ORIGINAL ARTICLE

Longitudinal effects of land-cover transitions on the periphyton community of a tropical stream

Bruna Suelen da Silva,[1]* Eugenia Zandonà,[1] Vinicius Neres-Lima,[1] Timothy P. Moulton,[1] Flavia Tromboni,[2] Steven A. Thomas,[3] Rafael Feijó-Lima[4]

[1]Postgraduate Program in Ecology and Evolution, Rio de Janeiro State University (UERJ), Rio de Janeiro, Brazil; [2]Rhineland-Palatinate Technical University of Kaiserslautern-Landau (RPTU), Landau, Germany; [3]Department of Biological Sciences, University of Alabama, Tuscaloosa, AL, USA; [4]Belle W. Baruch Institute of Coastal Ecology and Forest Science, Clemson University, Georgetown, SC, USA

ABSTRACT

Our study aims to investigate the longitudinal effects of two land-cover transitions on the periphytic algal community. We utilized datasets from three different studies conducted over a 5-year interval in a tropical headwater stream. The studied stream traverses two abrupt adjacent transitions from an upstream forest to a pasture and back to a downstream forest remnant. We performed a high-spatial resolution sampling and used generalized additive models (GAMs) to capture the non-linear gradient response of algal metrics to distance from land-cover transitions. Algal biomass presented a lagged response to increased light availability along the pasture section and decreased along a shorter distance in the downstream forest. Most algal metrics presented a lagged response to transitions, with chlorophyll-*a* taking up to 375 m to reach the maximum values inside the pasture and up to 300 m to return to reference conditions inside the downstream forest. In the downstream forested section, diatom richness and abundance were similar to the upstream forested section but did not return to reference conditions. The results were consistent across years. Our results indicate that, while riparian forest remnants can play an important role in buffering impacts related to land-cover changes in low order streams, both the magnitude and directionality of these effects might be influenced by longitudinal effects caused by the flow of water. Riparian forest remnants can have a longitudinal effect in stream conditions, influencing environmental characteristics even over non-forested reaches, to where the forest conditions can be propagated downstream by the flow of water.

INTRODUCTION

Deforestation resulting from agriculture and animal rearing significantly alters the structure and function of aquatic ecosystems (Fellows *et al.*, 2006; Silva-Araújo *et al.*, 2020). Riparian vegetation often serves as a protective barrier for adjacent aquatic ecosystems, mitigating soil erosion, reducing sediment and particulate nutrient input into streams, and regulating water temperature and light availability (Allan, 2004). Riparian vegetation also influences the balance between allochthonous and autochthonous energy inputs in stream reaches, impacting vital in-stream processes such as nutrient cycling, leaf litter decomposition, primary productivity, and the abundance and diversity of invertebrate species (Moslemi *et al.*, 2012; Tromboni *et al.*, 2019; Silva-Araújo *et al.*, 2020). In tropical streams, periphytic algae communities predominantly contribute to autochthonous primary production and serve as a crucial energy source for primary consumers, often supporting the entire food web (Bunn *et al.*, 1999; Brito *et al.*, 2006; Neres-Lima *et al.*, 2016).

Periphyton productivity is influenced by various factors such as herbivory, flow velocity, light availability, and nutrient levels (Lourenço-Amorim *et al.*, 2014; Calvo *et al.*, 2022). While forested reaches typically exhibit low periphyton productivity due to shading, deforested areas are characterized by increased algal biomass, with limitations imposed by nutrient availability, water velocity, or herbivory (Tromboni *et al.*, 2019). Therefore, periphyton communities may exhibit rapid responses to land-cover changes, with shifts in physiognomy observed following riparian deforestation (Pan *et al.*, 2006; Bere and Tundisi, 2011). In tropical regions, where human activities have fragmented landscapes, deforestation potentially affects riparian forests and their ability to buffer adjacent streams from land use changes (Neill *et al.*, 2001). Hence, human activities may alter periphyton abundance and community composition, thereby influencing the entire lotic food web through bottom-up processes (Machado-Silva *et al.*, 2022).

Studies have focused on determining the minimum lateral ex-

*Corresponding author: bruna_suelen_04@hotmail.com

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tension of riparian forests necessary to maintain aquatic ecosystem integrity and protect lotic systems from upstream land-cover changes (Broadmeadow and Nisbet, 2004; Lorion and Kennedy, 2009). In Brazil, riparian forests are designated as priority conservation areas with legislation, mandating a minimum lateral extension of riparian forest buffers based on river size (Brazilian Forest Code, No. 12.727/2012). However, there remains a gap in understanding the longitudinal propagation of deforestation effects on downstream reaches and their impacts on abiotic and biotic characteristics. Due to the continuous and unidirectional flow of water in streams, the effects of local land-cover are expected to propagate some distance downstream (Feijó-Lima *et al.*, 2018). This longitudinal linkage between upstream and downstream reaches would create ecological gradients as streams traverse discrete changes in riparian conditions and biological communities adjust to new physical, chemical and biological conditions (Feijó-Lima *et al.*, 2018). Some studies have identified longitudinal effects of abrupt transitions in land-cover in water temperature, invertebrate communities, algae, and ecosystem function (Scarsbrook and Halliday, 1999; Rutherford *et al.*, 2004; Suga and Tanaka, 2013; Tanaka *et al.*, 2016; Feijó-Lima *et al.*, 2019). These previous studies suggest that biotic and abiotic variables may have a spatial lag in their response to land-cover transitions and that forested reaches may have the capacity to cushion ecological conditions in downstream reaches that do not have a forest (Feijó-Lima *et al.*, 2018, 2019).

In this study, we examine how stream algal communities change longitudinally in response to abrupt changes in riparian forest conditions. We chose to assess periphyton as a response variable because of its capacity to respond to changes in canopy cover and light-condition over short distances (Scarsbrook and Halliday, 1999; Feijó-Lima *et al.*, 2019). Specifically, our study examines how two successive transitions in land-cover, from an upstream forest to pasture and from that same pasture to a downstream forest, influence periphyton abundance and composition. We relied on datasets collected from one stream in three different years to assess the distances over which algal communities respond to discrete land-cover transitions and subsequent gradients in physical, chemical and biological conditions they create. We expected that, if upstream conditions were dampening the responses to local riparian vegetation in downstream sections, we would observe a gradual alteration in key variables related to the algal community, which would persist across different land use types rather than abruptly changing at their boundaries.

METHODS

Study area

The study was carried out in a second-order stream (Fig. 1), located in the Guapiaçu-Macacu watershed in Cachoeiras de Macacu, Rio de Janeiro state, Brazil (22°27.251' S, 042°40.756' W). The region is part of the Atlantic Rainforest biome. Average annual temperatures are ~22°C and most of the rain occurs in the summer, with average precipitation of 2280 mm per year and July being the driest month with 54 mm of rain (https://en.climate-data.org/, 2022). Guapiaçu-Macacu river basin has a drainage area of 1,260 km² and provides water to approximately 2.5 million people (da Silva *et al.,* 2012). The basin has a mixed land use, with approximately 43.6% of the total area occupied by pasture and 42.4% by forested areas in an advanced successional state (Carvalho *et al.*, 2009). The headwaters of the stream examined in this study is an undisturbed forest adjacent to the Três Picos State Park. The focal stream flows from this well-preserved forest through a deforested area used as a pasture for non-intensive animal rearing, where cattle and horses freely access the stream channel. At the downstream end of the pasture, the stream flows into a forested reach that shows some signs of past logging and is adjacent to a dirt road. There were no tributaries entering the studied stream reach.

Sampling design

Throughout these two transitions we established sampling sites every 75 m over a total reach length of approximately 1.6 km. The sampling sites located between 0 and 525 m are within the upstream forest, those between 600 and 1050 m are in the pasture, and those between 1125 to 1650 m are in the downstream forest (Fig. 1). From here on, the first land-cover transition will be addressed as "forest-pasture" (T1, between 525 and 600 m) and the second transition in land-cover as "pasture-forest" (T2, between 1050 and 1125 m). The transition points were chosen based on canopy cover data from 2015. Establishing fixed transition points helped us to understand the extension of riparian vegetation recovery when we compared different years. It is expected that physical, chemical and periphytic biofilm characteristics change their behavior after the shift in land-cover has occurred. A longitudinal effect is represented by a lag in the variable's response after the change in canopy cover. A gradual change in the variables throughout the reach suggests that the stream is responding to physical and chemical drivers from upstream and are not interpreted as an immediate response to local riparian conditions. If the variables were responding only to local conditions, we would expect an immediate change at the land-cover transitions.

Field sampling and laboratory analyses

Sampling was carried out during the dry season in 2014, 2015 and 2019. Variables examined in each year in this study are summarized in Tab. 1 and Tab. S1. Canopy cover was measured in all years using a spherical densiometer (Forest densiometer, Bartlesville, OK, USA). We measured chlorophyll-*a* (chl-*a*) and ash free dry mass (AFDM) from periphyton standing stocks at 15 sampling sites (placed along the forest-pasture transition) in 2014 and 19 sampling sites (placed along the two transitions) in 2019. For that we chose three well colonized rocks in each sampling site to compose one sample, scraped the biofilms and measured the total length and width of each rock and estimated the area using the ellipse formula. In 2019 and 2015 sampling, ceramic tiles of 25 cm² were placed in the stream in 19 and 21 sampling sites, respectively, along the two transitions for 7 days. The colonization time of 7 days was chosen because it was the best data set available for 2015 and 2019 experiments. Among the available data for both years, 7 days of colonization was the only that did not suffer loss of biomass due to natural disturbances (*i.e.*, rain). In 2015, we analyzed chl-*a*, AFDM and the algal community composition on the ceramic tiles by phyto-PAM and microscopy. For the 2019 experiment, we quantified the same variables, but the algal community composition accrued on ceramic tiles was investigated only using the Phyto-

PAM approach. Additionally, we also sampled the chl-*a* and AFDM from periphyton standing stocks.

Chl-*a* and AFDM were obtained by scrubbing the substrates, rocks and titles, and the resulting slurry was homogenized and filtered using pre-ashed GF/D glass fiber filters (Whatman, Maidstone, Kent, UK). In addition, part of the slurry was reserved for periphyton taxonomic composition analysis (phyto-PAM and microscopy). In 2015, two tiles were scrubbed to compose one sample, due to the necessity of more material to perform the analysis while in 2019 we utilized just one tile per sample. Chl-*a* samples were extracted in opaque containers, using 10 mL of 90% ethanol at room temperature, stored overnight under 0°C and read within

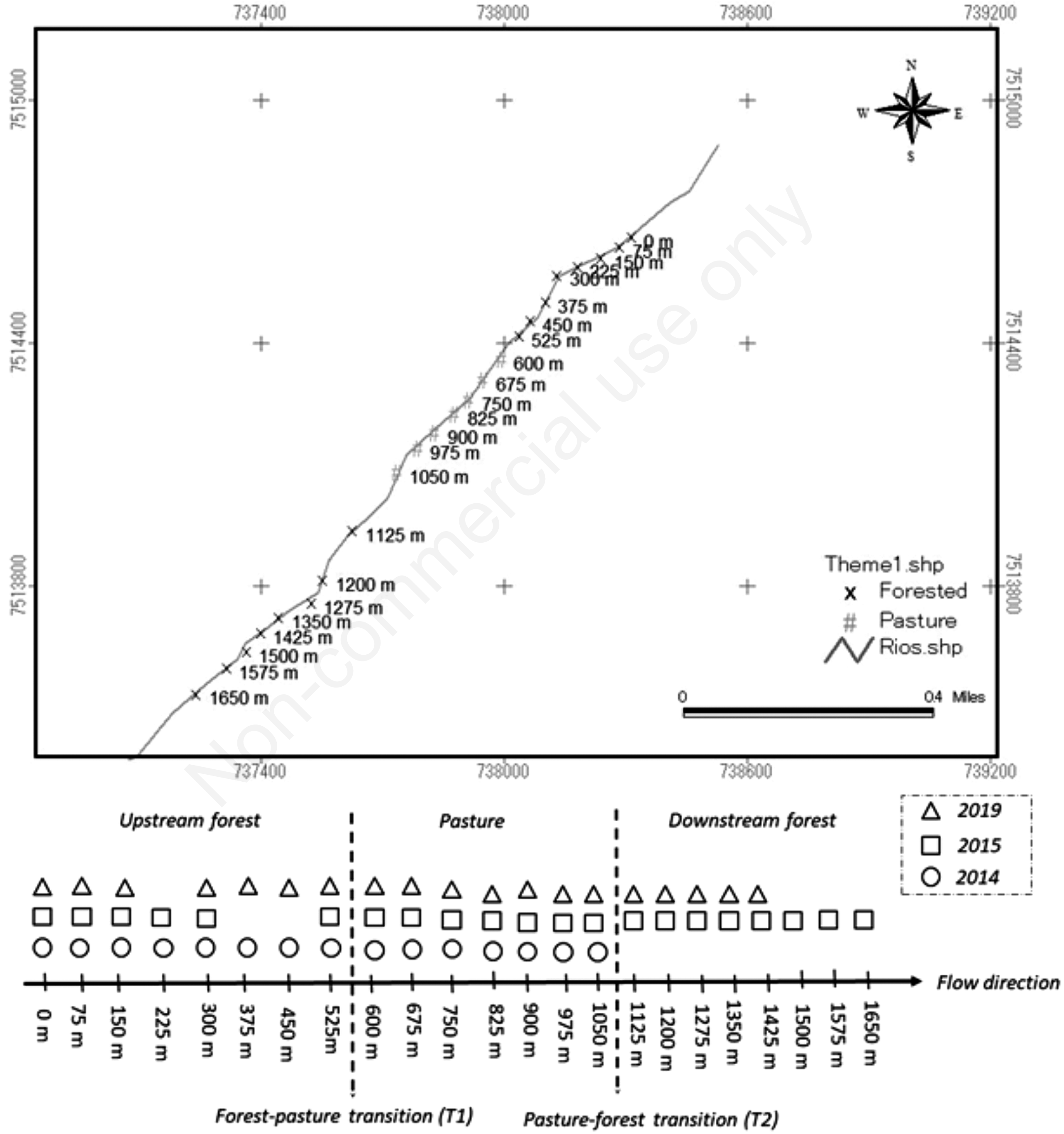

Fig. 1. Experimental design showing the two land-cover transitions along the stream and the sampling points assessed for each year. The layout of the sampling sites is as follows: upstream forest (0-52 5m), pasture (600-1050 m) and downstream forest (1125-165 0m). Each sampling site is placed 75 m apart from the next, ensuring systematic coverage across the different land-cover types along the stream. This design enables a comparative analysis of ecological variables across the transitions from forest to pasture and back to forest.

24 h of extraction in a fluorometer. To obtain AFDM we dried the filters in a drying oven for 72 h at 60°C and we then combusted them in a muffle furnace at 550°C for 1 h.

In 2015, we also measured physical and chemical variables, such as flow velocity, using a flow meter (Flow Probe, Global Water, Gold River, CA, USA), the concentrations of soluble reactive phosphorus (SRP) and ammonium (NH_4^+) for each sampling site. We collected three replicates of nutrient samples and filtered them with pre-ashed GF/F glass fiber filters (Whatman). For SRP concentrations, samples were measured through absorbance using the molybdenum-antimony blue colorimetric technique (Murphy and Riley, 1962). We measured NH_4^+ using the OPA fluorometric method with a fluorometer (Trilogy, Turner Designs Inc., Sunnyvale, CA, USA), considering the background fluorescence (Koch *et al.*, 2007).

Periphyton taxonomic composition

We performed two different procedures for the determination of the photosynthetic biofilm taxonomic composition, Phyto-PAM measurements (2015 and 2019) and microscopic identification (2015). Microscopic algae and cyanobacteria identification was performed for 12 sampling sites along the two transitions (four samples from each type of land-cover reach) at the following sampling points: 0 m, 75 m, 150 m, and 300 m in the upstream forest reach; 600 m, 750 m, 900 m, and 1050 m in the pasture reach and 1200 m, 1350 m, 1500 m, and 1650 m in the downstream forest reach. A 2 mL sub sample of the slurry obtained from the scrubbed substrates was fixed with Lugol and prepared in sedimentation chambers. After 24-h fixation time, the chambers were visualized and photographed in an inverted microscope, by sorting 30-35 randomized fields. We identified the individuals found in the pictures at the genus level (Bicudo and Menezes, 2005). The number of individuals counted was corrected by the slurry sample volume and by the tile area to estimate the total algal the total algal density (individuals m^{-2}).

Phyto-PAM technique consists of an *in vivo* fluorometric method for determining the photosynthetic biofilm composition, which measures wavelengths in different bands (470, 520, 645 and 665 nm). The procedure separates the photosynthetic biofilm (Heinz Walz GmBH, Effeltrich, Germany) into different groups, classifying them into “green”, “brown” and “blue”. Green algae present chl-*a* fluorescence excitation peaks at 480 nm and 650 nm. In diatoms, the peak occurs at 525 nm and cyanobacteria show the chl-*a* peak around 630 nm (Jakob *et al.*, 2005). Phyto-PAM classification into blue, green and brown groups can be associated with the taxonomic classification of different algal and cyanobacterial groups. Green is associated with Chlorophyta and Euglenophyta, blue with cyanobacteria and brown with diatoms (Garfield and Yokota, 2017). The use of phyto-PAM has the advantage of being a rapid algae assessment method, serving as a tool for the continuous monitoring of aquatic ecosystems (Garfield and Yokota, 2017). We analyzed all Phyto-PAM samples within 24 h of collection to ensure that the photosynthetic biofilm was still alive at the time of reading.

Statistical analysis

Data of canopy cover and chl-*a* of different years were converted into proportion, dividing each value by the maximum value, aiming to simplify comparison of data. Then data were related against the distances of the sampling sites, where 0 m is the most upstream sampling site and the remaining sampling sites were measured downstream every 75 meters, to understand how variables respond and to measure the distance it takes to achieve a new state after a land-cover transition. For this we used generalized additive models (GAMs) to capture the non-linear relationship between the response variables and the distance. GAMs were fitted using the method REML in the ‘mgcv’ package (Wood, 2017). To understand how the photosynthetic biofilm composition changes between the land-cover patches (upstream forest, pasture and downstream forest) we performed a non-metric multidimensional scaling analysis (NMDS) using the MASS package (Venables and Ripley, 2002). All analyses were performed using the R software (version 4.0.4).

RESULTS

In 2015, SRP had overall higher concentrations in the upstream forest and declined throughout the pasture where it reached the minimum value. After the pasture-forest transition, back to a forested environment, the SRP concentrations increased again (GAM model: r^2 adjusted=0.381, F=5.109, p=0.02; Fig. 2A). NH_4^+ concentrations showed little variation along the transitions. There was a trend for NH_4^+ concentrations to increase in the pasture and decrease in the downstream forested reach (GAM model: r^2 adjusted=0.737, F=15.52, p<0.001; Fig. 2B). Flow velocity presented a great variation within each type of land-cover category,

Tab. 1. Set of variables available for each year and the number of samples taken (N).

	2014	N	2015	N	2019	N
NH_4 concentration	-	-	x	63	-	-
PO_4 concentration	-	-	x	63	-	-
Flow velocity	-	-	x	21	-	-
Canopy cover	x	15	x	21	x	19
Chl-*a* tiles			x	21	x	19
Chl-*a* rocks	x	15	-	-	x	19
AFDM tiles	-	-	x	21	x	19
Algae microscopy	-	-	x	12	-	-
Phyto-PAM	-	-	x	21	x	19

AFDM, ash free dry mass.

upstream forest, pasture and downstream forest (GAM model: r² adjusted=0.101, F=2.239, p=0.25; Fig. S1), however both the maximum absolute value and the highest mean value was recorded in the pasture reach.

Over the years, we observed a gradual recovery of native vegetation in the forest-pasture transition along the final 150 meters of the upstream forest reach (Fig. 3A). In 2014 the proportion of canopy cover abruptly decreased from 0.3 to 0.09 in the first 75

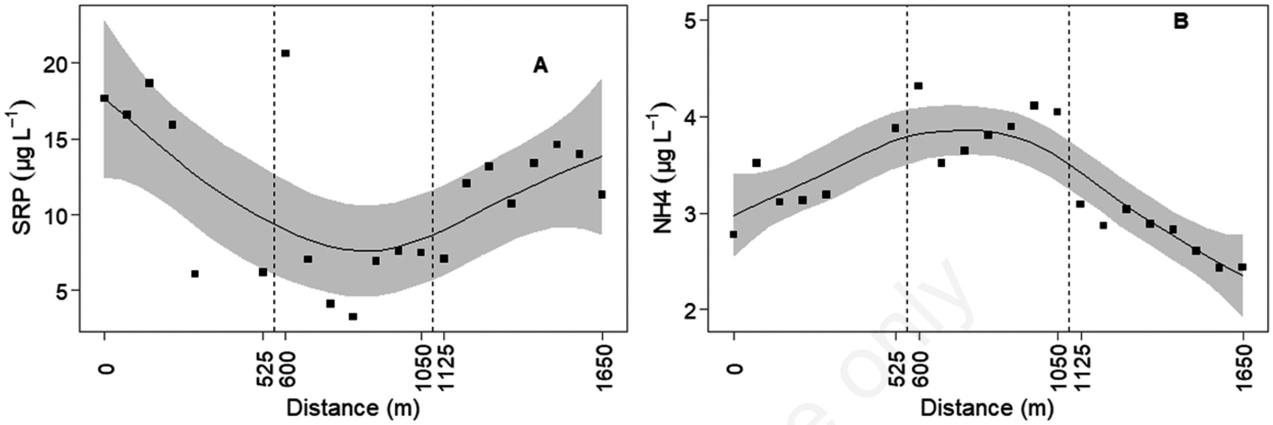

Fig. 2. Generalized additive models showing the nutrients along the two land-cover transitions in 2015 (A) soluble reactive phosphorus concentrations and (B) NH_4^+ concentrations. The dashed lines represent the land-cover transitions. The forest-pasture transition (T1) is placed between the last sampling site in the upstream forest (525 m) and the first sampling site in the pasture reach (600 m). The pasture-forest transition (T2) is between the last sampling site in the pasture (1050 m) and the first sampling site in the downstream forest (1125 m).

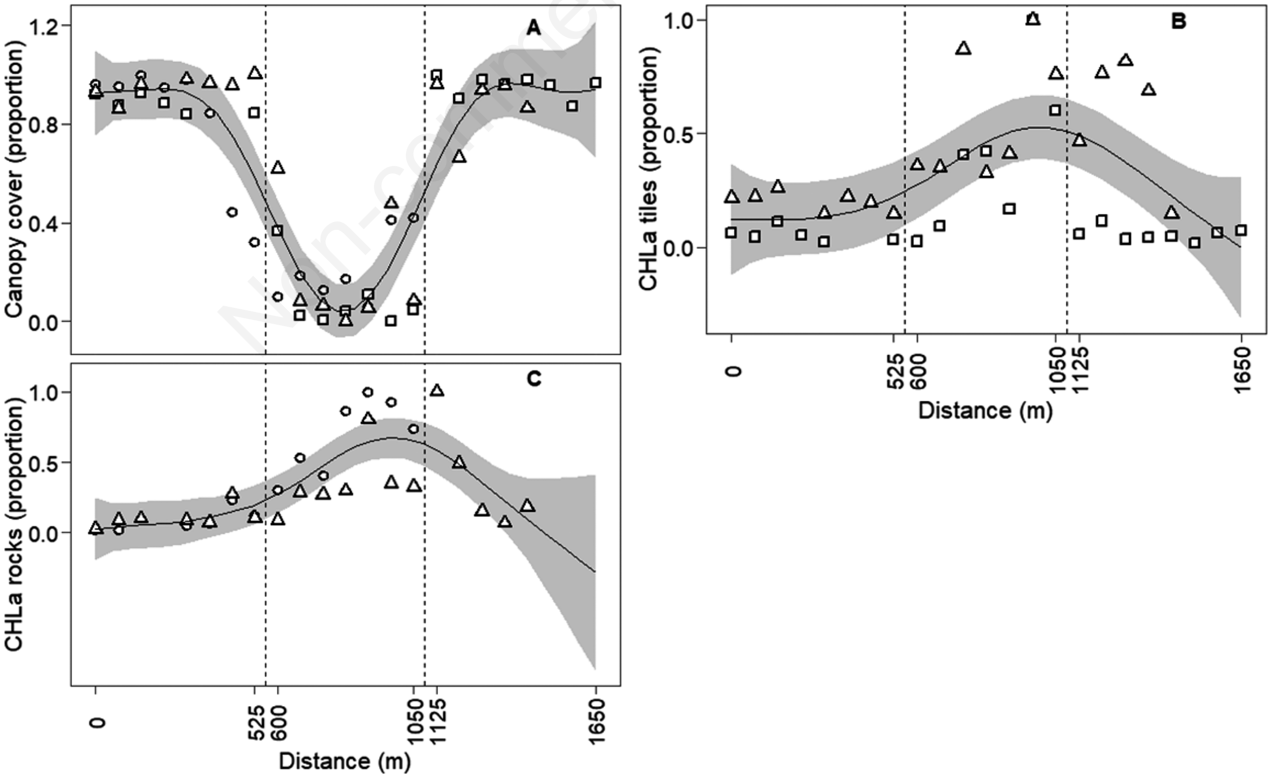

Fig. 3. Generalized additive models models showing the proportions of canopy cover (A), chl-*a* accrued in the tiles on day 7 (B) and chl-*a* present in natural rocks (C) varying along the land-cover transitions. The years are represented by different symbols, where the circles represent 2014 data, the squares 2015 and the triangles 2019.

meters of the land-cover transition. In 2015 and 2019 there was a clear regrowth of native shrubs and small trees along the forest-pasture transition and the observed decrease in canopy cover was smoother, transitioning from 0.8 to 0.4 in 2015 and from 1 to 0.6 in 2019 (Fig. 3A). In the upstream forest, all but one but one sampling site (450 m) increased in canopy cover proportion from 0.4 in 2014 to 0.9 in 2019 while in the last sampling site (525 m) it increased from 0.3 in 2014 to 1 in 2019. The proportion of canopy cover in different years along the two land-cover transitions explained approximately 81% of the variance in the data (GAM model: r^2 adjusted=0.808, F=34.07, p<0.001; Fig. 3A).

Chl-*a* proportion showed a lagged pattern of increasing concentrations after the forest-pasture transition and decreasing it shortly after the pasture-forest transition (Fig. 3B). In 2015, tile chl-*a* proportion showed a small decrease from 0.03 to 0.02 in the forest-pasture transition, taking more distance inside the pasture reach to achieve the maximum values, while in the pasture-forest transition the tile chl-*a* proportion decreased quickly from 0.6 to 0.06 after 75 m into the downstream forest. In 2019, tile chl-*a* proportion increased from 0.15 to 0.36 in the forest-pasture transition and decreased from 0.8 to 0.5 in the pasture-forest transition. In both years, the peak in chl-*a* concentrations was observed at the 975 m sampling site, 375 m into the pasture (GAM model: r^2 adjusted=0.319, F=4.966, p=0.003, Fig. 3B). Chl-*a* proportion from natural rocks (Fig. 3C) in the forest-pasture transition increased from 0.1 to 0.3 in 2014 and decreased from 0.1 to 0.08 in 2019. Comparing years, the proportions of chl-*a* from natural rocks in the upstream forest were similar between 2014 and 2019, however chl-*a* proportion was higher throughout the pasture reach in 2014. In 2014, the maximum chl-*a* proportion was achieved at the 900 m sampling site, 300 m into the pasture reach, while in 2019 the highest proportion was observed at the 1125 m sampling site, the first sampling site in the downstream forest (GAM model: r^2 adjusted=0.61, F=11.58, p<0.001, Fig. 3C). In 2015, tiles chl-*a* concentrations decreased from 72 µg m^{-2} to 59 µg m^{-2} after the transition in land-cover (T1), taking 375 m inside the pasture to achieve the maximum value of 2154 µg m^{-2}. In the pasture-forest transition the algal biomass decreased immediately from 1297 µg m^{-2} to 128 µg m^{-2} after the transition in land-cover (T2). As soon as the stream returned to a forested and light-limited area inside the downstream forest, the algal biomass quickly decreased by nearly 10 times over 75 m (GAM model: r^2 adjusted=0.359, F=3.03, p=0.07). Periphyton AFDM from 2015 and 2019 did not show the pattern of lagged response observed in chl-*a* after the transitions in land-cover. AFDM from the periphyton tile samples showed a wide variation inside each type of land-cover reaches. In 2015 the minimum value recorded was 1.11 g m^{-2} in the upstream forest and the maximum value was 11.44 g m^{-2} in the downstream forest. In 2019, AFDM had similar values with a minimum of 2.10 g m^{-2} in the pasture reach and a maximum of 11.76 g m^{-2} in the upstream forest (GAM model: r^2 adjusted= 0.137, F=1.869, p=0.127; Fig. S2).

Considering all the samples analyzed, we counted a total of 1425 individuals of algae. Diatoms corresponded to 91% of the total abundance, cyanobacteria about 0.7% and green algae together (Chlorophyceae, Euglenophyceae and Zygnemaphyceae) to 8%. In all samples, seven genera together corresponded to 72% of the total abundance, *Navicula, Pinnularia, Frustulia, Nupela, Nitzschia, Mougeotia* and *Zygnema.* All genera recorded in the upstream forest were also recorded in the pasture section, although some new algae genera appeared in the pasture, such as the diatoms *Encyonema*, *Surirella* and *Cyclotella*, the cyanobacteria *Planktothrix* and the green algae *Trachelomonas*, *Netrium*, *Closterium navicula* and *Cosmarium*. In the downstream forested reach, among all the algae genera only the diatom *Hantzschia* was not recorded. Algae density increased along the pasture, achieving the maximum value of 1,442,000 individuals m-2 recorded 150 meters into the pasture reach (GAM model: r^2 adjusted=0.106, F=0.735, p=0.4; Fig. 4A). Algal genus richness showed the same pattern as density, increasing inside the pasture reach and remaining high throughout the downstream forest (GAM model: r^2 adjusted=0.28, F=5.231, p=0.04; Fig. 4B), where it reached the maximum value of 19 genera recorded. Diatoms were the most abundant algal group in the periphyton samples with a maximum of 3,626,000 individuals m^{-2} recorded inside the pasture and a minimum of 175,000 individuals m^{-2} in the upstream forest. NMDS analysis obtained a good representation of the data (stress <0.2). Algal community composition shifted along the first transition in land-cover (forest-pasture). Furthermore, the algal community did not rebound to a composition similar to the upstream

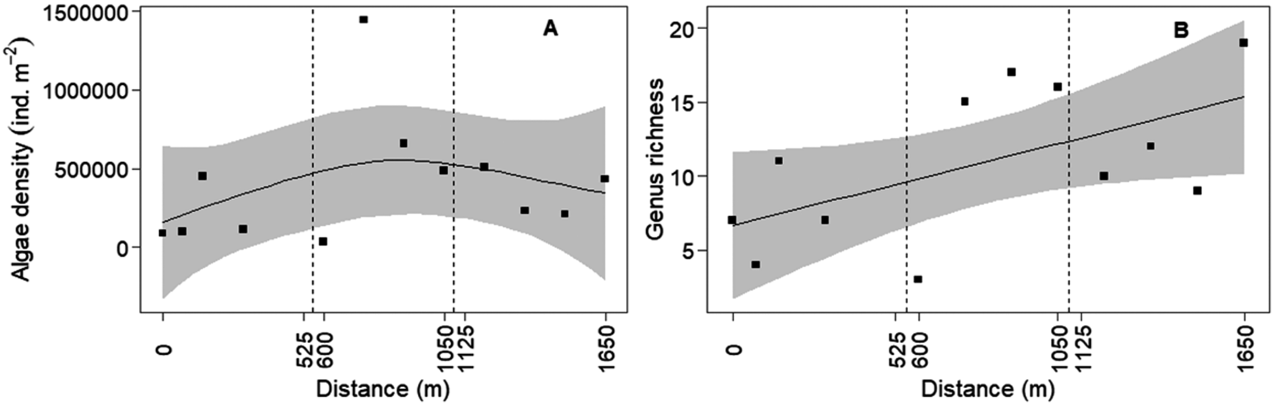

Fig. 4. Algae density (A) and genus richness (B) varying along the two land-cover transitions. For taxonomy we had 12 samples of periphyton from tiles collected in 2015.

forest along the downstream forest remnant. Algal community composition in the downstream forest lies between that registered in the pasture reach and from the upstream forest (Fig. 5). According to the Phyto-PAM results in 2015, brown algae decreased in the forest-pasture transition (Fig. 6A), delaying about 375 meters inside the pasture to achieve its maximum concentration. Whilst in the pasture-forest transition, brown algae group decreased, taking 75 m to change from 5524 µg m^{-2} to 910 µg m^{-2}, holding lower concentrations over the downstream forest and showing similar values to those recorded in the upstream forest (GAM model: r² adjusted=0.169, F=2.181, p=0.08; Fig. 6A). In 2019, we observed overall lower concentrations of all algae groups in our samples. Brown algae presented changes in both transitions, increasing concentrations in the forest-pasture and decreasing in the pasture-forest transition (Fig. 6A). In 2019 we observed a lagged response of brown algae taking about 375 m after the forest-pasture transition to achieve its maximum concentration and about 300 meters after the pasture-forest transition to reach its minimum concentration, recorded inside the downstream forest. Although there was a trend in reducing values over the downstream forest, brown algae concentrations remained higher than those recorded in the upstream forest. Blue and green algae were less representative in the periphyton community. In 2015, green algae (GAM model: r² adjusted=-0.0122, F=0.531, p=0.5; Fig. 6B) showed overall constant concentration along the transitions in canopy cover, and the maximum concentration was recorded in the pasture reach. In 2019, the maximum concentration was recorded in

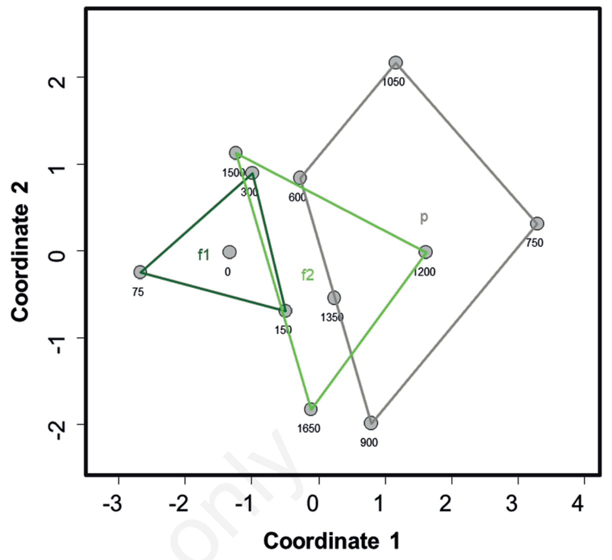

Fig. 5. Non-metric multidimensional scaling (NMDS) showing the composition of the algae community in response to land-cover transitions. NMDS analysis was conducted using data from microscopic identification of tile samples collected in 2015. f1, upstream forest section; f2, downstream forest section; p, pasture section.

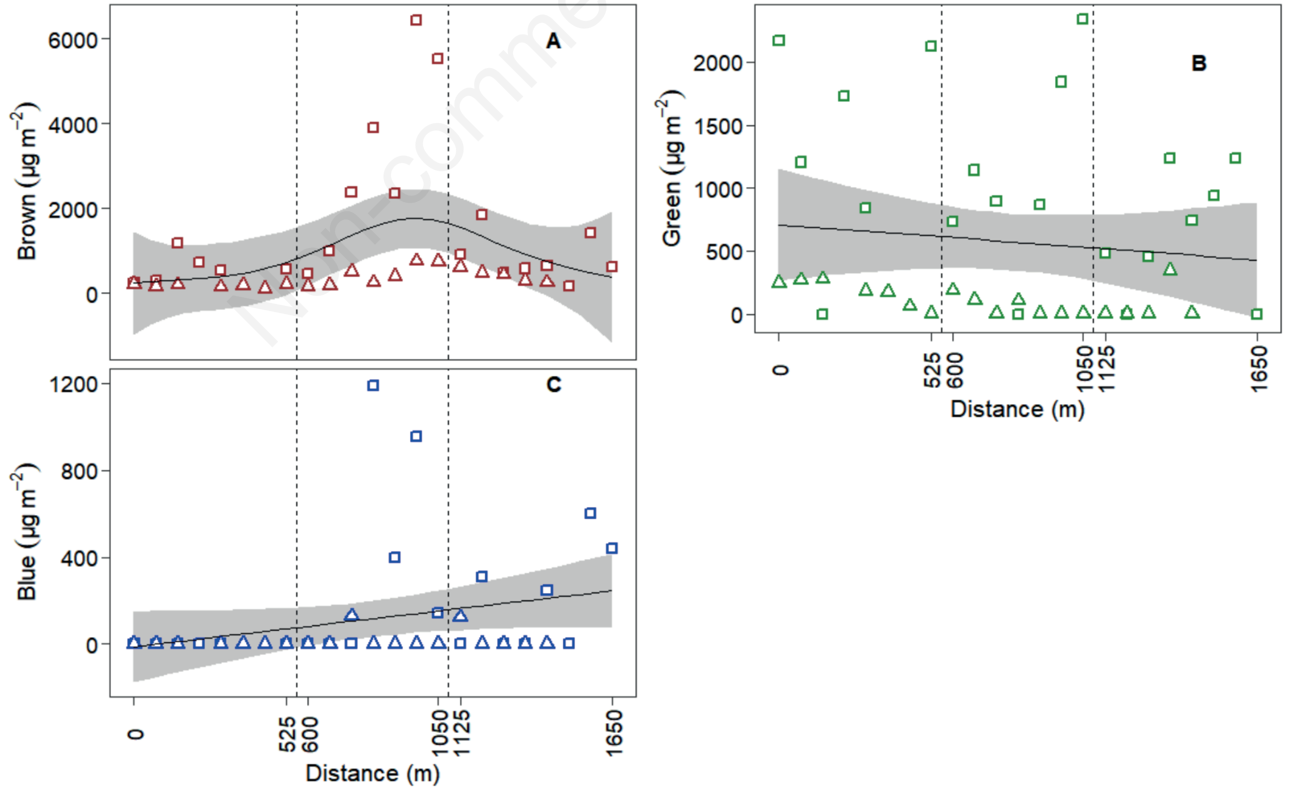

Fig. 6. Phyto-PAM data from tiles samples from 2015 (squares) and 2019 (triangles), where we can observe brown (A), green (B) and blue algae (C) varying between years and along the land-cover transitions.

the downstream forest. In 2015, blue algae (GAM model: r^2 adjusted=0.0562, F=3.321, p= 0.08; Fig. 6C) were first recorded after 225 m within the pasture and persisted along the downstream forest (Fig. 6C). The blue algae maximum concentration was much higher in 2015 than in 2019, where it first appeared in the stream 300 m into the pasture reach. However, unlike in 2015, this group was recorded just up to the first sampling site of the downstream forest and was not found further downstream.

DISCUSSION

Our study showed that the periphyton variables responded strongly but gradually to canopy cover changes: there was indeed a lagged response of chl-*a* after the two transitions. The patterns observed were very similar and consistent across years, showing a clear effect of land-cover transitions on periphyton variables. The downstream forest was able to buffer the effect of pasture in terms of chl-a concentrations that went back to values similar to the upstream forest, but not for the periphytic algal community. Algae community composition change was indeed more pronounced in the forest-pasture transition and the pasture altered the algae community physiognomy strongly enough that the downstream forest was not capable of rebounding it to control conditions (*i.e.*, those observed in the well-preserved forest).

The longitudinal effect of land-cover transitions on the lagged response of the periphyton community

In the forest-pasture transition, the increase in chl-*a* concentrations was gradual after the loss in canopy cover. The maximum value of algal biomass was achieved 375 m into the pasture, showing a lagged response of the algal community to increased light availability in the pasture reach. Our finding agrees with other studies conducted in land-cover transitions. A similar trend of gradual decrease in chl-*a* of natural rocks after a land-cover transition from a pasture to a forest, observing a stabilization of significant lower algal biomass values 300 m into the forested environment was reported for New Zealand streams (Scarsbrook and Halliday, 1999). These results suggest that periphyton algae does not respond immediately to changes in light availability. In 2015, chl-*a* concentrations in the two forested sections achieved similar values showing that the downstream forest reach after 75 m was capable of buffering algal biomass. Nevertheless, in 2019, the decrease after the pasture-forest transition was slower than in 2015, lagging about 300 m inside the downstream forest to achieve levels of algal biomass similar to those in the upstream forest. In 2019 we observed that the second sampling site inside the downstream forest lost canopy cover due to a landslide and this local loss of canopy cover might have had a role in the response of chl-*a* in 2019, leading to a slower decline of algal biomass along the downstream forest when compared to 2015.

When we compared chl-*a* proportion from the tile essays and from natural rocks we observed that the lag in algal biomass response after the land-cover change is consistent among years. Although the patterns across land-cover types were consistent between tiles and natural rocks, we observed that the algae biomass accrued on the tiles showed greater variability than in natural standing stocks collected from rocks (Fig. 3). This greater variation in the algae biomass accrued on artificial substrates, such as tiles, might be attributed to a younger and less stable community compared to the periphytic community present in the natural standing stocks (Cattaneo and Amireault, 1992). We observed that the maximum value of chl-*a* present in natural standing stocks after the forest-pasture transition was shifted downstream through the years. In 2014, we observed the maximum value of chl-*a* present in natural standing stocks about 300 m after the forest-pasture transition, while in 2019 the maximum concentration was achieved further downstream. Over a 5-years interval, in 2019, the upstream forest grew about 150 m into the pasture section. This shows the advance of forest inside the pasture reach over the years and this gain of forest could have affected the algal behavior along the pasture. This recovery of upstream forest in 2019 was capable of buffering pasture impacts on periphyton response, delaying algal biomass increase for a longer distance.

Another factor that has a strong influence on the proliferation of algae is the concentration of nutrients (Pringle, 1990; von Schiller *et al.*, 2007). We expected to find an increase of SRP along the pasture section due to manure runoff and a decrease of this nutrient along the downstream forest, but we observed the opposite trend. Concentrations of dissolved phosphate decreased abruptly upon entering the pasture area and increased along the downstream forest reach. Other studies conducted in land-cover abrupt transitions also found the same pattern of decreasing SRP concentrations within the pasture reach (Goss *et al.*, 2014; Feijó-Lima *et al.,* 2018). This reduction of phosphorus along the pasture matches the increase in algal biomass, suggesting that this depletion might have been caused by algal uptake (Neill *et al.*, 2007; Bott and Newbold, 2013). Non-intensive animal rearing in pastures can have a minor contribution on stream nutrient input when compared to other land uses such as cropland (Allan, 2004) and in the State of Rio de Janeiro, urbanization has been found to be the main driver of instream nutrient concentrations and not agriculture or pasture (Tromboni and Dodds, 2017). Furthermore, our samples were collected during the dry season, where diminished rainfall may reduce lateral inputs of nutrients from the pasture to the stream. In deforested reaches, light availability commonly acts as a driving force on periphyton algal growth (Calvo *et al.*, 2022), influencing its response to nutrient availability (Johnson *et al.*, 2009). This suggests that a low contribution of phosphorus coming from the pasture combined to a higher light availability may have led to a P limitation in algal growth within the pasture reach.

Phyto-PAM results showed a shift in algae community physiognomy with the emergence of blue algae and the numerical dominance of brown algae in the pasture community. Over the downstream forest, we observed a second shift, in which there was a decrease in brown algae. Such short distance change reinforces the strong sensibility of periphytic algae as indicators of impacts related to land-cover changes (Bere and Tundisi, 2011; Vázquez *et al.*, 2011). Blue pigments that represent cyanobacteria showed up after pasture disturbance in both years, which is explained by some characteristics of this group such as light and nutrient tolerance (Vázquez *et al.*, 2011). In the downstream forested reach, cyanobacteria exhibited a trend of decreasing concentrations, showing the potential of riparian vegetation in buffering pasture impacts. Brown algae (diatoms) mirrored chl-*a* behavior of increasing concentrations along the pasture and decreasing over the downstream forest, showing a lagged response to higher light availability. Over the downstream forest reach, after pasture disturbance, brown algae concentrations declined, although in 2019 the values were still higher than those from the upstream forest.

The downstream forest in 2019 was less efficient in returning the algae community to its undisturbed status along the same distance as in 2015. This may be caused by vegetation structure in the downstream forest being composed of a younger and less stable flora, with a consequent unstable shading capability when compared to the upstream forest. Although there is strong evidence of the importance of forest remnants in protecting stream ecosystems (Scarsbrook and Halliday, 1999; Niyogi *et al.*, 2007; Goss *et al.*, 2014; Feijó-Lima *et al.*, 2018), studies have pointed out the role of vegetation structure such as age, composition and density in determining the efficiency of a forest remnant in ameliorating ecological conditions (Harding *et al.*, 2006; Souza *et al.*, 2013; Fernandes *et al.*, 2014).

Optical microscopy revealed that diatoms dominated numerically in both transitions, and green algae divisions did not show higher numbers inside forested reaches confirming the trends observed in Phyto-PAM results. Cyanobacteria appeared at one location of the upstream forest, showing a larger number of individuals over the pasture reach. The group of blue algae was detected later by the Phyto-PAM method where cyanobacteria was recorded only after the stream flowed within the pasture. These results indicate a greater sensibility of microscopy, when compared to Phyto-PAM analysis to accurately detect the presence of different algae groups in periphyton samples (Garfield and Yokota, 2017). Although the expected pattern is that diversity tends to decrease along an impact gradient induced by changes in land-cover (Bere and Tundisi, 2011), the present study had an opposite result. We observed an increasing taxon richness along the pasture reach. One possible explanation might be that pasture impact was not strong enough to cause a profound worsening in water quality. That is, the community of algae ended up having only an increment of light that favored its development. However, we observed that pasture impact favored the numerical expansion of diatom genera and the emergence of blue algae (*i.e.*, cyanobacteria).

In our studied stream, we observed an increase in fine sediment in the pasture (not quantified) that might have had a role in shaping species composition of the algae community. The presence of fine sediment can strongly influence algae community physiognomy, increasing diatom abundance (Piggott *et al.*, 2015) and negatively affecting green algae abundance (Izagirre *et al.*, 2009). The most abundant diatom genus in our samples, *Navicula* presents gliding motility (Passy, 2007). The motility of some diatom algae as *Navicula* and *Nitzschia* might have conferred advantage in competing for habitat in the presence of sediment deposition, since motile algae can handle resource limitation and disturbance stress for its ability of selecting the most suitable environment (Passy, 2007). Species traits such as the organism's adherence form is an important factor that interferes in its capacity to disperse downstream, because loosely attached organisms present a higher chance to disperse and colonize new environments (Algarte *et al.*, 2017).

In our study, we observed different responses in the two land-cover transitions. After the forest-pasture transition we saw a gradual increase in density and richness of algae, showing a spatially lagged response to greater light availability in the pasture. This delay can be interpreted as a longitudinal effect mediated by the upstream forest on the pasture algae community even after the loss of canopy cover, delaying the community response to new environmental conditions. Algal variables responded to both transitions, but in general, the displacement of this response was greater in the forest-pasture than in the pasture-forest transition. This indicates that the conditions of the upstream forest may be moving for a greater distance in the pasture than the pasture conditions in the downstream forest, showing that the longitudinal effect was not symmetrical. The low intensity of the pasture impact which did not alter nutrient concentration, for instance, may have weakened the influence of the pasture over the downstream forest. However, the downstream forest was able to ameliorate and not to completely mitigate the conditions coming from the pasture. The algae biomass in forest fragments that are located downstream of agricultural impacted sites might present higher algae biomass in comparison with forested sites that do not present loss of canopy cover upstream (Harding *et al.*, 2006). In our study, the pasture impact modified some characteristics such as taxonomic composition that did not return to control conditions. The taxonomic composition in the downstream forest being different from the upstream forest might be caused by changes in stream physico-chemical characteristics that modifies the availability of light that reaches the streambed, which are known as controllers of algae community assemblage, such as turbidity (Atkinson and Cooper, 2016) that can be enhanced by fine sediment transported from the pasture to the downstream forest by the flow of water. Pasture impact also modifies the availability of allochthonous material entering the streams (Martínez-Atencia *et al.*, 2020), which in turn influences the macroinvertebrate community (Silva-Araújo *et al.*, 2020) and can subsequently affect the algae community composition. Deforestation leads to higher light regimes in streams, boosting algae biomass and the abundance of scraper taxa (Tonin *et al.*, 2018). Grazing pressure can regulate algae biomass and shape community composition by removing overstory algae (Martina *et al.*, 2014).

In this study, we assessed the longitudinal effects of two subsequent abrupt land-cover transitions in a tropical stream. We found that abrupt changes in land-cover produced lagged changes on chemical variables, on periphyton characteristics and community. Our findings are in accordance with other studies conducted in low-order streams exposed to land-cover transitions that evaluated the effect of forest remnants on buffering impacts (Niyogi *et al.*, 2007; Suga and Tanaka, 2013; Goss *et al.*, 2014; Tanaka *et al.*, 2016). The combined evidence is meaningful because this landscape configuration is common in tropical countries, where native forests and riparian vegetation are often cleared for agriculture and animal rearing (Bringhurst and Jordan, 2015; Tromboni *et al.*, 2019; Silva-Araújo *et al.*, 2020). Moreover, these spatial settings are likely to become even more common in the future. For example, it is estimated that in the one-year interval from 2020 to 2021 Brazil lost 21,642 hectares of Atlantic Rain Forest - this deforestation rate was 66% higher than the previous year (Fundação SOS Mata Atlântica and INPE, 2018).

CONCLUSIONS

The rapid loss and fragmentation of forest in the tropics is threatening functioning and diversity of streams. The condition of the studied stream, with patches of different types of land-cover and irregular riparian vegetation, is very common in low-order streams located in deforested landscapes, such as the Atlantic Rainforest in Brazil. As far as we know only few studies evaluated the response of periphyton biomass after abrupt transitions in land-cover (Scarsbrook and Halliday, 1999; Feijó-Lima *et al.*, 2018, 2019) but none of them assessed the communities' taxonomic responses. Beyond that, differently from previous studies, we had two continuous land-cover transitions along the same stream, which enabled us to evaluate the potential of a downstream forested reach in mitigating the changes caused by deforestation, reestablishing reference conditions from the upstream, non-impacted forest. The intensive sampling, both spatially and temporally (across different years), gave us the possibility of having high-spatial resolution patterns with a precise modeling of environmental gradients that were consistent across years.

Is not a consensus about the role of discontinuous forest remnants in preserving the ecological integrity of stream ecosystems. Harding *et al.* (2006) found that forest remnants of 5-7 ha were not capable of returning the stream to reference conditions after agricultural disturbance. Nevertheless, other studies have concluded that discontinuous forest patches were important to restore or maintain stream ecosystem function (Storey and Cowley, 1997; Danger and Robson, 2004; Goss *et al.*, 2014; Tanaka *et al.*, 2016) and invertebrate community (Scarsbrook and Halliday, 1999; Niyogi *et al.*, 2007; Chakona *et al.*, 2009; Suga and Tanaka, 2013). We observed a lagged response of the periphyton algae community to new environmental conditions after a forest-pasture transition and that a downstream forest was capable of reducing algal biomass. Our study brings more evidence that riparian forest remnants can have a longitudinal effect in stream conditions, influencing environmental characteristics even over non-forested reaches, to where the forest conditions can be propagated downstream by the flow of water. Nevertheless, more studies are needed to better understand how the longitudinal connection between riparian forest patches acts to preserve and modify conditions in streams exposed to riparian fragmentation. With more studies like these, it may be possible to inform restoration practices by determining the amount of riparian forest necessary to ensure stream integrity.

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Online supplementary material:

Tab. S1. Mean and standard deviation of the variables collected in 2014, 2015 and 2019 for the 3 land-cover types.

Fig. S1. GAM model showing the flow velocity varying along the land-cover transitions.

Fig. S2. AFDM from the tiles samples varying along the two land-cover transitions in 2015 and 2019.