion of stream bank eroded, **F)** ln riparian condition index. Pearson's R^2 and associated p-values listed. The deforestation history index for the catchment significantly predicted six habitat variables (Table 2). The other 14 were non-significant (only p<0.1 visualized here).

Figure 10 (cont'd)



G) ArcSIN transformed overhanging vegetation % cover, **H)** ArcSIN transformed instream live trees and roots % cover, and **I)** ArcSIN transformed periphytic macroalgae % cover.

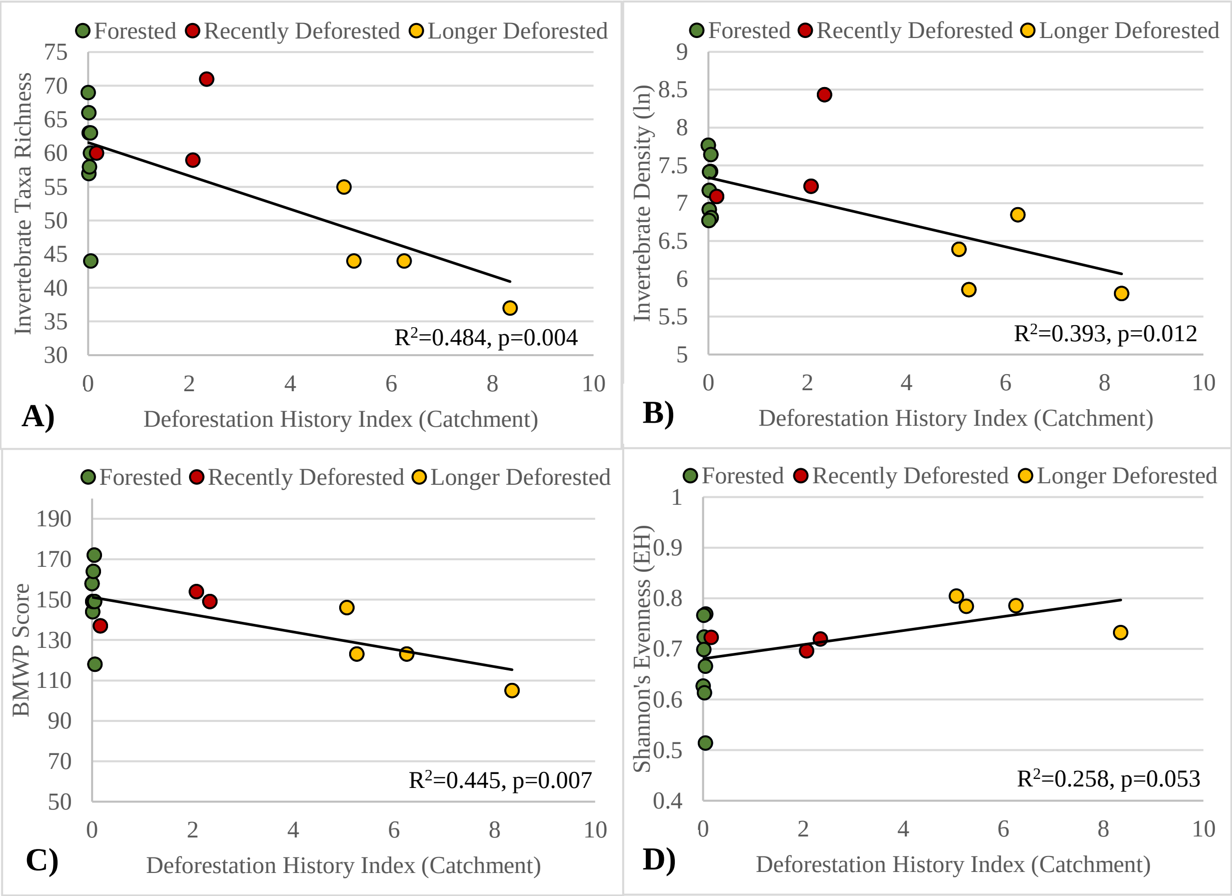
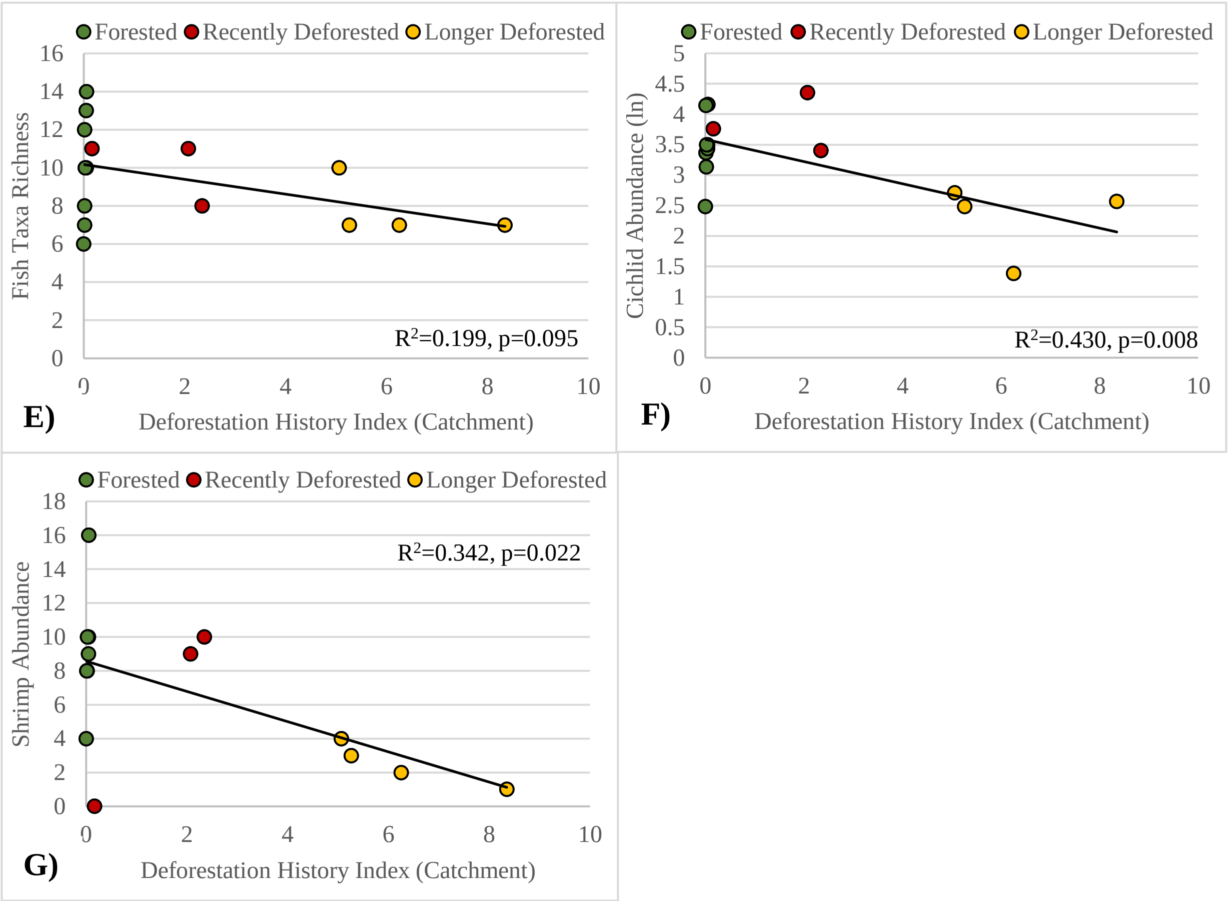


Figure 11: Single regression comparisons of the deforestation history index at the catchment scale (X) as a predictor of macroinvertebrate, fish, and shrimp responses (Y). A) Invertebrate taxa richness, **B)** ln invertebrate density (per m^2). **C)** BMWP score **D)** Invertebrate evenness (Shannon's). Pearson's R^2 listed and associated p-values listed. The deforestation history index for the catchment was the best predictor at the landscape scale (except for with evenness and cichlid abundance, where the index at the buffer scale was better) and predicted best or second best when compared to all 20 other habitat predictors (Tables 6 & 7).

Figure 11 (cont'd)



E) Fish taxa richness **F)** Natural log transformed cichlid abundance, **G)** Shrimp abundance.

DISCUSSION

Deforestation and subsequent land use change can cause a variety of different impacts to stream biota and habitat, depending on its extent, timing, type of land use, and natural conditions (Allan, 2004; Leitão et al., 2017). In the Rama-Kriol territory and reserves of Southeast Nicaragua the impacts of deforestation and subsequent conversion to pasture on streams are distinct yet, as hypothesized, align closely with what has been found in many other tropical stream studies: deforestation and cattle ranching had pronounced impacts on stream biota, mediated by changes in stream habitat, which were strongly predicted by *level of* deforestation and *time since* deforestation at the catchment scale, as integrated by the calculated "deforestation history index." Although there are few tropical studies that consider the role of time since deforestation, it appears that it plays a substantial role in structuring stream habitat and biotic responses when cattle ranching is the main subsequent land use.

Instream habitat response mediated by deforestation effects

There were strong impacts of deforestation and cattle ranching on instream habitat, which were generally more severe for streams whose catchments were deforested longer and to a larger extent. Metrics of bank disturbance and instream habitat evidence this trend. Bank erosion varied from 0-12 % in forested conditions to 25-48% in deforested conditions and was significantly explained by the deforestation history index. One reach in Pijibaye and one in Kukra had lower bank erosion (7 % and 5 %, respectively), but both also had more intact riparian forest and were mostly fenced off to cattle. Cattle access to streams appeared to be a major contributor to instream and bank destabilization, as shown in many studies (Strand & Merritt, 1999; Wantzen & Mol, 2013).

Both autochthonous and allochthonous sources of plant material were lowest in longer deforested streams (Table 1) and were significantly explained by the deforestation history index (Table 2). Lower amounts of large wood and small woody and leafy debris in streams is a common impact of deforestation in a catchment (Bojsen & Barriga, 2002; Benstead et al., 2003; Bojsen & Jacobsen, 2003; Wright & Flecker, 2004; De Paula et al., 2011; Leal et al., 2016; Leitão et al., 2017; Brejão et al., 2018; Montag et al., 2019), and is related to reduced riparian vegetation. It could also be related to decreased flow consistency, as deforestation could be resulting in increasingly flashy streams (Chaves et al., 2008; Recha et al., 2012; Peña-Arancibia, Bruijnzeel, Mulligan, & van Dijk, 2019) with less stabilizing large wood structure which tends to flush out leaf litter and smaller debris (Bilby & Likens, 1980).

Notably, aquatic vegetation (macrophyte % cover) was highest in forested streams, and at 0 % cover in all longer deforested, one recently deforested, and 1 more erosional forested stream, and was significantly predicted by the deforestation history index. Periphytic macroalgae had the highest percentage in more recently deforested streams, but lowest in longer deforested streams.

In other systems, increases in both metrics is often associated with more available sunlight to the stream channel because of riparian deforestation (Bojsen & Jacobsen, 2003; Lobón-cerviá et al., 2016; Leitão et al., 2017; Feijó-Lima et al., 2018). This sunlight-instream productivity subsidy effect (Allan, 2004) may be occurring with macroalgae recently deforested streams and in streams affected by the hurricane, but the opposite was true for longer deforested streams. This indicates that there may be a threshold of stream stability above which/below which macroalgae can flourish in deforested streams. Sediment from eroded banks could be smothering aquatic vegetation and macroalgae and scouring the stream bottom of suitable stable substrates for establishment (Mažeika et al., 2004; Schwendel et al., 2010), despite positive sunlight conditions for growth.

Although sedimentation and decreased bed stability were not effectively recorded in this study, they were apparent in longer deforested streams (Figure 12). Percent embeddedness in riffles and rapids, % fines, and % sand were intended to capture these dynamics (Allan, 2004; Mažeika et al., 2004; Kaufman et al., 2008; Lorion & Kennedy, 2009a), and results showed higher embeddedness in longer deforested streams, but results were nonsignificant. Bed stability can be measured by a variety of different techniques (Schwendel et al., 2010), all of which involved more time and labor-intensive measurements than possible in this study. Yet given that these streams were relatively high gradient, it is possible that sediments move through the system rapidly, and therefore bed instability would not be captured by measurements of instream fine substrates and embeddedness (Mažeika et al., 2004). The relatively high gradient nature of these streams appeared to determine substrate parameters more than any feature associated with disturbance in this system. When considering the high rates of bank erosion and relatively high gradient of streams, in addition to the declines in aquatic vegetation, macroalgae, small woody and leafy debris, and macroinvertebrate density in the most impacted streams, it is likely that deforestation is causing decreased bed stability. Increasing flashiness and flooding from deforestation (Bradshaw et al., 2007; Chaves et al., 2008; Recha et al., 2012; Peña-Arancibia et al., 2019) could exacerbating these issues, but seasonal patterns in discharge rates were not measured for these streams.

Changes in riparia caused by hurricane and deforestation effects

Riparian habitat was clearly degraded around all deforested streams, according to the riparian condition index. Understory riparian plant metrics (particularly mid-canopy plant %

cover) also captured this, as they were significantly higher in forested reaches, and significantly explained by deforestation history index (Table 2). The impacts of Hurricane Otto are shown by the finding that upper canopy large trees % cover and % shade were significantly lower and large wood and small woody and leafy debris were significantly higher at reaches impacted by the hurricane. The hurricane downed many of the large riparian trees, which ended up in the streams, opening up the canopy. The effects of this on stream habitat and biota could be substantial while the forest regenerates, including increases in temperature or algal growth. Because of these hurricane dynamics, upper canopy large tree % cover did not differ significantly between forested reaches and recently deforested or longer deforested reaches. But streams in the Corn River watershed had consistently high large tree cover (>50-57%) whereas recently deforested and longer deforested streams had variable large tree cover (10-48% and 19-53%, respectively).

These results together show that cattle ranchers in the study area often maintain large riparian trees but remove the woody understory for pasture, often right up to the stream bank. In fact, at most deforested sites there was evidence of active cattle grazing right up to the stream bank. This could also affect future riparian tree recruitment, as cattle trampling and grazing could limit seedling recruitment (Griscom, Griscom, & Ashton, 2009; De Paula et al., 2011).

Consistent reductions of macroinvertebrates, shrimp, and fish

Comparisons of macroinvertebrate community metrics showed significantly lower taxa richness and density only in streams where deforestation in the catchment has been occurring for a longer time and to a larger extent (Kukra watershed), whereas recently deforested streams were more like forested streams. BMWP score showed the same pattern (Figure 5). This aligns with studies that have found decreases in taxa richness (Paaby et al., 1998; Iwata et al., 2003; Lorion & Kennedy, 2009a; Iñiguez–Armijos et al., 2014; Fugère et al., 2016; Tanaka et al., 2016;

Montag et al., 2019) and density (Paaby et al., 1998; Iwata et al., 2003) in streams with deforested catchments. NMDS and PERMANOVA showed the same trend, where forested streams were significantly grouped apart from deforested streams, but where forested streams and recently deforested streams group more closely together than longer deforested streams (Figure 9). Given both of these results together, it follows that the macroinvertebrate communities in streams in the Pijibaye watershed, which have been deforested less time and to a lesser extent, have not yet been impacted the same amount as the communities in streams in the Kukra watershed, which have been deforested longer, and to a larger extent. The importance of deforestation not just in extent but also over time is also captured by the deforestation history index and its explanatory power (Table 6, Figure 11; see discussion below).

Forested streams were also more similar to each other (cluster more tightly) than deforested streams, which has been seen in other tropical studies (Figure 9) (Benstead et al., 2003; Lorion & Kennedy, 2009a; Iñiguez–Armijos et al., 2014; Fugère et al., 2016). This suggests that deforestation changes the macroinvertebrate community in an inconsistent way over time between streams. This explanation is supported by the indicator analysis, which shows four indicator taxa in the more recently deforested reaches (Pijibaye) and only one (*Moribaetis*) in the longer deforested reaches of the Kukra watershed. This implies that fewer taxa consistently thrive in the most impacted conditions (Table 5).

In this study, higher evenness was not an appropriate measure of macroinvertebrate community health. Evenness was significantly lower in undisturbed forested streams compared to deforested streams. This is contrary to other tropical studies, which found either no difference (Iwata et al., 2003; Iñiguez–Armijos et al., 2014) or higher evenness in forests (Fugère et al., 2016). Evenness was negatively correlated with BMWP score, and positively correlated with the deforestation index. In this study, the trend in evenness was driven by the dominance of Chironomidae at forested reaches. This has also been reported in the literature for forested tropical streams (Suga & Tanaka 2013; Gutiérrez-Fonseca, Ramírez, & Pringle, 2018).

Functional feeding group assignments can provide useful information to assess ecological impacts of disturbance (Ramírez & Gutiérrez-Fonseca, 2014). In this study, all four indicator taxa for deforested streams were relatively mobile (swimming and clinging) genera of collector-gatherer mayflies (in two families; Table 3), as was the only indicator for longer deforested streams (*Moribaetis*). Forested and recently deforested sites had a variety of other feeding groups present as indicators. Baetid and Leptohyphid mayflies may be more resilient to disturbances, as they fill a flexible niche and their mobility allows them to actively seek cover to escape flashes of high flow and elevated sediment load.

Fish and shrimp were also impacted in deforested streams. Comparisons of fish community metrics followed the same patterns as macroinvertebrate metrics, but differences were less pronounced. Shrimp abundance and Cichlid abundance were significantly affected by deforestation, especially where it has been occurring for a longer time and to a larger extent (Kukra). Fish taxa richness was also higher at forested reaches, but differences were not significant. But the finding that all 20 species found in the whole study were found in forested streams, while 7 of these were not found in deforested streams, points to some impact on diversity and abundance occurring in deforested streams. Limited sampling effort and low sample size limit power and interpretation of fish results.

Only the four commonly fished species were significantly smaller at deforested reaches, while the rest of the smaller, less desirable species did not differ between forested and deforested streams. Larger individuals of *Brycon guatemalensis, Parachromis dovii,* and *Tomocichla tuba* were nearly absent in both recently deforested and longer deforested streams compared to forested reaches (Figure 7). These findings could be attributed to either fishing pressure or the habitat effects of deforestation and cattle pasture. Though fishing pressure was not measured, it is known that fishing is common in these cattle ranching communities, and the data likely speak to its effects—given that only the length of larger, more heavily fished species was significantly reduced.

These reductions in size and abundance could pose a threat to the local fishery, especially if these species are not allowed to reach prime reproductive age or size. In Nicaragua, there are no size restrictions or limits on freshwater fish take in streams outside of protected areas. Even fishing bans for illegal occupants of Indio-Maíz are ignored (GTRK, unpublished data). Regulation in these remote areas is nil, and the life histories of many of the species in these rivers are poorly studied, so the foundation for establishing effective size limits and take restrictions is weak. Given these results, regulators should consider further study in these systems, and establishment of size and take limits, before fisheries are further reduced.

Taxa response and stream habitat

Associating specific changes in the habitat with specific changes in the biotic community is a consistent problem in stream studies (Gergel et al., 2002). In this study it was clear that deforestation caused many cooccurring impacts to stream habitat, all of which interact with biota in unique but interrelated ways. Linear regression analyses helped to elucidate these patterns. The dominating influence on macroinvertebrates in this study appears to be stream channel and bed instability as it influences instream habitat and food availability. Since periphytic macroalgae (especially when considering a logarithmic relationship), embeddedness in riffles and rapids, stream bank erosion, small woody and leafy debris, and large wood are all related to

Figure 12: Examples of streams in each watershed, featuring typical levels of disturbed banks and riverbed. **(A)** Indian River tributary. Note high levels of understory growth and large wood and debris from Hurricane Otto. **(B)** Corn River tributary. Note the intact primary forest canopy and instream debris. **(C)** Pijibaye River tributary. Note the pasture up to the stream bank, as well as some maintained larger riparian trees but no forest understory. **(D)** Kukra River tributary. Note the sluffing eroded banks, pasture up to the stream bank, and bank sediment covering the stream bottom. This was a particularly affected reach.

stream channel and bed instability, this was likely the main mediator of macroinvertebrate response to deforestation. Wood as a direct provider of habitat (Valente-Neto et al., 2015), and macroalgae and debris as sources of food could also be important mediators.

Nutrient enrichment and contaminant pollution were not measured and could also be contributing to patterns in biotic response (Allan, 2004). Given that habitat conditions in longer deforested streams were especially not stable, and it was in these streams where the strongest taxa response was observed, deforestation over time as it impacts instream and bank stability was the most likely cause of invertebrate declines. Multiple studies, both temperate and tropical, have found stream channel and bed instability to be some of the most important factors in determining patterns in the macroinvertebrate community (Townsend, Scarsbrook, & Dolédec, 1997; Schwendel et al., 2010; Ferreira et al, 2014). Shrimp abundance was also predicted significantly by embeddedness and riparian condition metrics, and followed similar patterns to macroinvertebrate density, which lends to the conclusion that shrimp were also sensitive to decreases in stream channel and bed stability in deforested streams (Table 7).

Observed evenness patterns could also be described by stream channel and bed instability. Miyake, Hiura, & Nakano (2005) found that frequent bed disturbance in a Japanese stream raised evenness in stream patches because Chironomidae were not able to effectively colonize, whereas they were the dominant taxa at undisturbed patches. These dynamics could be driving evenness patterns in this study, since the sites with the lowest numbers of Chironomidae were the longer and more deforested sites, which were also the most eroded and least stable. Schwendel et al. (2010) also observed increased evenness with increased bed stability.

Many studies have also associated the impacts observed in this study with changes in the fish community, for example: decreased bed stability (Leitão et al., 2017), eroded banks and sedimentation (Iwata et al., 2003), algae abundance (Bojsen & Barriga, 2002; Lobón-cerviá et al., 2016), decreased large wood (Wright & Flecker, 2004), and lower woody and leafy debris (Bojsen & Barriga, 2002). This could be impacting the fish community in this study, but changes in the fish community observed in this study were less pronounced, and associations with habitat metrics were weaker (Table 7). The lack of information on the feeding habits and reproductive needs of many species in this study also make further interpretation difficult (Bussing, 1998).

History of deforestation as the best predictor of taxa responses

Notwithstanding all of these relationships between habitat and biotic response, the deforestation history index for the catchment draining to each reach was the best linear predictor of all invertebrate taxa responses—better than all other habitat metrics, and better than % forest cover at the catchment or 100 m buffer scale and the deforestation history index at the 100 m buffer scale (Table 6). Only for evenness did the index for the buffer and forest cover for the catchment better predict than the index for the catchment. The deforestation history index for the catchment was also a top-three predictor for all fish and shrimp community metrics, in every case predicting better than % forest cover at catchment and buffer scales (Table 7). This supports the idea that land use change at the catchment scale is an integrator of habitat impacts and can serve as an important predictor for impacts to stream ecosystems (Gergel et. al., 2002; Heartsill-Scalley & Aide, 2003; Leal et al., 2016; Molina et al., 2017; Brejão et al., 2018; Zeni et al., 2019). The fact that the deforestation index, which integrates both forest cover extent, and time since deforestation, better predicted biotic response than raw forest cover extent, emphasizes the importance of the temporal component of impacts of land use (Harding et al., 1998; Iwata et al., 2003; Brejão et al., 2018; Zeni et al., 2019). In this context, stream processes set into motion by deforestation, and then exacerbated by cattle ranching, increasingly affect stream habitat and biota over time.

Thresholds of habitat and biotic disturbance

The presence of thresholds of disturbance for aquatic habitat and biota is a pillar of stream disturbance ecology (Allan, 2004). Although detailed threshold analysis was not carried out, presence of a threshold response is anecdotally supported by this study. It appears that some threshold of impact after which macroinvertebrate, shrimp, and many habitat metrics declined has not yet been achieved in the more recently and less deforested streams (Pijibaye), whereas it has in longer and more deforested streams (Kukra) (see Figures 10 & 11). Stream channel and bed stability have been shown to decline after a threshold of anthropogenic land use change occurs (Kaufmann, Larsen, & Faustini, 2009), as have metrics of stream biota in response to thresholds of bed stability (Schwendel et al., 2010). This could serve as an explanation for the patterns seen in this study.

The BMWP index appropriate for assessing deforestation impacts to streams?

Taxa associated with forested and deforested streams were often contrary to what would be expected by the BMWP index (where taxa with low scores are usually associated with disturbed conditions). For example, the four mayfly genera that indicated deforested habitat all have a BMWP score of 5. If these genera indeed indicate habitat degraded by deforestation, a BMWP value of 5 could be incorrect in the context, and these genera should be assigned a lower score. This would have to be verified by additional studies. Two of the seven indicators for forested streams had a BMWP score of 1, and Chironominae, with a BMWP score of 2, was an indicator at forested streams in Corn River watershed. The presence of these “tolerant” taxa could be expected at pristine locations, but not their dominance, according to index theory, which typically also considers relative abundance (Hilsenhoff, 1988). This puts into question the utility of the index for evaluating impact to streams from deforestation and conversion to cattle pasture. Indeed, the index was created to generally assess the “physical-chemical factors” or vaguely “water quality” (Hawkes, 1998), and is limited because it functions only at the family level, while actual tolerances vary at the species level (Hilsenhoff, 1988). But it has been applied to assess impacts of a variety of types of disturbance in Costa Rica and Nicaragua (Kumar, Colton, Springer, & Trama, 2013; Salvatierra, 2014). Deforestation affects “water quality” but also benthic habitat, so the index may not be fully appropriate. Much clearer trends can be found by looking at community measures of diversity and density, and functional feeding groups or life history traits of each taxa as it relates to changes in habitat, and thus analyzing these factors may be a more useful approach than considering the index for evaluating deforestation impacts.

Study limitations

Sampling methods used and variables measured limit this study in many regards. Fish sampling techniques selected for species that are active in the daytime (both methods), eat worms and can bite at least a size 14 hook (hook and line) or are found in the open channel (cast net). Sampling effort was surely not enough to capture all the species present in each stream or even the reach. Terra et al. (2016), who used the same reach length as this study in streams in Brazil, described that even electrofishing was not sufficient to estimate species richness because of the presence of so many relatively rare taxa. But other metrics of assemblage condition can still be useful for environmental assessment (Terra et al., 2016).

Fishing with pesticides (mainly cypermethrin) occurs in many of these communities, and likely also has played a role in structuring fish and invertebrate communities. Forthcoming research will further assess the extent of this problem (JT Betts, unpublished data).

In summing and averaging of habitat and invertebrate metrics from all 11 transects to attain reach level values, specific information was lost. Although reach-scale analysis is valuable for landscape-level studies, potentially important finer scale impacts of disturbance were not assessed. Further analysis which separates habitat and invertebrate metrics by transect will be useful, especially in evaluating taxa-specific habitat preferences and responses to disturbance.

Given the “rapid assessment” nature of this study design (Kaufman et al., 1999), some important stream habitat processes were impossible to capture. Metrics that vary widely depending on weather and seasonal conditions—such as temperature, pH, dissolved oxygen, nutrient concentrations, turbidity, discharge, bed stability, and sediment transport, were not possible to accurately measure since sampling at each reach occurred in 2-3 days. For this same reason, abundances of certain taxa which move in the stream system seasonally may have been over or underestimated. True algal biomass was not recorded, given that it was a visual assessment of larger (clearly visible) filamentous algae, not even all periphytic algae. This limits interpretations about subsidy effects from increased sunlight and nutrients. These limitations were anticipated, but future study could benefit by considering longer term monitoring at sites and quantification of algal biomass.

The informative power of this study was limited for a variety of reasons. A sample size of 15 is too low to significantly capture many relationships and differences that may be present in both the habitat and biotic community. For example, low sample size relative to number of habitat variables (20) made it inappropriate to apply multivariate techniques like DCA, PCA, and Random Forest analysis, which have been very informative in similar studies with higher sample size (Terra et al., 2016; Leal et al., 2016). More reaches were planned, but when the political crisis arose in April of 2018, the field study was immediately terminated by the funding source

(US government). This speaks to the challenges of carrying out research in politically unstable contexts. Although reaches were independent of each other (no catchment overlap), some spatial autocorrelation was likely in this study, since sampling was carried out in just 4 larger watersheds. The relevance of this study is not its large sample size, but the paucity of any prior data from the study area, and impending threats to conservation of the region's largely undescribed stream fauna. Difficulty of access, lack of infrastructure and communication, and political instability in southeast Nicaragua are likely reasons why studies from this area are so rare, compared to other ecologically similar regions like northeast Costa Rica.

Novel findings and future research priorities

Given that this study is the first formal aquatic study in any of these streams, and one of the only for the Indio-Maíz Biological Reserve, there were many novel findings and future research opportunities. Many of the reported genera are new reports for Nicaragua (JM Maes, pers. comm.), and it is likely that some are undescribed taxa, since this study is the first published macroinvertebrate study from any of these watersheds. For example, one caddisfly genus (Hydroptilidae: Leucotrichini, genus undet.) has never been associated with its adult (M Springer, pers. comm.), and description is underway. Notably, the mayfly family Euthyplociidae (*Euthyplocia*) had not yet been recorded for the country (Maes & Salvatierra-Suarez, 2014). Thiaridae, an invasive family of aquatic snails, was found only in deforested reaches. It is likely that it is *Melanoides tuberculata*, as this is the only species of Thiaridae reported for the country (Pérez & López de la Fuente, 1993). Introduced in the aquatic plant trade, it poses risk to native fauna and is a potential disease vector and has been shown to dominate in disturbed stream conditions (Gutiérrez-Gregoric & Vogler, 2010).

Sicydium altum was a new fish species register for Nicaragua, not known to extend north of Costa Rica (Bussing, 1998). *Hypostomus* sp. (possibly *H. niceforoi*), an invasive Loricariid catfish, was found in the upper reaches of Indian River. This genera has been recorded in Nicaragua, only in the San Juan River drainage (Corea, Hernández, Solís, & Aguilar, 2014; Härer et al., 2017), and evidence from interviews from a study by the authors (publication forthcoming) with fishermen indicates that it is a recent arrival and could be present in other watersheds as well. In prior publications it was recorded as *H. panamensis,* a Central American cogener native to south of Nicaragua, but recent genetic evidence from samples from the San Juan drainage suggests it is likely *H. niceforoi*, a species from Columbia (N Lujan, pers. comm.). Invasive loricariid catfish have been shown to dominate in disturbed stream conditions (Bojsen & Barriga, 2002; Leitão et al., 2017). Loricariid catfish are of little use to fisheries (Capps & Flecker, 2015) and have limited predators in invaded systems (Nico, 2010). They have been shown to reach high densities in some streams in which the invasion has progressed significantly (up to ~2 per m^2 at some sites), where they can be a significant threat to fisheries and river ecosystem function by degrading the amount and quality of primary resources (Capps & Flecker, 2015). Effort will be made to incorporate these species and genus registers into country and regional taxa lists, and future effort to further identify aquatic insect and shrimp specimens to species could yield important range expansions and even new species.

The number of important findings even given the limited extent of this study (only 15 headwater streams) justifies further intensive surveying of the region. There are many reasons it could be important for regional conservation. For example, species such as the Bobo (or hognose) mullet (*Joturus pichardi*) are of conservation concern in Costa Rica due to overharvest and dams (Anderson, Pringle, & Rojas, 2006), and appear to be common in at least Indian River.

But the potential of these rivers as population strongholds and threats to these populations has not been studied. Another species of concern, the American Eel (*Anguilla rostrata*), is likely present in these rivers (unpublished data, JT Betts), yet no data exists on its presence anywhere from northern Costa Rica to northern Nicaragua (Benchetrit & McCleave, 2015).

A new index

The predictive power of the novel "Deforestation History Index" for describing landscape driven processes is another important finding of this research. Since land use data has become increasingly accessible, there have been many efforts to find the most useful landscape predictors of stream conditions (Hawkins et al., 2000; Macedo et al., 2018; Sandric et al., 2019). Brejão et al. (2017) used time since deforestation and deforestation as separate indicators of impacts to streams. Other studies have considered land use history in addition to extent of land use change in how it impacts streams (Harding et al., 1998; Iwata et al., 2003; Zeni et. al., 2019). But this study appears to be the first to integrate the time and extent components of land use change into one index.

Given that the Deforestation History Index was easily generated with widely accessible software (GIS, Excel) using publicly available data (Hansen et al., 2013), this index could be a useful as a landscape predictor in a variety of contexts. It is useful when the impacts of deforestation are accumulative over the years—where current percent deforestation in a study area does not fully capture its impact on a study system. As shown in this study, this is true for conversion of rainforest to pasture as it impacts streams. If integrated with other land use datasets, this index could also be adapted to more complicated land use history situations, where multiple land uses (not just binary forest cover) are considered. It could also easily consider forest gain, as the Hanson et al. (2013) dataset also includes a forest gain layer. In this analysis the gain layer was not included because it currently only includes data up to 2012. Other land uses were not considered because deforestation almost always meant conversion to cattle ranch in SE Nicaragua.

Relevance to conservation

The findings of this study show that the agricultural frontier has had serious detrimental effects on stream ecosystems and associated fisheries in the Rama-Kriol territory. Cattle ranchers are increasingly invading the Indio-Maíz Reserve to remove the forest and create pasture. With these changes in the headwaters of the Indian, Corn, Pijibaye, and Bartola Rivers which drain the reserve, degradation of stream habitat and subsequent degradation of stream macroinvertebrate, fish, and shrimp populations should be expected. In the case of fish and *Macrobrachium* shrimp declines, this could also threaten the subsistence of Rama and Kriol communities who rely on these animals for food. In more invaded watersheds, older Rama community leaders have complained about the loss of reliance on rivers for food compared to before the invasion (unpublished data, JT Betts). Indeed, finding hard evidence for these concerns was an important goal of this study.

Conservation recommendations

The action plan for Indio-Maíz was finalized in 2017 by the Rama-Kriol territorial government, and includes as an action to “monitor key indicators for the condition of Indio Maíz and its flora and fauna” and to “conduct regular analyses of monitoring results and use these to plan protection and management activities” (Gobierno Territorial Rama y Kriol, 2018). This project serves as one such monitoring effort. As the action plan for Indio-Maíz is implemented, these current and projected negative impacts of the invasion to streams and their fisheries need to be considered. The following damage mitigation and prevention efforts, not only for Indio-Maíz, but for the whole territory are recommended:

1) **Promotion of forest conservation and restoration.** Maintaining the most primary forest possible in catchments and restoring forest where it has been lost are the best ways to promote aquatic ecosystem health and a healthy fishery. Given these results, any deforestation within a catchment will likely have some effect on stream habitat and biota over time.
2) **Encouragement of ≥30 m riparian buffers along streams.** Riparian buffers along streams of every order, including ephemeral streams, can mitigate the impacts of land use change on streams such as like temperature increase, nutrient increase, bank erosion, and decreased large wood and leaf litter inputs, among others (Luke et al., 2019). Many studies have shown the effectiveness of buffers in maintaining stream macroinvertebrate and fish communities (Lorion and Kennedy, 2009a,b; Chellaiah & Yule, 2018). Based on extensive review of the literature, Sweeney & Newbold (2014) recommended buffers of ≥ 30 m.
3) **Removal of illegal ranches in Indio-Maíz and the Rama-Kriol Territory.** The national and territorial laws of the reserves and indigenous territories of Nicaragua prohibit the establishment of new cattle ranches and farms within Indio-Maíz and the Rama-Kriol Territory unless in accordance with indigenous communal property laws under law 445 (Saenz, unpublished report, 2019). The Rama-Kriol authorities have filed numerous legal complaints against new illegal ranches (Gobierno Territorial Rama y Kriol, 2018). The Nicaraguan authorities should respond to these legal complaints and support removal of illegal ranches.

4) **Alternatives to cattle ranching like sustainable agriculture and agroforestry.** Cattle ranching is particularly damaging to streams compared to many other forms of agriculture (Strand & Merritt, 1999). Where agriculture is necessary, agroforestry techniques and traditional cropping systems such as banana, coconut, and fruit tree systems, or corn and bean intercropping and root vegetables crops like malanga, as grown typically by the Rama and Kriol inhabitants of the region are much less degrading alternatives to cattle ranching.
5) **Fencing and restricted stream access for livestock.** Where cattle or other livestock are present, restricting the access to the stream channel using fences can reduce stream bank erosion and trampling of the riparian zone. Having alternative water sources, or only allowing a few access points to a stream within a pasture can greatly reduce impacts (O'Callaghan et al., 2018).
6) **Fish size restrictions and take limits.** Size and abundance of important fish species was severely affected in cattle ranching communities. Establishing and enforcing fishing regulations could help overfished species like *Brycon guatemalensis* or *Parachromis dovii* to recover and maintain enough large, reproductive age individuals for a sustainable river fishery, even in areas of higher fishing pressure.
7) **Removal of Loricariid catfishes.** The Loricariid catfish invasion could become a significant threat to the fishery (Capps & Flecker, 2015). When caught, individuals should not be thrown back. Targeted harvest and removal of Loricariids could also be beneficial to help limit the effects of this nuisance species.
8) **Educational activities about the impacts of deforestation and cattle ranching on streams.** Although there is general concern, there is little awareness about the

mechanisms of impacts of deforestation and cattle ranching to streams in the communities where the research was conducted. The results of this study could be used to create educational materials to disseminate into the communities, to increase awareness and help motivate the adoption of some of these recommendations.

Conclusion

The case of deforestation in Rama-Kriol territory in Southeast Nicaragua is an important example of how rainforest loss impacts aquatic organisms and ecosystems processes, as well as the people who rely on the services they provide (Foley et al., 2007). Although they are an important component of biodiversity, stream organisms are often neglected in conservation initiatives, compared to more charismatic fauna. As the agricultural frontier continues to threaten the Indio-Maíz Biological reserve and the rest of the Rama-Kriol territory, the distinct threats it poses to stream biodiversity and ecosystem function needs to be considered, if these rivers and the life they support are to be conserved.

APPENDICES

APPENDIX A

Raw Data

Table A.1: Reach details, including local stream names, reach codes, date of first day sampling at the reach, and base transect coordinates. Creeks with asterisks were names that the team created upon arrival, if there was not a known local name. Caño Boca Tapadas and Caño Moga are considered the same creek on topographic maps but are different streams with confluences near each other.

Watershed	**Indian River Watershed**					**Corn River Watershed**		
Stream Name	Mountain Cow Creek*	Caño Guinea	Caño Banana Vieja*	She Tiger Creek	Long Falls Creek	Caño Boca Tapadas	Caño Moga	Caño La Combinación
Study Reach Code	IR18MC	IR18GU	IR18BV	IR18ST	IR18LF	CR18BT	CR18MG	CR18CO
Date Sampled	2/19/2018	2/22/2018	2/24/2018	2/26/2018	3/12/2018	4/10/2018	4/12/2018	4/14/2018
Coordinates (N)	11.13290	11.11850	11.12733	11.13787	11.12330	11.28167	11.28114	11.26783
Coordinates (W)	84.04524	84.09462	84.08104	84.06307	84.05836	84.00817	84.00561	83.99248
Watershed	**Pijibaye River Watershed**			**Kukra River Watershed**				
Stream Name	Caño El Coco	Caño La Perra	Caño El Salto	Caño Papa Abrahán	Caño El Limón	Caño Chacalín	Caño Limonero	
Study Reach Code	RP18EC	RP18LA	RP18SA	KR18PA	KR18EL	KR18CH	KR18LM	
Date Sampled	4/19/2018	4/21//2018	4/23/2018	2/7/2018	2/9/2018	3/22/2018	3/25/2018	
Coordinates (N)	11.45131	11.43747	11.43631	11.76249	11.73801	11.79634	11.80070	
Coordinates (W)	83.95861	83.96941	83.93757	84.08453	84.10820	84.11238	84.10738	

Table A.2: Full list of macroinvertebrate taxa abundances, by reach. Based on sum of eleven Surber samples (0.092903 m^2). Codes correspond to the “Study Reach Code” in Table A1. Organized as in Domínguez & Fernández (2009). Hydroptilidae: Leucotrichini, genus undet. is a unique taxon, likely undescribed (M Springer, pers. comm.). Grayed out columns are unknowns that were not considered unique taxa unless there were no other reports from the respective family at a site. These taxa were not included in determination of richness or diversity measures. These taxa, and taxa with <5 individuals in the study total were not included for NMDS, PERMANOVA, SIMPER, and indicator analyses. Taxa with ** were unconfirmed ID’s but distinct taxa, which are still in the UCR museum (Crambidae undet., Planiplax, Tholymis, and Phoridae).

Family	**Genus (or Subfamily)**	**IR18MC**	**IR18GU**	**IR18BV**	**IR18ST**	**IR18LF**	**CR18BT**	**CR18MG**	**CR18CO**	**RP18EC**	**RP18LA**	**RP18SA**	**KR18PA**	**KR18EL**	**KR18CH**	**KR18LM**	**Study Total**
							Arthropoda: Collembola: undet.										
undet.	undet.	1	0	0	0	0	0	2	2	0	0	0	1	0	0	0	**6**
							Arthropoda: Insecta: Ephemeroptera										
Baetidae	*Americabaetis*	1	0	0	4	7	3	0	0	7	0	3	0	1	6	0	**32**
	Apobaetis	0	0	0	0	1	5	0	2	2	0	1	0	0	0	0	**11**
	Baetodes	1	17	2	5	7	1	3	2	8	0	0	0	0	3	44	**93**
	Camelobaetidius	3	13	14	4	26	1	3	2	8	0	2	1	5	4	4	**90**
	Cloeodes	0	0	0	0	0	0	2	0	1	0	1	0	1	2	0	**7**
	Fallceon	1	2	0	4	2	7	3	0	2	5	10	1	7	13	6	**63**
	Guajirolus	0	0	0	0	0	0	0	0	17	0	0	0	0	2	0	**19**
	Mayobaetis	0	1	0	0	1	0	0	0	1	0	0	0	0	0	0	**3**
	Moribaetis	0	0	0	0	0	0	0	0	10	0	0	2	1	2	5	**20**
	Paracloeodes	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	**2**
	undet.	3	2	0	0	10	7	1	3	4	0	1	1	6	1	0	**39**
Caenidae	*Caenis*	1	0	0	0	0	26	5	7	5	7	29	0	0	1	0	**81**
Euthyplociidae	*Euthyplocia*	2 specimens from He Tiger Creek and 2 from Guinea Creek, Indian River, May 23-5, 2017, verified by L. Jacobus															
Heptageniidae	*Maccaffertium*	0	0	2	0	1	2	0	0	0	0	0	0	0	0	0	**5**
Leptohyphidae	*Asioplax*	13	0	3	9	10	2	19	2	11	5	0	1	1	12	7	**95**
	Cabecar	0	0	0	0	3	3	2	0	1	0	2	0	0	1	0	**12**
	Epifrades	0	0	1	2	0	1	1	9	2	1	28	0	0	2	0	**47**
	Leptohyphes	6	86	28	48	1	8	2	5	311	71	26	11	6	49	114	**772**
	Tricorythodes	72	37	18	41	54	35	41	44	344	190	112	4	14	45	4	**1055**
	Vacupernius	2	12	0	1	0	0	0	0	6	51	137	0	4	17	0	**230**
	undet.	0	0	2	0	0	0	0	0	0	0	0	4	0	0	1	**7**

Table A.2 (cont'd)

Leptophlebiidae	*Farrodes*	40	5	5	9	41	52	19	49	114	37	47	2	45	14	7	**486**
	Hagenulopsis	1	1	0	2	4	3	0	6	2	1	1	2	0	0	1	**24**
	Hydrosmilodon	0	2	0	3	0	0	0	0	0	0	0	0	0	0	0	**5**
	Thraulodes	10	77	0	32	4	70	27	85	34	56	14	18	90	8	92	**617**
	Traverella	1	2	1	1	0	0	0	0	115	10	0	0	0	2	11	**143**
Arthropoda: Insecta: Odonata																	
Calopterygidae	*Hetaerina*	0	0	0	0	0	0	0	0	2	0	0	0	0	0	1	**3**
Coenagrionidae	*Argia*	6	8	1	6	2	10	10	6	91	18	32	1	9	4	5	**209**
Gomphidae	*Agriogomphus*	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	**1**
	Desmogomphus	3	0	0	0	0	0	1	1	0	2	3	0	0	0	0	**10**
	Epigomphus	1	0	0	1	2	3	0	0	1	3	7	0	1	1	0	**20**
	Perigomphus	1	5	6	4	1	2	0	2	3	0	2	4	0	0	0	**30**
	Phyllocycla	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	**1**
Libellulidae	*Brechmorhoga*	0	0	6	3	8	0	0	1	14	1	6	0	4	0	9	**52**
	Libellula	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	**1**
	*Planiplax***	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	**1**
	*Tholymis***	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	**1**
	Libellulinae undet.	3	1	0	0	0	0	0	0	4	1	0	6	2	0	2	**19**
Megapodagrionidae	*Heteragrion*	0	0	0	0	0	0	1	1	0	2	0	0	0	0	0	**4**
Platystictidae	*Palaemnema*	6	34	46	28	20	50	29	35	12	19	2	7	2	29	26	**345**
Arthropoda: Insecta: Plecoptera																	
Perlidae	*Anacroneuria*	2	21	1	4	2	16	1	15	109	3	0	13	11	4	47	**249**
Arthropoda: Insecta: Hemiptera																	
Gerridae	undet.	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	**2**
Mesoveliidae	*Mesoveloidea*	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**
Naucoridae	*Cryphocricos*	9	11	39	3	26	22	8	9	12	14	0	5	0	1	0	**159**
Naucoridae	*Limnocoris*	4	1	1	4	0	0	1	0	36	9	32	12	5	0	0	**105**
Veliidae	*Rhagovelia*	0	0	0	4	0	1	1	3	0	1	0	0	0	0	0	**10**
Arthropoda: Insecta: Megaloptera																	
Corydalidae	*Chloronia*	0	0	0	0	0	0	2	0	0	0	1	0	2	0	0	**5**
Corydalidae	*Corydalus*	0	6	0	3	0	1	4	1	74	8	0	0	0	0	3	**100**
Arthropoda: Insecta: Trichoptera																	
Calamoceratidae	*Phylloicus*	0	0	0	0	0	2	0	1	0	0	0	0	0	0	0	**3**
Glossosomatidae	*Culoptila*	0	0	0	0	0	1	12	3	0	0	11	0	0	1	0	**28**
	Mortoniella	0	0	3	0	0	2	1	1	8	1	0	0	0	0	0	**16**

Table A.2 (cont'd)

	Protoptila	0	0	0	0	1	0	0	0	3	0	8	0	0	0	0	**12**
	undet.	0	4	0	0	0	0	0	0	0	0	48	0	0	8	5	**65**
Helicopsychidae	*Helicopsyche*	0	0	1	5	4	4	0	0	0	0	0	0	0	0	0	**14**
Hydrobiosidae	*Atopsyche*	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	**2**
Hydropsychidae	*Centromacronema*	0	0	1	0	8	0	0	0	0	0	0	0	0	0	1	**10**
	Leptonema	5	34	44	20	38	98	36	53	105	21	6	9	9	33	66	**577**
	Macronema	9	0	0	1	0	11	11	10	0	8	2	0	0	1	0	**53**
	Macrostemum	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	**2**
	Smicridea	20	142	214	61	54	92	131	74	459	83	18	29	3	56	49	**1485**
Hydroptilidae	*Alisotrichia*	0	0	0	0	3	0	0	0	0	0	0	0	0	0	1	**4**
	Hydroptila	6	0	76	0	3	0	38	0	120	0	7	0	0	0	0	**250**
	Leucotrichia	0	1	1	0	0	3	0	0	0	0	0	0	0	0	0	**5**
	Mayatrichia	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	**1**
	Metrichia	30	1	16	8	34	2	0	8	15	0	0	1	0	5	19	**139**
	Neotrichia	4	0	1	2	1	0	0	0	7	0	0	0	0	1	2	**18**
	Ochrotrichia	0	0	3	13	2	0	0	0	0	8	6	1	0	42	10	**85**
	Oxyethira	3	0	1	2	12	1	1	0	1	1	5	0	0	0	0	**27**
	Zumatrichia	2	2	0	0	0	0	0	1	0	0	0	0	0	0	1	**6**
	Leucotrichini undet.	92	0	3	5	1	0	2	0	0	0	0	0	0	0	0	**103**
	undet.	26	5	19	8	4	0	0	0	2	0	0	0	1	0	25	**90**
Leptoceridae	*Nectopsyche*	0	0	1	2	3	4	0	0	0	2	5	0	0	0	0	**17**
	Oecetis	5	0	9	2	0	1	0	1	10	4	12	1	0	3	3	**51**
	Triaenodes	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	**1**
Philopotamidae	*Chimarra*	2	19	7	10	9	19	10	11	189	8	2	1	1	0	7	**295**
Polycentropodidae	*Cernotina*	13	0	0	4	0	0	3	0	0	2	0	0	1	0	0	**23**
	Polycentropus	0	0	2	0	0	0	0	0	0	2	0	0	0	4	0	**8**
	Polyplectropus	4	9	1	9	0	0	0	0	0	46	1	0	0	4	0	**74**
Xiphocentronidae	undet.	1	0	0	3	0	7	0	1	0	0	0	0	0	3	0	**15**
undet.	undet.	25	1	3	3	0	8	41	0	0	2	28	0	0	2	4	**117**

Arthropoda: Insecta: Lepidoptera

Crambidae	*Petrophila*	27	8	111	29	7	4	13	10	79	29	54	4	0	6	16	**397**
	undet.**	6	0	0	1	19	0	0	0	0	1	0	1	0	0	0	**28**

Arthropoda: Insecta: Diptera

Ceratopogonidae	Ceratopogoninae	2	0	0	2	6	17	40	16	23	15	5	0	1	4	0	**131**
	Dasyheleinae	0	0	0	0	1	0	0	1	2	0	0	0	0	0	0	**4**
	Forcyponinae	0	0	0	1	0	2	0	0	3	1	0	0	0	0	0	**7**

Table A.2 (cont'd)

Chironomidae	Chironominae	185	66	144	158	152	501	1090	646	478	323	281	65	37	65	56	**4247**
	Orthocladiinae	112	122	109	39	619	250	159	246	389	64	42	39	8	36	124	**2358**
	Tanypodinae	10	1	2	7	7	5	8	19	40	15	14	1	1	1	1	**132**
Empididae	*Hemerodromia*	3	0	6	0	3	0	1	1	15	0	2	3	0	0	15	**49**
	undet.	5	1	0	2	0	4	0	0	0	0	0	0	0	4	0	**16**
Phoridae**	undet.	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	**2**
Psychodidae	*Maruina*	0	0	2	2	1	5	1	1	10	4	1	1	0	1	3	**32**
	undet.	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	**3**
Stratiomyidae	undet.	0	8	20	15	14	34	14	30	31	1	2	0	36	8	83	**296**
Simuliidae	*Simulium*	5	0	0	0	0	0	0	0	0	0	0	41	0	0	1	**47**
Tipulidae	*Hexatoma*	1	7	0	1	0	3	1	0	0	1	0	5	0	2	2	**23**
	undet.	2	1	4	0	0	5	0	0	0	0	0	0	1	0	2	**15**
undet.	undet.	0	0	0	20	0	1	0	0	0	0	2	0	0	0	1	**24**
Arthropoda: Insecta: Coleoptera																	
Dryopidae	*Dryops*	0	0	0	0	0	0	0	0	22	0	0	0	0	1	0	**23**
Elmidae	*Austrolimnius*	7	2	5	1	19	1	5	4	16	1	4	3	3	3	0	**74**
	Cylloepus	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	**1**
	Heterelmis	1	3	4	5	6	4	0	10	77	1	1	4	0	0	0	**116**
	Hexacylloepus	3	0	2	4	1	0	0	0	0	0	5	0	0	0	0	**15**
	Hexanchorus	0	0	0	0	11	0	0	0	1	0	0	0	0	0	0	**12**
	Macrelmis	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	**3**
	Microcylloepus	116	48	179	67	235	80	30	66	752	31	23	18	3	0	19	**1667**
	Neocylloepus	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	**3**
	Neoelmis	7	4	2	3	10	10	1	10	60	3	4	2	4	3	6	**129**
	Phanocerus	0	3	5	10	11	11	0	9	82	5	0	6	2	0	0	**144**
	Stenhelmoides	1	1	2	2	9	0	3	0	2	1	0	1	0	0	0	**22**
	Xenelmis	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	**3**
	undet.	5	1	0	1	0	2	0	4	126	3	0	7	2	0	1	**152**
Gyrinidae	undet.	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	**1**
Hydroscaphidae	undet.	5	0	0	0	88	8	11	5	4	6	2	0	0	1	0	**130**
Lutrochidae	*Lutrochus*	3	0	0	2	3	2	2	0	0	0	1	0	0	0	0	**13**
Psephenidae	*Psephenus*	28	70	28	90	51	99	42	99	106	173	77	11	5	13	35	**927**
Ptilodactylidae	*Anchytarsus*	2	0	0	2	4	8	1	3	3	1	0	1	0	0	0	**25**
Staphylinidae	undet.	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	**1**
Arthropoda: Malacostraca: Decapoda																	
Atyidae	*Atya*	0	0	0	0	0	7	1	5	0	0	0	1	0	0	0	**14**
Palaemonidae	*Macrobrachium*	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	**1**

Table A.2 (cont'd)

Pseudothelphusidae	undet.	0	0	2	0	0	0	0	0	0	0	0	0	0	0	1	**3**
undet.	undet.	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	**1**
Arthropoda: Malacostraca: Ostracoda																	
undet.	undet.	0	0	0	0	1	0	3	0	0	0	2	0	0	0	0	**6**
Arthropoda: Arachnida: Hydrachnidia																	
undet.	undet.	5	0	2	3	5	2	3	3	9	1	1	2	1	5	3	**45**
Annelida: undet.																	
undet.	undet.	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	**3**
Annelida: Oligochaeta: Clitellata: undet.																	
undet.	undet.	36	16	110	35	400	36	38	43	52	0	11	1	3	49	10	**840**
Mollusca: Bivalvia: Veneroida																	
Sphaeriidae	undet.	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	**1**
Mollusca: Gastropoda: Basommatophora																	
Ancylidae	undet.	6	0	0	0	0	0	1	0	21	9	13	0	0	4	0	**54**
Planorbidae	undet.	0	0	0	0	0	0	0	0	0	1	0	0	0	4	0	**5**
Mollusca: Gastropoda: Neotaenioglossa																	
Thiaridae	undet.	0	0	0	0	0	0	0	0	0	0	2	0	0	5	0	**7**
Hydrobiidae	undet.	4	0	0	5	0	4	2	2	0	5	11	2	0	5	1	**41**
Nematoda: undet.																	
undet.	undet.	2	0	1	0	79	0	181	3	2	0	0	0	0	0	0	**268**
Platyhelminthes: Trepaxonemata: undet.																	
undet.	undet.	1	0	2	1	6	6	0	2	5	1	4	0	0	1	0	**29**
Macroinvertebrate Community Metrics																	
Taxa Richness		63	44	57	66	69	63	60	58	71	59	60	44	37	55	44	-
BMWP Score		149	118	144	149	158	172	149	164	149	154	137	123	105	146	123	-
Abundance		1029	925	1328	893	2189	1701	2129	1696	4696	1400	1225	357	340	608	962	-
Density		1007	905	1299	874	2356	1664	2083	1660	4595	1370	1199	349	333	595	941	-
Shannon's Diversity (H)		3.00	2.91	2.83	3.21	2.65	2.76	2.10	2.49	3.07	2.84	2.96	2.97	2.64	3.22	2.97	-
Shannon's Evenness (EH)		0.72	0.77	0.70	0.77	0.63	0.67	0.51	0.61	0.72	0.70	0.72	0.78	0.73	0.80	0.79	-

Table A.3: Full list of fish taxa, by reach. Codes correspond to the "Study Reach Code" in Table A1. Organized as in Bussing (1998). Numbers are raw abundances from the study. P indicates present, but not caught. * indicates possibly caught but not identified, in just one case. For individuals not caught as part of the study, # caught, location, and date of capture are listed.

Family	Scientific Name	Rama-Kriol Name	IR18MC	IR18GU	IR18BV	IR18ST	IR18LF	CR18BT	CR18MG	CR18CO	RP18EC	RP18LA	RP18SA	KR18PA	KR18EL	KR18CH	KR18LM
Osteriophysi: Characiformes																	
Characidae	Characidae spp. (likely *Astyanax* spp.)	Bilam	20+	20+	3	20+	20+	20+	20+	20+	20+	20+	20+	20+	20+	20+	20+
	Bramocharax bransfordii	Bilam	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
	Brycon guatemalensis	Machaca	7	17	0	19	0	1	1	0	0	9	1	0	0	1	0
	Roeboides bouchelli	Bilam	1	0	0	3	0	0	0	0	12	26	3	3	3	6	0
Osteriophysi: Siluriformes																	
Heptapteridae	*Rhamdia nicaraguensis*	Mulung	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
	Rhamdia sp.	Mulung	0	0	1	0	0	1	0	1	0	0	0	P	8	0	1
Loricariidae	*Hypostomus* sp.	Devil Fish	1 spec. from Indian R. near Guinea Creek, May 23, 2017. Species likely H. niceforoi (N Lujan, pers. comm.)														
Acanthopterygii: Cyprinodontiformes																	
Poeciliidae	*Alfaro cultratus*	Tush-Tush	0	0	P	0	0	0	1	0	0	0	1	0	0	0	0
	Phallichthys amates	Tush-Tush	0	0	P	0	0	0	0	0	0	0	0	0	0	0	0
	Poecilia gillii	Tush-Tush	0	2	*	0	1	19	1	9	8	35	11	P	0	5	0
	Priapichthys annectens	Tush-Tush	0	0	P	0	3	0	0	0	0	0	0	0	0	0	0
Acanthopterygii: Atheriniformes																	
Atherinopsidae	*Atherinella hubbsi*	NA	1 specimen from Indian River near She Tiger Creek, May 23, 2017, verified by A Angulo Sibaja, UCR														
Acanthopterygii: Mugiliformes																	
Mugilidae	*Agonostomus monticola*	Salin	2	8	4	10	1	1	1	4	4	11	6	0	1	8	3
	Joturus pichardi	Salin/Bobo	1 specimen from Indian River near She Tiger Creek, May 26, 2017, verified by J Betts														
Acanthopterygii: Perciformes																	
Caranjidae	*Caranx* sp.	Jackfish	1 specimen from Indian River near Long Falls Creek, Mar. 13, 2018, verified by A Angulo Sibaja, UCR														
Haemulidae	*Pomadasys* sp.	Droma	1 specimen from Indian River near Guinea Creek, Feb. 21, 2018, verified by A Angulo Sibaja, UCR														
Cichlidae	*Amatitlania nigrofasciata*	Contrayat	0	6	0	2	0	1	1	1	17	25	24	6	3	6	3
	Amatitlania septemfasciata	Contrayat	1	2	31	1	5	12	6	14	0	0	0	0	0	0	0
	Amphilophus citronellus	NA	1 specimen from Indian River near Guinea Creek, Feb. 25, 2018, verified by A Angulo Sibaja, UCR														
	Cribroheros alfari	Shine-Thru	9	32	32	6	7	16	18	10	9	33	11	2	0	2	0
	Cribroheros rostratus	Shine-Thru	1 specimen from Indian River near Long Falls Creek, Feb. 19, 2018, verified by J San Gil, UCR														

Table A.3 (cont'd)

	Hypsophrys nicaraguensis	NA	1 specimen from Indian River near Long Falls Creek, Feb. 19, 2018, verified by A Angulo Sibaja, UCR														
	Neetroplus nematopus	Contrayat	0	9	0	2	0	0	0	0	0	0	0	0	0	0	0
	Parachromis dovii	Sasin	13	9	0	9	0	2	8	8	4	13	8	4	0	1	1
	Parachromis loisellei	Sasin	1 specimen from Indian River near Guinea Creek, Feb. 21, 2018, verified by J San Gil, UCR														
	Tomocichla tuba	Moga	0	8	0	9	0	0	0	0	0	7	0	0	10	6	P
	Vieja maculicauda	Tuba	1 specimen from Corn River near Chirripo Creek, Apr. 8, 2018, verified by J Betts in field														
Gobiidae	*Awaous banana*	NA	0	1	0	0	0	0	P	P	0	1	1	0	1	0	0
	Sicydium altum	NA	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0
Eleotridae	*Eleotris pisonis*	Elik	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
	Gobiomorus dormitor	Elik	0	1	0	2	0	3	P	2	1	3	1	0	0	1	1

Fish and Shrimp Community Metrics

Fish Taxa Richness	7	14	8	12	6	10	13	10	8	11	11	7	7	10
Cichlid Abundance	23	64	63	29	12	31	33	33	30	78	43	12	13	15
Shrimp Abundance	8	16	8	8	4	9	10	10	10	9	0	3	1	4

APPENDIX B

Additional statistics and graphs.

Table B.1: Correlations of taxa response metrics. Pearson's R and P are listed. Bolded items are significant (p≤0.05).

		Invert. Taxa Richness	**BMWP Score**	**Invert. Density (LN)**	**Invert. Diversity (H)**	**Invert. Evenness (EH)**	**Fish Taxa Richness**	**Cichlid Abundance (LN)**	**Shrimp Abundance**
Invert. Taxa Richness	**R**	-	0.839	0.787	0.034	-0.417	0.060	0.324	0.250
	P		**0.000**	**0.000**	0.905	0.122	0.831	0.238	0.368
BMWP Score	**R**	0.839	-	0.674	-0.156	-0.53	0.117	0.325	0.326
	P	**0.000**		**0.006**	0.578	0.042	0.678	0.238	0.235
Invert. Density (LN)	**R**	0.787	0.674	-	-0.266	-0.589	0.117	0.333	0.439
	P	**0.000**	0.006		0.338	**0.021**	0.678	0.225	0.101
Invert. Diversity (H)	**R**	0.034	-0.156	-0.266	-	0.893	-0.141	-0.122	-0.173
	P	0.905	0.578	0.338		**0.000**	0.616	0.665	0.538
Invert. Evenness (EH)	**R**	-0.417	-0.53	-0.589	0.893	-	-0.178	-0.279	-0.278
	P	0.122	**0.042**	**0.021**	**0.000**		0.526	0.314	0.315
Fish Taxa Richness	**R**	0.060	0.117	0.117	-0.141	-0.178	-	0.632	0.575
	P	0.831	0.678	0.678	0.616	0.526		**0.011**	**0.025**
Cichlid Abundance (LN)	**R**	0.324	0.325	0.333	-0.122	-0.279	0.632	-	0.635
	P	0.238	0.238	0.225	0.665	0.314	**0.011**		**0.011**
Shrimp Abundance	**R**	0.250	0.326	0.439	-0.173	-0.278	0.575	0.635	-
	P	0.368	0.235	0.101	0.538	0.315	**0.025**	**0.011**	

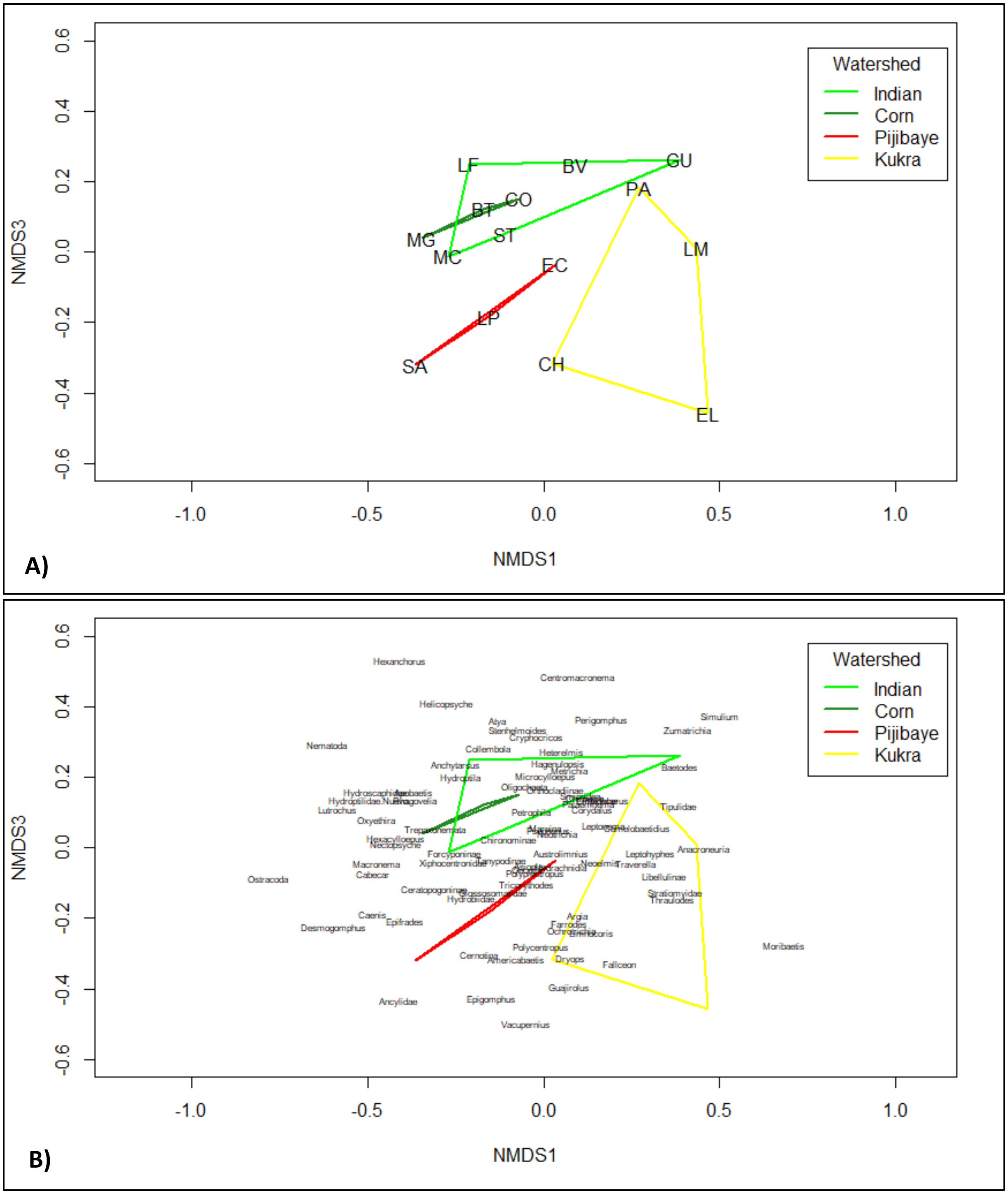
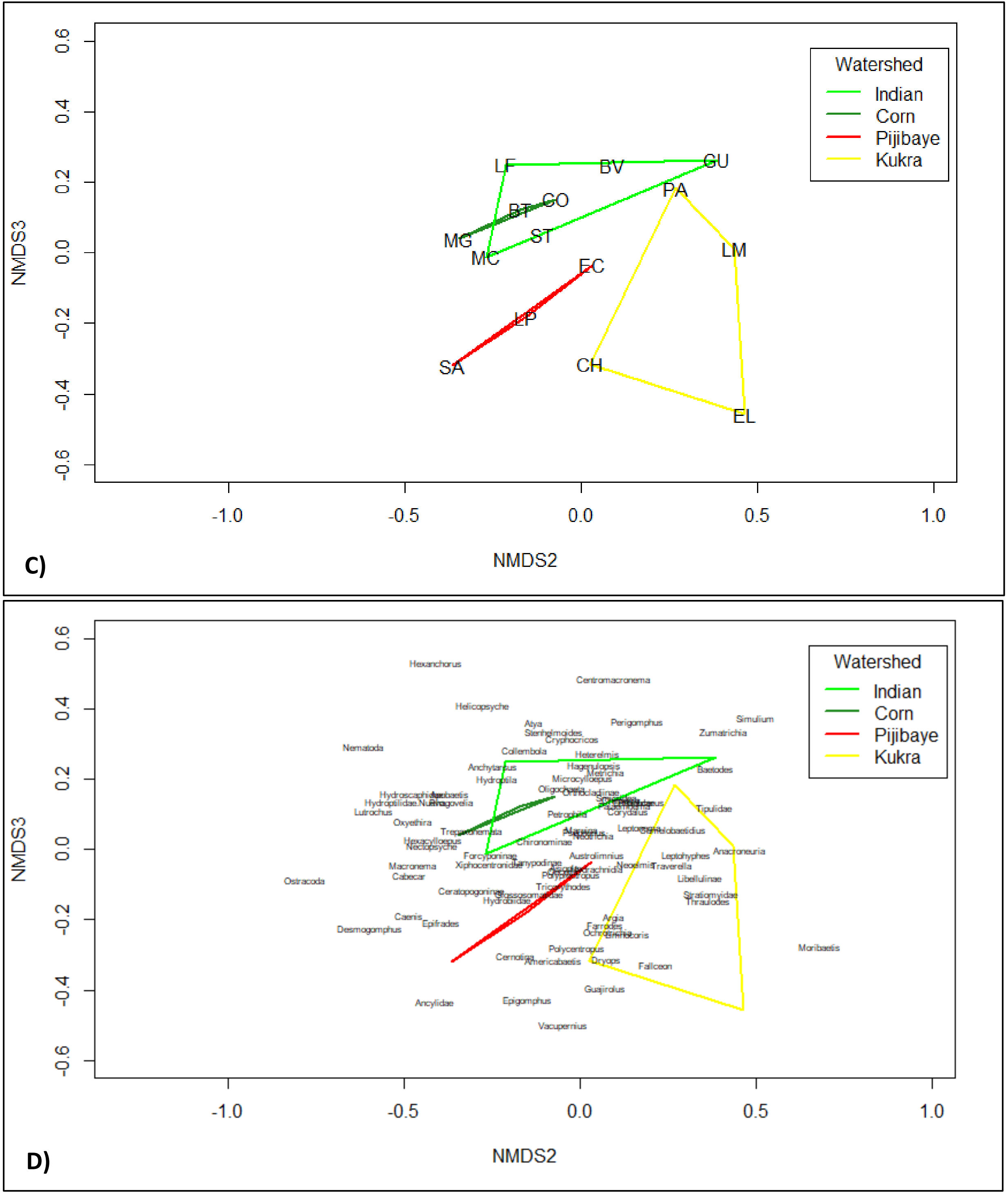


Figure B.1: Non-metric multidimensional scaling ordination plots of macroinvertebrate community matrix (taxa densities by reach). Axis combinations not featured in the main text are visualized. Polygons show watershed groupings. According to PERMANOVA, reaches group significantly as forested (Indian, N=5 and Corn, N=3) and deforested (Pijibaye, N=3 and Kukra, N=4) (F=1.88, p=0.0317). Reaches group with higher significance by watershed (F=2.445, p=0.0001). **A)** Ordination plot of Axis 1 and 3 with reaches visualized. **B)** Ordination plot of Axis 1 and 3 with taxa visualized.

Figure B.1 (cont'd)



C) Ordination plot of Axis 1 and 3 with reaches visualized. **D)** Ordination plot of Axis 1 and 3 with taxa visualized.

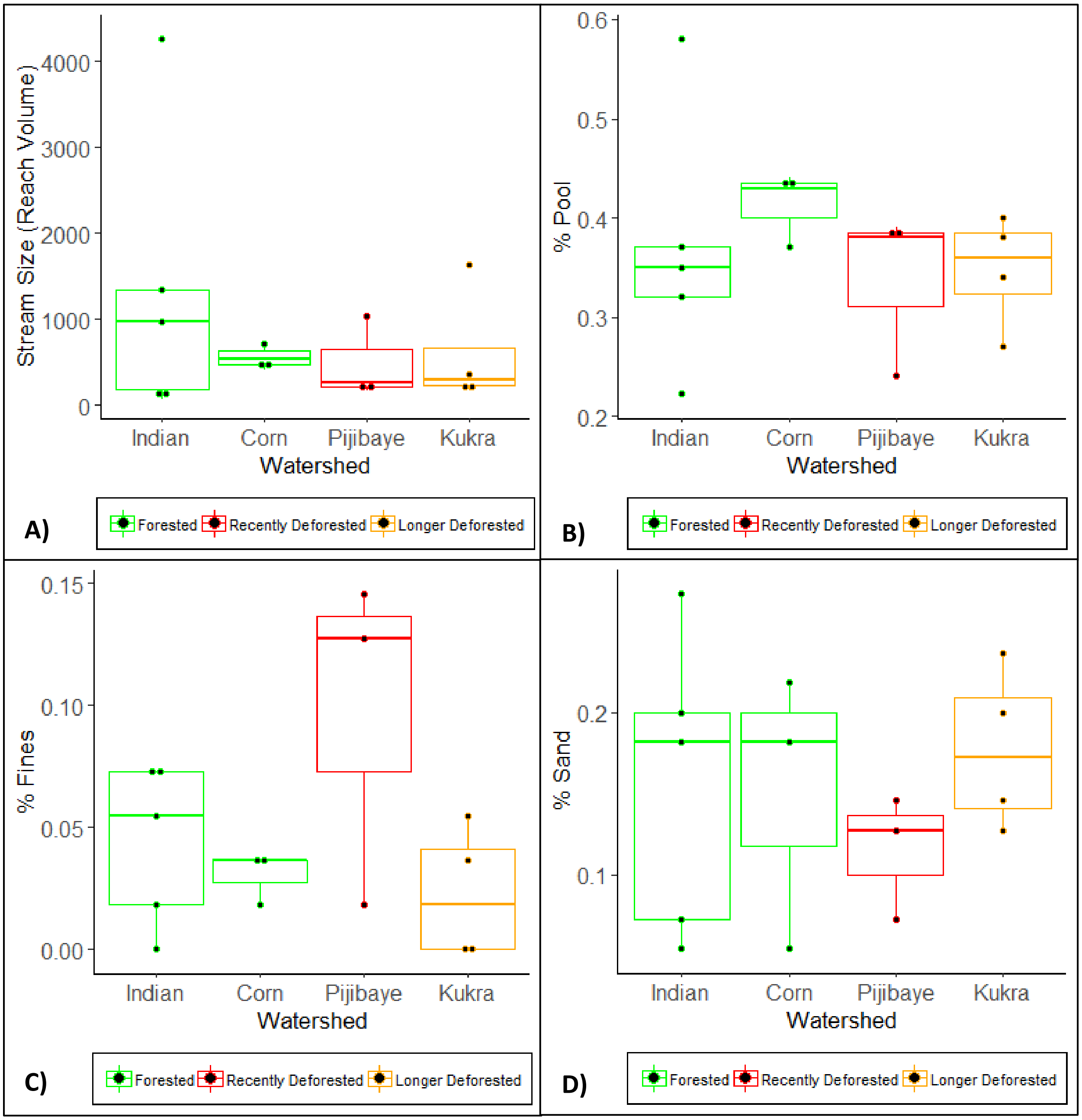
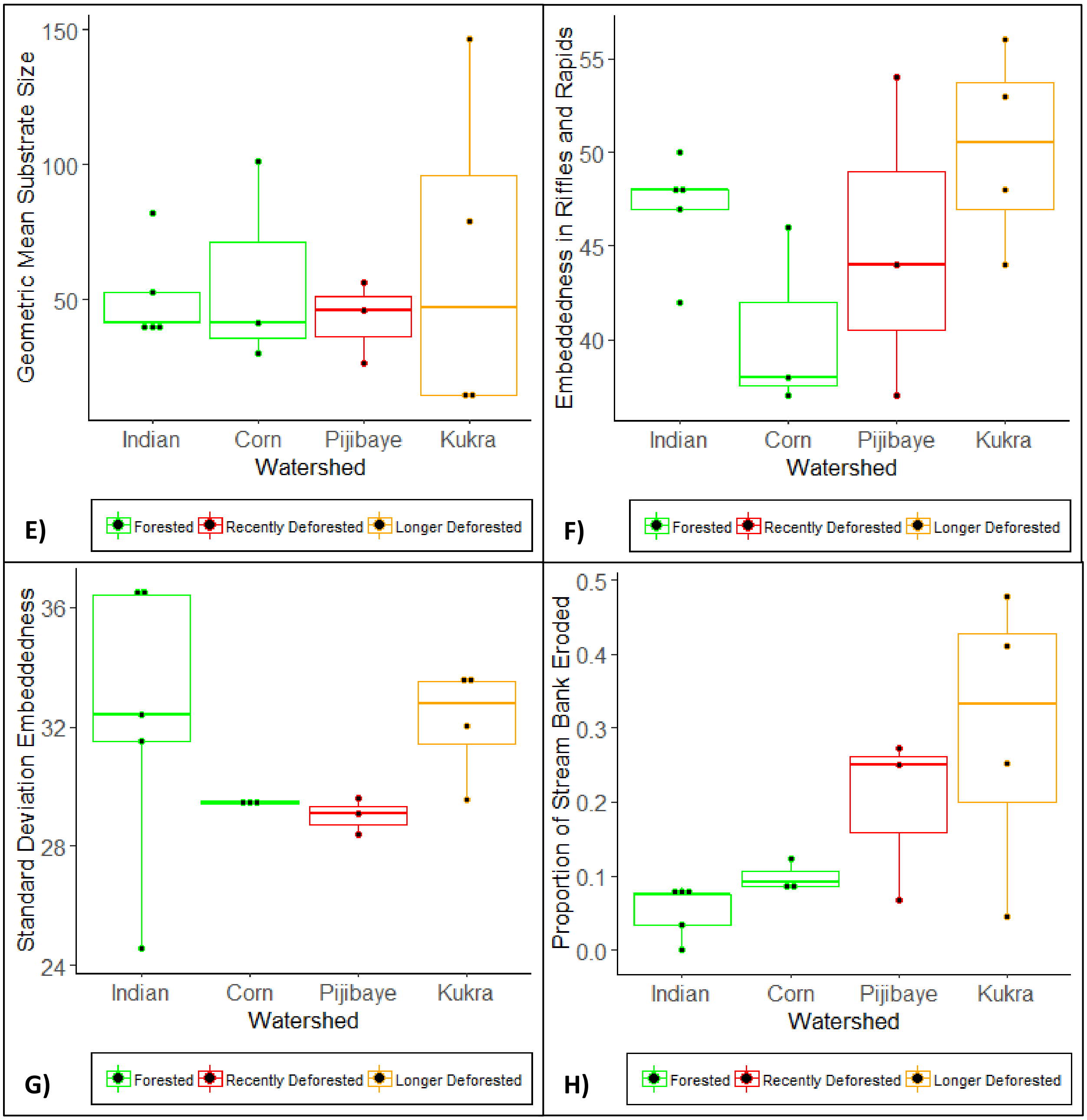


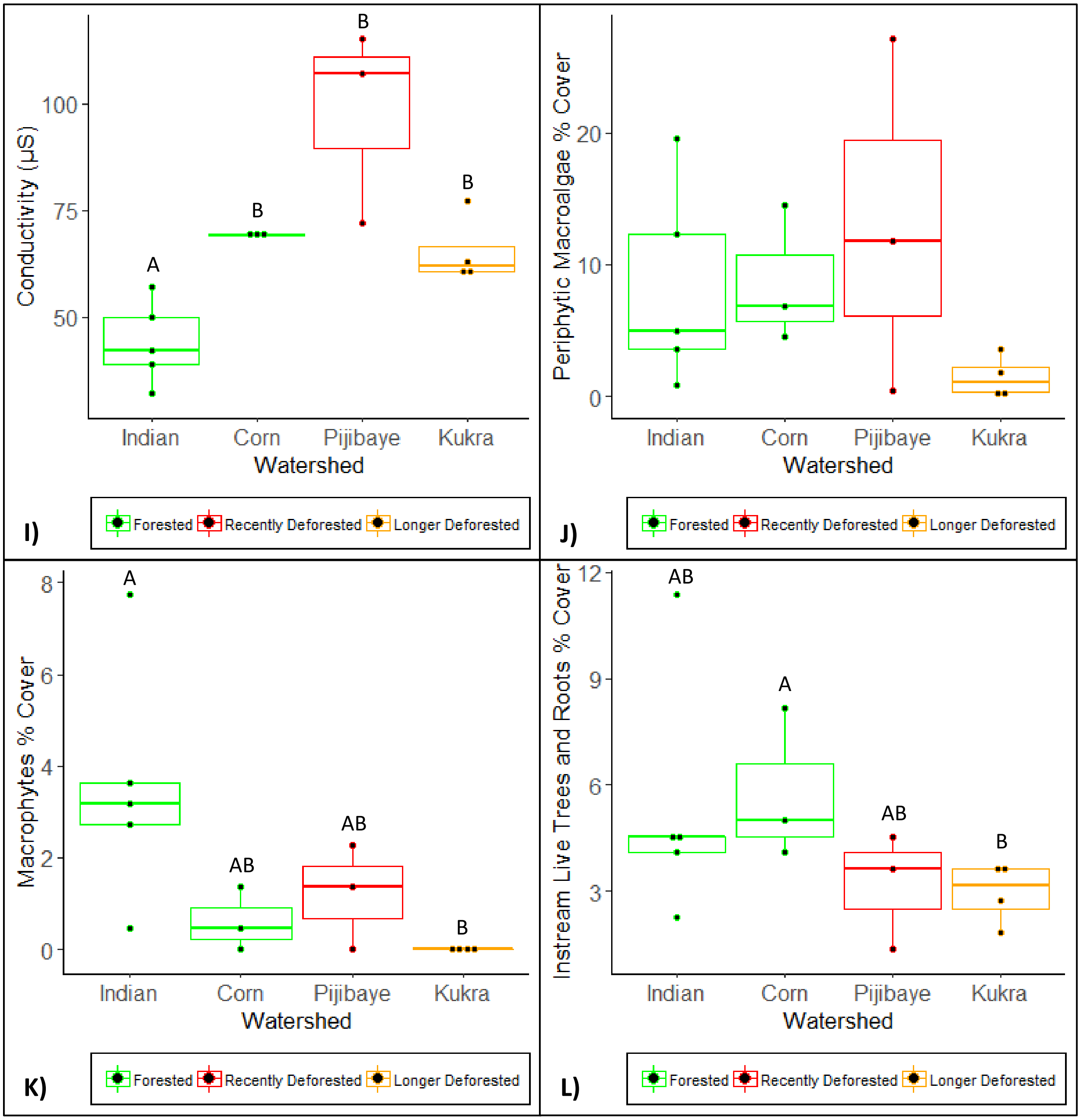
Figure B.2: Habitat metrics for two forested watersheds a recently and less recently deforested watershed. A) Stream size (reach volume in M^3). **B)** % Pool. **C)** % Fines. **D)** % Sand. Reach values represented by points. See methods for calculations of values (Most values based on mean of 11 transects and associated subsamples). Mann-Whitney U tests were carried out lumping forested and deforested reaches. Kruskal-Wallis and pairwise Mann-Whitney U nonparametric tests were run between each watershed (see Table 4). Letters represent significance groupings of watersheds ($\alpha = 0.05$). No letters implies no significance.

Figure B.2 (cont'd)



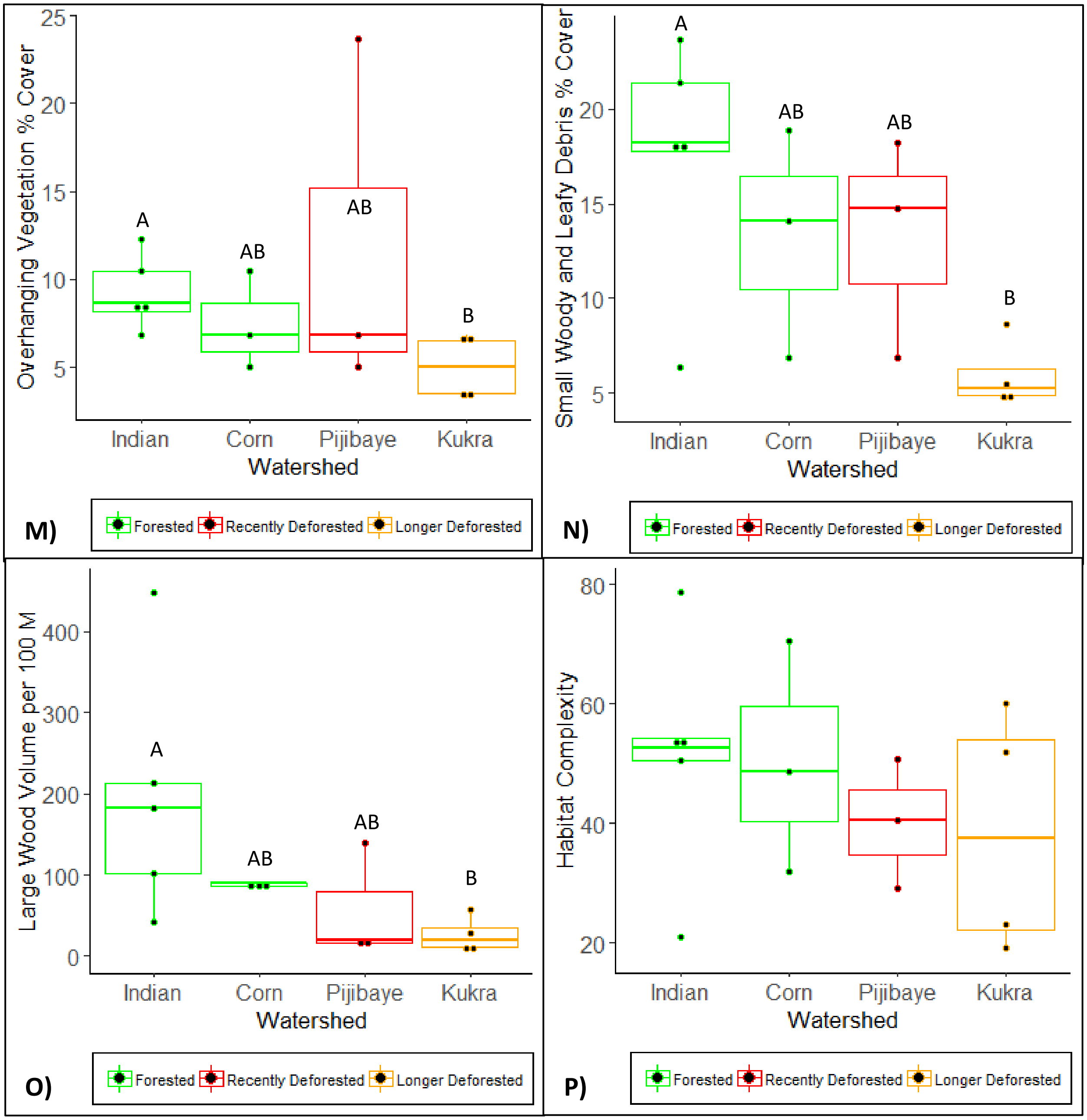
E) Geometric mean substrate size. **F)** Embeddedness in riffles and rapids **G)** Standard deviation of embeddedness. **H)** Proportion of stream bank eroded.

Figure B.2 (cont'd)



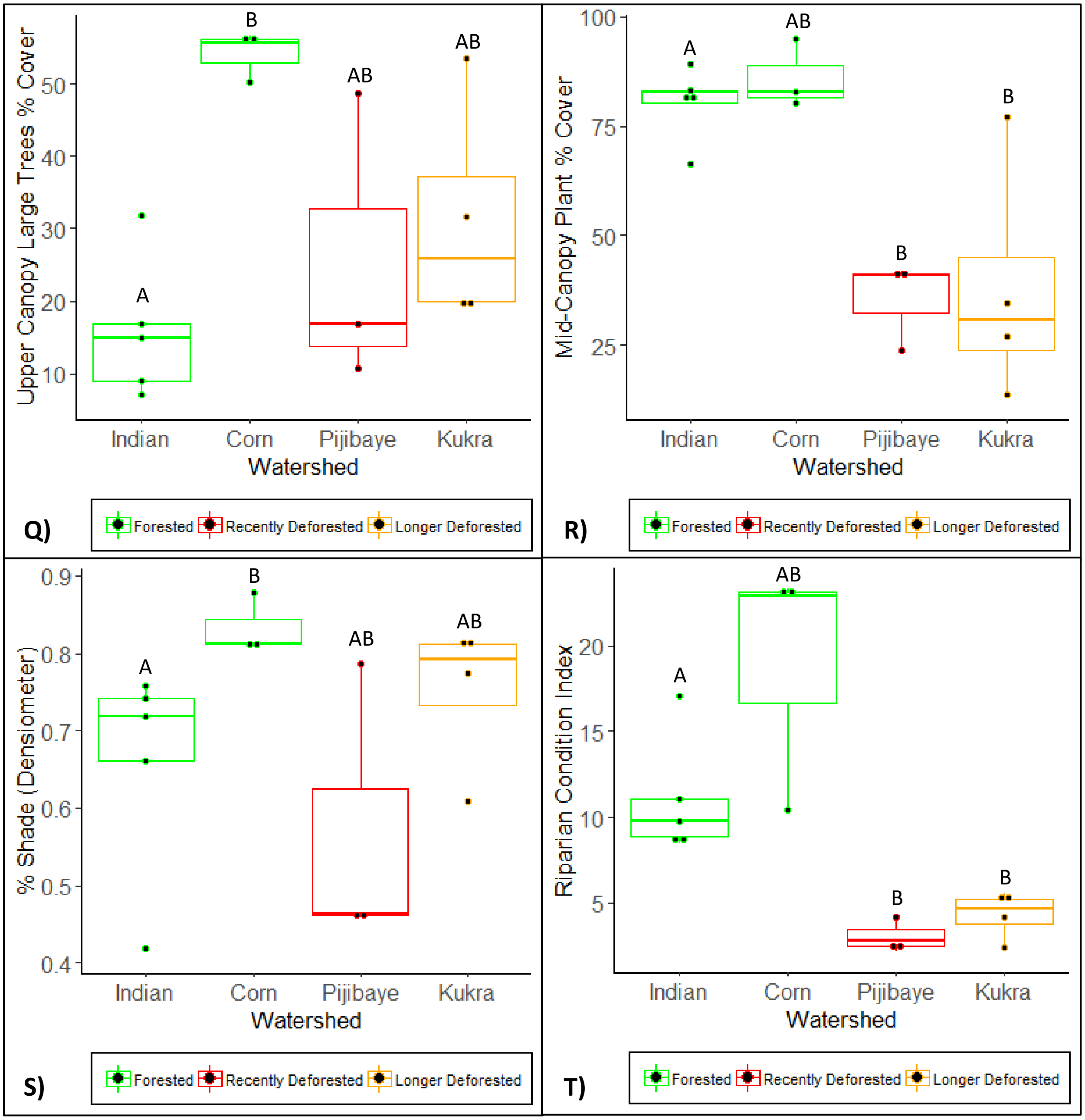
I) Conductivity (µS) **J)** Periphytic macroalgae % cover. **K)** Macrophytes % cover**. L)** Instream live trees and roots % cover

Figure B.2 (cont'd)



M) Overhanging Vegetation % Cover **N)** Small Woody and Leafy Debris % Cover. **O)** Large Wood Volume per 100 M**. P)** Habitat Complexity.

Figure B.2 (cont'd)



Q) Upper canopy large trees % cover**. R)** Mid-canopy plant % cover**. S)** % Shade (densiometer). **T)** Riparian condition index.

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