Nutrient concentrations and nitrogen speciation in tropical watersheds of central Panama

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Abstract

We present chemical analyses from rivers and streams in five partly to near-fully forested watersheds in the humid tropics of central Panama. Contrary to the situation observed for temperate watersheds in the Northern Hemisphere, the concentration of dissolved inorganic nitrogen in the Panamanian watersheds is low (mostly <2.6 µmol L^{-1}), whereas concentrations of organic nitrogen are several times higher, mostly >10 µmol L^{-1}. We provide evidence that almost all NH_4^+ and much of the NO_3^- from precipitation are being converted to DON as nitrogen is cycled from the rainforest ecosystem to watershed rivers and streams, and that nitrogen loss from these pristine watersheds occurs mainly via dissolved organic N compounds. Based on this information we conclude that these Panamanian forests are not nitrogen saturated and are sinks for inorganic N. These Panamanian streams have lower DIN concentrations and higher DON concentrations than comparable montane forested streams in the Caribbean and Central America. Dissolved soluble phosphate concentrations are also very low (<1 µmol L^{-1}). The TDN, DON and SRP yields are 4.45, 4.28 and 0.26 kg ha^{-1} yr^{-1}, respectively. These are similar to those calculated for Costa Rican tropical rain forest streams, with the Panama sites having lower TDN and SRP yields but higher DON yields. The central Panama TDN yield estimate is within the range determined in other tropical undisturbed watersheds (0.57 – 9.40 kg ha^{-1} yr^{-1}), with the DON yield for Panama at the higher end of the range for tropical watersheds.

Introduction

Human activities have more than doubled the rate of nitrogen entering the land-based N cycle from natural biological N_2 fixation, and this rate is continuing to climb [1-3]. This supply of excess nitrogen is stimulating algal and microbial production in aquatic ecosystems, as well as accelerating losses of biological diversity [4,5], contributing to the long-term decline in coastal marine fisheries [6], increasing global concentrations of the potent greenhouse gas nitrous oxide [7], increasing acidification of soils and waters [8-10], and reducing long-term soil fertility [1,9,11]. Such drastic consequences have generated increased interest in the understanding of processes that control the terrestrial N cycle, in particular the export of N from watersheds to inland lakes and coastal waters, and the chemical speciation of this exported N. In addition, despite the increased nutrient inputs from human activities, most N added to watersheds does not reach coastal systems, and only about 20% of N inputs are exported by rivers to the ocean [12,13]. Denitrification, the microbial reduction of NO_3^-, has been suggested to account for most of the N loss in the northeastern USA [13] and northern Europe [14]. Streams from these regions, however, even those in undisturbed forested watersheds, already contain elevated levels of dissolved inorganic nitrogen (DIN) and the NO_3^- fraction of DIN is much higher than the NH_4^+ or NO_2^- fractions [15-17]. As such, it is not a surprise that these temperate regions have elevated denitrification rates, even though the efficiency of these processes decreases with increasing NO_3^- concentration [18]. In these temperate forested ecosystems, N limitation has been reversed, leading to what is called nitrogen saturation, resulting in excessive loss of NO_3^- from streams [19].

The few studies from forested watersheds elsewhere have revealed patterns of N loss that are more complex than what is predicted by current conceptual models derived from studies of nutrient dynamics in temperate regions of Europe and the USA. For instance, hydrologic N losses in pristine temperate forested ecosystems in southern Chile has been shown to occur nearly exclusively as DON (95% of the total N), and that NO_3^- concentrations represent only 0.2% of the total dissolved nitrogen (TDN), with NH_4^+ constituting 4.8% of the total [20]. Stream chemistry data from 100 unpolluted primary forests in temperate South America has shown the same strong dominance of dissolved organic nitrogen (DON) over inorganic losses of N, as well as extremely low stream water NO_3^- concentrations [21]. Some have suggested that the strong dominance of organic over inorganic losses of N in these unpolluted streams is a consequence of their low mean annual temperature (4-11°C), arguing that such low temperatures may inhibit the conversion of DON to NH_4^+ and then to NO_3^- [22]. However, others have documented a similar dominance of DON transport in tropical forest systems, where temperature is higher and less variable, suggesting that temperature, although important, may not be the major control on the dominance of organic over inorganic N fractions in undisturbed tropical forested watersheds [23,24]. Work on coastal streams in southwestern Panama has also demonstrated that DON is the dominant fraction of dissolved N entering the coastal zone in both forested and pasture watersheds, at a molar ratio of ~3:1 [25]. Our results support these observations. We report dissolved nutrient concentrations from stream samples collected in the humid tropics of central Panama, within the northeastern portion of the Greater Panama Canal Watershed, where the mean annual temperature is about 27°C with a monthly mean annual range of less than 2º C. These data provide a significant contribution to the limited literature on the dynamics of N species and the hydrologic export of DON and DIN in tropical watersheds.

Material and methods

Study area

The area investigated in this study lies in the northeastern eastern portion of the Greater Panama Canal Watershed, which consists of 13 sub-basins, rivers, and dammed lakes that extend over 3,000 km^2 in the central portion of Panama and comprises five river systems (Fig 1): the Nombre de Dios and Cuango watersheds, which flow northward into the Caribbean Sea; the Pequini and Chagres watersheds, which flow southwestward into the Lago Alahuela (a dammed lake that provides water to operate the Panama Canal and generate electricity); and the Pacora watershed, where flow is initially east and then southward into the Pacific Ocean.

Fig 1. Locations of watershed boundaries in the Upper Chagres region of central Panama and sites sampled in this study.

The headwaters of these rivers lie in pristine tropical rainforest of the Chagres National Park, at elevations between 400 to 1000 meters. The study region has been affected by anthropogenic influences to differing extents and degrees. The central core area around the headwaters of the Nombre de Dios, Cuango, Pequini and Upper Chagres (excluding its Rio Indio tributary river) is pristine tropical rainforest. The Rio Indio tributary has been impacted by low-density local residential and farm development. The limited removal of forest for subsistence farming is common in the lower reaches of the Nombre de Dios, Cuango, Pequini and Upper Chagres, while the middle to lower reaches of the Pacora watershed have been deforested for residential, agricultural, and/or light industrial land use (Fig 2).

Fig 2. Land use in the Upper Chagres region showing the 24 sites sampled in this study.

The climate of central Panama is humid tropical as a consequence of its near-equatorial position at 7-10° N latitude and the occurrence of moisture-laden winds that alternate seasonally off the Pacific and Caribbean coasts of the isthmus. The region has warm temperatures that vary from 23-27 °C along the coast to about 19 °C in the interior highlands [26]. Seasonal wind patterns determine precipitation over Panama, with most rainfall (~90%) occurring during the May to

December wet season. The Caribbean coastal region (windward of the continental divide) has higher annual rainfall (>3000 mm), compared to the Pacific side of the isthmus (~2000 mm), mainly due to orographic precipitation [27].

Orographic enhancement of precipitation at the headwaters of the rivers sampled in this study is pronounced. The Upper Chagres watershed receives approximately 3500 mm of annual rainfall, producing over 2000 mm of annual runoff. Runoff in this watershed is dominated by groundwater discharge [28] and a similar situation is expected for the Nombre de Dios, Cuango, and Pequini rivers. From 1998 to 2006, the average annual discharge for the Upper Rio Chagres measured at the Chico monitoring station on the lower reaches of the river was 32.2 m^3 sec^{-1}. The hydrographs from storm events are very flashy with steep rises and falls [29]. Work using geochemical tracers has indicated that depending on the size of the rain event, water flowpaths from the surface landscape into the streams can vary between groundwater (i.e. baseflow), canopy throughfall, and shallow soil water inputs [30]. Preferential flows in the forested landscape can significantly increase soil infiltration capacity in these systems [31].

Geomorphologically, the mountainous portion of the study area is a strongly dissected landscape, covered with dense tropical forest, with most hillslopes having low-order streams that flow for only short distances before reaching a higher-order channel. The forested area (Fig 2) typically is characterized by a multi-story canopy that extends 20-50 meters above the ground. The tree species diversity in the rainforest of central Panama is high, about 90 species ha^{-1} [32]. Of the total 1,162 tree species catalogued in the Upper Rio Chagres area, 495 are found only on the Atlantic side of the Upper Chagres region, 101 are found on the Pacific side only, and 198 are widespread, among which the most common is *Podocarpus oleifolius* D. Don ex Lamb [33].

The bedrock geology of the Upper Chagres region consists primarily of Late Cretaceous to Early Tertiary age hydrothermally-altered andesites, with lesser amounts of younger mafic and felsic igneous rocks locally predominant [34]. For the Nombre de Dios, Cuango, and most of the Upper Chagres watershed, the outcropping geology is a mixture of all these lithologies. By contrast, mafic gabbro and diorite underlie much of the Rio Indio and Rio Chico sub-basins of the Upper Chagres watershed and all but the lower portions of the Pacora watershed, which is developed on Tertiary marine sediments.

Like other tropical soils worldwide, those in the study area of central Panama are strongly weathered, have high clay but low organic material content, and are enriched in residual elements like Fe, Al, and Si [35]. Translational mass movement, which has rafted weathered soil regolith downslope, appears to be the dominant geomorphic processes, and the base of the translational mass movements appears to be the contact between the pedogenic soil profile and saprolite [35]. Within the highly dissected mountainous portions of the five watersheds, soils developed in transported regolith form the majority (60%) of the land surface within the drainages. In contrast, more stable soil profiles, with higher clay contents and deeper weathering profiles, are present in upper slope positions, and form an estimated 10% of the total land surface area [35].

The major ion chemistry of the upper portions of these rivers reflects the variations of bedrock types within the watersheds [36,37]. For example, the tributaries draining gabbro lithologies have relatively higher total dissolved solid loads and contain more dissolved Ca than those draining basaltic lithologies. Bedrock variations in Panama have also been shown to have a great influence on the concentrations and yields of dissolved organic carbon (DOC), with the highest values associated Tertiary marine sedimentary rocks compared to the igneous dominated terranes [38]. Besides influencing stream compositional character, lithologic distribution exerts an important geological control on the drainage system of the Upper Chagres watershed and its tributary rivers [34].

Sampling procedures

Streams in five watersheds in central Panama (Fig 1) were sampled during a 3-day period between 27 February and 1 March 2007. The physical characteristics of the five watersheds are given in Table 1. Temperature, dissolved solid content, acidity, and dissolved oxygen content were measured in the field using portable meters. Water samples were collected by hand in the center of the stream channel by an individual wearing clean polyvinyl gloves reaching into the flow upstream from the sampler's body. Pre-cleaned 60 mL polyethylene bottles were rinsed three times with river/stream water prior to sample collection. Bottles were cleaned as outlined in [39]. After collection, samples were placed in dark, plastic coolers and filtered upon return to Panama City from the field no more than 12 hours after collection. Samples were filtered through 0.4 µm pore-size Nuclepore filters, using a bell jar and pre-cleaned plastic filter towers, directly into sample bottles. After filtration, the samples were frozen and shipped back to The Ohio State University (Columbus, OH, USA) in a frozen state and kept frozen until analyzed. Samples were thawed and analyzed for NO_2^-+NO_3^-, NO_2^-, NH_4^+, total nitrogen (TN) and soluble reactive phosphorus (SRP) using standard techniques on a Lachat FIA analyzer. Dissolved organic nitrogen (DON) was calculated as the difference between total nitrogen (TN) and the sum of the dissolved inorganic N species. Analytical precision of the measurements is ≤3%. Detection limits for NH_4^+, NO_2^-, and SRP are 0.2, 0.9, and 0.3 µmol L^{-1} respectively. Filtration blanks for NH_4^+, NO_3^-, NO_2^-, and SRP were all below detection.

Table 2. Geomorphic characteristics of the five river basins examined in this study.

Watershed	Area (ha)	Max elevation (m)	Min elevation (m)	Mean elevation (m)	Average slope (%)	Length (km)
Nombre de Dios	6,591	483	0	115	14	15
Cuango	17,435	728	0	205	14	30
Pequini	17,445	836	60	290	14	29
Chagres	55,348	1,008	60	452	16	55
Pacora	36,045	939	0	280	10	44

Sampling locations

The Rio Nombre de Dios watershed (~6,600 ha) was sampled in its lowermost downstream reach ~500 m upstream from its outflow point to the Atlantic Ocean (PAN-492). The Rio Cuango watershed (~17,400 ha) was sampled at five locations: the Rio Cuango in its lowermost downstream reach ~500 m upstream from its outflow point to the Atlantic Ocean (PAN-424); in its middle reaches at the upstream limit of forest clearance for subsistence farming (PAN-425); downstream of PAN-425, at the confluence with one of the Rio Cuango major tributary rivers (PAN-428); at a small tributary river to the Cuango (PAN-431); and in the upper reaches of the Rio Cuango, in pristine rainforest just upstream of its confluence with the second large tributary river (PAN-426).

The Rio Pequini watershed (~17,500 ha) was sampled in three locations: in the Pequini lower reaches, a few kilometers upstream of its outflow into Lago Alajuela, where some deforestation for subsistence farming and livestock grazing has occurred (PAN-432); in its pristine forested upper reaches, just upstream with the Rio San Miguel (PAN-433); and at the Rio San Miguel, the major tributary river of the Rio Pequini (PAN-434).

The Rio Chagres is the major river system of the region. It drains about 55,300 ha, most of which is protected by the Panamanian government as the Chagres National Park. The Upper Rio Chagres was sampled in two places: in its pristine upper headwater reaches (PAN-437), and in its lower reaches, a few kilometers upstream of its inflow into Lago Alajuela (PAN-435). Two Upper Rio Chagres tributary rivers in pristine tropical rainforest and two tributary rivers affected by partial deforestation were also sampled.

Four major tributary rivers of the Upper Rio Chagres were sampled – the Esperanza, Chagricito, Piedras, and Indio. The upper reaches of the Esperanza (PAN-449) and the lower reaches of the Chagricito (PAN-450) are deep in unspoiled rainforest. The Piedras tributary was sampled at a gauge site (PAN-451) approximately one kilometer upstream of its confluence with the Upper Chagres. The Indio tributary was sampled in its upstream reaches (PAN-455) at a large waterfall, in its upper-middle reaches (PAN-456) at the site of a former hydroelectric plant, and in its middle reaches (PAN-454) in an area of subsistence farming. A small tributary stream to the Rio Indio, whose upper reaches drains an area of sparse residential and farm settlements, was also sampled (PAN-457).

The Rio Pacora watershed (~36,000 ha) was sampled in four locations: in its upper-middle reaches (PAN-462) a few kilometers downstream of where deforestation for pastureland commences; in its middle reaches (PAN-461) at the village of San Miguel; in its lower-middle reaches (PAN-460) at the village of Juan Gil; and in its lower reaches (PAN-459) upstream of the Rio Cabobre confluence where it crosses the Pan-American Highway. The Rio Cabobre, sampled just upstream of its confluence with the Rio Pacora (PAN-482), is a major tributary river (~26,500 ha) that joins the Rio Pacora about halfway along its flow across the broad Pacific coastal plain in this region of central Panama that has been entirely deforested and currently supports livestock grazing, agriculture, light industry, and residential land uses.

The general physical and chemical characteristics and a brief description of the 24 sites sampled are provided in Table 2.

Table 2. Chemistry and nutrient concentrations for the 24 sampling sites in central Panama.

Location	Sample #	Land use	Temp (°C)	SPC (mS cm^{-2})	pH	DO (%)	NO_3^- (μmol L^{-1})	SRP (μmol L^{-1})	NH_4^+ (μmol L^{-1})	DON (μmol L^{-1})
1	PAN-492	Deforested	26.63	392	7.69	92	2.58	0.38	ND	17.3
2	PAN-424	Deforested	27.51	286	7.59	101	ND	0.28	ND	8.28
3	PAN-428	Farm/pasture	26.37	272	7.39	96	2.24	0.50	ND	14.4
4	PAN-425	Forested	26.51	269	7.26	81	1.32	0.39	ND	22.4
5	PAN-431	Farm/pasture	26.84	288	8.40	121	1.06	0.69	ND	8.92
6	PAN-426	Forested	26.02	281	7.63	107	2.12	0.91	ND	13.0
7	PAN-433	Forested	26.03	273	8.06	109	ND	0.92	ND	35.6
8	PAN-434	Forested	26.11	282	8.11	115	0.21	0.70	ND	7.42
9	PAN-432	Farm/pasture	27.12	322	7.76	103	ND	0.64	ND	32.3
10	PAN-437	Forested	24.09	148	6.94	96	1.46	0.36	1.59	42.9
11	PAN-450	Forested	25.89	181	8.08	105	0.29	0.24	ND	14.7
12	PAN-449	Forested	26.86	178	8.31	104	0.37	0.24	ND	66.3
13	PAN-451	Farm/pasture	26.14	236	8.02	103	2.40	0.33	ND	19.5
14	PAN-453	Deforested	26.25	223	8.27	114	1.22	0.58	ND	22.1
15	PAN-435	Deforested	27.10	220	7.88	109	ND	0.35	ND	11.5
16	PAN-455	Farm/pasture	23.97	166	7.87	94	11.4	0.08	ND	22.8

17	PAN-456	Farm/pasture	25.05	174	7.93	91	32.4	0.09	ND	19.1
18	PAN-457	Farm/pasture	25.16	190	7.93	102	1.75	0.54	ND	107.8
19	PAN-454	Farm/pasture	28.80	234	8.23	109	2.23	0.14	ND	30.5
20	PAN-462	Farm/pasture	29.34	313	8.40	107	ND	0.45	ND	6.80
21	PAN-461	Developed	29.82	319	7.96	105	ND	0.24	ND	18.1
22	PAN-460	Developed	27.61	337	8.27	112	ND	0.23	ND	10.5
23	PAN-482	Farm/pasture	30.25	330	8.24	112	ND	0.02	ND	26.1
24	PAN-459	Developed	34.03	340	8.07	118	0.24	0.22	0.12	18.4

ND = not detected; SPC = specific conductance. Detection limits for NH_4^+, NO_3^-, and SRP are 0.2, 0.9, and 0.3 µmol L^{-1} respectively.

Sample site descriptions:

1. Rio Nombre de Dios, downstream reach ~500 m upstream from Atlantic coast
2. Rio Cuango, downstream reach ~500 m upstream from Atlantic coast
3. Rio Cuango lower-middle reaches at 3-tributary farm, ~10m upstream of large tributary
4. Large unnamed tributary to Rio Cuango at 3-tributary farm
5. Mid-sized tributary to Rio Cuango at 3-tributary farm
6. Rio Cuango middle-upper reaches upstream of confluence with large tributary river
7. Rio Pequini, upstream of Rio San Miguel confluence
8. Rio San Miguel tributary river to Rio Pequini, ~10 upstream of confluence
9. Rio Pequini, lower reaches immediately downstream of Embara village
10. Upper Rio Chagres, upstream
11. Rio Chagricito tributary to Upper Rio Chagres, ~10 m upstream of confluence
12. Rio Esperanza tributary to Upper Rio Chagres in middle
13. Rio Piedras tributary to Upper Rio Chagres at ACP gauge site
14. Rio Chico tributary to Upper Rio Chagres, ~10 m upstream of confluence
15. Upper Rio Chagres, lower reaches downstream of Embara village
16. Rio Indio tributary to Upper Rio Chagres, upstream at waterfall
17. Rio Indio tributary to Upper Rio Chagres, upper reaches at former hydro-electric plant
18. Small upstream tributary to Rio Indio tributary to Upper Rio Chagres, in middle reaches
19. Rio Indio tributary to Upper Rio Chagres, in middle reaches
20. Rio Pacora, middle reaches at road crossing
21. Rio Pacora, at San Miguel village
22. Rio Pacora, middle reaches at Juan Gil village
23. Rio Cabobre tributary to Rio Pacora, lower reaches, ~10 m upstream of confluence

24 Rio Pacora at Highway 1, lower reaches ~10 m upstream of Rio Cabobre confluence

Results

Measured field data of temperature, dissolved solid content, acidity, and dissolved oxygen content are reported in Table 2. Water temperatures for the 24 sampling sites ranged from 24.1 to 34.0 ºC. Total dissolved solid contents, measured as specific conductance values, varied from 166 to 392 mS cm^{-2}. All waters were near neutral to slightly alkaline in acidity (pH = 6.9 to 8.4) and well aerated (dissolved oxygen = 81 to 121% of saturation). Water from the main-stem Upper Rio Chagres contained the lowest solute load and that from the Rio Nombre de Dios the highest, with the four rivers sampled at multiple points each exhibiting a general trend of increasing solute load downstream.

Nutrient concentrations at the sampling sites are listed in Table 2 and shown in Fig 3. The dissolved N fraction was dominated by organic species. DON concentrations varied between 6.8 and 108 µmol L^{-1}, while inorganic species (DIN) represented, on average, only about 8% of the dissolved fraction. Overall, observed NO_3^- concentrations were low, with all but two samples having concentrations below 2.6 µmol L^{-1} and 14 of the 24 samples having NO_3^- concentrations below 1.0 µmol L^{-1}. The highest NO_3^- concentration (32.4 µmol L^{-1}) was observed in the middle reaches of the Rio Indio tributary to the Rio Chagres, downstream from a small farm and livestock pasture (PAN- 454). The Rio Indio headwater sample (PAN-455) also has relatively high NO_3^- value (11.4 µmol L^{-1}). This headwater area receives a diffuse input of waste runoff from a large industrial chicken farming and processing operation.

Fig 3. Nutrient concentrations (in µmol L^{-1}) at the stream sampling sites in central Panama.

Average NO_3^- concentration from forested sites is 0.96±0.78 µmol L^{-1}, while the average from farm/pasture sites is 7.64±11.48 µmol L^{-1}. Average DON concentration from forested sites is 28.9±20.8 µmol L^{-1}, while the average from farm/pasture sites is 31.9±34.2 µmol L^{-1}. All NO_2^- concentrations were below our detection limit and only two river sites, PAN-437 (the headwater reaches of the Upper Rio Chagres) and PAN- 459 (the lower reaches of the Rio Pacora), had NH_4^+ concentrations above detection. Concentrations of NO_3^- were below detection at the two Rio Pequini sites (PAN-433 and PAN-432), at the lower Rio Cuango River near the Atlantic coast (PAN-424), at the downstream Upper Rio Chagres site upstream of its discharge point into Lago Alajuela (PAN-435), for three of the four Rio Pacora sites (PAN-460, PAN-461, and PAN-462), and for the Rio Cabobre tributary (PAN-482).

Concentrations of soluble reactive phosphorus (SRP) were also low (overall average of 0.40±0.24 µmol L^{-1}). Average SRP concentration from forested sites is 0.54±0.30 µmol L^{-1}, while the average from farm/pasture sites is 0.34±0.24 µmol L^{-1}. The highest concentrations (0.92 and 0.91 µmol L^{-1}) were observed at two of the pristine rainforest sites, the Rio Pequini upstream site (PAN-433) and Rio Cuango upstream site (PAN-426), respectively, while the lowest concentrations (0.02, 0.08, and 0.09 µmol L^{-1}) were all observed in deforested sites where the land is being used for pasture or subsistence crop (respectively, PAN-482, PAN-455, and PAN-456).

Discussion

Nutrient concentrations in Panama's precipitation have been measured in rainfall between 2009-2011 at an island located just off the coast of southwestern Panama [40]. The volume weighted mean annual concentrations were 5.3, 3.7, 0.5, and 17.4 µmol L^{-1} for NO_3^-, NH_4^+, PO_4^{3-}, and DON, respectively. For a low elevation rainforest in Costa Rica – the neighboring country to the west – the respective weighted mean nutrient concentrations in rainwater are 4.1, 7.1, 6.0 and

<0.3 µmol L^{-1} for NO_3^-, DON, NH_4^+ and SRP [41]. These values are considered to be minimally affected by anthropogenic inputs and representative of uncontaminated precipitation. Other work on nitrate and ammonium deposition in tropical forested sites span a wider range of values with modal concentrations of ~3 and ~4 µmol L^{-1} for NO_3^- and NH_4^+, respectively [40]. The majority of our stream waters in central Panama have mean values for NO_3^- concentrations that are similar to, or less than, these precipitation values, and NH_4^+ concentrations that are less than those observed in both coastal Panama and Costa Rican precipitation. Previous research has clearly demonstrated that a large percentage of the atmospheric input of inorganic species of N from precipitation in Panama is retained within the watersheds, with fully forested catchments retaining the least, only 65-80% [40]. If Panamanian rain forest precipitation has a character similar to that in Costa Rica, almost all the NH_4^+ and much of the NO_3^- from precipitation may be converted to DON as nitrogen is cycled from the rainforest ecosystem to rivers and streams in the watershed.

More recently, the global concentrations of dissolved and total nitrogen and phosphorus have been modeled and mapped for over 1400 rivers using data from 1990 to 2016 [42]. From this study, tropical rivers have median concentrations of 4.68, 7.21, 0.08, 49.55, and 2.26 µmol L^{-1}, for NO_3^-, NH_4^+, SRP, TN, and TP, respectively. These median concentrations are significantly different than those from temperate rivers of North and South America and Europe: NO_3^- values from tropical rivers are 34% lower, NH_4^+ values are 35% lower, and SRP values are 20% lower, while TP values are only 4% lower and TN values from tropical rivers are 93% higher than their temperate counterparts [42]. This extensive dataset also corroborates the assertion that the dissolved nitrogen fraction – and, to some extent, the dissolved phosphorus fraction as well – are dominated by organic forms in tropical rivers.

Little work has been undertaken on the nutrient geochemistry of streams in Panama. The Panama Canal Authority collects monthly samples from eight streams of the Greater Panama Canal Watershed and there are abundant data from Costa Rica and other forested tropical regions for comparison. NO_3^- concentrations in the Chagres and Pequini collected monthly by the Panama Canal Authority have means of 5.7 and 5.0 µmol L^{-1}, respectively [43,44], and both rivers had NO_3^- concentration ranging from 0.7 and 23 µmol L^{-1} between 2003-2019. The coastal streams entering the ocean in southwestern Panama have concentrations of 0.83, 2.45, 3.28, 9.73, and 0.37 µmol L^{-1} for NH_4^+, NO_3^-, DIN, DON, and PO_4^{3-}, respectively.

Analyses from six undisturbed streams of various sizes in Costa Rica [45] have weighted mean concentrations ranging from 8.6 to 21.0 µmol L^{-1} for NO_3^-, 3.6 to 10.0 µmol L^{-1} for DON, and 0.26 to 0.93 µmol L^{-1} for SRP. These NO_3^- values, although in the similar range of our farm/pasture sites, are about 3-fold higher than the concentration range of our forested sites. Regarding DON concentrations, the opposite situation is observed: our values (for both forested and deforested sites) are between 3 and 10 times the concentrations observed in Costa Rica. As for SRP, our values are in a range similar to those from Costa Rica.

Our nutrient values (mean ±SE) for the five central Panama watersheds are 2.64±6.76 µmol L^{-1} NO_3^-, 24.9±22.1 µmol L^{-1} DON, and 0.40±0.25 µmol L^{-1} SRP. These results are much closer to those observed in forested catchments from the Caribbean. Streams from the islands of Dominica, St. Lucia, and St. Vincent [46] have respective NO_3^-, NH_4^+ and SRP concentrations of 5.7, 1.7 and 0.4 µmol L^{-1} (Layou River, Dominica), 4.6, 3.4 and 0.1 µmol L^{-1} (Troumassee River, St. Lucia), and 32.8, 10.0 and 0.2 µmol L^{-1} (Buccament River, St. Vincent). As in our study, higher NO_3^- concentrations in the St. Vincent stream reflect high anthropogenic influence in its catchment, which has a population density 77% higher than the Troumassee River catchment and 181% higher than the Layou River catchment [46].

Our results are also comparable to that of Puerto Rico, another Caribbean Island, where the mean concentrations of nutrients in three tropical montane streams are 0.98 μmol L^{-1} NO_3^-, 0.66 μmol L^{-1} NH_4^+, 9.28 μmol L^{-1} DON, and 0.06 μmol L^{-1} TDP [23]. Like our findings in Panama, the highest nitrate concentrations in this study are associated with locations downstream from a small farm and pasture area. These results suggest that even small-scale farming operations can have a significant impact on the input of dissolved nitrogen into local drainages.

Although the median SRP concentrations in tropical rainforest streams are usually less than 1 μmol L^{-1}, values as high as 9.7 μmol L^{-1} have been recorded at low elevations in pristine streams in Costa Rica [47]. These high SRP values correlate with higher Na^+, Ca^{2+}, Mg^{2+}, Cl^-, and SO_4^{2-} values, and could potentially be derived from the chemical weathering of young basaltic rocks in these watersheds. As noted previously for volcanic terrains [48], P is derived from rock weathering and can be readily depleted in the soils in relatively short periods of geological time, unless it is replaced through continued volcanism or perhaps aeolian dust input. We have argued that, in tectonically active areas where physical weathering continually provides fresh mineral surfaces, P is continuously solubilized for ecosystem use [49]. The Upper Chagres region is such an area in that physical weathering and erosion yields are quite high at 269 ± 63 tons km^{-2} yr^{-1} [50] which, in turn, can lead to high chemical weathering rates [36]. P concentrations in stream sediments of the Upper Chagres watershed range from 5.6 to 18.2 μmol L^{-1} g^{-1}, with mean concentration of 10.3 μmol L^{-1} g^{-1} [51]. These values are much lower than the average value of 93.5 ± 52 μmol L^{-1} g^{-1} P measured in soils within the lower reaches of the Canal Zone drainage [52] and may indicate significant loss of P from both the soil and the stream sediment, as soils are produced and then eroded into the river system. These soils/sediments readily provide SRP to the terrestrial and aquatic ecosystems.

Of the five watersheds sampled, mean annual flow data are available only for the lower Rio Pequini, the Upper Chagres, and its Rio Piedras tributary river, so we can only estimate nutrient yields from these sub-basins. The TDN-yields have been calculated using the Panama Canal Authority monthly data collected from the aforementioned eight watersheds draining into the Panama Canal between 2003-2019, and the US Geological Survey's LOADEST model [43,44]. These and our study have two watersheds in common: the Chagres and the Pequini. Over the 17-year sampling period, the nitrate-N yields in these watersheds varied between 1.55 and 4.49 kg ha^{-1} yr^{-1}. The average yield of the Charges and Pequini in 2007, the year our calculations were made, was 3.83 kg ha^{-1} yr^{-1}, while mean value for all our watersheds was 4.45 kg ha^{-1} yr^{-1}. These values are also comparable to those calculated for Costa Rican tropical rain forest streams (7.47, 2.32 and 0.41 kg ha^{-1} yr^{-1}, respectively) [45], with our Panama sites having lower TDN and SRP yields but higher DON yields. The central Panama TDN yield estimate fits well within the range and the mean (0.57 – 9.40 kg ha^{-1} yr^{-1}; mean of ~3.7 kg ha^{-1} yr^{-1}) determined in other tropical undisturbed watersheds [24], with the DON yield for Panama at the higher end of the range for tropical watersheds.

Compared to temperate regions, our central Panama data more closely resemble concentrations and yields from undisturbed forested watersheds in the Southern Hemisphere (Fig 4). The first-order streams used for comparison (old-growth forests with little or no evidence of human disturbance in southern Chile and Argentina) have extremely low NO_3^- concentrations (mean = 0.14 µmol L^{-1}), very low NH_4^+ (mean = 0.35 µmol L^{-1}), but relatively high DON values of 0.6 – 9.6 µmol L^{-1} [21]. The consequent N yields from these streams are also quite low (0.2 –

3.5 kg ha^{-1} yr^{-1}), with most coming from DON [21]. There has been much debate about the reason for this excess of DON over DIN. Some have suggested that an excess of DON over DIN implies plant uptake of DON as well as DIN and that DON might be colloidal in character [53], whereas others have suggested it to be due to temperature [22]. Our data and some others [23,54-56] strongly indicate that the enhanced DON concentrations and yields are not due solely to differences in mean annual temperature.

Fig 4. Comparison between dissolved nitrogen concentrations in streams from old growth, undisturbed forested watersheds in tropical (this study) and temperate regions of the Northern Hemisphere [16,21] and Southern Hemisphere [21]. SE = Southeastern US (64 streams); W = Western US (90 streams); NE = Northeastern US (102 streams); TN = Great Smoky Mountains, Tennessee, US; PA = Tionessa National Forest, Pennsylvania, US.

Ecosystems vary widely in their capacity to retain N [19], but the lack of NO_3^- loss from these montane forested sites in Panama clearly suggests that they are currently not in a state of N saturation. Furthermore, with the abundance of SRP in these forested watersheds, even though at relatively low concentrations, we suggest the system is more N limited in these higher elevation watersheds. It has been previously suggested that montane tropical forests are N limited whereas lowland ones are P limited [57]. Small-scale spatial analysis indicates that the relationship may be more complex, with the relative amounts of one nutrient to the other being as important as their individual concentrations in soils [52].

In addition to the samples presented in this study, a large number of samples from these Panamanian river systems were analyzed over the period 2005-2009, using ion-chromatographic

(IC) techniques. These samples were also filtered through 0.4µm filters, but not preserved in a way to stabilize their nutrient concentrations, especially at low concentrations. These samples had concentrations about 12 to 15% higher than the samples presented in this study, which were analyzed with a Lachat FIA system. This historical dataset is shown in Table 3. Assuming that the IC data are within 15% of the FIA values for concentrations above 10 µmol L^{-1}, the following observations can be made: the Piedras site at the ACP gauge (site 13) and the Rio Indio site (17) at the former hydroelectric plant, in general, give measurable values of nitrate through our overall sampling period. As noted in Table 2, these are both farmland/pastureland locations, implying that the higher concentrations over time at these sites are directly related to agricultural activities. Sites 2, 3, 9, and 15 also yielded IC-measurable NO_3^- on at least one sampling period (Table 3). These are all locations impacted by anthropogenic activities. The two forested, most pristine locations, sites 10 and 12, yielded the comparatively lowest IC-measurable concentrations. Although this is a limited dataset, it does suggest generally lower background concentrations of inorganic nutrient species, and that anthropogenic activities such as agriculture are the major contributions to fixed nitrogen input into these waters.

Table 3. Concentration of NO_3^- (µmol L^{-1}) measured by a Dionex Ion Chromatography from samples collected at various time at some of the locations listed in Table 2.

Location	Feb 2005	Oct/Nov 2005	Jan 2006	Mar 2006	Jul 2007	Feb/Mar 2008	Mar 2009
2					16.0		
3			246				
9				10.4			
10				10.9			

12					10.7		
13		12.3		20.3	14.2		
15					32		
17	7.0	46		28.3	261	74	44

Conclusion

Our results indicate that the dissolved inorganic nitrogen (DIN) and soluble reactive phosphorus (SRP) concentrations for rivers of central Panama are very low, but that dissolved organic nitrogen (DON) concentrations are relatively high. In this respect, the situation is similar to what has been observed in other pristine forested watersheds in both the tropics and temperate regions of Central and South America and the Caribbean. Based on this information, we conclude that these Panamanian forests are not nitrogen saturated and are sinks for inorganic N. Nutrient yields are similar to those from rainforests in nearby Costa Rica. Others have argued that stream ecosystems play a fundamental functional role in watershed landscapes by documenting that small headwater streams can alter the NO_3^- flux in a temporally dynamic manner [58]. Further work in central Panama will focus on examining seasonal differences in nutrient cycling to refine our estimates of N export and identify any variability of N fluxes between baseflow and stormflow conditions.

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The laboratory work and writing of the paper were conducted at the Ohio State University, which is the located on the ancestral and contemporary territory of the Shawnee, Potawatomi, Delaware, Miami, Peoria, Seneca, Wyandotte, Ojibwe, and Cherokee peoples. We recognize the historical contexts that have affected and continue to affect Indigenous peoples of this land.

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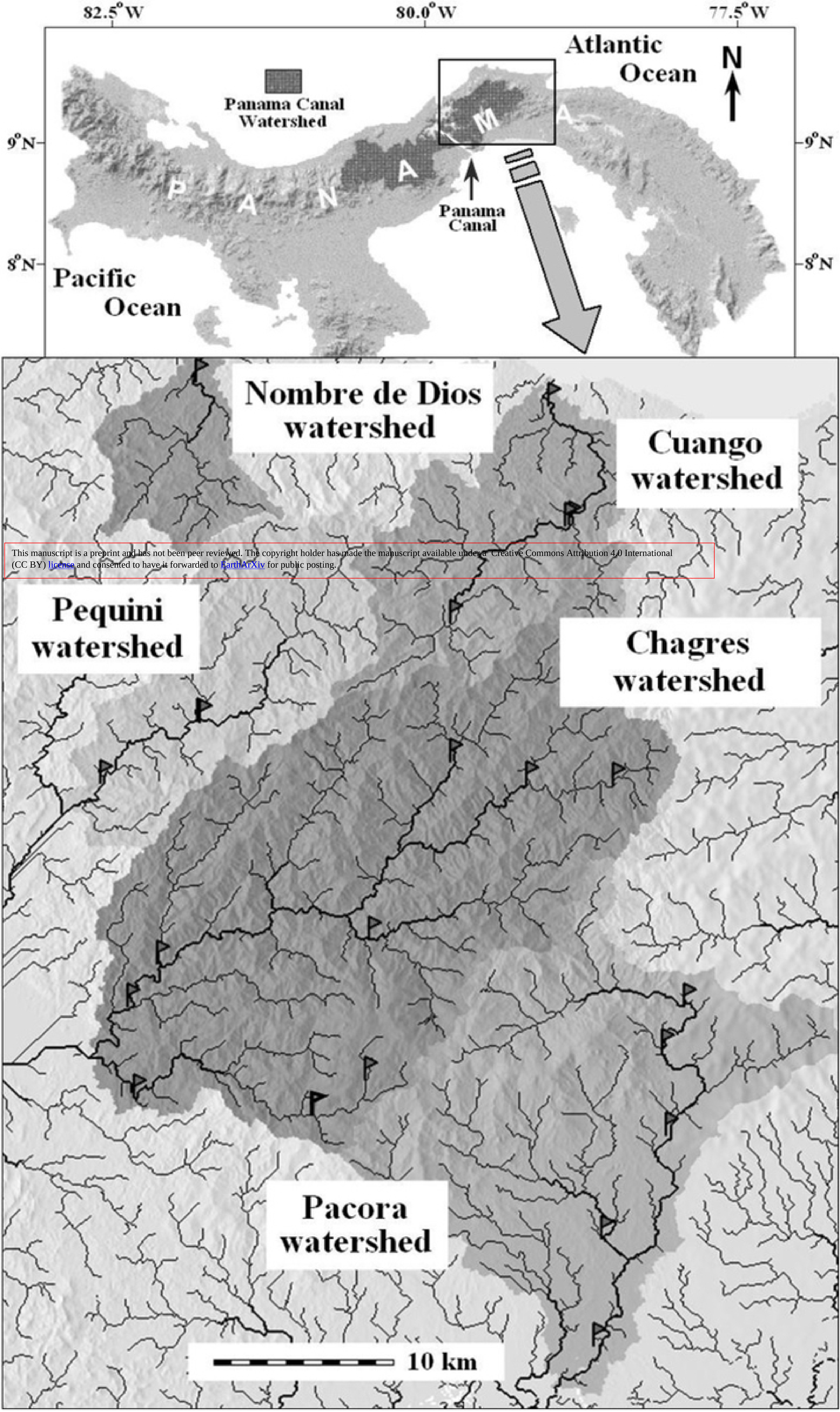
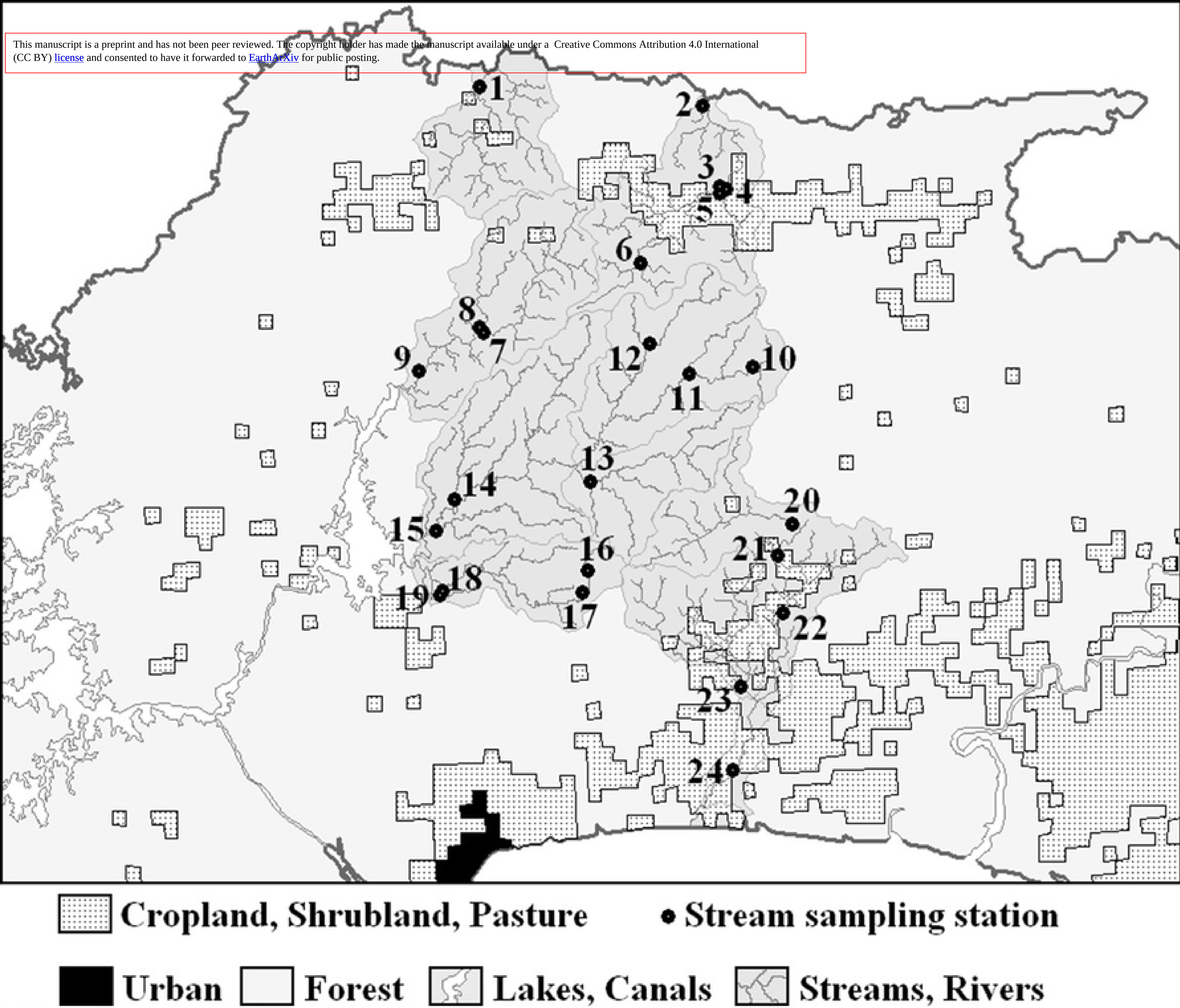

82.5°W
80.0°W
77.5°W
9°N
8°N
Atlantic Ocean
N
Panama Canal Watershed
PANAMA
Panama Canal
Pacific Ocean
Nombre de Dios watershed
Cuango watershed
Pequini watershed
Chagres watershed
Pacora watershed
10 km

Figure 1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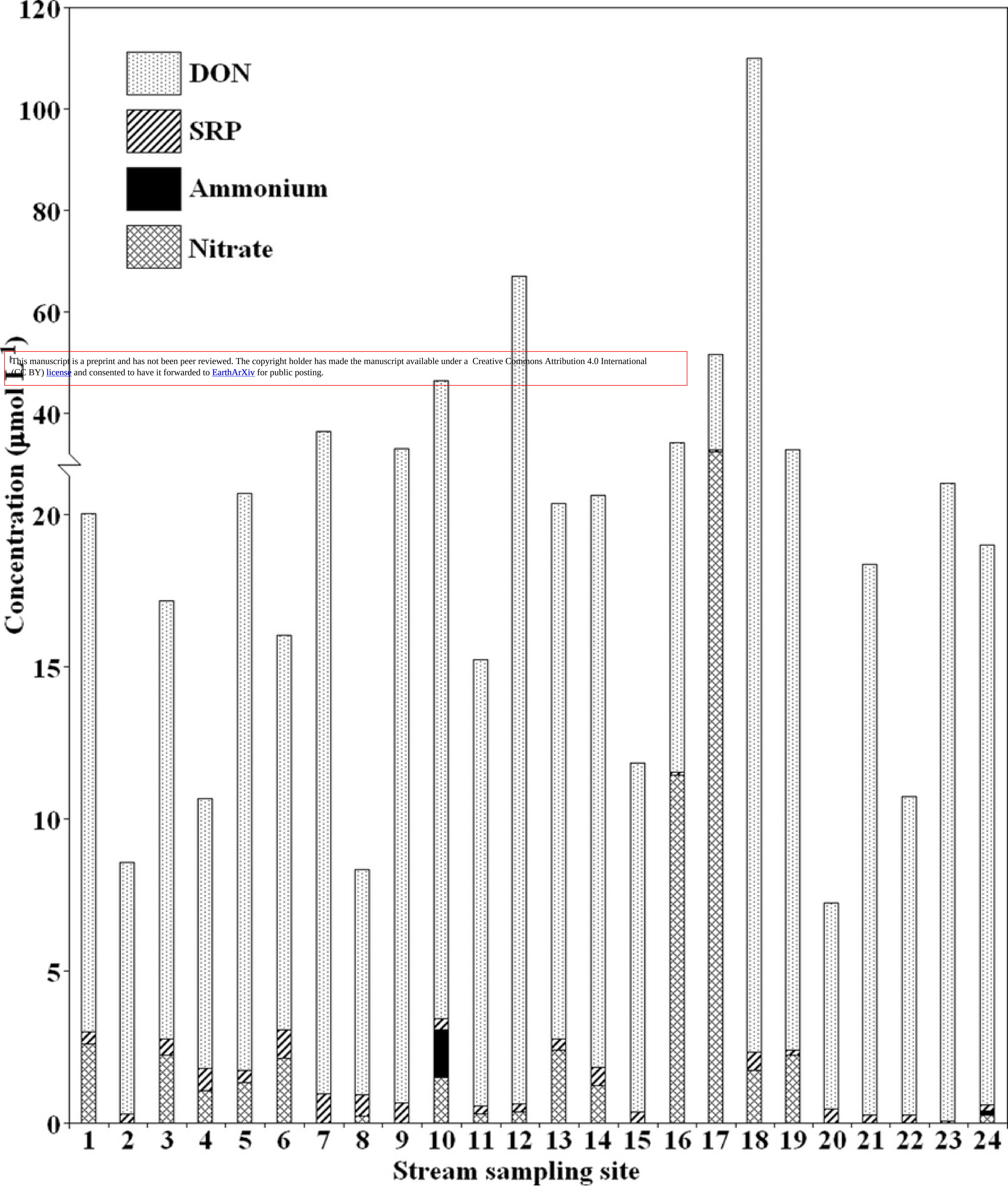
Cropland, Shrubland, Pasture
Stream sampling station
Urban
Forest
Lakes, Canals
Streams, Rivers

Figure 2



120
100
80
60
40
20
15
10
5
0
DON
SRP
Ammonium
Nitrate
Concentration (µmol L-1)
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
Stream sampling site

Figure 3

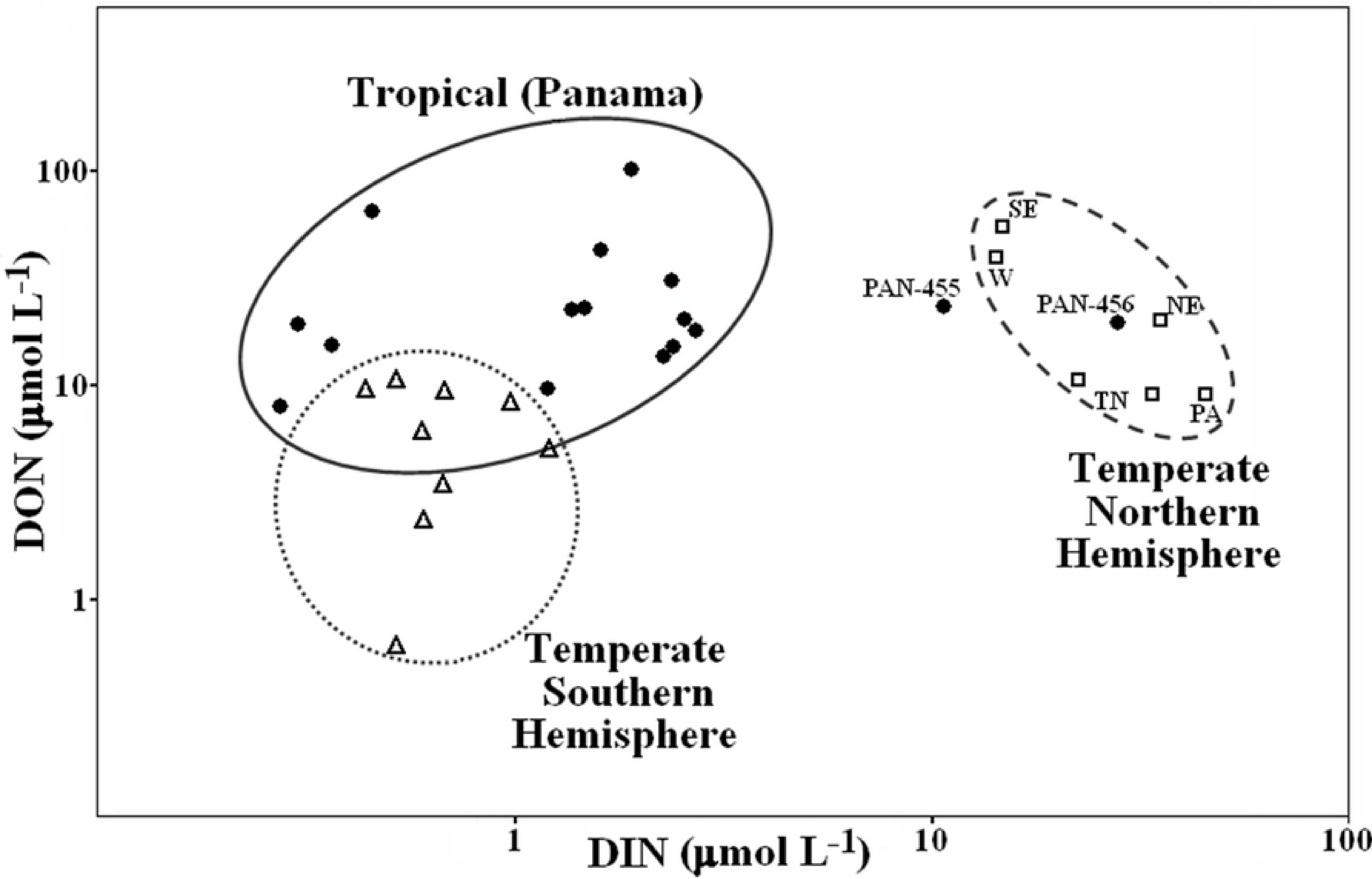

Tropical (Panama)
Temperate Southern Hemisphere
Temperate Northern Hemisphere
PAN-455
PAN-456
SE
W
NE
TN
PA
100
10
1
1
10
100
DON (µmol L^{-1})
DIN (µmol L^{-1})

Figure 4