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Amazon deforestation alters small stream structure, nitrogen biogeochemistry and connectivity to larger rivers

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Abstract Human activities that modify land cover can alter the structure and biogeochemistry of small streams but these effects are poorly known over large regions of the humid tropics where rates of forest clearing are high. We examined how conversion of Amazon lowland tropical forest to cattle pasture influenced the physical and chemical structure, organic matter stocks and N cycling of small streams. We combined a regional ground survey of small streams with an intensive study of nutrient cycling using ^{15}N additions in three representative streams: a second-order forest stream, a second-order pasture stream and a third-order pasture stream. These three streams were within several km of each other and on similar soils. Replacement of forest with pasture decreased stream habitat complexity by changing streams from run and pool channels with forest leaf detritus (50% cover) to grass-filled (63% cover) channel with runs of slow-moving water. In the survey, pasture streams consistently had lower concentrations of dissolved oxygen and nitrate (NO_3^-) compared with similar-sized forest streams. Stable isotope additions revealed that second-order pasture stream had a shorter NH_4^+ uptake length, higher uptake rates into organic matter components and a shorter $^{15}NH_4^+$ residence time than the second-order forest stream or the third-order pasture stream. Nitrification was significant in the forest stream (19% of the added $^{15}NH_4^+$) but not in the second-order pasture (0%) or third-order (6%) pasture

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stream. The forest stream retained 7% of added ^{15}N in organic matter compartments and exported 53% ($^{15}NH_4^+ = 34\%$; $^{15}NO_3^- = 19\%$). In contrast, the second-order pasture stream retained 75% of added ^{15}N, predominantly in grasses (69%) and exported only 4% as $^{15}NH_4^+$. The fate of tracer ^{15}N in the third-order pasture stream more closely resembled that in the forest stream, with 5% of added N retained and 26% exported ($^{15}NH_4^+ = 9\%$; $^{15}NO_3^- = 6\%$). These findings indicate that the widespread infilling by grass in small streams in areas deforested for pasture greatly increases the retention of inorganic N in the first- and second-order streams, which make up roughly three-fourths of total stream channel length in Amazon basin watersheds. The importance of this phenomenon and its effect on N transport to larger rivers across the larger areas of the Amazon Basin will depend on better evaluation of both the extent and the scale at which stream infilling by grass occurs, but our analysis suggests the phenomenon is widespread.

Keywords ^{15}N · Ammonium uptake length · Brazil · Nitrification · Nitrogen cycling · Pasture · Stable isotopes · Stream ecosystem · Tropical forest

Introduction

Human activities that modify land cover have the potential to alter the physical structure of small streams and the manner in which nitrogen (N) is transformed and transported in stream networks (Sweeney et al. 2004; Mulholland et al. 2008). The Amazon Basin contains more than 4 million km^2 of tropical forest and the earth's largest river network. It also has the world's highest rate of rainforest clearing, primarily to pasture for cattle ranching (Skole and Tucker 1993; Lepers et al. 2005). Approximately 697,830 km^2 of forest have been cleared in Brazil since 1970 (INPE 2010). This clearing has the potential to alter the structure and chemistry of the thousands of km of small streams that constitute three-fourths of stream channel lengths in the Amazon Basin (McClain and Elsenbeer 2001; Goulding et al. 2003).

Small streams are the primary receptors for nutrients and organic matter inputs from terrestrial ecosystems and play a key role as regulators of downstream flows of materials to larger rivers (Vannote et al. 1980; Alexander et al. 2000; Peterson et al. 2001). In the Amazon, streams act as key connections with terrestrial ecosystems (McClain and Elsenbeer 2001) and also are important habitat for fishes and aquatic organisms (Agostinho et al. 2005). Previous work conducted in the Large-Scale Biosphere–Atmosphere (LBA) Experiment in Amazonia showed that clearing of Amazon forest for pasture can change the flowpaths of water reaching streams (Germer et al. 2009), the structure and hydrology of stream channels (Neill et al. 2006) and the chemistry of streamwater (Thomas et al. 2004; Biggs et al. 2004; Neill et al. 2006). Establishment of cattle pasture has also been shown to alter terrestrial N cycling by reducing the production of nitrate (NO_3^-) in soils, resulting in low concentrations of NO_3^- in soil solution and reducing the potential for NO_3^- movement from land into small streams (Markewitz et al. 2004; Neill et al. 1996, 1997; Chaves et al. 2009).

There are several reasons why the dynamics of N transport and retention in Amazon streams may be different from streams in temperate regions where streams are recognized as important locations of N uptake and transformation (Peterson et al. 2001). High concentrations of N and low ratios of nitrogen to phosphorous (N:P) in tropical forest foliage and litter suggest that N is not limiting to forest vegetation (Vitousek 1984; Davidson et al. 2007). Relatively high rates of soil N mineralization and nitrification (Neill et al. 1995), abundant soil solution NO_3^- (Markewitz et al. 2004; Neill et al. 2006) and high soil emissions of N_2O (Verchot et al. 1999; Melillo et al. 2001) all indicate natural N "saturation" (Hall and Matson 1999) of the forest, which could lead to high transport of inorganic N in soil and ground water to forest streams. Under these conditions, we would expect tropical forest streams to be less retentive of N than similar-sized streams in temperate regions. Because clearing of Amazon forest for pasture introduces conditions that indicate greater N limitation of vegetation, including lower N concentrations in foliage and litter, lower rates of soil nitrification and less NO_3^- in soil solution (Davidson et al. 2007; Chaves et al. 2009), we would also expect pasture streams to be more retentive of N than forest streams.

Much of our recent understanding of stream N dynamics has come from experiments in which low levels of dissolved inorganic N enriched with ^{15}N, either as nitrate ($^{15}NO_3^-$) or ammonium ($^{15}NH_4^+$), have been added to streams for days to weeks then the fate of the added ^{15}N is assessed by quantifying fluvial export or retention into different inorganic and organic matter compartments in the stream channel (Peterson et al. 2001). Most experiments have introduced $^{15}NH_4^+$, which allows quantification of nitrification and subsequent uptake of produced NO_3^- as well as uptake of NH_4^+ into biomass compartments (Mulholland et al. 2000). Because they have been conducted in a number of streams ranging from Alaska to Puerto Rico using similar methodology, these experiments can now be used to compare N dynamics across different sites (Webster et al. 2003).

We quantified how clearing moist tropical forest for cattle pasture along small, lowland streams in one of the Amazon's deforestation hotspots, central Rondônia, influenced stream physical and chemical structure, and stream channel N uptake, transformation and retention. We combined a regional ground survey of small streams with an intensive study of nutrient cycling using ^{15}N additions in three representative streams: a second-order forest stream, a second-order pasture stream and a third-order pasture stream. These streams were within several km of each other, in the same stream network and on similar soils. We used the results to infer how forest clearing influence stream structure, the dynamics of N biogeochemistry in the stream channel and the role that small streams play in controlling the movement of N in stream networks in forested and deforested regions of the Amazon.

Methods

Regional stream survey

We surveyed physical and chemical characteristics of first- and second-order streams that drained watersheds (0.1–17.8 km^2) dominated by either forest (six streams) or pasture (12 streams) near Nova Vida, Rancho Grande and Ji-Paraná in central Rondônia in August 2005 (Fig. 1; Table 1). Target streams were identified from Landsat 7-ETM+ images (Ballester et al. 2003). We then combined an analysis of land cover and stream networks derived from Landsat 7-ETM+ and IKONOS remote sensing in the 74,057 km^2 Ji-Paraná River Basin (Fig. 1) to estimate the extent to which deforestation has altered streams at the river-basin scale. Aerial images analysis was used to determine the extent of *Paspalum repens* infilling of stream channels by combining the Landsat ETM image with low level videography data (obtained from INPE 2010) and IKONOS data (obtained from EOS-WEBSTER 2009). IKONOS images are color composites of the multispectral bands of 2000–2002 IKONOS with a spatial resolution of 4 × 4 m acquired and licensed to NASA LBA-Ecology Program, the NASA Scientific Data Buy Project and The University of New Hampshire Earth Science Information Partner (EOS-WEBSTER). Selected images were ground-truthed during the regional stream survey (above) and used to classify the full array of IKONOS and videography images.

Streams were classified as "forest" streams if >75% of the catchment was in native forest and "pasture" streams if >65% of the catchment was in pasture. Native forest vegetation is perennial evergreen broadleaf trees with a high number of palms (Pires and Prance 1986). Forest is typically cleared for pasture to the stream edge to allow access by cattle (approximately 1–1.5 animal per ha) and converted directly to pasture by planting with introduced forage grasses of the genus *Brachiaria* in upland areas. Riparian areas are often dominated by the native grass *P. repens* (Neill et al. 2006). Pasture in this region is never fertilized with N and only rarely is P added. The climate of central Rondônia is humid tropical, with a mean annual temperature of 26°C, mean annual precipitation of about 2,200 mm year^{-1} and a dry season that last approximately 5 months (June to October; Bastos and Diniz 1982). Sites were in areas of gently rolling topography underlain by Pre-Cambrian granite with well-drained Kandiudults and Paleudults soils that cover approximately 22% of the Brazilian Amazon (Moraes et al. 1995).

We surveyed stream width, depth and benthic substrate type (classified as tree leaf pack, living riparian grass, sand, fine organic, wood, or other) with 11 cross-sectional point transects in 100 m (first-order streams) or 800 m (second-order streams)

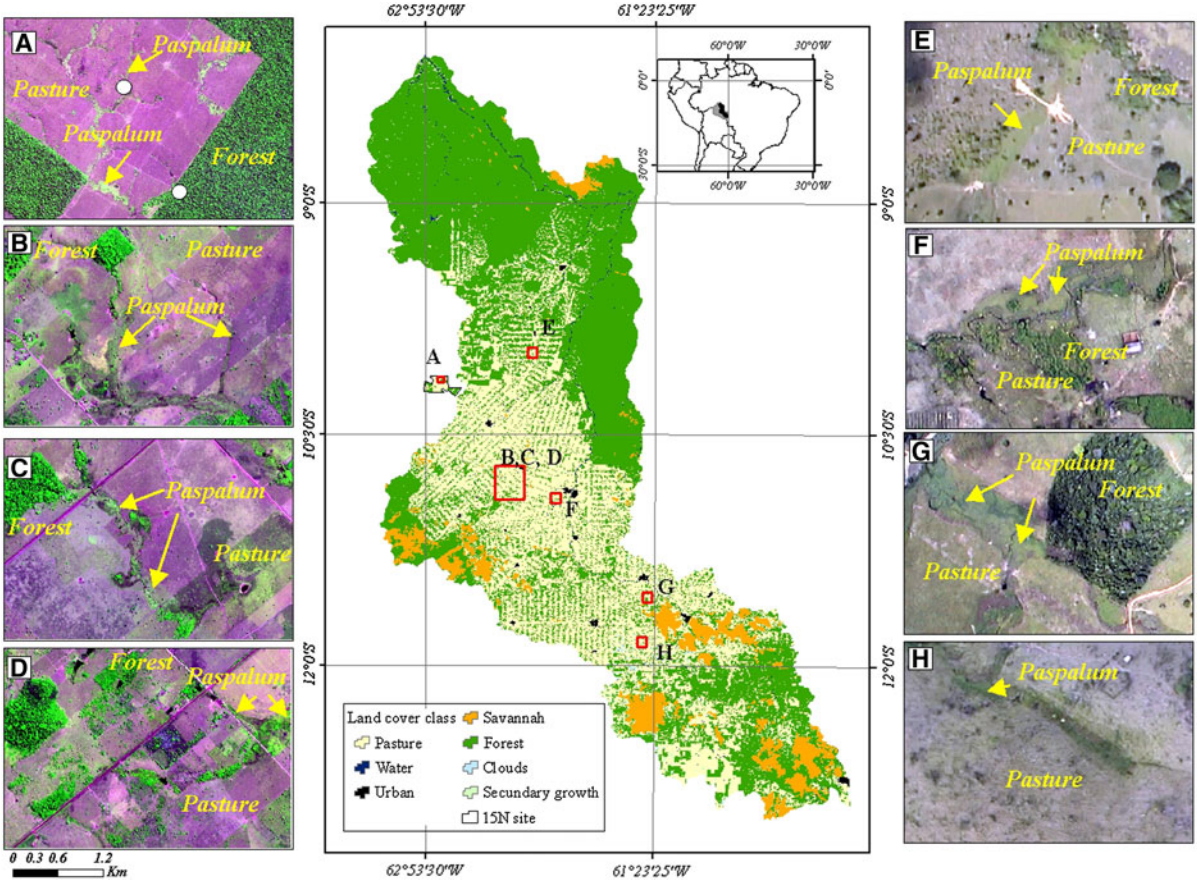

Fig. 1 Land use in the Ji-Paraná River Basin and images of Rondônia forest and pasture streams and streams used for the ^{15}N additions. The Ji-Paraná map (*middle*) is derived from a Landsat ETM composite from 1999. Detailed *images* (*side panels*) show the widespread infilling of stream channels with riparian grasses (primarily *P. repens*) determined from Landsat (*left side*: **a**), IKONOS (*left side*: **b–d**) and videography (*right side*: **e–h**). **a** is a Landsat image of Nova Vida Ranch near the city of Ariquemes. The *white circles* indicate the second-order forest and pasture streams, while the third-order pasture stream runs along the forest boarder near the bottom left of the image. The *IKONOS images* show representative channel and riparian area infilling by grasses (*lime green coloration*), the extent of pasture (*pink*) and forest (*dark green with texture*). *Paspalum* in streams and adjacent floodplains are evident in the fine scale videography (*right panel*)

stream reaches. Conductivity and dissolved oxygen (YSI Model 58) and pH (Orion 290A+ meter) were measured in the field. Discharge was determined from cross sectional area and flow velocity (FP-201 Global Water flow meter). Water samples for NH_4^+, NO_3^- and soluble reactive phosphate (SRP) were filtered in the field through ashed GFF filters and frozen. Whole water samples were returned to the lab for alkalinity and suspended particulate organic matter (SPOM) analysis (see lab methods below).

We analyzed differences in mean physical, structural and chemical characteristics of forest and pasture streams using one-way analysis of variance (SAS Institute 2002). Tests for percent cover were performed after arcsin-square root transformation (Zar 1984). Other environmental variables were tested on non-transformed data.

Stream ^{15}N additions

We selected three streams typical of the region located on Nova Vida Ranch (Fig. 1, 10°09′ S, 62°49′ W) for whole-stream additions of $^{15}NH_4^+$: (1) a second-order forest stream; (2) a second-order pasture stream and; (3) a third-order pasture stream located approximately 2 km downstream of the confluence of the second-order forest and pasture streams. Pastures were cleared in 1989 (second-order

Table 1 Mean physical and chemical characteristics and benthic habitat cover for first- and second- order forest ($n = 6$) and pasture ($n = 12$) streams surveyed in central Rondônia (±1 SE)

	Forest	Pasture	*F*-value	*P*-value
Physical characteristics				
Basin area (km^2)	3.6 ± 2.8	2.4 ± 0.9	0.27	0.612
Forest cover (%)	93 ± 4	7 ± 4	163.2	<0.0001
Discharge (l s^{-1})	22 ± 14	7 ± 3	0.15	0.705
Mean depth (cm)	9 ± 3	15 ± 3	3.11	0.097
Mean total wetted width (m)	2.1 ± 0.5	10.2 ± 3.2	6.65	0.020
Benthic cover characteristics				
Grass (%)	0 ± 0	63 ± 9	20.14	0.0004
Leaf pack (%)	50 ± 4	1 ± 1	194.03	<0.0001
Sand (%)	19 ± 5	2 ± 1	14.99	0.0014
Fine organic (%)	22 ± 5	19 ± 5	0.07	0.800
Wood (%)	5 ± 1	1 ± 0	14.29	0.0016
Other (%)	4 ± 3	13 ± 3	3.64	0.075
Chemical characteristics				
pH	6.3 ± 0.2	6.1 ± 0.1	1.76	0.201
Alkalinity (mg l^{-1})	15 ± 3	24 ± 3	3.63	0.075
Conductivity (µS cm^{-1})	34 ± 5	56 ± 8	3.36	0.085
NH_4^+ (µmol l^{-1})	0.9 ± 0.7	4.4 ± 1.9	1.06	0.320
NO_3^- (µmol l^{-1})	6.1 ± 1.7	0.7 ± 0.3	32.16	<0.0001
Total suspended solids (mg l^{-1})	6.9 ± 1.2	26.3 ± 9.5	4.49	0.0500
Dissolved oxygen (mg l^{-1})	5.6 ± 0.9	2.7 ± 0.7	6.74	0.0016

One-way analysis of variance (SAS Institute 2002) on percent cover was performed after arcsin-square root transformation; other environmental variables were tested on non-transformed data

stream) or 1983 (third-order stream) and planted directly to *Brachiaria brizantha*. These streams were in similar landscape positions and on similar soils (Kandiudults) (Moraes et al. 1996). Our interpretation uses the "space for time" substitution for land use (Allan 2004). This approach assumes that for locations that differ in land use but are similar in other respects, differences between sites can be viewed as equivalent to changes over time in a single location. There was no third-order stream in a forested watershed available for study in this region of expanding deforestation and fragmented forests.

The second-order forest stream (watershed area 17.8 km^2) was shaded, had a pool and run stream channel with a sandy bottom, a mean wetted width of 4 m, a maximum depth of 42 cm and dry season discharges of 15–40 l s^{-1}. The second-order pasture stream (watershed area of 8.4 km^2) was bordered by the C4 grass *P. repens* (Medina et al. 1976) along its entire length, had slow-moving deep runs with extensive channel infilling by grass, deep (>15 cm in some places) organic sediments underlain by sand with a mean wetted channel width of 5.2 m, an open water channel width of 1.4 m and a mean depth of 42 cm. Dry season discharges range from 14 to 90 l s^{-1}. The third-order pasture stream (watershed area of 27 km^2) had high sandy banks, a pool and run channel structure with a generally sandy bottom and lacked extensive growth of grass in the stream channel. Although this stream had some riparian trees, the canopy was relatively open and most of the stream was exposed to the sun. It had a wetted channel width of 3.6 m, a nearly identical open water channel width of 3.5 m and a mean depth of 34 cm. It had dry season discharges of 45–100 l s^{-1}. We selected representative reaches of 800 m (forest stream), 500 m (second-order pasture stream) and 760 m (third-order pasture stream) that had no obvious tributaries or other obvious surface water inputs.

Our ^{15}N addition methodology, sample analysis and calculations followed the protocols in LINX (Lotic Intersite Nitrogen eXperiment) (Mulholland et al. 2000; Peterson et al. 2001). We determined physical characteristics, organic matter standing stocks and background natural abundance levels of ^{15}N for each stream reach. We then added 98.5% enriched ^{15}N-labeled NH_4Cl at a constant rate to each stream for 21 days during the dry season to achieve an expected δ^{15}N of NH_4^+ of 500‰ (0.28 g day^{-1}, totaling 5.90 g in the forest stream, 0.98 g day^{-1}, totaling 21.50 g in the second-order pasture stream and 0.86 g day^{-1}, totaling 18.90 g in the third-order pasture stream). We measured ^{15}N in major ecosystem compartments upstream and downstream of the addition site before, during and for 14 days after the addition. The forest addition began on 12 August 2001 and the two pasture stream additions began on 15 August 2003. Although the third-order stream was downstream of the second-order pasture stream and the ^{15}N additions were done simultaneously, ^{15}N values at the start of the third-order stream reach were never elevated above baseline. Additionally, solute additions demonstrated that N added to the second order stream did not reach third-order pasture stream (Neill et al. 2006).

Water level, dissolved oxygen concentration, and conductivity were recorded every 15 min throughout the ^{15}N additions (YSI 600XL multi-parameter sondes). Streamwater samples were collected every 2–3 days and discharge determined every 3–7 days or when rains caused notable changes to stream flow (see Regional Survey for field methods). Multiple sodium chloride additions following standard solute injection methods (Stream Solute Workshop 1990) were used in our previous work (Neill et al. 2006) and during the ^{15}N additions at characteristic discharges to determine the extent of groundwater and surface water inputs in each reach. During the ^{15}N additions, we completed two Cl^-additions (discharges of 30 and 45 l s^{-1}) in the forest, one in the second-order pasture (discharge 45 l s^{-1}) and one in the third-order (discharge 105 l s^{-1}) stream. In all three streams, no surface water channels were observed flowing into the stream reaches and no measurable gains or losses of Cl^- tracer were detected over the study reaches. These measurements suggest that these stream reaches were neither measurably gaining nor losing water during the experiments.

We combined measurements of organic matter biomass with estimates of the area of each benthic habitat type to calculate standing stocks of organic matter and N for the stream reaches. Stream depth and benthic substrate area and type (classified as grass, leaf pack, sand, detritus, thin layer of fine organic matter over sand, clay, gravel, and woody debris) were determined using cross-sectional point transects in each reach ($N = 75$ cross sections in forest, 45 in second-order and 39 in third-order pasture streams). Leaf pack, detritus and fine organic matter were layers of varying thickness (from a few cm to mm) over a sandy substrate. Very small patches of filamentous algae were found but their area (<0.01% of stream bottom) did not warrant a separate habitat class.

Biomass of leaf pack (nearly entire, identifiable tree leaves), coarse benthic organic matter (CBOM; unidentifiable leaf fragments and organic material >1 mm) and fine benthic organic matter (FBOM, <1 mm) were quantified by pressing an open-ended cylinder (0.0573 m^2) 5 cm into the sediment, collecting and sieving all organic matter in the cylinder. The riparian *P. repens* grass habitat was divided into: (1) channel edge (submersed or emergent in the stream channel), and (2) floodplain (2 m from the open channel but out of direct contact). Both channel edge and floodplain grass habitats were found in the second-order pasture, while only the channel edge grass habitat was found in the third-order pasture stream. No riparian grass was present in the forest stream. Leaves (above-water green tissue) and roots and rhizomes (below-water) biomass were estimated using 0.25 m^2 quadrates. All organic matter samples were rinsed with tap water and dried at 60°C.

We measured the ^{15}N content of NH_4^+ and NO_3^- and the ^{15}N content in organic matter compartments (CBOM, FBOM, SPOM, filamentous algae and leaves) in longitudinal transects (7–8 stations in the reach) once before the start, 5 times during, and 4 times post ^{15}N addition. We sampled *P. repens* on day 20. We examined ^{15}N uptake by the microbial community on ceramic tiles conditioned for 7-day prior to ^{15}N addition. We simultaneously measured δ^{13}C (‰) in the organic matter compartments to examine the origin of organic matter in the stream channel.

Laboratory analyses

Concentrations of NO_3^-, NH_4^+, SRP and total dissolved nitrogen (TDN) were determined by ion chromatography (Dionex DX-500) or by autoanalyzer. NH_4^+ was measured by the phenol-hypochlorite method (FIAstar method AN5220), nitrate (as $NO_3^- + NO_2^-$) was measured by cadmium reduction (FIAstar method AN5201) and SRP was measured by the antimony/molybdate and ascorbic acid method (Alpkem method A303-S200-00). TDN was measured by alkaline persulfate digestion (Eaton et al. 1995). DON was calculated from the difference between TDN and ($NH_4^+ + NO_3^-$). SPOM was estimated gravimetrically. Alkalinity was determined by two-point fixed pH end-point (pH = 4.5 and 4.2) titration with H_2SO_4 (Hach 16900-01 digital titrator).

The $\delta^{15}N$ content of organic matter compartments was determined with a Finnigan Delta-plus mass spectrometer. The $\delta^{15}N$ content of NH_4^+ and NO_3^- were determined by diffusion (Sigman et al. 1997; Holmes et al. 1998). All $\delta^{15}N$ values were corrected for background ^{15}N by subtracting the average of $\delta^{15}N$ value of samples collected prior to the start of the ^{15}N addition and from the upstream station (−90 m) during the addition. DON in these streams typically comprises about one-third to one-half total dissolved N. Because laboratory incubation experiments indicated that DON material was not reactive in the time scale of about 2 h it took for streamwater to move through the study reaches, we did not correct for breakdown of DON. In 2 week laboratory incubations, we detected no consistent change in DON concentrations (Krushe, pers. comm.)

Calculations

We calculated the mass of ^{15}N in different compartments based on NH_4^+ and NO_3^- concentrations, discharge, estimates of the biomass of organic matter pools and ^{15}N of each compartment. We used the rate of increase and final distribution of the ^{15}N label in NH_4^+ and NO_3^- to calculate ^{15}N uptake kinetics (Mulholland et al. 2000). We used the concentration of ^{15}N and the mass of different organic matter components to estimate the amount of the added ^{15}N retained in each compartment. Total export in water was computed as the sum over the 21-day experiment of particulate and dissolved N transported out of the reach determined from water flux and the concentrations and ^{15}N content of NH_4^+, NO_3^- and SPON.

We used a simple mixing model (Phillips et al. 2005) to estimate the range of potential sources of organic matter (forest leaves, riparian grass, algae) to stream CBOM, FBOM and SPOM.

Regional river basin nitrogen budgets

We combined an analysis of land cover and stream networks from the regional survey with the ^{15}N uptake dynamics to estimate the extent to which deforestation has altered streams and nitrogen movement at the river-basin scale. We used the extent of streams in different land cover classes and the information on regional stream infilling by riparian grasses plus the uptake rates per m^2 of stream bottom to calculate total N uptake in first- and second-order forest and pasture streams. We used budgets of the fate of ^{15}N to calculate N retained in the first- and second-order stream reaches. The total N uptake and retention were determined for two scenarios: (1) entire Ji-Paraná basin covered by forest (pre-settlement scenario) and (2) under current land use (27% deforested in 1999; non-forest land use was 93% pasture).

Results

Regional survey

Geomorphological and ecological changes brought about by forest conversion to pasture produced widespread changes in physical structure and function of small streams. Across the region, forest and pasture streams had similar mean basin area, discharge and depth but forest streams had a narrower wetted width and more benthic cover of leaves (50%) and sand than pasture streams (Table 1). Pasture streams were wider, with slow moving water and deep accumulations of fine organic material (19% cover). Usually a small open water channel was present in pasture streams lined with floating mats of *P. repens* on both sides (63% riparian grass cover). Forest and pasture streams had similar pH, alkalinity and conductivity but pasture streams had lower concentrations of NO_3^- and dissolved oxygen (often near zero) and higher total suspended solids than forest streams (Table 1).

Landscape scale analysis of images of the Ji-Paraná watershed (LANDSAT, videography and IKONOS) showed that deforestation of 27% of the Ji-Paraná watershed altered 7,102 km (34% of total) first- and second-order channels. Infilling by *P. repens* was easily recognized in IKONOS and videography images (Fig. 1) and when combined with the on-the-ground survey and observations, indicated that almost all small pasture streams were dominated by riparian grass infilling.

^{15}N additions

Benthic habitats

The distribution of benthic habitats in the second-order forest stream used for ^{15}N addition was similar to that of forest streams in the regional survey (Table 2). Leaf pack (51%), sand (28%) and areas of sand overlain with a thin (a few mm) layer of fine organic matter (16%) were the dominant habitats. There were no extensive or deep accumulations of fine or coarse organic matter even in pools. Filamentous macroalgae were rare. The benthic habitat of the second-order pasture stream used for ^{15}N addition was also similar to second-order pasture streams in the regional survey. Benthic habitat cover was dominated by *P. repens* (55%) with water flowing through the root zone (Table 2). Grass detritus, sand and fine organic matter made up the remainder of benthic habitat. In the third-order pasture stream, riparian grass was found only on point bars (6%) and much of the stream had a sandy bottom. Benthic habitat was dominated by sand (42%), leaf and grass detritus (23%) and areas with a thin layer of fine organic matter over sand (14%). Filamentous macroalgae occurred attached to hard substrate (which was rare) or riparian grass in both pasture streams but were not common.

Table 2 Benthic habitat cover and N content of organic matter components in the streams receiving ^{15}N addition

Stream and habitat	Cover (%)	N content (g N m^{-2} of stream channel)			
		CBOM	FBOM	Leaf or grass	Total
Second-order forest					
Open channel					
Fine organic	16	0	0.003	0.134	0.137
Sand	28	0	0.001	0.000	0.001
Leaf pack	51	0.087	0.049	3.815	3.951
Wood	5				
Total	100	0.087	0.053	3.949	4.089
Second-order pasture					
Open channel		0.05	0.07		0.12
Find organic	12				
Sand	12		0.01		0.01
Detritus (grass)	17	0.19	0.10		0.29
Wood	5				
Grass channel habitat	55	12.74	16.00		28.74
Leaves				2.73	2.73
Roots and rhizomes				20.20	20.20
Total	100	12.98	16.18	22.93	52.09
Third-order pasture					
Open channel					
Fine organic	14		0.06		0.06
Sand	42		0.33		0.33
Detritus (grass, leaves)	23	0.05	0.36		0.41
Wood	5				
Gravel	3				
Clay	7				
Grass channel habitat	6				
Leaves				0.06	0.06
Roots and rhizomes		0.15	0.97	0.40	1.52
Total	100	0.20	1.73	0.46	2.38

Nitrogen content and biomass of wood was not measured

Water chemistry

The chemical characteristics of the second-order forest and pasture streams were similar to those in the regional survey (Fig. 2; Table 3). All forest and pasture streams had similar mean pH, alkalinity, conductivity, NH_4^+ concentrations. The second-order pasture stream had lower concentrations of NO_3^- and dissolved oxygen (range 0.1–2.8 mg l^{-1}) and higher SRP than the forest stream or the third-order pasture stream. DON was generally one third to about one half of the total dissolved N (Fig. 2). NH_4^+ and NO_3^- increased as discharge decreased in the forest, but declined in proportion to discharge in the second-order pasture stream. There was no clear pattern with discharge in the third-order pasture stream. The ratio of dissolved inorganic N:P was highest in the forest stream (105), lowest in the second-order pasture stream (2) and intermediate (17) in the third-order pasture stream.

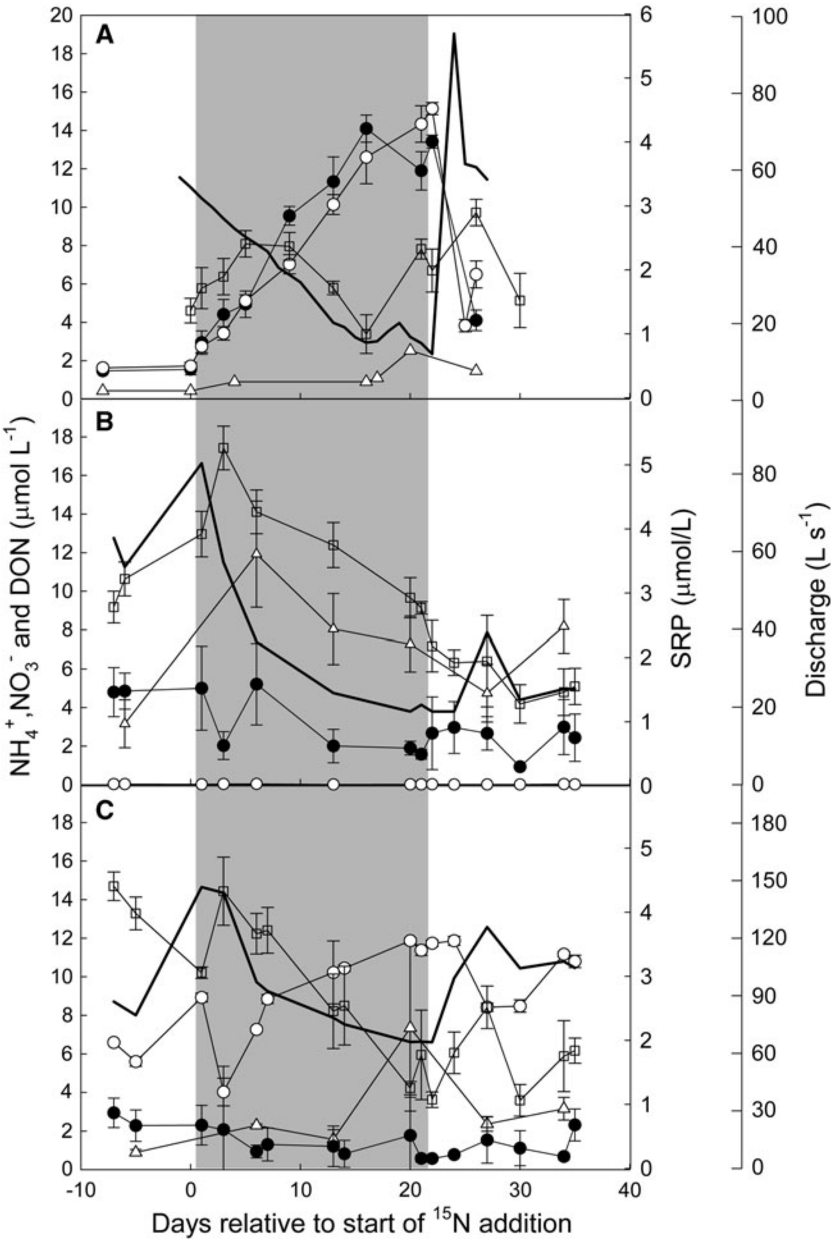

Fig. 2 Environmental conditions during the course of the ^{15}N addition experiments. *Plots* are mean concentrations of NH_4^+ (*closed circles*), NO_3^- (*open circles*), SRP (*open triangles*), DON (*open squares*) and discharge (*solid line*) during the ^{15}N addition experiment in the second-order forest stream (**a**), the second-order pasture stream (**b**) and the third-order pasture stream (**c**). Solute concentrations represent averages (±1 SD) of 3–7 stations over the experimental reach, except for SRP in the forest stream, which was measured at only one station at the downstream end of the reach on each date. *Shaded area* represents the period of $^{15}NH_4^+$ addition

Table 3 Chemical characteristics (mean and range) of the second-order forest stream and the second- and third-order pasture streams during the 21-day ^{15}N additions

	Second order		Third order
	Forest	Pasture	Pasture
pH	6.6 (5.2–7.4)	6.1 (4.1–6.5)	6.1 (6.8–9.7)
Alkalinity (mg l^{-1})	18.1 (14.5–22.0)	22.6 (18.0–32.2)	17.6 (15.9–20.9)
Dissolved oxygen (mg l^{-1})	6.7 (4.9–7.7)	1.4 (0.1–2.8)	7.5 (6.2–7.8)
Conductivity (mS cm^{-1})	0.053 (0.044–0.068)	0.1 (0.1–0.2)	0.1 (0.0–0.1)
NH_4^+ (μmol l^{-1})	7.3 (1.5–13.4)	3.2 (0.8–12.1)	1.5 (0.3–10.2)
NO_3^- (μmol l^{-1})	7.5 (1.7–15.1)	0.1 (0.0–0.7)	9.1 (3.6–12.1)
Dissolved organic N (μmol l^{-1})	12.2 (5.1–16.2)	9.5 (1.4–25. 8)	8.8 (1.2–20.7)
SRP (μmol l^{-1})	0.2 (0.1–0.3)	2.1 (0.5–4.2)	1.0 (0.2–5.1)
DIN:DIP	105 (16–503)	2.4 (0.7–10.7)	17.4 (2.3–40.5)

Organic matter and N standing stocks

The second-order pasture stream had 10 times more total N m^{-2} of stream reach (52. 1 g N m^{-2}) than either the second-order forest (4.1 g N m^{-2}) or the third-order pasture stream (2.7 g N m^{-2}) (Table 2). The location of N stocks in stream channels also differed. In the forest stream, leaf pack habitat had more than 25 times the N stock than depositional areas of fine organic sediments. In the second-order pasture stream, the large area of grass cover, high grass standing stock and abundance of CBOM and FBOM in grass habitat led to very high N stocks. There were typically accumulations (10–50 cm thick) of dead organic material in some of the deeper areas of the open stream channel and under the riparian grasses in the small pasture stream. In the third-order pasture stream, grass cover and grass standing stock were low and the stream had total N stocks and a distribution of N stocks that were similar to the forest stream.

Organic matter $\delta^{13}C$

In the forest stream, the $\delta^{13}C$ of organic matter compartments ranged from −26.2‰ in SPOM to −31.5‰ in biofilms (Table 4). The $\delta^{13}C$ of riparian grass leaves and roots and rhizomes ranged from −12.7 to −17.6‰ (Table 4). All organic matter classes (CBOM, FBOM and SPOM) in the forest stream had isotopic values consistent with being derived 100% from inputs of terrestrial C3 vegetation.

Table 4 Natural abundance of $\delta^{13}C$ in stream organic matter compartments

	$\delta^{13}C$ (‰)		
	Second-order forest	Second-order pasture	Third-order pasture
Leaf pack	−31.0 ± 0.8 (13)		
Biofilm	−31.5 ± 1.8 (19)	−21.4 ± 1.4 (15)	−26.4 ± 0.9 (15)
Algae	−28.3 ± 3.5 (26)	−21.3 ± 0.9 (8)	−19.4 ± 2.2 (5)
Riparian grass			
Leaves		−12.7 ± 0.4 (15)	−12.9 ± 0.5 (6)
Rhizomes		−13.6 ± 2.1 (16)	−17.6 ± 4.4 (19)
CBOM	−30.4 ± 0.9 (39)	−17.9 ± 4.2 (25)	−20.2 ± 4.7 (19)
FBOM	−29.2 ± 1.3 (25)	−19.8 ± 1.4 (22)	−22.4 ± 1.3 (20)
SPOM	−26.2 ± 1.3 (25)	−20.2 ± 0.9 (16)	−24.5 ± 0.5 (9)

Isotope values were from samples taken along the entire reach before the ^{15}N addition. Values are ±1 SD (sample size in parentheses)

The $\delta^{13}C$ of CBOM, FBOM and SPOM in the pasture streams was enriched compared with the forest stream, suggesting inputs of C4 grasses or algae. In the second-order pasture stream, contributions to CBOM came 90–100% from C4 grass with the remainder derived from algae (10%). For FBOM, contributions were smaller (70%) from grass and larger (30%) from algae. In the third-order pasture stream, contributions to CBOM were from grass (50–80%), trees (30–55%) and algae (10%) and contributions to FBOM were from grass (20–40%), trees (50–60%) and algae (2–30%). In both pasture streams, algae provided a larger contribution to FBOM ($\sim$20%) than to CBOM ($\sim$ 10%). SPOM was derived from similar sources as FBOM in all streams.

$^{15}NH_4^+$ and $^{15}NO_3^-$

In all streams, $\delta^{15}NH_4^+$ decreased with distance downstream from the injection point, and differences in the change of NH_4^+ indicated that NH_4^+ uptake differed among the streams (Fig. 3). In the forest stream, $\delta^{15}NH_4^+$ decreased over the course of the experiment because despite decreasing discharge, streamwater NH_4^+ concentration increased sevenfold (Fig. 2). This resulted in a relatively constant NH_4^+ during the experiment. In both pasture streams, $^{15}NH_4^+$ enrichment increased during the experiment because of declining discharge and either declining or stable NH_4^+ concentrations. Declining discharge in these streams led to a small decrease in NH_4^+ flux during the experiment.

The second-order pasture stream had a shorter NH_4^+ uptake length and a shorter NH_4^+ residence time than either of the other streams (Table 5). The third-order pasture steam had a NH_4^+ uptake rate, a NH_4^+ uptake length and a NH_4^+ residence time similar to the forest stream (Table 5). NH_4^+ uptake velocity showed a different pattern and was slightly higher in the forest stream compared with the second-order pasture stream and lowest in the third-order pasture stream (Table 5). We saw no significant increase in $\delta^{15}NH_4^+$ in the post-addition phase of any of the addition experiments, indicating that regeneration of NH_4^+ was minor in all of the streams. On day 22 (post-addition day 1), $^{15}NH_4^+$ returned almost to background levels in all streams and remained constant for the remainder of the post-addition period (Fig. 3).

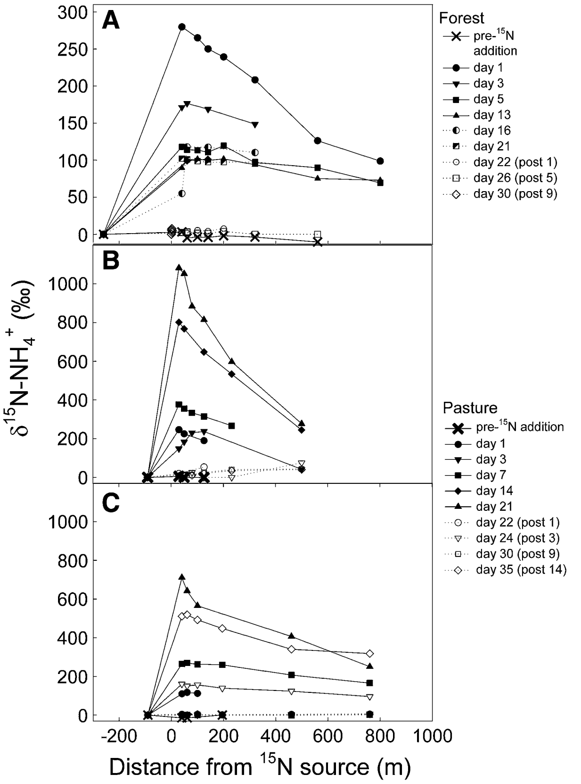

Fig. 3 The $\delta^{15}N$ of NH_4^+ in the second-order forest stream (**a**), second-order pasture stream (**b**) and third-order pasture steam (**c**). Profiles are $\delta^{15}NH_4^+$ in stream water over the study reach on one date prior to the start, five dates during and four dates after the ^{15}N addition ended. All values were normalized to upstream $\delta^{15}NH_4^+$ values on each date

In the second-order forest stream, nitrification was significant and increased $\delta^{15}NO_3^-$ downstream of the ^{15}N addition site (Fig. 4a). Mean NO_3^- uptake lengths in the forest stream ranged from 125 m to infinity and averaged 717 m (Table 5). Uptake by direct nitrification accounted for 22% of the whole-stream NH_4^+ uptake rate (10.1 of 46.6 µg N m^{-2} min^{-1}) and was the most significant removal pathway of NH_4^+ (Table 5). Very low concentrations of NO_3^- (range 0.0–0.7 µmol l^{-1}) in the second-order pasture stream made it impossible to reliably measure the $\delta^{15}NO_3^-$ and limited our ability to estimate the nitrification rate. Low dissolved oxygen (range 0.1–2.8 mg l^{-1}) combined with the very low NO_3^- concentrations implied that nitrification did not occur in the second-order pasture stream. In contrast, in the third-order pasture stream $^{15}NO_3^-$ was absent on day 1, but clearly present by day 3 (Fig. 4b). The lack of $^{15}NO_3^-$ on day 1

Table 5 Whole stream nitrogen processes during the 21-day ^{15}N addition

Attribute	Parameter	Units	Second-order forest	Second-order pasture	Third-order pasture
NH_4^+ dynamics	Uptake rate	μg N m^{-2} min^{-1}	46 ± 4	64 ± 65	49 ± 18
	Nitrification	μg N m^{-2} min^{-1}	10.1	0	5.1×10^{-5}
	Uptake velocity (V_f)	mm s^{-1}	0.089 ± 0.015	0.060 ± 0.014	0.018 ± 0.011
	Uptake length	m	1623 ± 327	410 ± 127	1264 ± 330
	Residence time	min	369 ± 75	168 ± 52	310 ± 81
NO_3^- dynamics	Uptake length	m	717 ± 824	nd	No uptake
	Nitrification (k_n)	m^{-1}	0.028	nd	0.00003
	$A_o \times K_n$		0.130 ± 0.051	nd	0.029 ± 0.062

There was no measureable uptake of NO_3^- in the third-order pasture stream

nd not determine because of very low NO_3^- concentrations

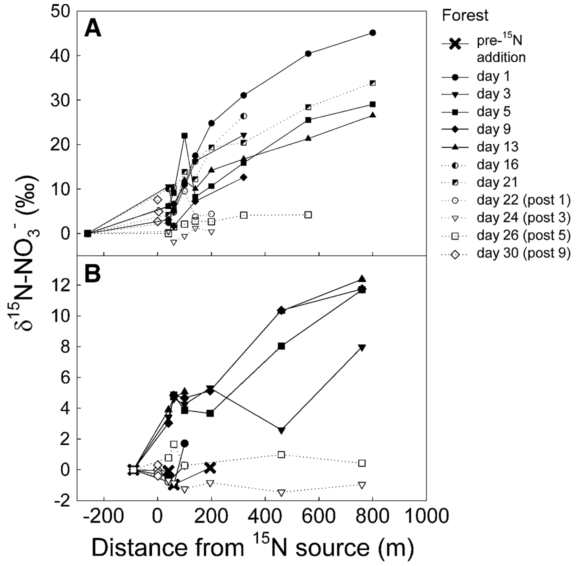

Fig. 4 The δ^{15}N of NO_3^- in the second-order forest stream (**a**) and the third-order pasture steam (**b**). Profiles are $\delta^{15}NO_3^-$ in stream water over the study reach on one date prior to the start, five dates during and four dates after the ^{15}N addition ended. The forest stream had the highest rate of nitrification as reflected in the increase in $\delta^{15}NO_3^-$. Nitrate concentrations in the second-order pasture stream were too low to reliably measure $^{15}NO_3^-$. *Closed symbols* were during the addition, *open symbols* were post-addition. The δ^{15}N values were normalized to upstream reference $\delta^{15}NO_3^-$ on each date

indicated that direct nitrification ($^{15}NO_3^-$ production from added ^{15}NH4$^+$) was minimal and that indirect nitrification (the production of $^{15}NO_3^-$ from $^{15}NH_4^+$ mineralized from ^{15}N-labeled organic matter) was responsible for formation of $^{15}NO_3^-$ on days 3–21. Nitrification accounted for none of the $^{15}NH_4^+$ uptake in the second-order pasture stream and less than 1% of $^{15}NH_4^+$ uptake in the third-order pasture stream (Table 6). No $^{15}NO_3^-$ uptake was measured in the second- and third-order pasture streams.

^{15}N in organic matter

In all streams, added ^{15}N accumulated in the organic matter compartments during the addition and then was lost relatively quickly after the addition ended (Fig. 5). In the forest stream, algae and biofilm, had the highest enrichments (Fig. 5a) and fastest post addition declines. In the forest stream, ^{15}N in FBOM increased sharply during the experiment and declined quickly post-addition. The forest stream CBOM accumulated and lost ^{15}N slower than FBOM, returning to background within 5 days (Fig. 5a).

In both pasture streams, algae were more highly labeled than microbial biofilm, FBOM or CBOM (Fig. 5b, c). In the second-order pasture stream, FBOM was more enriched than CBOM after 7 days (Fig. 5b). In contrast, in the third-order pasture stream, the CBOM was more enriched than FBOM after 7 days (Fig. 5c). The ^{15}N enrichment in all of these compartments was still increasing at the end of 21 days and tracked the increase in $\delta^{15}NH_4^+$ that occurred over the course of the addition.

In both pasture streams, the ^{15}N in all biomass compartments was highest in the stations 30–100 m downstream of the addition point and then declined downstream, while the forest stream had a much more uniform distribution of ^{15}N over the reach (Fig. 6). The highest enrichments did not always occur at the station nearest the ^{15}N addition point

Table 6 Mass balance of ^{15}N added to stream reaches

	Second-order				Third-order	
	Forest		Pasture		Pasture	
	^{15}N (g)	% of added	^{15}N (g)	% of added	^{15}N (g)	% of added
Total ^{15}N added	5.90		21.50		18.90	
Retained						
CBOM	0.01	0.2	0.4	2.0	0.1	0.5
FBOM	0.01	0.1	0.8	3.7	0.4	2.2
Leaf pack	0.42	7.1				
Grass—channel edge			11.2	52.2	0.3	1.8
Grass—floodplain			3.7	17.4		
Total retained	0.43	7.4	16.2	75.3	0.8	4.5
Exported in stream water						
NH_4^+	1.98	33.6	0.7	3.7	1.8	9.3
NO_3^-	1.13	19.2	0.0	0.0	1.0	5.6
SPON	0.01	0.1	1.6	7.4	2.1	11.0
Total exported	3.12	52.9	2.3	11.1	4.9	25.9
Total ^{15}N recovered	3.55	60.3	18.6	86.2	5.7	30.4

where $\delta^{15}NH_4^+$ was highest. This may have been caused by influx of unlabeled organic matter from upstream of the addition point in the case of CBOM or FBOM, or by sloughing or loss of the most labeled portions of algae or biofilm.

Riparian grass was highly labeled and both stream channel edge and floodplain grass became labeled (Fig. 7). In the second-order pasture stream, stream channel edge leaves and roots and rhizomes became highly labeled 30–50 m downstream of the addition point and were still highly labeled (>50‰) at 500 m (Fig. 7a). The leaves became more highly labeled than the roots and rhizomes downstream of 100 m, suggesting prompt translocation of acquired N into newly produced leaves. Grass in the floodplain also became labeled, with the highest label 120–230 m below the addition point (Fig. 7a), indicating that water moving below the grass and carrying the $^{15}NH_4^+$ spread out away from the stream channel downstream of the addition point. In the third-order pasture stream, the grass roots and rhizomes were more highly enriched (100–130‰) than the leaves (10–50‰), indicating N uptake and storage in rhizomes (Fig. 7b).

The biomass compartment-specific uptake rates of NH_4^+ were higher in the pasture streams than in the forest stream. Uptake of NH_4^+ was 2 times higher into grass leaves (6.4 versus 3.3 μg N m^{-2} min^{-1}) and 7 times higher into roots and rhizomes (67 vs. 10.8 μg N m^{-2} min^{-1}) in the second-order pasture stream compared to the third order pasture stream. Uptake of NH_4^+ into CBOM in the second-order pasture stream (1.7 μg N m^{-2} min^{-1}) was 85 times higher than in the forest stream (0.02 μg N m^{-2} min^{-1}) and 2 times higher (1.0 μg N m^{-2} min^{-1}) than the third-order pasture stream. A similar pattern was seen for rates of uptake into FBOM, which were 2.7 μg N m^{-2} min^{-1} in the second-order pasture stream, 0.01 μg N m^{-2} min^{-1} in the forest stream and 2.4 μg N m^{-2} min^{-1} in the third-order pasture stream. ^{15}N uptake into leaf pack in the forest steam (0.64 μg N m^{-2} min^{-1}) was half the rate of uptake into forest CBOM.

Turnover times of N in CBOM and FBOM in the forest streams were 2.5–5 times faster than their turnover in both pasture streams. The turnover time for CBOM was 5 ± 1 day in the forest stream, 26 ± 16 day in the second-order pasture stream and 16 ± 5 days in the third-order pasture stream. The turnover time for FBOM was 4 ± 2 days in the forest stream, 15 ± 5 days in the second-order pasture stream and 10 ± 3 days in the third-order pasture stream. The turnover time of N in forest leaf pack was 7 ± d. These turnover times assumed no uptake of

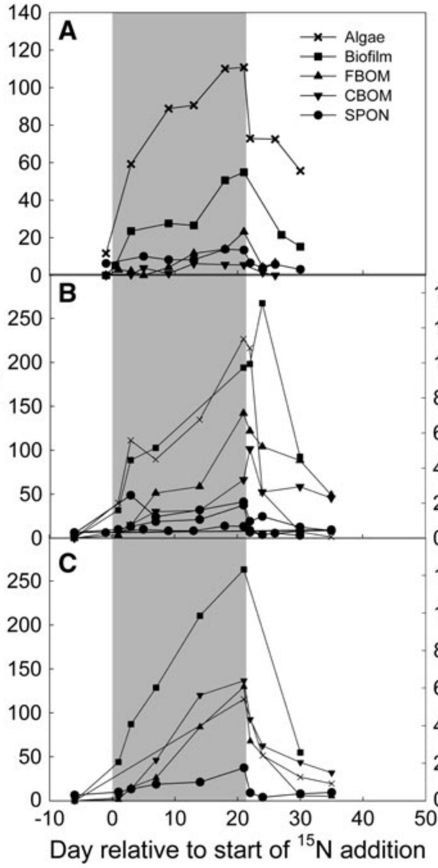

Fig. 5 Time course of δ^{15}N in biofilm, FBOM and CBOM (all *left axis*) and algae (*right axis* in pasture streams) at the 40 m station in the second-order forest stream (**a**), the 50 m station in the second-order pasture stream (**b**) and the 40 m station in the third-order (**c**) pasture stream. The δ^{15}N values were normalized to upstream values. *Shaded area* represents the period of $^{15}NH_4^+$ addition

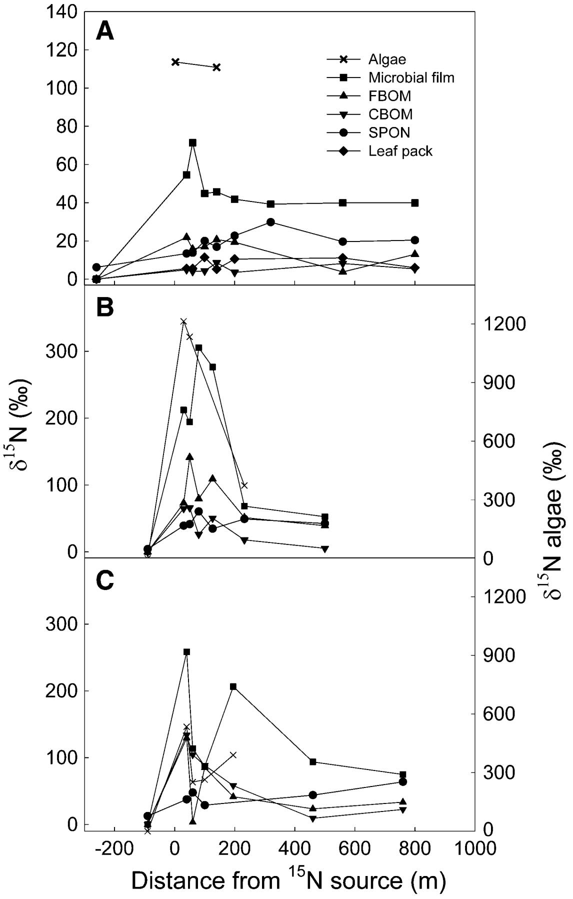

Fig. 6 Longitudinal transects of ^{15}N values in organic matter compartments on the final day of the ^{15}N addition. Values are δ^{15}N in algae (*right axis* in pasture streams), biofilm, FBOM and CBOM in the second-order forest stream (**a**), second-order pasture stream (**b**) and third-order pasture stream (**c**)

regenerated N and were likely underestimates of actual turnover time.

Nitrogen mass balance

A mass balance accounting of added ^{15}N indicated a change from predominantly N pass-through and export in the forest stream to N retention in the second-order pasture stream. In the forest stream, the predominant fate of N was export as DIN (Table 6). Fifty- seven percent of $^{15}NH_4^+$ added was exported as $^{15}NH_4^+$ and 8% was exported as NO_3^-. Seven percent of the added NH_4^+ entered organic matter pools and export of N as suspended particulate organic matter was minor. Forty percent of ^{15}N added to the forest stream was not accounted for at the end of the addition.

In contrast to the forest, in the second-order pasture stream almost 75% of added ^{15}N was retained in biomass compartments, predominately riparian grass. Export accounted for 11% of added ^{15}N, either as $^{15}NH_4^+$ or in particulate form, and no ^{15}N was exported as $^{15}NO_3^-$. Most of the total ^{15}N recovered in biomass compartments in the second-order pasture stream was retained by riparian grass. Fourteen percent of ^{15}N added in the second-order pasture stream was not accounted for.

The pattern of export and retention in the third-order pasture stream differed from that in the second-order pasture stream, with only 5% of added N retained and 26% exported as NH_4^+ (9%),

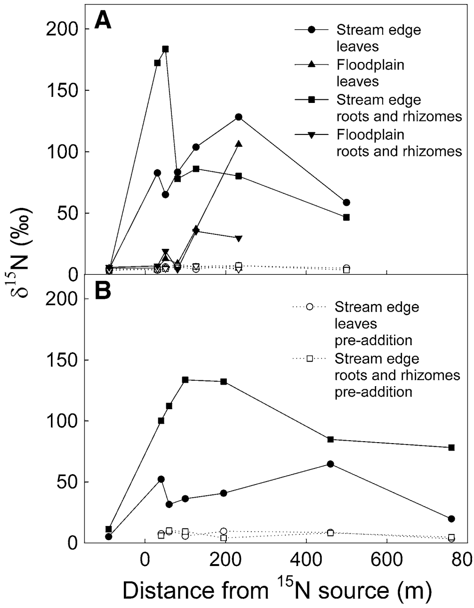

Fig. 7 The δ^{15}N in the riparian grass *P. repens* on day 20 in the second-order pasture stream (**a**) and third-order pasture stream (**b**). *Open symbols* represent pre-addition values, *closed symbols* are day 20. All δ^{15}N values were normalized to upstream values

NO_3^- (6%) and particulate N (11%). Two percent or less of the added ^{15}N was stored as CBOM, FBOM or riparian grass. Seventy percent of added ^{15}N was not accounted for.

Scaling to regional river basin N budgets

We estimate based on length of stream channel altered derived from remote sensing and changes to N cycling based on the ^{15}N additions that current deforestation of the Ji-Paraná basin of 27% has resulted in a sevenfold increase in basin-wide NH_4^+ uptake (20, 279 kg N day^{-1} under current land use versus 2,817 kg N day^{-1} in the fully forested watershed) and a 16-fold increase in NH_4^+ retention compared to the watershed in the fully forested state (15,151 kg N day^{-1} under current land use versus 929 kg N day^{-1} in the fully forested watershed). The fourfold greater uptake rates of ammonium, lowered nitrification and high retention in riparian grass in small pasture streams resulted in retention of more than 14,000 kg of N day^{-1} that would have been delivered downstream to third-order streams, and then flowed further downstream to larger rivers, had deforestation not occurred.

Discussion

Stream structure and water chemistry

Forest conversion to pasture in the watershed of second-order streams transformed stream morphology by eliminating the pool and run structure of the forest and replacing it with a narrow run of open water and a wide, wet, marshy bordering area created by extensive infilling with riparian grass in the stream and adjacent pasture. This led to high biomass of grass, CBOM and FBOM, hypoxic conditions, lower concentrations of NO_3^- and higher concentration of SRP in the pasture stream. These characteristics are linked to slower water velocities and greater transient storage of water and higher inputs of organic matter in pasture streams (Neill et al. 2006). Low dissolved oxygen has been associated with low concentrations of NO_3^-, low DIN:DIP and inducement of N limitation of pasture stream periphyton (Neill et al. 2001). The high ratio of dissolved inorganic N:P of 105 in the forest stream and 2.4 in the second-order pasture stream also indicated P limitation of algal and bacterial growth in the forest stream but N limitation in the pasture stream (Redfield 1958; Elser et al. 2007). The source of CBOM and FBOM in the second-order pasture stream also shifted to C4 grass sources from the C3 vegetation in the forest. Because of the large biomass and proximity of the streamside C4 grass *P. repens* it was the most likely source of C4-derived CBOM and FBOM in the second-order pasture stream.

The extensive infilling of first- and second-order streams by riparian grasses was widespread based on our ground survey and image analysis, and led to similar physical and chemical conditions across a wide range of locations. While the stabilization of banks by grasses and narrowing of stream channels occurs in meadow and pasture streams in different environments (Trimble 1997; Hession et al. 2003; Sweeney et al. 2004), the development of wide, marshy flooded streambanks in pasture represents a structural change not reported for other areas of the world. The condition in these altered streams were similar to large Amazon floodplain lakes, where dense mats of floating aquatic vegetation are widespread and high organic matter inputs lead to hypoxic conditions (Junk 1973; Welcomme 1985). Similar pasture stream infilling by grasses occurs elsewhere in deforested regions of the lowland Amazon, such as in eastern Pará state (R. Figueiredo, personal comm.), but is poorly documented.

In contrast to the second-order pasture stream, forest conversion to pasture in the watershed of the third-order stream resulted in less infilling of the channel by grass, lower streamside grass biomass and associated lower biomass of CBOM and FBOM. Third-order pasture streams also did not have the hypoxic conditions, low NO_3^- and higher concentrations of SRP found in the second-order pasture stream. In these ways, both physical and chemical conditions of the third-order stream more closely resembled conditions in the forest stream. The extent of forest clearing to the stream edge in the third-order pasture stream was also less than in the small streams in the regional survey. This may be related to the difficulty of clearing trees from the larger and wetter floodplains of larger streams. There was still a substantial shift in the origin of CBOM and FBOM from forest vegetation to C4 grasses in the third-order pasture stream. We could not distinguish between potential C4 sources in *P. repens* near the stream channel or the *B. brizantha* that occupied most of the upland portion of the watershed and some fraction of CBOM and FBOM may reflect the upland grass source.

These findings suggest that many of the most important structural and chemical changes to streams following deforestation depend on stream scale and that the largest changes occur at the smallest stream orders. The differences in channel structure between the second- and third-order pasture streams are potentially explained by an increase in erosive power per unit of streambed area with increasing discharge (Bagnold 1966). This higher erosive power of third-order streams relative to second-order streams may contribute to the lack of grass infilling if stream edge riparian vegetation provides little effective bank protection during channel-forming flows (Davies-Colley 1997). While we found virtually no NO_3^- in the second-order pasture streams, in a survey of mostly larger streams and rivers in Rondônia Biggs et al. (2004) found a positive relationship between NO_3^- concentration and percentage of the watershed in pasture, indicating a change in this relationship with stream size. Land-use practices may also play a role in the scale-dependence of stream structural changes. Ranchers typically clear trees from land immediately adjacent to small perennial streams to provide cattle with access to water and encourage grass infilling of stream courses to provide a source of actively growing forage during the dry season, but clearing the wider riparian forest adjacent to larger streams is more difficult and sometimes not done. By these practices, ranchers may be encouraging the differences we measured.

We found that the change in land use from forest to pasture surrounding second-order streams led to a dramatic shift in the sources of both coarse, fine and suspended organic matter from forest-derived leaves to riparian grass and that this shift took place rapidly (within a few years) following land-use conversion. This was consistent with the more enriched $\delta^{13}C$ values of POC in tributaries of the Ji-Paraná River in Rondônia that had higher proportions of pasture in their watersheds (Bernardes et al. 2004). The $\delta^{13}C$ values we found in second-order pasture streams were much more enriched in ^{13}C and had a higher C4 grass-derived fraction than those in larger rivers (>third-order), most likely because larger rivers still contain substantial fractions of forest in their watersheds and because riparian and floodplain forests can disproportionately deliver fresh particulate organic C to larger rivers (Mayorga et al. 2005).

Forest stream NH_4^+ uptake and transformations

In the forest stream, uptake into CBOM, FBOM and POM was low, NH_4^+ uptake velocity was low, the uptake lengths of both NH_4^+ and NO_3^- were long and 53% of ^{15}N added was exported from the reach as dissolved inorganic N. The fate of the 40% of added ^{15}N that was not recovered was not clear. While denitrification was possible in anoxic locations in the channel such as the hyporheic zone, we did not observe the required NO_3^- uptake. We did not measure $DO^{15}N$ export, but production of $DO^{15}N$ presumably would have been low given that we did not have strong uptake of ^{15}N into any abundant rapid turnover compartments, such as algae (rare in forest). Fluvial fluxes were well quantified and there were no major discharge events or measurable loss of water to hyporheic flows that might have resulted in large amounts of unquantified ^{15}N export.

The forest stream had lower NH_4^+ uptake velocity and a roughly tenfold longer uptake length than forested temperate and tropical North American streams with similar discharge and NH_4^+ concentrations (Mulholland et al. 2000; Peterson et al. 2001; Webster et al. 2003). The North American streams with the most similar uptake lengths (475–1,350 m) were in agricultural watersheds very high N concentrations, suggesting that NH_4 was not tightly cycled or limiting in these agricultural streams (Hamilton et al. 2001; Webster et al. 2003). The nitrification rate in our forest stream was comparable to temperate North American streams (Webster et al. 2003), but substantially lower than the rate (50–60%) for a tropical forest stream in Puerto Rico (Merriam et al. 2002). Among temperate streams, no consistent control of nitrification has been identified. Higher temperatures have been shown to increase nitrification (Warwick 1986), suggesting that our streams should have had higher rates of nitrification than the temperate streams and rates more comparable to the tropical Puerto Rican forest stream. Nitrification generally occurs in sediment and biofilms (Stream Solute Workshop 1990) and requires oxygen and NH_4^+. Tank et al. (2000) found almost no nitrification in a North American forest stream and attributed the low nitrification rate to low NH_4^+ concentrations and poor stream sediment quality for colonization by nitrifying bacteria. In contrast, in other temperate streams with low NH_4^+ concentrations, 10–50% of the total NH_4^+ uptake from streamwater was attributed to direct nitrification (Dodds et al. 2000; Mulholland et al. 2000; Ashkenas et al. 2004), similar to our forest stream. The export of inorganic N in the second-order forest (57% NH_4^+ and 8% NO_3^-) was on the high end of export as NH_4^+ (1–65%) and the low end of export as NO_3^- (1–50%) and export of SPON (1–12%) reported for temperate streams (Hall et al. 1998; Dodds et al. 2000; Mulholland et al. 2000; Tank et al. 2000; Hamilton et al. 2001; Ashkenas et al. 2004).

Long uptake lengths, moderate concentrations of DIN and high N:P all suggested algal and bacterial production in the forest stream was not limited by nutritional demand for N. Uptake of $^{15}NH_4$ by CBOM, FBOM and leaf biomass was slower than $^{15}NH_4$ uptake by nitrification. Combined, the biomass compartments accounted for only 1% of the whole stream NH_4 uptake and 6% of the total $^{15}NH_4$ uptake. The low $^{15}NH_4$ uptake rates by biomass compartments coupled with the high nitrification rates indicated low demand for N as a nutrient but use of NH_4^+ as an energy source by nitrifying bacteria in the stream channel. Low rates of NH_4^+ uptake were consistent with shaded conditions that limit algal productivity in forested lowland Amazon headwater streams (Fittkau 1967; Lowe-McConnell 1987). NH_4^+ uptake but no NO_3^- uptake was also consistent with a general preference for NH_4^+ assimilation by stream biota (Reynolds 1984; Fenchel et al. 1998) and by phytoplankton in Amazon River floodplain lakes (Fisher et al. 1998). Assimilatory uptake of NO_3^- has been found to contribute total inorganic N uptake in some temperate urban and agricultural streams (Arango and Tank 2008, Arango et al. 2008) but that was not an important process in any of our streams.

Several characteristics of mature lowland Amazon tropical forest suggest an open N cycle and the absence of strong N limitation of the forest ecosystem. These include high concentrations of N in leaves and litter, high concentrations of NO_3^- in forests soil solution and high ratio of NO_3^-:NH_4^+ (Markewitz et al. 2004; Neill et al. 2006; Chaves et al. 2009), high soil emissions of N_2O (Vitousek 1984; Davidson et al. 2007), and high rates of soil nitrification (Neill et al. 1997; Verchot et al. 1999). The result of the forest stream ^{15}N addition indicated that the relatively open N cycle of tropical forests extends to small forest stream channels and further contributes to open N cycling and the absence of strong N retention at watershed and landscape scales in forested regions.

Pasture stream NH_4^+ uptake and transformations

The second-order pasture stream had a much higher uptake of NH_4^+ than the forest stream. This was evident in the shorter NH_4^+ uptake lengths, faster rates of uptake into organic matter compartments, a shorter NH_4^+ residence time and very low export of $^{15}NH_4^+$. The most important reason for the higher NH_4^+ uptake was the presence of riparian grasses in the stream channel. This grass accounted for 75% of recovered ^{15}N. A slightly lower $^{15}NH_4^+$ uptake velocity in the second-order pasture stream compared with the forest stream was unexpected and not easily explained given the high measured total uptake into riparian grass.

Low dissolved oxygen concentration inhibits nitrification and promotes denitrification of NO_3^- (Seitzinger 1988; Christensen et al. 1990; Kemp and

Dodds 2001). The hypoxic conditions in the second-order pasture stream channel limited nitrification and NO_3^- export was zero. The very high biomass of grass, CBOM and FBOM led to more export as PON (7%) than in the forest stream (0.1%). Floodplain grass, even 2 m away from the stream channel, was a significant sink for added $^{15}NH_4^+$. Increases in the amount of ^{15}N detected in floodplain grass with distance downstream indicated that water spread away from the open stream channel and moved underneath the grass mat. This allowed a much larger area of grass to interact with streamwater and increase the total amount of N retained in the stream channel-floodplain system. Relatively little (14%) of ^{15}N added to the second-order pasture stream was not accounted for. Because of the large grass biomass, variability in quantifying grass biomass and $\delta^{15}N$ of the grass were the most likely sources of this discrepancy.

In the third-order pasture stream, most measures of N biogeochemistry were intermediate between the second-order forest and pasture streams and N export dominated over N retention. The third-order pasture stream had low uptake of ^{15}N in CBOM, FBOM and streamside grasses and some NH_4^+ export (9%). Some nitrification occurred in the well-oxygenated streamwater but NO_3^- export was low (6%). Export of PON (11%) was also relatively high. The most puzzling aspect of the third-order addition was the low recovery (30%) of the added ^{15}N. There were no major discharge events that were not measured or detectable loss of water to hyporheic flows that might have resulted in large amounts of unquantified ^{15}N export. Errors associated with uptake into organic compartments were relatively low as total organic biomass was relatively low. It is tempting to invoke denitrification, however, nitrification accounted for less than 1% of $^{15}NH_4^+$ uptake and no $^{15}NO_3^-$ uptake was measured in the third-order pasture stream.

Landscape-scale implications for N retention

Changes in stream structure and biogeochemistry of N of small streams suggest that the connection to larger rivers via downstream transport of N typical of forested systems is weakened substantially by deforestation. Small forest streams function largely as transformers of NH_4^+ to NO_3^- and long-distance conduits for transport of inorganic N. Deforestation around small streams results in infilling of the stream and floodplain by grass and ultimately causes retention of large amount of N in grass biomass and preventing downstream N transport, at least over the time scales (weeks to months) measured by the ^{15}N addition experiment. At the regional watershed level, changes to N cycling from clearing 25% of the watershed caused a 16-fold increase in N retention in first- and second-order pasture streams compared with forest streams. Larger (third-order) pasture streams were not as retentive of N as second-order pasture streams, but N retention as a percentage of recovered N is higher than small forest streams, suggesting deforestation for pasture creates a break in transport of NO_3^- and diminishes the flow of total N down small stream corridors to larger rivers.

Significant nitrification in streams indicated that NO_3^- forest and pasture streams was derived from nitrification of NH_4^+ in situ rather than direct transfer from NO_3^--rich soil solution to streams via groundwater pathways. This is consistent with the Chaves et al. (2009), who found removal of NO_3^- in deep pasture soils in Rondônia and low concentrations of NO_3^- in groundwater. It is also consistent with the finding of Brandes et al. (1996) who used natural abundance of $^{15}NO_3^-$ to infer that NO_3^- in the streamwater of a small primary forest watershed near Manaus originated from in-channel nitrification. Our finding of low NO_3^- concentrations in small pasture streams combined with observed low production of NO_3^- in soils (Neill et al. 1997) and low NO_3^- concentrations in all potential hydrologic flowpaths from pasture (Chaves et al. 2009) indicate that NO_3^- in larger pasture streams is also likely derived from nitrification in the stream channel rather than NO_3^- inputs from the watershed. The second-order pasture stream had no measureable levels of NO_3^-.

High N retention in small pasture streams is very different than the result from the temperate zone in which streams running through pasture can have lower rates of N uptake than streams in forest because narrower streams in pasture leads to less total area of stream bottom per unit stream length (Sweeney et al. 2004). There is some evidence that riparian vegetation along temperate forest streams may play a role in stream channel N cycling (Ashkenas et al. 2004), but the role of riparian grasses on stream N processing is not well studied.

These results contradict the trend in temperate latitudes of generally higher N export from agricultural compared with forested watersheds (Peterson et al. 2001; Allan 2004; Green et al. 2004) and the suggestion of Matson et al. (1999) that increased N additions to tropical terrestrial systems will result in large losses of N to the ocean in tropical locations because of the absence of strong N limitation to terrestrial vegetation. Higher export from temperate agricultural areas results from a combination of changes in stream structure and N processing to favor export and runoff of N added as fertilizer. Our agricultural pastures are not fertilized, however, the changes in N cycling favor retention of any N that reaches the streams from land. Our work suggests a more nuanced view than proposed by Matson, which implied that streams would simply pass N received from forests downstream unchanged. Stream N cycling changes in response to land-use resulting in high N retention in deforested portions of stream networks (primarily through grass infilling of smaller streams) and less N retention were deforestation does not result in the same degree of changes to stream structure and N cycling.

There are several potential limitations to our interpretation of larger-scale changes within stream networks. We did not examine larger forest streams (third-order or higher) because forest clearing has severely reduced the extent of large forested watersheds in central Rondônia. We performed our ^{15}N additions in the dry season, which represents only half of the year (May–October) and our experiments were limited to a small number of streams. Further work to examine net N retention for long periods and during the wet season is needed to understand the role of stream channels in landscape N retention over a complete annual cycle. In the wet season, it is possible that N transport in both forest and pasture streams will increase because of more frequent and higher discharge events with faster current velocities. The effects of increased wet season discharge on downstream flux may be moderated in pasture streams because the grass in stream channels remains vigorous year-round, is not scoured out annually, and serves to slow water velocities and filter out particulates, all suggesting the pattern of high retention in the grass is likely to remain in the wet season. It is also possible that the higher current velocities associated with wet season floods might dislodge particulates trapped in the riparian vegetation and increase episodic particulate transport.

Conclusions

Conversion of land use change from forest to pasture resulted in a cascade of effects that altered stream structure and N biogeochemistry. Deforestation simplified second-order stream structure by promoting channel infilling by streamside grasses and eliminating tree leaf detritus, creating streams with continuous slow moving deep runs and thick deposits of coarse and FBOM. The infilling of small pasture streams with grass created high organic matter loading, hypoxia and a 16-fold increase in N retention. The same high N retention did not occur in larger pasture streams where grass infilling was much less. Our findings of widespread infilling of first- and second-order pasture stream channels by riparian grass and the accompanying of this phenomenon with lower dissolved oxygen and increased N uptake and retention suggest that deforestation now alters stream ecosystem structure and N retention over many thousands of km of small Amazon stream channels. These structural changes and high N retention are largely restricted to second-order pasture streams. Better estimates of the extent and spatial scales at which small stream infilling occurs and a better understanding of where N gets delivered to streams will further improve our understanding and prediction of how N is transported within Amazon stream networks.

These results have several potential implications for the ecological function and conservation management of the lowland Amazon's streams. Small streams constitute three-fourths of stream channel length in the Amazon (Junk 1997; Goulding et al. 2003; McClain and Elsenbeer 2001). Small streams are vital to the life cycles of many fish important in commercial and subsistence fisheries and they contain the world's richest diversity of freshwater fishes and aquatic organisms, many of them endemic (Goulding 1980; Barthem 2004; Agostinho et al. 2005). Low dissolved oxygen and greatly altered habitat structure in second-order pasture streams are likely to have implications for a variety of stream organisms, including fishes. Because grass infilling in small streams is related to clearing of stream-edge forest, conserving streamside forest could reduce to grass infilling and preserve stream physical structure and N patterns of N uptake and retention more like those of the original forest.

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