Changes of water temperature caused by deforestation are of major concern for the future of many species of *Apistogramma* (Regan, 1913) (Teleostei, Perciformes, Cichlidae, Geophaginae)

Veränderungen der Wassertemperatur durch Entwaldung sind für die Zukunft vieler *Apistogramma*-Arten (Regan, 1913) (Teleostei; Perciformes; Cichlidae; Geophaginae) von großer Bedeutung

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Summary: The Iquitos Paleoarch is decisive for the restricted distribution of many *Apistogramma* species in the region. Distinguishing it from large parts of the Amazonian basin, only few seasonal rhythmic inundations trigger frequent isolation events and create a setting favourable for diversification and speciation. Iquitos, probably the fastest expanding city in Amazonia, is located within the Iquitos Paleoarch. Here local resource harvesting frequently leads to small-scale deforestation. Simultaneously, the forest plays a decisive role in the aquatic ecology of streams and ponds by regulating the temperature regime and providing dead plant material, resulting in low pH and conductivity levels, properties typical of blackwater. We conducted field measurements of water parameters in selected areas inhabited by *Apistogramma atahualpa*. Our results show that the temperature regime varies widely in streams and ponds, and temperature increases are especially abrupt at the transition from forested habitats to deforested, open areas. We elaborated how this effect of small-scale deforestation and associated temperature change can impact the breeding biology of *A. atahualpa*. Due to all *Apistogramma* species studied so far exhibiting temperature dependent sex determination (TSD) of offspring, we anticipate changes in population structure following such abrupt alterations in ecological conditions of aquatic habitats. Additional isolation events typical for this region may further impact populations and induce diversification. Our findings highlight the need for more detailed assessments of the impact of deforestation and other ecological alterations on blackwater habitats at small spatial scales, as they can pose a serious threat to many aquatic species.

Key words: Amazonia, Peru, diversification, human Impact, urban sprawl, local adaptation, neotropics; environmental sex determination, biodiversity

Resumen: El Paleoarco de Iquitos juega un papel decisivo en la distribución restringida de varias especies de Apistogramma en la región. A diferencia de otras partes de la bacía Amazónica, acá algunas inundaciones rítmicas estacionales provocan eventos frecuentes de aislamiento, creando condiciones favorables para diversificación y especiación. El hábitat de *Apistogramma atahualpa* se ubica en el Paleoarco de Iquitos y entonces al alcance inmediato de Iquitos, una de las ciudades de mas rápida expansión en la Amazonia,

donde ocurre frecuentemente deforestación de pequeña escala. El bosque tiene un papel importante en la ecología de los arroyos y pequeños lagos donde vive *A. atahualpa*: regula el régimen de temperatura y provee material vegetal en descomposición que facilita bajos niveles de conductividad y pH, típicos de las aguas negras. Hemos medido diferentes parámetros de aguas and áreas selectas dentro de la zona documentada de distribución de *A. atahualpa*. Nuestros resultados muestran que los régimen de temperatura en los arroyos y lagos muestreados varían mucho y los cambios son particularmente abruptos en las zonas de transición entre el bosque y las zonas deforestadas abiertas. Considerando que en todas las especies de *Apistogramma* testeadas hasta ahora, el determinismo del sexo depende de la temperatura (temperature-dependent sex determination, TSD), discutimos los efectos potenciales de la deforestación de pequeña escala y los cambios de temperatura asociada sobre A. atahualpa. Anticipamos cambios en las estructuras poblacionales a consecuencia de la abrupta transición ecológica de los sistemas acuáticos impactados. Eventos de aislamiento adicionales, típicos de esta región, impactaran aun mas las poblaciones e inducirán diversificación. Nuestros resultados ilustran la necesidad de realizar mas estudios de impactos la deforestación y de las otras alteraciones de los hábitats de agua negra de la región, ya que sin destruirlos de manera permanente, ocasionan serias amenazas, y no solamente para las especies de *Apistogramma*.

Palavras claves: Amazonia, diversificación, impacto humano, expansión urbana, adaptación local, neotrópicos, determinación del sexo ambiental, biodiversidad

Zusammenfassung: Der Iquitos-Paläoarch ist entscheidend für die eingeschränkte Verbreitung vieler *Apistogramma*-Arten in der Region. Anders als in großen Teilen des Amazonas-Beckens führen die hier seltenen saisonalen Überschwemmungen zu häufigen Isolationsereignissen und schaffen günstige Bedingungen für Diversifizierung und Artbildungsprozesse. Iquitos, die wohl am schnellsten wachsende Stadt Amazoniens, liegt im Bereich des Iquitos Paläoarch. Hier führt lokale Ressourcennutzung immer häufiger zu kleinräumiger Abholzungen. Gleichzeitig spielt der Wald, insbesondere ein zusammenhängendes Baumkronendach, eine entscheidende Rolle für die aquatischen Ökologie von Bächen und Teichen, die von vielen *Apistogramma*-Arten bewohnt werden: Er reguliert deren Temperaturregime und liefert abgestorbenes Pflanzenmaterial, was – für Schwarzwasser typisch – zu niedrigen pH-Werten bei geringer Leitfähigkeit führt. Wir führten Feldmessungen von Wasserparametern in solchen Gewässerbereichen durch, die von *Apistogramma atahualpa* besiedelt waren. Unsere Ergebnisse zeigen, dass das Temperaturregime in Bächen und Teichen stark variiert und der Temperaturanstieg beim Übergang von bewaldeten Abschnitten zu entwaldeten, offenen Gebieten besonders abrupt ist. Da alle bisher untersuchten *Apistogramma*-Arten eine temperaturabhängige Geschlechtsbestimmung (TSD) von Nachkommen aufweisen, diskutieren wir mögliche Auswirkungen kleinräumiger Entwaldung und damit verbundener Temperaturänderungen auf *A. atahualpa*. Wir erwarten Veränderungen in der Populationsstruktur nach solch abrupten Änderungen der ökologischen Bedingungen in den Gewässern. Zusätzliche für diese Region typische Isolationsereignisse könnten lokale Fischpopulationen beeinträchtigen und zu weiterer Diversifizierung führen. Unsere Ergebnisse unterstreichen die Notwendigkeit einer detaillierteren Bewertung der Auswirkungen von Entwaldung und anderen ökologischen Veränderungen auf Schwarzwasserhabitate in der Region und im Allgemeinen, da sie viele Arten ernsthaft gefährden könnten, in unserem Fall speziell *Apistogramma*-Arten.

Schlüsselwörter: Amazonien, Diversifizierung, Menschlicher Einfluss Zersiedelung; Lokale Anpassung, Neotropen, umweltabhängige Geschlechtsbestimmung, Biodiversität

1. Introduction

Apistogramma (Regan, 1913) is a well-known genus of South American dwarf cichlids (Teleostei: Cichlidae) (summarised in RÖMER 2000, 2006). The total number of *Apistogramma* species is estimated at 250-400 or more valid taxa (READY 2006; RÖMER et al. 2004; RÖMER 2006),

94 have received valid, 16 more doubtful scientific classification and descriptions and many more are already known from the aquarium trade (KOSLOWSKI 2002; RÖMER 2000, 2006; STAECK 2003; STAWIKOWSKI 2005). By the late 1980s KULLANDER (1976, 1979, 1980, 1986) had already described numerous *Apistogramma* species, specifically from within the Iquitos Pa-

leoarch, Loreto and other parts of Peru. More recent investigations in Loreto led to the discovery and description of 17 more species of *Apistogramma* (see tab. 1). Many of the 28 Peruvian *Apistogramma* taxa have a restricted distribution (RÖMER 2006): *Apistogramma cinilabra* is known only from a single small pool (locally referred to as a 'cocha'), which has led to its inclusion in the IUCN Red List as vulnerable (criterion D2) (IUCN 2017); *Apistogramma eremnopyge* is known only from a single short river, the Rio Itaya (READY & KULLANDER 2004); *Apistogramma nijsseni* Kullander, 1979 has been collected only at the type locality and a small river within about 40 km distance (DE RHAM & KULLANDER 1983; RÖMER 1998); sampling sites for the recently described *Apistogramma paulmuelleri* all lie within a couple of hundred metres of each other in the same small brook (locally referred to as a 'quebrada'), in spite of the fact that a much larger area has been sampled, and hence, on the basis of current knowledge, this species falls into the same IUCN category as *A. cinilabra*. Species classified following criterion D2 (tab. 1) have a very limited distribution (less than 20 km² or five or less known locations) which is vulnerable to changes caused either by natural events [e.g. volcanism or tsunamis (HAHN et al. 2013, 2014)] or by human impact, such as deforestation or other resource exploitation characteristic of urban sprawl (see e.g. ALIANZA ARKANA 2014; FINER et al. 2012; IUCN 2013; TRITSCH & LE TOURNEAU 2016; WARD & STANFORD 1989).

Recently LAURANCE et al. (2014) reviewed possible future changes of land use and highlighted agricultural expansion as a major driver for increasing conflicts between human-dominated landscapes and nature conservation, especially in Sub-Saharan Africa and South America. In addition to conversion of forest areas into land for agriculture, changes in water properties, harvesting of wood for fuel, and over-hunting are cited as likely to impact biodiversity, especially given a proximity to major roads and other transportation routes, as well as poverty, exacerbating these effects. Numerous of the newly

Tab. 1: Peruvian species of the genus *Apistogramma*. Known species distribution, status, documented range, and current risk status.
Tab. 1: Peruanische Arten der Gattung *Apistogramma*. Verbreitung, Artstatus, und aktueller Gefährdungsstatus.

species	description	known range of distribution within Peru	state	taxon status	IUCN criteRion
agassizii	(Steindachner, 1875)	widespread, all over lower Ucayali and Amazonian lowland	Loreto	multi-species cluster	unknown/data deficient
aguarico	Römer et al., 2013	uncertain, tributaries of Rio Napo connected to Rio Largatococha	Loreto (?)	valid species	data deficient
alltpahuayo	Römer et al., 2012	local, lower Rio Nanay system	Loreto	valid species	stable
atahualpa	Römer, 1997	local, lower Rio Nanay system	Loreto	valid species	stable
baenschi	Römer et al., 2004	Rio Shanushi, lower Rio Huallaga system	San Martin (Loreto?)	valid species	unknown/data deficient
barlowi	Römer & Hahn, 2008	local, tributaries of Rio Ampiyacu near El Pozo	Loreto	valid species	unknown/data deficient
bitaeniata	Pellegrin, 1936	widespread, northern Ucayali and Amazonian lowland	Loreto	multi-species cluster	unknown/data deficient
cacatuoides	Hoedeman, 1951	widespread, all over Ucayali and Amazonian lowland downstream from Rio Pachitea	Loreto	multi-species cluster ?	unknown/data deficient
cinilabra	Römer et al., 2011	extremly restricted, ony 1 location	Loreto	valid species	vulnerable/D2
cruzi	Kullander, 1986	tributaries of Rio Mazán and Rio Aguarico, Rio Napo system	Loreto	valid species	unknown/data deficient
eremnopyge	Ready & Kullander, 2004	local, endemic to Rio Itaya system	Loreto	valid species	potentially endangered/overfishing
emotus	Kullander, 1981	uncertain, widespread over Rio Ucayali and Amazonian lowland	Loreto	multi-species cluster ?	unknown/data deficient
feconat	Römer et al., 2015	lower Rio Pucacuro, middle of Rio Tigre system	Loreto	valid species	unknown/data deficient
huascar	Römer et al., 2006	middle and upper Rio Tapiche system	Loreto	valid species	unknown/data deficient
luelingi	Kullander, 1976	tributaries of Rio Madre de Dios and Tambopata (Chaparé and Chimoré)	Madre de Dios (Loreto?)	valid species	unknown/data deficient
martini	Römer et al., 2003	restricted, only one location, quebrada in lower Rio Tigre system	Loreto	valid species	potentially endangered/D2
megastoma	Römer et al., 2017	tributaries of the Rio Ucayali near Leticia, Rio Jutai	Loreto	valid species	unknown/data deficient
nijsseni	Kullander, 1979	local, quebrada Carahuayte, tributary of Rio Copál near Genaro Herrera	Loreto	valid species	potentially endangered/D2
norberti	Staeck, 1991	Quebrada Nueva Horizonte, Rio Tahuayo and Rio Carahuayte system	Loreto	valid species	unknown/data deficient
ortegai	Britzke et al., 2014	local, tributaries of Rio Ambiyacu near Pebás	Loreto	multi-species cluster	vulnerable/overfishing
panduro	Römer, 1997	Rio Tahuayo and Rio Tamshiyacu system	Loreto	valid species	unknown/data deficient
pantalone	Römer et al., 2006	several tributaries of lower Rio Tigre system	Loreto	valid species	unknown/data deficient
paulmuelleri	Römer et al., 2013	restricted, tributaries of Rio Ucayali near Nauta	Loreto	valid species	potentially endangered/D2
playayacu	Römer et al., 2011	local, Quebrada Playayacu and tributaries of Rio Napo near Limoncocha	Loreto	valid species	unknown/data deficient
rositae	Römer et al., 2006	uncertain, tributaries of Rio Marañon between Nauta and Baranca	Loreto	valid species	unknown/data deficient
rubrolineata	Hein et al., 2002	local, endemic to Rio Tahuamano system	Madre de Dios	valid species	unknown/data deficient
urteagai	Kullander, 1986	uncertain, Rio Madre de Dios system close to Puerto Maldonado	Madre de Dios	valid species	unknown/data deficient
wolli	Römer et al., 2015	local, small tributaries of Rio Napo near Cabo Pontoya	Loreto	valid species	unknown/data deficient

described species of *Apistogramma* from the department of Loreto in Peru currently face the above-mentioned threats and the entire known global distribution of many of these species is restricted to this area (READY & KULLANDER 2004; RÖMER & HAHN 2008; RÖMER et al. 2003, 2004, 2006, 2011a, b, 2012, 2013, 2015, 2017). This region of north-eastern Peru is bounded by the Peruvian Amazon basin and the Iquitos Paleoarch, a major geological structure in Loreto area that separates the Peruvian Upper Amazon from the Brazilian Solimoes basin to the east (RODDAZ 2005). The paleoarch, with its unique hilly structure, has been identified as a possible driver for the region's high level of diversity in fishes in general and in *Apistogramma* species in particular (cf. RÖMER 2000, 2006), as periods of isolation of water bodies are frequent and of prolonged duration (ORTEGA & VARI 1986; ORTEGA et al. 2011, 2012). Laboratory studies revealed that as a result of temporary isolation, mate preferences in cichlids may change (EN-GELKING et al. 2010), and could trigger speciation within comparatively small geographical areas and within short time (RÖMER & BEISENHERZ 2005; READY et al. 2006; ESTIVALS et al. in print). The specific natural ecological conditions shaping behavioural traits and physiological adaptations in *Apistogramma* still remain largely unknown, as most of the available data comes from laboratory experiments and observations. Only a few studies have been carried out in the field, and these have usually focused on other aspects of biology or, in most cases, on the collection of species for scientific description (ITUASSÙ & CHAO 2006; RODRIGUEZ et al. 2009, 2011; RÖMER 1992, 1993, 1994, 2000a, 2006). Aquarists have added considerably to the knowledge of the preferred living conditions for many *Apistogramma* species, estimating species-specific tolerances for parameters such as acidity, oxygen level, temperature, and conductivity. Yet a systematic and standardised quantification of ecological parameters in the field is lacking. Although some data has been published by MAYLAND & BORK (1997), STAECK (2003), STAECK & LINKE (2006), RÖMER (summarised in 2000, 2006), most of this information, except in the last two publications,

is no more than the result of random sampling at various locations distributed across all three of the major river systems in cis-Andean South America: the Rio Amazon, the Rio Orinoco, and the Rio Paraguay. The study presented here is a start in recording standardised ecological data sets for *Apistogramma* in the field in a systematic way (see RÖMER et al. 2011b, 2012, 2013).

With a focus on *Apistogramma atahualpa* (Fig. S1, S2)*,* a species with a restricted distribution near to a major road and the city of Iquitos, we present a quantification of ecological parameters in the field. We took standardised measurements at 13 sites a few kilometres apart along a dust road southwest of Iquitos, in an attempt to assess (1) the degree to which the species' habitat is affected by deforestation, (2) the effect of the latter on pivotal water parameters and (3), breeding activity of individuals at sites. Furthermore, and based on these findings, we discuss (4) the possible impact of these factors on the species' ecology.

2. Study area

The study area (fig. 1a), around 20 km southwest of Iquitos, is situated in the Iquitos Paleoarch with a maximum altitude above sea level of between 110 and 132 metres. While rhythmic fluctuation of water levels of up to 15 m is not unusual elsewhere in the Amazonian lowland floodplains (RÖMER 2000b, 2006), water levels in this hilly terra firme region are more stable and may vary by no more than 10-20 cm between seasons (RÖMER et al. 2011b). In 2011 and 2012 we sampled *A. atahualpa* at thirteen sites, eleven of which are located within about five kilometres of one another. Only sample sites 12 and 13 are situated further away, about 4 km south and 15 km southwest of the other locations. Eleven of the sample sites are blackwater *quebradas*, and the other two clearwater. The *quebradas* comprising the eleven neighbouring sample sites along the dirt road from Varillal to Llanchama all drain into a tributary of the Rio Nanay, but are not otherwise linked (fig. 1b). All the study sites are located either within the Reserva Nacional
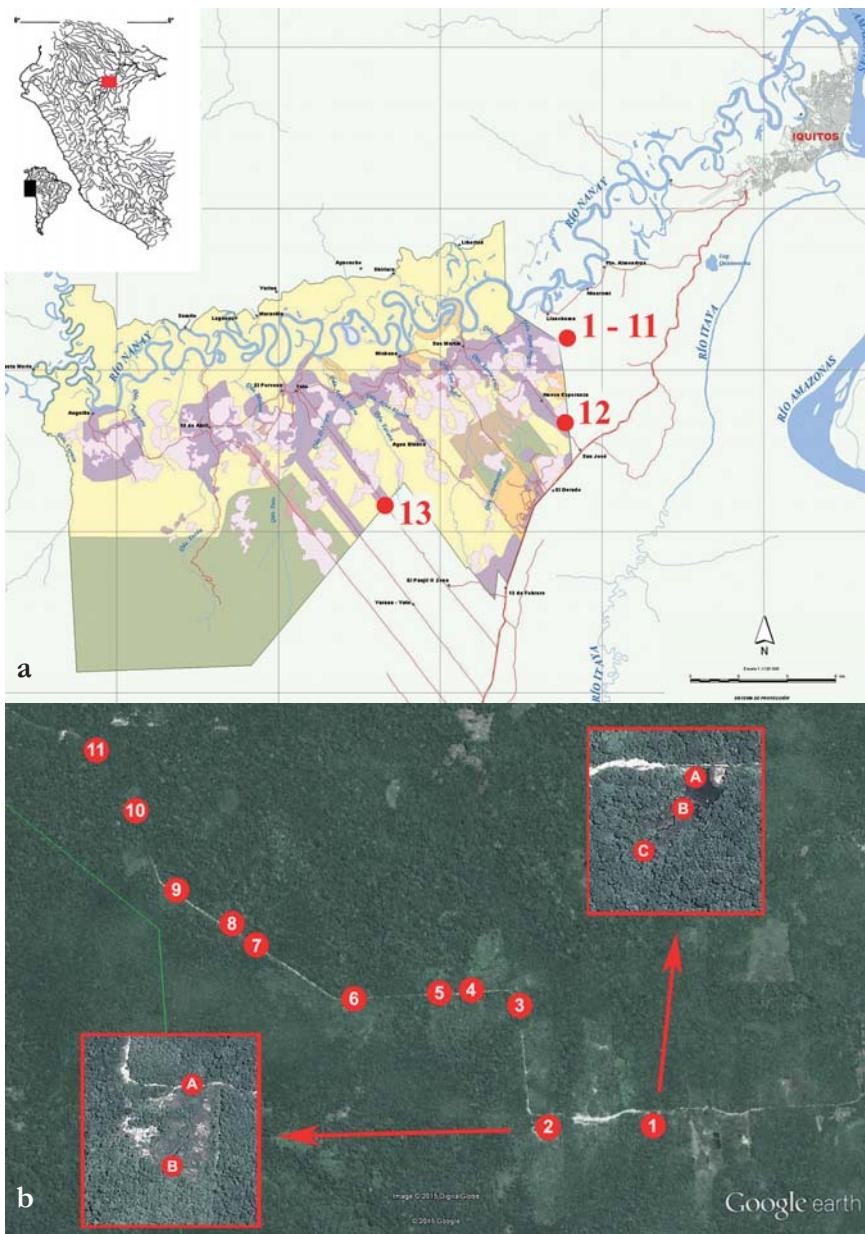
Fig. 1: a Research sites in the Amazon investigated in 2011 and 2012. The 13 sites cover the complete known range of *Apistogramma atahualpa,* located in and around the eastern half of the "Reserva Nacional Allpahuayo Mishana (RNAM)", Loreto, Peru. **b** Research sites 1 to 11, all are located just outside the RNAM close to a dirt road. Border of RNAM indicated by green line. Enlarged sections from sites 1 and 2 show transitions from forested to small scale clear-cut areas as well as measuring spots A to C. Map modified from Google Earth.

Abb. 1: a In den Jahren 2011 und 2012 in Amazonien untersuchte Fundorte. Die 13 Fundorte decken das gesamte bekannte Verbreitungsgebiet von *Apistogramma atahualpa* in und um das „Reserva Nacional Allpahuayo Mishana (RNAM)", Loreto, Peru, ab. **b** Fundorte 1 bis 11 befinden sich außerhalb der Grenze des RNAM (dargestellt durch eine grüne Linie), entlang einer Lehmstraße. Vergrößerte Ausschnitte der Standorte 1 und 2 zeigen den Übergang von Wald hin zu kleinräumiger Abholzung sowie die Messpunkte A-C. Karte modifiziert aus Google Earth.
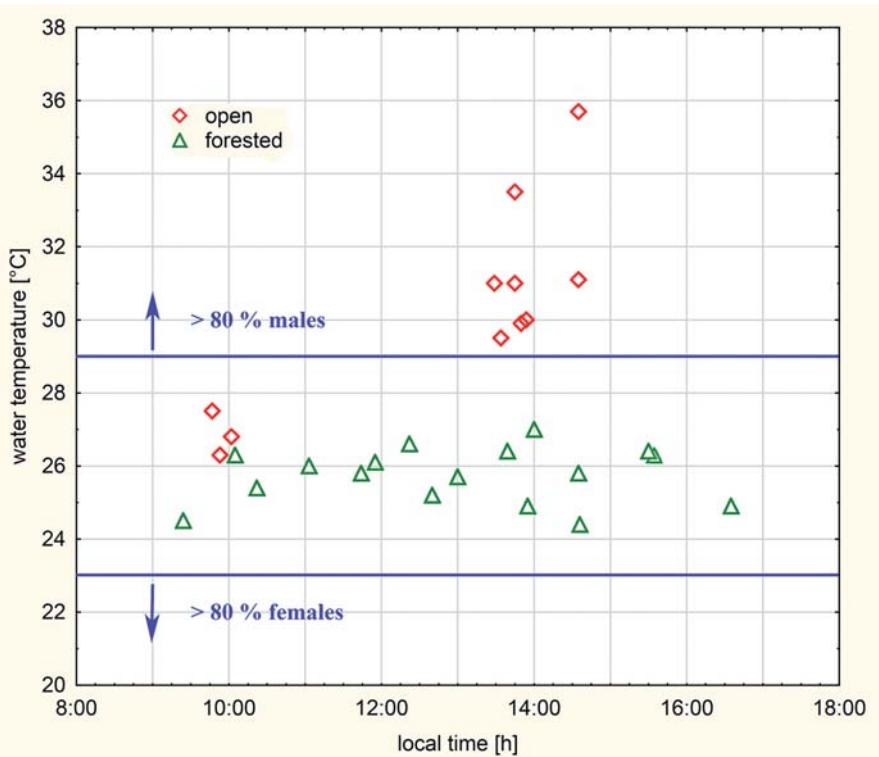
Fig. 2: Temperatures measured in the natural habitat of *Apistogramma atahualpa* during the day. Green triangle: data from waters shaded by the forest canopy; red diamond: data from open sites. Blue lines indicate estimates of reproductive sex ratio (RSR) based on previously published findings of temperature dependent sex determination (TSD) in species of *Apistogramma* (Römer & Beisenherz 1996). Constant temperatures below the lower blue line induce over 80 percent female-biased sex ratios, above the upper blue line over 80 percent male-biased broods (all analysed *Apistogramma* species have TSD).

Abb. 2: Temperaturen des Lebensraum von *Apistogramma atahualpa,* gemessen im Tagesverlauf. Grünes Dreieck: Werte von Messpunkten an durch Wald beschatteten Standorten; roter Rhombus: Werte von Messpunkten in offenen, abgeholzten Standorten mit direkter Sonneneinstrahlung. Blaue Linien zeigen das vermutete reproduktive Geschlechterverhältnisses (RSR) von *Apistogramma atahualpa*, basierend auf veröffentlichten Daten zur temperaturabhängigen Geschlechtsdetermination (TSD) bei nah verwandten *Apistogramma*-Arten (Römer & Beisenherz 1996). Konstante Temperaturen unter der unteren blauen Linie induzieren über 80 % Weibchenanteil, über der oberen blauen Linie über 80 % Männchenanteil in Bruten (alle untersuchten *Apistogramma*-Arten zeigen eine TSD).

Forrestal Allpahuayo Mishana (RNAM) or in the surrounding buffer zone. The distance between the sampling sites and the confluences of the individual *quebradas* with the nameless tributary of the Rio Nanay ranges from 3.1 to 4.3 km. Local fishermen informed us that all the *quebradas* sampled were normally isolated for their entire length even during the rainy season; and inundation only very rarely, if ever, temporarily connects adjacent *quebradas*.

3. Environmental data, behavioural observations and fish sampling

Field work was carried out on the 2nd and 4th of August 2011, as well as on the 23rd and 24th of July 2012. Collection attempts in August 2013 failed as the access road was impassable due to continuous rainfall.

Apistogramma populations at the sites were observed for a period of ca. 20 min to determine

potential breeding activity. To determine the identity of the specimens observed, they were caught using the expertise of local fishermen (using a 1 metre diameter net with 2 mm mashes) and by setting out specially-designed movable traps made of spring wire, expanding to a size of 25 cm x 25 cm x 50 cm, covered by 5 mm nylon mesh and with an entrance at each end. Some of the specimens captured were transported to and housed in the IIAP laboratory for precise identification of live individuals, and some preserved for subsequent taxonomic examination and storage in the collections of the Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, in Lima (MUSM) and the fish collection of the Museum für Tierkunde in Dresden (MTD F): location F1: MTD F 32652 (3 specimens), MUSM 41823 (3); F2: MTD F 32651 (3), MTD F 32691 (2), MUSM 41819 (3), MUSM 42054 (2); F6: MTD F 32692 (2), MUSM 41822 (2); F9: MTD F 32653 (3), MTDF 32690 (4), MUSM 41820 (3), MUSM 42056 (4), MUSM 42053 (1). For locality nomenclature and GPS data see tables S1 & S2. Museum acronyms follow Leviton et al. (1985).

Voucher specimens were preserved following the Low Temperature Preservation Protocol (LTPP) as described in Römer & Hahn (2008). Documentation of specimens and determination of vouchers follows Römer et al. (2011b). Due to time limitations, the fishing procedures were unable to cater for statistical comparison of the numbers of fishes caught at each site, hence catch data provide only qualitative information.

In 2011 one stream was assessed in more detail, with measurements taken over the course of the day, while all other sites were visited at least once a day each in both 2011 and 2012. Habitats were characterised on the basis of the surrounding vegetation, plus the depth, width, and temperature of the water, as well as its pH, conductivity (measured using a WTW multi 3210), and oxygen content (using a Hexis oxymeter YSI 55). Whenever possible, measurements were taken at least twice over the course of the day (between 0900 and 1635 l. t.). If the habitat surrounding a sample site and/or

within the water body itself varied greatly we took additional measurements representative of each of the surrounding habitat types (forested or deforested/open) and/or water body types (cocha or quebrada). Measurements of water parameters were taken only on days where there had been no rain during the preceding 24 hours, in order to minimise the direct influence of rainfall on waterchemistry data.

Photographs were taken to document all the sampling sites using Nikon camera systems (D200 & D300). Data recorded in the field were later back-checked against metadata from these photographs by using the auto-transformation functions of Adobe Photoshop Lightroom 4.4. GPS locality data, including altitude above sea level, were taken for all sampling sites using a GPSmap 76 CSx (Garmin International Inc., Lenexa, USA) and a Solmeta Geotagger N3-A-Kompass (MBK, Hüfingen, Germany) for Nikon cameras.

4. Results

We detected *Apistogramma atahualpa* at eight locations in 2011, and at another five during the 2012 field trip. *A. atahualpa* was the only species found at nearly all of the sampling sites, and was the numerically dominant cichlid species at ten of them; at site 7 only one *A. atahualpa* individual was found amongst more than 50 specimens of *A. allpahuayo*. At site 13 two other species, *A. allpahuayo* and *Apistogramma* cf. *cruzi*, were found together with *A. atahualpa*. Other species collected at the sample sites are listed in table S2. The vegetation surrounding the sampling sites varied significantly from deforested areas to patches of primary forest (tab. S1). Locations 1 and 2 are sited partially in secondary forest as well as in open, deforested terrain, with only grass or bushes, if any plant cover is present at all, next to the water in open areas and hence little or no shade provided by vegetation. Sites 3-7 and 12-13 are set in secondary forest, with tall vegetation shading the water's surface at all times. At sites 4 and 5 logging had taken place between the sampling in 2011 and that in 2012, leading to reduced canopy cover above the

Fig. 3: Site 1B, black-water creek (*quebrada*) in a situation typical for deforested patches in the area around Iquitos, Loreto, Peru. View from site 1B in direction SSW to site 1C (compare Figure 1b). Full sunlight exposure of water surface during the whole day. Structuring elements like leaf litter and driftwood are nearly absent. Submerged plants are missing.

Abb. 3: Fundort 1B, ein Schwarzwasserbach (quebrada) in einem entwaldeten Bereich, wie sie häufig auftreten in der Nähe von Iquitos, Loreto, Peru. Von Punkt 1B aus blickend nach SSW, in Richtung von Punkt 1C (siehe Abbildung 1b). Die Wasseroberfläche ist ganztägig sonnenexponiert. Strukturierende Elemente wie Falllaub und Totholz fehlen fast vollständig. Wasserpflanzen fehlen.
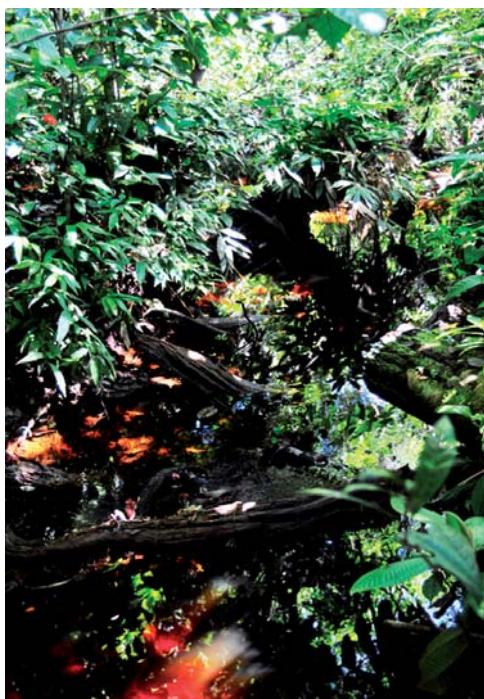
Fig. 4: Site 9, view into SW-direction, a typical small black-water forest creek (*quebrada*) with only sparse sunlight reaching the water surface. Leaf litter and a multitude of driftwood covering the bottom, submerged plants generally missing.
Abb. 4: Fundort 9, Blick in SW-Richtung, ein typischer Schwarzwasser-Waldbach (quebrada), dessen Wasseroberfläche nur spärlich von Sonnenlicht erreicht wird. Falllaub und zahlreiches Totholz bedecken den Boden, Wasserpflanzen fehlen vollständig.

water of the *quebradas* in question. Sites 8-11 are located in either rudiments of primary or long-established secondary forest areas. Overall, temperature readings averaged across the sampling sites were not significantly different between 2011 and 2012 (Welch T-test: t = -0.27, df = 26, p-value = 0.788), ranging from 24.4 °C to 35.7 °C (2011: Ø 27.4 °C ± 3.2 SD; 2012: Ø 27.7 °C ± 2.5). We therefore combined data from both years for further analysis of the effect of reduced canopy cover and the resulting exposure of the habitat.

The pH of the water was the most consistent parameter between sites, with an average range of 3.5-4.6 (average 4.1 ± 0.3 SD) and showed no

difference between the two years (Welch T-test: t = 0.723, df = 23.07, P = 0.477) or habitat type (ANOVA: df = 1, SS = 0.028, F = 0.37, P = 0.55). Conductivity ranged from 154 up to 206 µS/cm (Ø 172 µS/cm ± 14 SD) in 2011, but was lower in 2012 (Welch T-test: t = 12.825, df = 16.44, P < 0.001) and did not change depending on habitat type (ANOVA: df = 1, SS = 475, F = 0.142, P = 0.71). Oxygen levels varied between 1.0 and 9.8 mg/L (Ø 4.1 mg/L ± 2.1 SD) and were recorded only in 2011.

Temperature and oxygen levels within the waterbody were significantly different for forested and open sites (ANOVA: temperature: df = 1, SS = 125.24, F = 34.93, P = 0.001; oxygen: df = 1, SS = 19.66, F = 6.24, P = 0.028; Fig. 2). Oxygen levels were significantly higher in open-habitat locations compared to forest sites (Spearman rank correlation: R = -0.609, P = 0.02). Temperatures within forest quebradas were stable and fairly uniform over the course of the day (Spearman rank correlation: N = 17, coefficient = 0.151, P = 0.621), whilst temperatures in open-area quebradas increased significantly over the same period (Pearson's correlation: N = 11, coefficient = 0.766, P = 0.002) (fig. 4).

A maximum temperature difference of 11.3 °C was measured between all sampling sites. At individual sampling sites a temperature difference of 9.5 °C occurred over the course of the whole day whilst differences during the first half of the day were much lower, reaching only 3 °C.

During all visits to locations site 1 and site 2 several brood caring females of *A. atahualpa* were observed tending eggs, larvae, and small fry. At all study sites individual observations were made of brood care behaviour in females exhibiting yellow brood care coloration, indicating local breeding activity, although no actual offspring were seen in some cases.

5. Discussion

The ecological parameters of *Apistogramma atahualpa* habitats, also the low levels of oxygen, are characteristic of water bodies where rotting plant material covers the bottom (RÖMER 2000a,

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b, 2001, 2006; Römer et al. 2011b, 2012). This is especially the case in forest brooks, creeks, and rivers, where a thick layer of leaf litter, and in many cases driftwood, covers the bottom. Bottoms of lakes and rivers in open habitat frequently lack such a covering of detritus. We assume that lower water levels and episodic rainfall during our 2011 field study may have led to extremely high concentrations of organic material such as dissolved humic acid components in the small forest quebradas, significantly increasing conductivity. Rodrigues (2009, 2011), one of a few researchers to detail habitat parameters in the field, recorded a stable temperature of 24-26 °C throughout the day in a small forest streamlet in Brazilian Central Amazonia, the habitat of *Apistogramma hippolytae* Kullander, 1982, comparable with the average value of 25.7 °C (± 0.5 SD) we found at forested sites for *A. atahualpa*.

Most strikingly, our results demonstrate the pronounced effect of small-scale logging on the temperature regime of forested and open stretches of a quebrada, emphasising the local effects increasing urbanisation and subsequent resource utilisation can have on aquatic habitats. Our data show that deforestation is indeed leading to a strong divergence in water temperature between open and forested sites, affecting the habitat of *A. atahualpa*, and that a significant number of individuals of the species continue to breed on both habitat types. We know from earlier studies that temperature may modify the sex ratio of fish offspring within a brood (literature reviewed in Ospina-Alvarez & Piferrer 2008). In particular species of the genus *Apistogramma* are affected (Römer & Beisenherz 1996): temperature-dependent sex determination (TSD) was found in all 33 species of *Apistogramma* investigated. This study showed that temperature extremes lead to extremely biased sex ratios within any given brood, with 80 percent or more female offspring at low temperatures and 80 percent or more male offspring at high temperatures. These extremely biased sex ratios are seen only at temperatures not typically encountered in the natural, forested and unmodified habitat of *A. atahualpa*. In the light of this,

the strong divergence in temperature we found between adjacent forested and open stretches of habitat is notable. Although *A. atahualpa* was not included in the systematic study of TSD in *Apistogramma* by Römer & Beisenherz (1996), that study demonstrated that rising temperature is strongly correlated with increased frequency of male offspring in some of its closest relatives, namely *Apistogramma nijsseni* Kullander, 1979 (Kullander 1979) and *Apistogramma norberti* Staeck, 1991 (Staeck 1991), both members of the same *A. steindachneri* phylogenetic lineage (nomenclature following Römer 2006), representing clade A2 in the genetic phylogeny presented by Tougard et al. (2017). Furthermore, male-biased sex ratios at increased temperatures recorded by local commercial breeders in Iquitos, including for *A. atahualpa* (C. Chiquipiondo pers. comm. 2011), and as yet unpublished laboratory data from ourselves, corroborate the probability that assumptions regarding TSD are also valid for *A. atahualpa*. Preliminary laboratory experiments on TSD carried out on *A. atahualpa* show high rates of male offspring at high (29 °C) and low rates of males at low temperatures (23 °C). As predicted, further data needs to be collected for a statistical analysis as defined in Römer & Beisenherz (1996). Under the assumption that (1) TSD generally applies to the breeding biology of *A. atahualpa*, and its effect on the sex ratio of this species' offspring is similar to that observed in its closest relatives, *A. nijsseni* and *A. norberti* (Römer & Beisenherz 1996; preliminary data), and that (2) the rate of deforestation of habitats will not decline but most likely increase in the near future (Laurance et al. 2014), we argue that the population demography of *A. atahualpa* will become highly dynamic and that populations will likely be fragmented, as discussed below.

5.1. TSD and RSR

Römer & Beisenherz (1996) have shown that the reproductive sex ratio (RSR) of offspring in the Peruvian *Apistogramma nijsseni*, a close relative of *Apistogramma atahualpa*, is determined by temperature following fertilisation, ranging from about 20 percent males at a constant tempera-

ture of 23 °C to 75-95 percent males at a constant 29 °C, co-varying with the acidity of the water (pH). The pH values recorded at our open water sampling sites (like in location 1A in Table S1) might even lead to extreme sex ratios with about 95 percent male offspring, comparable to the laboratory data for *Apistogramma nijsseni* (Römer & Beisenherz 1996). In forested sampling sites, with average temperatures of about 26 °C, more balanced sex ratios can be expected for *A. atahualpa* (Römer & Beisenherz 1996). These authors also demonstrated that temperature affects sex ratios cumulatively. During a period of 34 days temperature was measured once per hour, and the resulting data summated to produce a cumulative temperature value (CTV) which correlated with the observed sex ratios within broods reared during the experiments. Broods of *Apistogramma trifasciata* (Eigenmann & Kennedy, 1903) that had experienced a CTV of 18,768 °C consisted of about 80 percent females, a CTV of 21,216 °C resulted in a balance between numbers of the two sexes, and a CTV of 23,664 °C led to more than 80 percent males (Römer & Beisenherz 1996). Based on a linear equation derived from these data, we have extrapolated from our temperature data measured in the field for a comparable period (34 days). To do so we conservatively estimated a temperature profile over the course of the day in the habitats of *A. atahualpa* from our data (Figure 4, Table S1), which produced an average daily temperature of 27.1 °C. This in turn produced a CTV of 22,134 °C putatively experienced by broods of *A. atahualpa* in open-habitat sites, resulting in an unbalanced operational sex ratio (OSR) with 62.2 percent males. The field data presented here, combined with laboratory data on TSD, highlight the potential effect small scale deforestation may have on local changes in OSR.

5.2. Temperature patterns, metabolic rate & changing habitats of *Apistogramma*

In the long term and in consideration of predicted population growth of the city of Iquitos and associated surge of local deforestation, open stretches of quebradas, where logging reduces canopy cover and increases temperature, will become more frequent throughout the distribution of many *Apistogramma* species. Next to potentially biasing OSR, rising temperatures in open habitats likely also result in a reduction of biological fitness at the population level (cf. Römer 1998, 2001), as the biological fitness of breeding individuals may diminish for two reasons. Firstly, high temperatures may lead to massive physiological stress and huge changes in the behaviour of *Apistogramma* (Eckert-Hetzel et al. 2001). In camera-monitored *Apistogramma* males, high temperature drastically increased energy expenditure for their basic metabolic rate, which resulted in significantly higher aggression against all other fish including conspecific females. In the wild this might significantly reduce the ability of females to practice brood care successfully in open habitat, and hence limit the survival of offspring. Secondly, permanently high temperatures induce permanent compensatory food consumption due to increasing metabolic rates, a behaviour that has previously been observed but was estimated to only be temporarily sustainable until temperatures reach 30 °C (Römer 1998, 2001). While *Apistogramma* females have been observed in the laboratory to exhibit reduced activity levels at extremely high temperatures, indicating a female survival strategy involving a reduction in total energy expenditure (Eckert-Hetzel et al. 2001; Römer 2001), overall, higher temperatures lead to significantly increased mortality, especially in offspring and eventually females (Römer 1998, 2001).

In addition to these effects on biological fitness of *Apistogramma* species, open stretches might also become barriers to movement as they increase in length fragmenting local populations genetically. Open stretches have a twofold effect on the water body, particularly in the dry season: (i) absence of adjacent vegetation can cause localised seasonal erosion, leading to deposition of sediments that create isolated segments within a *quebrada*, and (ii), in the long term, reduced leaf-litter deposits change the characteristics of the water body, chemically transforming it into less suitable habitat for *Apistogramma*

species. In the latter case, reductions in leaf-litter deposits causes a loss of both hiding places and food source, as most *Apistogramma* species pick up Aufwuchs growing on the surface of dead plant matter. As for the former, we have documented the effects of silt deposition from erosion at sampling site 2 (compare fig. S5A) and observed them in the habitats of several other *Apistogramma* species in the proximity of Iquitos and Pebas (RÖMER, unpublished data). Our current field observations show that *A. atahualpa* does not avoid open stretches of quebradas; on the contrary, females were observed defending broods in these stretches. Assuming a similar territory size for female *A. atahualpa* as is known from other *Apistogramma* species, namely 30-250 cm in diameter (RODRIGUES et al. 2011; RÖMER 1992, 1996, 2000, 2006), then only few territories will lie in the transition zones between habitat types, and the territories of most females will lie either in the cooler, forested habitats or in the warmer, open stretches. Although adaptation to local temperature patterns of different habitat types can be expected, the effects of disparate temperatures at population level remain unknown. The degree of interbreeding between open and forested populations will be decisive for population-level adaptations. Specialisation for and adaptation to specific habitat types and conditions may occur and stabilise at population level. But, as shown for localized bird populations, other still unknown factors resulting from changing conditions may negate the positive effects of these processes (DIAS & BLONDEL 1996).

5.3. Conclusion

The Peruvian Amazon in the vicinity of the city of Iquitos may serve as an example demonstrating how deforestation is affecting aquatic organisms by destabilising aquatic temperature patterns. In order to survive, *Apistogramma atahualpa* and its congeners will in all probability need to adapt to habitat changes, which are characterised by more frequent temperature isolation of segments of quebradas, as well as an increasing number of transition zones between these segments with unique and rapidly changing temperature patterns.

A more thorough investigation of urban expansion into the rainforest of the Iquitos Paleoarch, and its impact on the ecology of *Apistogramma* species, is overdue and urgently required. Due to the restricted distribution of *A. atahualpa* and most of its congeners in proximity of Iquitos, habitats at severe risk of being impacted by resource harvesting, threatening the global distribution of some *Apistogramma* species, such as in the cases of *A. atahualpa* or *A. cinilabra*. Non-selective, lethal fishing techniques have not been observed in the habitat of *A. atahualpa*, but deforestation has significantly impacted sites there in the past few years. Our second field trip in 2012 showed that deforestation had continued unabated during the period between the two sessions of sampling, despite most of the sampling sites for *A. atahualpa* being situated in the Reserva Nacional Allpahuayo Mishana, a protected forest reserve, or its adjacent buffer zone. Given the socio-economic pressures created by rapidly growing human populations in Neotropical cities such as Iquitos, threats are bound to become more frequent. This highlights how real the danger of extinction may be, especially given the limited distributions of many species of *Apistogramma*.

Acknowledgements

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Supplementary information

Tab. S1: Ecological data collected at 13 different sampling sites for *Apistogramma atahualpa* south-west of Iquitos, Department of Loreto, Peru. * = data taken at same site, but in different depth of water; ** = no data recorded; *** = site within protected area; # = site located in a different quebrada entering the Rio Nanay about 15 km upriver from Llanchama; bw = blackwater; cw = clearwater; f = forest habitat; o = open habitat.
Tab. S1: Ökologische Daten von 13 Fundorten von *Apistogramma atahualpa* südwestlich von Iquitos Department of Loreto, Peru. * = Daten vom gleichen Messpunkt, aber aus anderer Wassertiefe, ** = keine Daten erfasst; *** = Fundort liegt innerhalb Schutzgebiet: # = Fundort liegt in einer anderen quebrada, etwa 15 km flussaufwärts von Llanchama; bw = Schwarzwasser; cw = Klarwasser; f = bewaldetes Habitat; o = offenes Habitat.

Site No.	field station	date local time	altitude [m.a.0]	T [°C]	pH	O2 [mg/L]	conductivity [μS / cm]	water type	Habitat
1A	F1-P-2011-R a	2011.08.02 09:47	110	27.5	4.5	4.17	154	obw	open cocha, shore
1A	F1-P-2011-R a*	2011.08.02 09:53	110	26.3	4.6	4.40	154	obw	
1A	F1-P-2011-R a*	2011.08.02 14:35	110	35.7	4.4	9.77	157	obw	open cocha, deeper water
1A	F1-P-2011-R a*	2012.07.23 13:50	112	29.9	4.4	**	29	obw	
1B	F1-P-2011-R b	2011.08.02 10:02	110	26.8	3.5	3.68	206	obw	
1B	F1-P-2011-R b	2011.08.02 14:35	110	31.1	4.2	4.10	167	obw	open quebrada
1B	F1-P-2011-R b	2012.07.23 13:54	112	30.0	4.0	**	40	obw	
1C	F1-P-2011-R c	2011.08.02 10:22	110	25.4	4.2	2.90	162	fbw	
1C	F1-P-2011-R c	2011.08.02 14:35	110	25.8	4.2	3.27	164	fbw	forest quebrada
1C	F1-P-2011-R c	2012.07.23 14:00	107	27.0	4.4	**	44	fbw	
2A	F2-P-2011-R a	2011.08.02 13:45	116	33.5	4.1	6.51	179	obw	open quebrada
2A	F2-P-2011-R a	2012.07.23 13:45	114	31.0	3.9	**	76	obw	
2B	F2-P-2011-R b	2011.08.02 13:55	116	24.9	4.0	2.08	182	fbw	forest quebrada
3	F3-P-2011-R	2011.08.02 13:00	124	25.7	4.0	3.56	178	fbw	forest quebrada
3	F3-P-2011-R	2012.07.23 13:39	111	26.4	3.8	**	76	fbw	
4	F4-P-2011-R	2011.08.02 12:40	121	25.2	4.1	0.99	172	obw	open forest cocha
4	F4-P-2011-R	2012.07.23 13:34	117	29.5	3.9	**	65	obw	
5	F5-P-2011-R	2011.08.02 11:55	122	26.1	4.0	4.95	178	obw	open forest quebrada with cocha
5	F5-P-2011-R	2012.07.23 13:29	114	31.0	4.0	**	78	obw	
6	F6-P-2011-R	2011.08.02 10:05	118	26.3	4.0	2.57	180	fbw/cw	forest quebrada
7	F7-P-2011-R	2011.08.04 15:30	132	26.4	4.1	4.03	173	fbw/cw	forest quebrada with swampy cocha
8	F30-P-2012-R	2012.07.23 09:24	99	24.5	4.6	**	35	fbw	small forest quebrada ***
9	F31-P-2012-R	2012.07.23 11:03	111	26.0	3.8	**	84	fbw	small forest quebrada ***
10	F32-P-2012-R	2012.07.23 11:44	125	25.8	3.8	**	86	fbw	small forest quebrada ***
11	F33-P-2011-R	2012.07.23 12:22	124	26.6	3.8	**	80	fbw	small forest quebrada ***
12	F9-P-2011-R	2011.08.04 15:30	132	26.4	4.1	4.3	173	fbw	shallow quebrada pool ***
12	F9-P-2011-R	2011.08.04 16:35	132	24.9	3.6	4.3	176	fbw	shallow quebrada pool ***
13	F37-P-2012-R[#]	2012.07.24 14:36	121	24.4	4.2	**	114	fbw	wide forest quebrada ***

Tab. S2: Species collected together with *Apistogramma atahualpa* at 13 sites in and around the Reserva Forrestal Allpahuayo Mishana. * = data sets incomplete, as non-cichlids have not been determined at the time of submission of this manuscript; several other species have been collected from these sites. ** = phenotypic appearance, but final determination of species still in progress. *** = juvenile, species cannot be determined using conventional methods, DNA analysis in preparation.

Tab. S2: Arten, die zusammen mit *Apistogramma atahualpa* an 13 Fundorten in und um das Reserva Forrestal Allpahuayo Mishana gesammelt wurden. * Datensatz unvollständig, da die Nicht-Cichliden zum Zeitpunkt der Manuskripabgabe noch nicht bestimmt waren; zahlreiche andere Arten wurden an diesen Fundorten gesammelt. ** = phänotypisches Erscheinungsbild, aber abschließende Artbestimmung noch nicht abgeschlossen. *** = juvenil, Art kann mit konventionellen Methoden nicht bestimmt werden, DNA-Analysen sind in Vorbereitung.

site	number in this study	Sample sites												
		1	2	3	4	5	6	7	8	9	10	11	12	13
	original field number	F1-P-2011-R	F2-P-2011-R	F3-P-2011-R	F4-P-2011-R	F5-P-2011-R	F6-P-2011-R	F7-P-2011_R	F30-P-2012-R	F31-P-2012-R	F32-P-2012-R	F33-P-2012-R	F9-P-2012-R	F37-P-2012-R
genus	species													
									*	*	*	*		*
Apistogramma	*allpahuayo*							x						x
	atahualpa	x	x	x	x	x	x	x	x	x	x	x	x	x
	sp. *cf. cruzi* **													x
Aequidens	sp. "Bujurqui rocho" **	x	x				x				x		x	
Crenicichla	sp. (*saxatilis* group) ***		x											
Laetacara	*flavilabris*							x						
Hoplias	sp. (*cf. malabaricus*) **	x	x				x	x	x				x	
Hoplerythrinus	Indet.												x	
Crenuchus	*spilurus*	x	x	x	x	x	x	x	x				x	
Hemigrammus	sp.								x	x				
Hyphessobrycon	sp. 1	x												
	sp. 2						x							
Copella	sp.								x					
Pyrrhulina	sp.1	x	x						x	x	x	x		
	sp. 2						x							
Haplosternum	sp.						x	x						
Atinga	sp.						x							
Gymnotid	sp.1 (transverse bars)		x	x			x	x	x					
	sp. 2 (brown)								x					
Rivulus	sp. 1	x		x			x							
	sp. 3					x								

Fig. S1: *Apistogramma atahualpa* from sample site F1. **A** Adult male. **B** Adult female in brooding coloration. Picture taken in captivity. **C** Research site 1A: Open pool in deforested area (F1a-P-2011-R).
Abb. S1: *Apistogramma atahualpa* vom Fangplatz F1. **A** Adultes Männchen. **B** Adultes Weibchen in Brutpflegefärbung. Aquarienfotos. **C** Fundort 1A: Offene Teichfläche in entwaldetem Gebiet (F1a-P-2011-R).
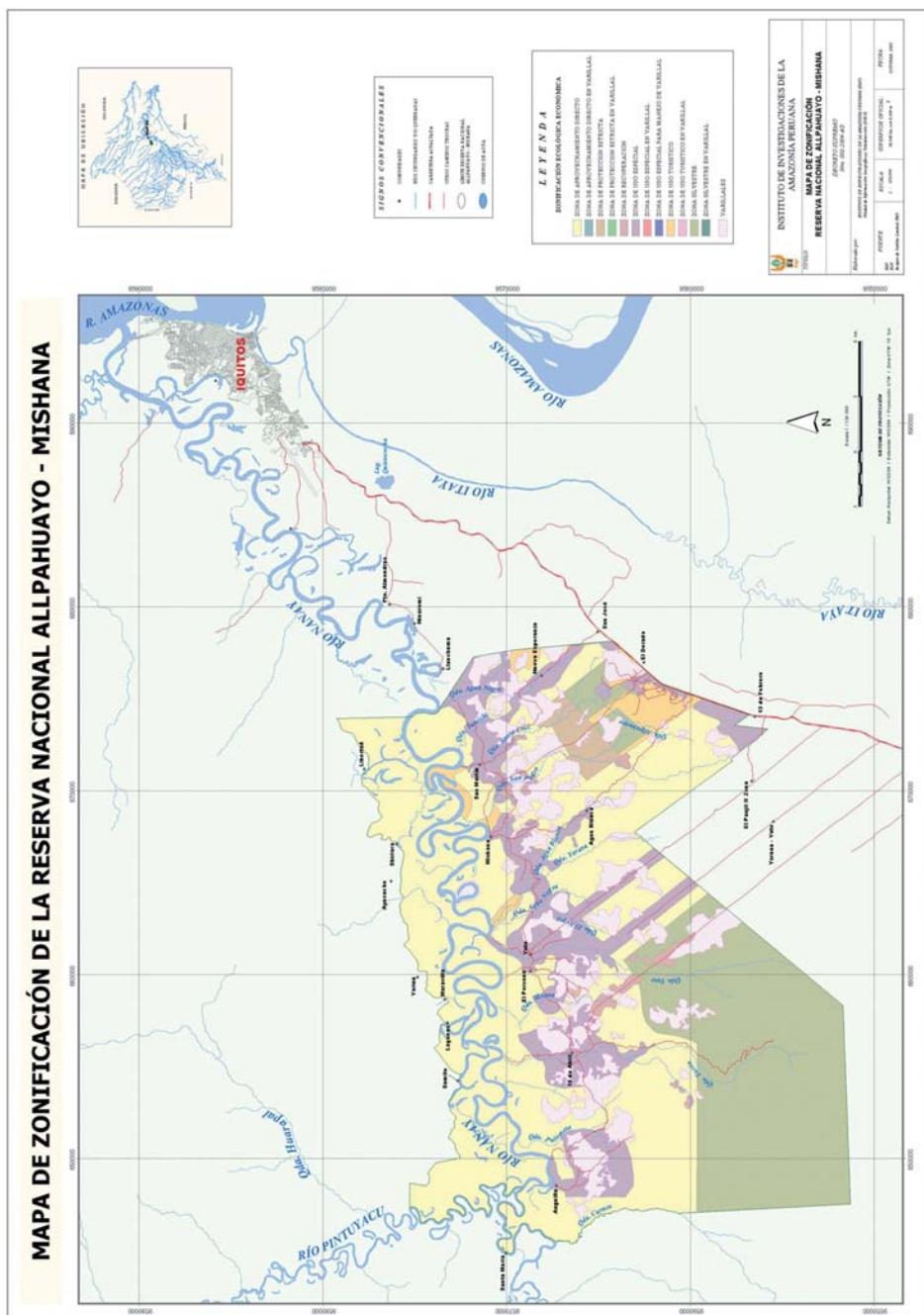
Fig. S2: Map showing different zones of land-use and protection station within the "Reserva Nacional Allpahuayo-Mishana (RNAM)", Loreto, Peru. Courtesy of the INSTITUTO DE INVESTIGACIONES DE LA AMAZONÍA PERUANA (IIAP).

Abb. S2: Karte der Zonierung der Landnutzung und Schutzstationen innerhalb des „Reserva Forrestal Allpahuayo Mishana (RNAM)", Loreto, Peru. Überlassen durch das INSTITUTO DE INVESTIGACIONES DE LA AMAZONÍA PERUANA (IIAP).

Fig. S3: A. Research site 1B: View from site closer to site 1C compared to figure 3 in main text (F1b-P-2011-R). **B**. Research site 1C: Brook at transition from (probably secondary) forest to deforested area (F1c-P-2011-R). **C**. Research site 1C: Close-up of brook at the transition zone (F1c-P-2011-R). **D**. Research site 2: Small brook (quebrada) (F2-P-2011-R).

Abb. S3: A. Fundort 1B: Blick von im Vergleich zu Abb. 3 im Haupttext zu Fundpunkt 1C näherem Standort (F1b-P-2011-R). **B**. Fundort 1C: Bach am Übergang vom (wahrscheinlich) Sekundärwald zur entwaldeten Fläche (F1c-P-2011-R). **C**. Fundort 1C: Nahaufnahme des Baches an der Übergangszone (F1c-P-2011-R). **D**. Fundort 2: kleiner Waldbach (F2-P-2011-R).

Fig. S4: A. Research site 3: Forest quebrada (F3-P-2011-R). **B**. Research site 5: Open forest quebrada with cocha (F5-P-2011-30 R). **C**. Research site 4: Open forest cocha (F4-P-2011-R).

Abb. S4: A. Fundort 3: Waldbach (F3-P-2011-R). **B**. Fundort 5: Bach in offenem Wald mit Teich-Erweiterung (F5-P-2011-R). 32 **C**. Fundort 4: Teich in offenem Wald (F4-P-2011-R).

Fig. S5: Research sites. **A** Research site 6: Forest quebrada (F6-P-2011-R). **B** Research site 7: Forest quebrada with swampy cocha (F7-P-2011-R). **C** Research site 8: Small forest quebrada (F30-P-2012-R). **D** Research site 9: Small forest quebrada (F31-P-2012-R). Aspect about 100 m south of sample site 9 within the same quebrade as shown on figure 4 in the main text.

Abb. S5: Fundorte. **A** Fundort 6: Waldbach (F6-P-2011-R). **B** Fundort 7: Waldbach mit sumpfartiger Teicherweiterung (F7-P-2011-R). **C** Fundort 8: Kleiner Waldbach (F30-P-2012-R). **D** Fundort 9: Kleiner Waldbach (F31-P-2012-R). Aspekt etwa 100 m südlich von Fundort 9 innerhalb des gleichen Baches wie in Abb. 4 im Haupttext.

Fig. S6: Research sites. **A** Research site 10: Small forest quebrada (F32-P-2012-R). **B** Research site 11: Small forest quebrada (F33-P-2012-R). **C** Research site 12: Shallow quebrada pool (F9-P-2011-R). **D** Research site 13: Wide forest quebrada (F37-P-2012-R).

Abb. S6: Fundorte. **A** Fundort 10: Kleiner Waldbach (F32-P-2012-R). **B** Fundort 11: Kleiner Waldbach (F33-P-2012-R). **C** Fundort 12: Flacher teichartige Bacherweiterung (F9-P-2011-R). **D** Fundort 13: Breiter Waldbach (F37-P-2012-R).