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Ecological Indicators

Low forest-loss thresholds threaten Amazonian fish and macroinvertebrate assemblage integrity

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ABSTRACT

Deforestation is a major threat globally, but especially in tropical regions because they are biodiversity strongholds and carbon storehouses. Some studies have reported changes in species richness and composition in lotic ecosystems with increased forest-loss in their catchment, presumably resulting from the replacement of sensitive taxa by more resistant or tolerant taxa. Also, sensitive taxa respond to deforestation in a non-linear manner and fish and macroinvertebrates have different sensitivities to landscape pressures. Therefore, it is useful to determine the effects of forest-loss on widespread sensitive or threshold taxa in aquatic ecosystems. We used Threshold Indicator Taxa Analysis (TITAN) to assess forest-loss and land use history impacts in 92 eastern Amazonian stream sites. We determined TITAN peak-change thresholds for fish at 1% and 6% of forest-loss at total-catchment and local-riparian spatial extents, respectively, and at 2% and 40% of land-use intensity change at total-catchment and local-riparian spatial extents, respectively. For macroinvertebrates, TITAN peak-change thresholds were 1% and 11% of forest loss at total-catchment and local-riparian spatial extents, respectively, and at 3% of land-use intensity change for both total-catchment and local-riparian spatial extents. Because of these thresholds, inherent ecoregional variability and key literature, we have three major recommendations. 1) Logging should be prohibited in riparian reserves that are at least 100-m wide on each side of headwater streams and in a network of catchments across all biomes and as many landscape types as possible. 2) An ecologically and statistically rigorous monitoring program with standard methods should be implemented to assess and regulate land uses better. 3) Conservation planning areas should consider aquatic biota as well as terrestrial biota.

1. Introduction

Deforestation is a global phenomenon, but it has accelerated in recent decades in tropical and subtropical regions because of increased demand for agricultural products (Laurance et al., 2014). This has been especially true in Brazil, where 18% of its Amazonian forest, 88% of its Atlantic Forest, and 80% of its Cerrado (neotropical savanna) have been converted to agricultural uses (Ribeiro et al., 2009; Ferreira et al., 2012;

Strassburg et al., 2017). Such conversions result in degraded physical habitat, water quality and biota in the streams draining previously forested catchments (Leal et al., 2016; Leitão et al., 2018; Silva et al., 2018; Hughes et al., 2019). Recently, Brazilian President Bolsonaro has continued to encourage further deforestation in Amazonia to bolster economic growth (Ferrante and Fearnside, 2019; Pereira and Vioa, 2019; Pelicice and Castello, 2021). Such a policy ignores the global importance of its rainforest in mitigating climate change (Baker and Spracklen, 2019; McGuffie et al., 1995), its role in providing drinking water for the entire nation (Baker et al., 2015), the increasing threats of uncontrolled wildfires (Brando et al., 2014; Barlow et al., 2020), its projected human emigration rate because of an unsuitable human climate niche (Xu et al., 2020) and its enormous reservoir of biodiversity (Barlow et al., 2007; Nobre et al., 2016; Leal et al., 2020). Most Amazonian biodiversity research has focused on terrestrial biota (e.g., Peres et al., 2010). However, threats to aquatic biota, particularly fishes and macroinvertebrates, have indicated that they are especially sensitive to small amounts of deforestation (Chen et al., 2017; de Faria et al., 2017; Oliveira-Júnior et al., 2017; Leitão et al., 2018, Cunha et al., 2020; Dala-Corte et al., 2020). The multi-faceted effects of climate change are expected to multiply these threats (Ripple et al., 2017; Masson-Delmotte et al., 2019; AFS, 2020) and this makes it essential to buffer streams by reducing deforestation. For example, increased water temperatures and reduced flows have already, and are predicted to, alter fish assemblage composition and reproductive dynamics and decrease survival and body size (Winfield et al., 2016). Such alterations can extirpate macroinvertebrate and fish species and impair ecosystem processes (Lawrence et al., 2010; Colvin et al., 2019), amplifying the negative effects of deforestation on aquatic biota.

To better assess the sensitivities of aquatic biota, it is useful to examine their threshold responses to anthropogenic stressors and pressures, instead of assuming linear responses (With and King, 1999; Davies and Jackson, 2006; Baker and King, 2010; King and Baker, 2010). Although the vast majority of threshold studies have focused on a single assemblage, it is important to assess threshold responses of different groups of organisms (e.g., fish and macroinvertebrates) because they play different roles in ecosystems and have differing sensitivities to stressors and pressures (Chen et al., 2017). For example, fish assemblages have been reported to be more sensitive than macroinvertebrates to landscape disturbance (Brazner et al., 2007; Montag et al., 2019), stream morphology alterations (Hughes et al., 2009), hydrological perturbations (Marzin et al., 2012a) and excess salinity (USEPA, 2016). On the other hand, macroinvertebrate assemblages were determined to be more sensitive than fish to excess fine sediments (Bryce et al., 2010), substrates (Juen et al., 2016), riparian vegetation (Oliveira-Junior et al., 2019), nutrients (USEPA, 2016) and water quality (Herlihy et al., 2020). However, Herlihy et al. (2020) reported that the relative strength of predictor variables varied considerably among nine USA ecoregions for both fish and macroinvertebrate assemblages and that local predictors usually explained more assemblage variability than catchment predictors.

1.1. TITAN: Global examples

TITAN (Threshold Indicator Taxa Analysis) has been shown to be especially useful for indicating the early (threshold) effects of land-use changes to sensitive taxa in some different settings, whether those taxa are genera, species, or putative species. Hilderbrand et al. (2010) reported that half the macroinvertebrate taxa could be lost from Maryland Piedmont streams when impervious catchment cover reached as little as 3%. In Thuringia, Germany, mountain stream sites at 4% urban land use in the upstream catchment resulted in a threshold decline in 5 macroinvertebrate taxa (Kail et al., 2012). In Texas, USA, intermittent stream sites at 3–11% impervious cover experienced a threshold decline in EPT (Ephemeroptera, Plecoptera, Trichoptera) taxa densities (King et al., 2016). In the Llanos region of Colombia, Pardo et al. (2018)

estimated thresholds of 45–75% oil palm cover for declines in mammalian species composition. In an assessment based on data from four continents (eight nations) and employing gradient forest analysis, Chen and Olden (2020) determined that freshwater fish assemblages demonstrated thresholds at 1–12% of catchment urbanization and 2–37% of catchment agriculture. They also determined that relative species abundances were more sensitive than total species richness and New Zealand, South Korea and Sweden had low thresholds for both urbanization (1.8–4.4%) and agriculture (2.5–6.4%). Thresholds differ by the assemblage, land use type, and geographic area studied.

1.2. TITAN: Brazil macroinvertebrates

TITAN was used in six recent Brazilian studies for assessing land use effects on aquatic macroinvertebrates. Shimano and Juen (2016) reported that the ephemeropteran, *Miroculis*, showed threshold declines in Pará state streams near oil palm plantations. Rodriguez et al. (2016) found negative threshold responses at 40–60% native riparian vegetation loss for six damselfly (Odonata) species (*Argia modesta, A. smithiana, A. subapicalis, Enallagma novaehispaniae, Epipleoneura venezuelensis, Hetaerina mortua*) in the Cerrado biome of Mato Grosso do Sul state. Studying Cerrado streams in Minas Gerais state, Firmiano et al. (2017) found Ephemeroptera genera at a threshold of < 1% of catchment urbanization (*Caenis*) and human riparian disturbance at a threshold of one-third of a site's 22 riparian plots (*Campylocia, Cryptonympha, Leptohyphodes, Miroculis*). Giehl et al. (2019) reported that *Ambrysus* (Heteroptera) reflected a negative change point threshold of 0.8 in site habitat integrity of Mato Grosso state streams. Brito et al. (2020) observed thresholds in macroinvertebrate assemblages at 9% of catchment forest loss and 1% of riparian forest loss in Pará (Amazonian) streams. However, they reported change points for taxa richness at 57% and 79% of the catchment and riparian forest-loss, respectively, indicating the weakness of total taxa richness for separating early decreases of sensitive from co-occurring increases in tolerant taxa. Dala-Corte et al. (2020) determined that thresholds for the effects of native riparian vegetation loss on macroinvertebrates varied by buffer extent, biome and assemblage, ranging from 2.9% (Amazonian, 50-m buffer) to 37% (Atlantic Forest, 500-m buffer). Thresholds were higher for larger riparian buffers. Generally, thresholds were lower for macroinvertebrates than for fish. Thus, for macroinvertebrates, thresholds differ by the assemblage, ecological indicator, study area extent, anthropogenic pressure, and biome studied.

1.3. TITAN: Brazil fish

Three recent Brazilian studies have used TITAN for assessing land use effects on fish assemblages. Ferreira et al. (2018) determined that total species richness was a poorer indicator of thresholds than species composition for assessing the effects of oil palm plantations on fish assemblages in Pará state (Amazonian) streams. They listed three species with thresholds that responded negatively to those plantations (*Apistogramma agassizii, Aequidens tetramerus, Microcharacidium weitzmani*). Sampling 75 stream sites in Rondônia state (Amazonian), Brejão et al. (2018) observed negative threshold responses in 10 and 6 species at < 10% catchment deforestation and < 10% riparian deforestation, respectively. *Pyrrhulina australis, Gymnotus coropinae, Brycoella pallidifrons*, and *Elachocharax pulcher* reflected negative threshold responses at both spatial extents. Dala-Corte et al. (2020) reported negative threshold responses in fish assemblages to native riparian vegetation loss ranging from 0.5% (Pampa, 50 m riparian buffer) to 77.4% (Atlantic Forest, 500 m buffer). As with macroinvertebrates, the thresholds were higher, the greater the riparian buffer. Clearly, the threshold responses of fish assemblages differ by the spatial extents and geographical regions of the studies.

As indicated above, TITAN offers useful early-warning signals of further ecological damage that can alert scientists and managers of

impending damages should such activities proceed or be considered elsewhere, thereby aiding the development of more protective land use standards (Hilderbrand et al., 2010, Roque et al., 2018, Chen and Olden, 2020). Therefore, our study of Amazonian streams had three objectives: 1) determine the levels of catchment and riparian forest loss and land use intensity that yield negative threshold responses in fish and macroinvertebrate taxa; 2) determine if macroinvertebrate taxa are more sensitive to catchment-extent or local riparian-extent forest loss and land use intensity than fish; and 3) determine fish and macroinvertebrate taxa that serve as early-warning signals of ecological damage from proposed deforestation projects. Based on the published literature, we expected to find that: 1) very low levels of forest loss and land use intensity would result in loss of sensitive taxa; 2) forest-dependent fish and macroinvertebrate taxa would show earlier responses to total catchment forest loss than local riparian forest loss; and 3) the number of sensitive macroinvertebrate taxa would be greater than the number of sensitive fish taxa and macroinvertebrates would show earlier responses than fish, both because of the greater number of macroinvertebrate taxa and the greater sensitivities of many macroinvertebrate taxa.

2. Methods

2.1. Study area & design

We sampled 92 wadeable stream sites within five river basins in the Paragominas (PGM) and Santarém-Belterra (STM) districts of Pará state, Brazil (Gardner et al., 2013). The sites were 150-m long and selected following field reconnaissance visits. The sites were chosen to encompass a gradient in the extent of riparian and catchment forest cover, resulting in 5, 32, 6, 25 and 24 sites in the Amazon (STM), Curuá-Una (STM), Tapajós (STM), Capim (PGM) and Gurupi (PGM) River basins, respectively (Appendix S1). There were too few sites in the Amazon and Tapajós basins for meaningful analyses, but the ranges in both catchment and riparian forest loss and land use intensity were slightly less in the Capim basin. We sampled 43 and 49 sites in June-August 2010 (Santarém-Belterrra) and 2011 (Paragominas), respectively. Our study comprised two different years, but year lacked a clear effect on our results. We observed no changes in weather or land/water use during those two years—certainly not relative to the historical natural and anthropogenic differences between municipalities (Chen et al., 2017)– nor did our sampling methods differ between years (Hughes and Peck, 2008). Furthermore, we restricted sampling to the dry season to limit the 'noise' of seasonal and daily weather variations (Hughes and Peck, 2008; Heino, 2014; Oliveira-Júnior & Juen, 2019).

Although our study design was based on a disturbance gradient instead of a probability design (Stevens and Olsen, 2004; Silva et al., 2018), we ensured that each site was located in a different named stream and sub-basin to minimize site autocorrelation (Leitão et al., 2018; Leal et al., 2020). Furthermore, the sites were dispersed across relatively large study areas (~1 million ha in Santarém-Belterra and ~ 1.9 million ha in Paragominas) to ensure that we captured the inherent natural variability in each study area. In addition, the sites varied widely in catchment area, slope, forest cover, agriculture and road crossings, as well as in riparian forest cover and forest change profile (Leal et al., 2016). This site distribution led to much higher among-site and among-basin taxa diversity than within-site taxa diversity, indicating that the taxa among basins and the sites within the basins are distinctly different from each other because of their high (78–82%) taxa turnover (replacement) versus taxa nestedness (addition or subtraction) (Leal et al., 2018). The Amazon, Curuá-Una and Tapajós sites in the Santarém-Belterra district are located near the Tapajós-Amazon Rivers confluence, and the Amazon and Tapajós sites are direct tributaries to those great rivers. The Capim and Gurupi sites in the Paragominas district were located 1400 km east and drained into the Tocantins-Araguaia River basin, which discharges into the Amazon River delta.

The state has a tropical climate with an average annual temperature

of 27 °C, an annual average rainfall of ~ 200 cm and a June-August dry season (~6 cm rainfall per month). Most of the landscape in both districts is covered by tropical rainforest, but various kinds of crops are grown, creating mosaics of primary and secondary forests, silviculture, pastures, croplands, and small villages. Santarém-Belterra was colonized over 350 y ago and has been intensively farmed for over 100 y, but cattle ranching and silviculture only began in earnest in Paragominas 60 y ago. Although both districts have comparable levels of cropland (2–4%), pasture (4% versus 21%) and secondary forest (10% versus 18%) are more prevalent in Paragominas. Primary forest is more common in Santarém-Belterra (84% versus 58%), but some of that forest in both districts has been degraded by selective logging, fire, and fragmentation (Barlow et al. 2016).

2.2. Land use assessment

Channel networks and catchment boundaries were determined from 30-m resolution elevation data from Shuttle Radar Topography Mission (SRTM) and hydrological modeling in ArcSWAT (Di Luzio et al., 2004). Annual Landsat TM and ETM imagery (30-meter resolution) from 1985 to 2010 were classified by the likelihood supervised method using bands 3, 4 and 5 (Leal et al., 2016). Using annual land-use maps, we determined the current amount of forest loss (forest loss) and the rate of accumulated forest loss via the Land Use Intensity index (LUI; Ferraz et al., 2009). Unlike current forest loss, the LUI considers the average time since deforestation. Percent non-forest cover was calculated for 2010 for the catchment above each site (total-catchment forest loss) and for a 100-m riparian buffer along both sides of each site (local-riparian forest loss; Leal et al., 2016). As complementary information, the degree of local deforestation was also estimated during site reconnaissance and during riparian forest cover assessments performed every 15 m at each site (Leal et al., 2016). The LUI was also calculated for both extents (total-catchment, local-riparian). A 100-m buffer was used because at the 30-m resolution of our land cover data, narrower buffers would tend to simply indicate forested or unforested, instead of a forest-loss gradient. Also, 100-m riparian buffers were recommended by Valle et al. (2013) for tropical forest streams and FEMAT (1993) for temperate forest streams. The same buffer widths were employed by Brejão et al. (2018) for Amazonian fish assemblages. Dala-Corte et al. (2020) reported that 100-m buffers had the least variable and lowest thresholds for Amazonian macroinvertebrate assemblages compared with 50, 200 and 500-m buffers, as well as the lowest forest-loss thresholds for fish assemblages in Atlantic Forest streams.

2.3. Biological sampling

Aquatic macroinvertebrate assemblages were sampled in three different ways in the mornings and before physical habitat structure or fish sampling disrupted stream substrates. Ephemeroptera, Plecoptera and Trichoptera (EPT) were sampled by disturbing 900 cm^2 of substrate upstream of a D-frame net (1 mm^2 mesh) at 10 systematic points 15 m apart and distributed in a zigzag pattern (left margin, midstream, right margin, left margin as described in Hughes and Peck, 2008). Heteroptera (Gerromorpha) were sampled from the water surface over the entire site using a hand sieve (18 cm diameter; 0.5 mm mesh; Dias-Silva et al., 2010; Cunha and Juen, 2020). Samples were washed in the field to remove fragile organisms, placed in plastic jars and preserved with 93% ethanol for subsequent taxonomic identification of all individuals in the samples to genus or species in the laboratory. Adult Odonata were collected for 90 min throughout each site using an insect net (65 cm deep, 40 cm diameter; Oliveira-Junior et al., 2017). Aquatic macroinvertebrate genus and species richness are known to increase with increased sampling effort at sites (Li et al., 2001; 2014;; Silva et al., 2016) because of high levels of within-site diversity (Ligeiro et al., 2010) driven by rare taxa (Cao et al., 2002; Schneck and Melo, 2010). However, Cao et al. (2002) showed that site classification strength stabilized

at 10 Surber samples and Li et al. (2014) reported that 5–10 samples usually yielded 70% of true taxa richness at sites through use of Jaccard similarity replicate analysis. For Odonata sampled in the manner we employed, Oliveira-Junior et al. (2015) reported 79% sampling efficiency in Amazonian stream sites as indicated by species accumulation curves and 78% for species-area rarefaction curves. Voucher specimens are located in, and their identifications were verified to genus or species at, the Instituto Nacional de Pesquisas da Amazônia (INPA) insect collection or the Universidade Federal do Pará Zoological Museum (Odonata and Heteroptera).

Fish assemblages were usually sampled in the afternoons throughout the entire 150-m long sites for 2 h by 2 persons using seines (6 × 1.5 m; 5 mm mesh) and semi-circular hand nets (0.8 m diameter; 2 mm mesh) (Leitão et al., 2018). As with macroinvertebrates, the level of sampling effort needed to determine true fish species richness is driven by the proportion of spatially rare species (Cao et al., 2002; Terra et al., 2013; Hughes et al., 2021). Our site lengths were 50 m longer than those reported by dos Anjos and Zuanon (2007) to yield 70–94% of true fish species richness in Amazonian stream sites as estimated from Jackknife, Bootstrap and species accumulation curves. Similarly, our site lengths were 50 m longer than the minimum lengths of Atlantic Forest sites that produced 81–98% of true species richness calculated from Bootstrap estimation (Terra et al. 2013). Specimens were euthanized in Eugenol, fixed in 10% formalin and transferred to the laboratory, where they were rinsed in water, identified and preserved in 70%. Vouchers are stored and species identifications were verified at INPA and Museu Paraense Emilio Goeldi.

2.4. Data analyses

We used TITAN to determine separate thresholds of fish and macroinvertebrate taxa loss along the forest-loss and LUI gradients at both total-catchment and local-riparian spatial extents. Taxa sampled from < 5% of our sites were excluded from TITAN as recommended by Arscott et al. (2006) and Baker et al. (2015) to reduce analytical bias and random errors and because they represent too little information along disturbance gradients to identify thresholds. In addition, we used the filtered TITAN results determined from taxa reliability and purity as recommended by Baker et al. (2015). Filtering uses only the sum(z) scores from taxa determined as being pure and reliable indicators. In general, filtered score patterns are similar to unfiltered patterns, but are lower in magnitude because they lack the scores of impure or unreliable taxa (Baker et al. 2015). TITAN employed standardized values of indicator species (z-values) to estimate change points from multiple taxa change peaks along the forest-loss and LUI gradients. The z-values were determined from normalized indicator values relative to random variability of abundances to yield abundance-normalized change points. Taxa z-values were standardized to the mean and standard deviation of permuted samples along the forest-loss and LUI gradients and the sum of z-values reflected the amount of assemblage change along a gradient (Baker and King, 2010). Synchronous change points for multiple taxa indicated an assemblage change threshold, which is where on the forest-loss or LUI gradient that the differences in taxon frequency and abundance were maximized. Taxa with negative (Z^-) and positive (Z^+) responses to forest loss and LUI were distinguished, as were their reliability and purity, which were determined by bootstrap resampling 1000 times with replacement for each taxon along with multiple levels of forest loss and LUI near the change point. Reliability was calculated as the percent of change points determined from resampling with significant TITAN results; purity was the percent of resamples with the same response direction. We also used bootstrapping to calculate change point confidence intervals (Baker and King, 2010). The TITAN analyses were run in the TITAN2 package (Baker et al., 2015) in R version 3.5.1 (R Core Team, 2020).

3. Results

We collected totals of 235 macroinvertebrate species or genera, 32 families, five orders, and 29,223 individuals, from which 117 rare taxa were excluded from analyses because of infrequent occurrences. Likewise, we collected 144 fish species, 26 families, seven orders, and 25,260 individuals, with 65 taxa excluded because of their rarity. Both total and accumulated (LUI) forest loss at the total-catchment extent ranged from 0 - ~65% and at the local-riparian extent ranged from 0 - ~100% (Supplementary Figs. S1; S21).

Correlations of forest loss and LUI between total-catchment and local-riparian spatial extents in all streams and in the three basins were weak to moderate. The correlation of forest loss in the total-catchment and the local-riparian was 0.38. If examined for each of the three basins separately, the correlations of forest loss between the two spatial extents were 0.19, 0.45 and 0.56 in the Curuá-Una, Gurupi and Capim basins, respectively. The correlation of LUI in the total-catchment and the local-riparian was 0.53. When examined for each of the three basins separately, the correlations of LUI between the two spatial extents were 0.15, 0.53 and 0.55 in the Curuá-Una, Gurupi and Capim basins, respectively. Clearly, the two disturbance indicators measured different environmental conditions and the three basins differed in their responses to those disturbances.

3.1. Forest loss

The macroinvertebrate TITAN peak-change thresholds and cumulative frequency distributions for current total-catchment and local-riparian extents for all 92 sites differed (Fig. 1). The Z^- peak change at the total-catchment extent occurred at 1% of forest loss with a 5th- 95th percentile confidence interval of 1–10% forest loss. At the local-riparian spatial extent, the Z^- peak change occurred at 11% of forest loss with a 5th- 95th percentile confidence interval of 0–15% forest loss. Although the Z^- peak changes differed between total-catchment and local-riparian extents, their confidence intervals were similar. If examined for each of the three basins separately, the Z^- peak changes at the total-catchment extent occurred at 1%, 9% and 17% of forest loss in the Capim, Gurupi and Curuá-Una basins, respectively (Table A10). At the local-riparian spatial extent, the macroinvertebrate Z^- peak changes occurred at 11%, 18% and 22% of forest loss in the Curuá-Una, Capim and Gurupi basins, respectively. Thus, the Z^- peaks indicated an earlier response by sensitive macroinvertebrate taxa to forest loss at the total-catchment spatial extent than at the local-riparian extent whether assessed regionally or by basin.

The fish TITAN peak-change thresholds and cumulative frequency distributions for current total-catchment and local-riparian extents also differed (Fig. 1). The Z^- peak change at the total-catchment extent occurred at 1% of forest loss with a 5th- 95th percentile confidence interval of 0–12% forest loss. At the local-riparian spatial extent, the Z^- peak change occurred at 6% of forest loss with a 5th- 95th percentile confidence interval of 0–43% forest loss. If examined for each of the three basins separately, the fish assemblage Z^- peak changes at the total-catchment extent occurred at 1% and 11% of forest loss in the Capim and Gurupi basins, respectively; however, no Z^- peak changes were recorded in the Curuá-Una basin (Table A11). At the local-riparian spatial extent, the fish Z^- peak change occurred at 3% and 9% of forest loss in the Capim and Curuá-Una basins, respectively; but no Z^- peak changes were observed in the Gurupi basin. Thus, both the peaks and confidence intervals tended to indicate a more distinct response to forest loss, i.e., a much clearer indicator of assemblage change relative to sensitive fish species, at the total-catchment spatial extent than at the local-riparian extent. However, there was greater forest-loss variability when basins were examined separately versus all sites combined.

Regarding macroinvertebrates versus fish as threshold indicators of forest loss at the total-catchment extent, the Z^- peak changes were the same (1% forest loss) but the macroinvertebrates had slightly narrower
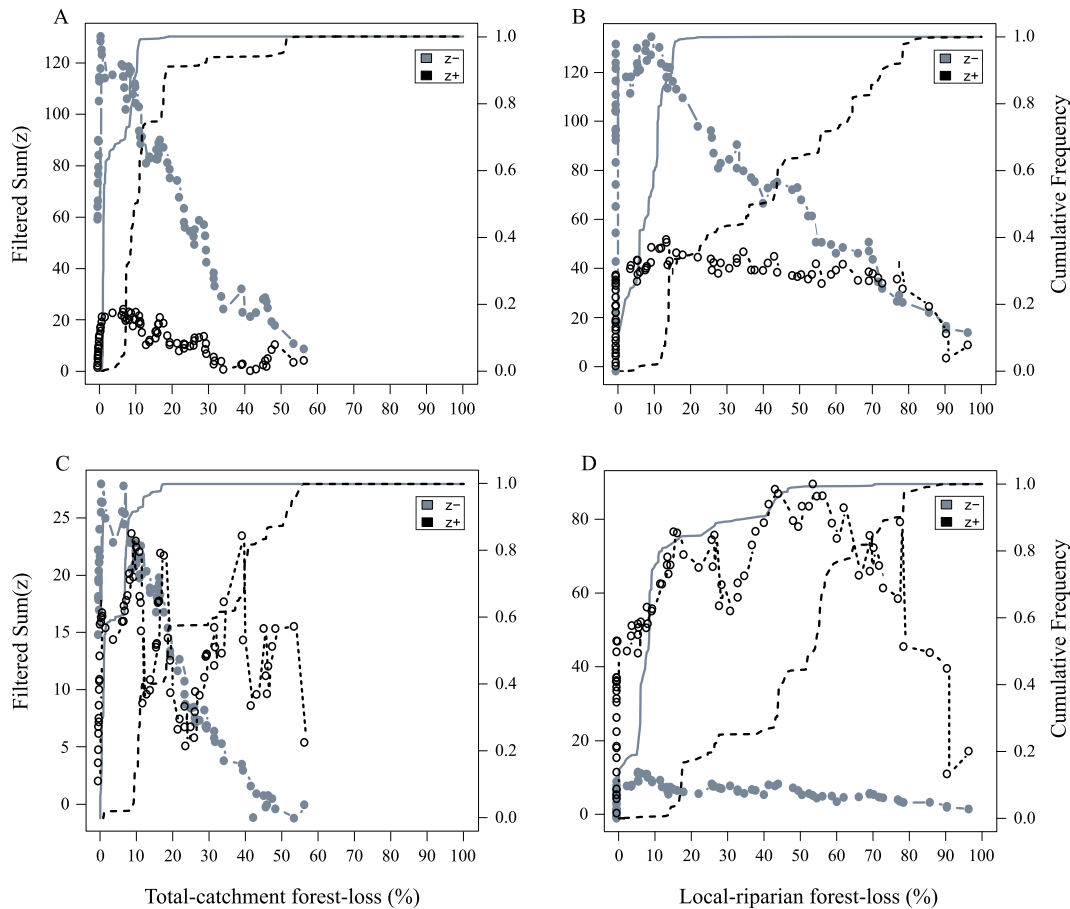
Fig. 1. TITAN assemblage sum Z⁻ and sum Z⁺ values indicating all change points (dots) versus the proportion of forest-loss for macroinvertebrates at catchment (A) and local-riparian (B) extents and for fish at catchment (C) and local-riparian (D) extents. Sum Z⁻ and sum Z⁺ peaks indicate synchronic decreases and increases of sensitive and tolerant taxa, respectively. Solid and dashed lines are the cumulative frequency distributions of change points for 1000 bootstrap replicates for sum Z⁻ and sum Z⁺, respectively.

confidence intervals (1–10% vs. 0–12%). However, their higher Z⁻ maximum values (140 vs. 24) indicated that macroinvertebrates offered a more distinct indicator of assemblage change and a clearer response to forest loss than fish. The 11% threshold does not support this conclusion for macroinvertebrates at the current local-riparian extent (versus 6% for fish), but it is supported by the much greater number of significant sensitive (Z⁻) macroinvertebrate taxa than fish species (Fig. 2).

We detected 24 reliable Z⁻ macroinvertebrate taxa at the total-catchment extent (Table A1) and 32 at the local-riparian extent for forest loss (Table A2; Fig. 2). Of all Z⁻ macroinvertebrate taxa, 16 were present in both extents. The Odonata (*Acanthagrion adustum, Mnesarete williamsoni, Tigriagrion aurantinigrum, Senithoptera lanei*) and Trichoptera (*Cyrnellus* sp., *Hydroptila* sp., *Macrostemum* sp., *Oxyethira* sp.) were recorded only at the total-catchment extent. The Heteroptera (*Rhagovelia jubata*), Odonata (*Chalcolpteryx radians, Epipleoneura capilliformis, Epipleoneura haroldoi, Heteragrion* sp., *Mnesarete smaragdina, Psaironeura tenuissima*), Ephemeroptera (*Amanahyphes* sp., *Campsurus* sp.) and Trichoptera (*Mortoniella* sp.) were recorded only at the local-riparian extent (Fig. 2).

We detected only 3 reliable Z⁻ fish species at the total-catchment extent (Table A3) and 6 at the local-riparian extent of forest loss (Table A4; Fig. 2). Of all Z⁻ fish taxa, 2 (*Erythrinus erythrinus* and *Gymnotus coropinae*) were present in both extents. *Apistogramma* aff. *regani, Helogenes marmoratus* and *Pyrrhulina* aff. *brevis* were recorded only at the total-catchment extent. *Apistogramma taeniata* was recorded only at the local-riparian extent (Fig. 2).

3.2. Land-use intensity index (LUI)

The macroinvertebrate TITAN peak change thresholds and cumulative frequency distributions for LUI total-catchment and local-riparian extents differed similarly to forest loss (Fig. 3). The Z⁻ peak change at the total-catchment extent occurred at 3% of the LUI with a 5th – 95th percentile confidence interval of 0–3%. At the local-riparian spatial extent, the Z⁻ peak change also occurred at 3% of the LUI, but with a 5th – 95th percentile confidence interval of 0–20%. When examined by the three basins separately, the macroinvertebrate assemblage Z⁻ peak changes at the total-catchment extent occurred at 3% and 10% of the LUI in the Capim and Curuá-Una basins, respectively, but no Z⁻ peak changes were recorded in the Gurupi basin (Table A10). At the local-riparian spatial extent, the macroinvertebrate Z⁻ peak change occurred at 13%, 27% and 82% of the LUI in the Curuá-Una, Capim and Gurupi basins, respectively. Thus, whether assessed regionally or by basin, the confidence intervals tended to indicate a more distinct response to the LUI, i. e., a much clearer indicator of assemblage change, relative to sensitive macroinvertebrate taxa at the total-catchment spatial extent than at the local-riparian extent. Again, there was greater LUI variability when basins were examined separately versus all sites combined.

The fish TITAN peak-change thresholds and cumulative frequency distributions for LUI total-catchment and local-riparian extents differed as well (Fig. 3). The Z⁻ peak change at the total-catchment extent occurred at 2% of the LUI with a 5th – 95th percentile confidence interval of 0–5%. At the local-riparian spatial extent, the Z⁻ peak change occurred at 40% of the LUI with a 5th – 95th percentile confidence interval of 11–49%. If examined by the three basins separately, the fish
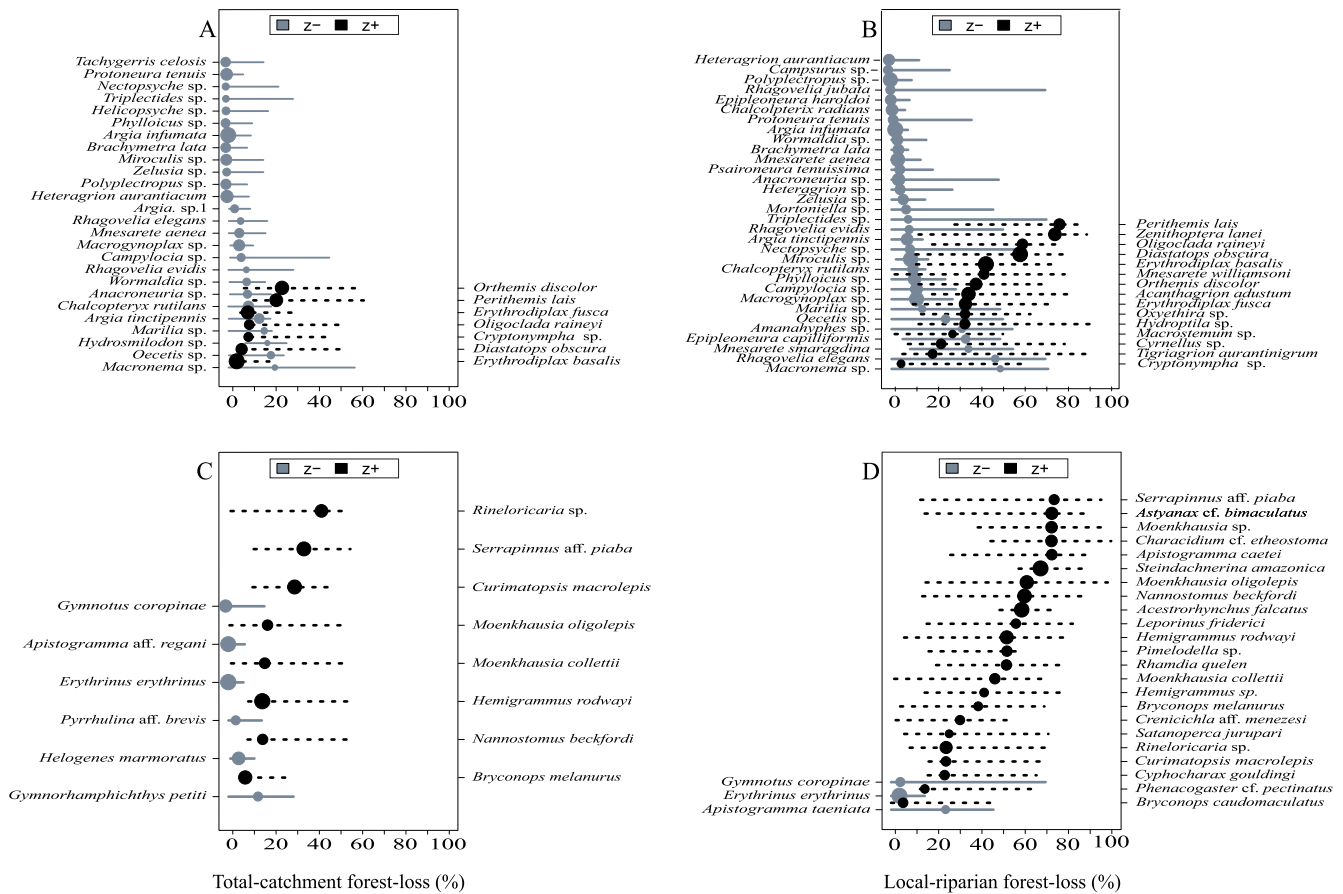
Fig. 2. TITAN threshold responses to forest-loss at total-catchment (macroinvertebrates: A; fish: C) and local-riparian (macroinvertebrates: B; fish: D) showing significant (p ≤ 0.05) indicator taxa. Z⁻ taxa decreased and Z⁺ taxa increased with forest loss. Circles are change points, their sizes are relative to their z-values, bars are 5th-95th percentiles from 1000 bootstrap replicates.

assemblage Z⁻ peak changes at the total-catchment extent occurred at 8% of the LUI in the Capim basin, but no Z⁻ peak changes were recorded in the Curuá-Una or Gurupi basins (Table A11). At the local-riparian spatial extent, the fish Z⁻ peak changes occurred at 4% and 13% of the LUI in the Capim and Curuá-Una basins, respectively, but no Z⁻ peak changes were observed in the Gurupi basin. Again, when examined regionally, both the Z⁻ peaks and confidence intervals indicated a more distinct LUI response, i.e., a much clearer indicator of assemblage change relative to sensitive fish species, at the total-catchment spatial extent than at the local-riparian extent. Like the macroinvertebrates, there was more LUI variability at the local-riparian extent when basins were examined separately versus all sites combined.

Regarding macroinvertebrate versus fish as LUI threshold indicators at the total-catchment extent, fish were slightly more sensitive as indicated by lower Z⁻ peak changes (2% vs. 3%), but with slightly wider confidence intervals (0–5% vs. 0–3%). However, their higher Z⁻ maxima (140 vs. 28) indicated that macroinvertebrates offered a more distinct indicator of assemblage changes and a clearer LUI response than fish. The 3% threshold further supports this conclusion for macroinvertebrates at the local-riparian extent (versus 40% for fish) as does the much greater number of significant sensitive (Z⁻) taxa than fish species at the total-catchment extent (Fig. 4).

We detected 24 reliable Z⁻ macroinvertebrate taxa for the LUI at the total-catchment extent (Table A5) and 32 at the local-riparian extent (Table A6; Fig. 4). Of all Z⁻ macroinvertebrate taxa, 23 were present in both extents. *Nectopsyche* sp. (Trichoptera) was recorded only at the total-catchment extent. The Heteroptera (*Hydrometra comatae*), Odonata (*C. radians, E. capilliformis, E. haroldoi, Heteragrion* sp., *M. smaragdina, P. tenuissima*), Plecoptera (*Enderleina* sp.) and Trichoptera (*Macronema*

sp.) were recorded only at the local-riparian extent (Fig. 4).

We detected 4 reliable Z⁻ fish species with the LUI at the total-catchment extent (Table A7) and 6 at the local-riparian extent (Table A8; Fig. 4). Of all Z⁻ fish taxa, 2 (*E. erythrinus* and *G. coropinae*) were present in both extents. *Apistogramma* aff. *regani* and *H. marmoratus* were recorded only at the total-catchment extent. *Aequidens epae, A. taeniata, Hyphessobrycon* sp*.,* and *Moenkhausia collettii* were recorded only at the local-riparian extent (Fig. 4). Thus, 5 fish species (*Apistogramma aff. regani, A. taeniata, E. erythrinus, G. coropinae, H. marmoratus*) were Z⁻ indicators for both LUI and forest loss.

4. Discussion

4.1. Forest loss & LUI thresholds for macroinvertebrates and fish

We determined that the levels of forest loss and LUI that yielded negative threshold responses in macroinvertebrate and fish taxa were very low and resulted in the loss of sensitive taxa at as little as 1–3% current forest loss or LUI decline at the total-catchment extent (Figs. 1, 3). Those values are comparable to those reported for macroinvertebrates by Firmiano et al. (2017) for percent urbanization (<1%) of Cerrado catchments and by Brito et al. (2020) for Amazonian local-riparian forest loss (1%). However, they are lower than those reported by Rodriguez et al. (2016) for Cerrado riparian forest loss (40–60%), Dala-Corte et al. (2020) for forest loss of Amazonian 100-m riparian buffers (12%), and Brito et al. (2020) for Amazonian total-catchment forest loss (9%). We suspect that the more considerable differences in thresholds result partly from sampling Cerrado (Rodrigues et al., 2016) versus Amazonian streams, Amazonian catchment- versus riparian-
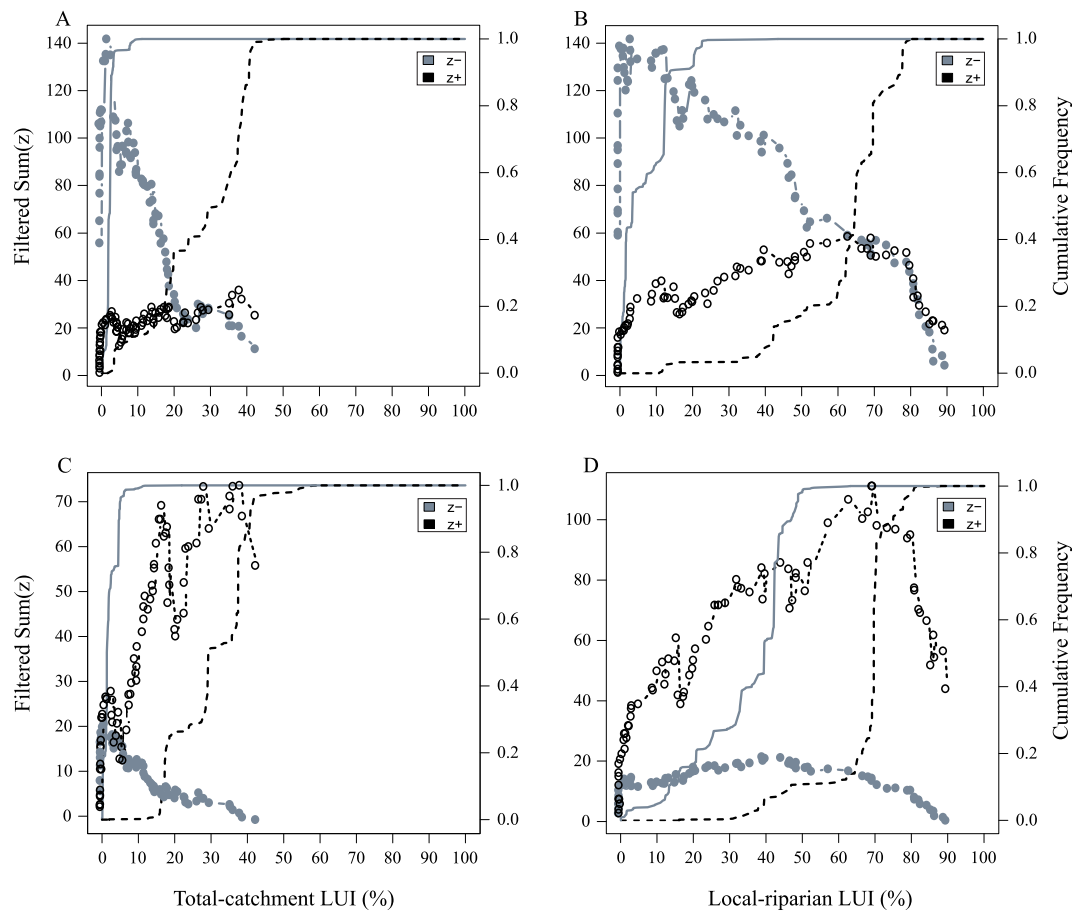
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Fig. 3. TITAN assemblage sum Z⁻ and sum Z⁺ values indicating all change points (dots) versus the Land Use Index (LUI) change for macroinvertebrates at catchment (A) and local-riparian (B) extents and for fish at catchment (C) and local-riparian (D) extents. Sum Z⁻ and sum Z⁺ peaks indicate synchronic decreases and increases of sensitive and tolerant taxa, respectively. Solid and dashed lines are the cumulative frequency distributions of change points for 1000 bootstrap replicates for sum Z⁻ and sum Z⁺, respectively.

extent (Dala-Corte et al., 2020) assessments, and twice as many Amazonian sites as sampled by Brito et al. (2020). Cerrado landscapes are naturally much more open and experience greater fire and forest retraction frequencies than Amazonian streams (Melo et al., 2018; Roque et al., 2018). Nonetheless, our macroinvertebrate riparian forest-loss and LUI thresholds (11% and 40%) were similar to or higher than the 12% of Dala-Corte et al. (2020) for Amazonian streams, possibly because of intra-biome, sample size, sampling method, and analytical differences.

For fish, our LUI and forest-loss thresholds (2% and 1%) were lower than that of Brejão et al. (2018) for total-catchment forest-loss (10%). Our LUI threshold (40%) was higher than their riparian forest-loss estimate (10%) but our riparian forest-loss threshold (6%) was lower and lower than the 49% reported by Dala-Corte et al. (2020) for Amazonian 100-m riparian forest-loss. Again, the differing thresholds in these results may be driven by regional, sampling methodology and analytical differences. For example, Dala-Corte (2020) reported threshold confidence intervals of 0.3% − 55% for fish and 4.4% − 26% for macroinvertebrates in Amazonian 100-m riparian forest-loss. Likewise, within the same state (Pará) for fish assemblages, Leal et al. (2018) found that there were high levels of environmental heterogeneity among river basins and regions and Leitão et al. (2018) determined that the importance of local-riparian and catchment forest-loss varied between regions. Agra et al. (2019) reported substantial variability among macroinvertebrate assemblages within a Cerrado ecoregion because of differing reference stream types within a relatively small area (64 km²). Likewise, Brasil et al. (2018) and Alves-Martins et al. (2019) found substantial regional biogeographic differences in Odonata among eastern Amazonian sites.

Such differences indicate the need for a much larger sample size distributed randomly across entire states and employing standard sampling methods (Olsen and Peck, 2008; Herlihy et al., 2020; Leal et al., 2020).

4.2. Forest loss & LUI thresholds for catchments vs. riparian zones

We found that fish and macroinvertebrate taxa were more sensitive to current total-catchment forest loss and LUI change (1–3%) than local-riparian forest loss and LUI change (3–40%) as expected. Brito et al. (2020) reached the same conclusion for macroinvertebrates based on half the number of sites, but Brejão et al. (2018) arrived at 10% thresholds for fish at both catchments and local-riparian forest-loss extents. Biotic conditions at stream sites are driven by both catchment and local anthropogenic pressures (Marzin et al., 2012b; Macedo et al., 2014; Leal et al., 2018; Leitão et al., 2018; Herlihy et al., 2020). However, the degree to which each spatial extent affects biota depends on the relative amount and intensity of disturbance at each of those extents. For example, Wang et al. (2006) concluded that biotic assemblages were most influenced by local pressures in largely undisturbed catchments, but that the importance of catchment pressures increased with greater catchment disturbance. However, they used a multivariate analysis of fish assemblage characteristics as opposed to TITAN, which we consider a more sensitive early-warning indicator of landscape disturbance. In addition, other co-varying anthropogenic pressures (agriculture type, roads, road-stream crossings, forest age, forest disturbance) add variability to estimates of forest loss (Leal et al., 2018, Leitão et al., 2018, Barlow et al., 2016, Brejão et al., 2018).
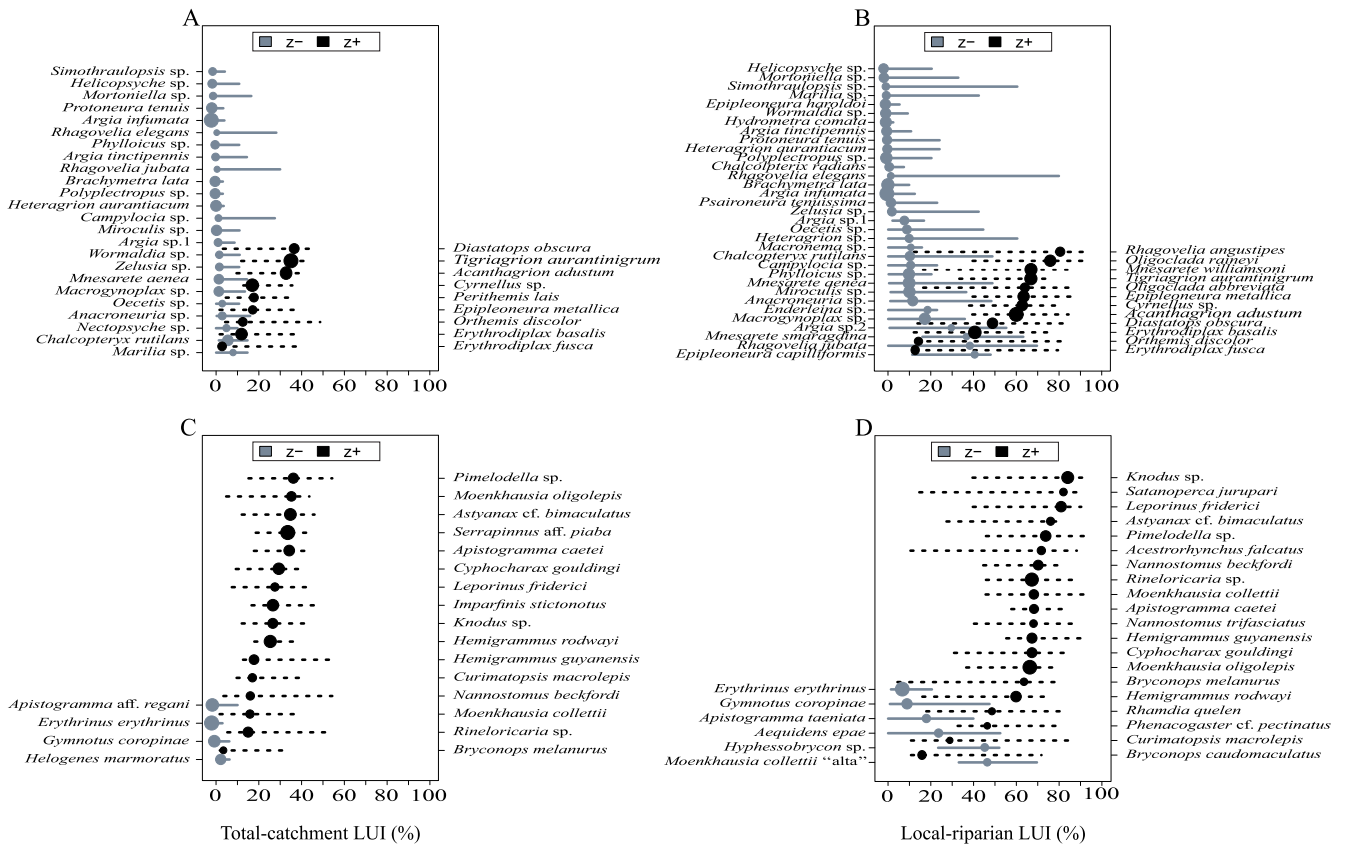
Fig. 4. TITAN threshold responses to Land Use Index (LUI) change at total-catchment (macroinvertebrates: A; fish: C) and local-riparian (macroinvertebrates: B; fish: D) showing significant (p ≤ 0.05) indicator taxa. Z⁻ taxa decreased and Z⁺ taxa increased with forest loss. Circles are change points, their sizes are relative to their z-values, bars are 5th-95th percentiles from 1000 bootstrap replicates.

4.3. Fish & macroinvertebrates as indicators of forest loss & land use intensity

Fish, and especially macroinvertebrates, taxa can serve as early-warning signals of ecological damage from forest loss as predicted. In addition to some EPT (Ephemeroptera, Plecoptera, Trichoptera), we determined that some Heteroptera and Zygoptera (Odonata) were sensitive to forest loss; however, some Anisoptera (Odonata) were tolerant to forest loss. EPT taxa richness and %EPT individuals are widely used in biomonitoring and bioassessment programs because of their general sensitivity to disturbance (Lenat and Penrose, 1996; Hering et al., 2006; Stoddard et al., 2008; Ruaro et al., 2020). Some Zygoptera species are especially sensitive indicators of riparian forest removal (Oliveira-Junior et al., 2015; 2017). They reported that the slender, delicate bodies of adults make them prone to dehydration and overheating, thereby limiting them to shadier habitats. Higher abundances and richness of Anisoptera occur in deforested areas because of their greater thermoregulatory efficiency than Zygoptera (Oliveira-Junior et al., 2015; 2017; Bastos et al., 2021). This different sensitivity pattern of these two Odonata suborders to environmental change is so evident that an index for assessing stream condition was created, based on Zygoptera/ Anisoptera richness and/or abundance (Oliveira-Júnior and Juen, 2019). Heteroptera are very dependent on local processes (Dias-Silva et al., 2020), which would explain their relationship with forest loss.

Regarding fishes, *Apistogramma aff. regani*, *A. taeniata*, *E. erythrinus*, *G. coropinae*, and *H. marmoratus* are widespread in small Amazonian streams and are complex microhabitat specialists over a range of foraging groups (Zuanon et al., 2015). They prefer dead-leaf packs and tree branches that are directly affected by deforestation. *Helogenes marmoratus* is the most specialized, feeding mostly on insects of allochthonous origin and frequently occurring in leaf packs and woody

debris from riparian forests (Sazima et al., 2006; Carvalho et al., 2013). *Apistogramma aff. regani* and *A. taeniata* commonly occur amongst tree branches near leaf packs in slow flows and are very sensitive to forest loss (Ferreira et al., 2018). They are invertivores, feeding diurnally on the benthos. *Gymnotus coropinae* occurs more commonly inside large leaf packs in slow flows and was very sensitive to forest loss (Brejão et al., 2020). It is an invertivore/piscivore feeding at night or in twilight. *Erythrinus erythrinus* is the least specialized in terms of microhabitat, occurring in leaf packs as well as temporary marginal ponds; but it is the most carnivorous/piscivorous of the four species.

4.4. TITAN & sampling limitations

Uncommon or rare taxa sampled from < 5% of our sites were not included in our TITAN analyses to reduce random errors and analytical bias. However, rare fish and macroinvertebrate taxa may also be very sensitive to environmental disturbances, especially conditions that limit their dispersal (Oliveira-Junior et al., 2017; Benone et al., 2020; Brasil et al., 2020). Rare taxa also tend to be habitat and functional specialists, so when they are eliminated from assemblages those traits often are as well (Leitão et al., 2016; Benone et al., 2020). Furthermore, our relatively short site lengths likely limited detection of rare taxa that would have been collected from longer sites or with increased sampling effort thereby increasing their occurrence frequencies (Kanno et al., 2009; Terra et al., 2013; Silva et al., 2016; Junqueira et al., 2020). Nonetheless, high levels of beta diversity amongst Brazilian stream sites hinder detecting many taxa unless both long and many sites are sampled (Ligeiro et al., 2010; Brasil et al., 2018, 2020; Leal et al., 2018; Pompeu et al., 2019), which is often logistically unfeasible (Hughes and Peck, 2008). Furthermore, the confidence intervals of the taxa thresholds that we observed are substantial, overlapping and river-basin dependent,

hence, our conclusions regarding spatial extents and biotic assemblages must be regarded with caution.

4.5. Fish versus macroinvertebrates as threshold indicators

The threshold and Z⁻ taxa results for percent forest-loss and LUI change yielded similar results for macroinvertebrates and fish at both total-catchment and local-riparian extents—except for fish at the local-riparian extent, where the forest loss threshold was 6% but the LUI threshold was 40% (Figs. 1, 3). However, in both cases those thresholds were less distinct (wider confidence intervals) than those for total catchment fish or total-catchment and local-riparian macro-invertebrates. This likely results from the weaker and more variable relationship between fish assemblages at the local-riparian extent than at the total-catchment extent. Leitão et al. (2018) reported stronger total-catchment than local-riparian relationships for Paragominas, but not for Santarém, fish species richness. In the same regions, Leal et al. (2018) found that the catchment-species abundance relationship was greater than the riparian-species abundance relationship in the Curuá-Una basin, but the opposite was the case in the Capim basin, and the relationships were similar in the Gurupi basin. Such differences among Pará regions and basins apparently weakened the threshold responses of fishes at the local-riparian extent more than at the local-catchment extent. In addition, the LUI assesses the dynamics of forest loss and regeneration (deforestation rate, time since deforestation, deforestation rate profile, secondary forest regeneration level). Those dynamics greatly affect the amount of wood, macrophytes (Faraes et al., 2020), bank integrity and channel complexity in and near sampling sites, thereby affecting the movement of and habitat quality for fish (Kauf-mann and Hughes, 2006; Zuanon et al., 2015; Leitão et al., 2018; Montag et al., 2019).

4.6. Management implications

Four other recent studies have indicated that low levels of deforestation can eliminate sensitive Amazonian fish and invertebrate taxa (Oliveira-Júnior et al., 2015; Brejão et al., 2018, Brito et al., 2020, Dala-Corte et al., 2020). Furthermore, Leal et al. (2018) and Dala-Corte et al. (2020) concluded that existing Brazilian legal statutes for protecting riparian vegetation were inadequate for conserving streams and their fish and macroinvertebrate assemblages. Brito et al. (2020) indicated that conservation protections are needed for entire catchments to protect their sensitive macroinvertebrate taxa. Leal et al. (2020) demonstrated that conservation planning based on both aquatic and terrestrial protections had markedly greater total value than either alone, but with insignificant loss in terrestrial protections. Such ideas are not new. The strong linkages between terrestrial and aquatic systems were clearly established by von Humboldt in 1819 (Pausas and Bond, 2019) and Marsh (1864). However, Brazil has high levels of fish and macro-invertebrate beta richness driven by turnover among sites, basins, regions, and biomes (Ligeiro et al., 2010; Brasil et al., 2018; Leal et al., 2018; Pompeu et al., 2019), which calls for protections of many large areas.

Therefore, should Brazil desire to protect its aquatic biota, particularly its sensitive fish and macroinvertebrate taxa, it would be wise to expand its riparian zone protections and protect several entire catchments across all biomes and as many ecoregions or landscape types within each biome as possible, as suggested in our study together with those of Brejão et al. (2018), Brasil et al., (2020), Dala-Corte et al. (2020), Firmiano et al. (2020) and Leal et al. (2020). Those catchments can be best selected via cost-benefit analyses based on current and potential conditions (Leal et al., 2020). One conservation model for Brazil from temperate rainforests is that of FEMAT (1993), which established riparian reserves that are 100-m wide on each side of permanent fish-bearing streams, as well as late-successional reserves and key catchments in which logging is prohibited or highly restricted. That

management plan resulted from the leadership of U.S. President Clinton and months of collaboration by multiple federal, state, and university scientists representing the disciplines of terrestrial and aquatic ecology, geography, economics, sociology and political science. But it was preceded by grass-roots protests and scientific concerns regarding threatened taxa (Spotted Owl *Strix occidentalis*, Marbled Murrelet *Brachyramphus marmoratus*, Chinook Salmon *Oncorhynchus tshawytscha*, Coho Salmon *O. kisutch*, Steelhead Trout *O. mykiss*). Finally, legal statutes without implementation, effectiveness, and assessment monitoring of status and trends are simply paper exercises. Therefore, a monitoring program is needed that incorporates a statistical survey design, standard sampling methods, multiple ecological indicators, a data management system, public reporting of results, and collaboration among citizen scientists, academicians, and state and federal agency employees (Mulvey et al., 2009; Gardner et al., 2013; Buss et al., 2015; Callisto et al., 2019; Bried et al., 2020).

Declaration of Competing Interest

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

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2021.107773.

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