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Small forest losses degrade stream macroinvertebrate assemblages in the eastern Brazilian Amazon

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ABSTRACT

Generally, habitat loss and fragmentation negatively affect biota, often in nonlinear ways. Such nonlinear responses suggest the existence of critical limits for habitat loss beyond which taxa experience substantial changes. Therefore, we identified change points for aquatic macroinvertebrate assemblages at both local-riparian and catchment extents in response to a forest-loss gradient in agriculture-altered landscapes of 51 small (1st to 3rd Strahler order) eastern Amazon streams. We used Threshold Indicator Taxa Analysis (TITAN) to identify change points for individual taxa and segmented regression analysis for assemblage richness. Considering the patterns of the cumulative frequency distributions of sum(Z^-) maxima across bootstrap replications, peak changes in macroinvertebrate assemblages were at ~9% (5–95 percentiles = 1–15%) of forest-loss at the catchment extent, and at ~1.4% (5–95 percentiles = 0–35%) of forest-loss at the local-riparian extent. Although the assemblage change point at the site extent was less than that detected at the catchment extent, the markedly lower percentile range indicates that biotic assemblages are more clearly responsive to forest-loss at the catchment/network-riparian extents than the site extent. For catchment and site extents, segmented regression analysis determined a change point for assemblage richness at 57% and 79% of forest-loss, respectively. This indicates the low capacity of total richness to separate early and synchronous decreases of sensitive taxa from gradual increases of tolerant taxa. Our results also show that it is not enough to focus management and conservation actions on riparian zones, but that conservation strategies should be expanded to entire catchments as well. The sharp decline of sensitive taxa in response to removal of a small portion of forest cover, even at catchment extents, indicates that the Brazilian Forest Code is insufficient for protecting stream macroinvertebrates. Consequently, we recommend strategies to reverse the potential collapse of aquatic biodiversity, particularly through avoiding deforestation and forest degradation, encouraging socio-economic incentives for restoring degraded areas, creating protected areas, and maintaining the current protected areas. We argue that reducing habitat loss should be a top priority for conservation planners in tropical forests because the sensitivity of aquatic biodiversity to removal of riparian forest-cover in Amazon rainforests is higher than previously thought. Therefore, the Forest Code regulatory framework needs complementary regulation that may be achived by more restrictive State and biome policies.

1. Introduction

Agricultural activities performed over large areas cause extensive alterations in the landscape, mainly from conversion, loss, and fragmentation of native vegetation (Laurance et al., 2014). These changes in the landscape significantly threaten ecosystem processes and biodiversity, especially in highly diverse ecosystems such as tropical forests (Barlow et al., 2016). Recently, the expansion of agriculture and cattle grazing in the Brazilian Amazon has resulted in the loss of ~18% of native forest (Ferreira et al., 2012). Moreover, such land use changes

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result in considerable impacts on the physical habitat structure of the dense and complex network of small Amazon streams (Leal et al., 2016). Unfortunately, increased removal of forest-cover is expected in the coming years, intensifying impacts in the Amazon region, the largest and most biodiverse expanse of tropical forest on the planet, which also hosts the largest river basin on Earth, the Amazon River Basin (Brando et al., 2013).

Habitat loss and fragmentation affect species distributions as a result of altered site rates of reproduction, mortality, dispersal, and extinction (Lindenmayer and Fischer, 2013). Forest-loss and fragmentation reduce population sizes or increase isolation of species sensitive to patch size and/or habitat specialists, consequently increasing extinction risks (Haddad et al., 2015). Usually, habitat loss and fragmentation effects on faunas are described as linear and negative; however, studies recording nonlinear responses are increasingly common (e.g., Barlow et al., 2016; Roque et al., 2018; Macchi et al., 2019). Nonlinear responses suggest the existence of critical limits in habitat loss from which taxa have change peaks and reach alternative states (Huggett, 2005). These faunal changes occur in response to small and continuous changes of one or more stressors (With and King, 1999).

Thresholds in biological assemblages are attributed to the simultaneous response of various taxa to small variations in stressors (Baker and King, 2010). Synchronic responses of different taxa require some relationships between them (e.g., similar attributes, narrow niches, facilitation), which may result from coevolution (King et al., 2011). Evaluating ecological thresholds facilitates prohibition, conservation, restoration, and mitigation actions before assemblages are most at risk, preventing biodiversity and ecosystem function losses (Baker and King, 2010). Such thresholds are useful for guiding conservation and restoration decisions on relatively short timescales in human altered systems, particularly for setting regulatory limits and defining conservation actions involving societal choices and negotiation of values and aims (Siding and Hobbs, 2009).

Aquatic macroinvertebrate taxa may be affected to different degrees and directions by loss of native forest in watersheds and riparian zones (Monteiro-Júnior et al., 2013; Martins et al., 2017a). Their variation in sensitivity to disturbance is a result of their differences in life cycles, morphologies, physiologies, and behaviors (Oliveira-Junior et al., 2017). Because of that variability and their high taxonomic and functional diversities, aquatic macroinvertebrates are good models to test the effects of riparian forest-loss on sensitivity to disturbance, geographic distribution, and habitat specialization (Lenat and Resh, 2001).

Conversions of native forest in catchments have strong negative effects on aquatic biota. In urban streams, a non-linear and synchronous decline of sensitive macroinvertebrate taxa in response to sedimentation and water quality degradation has been reported, indicating a strong assemblage threshold to those stressors (Baker and King, 2010). Similarly, the impacts of agriculture on aquatic fauna are relatively well documented, with consistent evidence of biodiversity decline (e.g., Brito et al., 2018; Miguel et al., 2017). However, threshold studies of tropical/subtropical stream assemblages in response to riparian forest-loss are scarce and with inconsistent results. In the Brazilian savannah, adult Odonata showed moderate evidence of nonlinear response at sites with native vegetation loss between 40% and 60% (Rodrigues et al., 2016). In the western Brazilian Amazon, fish assemblages had a negative threshold response to deforestation at < 20% of deforestation and soon after impact (< 10 years; Brejão et al., 2018). Tropical forests have high environmental stability (Juen and de Marco, 2011), unique climatic characteristics (humidity, shading, precipitation, and temperature), and numerous rare and sensitive taxa (e.g., Terra et al., 2013; Oliveira-Junior et al., 2017). Therefore, small amounts of forest conversion may result in extreme changes for those rare and sensitive taxa, resulting in non-linear changes in aquatic and terrestrial tropical forest assemblages (Leitão et al., 2016; Barlow et al., 2016). Currently, the highest rates of deforestation have been recorded in the tropics, led by Brazil and Indonesia (FAO, 2016).

Here, we aimed to detect change points in macroinvertebrate assemblages along a catchment- and riparian-forest cover gradient in Brazilian eastern Amazonian streams, a region marked by high endemism, high diversity, and threats to biodiversity (Juen and De Marco, 2012; da Silva et al., 2005). We hypothesized that threshold responses of macroinvertebrate assemblages would occur long before substantial riparian forest-loss. In small streams there is a strong connection between aquatic and terrestrial systems especially for insects, which usually have aquatic and terrestrial phases. In the latter case, the conditions of the terrestrial system will influence various aspects of the animal's adult life, especially the choice of areas for mating, oviposition, and dispersal. The latter could isolate nearby populations that are not hydrologically connected. In addition, the loss of catchment, network-riparian, and local-riparian vegetation results in markedly altered environments in tropical forests. For example, forest-loss increases light input and air and water temperatures while reducing wood and leaf debris in streams (Leal et al., 2016; Leitão et al., 2018). Such habitat changes negatively affect the abundance and frequency of occurrence of narrow-niche taxa by increased light (e.g., decreased Anisoptera; Oliveira-Junior et al., 2017), increased temperature (decreased Plecoptera; Hynes, 1976) and decreased leaf debris (decreased Trichoptera; Martins et al., 2017b).

2. Materials and methods

2.1. Study area

We studied 51 small (1st to 3rd Strahler order) stream sites located in the Capim and Gurupi River Basins in the eastern Brazilian Amazon state of Pará (Paragominas district, Fig. 1). The district climate is tropical equatorial humid with rainy (December to May) and drier (June to November) seasons. Mean annual air temperature is 27 °C, mean humidity is 81%, and mean annual precipitation is 1800 mm (EMBRAPA, 1986). The original vegetation of the region is classified as ombrophilous dense forest (RADAMBRASIL, 1974). In the last 65 years, many forests in this region have been converted into pastures and mechanized agricultural areas, resulting in a forest cover gradient (Gardner et al., 2013; Fig. A1). Sites were selected along a previously known gradient of land use impact, principally determined by the riparian forest cover along the streams (Gardner et al., 2013). Additional criteria used for site selection were stream size and number of sites in each microbasin (~3; Leal et al., 2018).

2.2. Landscape data acquisition

Catchment boundaries, physical attributes (elevation and slope), and channel networks were developed from TopoData (30-m resolution; INPE, 2016) via hydrological digital elevation modeling in the ArcSWAT program (di Luzio et al., 2004). Percent of forest cover (primary forest + secondary forest) were calculated from a digital land cover map (Landsat TM and ETM + images, 30-m resolution, year 2010) for three landscape extents: (1) the whole catchment upstream from the stream site (catchment extent); (2) a 100-m buffer along each side of the entire channel network upstream from the site (network-riparian extent); and (3) a 100-m riparian buffer along each side of the sampled site (local-riparian extent) (Leal et al., 2016). We used a 100-m buffer to calculate forest cover because at the resolution of our land cover data (30 m) narrower buffers would almost be binary (forested or not forested) rather than representing a gradient. In addition, riparian land use effects on streams within a 100-m buffer from the channel in tropical (Valle et al., 2013; Leal et al., 2016) and temperate (Wang et al., 2003) forests has been reported. The proportions of forest at each spatial extent (catchment, network-riparian, and local-riparian) were highly correlated (Fig. A2). Therefore, we used the local-riparian extent because of the low dispersion capacity of some aquatic invertebrates (e.g., Trichoptera; Saito et al., 2015) and the importance of site riparian

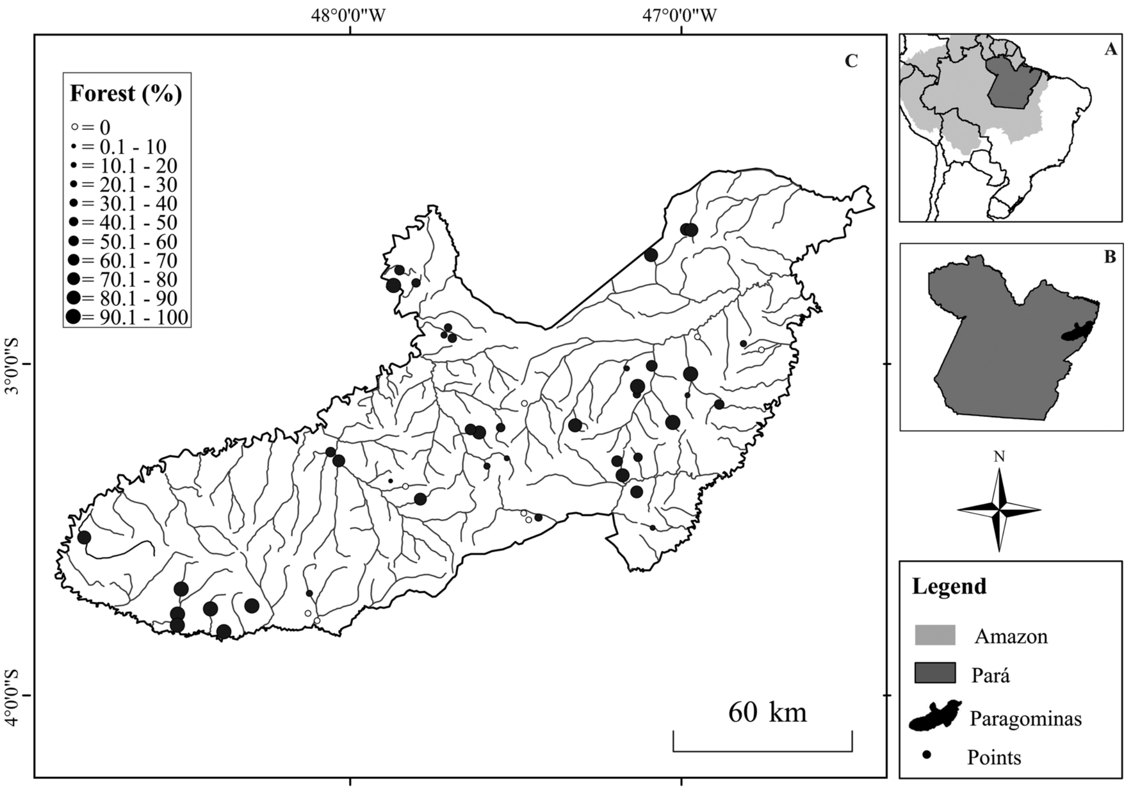

Fig. 1. Stream site locations (n = 51) in the Paragominas district. Circle sizes are proportional to forest cover percentage in the 100-m local-riparian buffers.

forest for these organisms (Saito et al., 2015). Because different landscape extents need different management measures, we included catchment extent results in our manuscript text and the network-riparian extent results in our supplemental material.

2.3. Aquatic macroinvertebrate sampling

We sampled sites from June to August 2011 with an aquatic D-frame net (1-mm^2 mesh). In each site, we collected a 900-cm^2 sample of bed substrate every 15-m for 150-m in a systematic zig-zag manner to sample the most frequent and abundant bed substrates (Peck et al., 2006; Hughes and Peck, 2008). The samples were preserved in 93% alcohol, transported to the laboratory, rinsed under running water in a metal sieve (125-µm), preserved in 80% alcohol, and then the macroinvertebrates were sorted over a light box. We identified each macroinvertebrate to the lowest taxonomic level possible through use of a regional key (Hamada et al., 2014) and with the help of taxonomic specialists (see Acknowledgments).

2.4. Data analyses

Before assessing thresholds, we tested autocorrelation between catchment, network-riparian, and local-riparian extents, using Pearson Autocorrelation Analysis (Legendre, 1993). Then to identify thresholds of aquatic macroinvertebrate taxa and assemblages along the forest-loss gradient, we used Threshold Indicator Taxa Analysis (TITAN). This analysis uses the standardized scores of an indicator species analysis (z-values) to detect potential change points through use of multiple taxa change peaks (frequency of occurrence and relative abundance) along an environmental gradient. The z-scores come from normalizing IndVals (indicator value scores) relative to random permutations of the abundances to obtain abundance-normalized change. Responses of taxa z-scores are standardized to the mean and standard deviation of permuted samples along the gradient. Thus, the sum of z-scores can be used to reflect the magnitude of assemblage change along an environmental gradient (Baker and King, 2010). Synchrony between the change points of multiple taxa is evidence of an assemblage change threshold (Baker and King, 2010). The change point is the value of the environmental gradient where the difference in taxon abundance and frequency is maximized in the observed sample (King and Baker, 2014). To minimize the potential effects of operation bias and random values, we excluded taxa collected from fewer than 5% of the sampled sites from the TITAN (Arscott et al., 2006). Prior to analyses, abundance data were log-transformed because of the wide ranges observed in taxa abundances. We used the filtered sum(z) results following Baker et al (2015), who recommended using the filtered version in most cases (see unfiltered in Fig. A3)

TITAN differentiates taxa with positive (Z^+) and negative (Z^-) responses to the forest cover gradient, with Z^+ (tolerant) taxa increasing in frequency and abundance from the change point and Z^- (sensitive) taxa decreasing. The response quality of each indicator taxon is measured by purity and reliability; both indices are obtained by resampling using the bootstrap method. This resampling procedure is realized with replacement and, repeated 500 times for every taxon. In resampling, a range of alternative observation sets is examined to assess relative sensitivity in the location of change points across taxa (Baker and King, 2010). Purity is the percentage of repetitions of the bootstrap analysis with the same response direction (positive or negative) and reliability is the percentage of change points obtained by bootstrap resampling in which the TITAN results are significant. Bootstrap resampling was also used to determine confidence intervals for a selected change point (Baker and King, 2010).

We used segmented regression (generalized linear model-GLM; Poisson distance) to determine thresholds in macroinvertebrate assemblage richness relative to the forest cover gradient in both extents (local-riparian and catchment). A strength of segmented regression analysis is that it can detect change points wherever they occur–including slight deviations from 100% forest cover. In segmented regression analysis, forest cover was split into two or more GLM regressions to locate points where the greatest changes in the relationship between explanatory and response variables occurred (Muggeo, 2003). The thresholds or breakpoints were estimated using different starting points and identified using the highest coefficient of determination value (R^2; Muggeo, 2003). All statistical analyses were performed in R software (R Development Core Team, 2010) using the segmented (Muggeo, 2004), ncf (Bjornstad, 2016), and TITAN (Baker and King, 2010) packages.

3. Results

We collected 25,142 invertebrates and 159 taxa distributed in 66 families and 143 genera (Table A1). Odonata (41 genera), Coleoptera (37 genera), Ephemeroptera (25 genera), and Trichoptera (21 genera) were the richest orders. Trichoptera (52%), Diptera (22%), and Ephemeroptera (14%) were the most abundant orders. We excluded 47 of the 159 taxa from TITAN because they were collected from fewer than 3 sites.

3.1. *Assemblage TITAN responses*

The TITAN cumulative frequency distributions (CDFs) of sum(Z) maxima across bootstrap replications for the total macroinvertebrate assemblages differed for catchment and both riparian extents (Fig. 2). Peak changes at the catchment extent were at ~9% of forest-loss. The 5th-95th percentiles covered 0.6–15% of catchment-extent forest-loss (Fig. 2). For the network-riparian extent, peak changes were slightly more than for catchments, at ~12% of forest-loss (Figure A4). The 5th-95th percentiles ranged from 1% to16% of network- riparian extent forest-loss. Peak changes at the local-riparian extent were the lowest of the three extents, occurring at ~1.4% of forest-loss. However, the 5th-95th percentiles were much wider, representing 0–35% of forest-loss (Fig. 2).

As suggested by their ranges described above, the peaks were more distinct in the CDF sum(Z^-) maxima for assemblage response to catchment forest-loss than for local-riparian forest-loss. The Z^- maxima values (indicating greater coincident change) associated with the catchment-level (~85) were higher than at the local-riparian level (~73) of forest cover (Fig. 2). This is a > 10% difference in biotic signal. However, the two extents had similar numbers of significant Z^- indicator taxa (19 catchment, 15 local riparian) and average indicator Z^- scores (~4.5 catchment, ~4.9 local riparian). The network-riparian sum(z) maximum was also ~73 (but for 13 Z^- indicator taxa; Figure A4) for an average indicator Z^- score of ~5.60. Therefore, catchment forest cover produced a clearer signal of assemblage change for sensitive taxa than did the local-riparian forest cover. However, the mean per-taxon signal was greatest for network-riparian forest cover. Moreover, the two different riparian extents yielded different z-scores and peak changes, despite being assessed from the same biotic dataset.

3.2. *Taxon-specific TITAN responses*

Considering the taxon-specific responses at the catchment extent, TITAN identified 24 taxa as indicators of forest-loss (purity ≥ 0.95; reliability 05 ≥ 0.95; Table A2; Fig. 3). The abundance and/or frequency of 19 sensitive taxa were negatively related to decreased forest cover (Z^-). Another 5 tolerant taxa increased in abundance and/or frequency of occurrence with increased forest-loss (Z^+). Odonata, Trichoptera and Ephemeroptera had the highest numbers of indicator taxa, representing ~68% of Z^- taxa (4 Trichoptera, 6 Odonata,3 Ephemeroptera) and 60% of Z^+ taxa (2 Odonata, 1 Ephemeroptera). Over half of the sensitive indicator taxa with negative (Z^-) responses responded below 10% of forest-loss, with moderate 0–95th percentiles; for example, 0–27 for *Oecetis* and 0–9 for Corydalidae.

At the local-riparian extent, TITAN identified 20 taxa as indicators of riparian forest-loss (purity ≥ 0.95; reliability 05 ≥ 0.95; Table A3; Fig. 3). The abundance and/or frequency of 15 taxa were negatively related to decreased forest cover (Z^-). Another 5 taxa increased in abundance and/or frequency of occurrence with decreased forest cover (Z^+). Again, Trichoptera, Odonata, and Ephemeroptera had the highest numbers of indicator taxa, representing ~80% of Z^- taxa (4 Trichoptera, 3 Odonata, 5 Ephemeroptera) and ~40% of Z^+ taxa (2 Trichoptera). Half of the indicator taxa with negative responses to forest-loss (sensitive, Z^-) responded below 10% of forest-loss; however, few taxa had narrow 5th-95 th percentiles in the bootstrap results (three taxa with 5%–95% ≤ 0–15%). Seven of those taxa responded synchronously between 0 and 2% of forest-loss, but with large 5th-95th percentiles; for example *Argia* at 0–54% of forest-loss. Other Z^- (sensitive) taxa decreased in abundance with less than ~15% local-riparian forest-loss, with large 5th-95th quartiles; for example, 0–32% for *Heteragrion* and 0–91% for *Campylocia*. On the other hand, Z^+ (tolerant) taxa increased in abundance with greater than ~ 6% local-riparian forest-loss, with large 5th-95 th quartiles; for example, *Cyrnellus* with 0–60% of forest loss.

We recorded 9 taxa (~50%) as Z indicators of forest-loss with significant purity and reliability (purity ≥ 0.95; reliability 05 ≥ 0.95) at all three landscape extents (Tables A2, A3 and A4; Fig. 3, A5). Of those 10 taxa, three were Ephemeroptera (*Campylocia, Miroculis, Zelusia*), two were Plecoptera (*Anacroneuria, Macrogynoplax*), two were Trichoptera

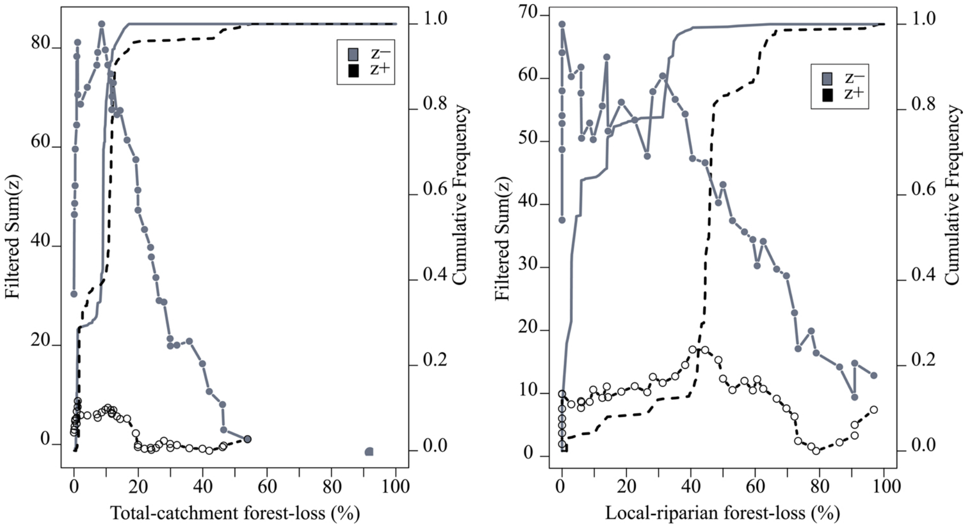

Fig. 2. Assemblage Threshold Indicator Taxa Analysis sum Z^+ and sum Z^- values corresponding to all change points along the riparian forest-loss at catchment (A) and local-riparian (B) extents. Peaks in the sums of Z^- and Z^+ are the sites along the gradient with synchronic decrease and increase of taxa, respectively. At the catchment extent, the highest peak for sum Z^- and sum Z^+ occurred at 9% and 2% of forest-loss, respectively. At the local-riparian extent, the highest peak for sum Z^- and sum Z^+ occurred at 1.4% and 42% of forest-loss, respectively. Sum Z^+ and sum Z^- values correspond to all candidate change points along the environmental gradient. Black dashed and gray solid lines represent the cumulative frequency distribution of change points for 500 bootstrap replicates for sum Z^+ and sum Z^-, respectively. Z^+ and Z^- = taxa increased or decreased in frequency of occurrence and abundance with increased forest-loss, respectively.

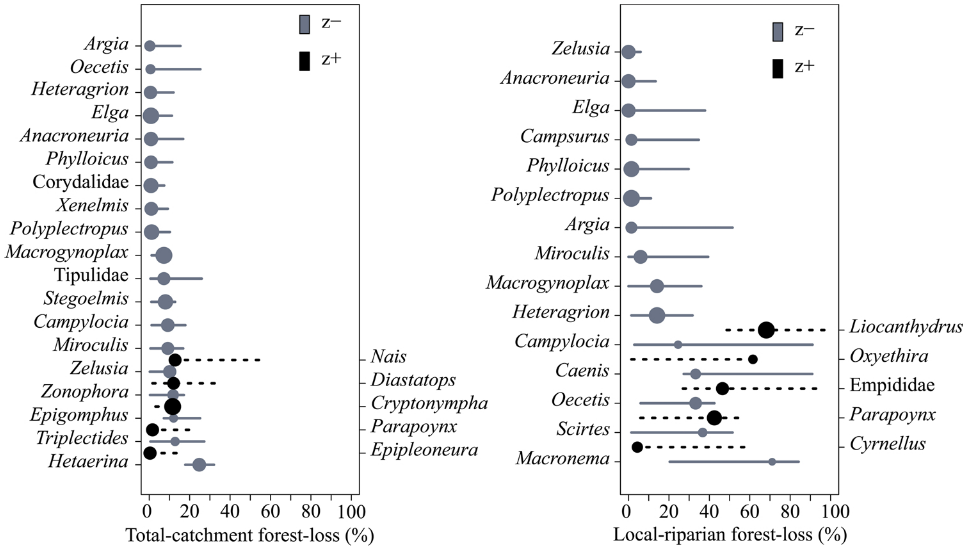

Fig. 3. Taxon-specific Threshold Indicator Taxa Analysis responses to forest-loss at catchment (A) and local-riparian (B) extents, showing significant indicator taxa ($p \leq 0.05$). Z^+ and Z^- = taxa increased or decreased in frequency of occurrence and abundance with increased forest-loss, respectively. Circles = change point of each taxon in proportion to the magnitude of the response. Circle sizes are proportional to Z^- score value. Error bars overlapping each circle represent 5th and 95th percentiles among bootstrap replicates (n = 500). The variations in error bars can be used to determine the change-zone width or confidence interval of an assemblage or taxon (Rodrigues et al., 2016).

(*Phylloicus, Polyplectropus*), two were Odonata (*Heteragrion, Elga*). The Ephemeroptera, Plecoptera, Trichoptera, and Odonata also comprised most of the significant and reliable indicator taxa at the network-riparian extent.

In the TITAN taxon-specific bootstrap results, taxa showed narrower 5^{th}-95^{th} percentiles at catchment (median: 0.5–15.4%) and network-riparian extents (median: 0.6–15.8%; Table A2, A4; Figure A6, A8) than at the local-riparian extent (median: 0.0–36.9%; Table A3; Figure A7). There also was far greater uniformity and tighter distributions for both Z^- and Z^+ indicator taxa associated with the catchment and network-riparian extents (Fig. 3, A5) versus those associated with the local-riparian extent for forest-loss (Fig. 3).

3.3. Assemblage richness responses

We observed a change point in segmented regression analysis for assemblage richness at 57 ± 3% (Model AIC = 433.93), 66 ± 5% (Model AIC = 456.65), and 75 ± 12% (Model AIC = 446.88) of forest-loss for catchment, network-riparian; and local-riparian extents, respectively (Figs. 4; A9). This total richness response occurred at much higher levels of forest loss than those indicated by TITAN at all three spatial extents and for both indicator taxa and total assemblages.

4. Discussion

4.1. Effects of forest-loss on macroinvertebrate assemblages

We found that a high percentage of riparian forest cover was necessary to avoid changes in macroinvertebrate assemblage composition in small Amazonian streams. The detection of an assemblage change point and alterations in assemblage composition with 9% and 1.4% of forest-loss at the catchment and local-riparian extent, respectively, indicates a very low forest-loss threshold for sensitive taxa. However, for total macroinvertebrate taxonomic richness, the change point was 57% and 75% of forest cover at catchment and local-riparian extents, respectively. These change-point differences indicate the low capacity of total richness to separate early and synchronous decreases of sensitive taxa from gradual increases of tolerant taxa. Thus, total richness can hide or mute such contradictory taxa responses to disturbance (Baker and King, 2010). The same phenomenon was observed for assemblage metrics or multimetric condition indices constructed with simulated data (King and Baker, 2010). This insensitivity is one reason that total taxa richness is often omitted from multimetric indices of assemblage condition for aquatic macroinvertebrates (e.g., Stoddard et al., 2008; Silva et al., 2017; Fierro et al., 2018) and fish (Hughes et al., 2004; Terra et al., 2013; de Carvalho et al., 2017).

The estimated thresholds (9% (1–15%) and 1.5% (0–35%) of forest-loss) of aquatic macroinvertebrate assemblages to catchment and local-riparian forest-loss were very low relative to previously determined values for terrestrial vertebrates in tropical forests (40–50%; e.g., Roque et al., 2018). These thresholds indicate that in the Amazon rainforest, the sensitivity of aquatic biodiversity to local-riparian forest-loss (as well as catchment forest-loss) are much higher than previously thought. The high dependence of some macroinvertebrate taxa to riparian and catchment forest cover can be related to three ecological factors. 1) Food webs of Amazonian streams are based on riparian and catchment inputs (Walker, 1985), and many taxa are strongly associated with resources and microhabitats provided by riparian forest (Henderson and Walker, 1986). 2) Some taxa have similar morphological, behavioral, and physiological adaptations in response to small variations in riparian zone conditions (King et al., 2011). 3) By definition, species with narrow functional niches (specialists) result in some taxa being less tolerant to conditions than taxa with broad functional niches (generalists) (Leitao et al. 2016). Brejão et al. (2018) also detected a low change threshold (< 20%) for fish assemblages experiencing deforestation along Amazonian streams. Clearly, our results indicate an intrinsic connection between forest streams and the riparian zone as has long been observed (Gregory et al., 1991). Moreover, the removal of small proportions of forest (at local-riparian, network-riparian and catchment extents) negatively affects aquatic macroinvertebrates, reinforcing their use as bioindicators of the effects of forest-loss and other anthropogenic disturbances more quickly than larger and less sensitive animals (e.g., Bryce et al., 2010; Brito et al., 2018). Therefore, our results further reinforce the importance of conserving stream-forest integrity to maintain not only macroinvertebrate species but entire ecosystems and the ecosystem services that streams provide for humans. Those services include organic material and nutrient processing, flood control and water supply, sediment trapping, biodiversity maintenance, and fisheries support (Cummins, 1974; Meyer et al., 2003; Colvin et al., 2019; Weber and Ringold, 2019).

In addition, our results indicate the importance of studying full forest gradients (forest cover: 0–100%) to detect thresholds in forests and to avoid the shifting baseline phenomenon (Pauly, 1995; Hughes, 2019). Studies that do not use the full gradient may overestimate thresholds and may evaluate only late responses. For example, in studies using reference areas having > 20% of forest-loss, the threshold for sensitive species may already have been surpassed.

We recorded taxa with negative (sensitive) responses (Z^-) and

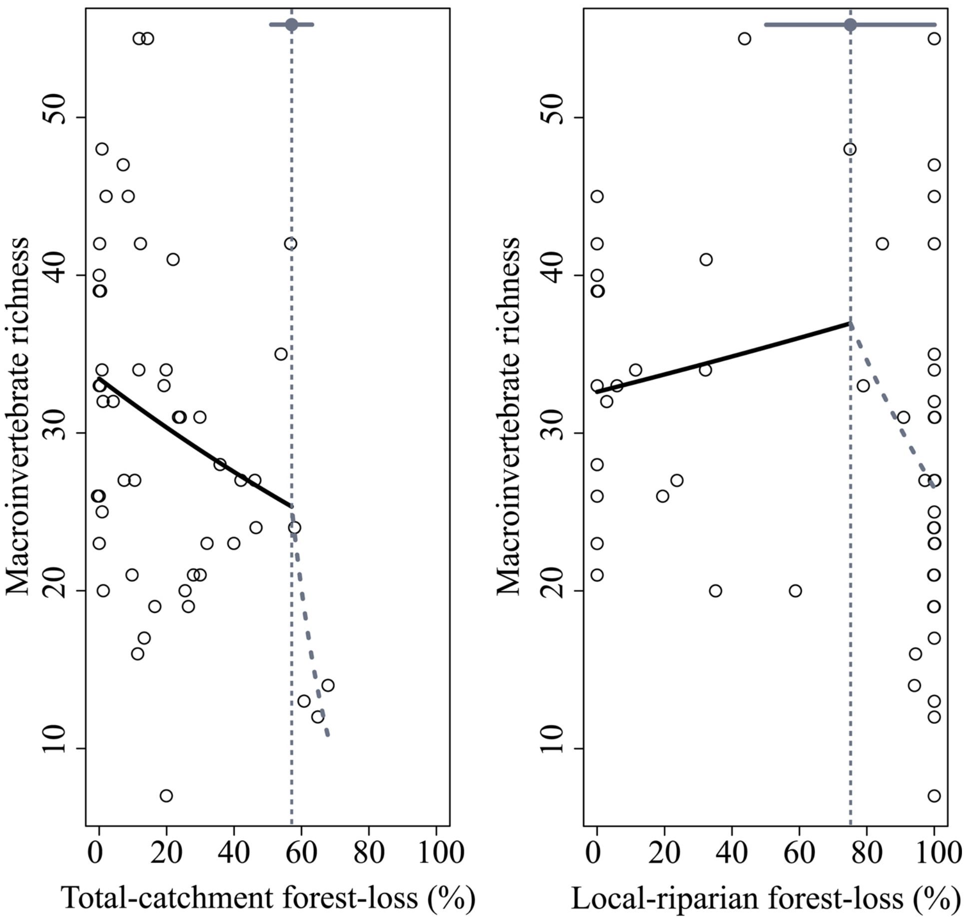

Fig. 4. Segmented regression analysis showing change points in species richness of macroinvertebrate assemblages relative to forest-loss at catchment (A) and local-riparian (B) extents. For richness, the change point is located at 57 ± 3% (mean and standard error) of forest-loss at the catchment extent and 75 ± 12% at the local-riparian extent.

others with positive (tolerant) responses (Z^+) to increased forest-loss. Response direction and specific attributes of each taxon help us to understand the mechanisms behind biotic changes caused by anthropogenic pressures (King et al., 2011) and may be directly associated with tolerances and requirements of each taxon (Poff, 1997). Riparian forest-loss (in general) results in alterations in source and quality of allochthonous organic matter available to macroinvertebrates and increased light inputs to streams (Siegloch et al., 2017). Such changes lead to increased abundance and/or frequency of occurrence of three types of taxa. 1) Taxa preferring or tolerant to open areas (e.g., *Diastatops*) tend to increase (Hamada and McCreadie, 1999; Oliveira-Junior et al., 2017). 2) Taxa feeding on algae and aquatic macrophytes (e.g., *Parapoynx,* and *Oxyethira*) tend to proliferate (Nessimian and da Silva, 1994). 3) Generally, tolerant taxa (for organic pollution and sedimentation) like *Nais* tend to multiply under stream degradation conditions (Simpson et al., 1993).

In general, mechanisms involving changes in aquatic macroinvertebrate assemblages are difficult to understand because of the great complexity of relationships (including biotic and abiotic components) and the lack of detailed information about natural history, biology, and ecology of specific taxa (Heino and Peckarsky, 2014). It is likely that different mechanisms account for the relationships between the Z^- taxa and the riparian forest that we documented, but we can identify characteristics that highlight certain mechanisms for some taxa. For instance, the stoneflies *Anacroneuria* and *Macroginoplax* are typical of forested areas and have low dispersion capacities (Briers et al., 2002) and physiological restrictions to elevated temperatures (Hynes, 1976). *Heteragrion* (Odonata, Zygoptera) has high habitat selectivity and limited dispersal capacity (Corbet, 1999; Loiola and de Marco, 2011; Oliveira-Júnior et al., 2015). In addition, the caddisfly *Phylloicus* is typical of forested areas and dependent on leaves from riparian forest for feeding and case construction (Martins et al., 2017b). In Brazilian savanna streams, the mayflies *Campylocia* and *Miroculis* were reported to be sensitive to riparian disturbances (Firmiano et al., 2017).

4.2. Influence of forest-loss on macroinvertebrates at different spatial extents

Potential mechanisms affecting populations, assemblages, and communities at different spatial extents include habitat change feedbacks and cascade effects (Levin, 1992). For instance, forest alterations at the site or reach extent may degrade the canopy structure of forests, enhancing light penetration, which facilitates food web changes and primary production in streams (Bunn et al., 1999; Mosisch et al., 2001; Kiffney et al., 2003).

Increased light facilitates the colonization of aquatic plants that subsequently change microhabitats, leading to non-linear assemblage changes, characterized by increased abundances of collectors and grazers (e.g, *Parapoynx*, and *Oxyethira*) versus shredders (e.g., *Phylloicus*, and *Triplectides*), as we detected in our study. Grazer abundance may also increase as a result of periphyton growth under increased light conditions after canopy alterations (Kiffney et al., 2003).

Land use changes at catchment extents may affect macroinvertebrates in many different ways, but one of the most pervasive is increased sedimentation and stream bed degradation caused by increased runoff after forest alterations. The impacts to streams from sedimentation include: 1) increased turbidity, scouring and abrasion (Sutherland et al., 2002); 2) impaired substrate suitability for biofilm production (Iwata et al., 2003; Chará-Serna and Richardson, 2018); 3) decreased food quality causing bottom-up effects through food webs; 4) increased substrate embeddedness that excludes crevice-occupying invertebrates and access to food resources (Sutherland et al., 2002; Iwata et al., 2003; Lecerf and Richardson, 2010; Chará-Serna and Richardson, 2018); 5) increased coating of gills and respiratory surfaces (Sutherland and Meyer, 2007); and 6) reduced stream habitat heterogeneity (Sutherland et al., 2002; Iwata et al., 2003).

Moreover, changes in the forest matrix at catchment extents can influence the permeability of the landscape for the movement of adult aquatic insects (Valente-Neto et al., 2016). These catchment-extent impacts can also have a synergistic effect, depending on the habitat loss, fragmentation and matrix type (Boesing et al., 2018), but how these interacting effects cause assemblage thresholds in aquatic communities is unclear. These non-linear effects of habitat loss and fragmentation on population abundances can cause dramatic shifts in assemblage composition when disturbances surpass certain levels.

Although the assemblage change point at the local-riparian extent was consistent and lower than that detected in the other extents, the TITAN sum(z) output indicates that macroinvertebrate assemblages were more sensitive and responsive to forest-loss at the catchment or network-riparian extent than at the local-riparian extent (Figs. 2, A3). Catchment forest-loss produced a stronger signal of assemblage change for sensitive taxa than did local-riparian forest-loss; however, the mean per-taxon signal was greatest for network-riparian forest cover. These extent differences indicate that broad upslope patterns of forest-loss have a stronger effect on assemblages than local-riparian measures. This idea is further supported by the cumulative frequency distributions (CFD) of sum(Z^-) maxima across bootstrap replications (Figs. 2; A3). Those CFD distributions reflect variation in the assemblage-level change points as a result of dataset resampling (Baker and King, 2010). More vertical CFD curves and narrower CFDs indicate greater certainty of the location of the change point and stronger support for the pattern expected from a threshold response (King et al., 2005). We observed tighter CFD distributions for the catchment and network-riparian extents than for the local-riparian extent. These CFD results indicate greater precision in the assemblage-level response for forest-loss assessed at the catchment or riparian-network extents than at the local-riparian extent. This is further supported when we analyze the individual taxa responses assessed via bootstrap uncertainty Figs. 3; A4). Although a few taxa show narrow 5–95 quartiles in their bootstrap results, the far greater uniformity and tighter distributions of bootstrap replicates associated with catchment and network-riparian rather than local-riparian forest cover supports the notion that the primary signal is being derived from catchment or network-riparian forest cover.

In general, studies have shown that macroinvertebrates are sensitive to native vegetation loss from local-riparian zones, probably because they are highly responsive to substrate quality and more directly dependent on the riparian zones for feeding, refuge and dispersal (e.g. Ruaro et al., 2016). Although our study indicates that macroinvertebrates in Amazonian streams respond to local-riparian forest-loss, the most impressive finding of our study is that macroinvertebrate change points across forest-loss gradients are more predictable from entire catchment and network-riparian extents than from local-riparian extents. This means that very low levels of local forest removal can produce biotic loss, but it does not have to and it may take greater local removal than catchment removal to produce a biotic response in some cases. Perhaps this occurs because local disturbances can be mitigated by upstream and downstream refuges with intact populations (Hughes et al., 2004; Colvin et al., 2019). Amazon fish assemblage responses to riparian and catchment deforestation reinforce our results (Brejão et al., 2018; Leal et al., 2018). Clearly, conservation strategies and management actions are needed at both riparian (local-riparian and network-riparian) and catchment extents. Similar conclusions were reached for USA temperate rainforest streams (FEMAT, 1993) and USA streams in general (Hill et al., 2017; Hughes et al., 2019; Hughes et al., 2006).

We emphasize that catchment and network-riparian forest-loss were autocorrelated. So for our study area, the amount of catchment forest cover can be used as a proxy for the network-riparian extent (and vice-versa), which allows us to make generalizations about the role of forest throughout the region. Van Sickle et al. (2004) reported a similar relationship for the temperate Willamette River basin, Oregon, USA. However, this should not be assumed to be a general pattern for all forests, because the relationship between the amount of forest in the catchment and riparian-network depends on the history and type of deforestation processes.

4.3. Conserving aquatic biodiversity in Amazonia

Our results have important implications for natural resource management policies in Brazilian riparian zones. The Brazilian Forest Code (Federal Law 12.651/2012) aims to protect ecological equilibrium and water resource quality. The Code requires a 30-m forested riparian buffer along each stream bank (for streams ≤10-m wide) as a Permanent Preservation Area. However, we found clear change points at catchment (9% forest-loss), network-riparian (12% forest-loss) and 100-m local-riparian buffer (1.4% forest-loss) extents, indicating that biota appear to be sensitive to forest-loss outside of 30 m. Thus, expanding the buffer width may be necessary, but perhaps not sufficient for protecting sensitive macroinvertebrate taxa in Amazonian streams. Thus, policy makers should also consider entire catchments, especially headwater catchments that may provide sources of biota for downstream reaches (Meyer et al., 2003; Colvin et al., 2019). Therefore, it would be wise for environmental planning to favor natural borders over political borders, unlike most Brazilian environmental legislation (Nunes at al, 2014).

Additionally, our results have three other important implications for Brazilian legislation and forest management. First, our findings indicate that the Legal Reserve area (reserve of native vegetation for private property) in the Forest Code is less than that necessary to ensure the maintenance of stream biodiversity. Our study indicates that a loss of about 10% of the catchment forest (90% forest retention) may cause important changes in macroinvertebrate assemblage structure. The Forest Code mandates conserving only 80% of forest on private property, 10% less than what we detected as a change point. In addition, property boundaries do not correspond to catchment divides, quantification typically ignores public infrastructure and pre-existing conditions, and there are multiple political and economic pressures to grant exceptions to existing rules—all of which result in shifting benchmarks (Pauly, 1995). Nonetheless, further studies in other Amazonian regions need to be conducted to establish an empirical value that can serve as a better reference for legislation and environmental protection. Second, we found that the macroinvertebrate fauna in Amazonian streams need large percentages of native forest coverage. That goes against the law for Consolidation Areas in Ecological-Economic Zoning Plans for Amazonia (Federal Law 12.651/2012). That law states that properties with more than 50% of their forest cover removed need only restore or compensate enough to reach 50%, which is much lower than that required for sensitive stream macroinvertebrates. Similar conclusions were obtained for fish assemblages in this same study area (Leal et al., 2018), and exceptions to existing rules are common as stated above. Third, it is important to evaluate the effects of interactions among landscape configuration, composition, matrix, and land use on biodiversity (Barlow et al., 2016; Boesing et al., 2018) before setting specific values. Lastly, laws are only paper. Without rigorous regulation monitoring and enforcement, even the best laws fail to meet their objectives (Nunes et al., 2014; Leal et al., 2018). Therefore, it is important to improve Brazilian legislation based on empirical evidence about ecological thresholds–and to enforce those laws–to reconcile agricultural production with nature protection in Amazonia.

In addition to the existing failures, concessions, omissions and gaps in Brazilian Environmental Law, the conservation of aquatic and terrestrial biodiversity in the Amazon is threatened by recent changes in the laws governing National Preservation Areas (NPAs; Ferreira et al., 2014; Mascia et al., 2014). Despite the conservation efforts of previous governments, downsizing and degazetting events have occurred since 2008 in the Brazilian Amazon. These events have been associated with increased agribusiness, hydroelectric energy, and mineral mining (Ferreira et al., 2014). Under the current Brazilian government, legal threats to NPAs have intensified. Consequently, empirical studies such as ours, besides helping to guide public policies, reinforce the importance of the permanence of NPAs for conserving biodiversity.

Regarding sensitive groups like macroinvertebrates and rare species (Leitão et al., 2016), there are at least four challenges for using our findings for guiding decision-making in forest-stream preservation, rehabilitation, and regulation. 1) We focused on two phyla (Arthropoda and Annelida), whereas we need information about thresholds from multiple taxa (e.g., Barlow et al., 2016). 2) Our study was restricted to a single Amazon region, but we need information about how ecological thresholds vary in multiple Amazon regions (e.g., Leitão et al., 2018). 3) We used catchment, network-riparian and 100-m buffer (local-riparian) extents to calculate forest cover (Valle et al., 2013). However, we still do not know the best survey design or extent (site-radius area, subcatchment area, network-catchment area) to calculate landscape pressures (Hughes et al., 2019). Also, we lack information about dispersal patterns and biology of most neotropical aquatic insects (Heino and Peckarsky, 2014). However, applying partitioned study designs (catchment, riparian-network, local-riparian, instream) such as those used herein and by others (Leal et al., 2016, 2018; Leitão et al., 2018) can help us discriminate key pressures, stressors, and spatial extents. Likewise, analyzing both natural and anthropogenic predictors at multiple extents aids us in determining the major drivers of ecosystem condition at those extents (Hughes et al., 2006, ; Macedo et al., 2014). In addition, assessing conditions at hundreds of sites over large regions helps us to understand how regional or basin differences alter predictor-response relationships (Chen et al., 2017; Leitão et al., 2018; Callisto et al., 2019; Herlihy et al., 2019). 4) Finally, applying more powerful analytical tools such as structural equation modeling (Leitão et al., 2018), partial constrained redundancy analysis together with variance partitioning (Marzin et al., 2012; Macedo et al., 2014), and random forest modeling (Breiman, 2001; Cutler et al., 2007) can enable us to analyze complex interactions among differing extents of predictor and response variables. Nonetheless, if we wait until the Amazon is irretrievably altered by humans before taking effective conservation actions, we will be doing a disservice to the biota and the humans throughout the planet that depend on maintaining its ecological integrity.

Although there is a lack of congruency between different aquatic assemblages regarding responses to anthropogenic impacts (Bryce et al., 2010; Heino, 2010; Hering et al., 2010), Brito et al. (2018) found clear responses with aquatic insects for Amazonian streams. Therefore, we recommend their scientifically rigorous monitoring to minimize risks of abrupt biodiversity losses as priorities in national and international public policies and research agendas, especially in the Amazon. Such foci have been implemented previously in the USEPA's National Aquatic Resource Surveys, the European Union's Water Framework Directive, and Australia's Sustainable Rivers Audit (Shapiro et al., 2008; Davies et al., 2010; Hering et al., 2010). Reversing the potential collapse of Amazonian aquatic biodiversity requires avoiding deforestation and halting the degradation of riparian forests and watercourses. Therefore, we support socioeconomic incentives for rehabilitating riparian and catchment forests and stream ecosystems, such as payment for the ecosystem services provided by farmers that protect their riparian forests and technical support to guide farmers to use riparian forests sustainably by avoiding riparian deforestation for pasture. We believe that payment schemes in Amazonia could benefit potential sellers who are exceeding regulatory requirements. Based on our results, sellers who are protecting > 30 m of riparian forest, as well as those who are protecting beyond the legal reserve across the catchment, are contributing to aquatic biodiversity and ecosystem services conservation, and it seems wise to pay them more for doing so.

There is accumulating evidence regarding the great sensitivity of Amazonian streams to landscape changes (e.g., Nobre et al., 2016; Martins et al., 2017a), particularly the loss of aquatic organisms, a phenomenon recently named Empty Rivers (Antunes et al., 2016). We agree that reducing habitat loss should be a top priority for conservation planners in tropical forests (Villard and Metzger, 2014). Nonetheless, we emphasize that in Amazon rainforests, the sensitivity of aquatic biodiversity to riparian and catchment forest-loss is much higher than previously thought. Therefore, applying the Forest Code regulatory framework will require much more restrictive policies, regulations and enforcement if aquatic biodiversity protection remains a goal.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2019.108263.

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