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THE AVIFAUNA OF THE RÍO TIGRE BASIN, NORTHERN PERÚ

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ABSTRACT · The Tigre river basin in the Amazonian lowlands of northern Perú harbors a hyperdiverse avifauna that remains under-surveyed and poorly known. We conducted the first comprehensive ornithological inventory of the basin. Observational fieldwork at 42 sites spread across the Peruvian portion of the basin resulted in a bird list of 584 species, reflecting several noteworthy patterns in the avian biogeography of northern Perú. These patterns include the distribution of several species that specialize on nutrient-poor habitats, such as weathered clay terraces and peatlands. Peatland forests are especially poorly studied in Perú and represent a novel habitat association for these species. We also report on the presence of a suite of species with primarily montane distributions that occur in low density across the Amazonian lowlands and in the study area. Current conservation challenges in the Tigre basin include deforestation and pollution associated with hydrocarbons extraction and infrastructure projects.

RESUMEN · Avifauna de la cuenca del río Tigre, Perú
La cuenca del río Tigre en las tierras bajas del norte de la Amazonía peruana tiene una avifauna súper diversa que sin embargo es muy poco conocida. Realizamos el primer inventario ornitológico de la cuenca. Observaciones de aves en 42 sitios resultaron en una lista de 584 especies de aves registradas en la zona de estudio. Un grupo particular de esta comunidad de aves son aquellas que se distribuyen en los bosques arcillosos pobres a lo largo del río Pucacuro y sobre bosques de turberas en el bajo río Tigre. Reportamos especies generalmente consideradas como especies facultativas u obligadas de hábitats de suelos de arena blanca en la zona de estudio. Los bosques sobre turberas aún se encuentran muy poco estudiados por los ornitólogos y representan un nuevo espacio para las especies que por lo general encontramos sobre los bosques de arena blanca. Adicionalmente reportamos un grupo de especies que generalmente son comunes en el pie de monte andino, pero que ocurren en bajas densidades en el área de estudio. Las amenazas actuales a la conservación de la zona incluyen la deforestación y la contaminación asociada con actividades petroleras y proyectos de infraestructura.

KEY WORDS: Amazon · Avian biogeography · Bird list · Loreto · Peatlands · Perú · White-sand forest

INTRODUCTION

The lowland rainforests of the Loreto region, Perú harbor exceptional biodiversity, with an estimated avifauna of 700–900 species (Pitman et al. 2013, Wiley et al. 2015). To date, biological investigation has focused primarily on accessible areas near Iquitos and along the Amazonas river (Pitman et al. 2013). Large portions of lowland Loreto remain poorly surveyed, especially the north-central region of the Tigre, Pastaza, and Morona river basins. These basins are within the Napo ecoregion, which is exceptional for its avian richness (Dinerstein 1995, Rodríguez & Young 2000).

The Tigre basin, in particular, has received little ornithological attention; almost no bird records have been published from the Peruvian portion of the basin except for a handful of noteworthy records from white-sand forest (Álvarez Alonso & Whitney 2003). More information is available from adjacent areas, provided by the collections of the Olalla brothers from 1925–1928 (especially on the Napo river near the mouth of the Curaray river,

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but some records may suffer from erroneously recorded collection localities; Stotz & Díaz 2007, Wiley 2010), and by a series of inventories conducted during the last two decades in the adjacent Pastaza basin, upper Nanay-Pintuyacu-Chambira basin, and Allpahuayo-Mishana National Reserve (IIAP 1999, Eckhardt 2003, Stotz & Díaz 2007). These investigations revealed an exceptionally rich biota and motivated the establishment in 2005 of the Pucacuro Reserved Zone (upgraded in 2010 to Pucacuro National Reserve) within the Pucacuro catchment.

In this paper, we catalog the exceptionally rich birdlife of the Tigre basin (including the Corrientes and Pucacuro catchments) based on extensive ornithological surveys conducted from 1991–2014 at 42 sites across various habitat types throughout the basin. We present an annotated checklist of birds for the basin, including information on the abundance and habitat associations of each species. This inventory fills a major gap in our knowledge of bird distribution in Amazonian Perú, and includes numerous records of special interest, which we highlight and synthesize below. We especially emphasize patterns of novel habitat associations for poor-soil specialist birds, and the occurrence of species more typical of Andean foothills across northern Peruvian Amazonia. We additionally discuss the distribution of birds typical of Amazonian river islands in the Tigre basin, the occurrence of Amazonian birds with very low population densities and/or patchy distributions, and several apparent vagrants to the study region. We discuss the conservation implications of our results, both in the context of contemporary threats to the Tigre basin and in terms of conserving white-sand specialists throughout their range.

METHODS

Study region. The Tigre river is a north-bank tributary to the Marañón, with a basin that covers approximately 54,222 km^2 in Perú and Ecuador. The Peruvian portion of the basin, including the catchments of the tributary Corrientes and Pucacuro rivers, is situated entirely in lowland Amazonia, and includes the recently created Pucacuro National Reserve. Throughout this paper, we use *Tigre basin* to refer to the entire drainage, and *Tigre catchment* to refer to the drainage exclusive of the Corrientes and Pucacuro catchments. The climate is wet and hot, with a mean annual temperature of 26°C, and a mean annual rainfall of 2400 mm (SERNANP 2013). The eastern side of the basin consists primarily of hilly *terra firme* forest, while the western side is dominated by vast swamps between the Tigre and Pastaza rivers. All three rivers (the Tigre, Corrientes, and Pucacuro) flow generally south across the Pebas-Nauta boundary, which marks the transition from the nutrient-rich lacustrine sediments of the Pebas formation (to the north) to the nutrient-poor alluvial sediments of the Nauta formation (to the south), and is the site of a dramatic discontinuity in forest composition (Higgins et al. 2011). Bird communities also respond to this boundary, with various poor-soil specialists (Álvarez Alonso et al. 2013) restricted to the nutrient-poor soils of the Nauta formation.

Important habitats within the region include tall *terra firme* forests on nutrient-rich clays of the Pebas formation (especially in the Perú–Ecuador border region), seasonally-flooded *várzea* forests along major rivers, and a wide variety of nutrient-poor habitats, including white-sand forest, clay terraces of the Nauta formation, and the swampy plain between the Tigre and Pastaza rivers, a region of blackwater scrub, *igapó*, and peatlands. In places, peat accumulation rises above the floodwater level, forming domed ombrotrophic peatlands that support a distinctive habitat termed “peatland pole forest” with structural and floristic affinities to white-sand forest (Draper et al. 2014). Additionally, anthropogenic habitats such as agricultural plots (*chacras*) and secondary forest are predominant around towns and settlements.

Fieldwork. We conducted fieldwork between 1991 and 2014 at 42 sites throughout the basin, including 24 sites in the Tigre catchment, 8 sites in the Pucacuro catchment, and 10 sites in the Corrientes catchment (Figure 1, Table 1). All survey points were georeferenced using a handheld GPS unit. We conducted observational surveys along rivers and trails, often with a special focus on *terra firme* and nutrient-poor habitats. Bird species were identified by sight or sound, and were voice-recorded and photographed when possible. Some of the voice recordings are deposited in the open-access Xeno-Canto online sound library (www.xeno-canto.org), and all photographs have been deposited online in the VIREO database (www.vireo.anps.org). Early fieldwork also employed the use of mist-nets and shotgun collecting (Álvarez Alonso & Whitney 2003).

We assigned every species that we detected to one of five qualitative abundance classes. *Common* species were observed in considerable number (≥ 10 individuals) on most days in appropriate habitat. *Fairly common* species were observed on most days in appropriate habitat (1–9 individuals on most days). *Uncommon* species were encountered at least three times during our sampling, but were not encountered on most days. *Rare* species were encountered 1–3 times during our sampling. *Accidental* species are those for which available biogeographic evidence suggests that their occurrence in the study area is abnormal. We additionally distinguish *locally common* and *locally fairly common* species that attain these abundances only in localized habitats or geographically restricted parts of the basin. Our identifications follow the taxonomy of Plenge (2015) for Peruvian birds, which is based on the taxonomy of the South American Checklist Committee of the American Ornithologists’ Union (Remsen et al. 2016).

Habitat-specialist birds. To facilitate our discussion of biogeographic patterns among poor-soil specialist

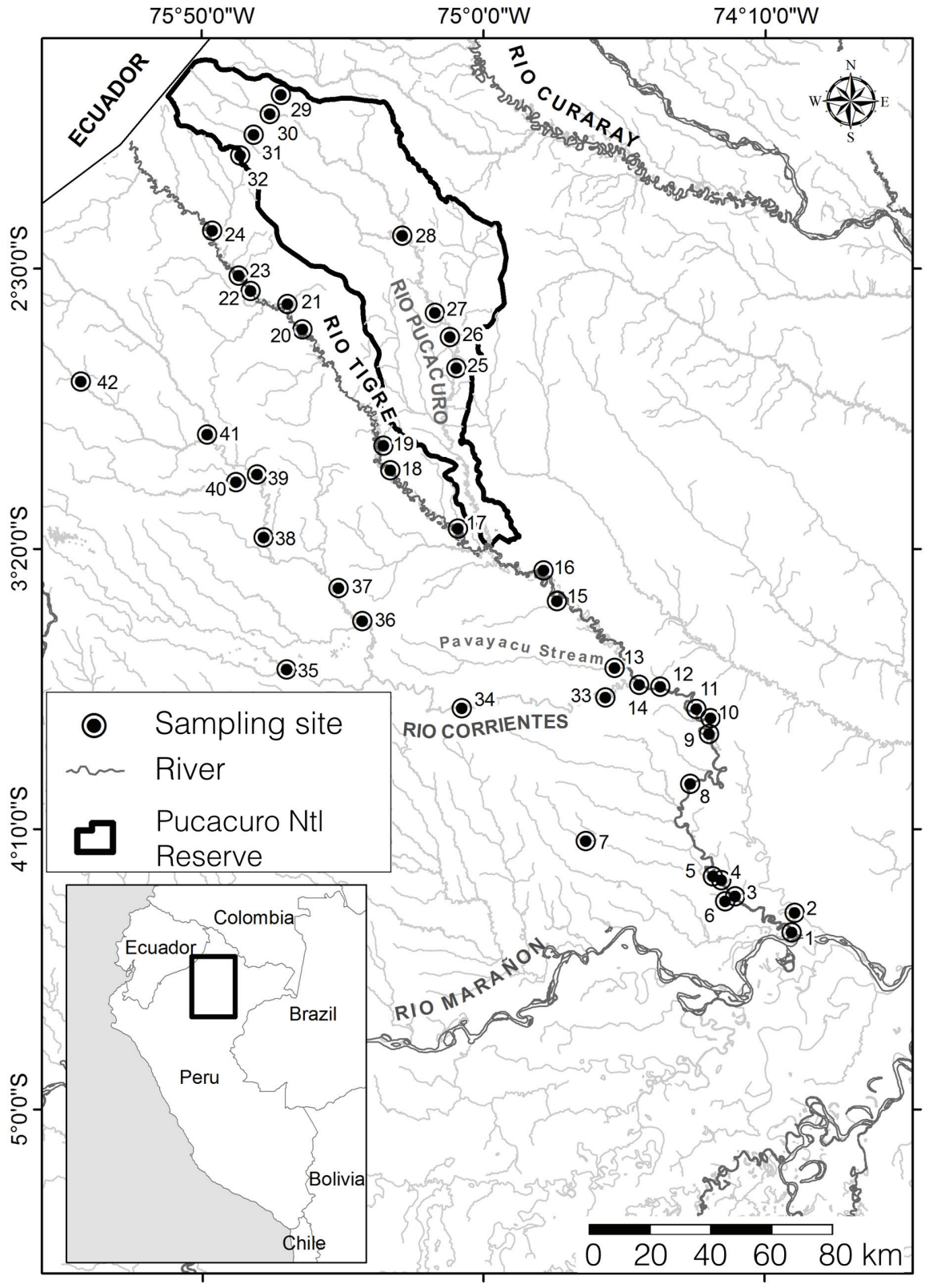

Figure 1. Sampling locations within the Tigre basin, Loreto, Perú. Numbers on the map are referenced to location names and geographic coordinates in Table 1.

birds in the study area, we rely heavily on the work of Álvarez et al. (2013), which examines the degree of white-sand specialization in the Peruvian avifauna. Álvarez et al. identify 39 species as white-sand specialists in the western Amazon, and subdivide this group into strict, local, and facultative specialists. We reference this classification repeatedly. Strict specialists are those believed at the time of publication of

Table 1. Study sites along in the Tigre river basin, Loreto, Perú. The habitat column lists the habitats visited at each site. Habitat codes are as follows: Tf - *Terra firme* forest; Fl - Floodplain forest, excluding swamps dominated by the palm *Mauritia flexuosa*; Np - Nutrient-poor forest habitats, including white-sand forest, weathered clay terraces, and peatland pole forest; Re - River-edge and lake-edge habitats; St - Forest streams; R - Rivers; L - Lakes; Ps - Palm swamp dominated by *Mauritia flexuosa*; F2 - Secondary forest; A - Agricultural plots and town centers.

#	Site name	Catchment	Coordinates	Observers	Years	Habitats
1	Boca del Tigre	Tigre	04°28’27’’S, 74°05’18’’W	JAA, JDA, JBS	1992–1995, 2002–2004, 2006, 2008–2011, 2013–2014	R, Re, Fl, Ps, A, F2
2	Quebrada Nahuapa	Tigre	04°24’59’’S, 74°04’45’’W	JBS	Aug–Sep 2013, Dec 2014	Fl, St, Np
3	Nueva York	Tigre	04°22’0.9’’S, 74°15’19’’W	JAA, JDA, JBS	1992–1995, 2003, 2004, 2006, 2008, 2010, 2013	Fl, R, Re, Ps, A, F2, L
4	Piura	Tigre	04°19’10’’S, 74°17’46’’W	JAA, JDA	1992–1995, 2003, 2004, 2006, 2008	Fl, R, Re, Ps, A, St, L
5	Monte Verde	Tigre	04°18’30’’S, 74°19’16’’W	JAA, JDA	1992–1995, 2003, 2004, 2006, 2008	Fl, R, Re, Ps, A, F2, St
6	Quebrada Supay	Tigre	04°22’57’’S, 74°17’04’’W	JBS	Sep 2013	Fl, St, Np
7	Zapotal	Tigre	04°12’11’’S, 74°41’52’’W	JAA	1992–1995	Fl, R, Re, Ps, A, St
8	Bellavista	Tigre	04°02’0.2’’S, 74°23’18’’W	JAA	1992–1995	Fl, R, Re, Ps, A, F2, St
9	Huacachina	Tigre	03°53’03’’S, 74°19’59’’W	JAA	1992–1995	Fl, R, Re, L, Ps, A, F2, St
10	Nueva Manchuria	Tigre	03°50’16’’S, 74°19’42’’W	JAA	1992–1995	Tf, R, Re, A, F2, St
11	Nueva Tarma	Tigre	03°48’35’’S, 74°22’14’’W	JAA	1992–1995	Fl, R, Re, L, A, F2, Tf, St
12	San Andres	Tigre	03°44’39’’S, 74°28’40’’W	JAA, JDA	1992–1995, 2006, 2010	Tf, Fl, Np, R, Re, F2, A, Ps, St
13	Nuevo Triunfo	Tigre	03°41’18’’S, 74°36’44’’W	JAA	1992–1995	Fl, R, Re, F2, A, Ps, St, L
14	Lores	Tigre	03°44’17’’S, 75°32’24’’W	JAA	1992–1995	Tf, Np, Fl, R, Re, F2, A, Ps, St, L
15	Intuto	Tigre	03°29’22’’S, 74°46’59’’W	JAA, JDA	1992–1995, 2007–2009, 2014	Tf, Np, Fl, R, Re, F2, A, Ps, St, L
16	Santa Andrea	Tigre	03°23’55’’S, 74°49’25’’W	JAA	1992–1995, 2007–2009	Tf, Fl, R, Re, A, F2, St, L, Ps
17	Bolognesi	Tigre	03°16’24’’S, 75°04’37’’W	JDA	2007–2009	Tf, Fl, R, Re, A, F2, St, L, Ps
18	Patria Nueva	Tigre	03°06’02’’S, 75°16’36’’W	JDA	2007–2009	Tf, Fl, R, Re, L, A, F2, Ps
19	Paiche Playa	Tigre	03°01’38’’S, 75°17’49’’W	JAA, JDA	1992–1995, 2007–2009	Tf, Fl, R, Re, A, F2, L, Ps
20	Lamas Tipishca	Tigre	02°40’52’’S, 75°32’09’’W	JAA, JDA	1992–1995, 2007–2009	Tf, Fl, R, Re, A, F2, Ps, L
21	Tnte. Ruiz	Tigre	02°36’18’’S, 75°34’48’’W	JAA	1992–1995	Tf, Fl, R, Re, Ps, L, A, F2
22	Vista Alegre	Tigre	02°33’59’’S, 75°41’20’’W	JAA	1992–1995	Tf, Fl, F2, R, Re, Ps, L, A
23	San Juan de Bartra	Tigre	02°31’14’’S, 75°43’28’’W	JAA	1992–1995	Tf, Fl, A, F2, R, Re
24	Doce de Octubre	Tigre	02°23’14’’S, 75°48’11’’W	JAA, JDA	1992–1995, 2007–2009	Tf, Fl, A, F2, R, Re, St
25	Posayo	Pucacuro	02°47’47’’S, 75°04’50’’W	JAA, JDA	2000, 2001, 2007, 2008	Tf, Fl, R, Re, L, St
26	Coconilla	Pucacuro	02°42’16’’S, 75°05’50’’W	JAA, JDA	2000, 2001, 2007, 2008	Tf, Fl, Np, R, Re, St
27	Salvador	Pucacuro	02°37’56’’S, 75°08’39’’W	JAA, JDA	2000, 2001, 2007, 2008	Tf, Fl, F2, R, Re
28	Baratillo-Tangarana	Pucacuro	02°24’10’’S, 75°14’29’’W	JAA, JDA	2000, 2001, 2007, 2008	Tf, Fl, R, Re, St

Álvarez et al. (2013) to be significantly associated with white sands and never found in other habitats. Local specialists are strict specialists only in part of their geographic distribution. Facultative specialists are those believed to be commonest in white-sand habitats, but potentially widespread in other forest

Table 1. Continuation.

#	Site name	Catchment	Coordinates	Observers	Years	Habitats
29	Point A	Pucacuro	01°58′59′′S, 75°35′57′′W	JDA	2007–2008	Tf, St, Np
30	Point B	Pucacuro	02°02′23′′S, 75°37′57′′W	JDA	2007–2008	Tf, St
31	Point C	Pucacuro	02°06′08′′S, 75°40′50′′W	JDA	2007–2008	Tf, St
32	Point D	Pucacuro	02°09′47′′S, 75°43′10′′W	JDA	2007–2008	Tf, St
33	San Carlos	Corrientes	03°46′34′′S, 75°38′22′′W	JAA	1992–1995	Fl, R, Re, Ps, A, F2
34	Trompeteros	Corrientes	03°48′28′′S, 75°03′55′′W	JAA, JDA	1992–1995, 2004, 2005, 2010	Fl, R, Re, A, Ps, F2
35	Copal	Corrientes	03°41′33′′S, 75°35′01′′W	JAA	1992–1995	Fl, Tf, A, Ps, St
36	Nuevo Peruanito	Corrientes	03°32′58′′S, 75°21′35′′W	JAA	1992–1995	Tf, Fl, R, Re, A, F2, St
37	Point E	Corrientes	03°27′01′′S, 75°25′48′′W	JAA	1992–1995	Tf, Fl, R, Re, A, F2, St, Ps
38	Tunchiplaya	Corrientes	03°18′01′′S, 75°39′05′′W	JAA	1992–1995	Tf, Fl, Np, R, Re, A, St
39	Nueva Valencia	Corrientes	03°06′47′′S, 75°40′16′′W	JAA	1992–1995	Tf, R, Re, A, St, L
40	Belen de Plantanoyacu	Corrientes	03°08′07′′S, 75°43′58′′W	JAA	1992–1995	Tf, R, Re, A, St
41	Sauki	Corrientes	02°59′28′′S, 75°49′04′′W	JAA	1992–1995	Tf, R, Re, A, St
42	Nueva Jerusalen	Corrientes	02°50′11′′S, 76°11′30′′W	JAA	1992–1995	Tf, Fl, A, R, Re, St

types. Our discussion of river-edge specialists draws on Rosenberg's (1990) description of the avifauna of Amazonian river-islands, and our discussions of Andean species and patchily-distributed species draw on the range maps presented by Schulenberg et al. (2010).

RESULTS

We recorded a total of 584 bird species from the Tigre basin, of which 554 were recorded inside the Pucacuro National Reserve, representing a hyper-diverse strictly lowland avifauna (Table S1). The majority of these species were geographically widespread, with 476 species present in all three of the basin's major catchments (the Tigre, Corrientes, and Pucacuro). Twenty-two species were found only in the Tigre catchment; 12 species only in the Pucacuro; 66 species shared only between the Tigre and Pucacuro; and 8 species shared only between the Tigre and Corrientes. Many of these species may in fact be more widespread, but poorly sampled; however, others may be genuinely restricted to localized habitats, including river-created habitats found only along the lower reaches of the Tigre (e.g. whitewater *várzea*); Pebas formation forests that are scarce along the Corrientes; and swampy habitats that are scarce along the Pucacuro.

Most observed species belong to the expected *terra firme* avifauna in northern Amazonia (including species typical of *chacras* and secondary forests). However, the avifauna included five distinct groups of special interest. The first is a set of species that are generally widespread on the lower slopes of the humid Andes, but that apparently occur sparingly across the Amazonian lowlands in northern Perú. These species include White Hawk (*Pseudastur albicollis*), Sapphire Quail-Dove (*Geotrygon sapphirina*), Black-throated Brilliant (*Heliodoxa schreibersii*), Lanceolated Monklet (*Micromonacha lanceolata*); Chestnut-throated Spinetail (*Synallaxis cherriei*), White-shouldered Antshrike (*Thamnophilus aethiops aethiops*), Scaled Antpitta (*Grallaria guatemalensis*), Golden-winged Tody-Flycatcher (*Poecilotriccus calopterus*), Long-tailed Tyrant (*Colonia colonus*), Rufous-browed Peppershrike (*Cyclarhis gujanensis*), Wing-banded Wren (*Microcerculus bambla*), White-breasted Wood-Wren (*Henicorhina leucosticta*), Half-collared Gnatwren (*Microbates cinereiventris*), and Slate-colored Seedeater (*Sporophila schistacea*). Some of these species were found in disturbed habitats, including river-created habitats and anthropogenic disturbance (*Colonia colonus*, *Cyclarhis gujanensis*, *Sporophila schistacea*); others were found primarily in very hilly terrain in far northern Perú (*Geotrygon sapphirina*, *Thamnophilus aethiops*, *Grallaria guatemalensis*, *Microcerculus bambla*, *Henicorhina leucosticta*); and still others are widespread but rare across northern Amazonian Perú (*Heliodoxa schreibersii*, *Micromonacha lanceolata*).

The second group is a set of species typical of Amazonian white-sand that we recorded on nutrient-poor clay terraces along the Pucacuro and peatland pole forests and blackwater scrub on the lower Tigre. Several bird species regarded as facultative or obligate white-sand specialists (Álvarez Alonso et al.

2013) occurred in these additional forest types, and we suggest that *poor-soil specialists* (rather than *white-sand specialists*) may be a more accurate descriptor for these species. Peatland forests, in particular, have received scant attention from ornithologists (Lähteenoja et al. 2009a), and represent a novel habitat association for many of the poor-soil specialists. Poor-soil specialists (white-sand specialists *sensu* Álvarez et al. 2013) detected from the peatlands of the lower Tigre include the following. For each species, we indicate its level of white-sand specialization (strict, local, or facultative) as given by Álvarez et al. 2013; note that these designations are based in part on JÁA's records discussed in this paper. Brown-banded Puffbird (*Notharchus ordii*, strict), Paradise Jacamar (*Galbula dea*, facultative), Pearly Antshrike (*Megastictus margaritatus*, facultative), Mishana Tyrannulet (*Zimmerius villarejoi*, strict), Zimmer's Tody-Tyrant (*Hemitriccus minimus*, strict), Cinnamon Manakin-Tyrant (*Neopipo cinnamomea*, local), Yellow-throated Flycatcher (*Conopias parvus*, local), Citron-bellied Attila (*Attila citrineiventris*, local), White-crowned Manakin (*Dixiphia pipra*, facultative), and Orange-crowned Manakin (*Heterocercus aurantiivertex*, local). Peatland pole forests also had dozens of more widespread *terra firme* species, including Gilded Barbet (*Capito auratus*), Rufous-capped Antthrush (*Formicarius colma*), and Brown-winged Schiffornis (*Schiffornis turdina*).

Poor-soil specialists detected from weathered clay terraces on the Pucacuro include *Megastictus margaritatus* (facultative), Ancient Antwren (*Herpsilochmus gentryi*, facultative), Allpahuayo Antbird (*Percnostola arenarum*, local), Short-billed Leaftosser (*Sclerurus rufigularis*, facultative), Duida Woodcreeper (*Lepidocolaptes duidae*, local), *Zimmerius villarejoi* (strict), Rufous-tailed Flatbill (*Ramphotrigon ruficauda*, facultative), Pompadour Cotinga (*Xipholena punicea*, strict), and *Dixiphia pipra* (facultative).

Only two sampling points were located in true white-sand forest, both on the middle Tigre. Here, we encountered a diverse white-sand avifauna that included additional specialists such as Gray-legged Tinamou (*Crypturellus duidae*, strict), Barred Tinamou (*C. casiquiare*, facultative), Saffron-crowned Tyrant-Manakin (*Neopelma chrysocephalum*, strict), Helmeted Pygmy-Tyrant (*Lophotriccus galeatus*, facultative), and Cinnamon-crested Spadebill (*Platyrinchus saturatus*, local). The most interesting of these records were discussed in detail by Álvarez & Whitney (2003).

The third group are species characteristic of river islands (Rosenberg 1990). In Perú, these species are known primarily from the major rivers: Amazon, Marañón, Ucayali, and Napo. Here we report that they enter the Tigre in river-edge habitats similar to those of the larger rivers, including *Cecropia* (Urticaceae) woodland, *Gynerium* (Poaceae) and *Tessaria* (Asteraceae) scrub, sand bars, and anthropogenic clearings. These species include Lesser Yellow-headed Vulture (*Cathartes burrovianus*), various shorebirds including Baird's Sandpiper (*Calidris bairdii*), Olive-spotted Hummingbird (*Leucippus chlorocercus*), Blue-winged Parrotlet (*Forpus xanthopterygius*), Leaden Antwren (*Myrmotherula assimilis*), Fuscous Flycatcher (*Cnemotriccus fuscatus*), Cinereous Becard (*Pachyramphus rufus*), Oriole Blackbird (*Gymnomystax mexicanus*), and Purple-throated Euphonia (*Euphonia chlorotica*).

The fourth group of special interest are species that are generally rare or poorly known in northeast Amazonian Perú (Schulenberg et al. 2010). These include Gray-bellied Hawk (*Accipiter poliogaster*), Buckley's Forest-Falcon (*Micrastur buckleyi*), Rufous-vented Ground-Cuckoo (*Neomorphus geoffroyi*), Rufous-headed Woodpecker (*Celeus spectabilis*), Brown-rumped Foliage-gleaner (*Automolus melanopezus*), Tawny-throated Leaftosser (*Sclerurus mexicanus*), Wing-banded Antbird (*Myrmornis torquata*), Brown-backed Antwren (*Epinecrophylla fjeldsaai*), Spotted Antpitta (*Hylopezus macularius*), Amazonian Scrub-Flycatcher (*Sublegatus obscurior*), Three-striped Flycatcher (*Conopias trivirgatus*), White-bellied Dacnis (*Dacnis albiventris*), Large-billed Seed-Finch (*Sporophila crassirostris*), and the migrants Nacunda Nighthawk (*Chordeiles nacunda*) and Slaty Elaenia (*Elaenia strepera*).

The fifth group comprised two species that are probably genuine vagrants to the region: Eared Dove (*Zenaida auriculata*), and Ash-colored Cuckoo (*Coccycua cinerea*). An additional vagrant, Black-and-white Warbler (*Mniotilta varia*), has already been discussed by Álvarez & Whitney (2003).

Species accounts. Table 1 gives the geographic coordinates and map number (from Figure 1) for all locations mentioned in the accounts below. The letters 'XC' followed by a number refer to recordings in the Xeno-Canto catalog.

Eared Dove (*Zenaida auriculata*)
JAA recorded single individuals in agricultural areas at Point E in October 1994 and at Intuto in March 1995. In Perú, this species primarily occurs west of the Andes and in dry intermontane valleys; the closest known populations occur near Tarapoto. Its presence in the Tigre basin is entirely unexpected and likely involves vagrant individuals. The possibility of human-assisted vagrancy must be considered, but the absolute lack of records near Iquitos suggests that human-assisted vagrancy to lowland Loreto is not common for this species.

Sapphire Quail-Dove (*Geotrygon sapphirina*)
JDA recorded single individuals in hilly *terra firme* at Point A and at Baratillo-Tangarana, both in December 2007. Both sites are within the newly created Pucacuro National Reserve. These records represent one of several apparently disjunct populations in northern Amazonia. The species is more frequent on lower Andean slopes and ridges, though still rare (Walker et al. 2006).

Ash-colored Cuckoo (*Coccycua cinerea*)
JAA recorded one individual of this species foraging low above the ground in an agricultural plot at Intuto on 19 February 1994. This species is a scarce Austral migrant to southeastern Perú. No additional records exist from Loreto, where its occurrence is presumably accidental.

Paradise Jacamar (*Galbula dea*)
This species is widespread in *terra firme*, particularly on nutrient poor substrates. We mention it here to report its presence in peatland pole forest at Quebrada Supay (JBS, 10 September 2013, one individual).

Brown-banded Puffbird (*Notharchus ordii*)
JDA recorded the species on weathered clay terraces at Coconilla in May 2007. JBS recorded up to two individuals from peatland pole forest at Quebrada Supay on 6 and 10 September 2013. These records establish a new habitat (peatland pole forest) for the species in Perú, and may be the first records west of the Tigre river. Otherwise, this species is primarily known in Perú from white-sand forests on both banks of the Amazon near Iquitos and along the Tigre (Álvarez & Whitney 2003), from a few records in Madre de Dios and Ucayali (Harvey et al. 2014), and from a few records on nutrient-poor substrates near Nauta and west of the lower Ucayali river (Socolar et al. in press).

Rufous-headed Woodpecker (*Celeus spectabilis*)
JAA encountered single individuals several times in *Cecropia*-dominated forest: at Copal in November 1992, at Intuto in July 1993, and at Doce de Octubre in October 1993. Elsewhere in its Peruvian range, this rare woodpecker has be hypothesized to be a bamboo specialist (Kratter 1997), but we found it in river-edge and secondary forest without a substantial bamboo element, consistent with records in *Cecropia* habitat in Ecuador and elsewhere (Winker & Christie 2002).

White-shouldered Antshrike (*Thamnophilus aethiops aethiops*)
JAA encountered the nominate subspecies in *terra firme* at Doce de Octubre in October 1993, and JDA voice-recorded the nominate subspecies in *terra firme* at Point A in December 2007 (XC298265). Although we lack physical documentation of the subspecific identification (which was based on visual observations), these records extend the Peruvian range of the nominate *T. a. aethiops* (previously known from Andean foothills and adjacent lowlands north of the río Marañón) far into lowland Amazonia. The Amazonian subspecies *kapouni* apparently occurs only south of the Amazon and Marañón (and possibly Huallaga) rivers. We mention the subspecific identification here because it situates these records within the broader pattern of Andean taxa that occur across the lowlands of northern Perú in hilly terrain.

Brown-backed (*Epinecrophylla fjeldsaai*) **and Stipple-throated Antwrens** (*E. haematonota*)
The status of *E. fjeldsaai* as specifically distinct from *E. haematonota* is controversial because genetic analysis reveals the former taxon to be nested within the latter (Whitney et al. 2013), and because of a phenotypically intermediate population at San Lorenzo, well to the west of the study area (18 km NW of the confluence of the Marañón and Pastaza rivers, 04°49'S, 76°33'W, Schmitt et al. in press). Despite these findings, our experience in the Tigre basin is consistent with the observation of Krabbe et al. (1999) that the species come into close parapatry without apparent intermediates in northern Perú, including along the middle Tigre. We have recorded both *E. fjeldsaai* and *E. haematonota* along each of the Tigre, Corrientes, and Pucacuro rivers, and at several sampling points on the left bank of the Tigre we encountered both taxa, but no apparent intermediates. We encountered birds phenotypically consistent with *E. haematonota* as far north as Baratillo-Tangarana, and birds consistent with *E. fjeldsaai* as far south as Copal and Nuevo Triunfo. Similar findings of parapatry and possible overlap without intermediates were obtained during a rapid inventory of the Nanay, Mazan, and Arabela catchments (Stotz & Díaz 2007).

Mishana Tyrannulet (*Zimmerius villarejoi*)
This species was recently described from white-sand forests in the Nanay basin, and a disjunct population (possibly a distinct species or subspecies) was subsequently rediscovered in San Martín (Álvarez & Whitney 2001, Whitney et al. 2013). We have obtained records from several additional sites that dramatically extend the range of the Nanay-basin form. JDA encountered this species on a highly weathered clay terrace at Coconilla in May 2007. This site is 200 km north of the tiny known range of this species in the lower Nanay basin. JBS recorded one individual (XC196765–196767) in peatland pole forest at the eastern edge of the Tigre floodplain at Quebrada Nahuapa on 31 August 2013, providing a range extension of over 50 km southwest from the lower Nanay. Recordings confirm that this individual belongs to the Nanay-basin form (Dan Lane pers. comm.). In addition to expanding its known range, these records establish new habitat associations for the Nanay-basin form of *Z. villarejoi*, which was previously regarded as an obligate white-sand specialist.

Helmeted Pygmy-Tyrant (*Lophotriccus galeatus*)
The first Peruvian record of this species was in bamboo-dominated white-sand forest near the Tigre river at Lores, and it has subsequently been found in similar habitat on the upper Nanay, as well as on clay soils east of the Napo river (Álvarez & Whitney 2003). JDA additionally recorded this species from a weathered clay terrace at Coconilla in August 2007.

Zimmer's Tody-Tyrant (*Hemitriccus minimus*)
In Perú, this species is known primarily from white-sand areas, though additional records exist from near the Yavarí and Ucayali rivers (Álvarez & Whitney 2003, Harvey et al. 2014). JBS detected the ringing day-song of a single individual in peatland pole forest west of the Tigre at Quebrada Supay on 6, 7, and 9 September 2013. This represents a new habitat for the species in Perú.

Long-tailed Tyrant (*Colonia colonus*)
In Perú, this species occurs primarily on Andean slopes, but a disjunct population exists in northern Loreto. We encountered this species in *terra firme* along the Tigre and Pucacuro rivers: JAA encountered four individuals at Doce de Octubre in August 1993, and JDA encountered six individuals at Baratillo-Tangarana and Point B in June 2007.

Pompadour Cotinga (*Xipholena punicea*)
This species was recently discovered in Perú on white-sand substrates in the Nanay basin (Álvarez & Whitney 2003). JDA encountered this species in white-sand forest at San Andrés in July 2006, and on a highly weathered clay terrace at Coconilla in August 2007. Along with records near Nauta and in the Tapiche basin (Socolar et al. in press) these are the first Peruvian records away from the Nanay basin and the first Peruvian records away from white-sand soil.

Orange-crowned Manakin (*Heterocercus aurantiivertex*)
This species is now known to be relatively widespread in white-sand and blackwater habitats in northern Perú (Álvarez & Whitney 2003, Schulenberg et al. 2010). We include it here to note that it attains exceptionally high densities in peatland pole forest on both banks of the Tigre river. For example, JBS encountered approximately 25 individuals along 4 km of trail at Quebrada Supay on 6 September 2013.

Cinereous Becard (*Pachyramphus rufus*)
This species is generally considered to be rare in forests along large Amazonian rivers, including on river islands. JAA encountered individuals in river-edge forest at Lamas Tipishca in August 1993 and at Belen de Plantanoyacu in December 1994.

Wing-banded Wren (*Microcerculus bambla*)
This poorly known species has a patchy range, with a few records from central and southern Perú (Harvey et al. 2011, Socolar et al. 2013, Dan Lebbin pers. comm.). JAA encountered this species in *terra firme* forest at Doce de Octubre in 1992–1993, and JDA in *terra firme* forest at Baratillo-Tangarana and Point B in August and December 2007.

Slate-colored Seedeater (*Sporophila schistacea*)
This species is known from northern Amazonian Perú exclusively from several individuals recorded in flowering bamboo along the middle Tigre in 1995 (Álvarez & Whitney 2003). We report two additional records from Corrientes and Pucacuro catchments, both from secondary forest. JAA encountered this species at Point E in October 1994, and JDA encountered the species at Salvador in August 2007. The occurrence in secondary habitats is consistent with an additional record from an agricultural plot at Madre Selva, some 200 km to the east (Socolar et al. in press).

DISCUSSION

Biogeographic patterns. Our results represent the first large-scale ornithological inventory of the Tigre basin, comprising roughly 75% of the avifauna of lowland Loreto (Wiley et al. 2015). We document two striking biogeographic patterns: the occurrence of typically Andean species far into the lowlands of northern Perú, and the occurrence of putative white-sand specialist birds in additional nutrient-poor habitats. These patterns carry several implications. The majority of Andean species in the study region are understory (frequently terrestrial) birds that we encountered at very hilly Amazonian sites. Therefore, we suggest that these species might select for hilly topography rather than altitude *per se*. Perhaps hilly terrain influences some yet-unknown aspect of terrestrial foraging important for these taxa. A few species stand in contrast to this general pattern. *Sporophila schistacea* was found in white-sand forest with seeding bamboo and also in secondary habitats. Its occurrence is likely tied to bamboo flowering events (Álvarez & Whitney 2003). *Micromonacha lanceolata* is widespread across upland forests in the study area. *Heliodoxa schriebersii* and *Cyclarhis gujanensis* occur in streamside or seasonally flooded habitats. We note that immediately south of the study area, in the Pacaya-Samiria basin, *C. gujanensis* occurs together with *Myrmotherula longicauda*, another Andean species, in broken-canopy flooded forest with extensive bamboo in the understory (Begazo & Valqui 1998). Immediately east of the study area in the Nanay basin, *H. schreibersii* has been found on stunted white-sand forest with waterlogged soil (Socolar pers. obs.). The peculiar distributions of these two species may be related to structural similarities between scrubby flooded forest and montane forest edge.

The occurrence of poor-soil specialist bird species (previously regarded as white-sand specialists) on weathered clay terraces and peatlands suggests that the floristic composition of white-sand forests is not the primary driver of avian specialization in those habitats. In the peatlands, the vast majority of white-sand tree species are absent, though the few tree species present in the peatlands are often shared with white sands (Frederick Draper, personal communication). Previous studies of bird distributions along soil nutrient gradients in this region found that avian community composition correlated more strongly with floristic composition than with soil cation concentrations (Pomara et al. 2012). We hypothesize that

floristic composition correlates strongly with an additional unseen driver (e.g., vegetation structure) across the sites studied by Pomara et al. (2012). Peatland pole forest is a previously unrecognized non-flooded habitat type in the Pastaza-Marañón-Tigre basin, which may facilitate the dispersal of *terra firme* species across this low-lying area, including to the isolated *terra firme* "island" at San Lorenzo (04°49'S, 76°33'W).

The river-edge specialist birds found during our inventory are a subset of the river-island avifauna documented by Rosenberg (1990). In general, we did not find the most specialized components of the island avifauna. For example, we did not detect any of the species that specialize on even-aged *Cecropia* stands, pure *Gynerium* canebreaks, or extensive *Tessaria* scrub. Those species that we did detect were often surprisingly widespread, occurring throughout much of the basin along the banks of the Tigre and its major tributaries. True river islands are largely absent from the Tigre basin.

Rare and patchily distributed bird species have long posed a puzzle for Amazonian biogeographers, as it is difficult to determine whether they are truly patchy in space or merely rare everywhere. Several of our records corroborate the idea that these birds have truly patchy distributions. Our records of both *Neomorphus geoffryi* and *Automolus melanopezus* are consistent with massive range disjunctions between northern and southeastern Perú (Schulenberg et al. 2010). We recorded *Conopias trivirgatus* exclusively near the mouth of the Tigre, which is consistent with the possibility that the vicinity of the Pacaya-Samiria basin is a population center for this species in Perú (Begaso & Valqui 1998, Schmitt et al. in press, Socolar et al. in press). Records of *Epinecrophylla fjeldsaii* and *Myrmornis torquata* are consistent with populations restricted to northern Perú (possibly to the rich soils of the Pebas formation). Most other species in this group, however, appear to be widespread but rare across much of Peruvian Amazonia.

Conservation implications. Our inventory highlights the Tigre basin as a region of conservation priority, both for its exceptional avian diversity and for its unique combination of habitats and biogeographic influences, including nutrient-poor habitats and foothill affinities. The basin includes many habitats and species with highly restricted distributions in Amazonian Perú, and is home to numerous species considered threatened or near-threatened both for Perú (SERFOR 2014) and at global scale (BirdLife International 2016). These include *Crypturellus duidae*, *Crypturellus casiquiare*, Blue-throated Piping-Guan (*Pipile cumanensis*), Salvin's Curassow (*Mitu salvini*), Jabiru (*Jabiru mycteria*), Wood Stork (*Mycteria americana*), Crested Eagle (*Morphnus guianensis*), Harpy Eagle (*Harpia harpyja*), Orange-breasted Falcon (*Falco deiroleucus*), Peregrine Falcon (*Falco peregrinus*), Scarlet Macaw (*Ara macao*), Red-and-green Macaw (*Ara chloropterus*), *Herpsilochmus gentryi*, Black-tailed Antbird (*Myrmoborus melanurus*), *Percnostola arenarum*, *Zimmerius villarejoi*, *Hemitriccus minimus*, *Xipholena punicea*, and *Neopelma chrysocephalum*, fourteen of which are protected within the Pucacuro National Reserve.

Although legislative protections afforded to these species and to the Pucacuro National Reserve are encouraging, enforcement remains a challenge, especially in light of the region's long and ongoing history of environmental degradation and threats. These principally consist of deforestation, overhunting, and pollution related to hydrocarbons exploration and extraction. From 1971–2003, toxic wastewater from petroleum extraction was dumped directly into local water bodies in the Tigre, Corrientes, Pastaza, and Marañón basins; efforts at mitigation and clean-up are ongoing (Dourojeanni 2013). Today, plans exist for a 207 km pipeline to transport crude oil from operations near the Ecuadorian border; this pipeline would cross a 30 km stretch inside the Pucacuro National Reserve, posing a major threat to the reserve. Concrete and aggressive regulatory measures are urgently needed avoid spills, which might irreversibly damage the area.

A separate threat involves plans to connect Iquitos to Yurimaguas via a route that traverses the basin, originally via a rail link, and more recently with high-voltage transmission lines. If and when such development occurs, measures must be taken to prevent widespread colonization and deforestation along the route, as has occurred along the Iquitos-Nauta highway (Mäki et al. 2001).

Our findings also have conservation implications that extend beyond the Tigre basin. The occurrence of white-sand specialists on peatland habitats is especially significant because radiocarbon dates for the onset of peat accumulation indicate that these formations are geologically quite young, with basal dates of < 4,000 years before present (Lähteenoja et al. 2009b). Therefore, the occurrence of white-sand specialist birds in peatlands strongly suggests ongoing/recent dispersal of these specialists between widely separated patches of suitable habitat. This situation highlights the urgent need for a metapopulation approach to the conservation of white-sand specialist birds, especially in light of extensive recent clearing of white-sand habitat along the Iquitos-Nauta highway (Mäki et al. 2001).

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