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## Avifaunal surveys in the central Peruvian Amazon clarify range limits and highlight links between avian and habitat diversity

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**ABSTRACT**—The bird life of the central Peruvian Amazon is poorly known. To better characterize bird diversity and distributions, we conducted 4 expeditions to this lowland area, totaling 114 field days in 2015, 2018, and 2019. We focused on sampling under-surveyed habitats, *terra firme* in multiple interfluvies, and sites around a recent river avulsion, and we detected 657 bird species across 22 study sites. Our results include the first extensive inventories of blackwater wetland systems, *Guadua* bamboo tracts, and riverine islands in central Peru; revised information on distributions with respect to river barriers, including documentation of contact and putative hybridization between parapatric forms; 28 first regional records; and new details on poorly known taxa. Together, these results provide a more complete picture of avian diversity in an area characterized by high species richness, high habitat diversity, and biogeographic interchange. Received 30 June 2020. Accepted 4 March 2021.

Key words: Amazonia, biodiversity, biogeography, contact zone, hybridization, river avulsion, Ucayali.

### Reconocimientos de avifauna de la Amazonía central del Perú clarifican límites en distribuciones y destacan el vínculo entre diversidad aviar y de hábitats

**RESUMEN** (Spanish)—La avifauna de la Amazonía central del Perú es pobremente conocida. Para caracterizar su diversidad y distribución, llevamos a cabo 4 expediciones en esta área de tierras bajas, con un total de 114 días de trabajo de campo en 2015, 2018 y 2019. Nos enfocamos en muestrear hábitats subestudiados, *terra firme* en múltiples interfluvios y sitios alrededor de avulsiones recientes de ríos. Detectamos 657 especies de aves en 22 sitios de estudio. Nuestros resultados incluyen los primeros inventarios extensos de sistemas de humedales de aguas negras, parches de bambú *Guadua* e islas en los ríos del Perú central; información corregida de distribuciones respecto a barreras ribereñas, incluida documentación de contacto e hibridación putativa entre formas parapátricas; 28 primeros registros regionales y nuevos detalles de taxa escasamente conocidos. En conjunto, estos resultados proveen una imagen más completa de la diversidad aviar en un área caracterizada por una alta riqueza de especies, una alta diversidad de hábitats e intercambio biogeográfico.

Palabras clave: Amazonia, avulsión de ríos, biodiversidad, biogeografía, hibridación, Ucayali, zona de contacto.

The central Peruvian Amazon lies within a global hotspot of bird species richness in the western Amazon Basin (Orme et al. 2005). This richness is tied to the diversity of avian habitats regionally (Terborgh 1985, Parker et al. 1996), including upland forest (*terra firme*), floodplain forest along silt-laden rivers draining out of the Andes (*várzea*), blackwater drainages with associated seasonally flooded forests (*igapó*), wetlands, riverine habitats, and associated islands (Ramsen and Parker 1983, Rosenberg 1990), *Guadua* (Poaceae) bamboo tracts (Kratte 1997, Parker et al. 1997, Lebbin 2007), stunted forest on nutrient-poor soils (Álvarez et al. 2013, Borges et al. 2016),

and, increasingly, agricultural land and settlements. Understanding how spatial patterns of avian diversity correspond to habitat diversity helps to clarify the ecological and evolutionary basis of diversity hotspots (Ramsen 1985, Terborgh 1985, Marra and Ramsen 1997). However, more information is needed on avian habitat associations and on the geographic distributions of habitat specialists in the western Amazon Basin.

The high species richness of the western Amazon Basin is also linked to avian biogeographic turnover across major landscape barriers such as rivers. The central Peruvian Amazon is at the headwaters of the Amazon River and at the confluence of avifaunas from the Napo area of endemism north of the Amazon and the Inambari area of endemism to the south (Cracraft 1985, Silva et al. 2005). Identifying the locations of range limits and the presence or absence of contact between closely related taxa in headwater regions can clarify not only patterns of species richness, but also how Amazonian species form and are maintained (Bates et al. 2004, Naka et al. 2012,

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Weir et al. 2015, Naka and Brumfield 2018). The central Peruvian Amazon is biogeographically complex, with the Ucayali, Urubamba, and Tambo rivers as well as outlying mountain ranges like the Cerros del Sira serving as distributional barriers. These barriers, moreover, are not fixed over time. The Ucayali River in particular is thought to have had a dynamic history even over recent timescales (Lathrap 1968, Dumont 1991), with a notable example being an avulsion that passively transferred ~2,000 km<sup>2</sup> of land near Pucallpa from the west to the east side of the river in the late 18th century (hereafter, the Ucayali avulsion; Pärssinen et al. 1996). High-resolution survey data are required to assess the role of these landscape barriers in shaping geographic distributions and contact zones between taxa.

The first major ornithological surveys of the central Peruvian Amazon were conducted in 1927–1928 by the Olalla brothers, Alfonso and Ramón, who collected ~2,000 specimens along the upper Ucayali River (Wiley 2010). Further surveys of similar scale by the Louisiana State University Museum of Natural Science (LSUMNS), Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos (UNMSM), and Centro de Ornitología y Biodiversidad (CORBIDI) have established general biogeographic patterns. These surveys include those at Yarinacocha from 1961 to 1972 (~900 specimens; O’Neill and Pearson 1974), near Balta in the upper Purús River drainage from 1963 to 1971 (~2,300 specimens; Lowery and O’Neill 1965, 1966, 1969; O’Neill 1969, 1974, 2003), along the Shesha River in 1987 in what is now the Sierra del Divisor National Park (park established in 2015; ~1,100 specimens; O’Neill et al. 1991; also see Schulenberg et al. 2006), and to sites around the upper Ucayali River in 2010–2011, particularly along the Cohengua River (~2,100 specimens; Harvey et al. 2014b). Additional surveys around Pucallpa (Traylor 1958, Dickerman 1975, Srinivas and Molina 2013, Srinivas and Koh 2016), the upper Purús River drainage (Angulo et al. 2016), upper Jurua drainage (Balta 2007), Mapuya and Caco Rivers (Goussard 1984), and lower Urubamba River (M.J. Miller, University of Oklahoma, unpubl. data), and more peripherally in the foothills of the Cerros del Sira (Terborgh and Weske 1975, González 1998, Mee et al. 2002, Harvey et al. 2011, Socolar et al. 2013), Gran Pajonal (Harvey et al. 2011), northern

foothills of the Cordillera Vilcabamba (Schulenberg and Servat 2001), and lowlands of Acre, Brazil (Whittaker and Oren 1999), provided important context for the work presented here.

Despite this long history, ornithological study in the central Peruvian Amazon has been patchy both in time and space. The area generally has not been the focus of intensive avifaunal surveys such as those conducted in the Loreto and Madre de Dios regions by ornithologists and amateurs alike (e.g., Graham et al. 1980, Parker 1982, Capparella 1987, Rosenberg 1990, Terborgh et al. 1990, Robinson 1997, Lebbin 2007, Álvarez et al. 2013, Díaz-Alván et al. 2017, Schmitt et al. 2017, Williams 2017, Socolar et al. 2018, Moncrieff et al. 2019), certainly in part due to much less developed infrastructure such as roads, research centers, and eco-lodges. Major habitats, particularly extensive blackwater wetlands and surrounding *igapó* forests, *Guadua* bamboo tracts, and riverine islands, remain largely unexplored. Knowledge of bird distributions with respect to rivers and the extent of hybridization between closely related taxa are also poorly known (but see Harvey et al. 2014b). Meanwhile, expanding human settlement is providing increased access, but threatens the very habitats in need of study.

Here, we report on surveys aimed at filling these avian knowledge gaps in the central Peruvian Amazon. We conducted the most extensive surveys to date of blackwater wetland systems, *Guadua* bamboo tracts, and riverine islands in the area, and targeted specific localities to assess the influence of the Ucayali River and its tributaries on the geographic ranges of birds, including sites within the ~2,000 km<sup>2</sup> land mass that switched riverbanks during the Ucayali avulsion.

## Methods

### Study sites

We surveyed 22 sites across central Peru over 114 d during 2015, 2018, and 2019 (Table 1; Fig. 1). The study area is largely located within the Ucayali Region, but also includes lowland sites in the Huánuco, Junín, and Cuzco regions (we restrict our usage of “region” to the first-level administrative subdivision in Peru previously known as a “department”). Sampling effort was focused along the Ucayali River and its main tributaries, the Urubamba and Tambo rivers, which join to form

**Table 1.** Summary of avifaunal surveys in the central Amazon of Peru.

Study sites	Dates surveyed	Surveyors	Species detected	Specimens collected	Species collected	Species with media <sup>a</sup>
Yarinacocha	19 Dec 2015; 25, 27 Jul 2019; 20, 31 Aug–1 Sep 2019	AEM, OJ, CFC, ECC, MLB, MGH	112	2	1	45
Pucallpa area	12 Dec 2015; 24–26 Jul 2019; 4, 7, 25, 29 Aug 2019; 1 Sep 2019	AEM, OJ, CFC, ECC, MLB, MGH, DFL	92	2	1	5
Tournavista area	2, 25–29 Aug 2019	AEM, OJ, CFC, ECC, MLB	192	55	34	69
Masisea island	23–24 Aug 2019	AEM, OJ, CFC, ECC, MLB	94	17	12	22
Headwater islands	6–7, 9–12 Oct 2015; 16 Aug 2018; 1, 26–27 Sep 2018	AEM, OJ, CFC, AEH, GFS	150	118	35	31
Middle Ucayali River	6, 11 Dec 2015; 5, 8–9, 19, 23–24 Aug 2019	AEM, OJ, CFC, ECC, MLB, MGH	72	0	0	10
Headwater rivers	6–7, 12 Oct 2015; 14, 16, 24–25 Aug 2018; 10, 24 Sep 2018; 1–2 Oct 2018	AEM, OJ, CFC, AEH, GFS	79	0	0	28
Preferida	31 Jul 2019; 1, 5–20 Aug 2019	AEM, OJ, CFC, ECC, MLB, MGH	298	310	108	127
Laguna Juanacha	18, 21–22 Aug 2019	AEM, OJ, CFC, ECC, MLB, MGH	197	25	11	76
Quebrada Caco	6–9 Dec 2015	MGH, EB	191	22	14	0
Breu	13–17 Dec 2015	MGH, EB	248	39	25	0
Atalaya area	6, 8 Oct 2015	AEM, OJ, GFS	102	0	0	10
Oventeni area	2–4 Jul 2015; 18–22 Sep 2015; 1–4 Oct 2015	AEM, OJ, GFS	221	101	62	26
Sira foothills	9, 13 Oct 2015	AEM, OJ, GFS	133	13	8	30
Cushireni	25 Sep–1 Oct 2018	AEM, CFC, AEH	77	48	22	7
Mayapo	27 Sep–1 Oct 2018	AEM, CFC, AEH	160	20	16	13
Serjali	13–14 Sep 2018	AEM, CFC, AEH	82	20	14	2
Sepa	11–13 Sep 2018	AEM, CFC, AEH	88	19	13	7
Nuevo San Martín	16–22 Sep 2018	AEM, CFC, AEH	171	38	18	11
~30 km NW Sepahua	2–9 Sep 2018	AEM, CFC, AEH	221	51	25	45
Sepahua	17–24, 29–31 Aug 2018	AEM, CFC, AEH	215	62	29	56
Camisea	25–29 Aug 2018	AEM, CFC, AEH	97	18	5	8

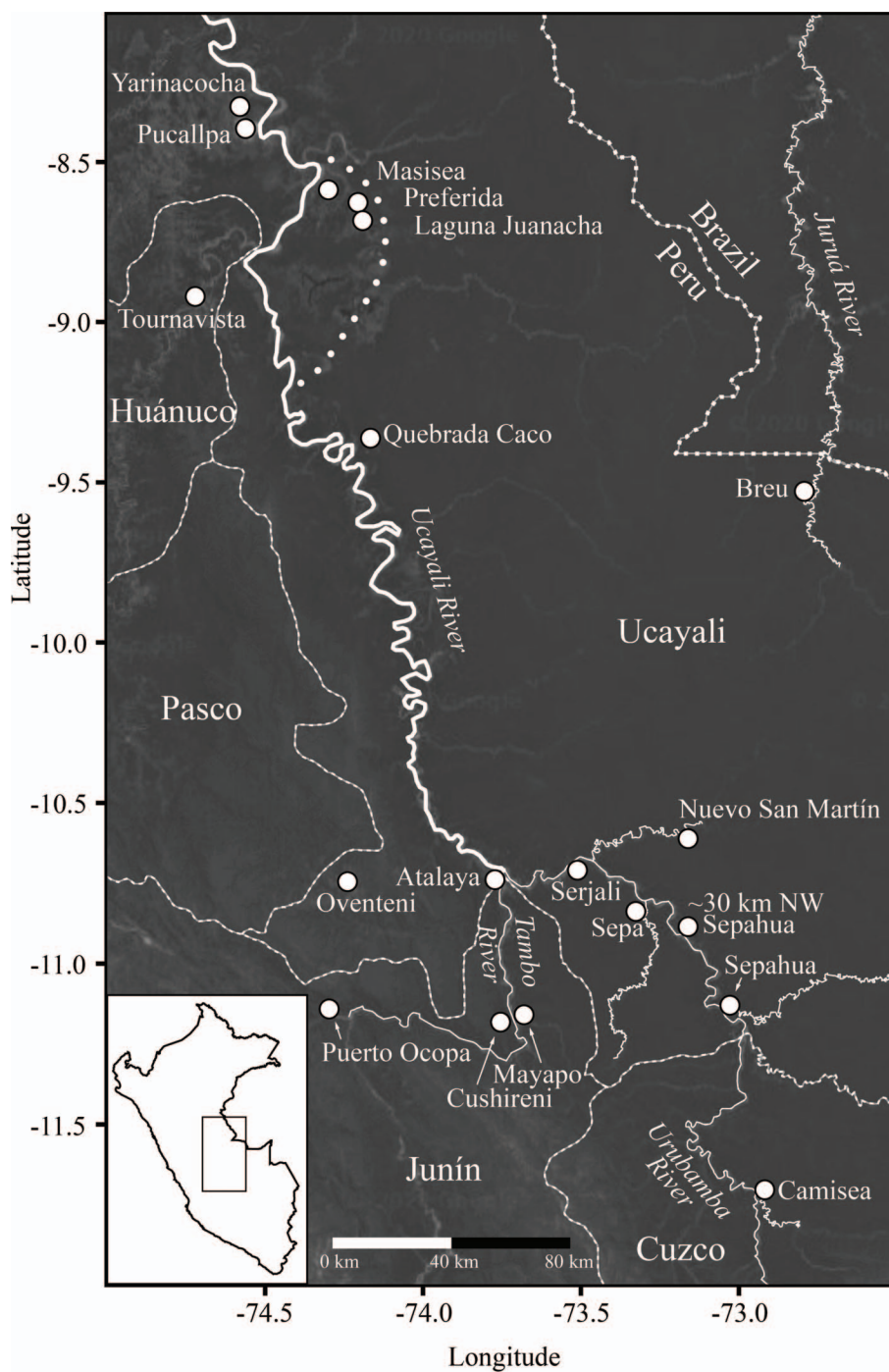
<sup>a</sup> Audio recording and/or photograph in Macaulay Library.

the Ucayali near the city of Atalaya. We also sampled along the upper Juruá River at Breu and at elevations up to 1,100 m in the Cerros del Sira foothills and Oventeni. Here we describe each of these 22 sites, which are listed roughly from north to south, with a few adjustments to cluster sites of the same habitat (rivers and riverine islands) or same riverbank/interfluvium.

*Yarinacocha*—Although it is located just north of Pucallpa, we present our surveys from Yarinacocha (8.344°S, 74.571°W; ~140 m elevation) as a distinct locality due to its historical importance as a research locality (e.g., O'Neill and Pearson 1974). We used boats to survey the eastern half of the lake, and we also traversed the eastern edge of the lake and adjacent forest by foot.

*Pucallpa area*—This locality includes surveys from within the city itself, such as around the Hotel Ecológico Manish, FAP Captain David Abensur Rengifo International Airport, and the principal Plaza de Armas, but also sites well outside the city. These more distant sites included a dirt track ~17 km SW Pucallpa (8.504°S, 74.638°W; ~160 m elevation) and sightings within the Ucayali Region along the principal roads between Pucallpa and Campoverde and between Campoverde and Tournavista.

*Tournavista area*—Survey effort for this locality was concentrated along a 2 km stretch of dirt road 13 km west of Tournavista (8.94°S, 74.83°W; ~240 m elevation), a town on the west bank of the Pachitea River, which served as our base during



**Figure 1.** Map of study area in the central Amazon of Peru. The dotted arc passing by the localities of Masisea, Preferida, and Laguna Juanacha denotes the approximate route of the Ucayali River prior to the Ucayali avulsion (see Pärssinen et al. 1996).

fieldwork. Although this stretch of road provided access to some of the most extensive patches of *terra firme* forest in the area, the habitat was highly fragmented and interspersed with open agricultural areas. Forest clearing and road building were actively taking place in the immediate surroundings. This locality also includes observations from within the Huánuco Region along the road between Tourmavista and Campoverde. The habitat along this road was open agriculture with scattered trees and occasional small roadside marshes, several of which we stopped to survey.

*Masisea island*—This locality refers to a 215 ha island in the Ucayali River ~10 km north of the town of Masisea. The island was near the east bank, from which it was mostly separated by a narrow channel (satellite imagery revealed that the southern end of the island had recently connected to the mainland shore). Our surveys covered the grassy perimeter and small patches of *Cecropia* (Urticaceae) on the eastern side of the island (8.514°S, 74.309°W). The thick vegetation (mostly grasses) and lack of trails made for difficult work conditions and prevented access to some of the larger patches of *Cecropia*.

*Headwater islands*—For our surveys of islands in the Tambo, Urubamba, and upper Ucayali Rivers, we targeted those not visited by Harvey et al. (2014b). We visited 2 islands downriver of Atalaya on the Ucayali River: Isla Cetical (10.642°S, 73.841°W) and Isla del Gallo (10.675°S, 73.797°W). On the Urubamba River we visited 3 islands to the east of Atalaya (Isla Escondida, 10.737°S, 73.606°W; Isla Pukani, 10.692°S, 73.543°W; and an unnamed island, 10.721°S, 73.566°W) and an island farther upriver near Sepahua (Isla Pajuya, 11.066°S, 73.105°W). We also surveyed the gravel beaches of a complex set of small islands in the Tambo River (11.164°S, 73.710°W) but did not have a chance to survey the island interiors. Three of the islands visited (Cetical, del Gallo, and Escondida) were moderate in size (150–400 ha) and contained typical riverine island scrub habitat: a mix of mature *Cecropia* forest at the island center, with scrub of decreasing stature toward the periphery dominated by *Gynerium* (Poaceae) cane and *Tessaria* (Asteraceae) shrubs. Isla Pajuya was smaller in size (35 ha) but with habitat similar to that of the islands described above. Isla Pukani was larger in size (290 ha), and

its forest was taller, taking on a more *várzea*-like stature. Finally, the unnamed island in the Urubamba River was small (25 ha) and little more than a gravel bar with scattered forbs and grasses. Both Isla Pukani and Isla del Gallo were close to the riverbank and appeared to be merging with the shoreline. Every surveyed island larger than 50 ha contained some amount of habitat clearing for agricultural use.

*Middle Ucayali River*—To access other field sites we regularly traveled along the middle Ucayali River in boats, and we took advantage of these trips to document birds along the riverbanks and gravel bars. All surveys for this locality were along the stretch of river between Pucallpa and Masisea, except for one between the mouth of the Pachitea River and Quebrada Caco (see locality below).

*Headwater rivers*—Our extensive boat travel along the upper Ucayali River around Atalaya, Urubamba River (from Atalaya to Camisea), and Tambo River (between Atalaya and Puerto Ocopa) provided opportunities to survey birds along the riverbanks and gravel bars. In this locality, we also have included sightings from the Atalaya waterfront.

*Preferida*—This locality includes surveys at an established camp on land of the Shipibo community of Preferida de Charasmaná (which locals referred to simply as “Preferida”), 10.8 km southeast of Masisea (8.685°S, 74.250°W; 150 m elevation). It also includes a few surveys in the town of Masisea and along the roads in the immediate area. This site is in the eastern portion of the ~2,000 km<sup>2</sup> land area passively transported from the west to the east bank of the Ucayali River by the Ucayali avulsion. The primary habitat was tall, relatively intact *terra firme*-like forest, but included some forest in swampy terrain, agricultural fields, and edge habitats.

*Laguna Juanacha*—We launched a boat from the lakeside town (*caserío*) of Charasmaná (8.693°S, 74.206°W; not to be confused with the community of Preferida de Charasmaná detailed above) to survey the northeastern end of Laguna Juanacha and surrounding forest (8.694°S, 74.201°W; 155 m elevation). Surveys for this locality also involved a short trip along the Tamaya River to Cocha Larga (8.679°S, 74.191°W), an oxbow lake 2 km northeast of Charasmaná. In contrast to Cocha Larga, Laguna Juanacha is a blocked valley lake

formed during the Ucayali avulsion (Neller et al. 1992). The habitat in the area surrounding Laguna Juanacha and nearby Cocha Larga was largely *igapó* forest. We visited during the dry season, but high-water markings suggest that much of this forest is flooded to a depth of ~1.5–2 m for part of the year. Near Laguna Juanacha the understory was particularly open, but near Cocha Larga the understory was dense and viny. Cocha Larga was marsh-like with little open water, whereas Laguna Juanacha held extensive open water. Large mats of aquatic vegetation along parts of Laguna Juanacha were dominated by *Polygonum* sp. (Polygonaceae) or a close relative, and the forested margins of the lake were of particularly short stature (~5–7 m).

*Quebrada Caco*—Our surveys at this locality (9.403°S, 74.163°W; 160–170 m elevation) in 2015 covered the lower stretch of this blackwater creek immediately upstream from the town of Pueblo Nuevo del Caco. Habitats surveyed included a large area of seasonally flooded scrubby swamp and grasslands and nearby seasonally flooded forest (*igapó*).

*Breu*—This locality lies near the Brazil border and is the only Peruvian town in the watershed of the Juruá River (9.534°S, 72.762°W; 240 m elevation). We conducted surveys near town on both sides of the Juruá River, covering habitats including floodplain forest (*várzea*) with some extensive swamps and *terra firme* forest on hilly terrain containing many clearings and viny tangles.

*Atalaya area*—Our surveys for this locality were limited to a marsh 10 km south of Atalaya (10.821°S, 73.760°W) and nearby low foothill forest at ~500 m elevation (10.820°S, 73.771°W) on 8 October 2015. We also include incidental records within the city of Atalaya.

*Oventeni*—We surveyed a marsh, *pajonales* (grasslands), and forest patches below 1,100 m elevation around Oventeni (10.759°S, 74.221°W; 1,000 m elevation), the principal town in the Gran Pajonal, and the Ashéninka community of Kirahuanero (10.699°S, 74.218°W; 6.5 km to the north). For most of our time in the Oventeni area we were based at a camp on the eastern edge of Kirahuanero.

*Sira foothills*—This locality encompasses numerous sites (700–1,100 m elevation) along the primary dirt road between Puerto Ocopa and Atalaya. We stopped regularly along this road to conduct short surveys and to collect specimens but

did not establish any camps. Stops included a logging track in humid forest ~20 km southwest of Atalaya (10.915°S, 73.905°W; 880 m elevation), scrubby dry forest 22.3 km southeast of Oventeni (10.904°S, 74.082°W; 800 m elevation), a *pajonal* 19.4 km southeast of Oventeni (10.894°S, 74.104°W; 1,060 m elevation), and humid forest 15.4 km south of Oventeni (10.899°S, 74.195°W; 780 m elevation).

*Cushireni*—We based our work along the Tambo River from our camp (11.153°S, 73.724°W) on the west bank ~5 km downriver from the Ashéninka community of Cushireni (11.197°S, 73.708°W). We boated most days to the community itself to access their well-maintained trails. The primary habitat was tall foothill forest, which we surveyed up to 450 m elevation. We also surveyed edge habitats around agricultural clearings.

*Mayapo*—We conducted surveys in a variety of habitats around the Ashéninka community of Mayapo (11.171°S, 73.694°W; 275 m elevation), including transitional *várzea/terra firme* forest, young second-growth and edge habitats around clearings, and small tracts of *Guadua* bamboo. To survey mature *terra firme* forest (400 m elevation), AEM also dedicated 2 d along the well-maintained trail connecting the communities of Mayapo and Nazareth and spent a single night on the trail ~9 km east of Mayapo (11.154°S, 73.614°W).

*Serjali*—We established a camp near this small town on the west (left) bank of the Urubamba River ~25 km east of Atalaya (10.715°S, 73.525°W). We focused our surveys primarily on the transitional *várzea/terra firme* forest ~2 km inland from the river (280 m elevation).

*Sepa*—We established a camp on the west bank of the Sepa River about 2 km upstream from the mouth (10.835°S, 73.296°W). The river was shallow in many places (~0.5 m) during our mid-September visit, and it was only by unloading and frequently pushing our boat that we reached our field site. We surveyed *várzea* and hilly *terra firme* forests as well as clearing edges (230–365 m elevation).

*Nuevo San Martín*—Our camp along the Inuya River was based on the south bank in the Amahuaca community of Nuevo San Martín (10.587°S, 73.173°W; 210 m elevation). We surveyed pristine *terra firme* habitats on both the south and north banks of the Inuya River, with the

north bank being notably hilly (up to 250 m elevation). We also surveyed several small tracts of bamboo on both banks, edge habitats surrounding the community, and the river margins.

~30 km NW Sepahua—Our camp at this locality (10.911°S, 73.175°W; 250 m elevation) was located on the east bank of the Urubamba River on the edge of extensive *várzea* forest. We established a trail northeast to a small oxbow lake (10.903°S, 73.168°W) and continued until reaching logging trails that allowed for easier hiking. As we hiked into slightly higher elevations, we encountered vast tracts of *Guadua* bamboo. We established a satellite camp (10.889°S, 73.161°W), where we stayed for 6 nights, in a large bamboo tract ~3 km northeast of our principal camp. From the satellite camp we also accessed hilly *terra firme* forest farther north (10.884°S, 73.163°W; 300 m elevation).

Sepahua—We established 3 different camps near the town of Sepahua (11.144°S, 73.044°W) in 2018: first at ~9 km southeast of Sepahua on the east bank of the Urubamba River (11.193°S, 72.979°W; 17–20 August; 270 m elevation); second at 10 km east-southeast of Sepahua on the south bank of the Sepahua River (11.165°S, 72.957°W; 20–24 August; 290 m elevation); and third at 10.5 km east-southeast of Sepahua on the north bank of the Sepahua River (11.165°S, 72.952°W; 29–31 August; 290 m elevation). The terrain at the first camp rose steeply from the river and allowed us to quickly reach hilly *terra firme* forest up to just over 400 m elevation. Treefall gaps were common, perhaps related to the steepness of the terrain, which fostered thick undergrowth and viny tangles. There was also an overgrown *chacra* with similarly dense habitat. The second camp was situated in relatively intact habitat (some evidence of selective logging) with easy access to rolling *terra firme* forest. The nearby third site was at the edge of an overgrown *chacra*, but upon hiking north from camp this quickly transitioned to hilly *terra firme* forest, which we surveyed up to 330 m elevation.

Camisea—Our Camisea camp (11.726°S, 72.921°W) was located on the north (right) bank of the Camisea River ~4 km southeast of the community of Camisea. From this base, we focused our surveys in hilly *terra firme* forest on both banks of the river (up to 400 m elevation on

the north bank) but also surveyed birds in the river-edge forest around camp.

### Fieldwork

Daily fieldwork consisted of a combination of mist-netting throughout the day and audiovisual surveys concentrated in the mornings and evenings. To collect specimens, we deployed mist nets and used shotguns. We also obtained sound recordings and photos of as many species as possible. We prepared study skins for most specimens and prepared a smaller number as skeletons. For all specimens, we flash-froze pectoral muscle, heart, and liver tissues in liquid nitrogen, with additional muscle and stomach content samples preserved in ethanol. For at least 1 individual per species, we also preserved the lower intestine in liquid nitrogen for gut microbiota studies. We submitted complete lists of species observed, often several per day, to the Avian Knowledge Network through the eBird portal (Sullivan et al. 2009), which is freely accessible online. We uploaded our bird photographs and audio recordings to the Macaulay Library (<https://www.macaulaylibrary.org>) through the eBird portal. ML numbers in the below text refer to supporting media archived online at the Macaulay Library and XC numbers refer to supporting audio recordings archived online at <https://www.xeno-canto.org>. LSUMZ numbers refer to catalogued specimens in the bird collection at the LSUMNS (formerly the Louisiana State University Museum of Zoology). We follow Remsen et al. (2021) for English and scientific names of birds.

### Results

We detected 657 species and collected 980 specimens of 294 species (Table 1; see Supplemental Table S1 for complete species list). We evenly divided specimen collections between CORBIDI and LSUMNS, and both institutions received tissue samples for all individuals. Below we describe avian communities associated with major habitat types and summarize novel biogeographic patterns. More detailed accounts for notable species are included in the Supplemental Appendix.



### Avifauna by habitat types

*Birds of upland/terra firme forest*—Our most intensive surveys in *terra firme* forest occurred around the Preferida camp within the area of land transported by the Ucayali avulsion. The forest here was swampier and had a thicker understory than is typical of *terra firme*. We detected species typical of *terra firme* forest such as White-throated Tinamou (*Tinamus guttatus*), Black-bellied Cuckoo (*Piaya melanogaster*), Blue-cheeked Jacamar (*Galbula cyanicollis*), Paradise Jacamar (*Galbula dea*), Spot-winged Antbird (*Myrmelastes leucostigma*), Blue-crowned Manakin (*Lepidothrix coronata*), White-crested Spadebill (*Platyrinchus platyrhynchos*), and Brownish Twistwing (*Cnipodectes subbrunneus*) but also some species typical of *várzea* or transitional forests such as Cinereous Tinamou (*Crypturellus cinereus*), Spotted Puffbird (*Bucco tamatia*), Rufous-necked Puffbird (*Malacoptila rufa*), White-shouldered Antbird (*Akletos melanoceps*), Band-tailed Manakin (*Pipra fasciicauda*), and Gray-crowned Flycatcher (*Tolmomyias poliocephalus*). Interestingly, this site also harbored some local species typical of forest on nutrient-poor soil such as Brown-banded Puffbird (*Notharchus ordii*) and Citron-bellied Attila (*Attila citriniventris*).

Other *terra firme* sites sampled on both banks of the Ucayali, Tambo, and Urubamba rivers overlapped with Preferida in avian species composition, but generally had more open understory and hilly terrain that reached higher elevations relative to the floodplain. This was likely responsible for the detection of additional *terra firme* bird species (Supplemental Table S1). In the foothills of the Sira these included notable species such as Foothill Elaenia (*Myiopagis olallai*) and Blackish Pewee (*Contopus nigrescens*), both of which are poorly known in central Peru (see Supplemental Appendix). In contrast to most *terra firme* sites, forest at our principal Tournavista site west of the Ucayali River was severely fragmented. Bird diversity was still high, and we encountered most of the common species detected in *terra firme* sites elsewhere. We failed, however, to detect some expected taxa including antthrushes (*Formicarius* spp.), Long-tailed Woodcreeper (*Deconychura longicauda*), White-chinned Woodcreeper (*Dendrocincla merula*), Wedge-billed Woodcreeper (*Glyphorynchus spirurus*), foliage-gleaners (*Phil-*

*ydor* and *Automolus* spp.), and Pipridae spp. (except for one male Blue-crowned Manakin). Further work is needed to identify whether these absences from the avian community are associated with fragmentation, which can lead to reduced diversity and even extirpation of mixed-species flocks (Rutt et al. 2020), or are due to limited sampling.

*Birds of floodplain/várzea forest*—Our surveys of *várzea* forest were restricted mostly to the banks of the Urubamba River. We surveyed this habitat most thoroughly near our camp ~30 km northwest of Sepahua, but our mist-netting and general survey efforts were limited in this habitat compared to those in *terra firme* forest at this and other sites. Still, we detected many species typical of *várzea* forest (Supplemental Table S1). We also detected in this habitat several species typical of *terra firme* forest, notably 2 Fulvous-chinned Nunlets (*Nonnula sclateri*) captured in mist nets a few meters up-bank from the river at our camp ~30 km northwest of Sepahua.

*Birds of blackwater flooded forests/igapó*—Our surveys at Quebrada Caco, Laguna Juanacha, and Cocha Larga are the most extensive conducted in blackwater habitats in the central Amazon of Peru. The previous lack of attention paid to this habitat is highlighted by our detection of 5 new species for the Ucayali Region in just 3 d of fieldwork: Band-tailed Nighthawk (*Nyctiprogne leucopyga*), Green-tailed Goldenthrout (*Polytmus theresiae*), Yellow-chinned Spinetail (*Certhiaxis cinnamomeus*), Amazonian Black-Tyrant (*Knipolegus poecilocercus*), and Gray-chested Greenlet (*Hylophilus semicinerus*). The avifauna at these sites resembles that noted in blackwater habitats at the Pacaya-Samiria National Reserve in the Loreto Region (Begazo and Valqui 1998). Characteristic forest species included Scarlet-crowned Barbet (*Capito aurovirens*), Plain-breasted Piculet (*Picumnus castelnaui*), Black-crested Antshrike (*Sakesphorus canadensis*), Amazonian Antshrike (*Thamnophilus amazonicus*), Stripe-chested Antwren (*Myrmotherula longicauda*), Black-tailed Antbird (*Myrmoborus melanurus*; at Cocha Larga), Yellow-crowned Elaenia (*Myiopagis flavivertex*), and Cinnamon Attila (*Attila cinnamomeus*). Green-tailed Golden-throat and Gray-chested Greenlet were common components of the avifauna in scrubby lakeside forest at Laguna Juanacha, and Band-tailed Nighthawk was abundant in the hour before dawn,

singing from lakeside vegetation and foraging over the lake. Additional species in edge and scrub habitats included Cinereous Becard (*Pachyrampus rufus*) and Dot-backed Antbird (*Hylophylax punctulatus*) at Quebrada Caco and Amazonian Black-Tyrant at Laguna Juanacha. Dense floating stands of aquatic *Polygonum* vegetation seemed to be the preferred habitat for Yellow-chinned Spine-tail, and Pied Water-Tyrant (*Fluvicola pica*) was also present at lake margins.

*Birds of Guadua bamboo*—During fieldwork in 2018 along the headwaters of the Ucayali, we detected most of Kratter's (1997) avian specialists of *Guadua* bamboo habitats of the southwestern Amazon Basin. The composition of the bamboo bird communities surveyed varied greatly depending on the extent of bamboo present. The largest and most mature bamboo tract was ~30 km northwest of Sepahua (10.889°S, 73.161°W; 300 m elevation) and ~3 km northeast of our camp on the bank of the Urubamba River. This tract extended for ~1 km along a trail and was composed of dense, ~10 m tall bamboo, bordered by *terra firme* forest to the northeast and cleared pasture to the southwest. Obligate and near-obligate bamboo specialists (Kratter 1997, Lebbin 2013) detected at this site included Pavonine Cuckoo (*Dromococcyx pavoninus*), Yellow-billed Nunbird (*Monasa flavirostris*), Rufous-headed Woodpecker (*Ceileus spectabilis*), Striated Antbird (*Drymophila devillei*), Manu Antbird (*Cercomacra manu*), White-lined Antbird (*Myrmoborus lophotes*), Goeldi's Antbird (*Akletos goeldii*), Dusky-cheeked Foliage-Gleaner (*Anabazenops dorsalis*), Peruvian Recurvebill (*Syndactyla ucayalae*), Brown-rumped Foliage-Gleaner (*Automolus melanopezus*), Flammulated Pygmy-Tyrant (*Hemitriccus flammulatus*), White-cheeked Tody-Flycatcher (*Poecilatriccus albifacies*), and Large-headed (*Ramphotriccus megacephalum*) and Dusky-tailed (*R. fuscicauda*) flatbills. Several facultative bamboo-associated species (Kratter 1997, Lebbin 2013) were also present in the area, including Chestnut-capped Puffbird (*Bucco macrodactylus*), Rufous-breasted Piculet (*Picumnus rufiventris*), Red-billed Scythebill (*Campylorhamphus trochilirostris*), and Long-crested Pygmy-Tyrant (*Lophotriccus eulophotes*). Notably, this was the only site where we detected Pavonine Cuckoo, Yellow-billed Nunbird, and Peruvian Recurvebill.

The tracts of bamboo we surveyed elsewhere were smaller, but each generally contained at least

a few bamboo specialists. Around Nuevo San Martín, the bamboo occurred on both sides of the Inuya River (10.599°S, 73.171°W and 10.573°S, 73.190°W), and several specialists recorded here represent some of the northernmost records for their species in Peru (e.g., Manu Antbird and White-cheeked Tody-Flycatcher). The bamboo at Mayapo was part of a matrix of habitat that included *terra firme*, cleared cultivated land, and viny tangles near water. We found many bamboo specialists here (see Supplemental Table S1), including 2 species not detected elsewhere: Ornate Antwren (*Epinecrophylla ornata*) and the recently described Rufous Twistwing (*Cnipodectes super-rufus*; Lane et al. 2007). At our first Sepahua locality, we collected a pair of the typically bamboo-associated Bamboo Antshrike (*Cymbilaimus sanctaemariae*) in a matrix of *terra firme* and viny tangles but failed to detect this species in bamboo at any of our study sites.

*Birds of riverine islands*—The bird communities of the 5 typical riverine islands (Masisea, del Gallo, Cetical, Escondida, and Pajuya) were similar between islands and were dominated by a combination of obligate riverine island species—of which we detected 14 of the 18 species found in western Amazonia (Rosenberg 1990)—and species typical of open country and disturbed Amazonian habitats (Supplemental Table S1). We detected all of the island specialists found by Harvey et al. (2014b) and added Brownish Elaenia (*Elaenia pelzelni*) and Bicolored Conebill (*Conirostrum bicolor*), both of which were seen only on the Masisea island. Riverine island specialists detected at Isla Pajuya (near Sepahua) were Olive-spotted Hummingbird (*Leucippus chlorocercus*), Parker's Spinetail (*Cranioleuca vulpecula*), Castelnau's Antshrike (*Thamnophilus cryptoleucus*), and Black-and-white Antbird (*Myrmochanes hemileucus*), the latter 2 species representing the southernmost records in Peru. The avifauna of Isla Pukani had a distinctly *várzea*-like component, with species such as Silvered Antbird (*Sclateria naevia*) and Amazonian Antpitta (*Myrmothera berlepschi*). Little more than an exposed gravel bar, the small unnamed island in the Urubamba River was depauperate, but the riverine island specialists Lesser Hornero (*Furnarius minor*) and River Tyrannulet (*Serpophaga hypoleuca*) were both present despite the extremely young age of the island. In addition to the riverine

island specialists, we detected a variety of boreal migrant shorebird species, both austral and boreal migrant passerine species, and 3 intra-tropical migrant *Sporophila* species on riverine islands.

*Birds of open country and wetlands*—We conducted occasional avifaunal surveys of open agricultural habitats, which are rapidly increasing in extent in the central Peruvian Amazon, particularly in the greater Pucallpa area (Bax et al. 2016, Vijay et al. 2018). In addition to a variety of expected open country species (Supplemental Table S1), we observed Crested Caracara (*Cara-cara plancus*), a recently arrived species in the area (Piana et al. 2012; see Supplemental Appendix), on several occasions. Marshes within agricultural areas along the dirt road between Tournavista and Campoverde held a variety of waterbirds including less expected species such as Snail Kite (*Rostrhamus sociabilis*) and Pied Water-Tyrant (*Fluvicola pica*). Naturally occurring open habitats and wetlands around Lago Yarinacocha provide an important foraging area for birds near the city of Pucallpa (Supplemental Table S1). Boreal-breeding migratory shorebirds are poorly surveyed in the central Peruvian Amazon, but our observations suggest Lago Yarinacocha may be an important stopover site. On 20 August 2019 we encountered ~700 Pectoral Sandpipers (*Calidris melanotos*) and ~450 Lesser Yellowlegs (*Tringa flavipes*) at Yarinacocha, and on 31 August 2019 we encountered ~250 Stilt Sandpipers (*Calidris himantopus*) and ~800 Lesser Yellowlegs. At Yarinacocha we also documented American Golden-Plover (*Pluvialis dominica*), Buff-breasted Sandpiper (*Calidris subruficollis*), and Wilson's Phalarope (*Phalaropus tricolor*), and along the Ucayali River we noted Black-bellied Whistling-Duck (*Dendrocygna autumnalis*), Brazilian Teal (*Amazonetta brasiliensis*), Franklin's Gull (*Leucophaeus pipixcan*), and Puna Ibis (*Plegadis ridgwayi*), all species poorly known in the Peruvian Amazon (see Supplemental Appendix).

We conducted additional surveys of open country in the *pajonales* around Oventeni and on the Puerto Ocopa–Atalaya Road (~1,000–1,100 m), areas previously surveyed by Harvey et al. (2011). We found many species typical of open country in the lowlands, but we also detected some species only in this area including Spot-tailed Nightjar (*Hydropsalis maculicaudus*), Ocellated Crane (*Micropygia schomburgkii*), Russet-

crowned Crane (*Anurolimnas viridis*), Rusty-backed Antwren (*Formicivora rufa*), Cinereous-breasted Spinetail (*Synallaxis hypospodia*), Yellow-bellied Elaenia (*Elaenia flavogaster*), Lesser Elaenia (*Elaenia chiriquensis*), Yellow-browed Tyrant (*Satrapa icterophrys*; austral migrant), Black-faced Tanager (*Schistochlamys melanopsis*), Wedge-tailed Grass-Finch (*Emberizoides herbicola*), and Plumbeous Seedeater (*Sporophila plumbea*).

### Species turnover across rivers

We found that species distributions nearly all conformed to previous findings for river-limited taxa in the central Peruvian Amazon (Harvey et al. 2014b). Harvey et al. (2014b) noted 9 species pairs with distributions limited by the middle Ucayali, and our surveys largely support those findings. Even at Preferida, which was on the west bank of the Ucayali River until ~230–250 years ago (Pärssinen et al. 1996), we found almost entirely east-bank taxa, including Blue-cheeked Jacamar (*Galbula cyanicollis*), Fulvous-chinned Nunlet (*Nonnula sclateri*), Bar-breasted Piculet (*Picumnus aurifrons*), White-bellied Parrot (*Pionites leucogaster*), White-throated Antbird (*Oneillornis salvini*), White-bellied Tody-Tyrant (*Hemitriccus griseipectus*), and Moustached Wren (*Phlegopedius genibarbis*). However, we did find 2 apparent instances of west-bank taxa at Preferida: a specimen of Rufous-rumped Foliage-Gleaner (*Philydor erythrocerum*; LSUMZ 228870) that closely resembles the darker brown *P. e. subfulvum* from west of the Ucayali River rather than the expected *P. e. lyra* and a specimen of Double-banded Pygmy-Tyrant (*Lophotriccus vitiosus*; LSUMZ 228926) that shows gray crest margins similar to *L. v. vitiosus* from west of the river rather than the buffy or olive crest margins of *L. v. congener*, the expected taxon east of the river. In addition, we noted 2 striking cases of apparent hybridization in the area of the avulsion.

First, we found evidence of introgressive hybridization between White-bellied Parrot and Black-headed Parrot (*Pionites melanocephalus*) along the middle Ucayali River (Fig. 2a). Haffer (1977) had previously noted several specimens with characteristics intermediate between these species in eastern Peru: White-bellied Parrots with different combinations of scattered black crown



**Figure 2.** Specimens of 2 species pairs bounded by the Ucayali River show evidence of introgression across the river. In each panel, a blue line indicates the divide between west/left bank birds from Tournavista and east/right bank birds from Preferida, which is located within the patch of *terra firme* forest that was transported from the west bank to the east bank during the Ucayali avulsion. (a) *Pionites* parrots: Black-headed Parrot (*P. melanocephalus*) is expected on the west bank and White-bellied Parrot (*P. leucogaster*) on the east bank. The 3 west bank individuals (left to right: LSUMZ 228716, 228718, 228713) show largely *P. melanocephalus* phenotypes but with varying degrees of *leucogaster*-like traits: LSUMZ 228716 appears close to the parental type, but the other 2 show orange feathering in the forehead and crown and the amount of green in the lores is reduced, especially in LSUMZ 228713. Six individuals from the east bank at Preferida are shown (left to right: LSUMZ 228725, 228726, 228720, 228727, 228729, 228730). One east bank individual, LSUMZ 228725 (fourth from left overall), shows a *melanocephalus*-like phenotype, despite being on the “wrong” side of the Ucayali River. Like *P. melanocephalus* it has a fully black crown, bill, and orbital skin, but unlike *P. melanocephalus* it has very little green in the lores. Among the other more *leucogaster*-like individuals, there is substantial variation in the presence of *melanocephalus*-like traits, such as black feathers in the crown, dark coloring of the bill and orbital skin, and green feathers in the lores. (b) *Pheugopedius* wrens: Coraya Wren (*P. coraya*) is expected on the west bank and Moustached Wren (*P. genibarbis*) on the east bank. The individual from the west bank (LSUMZ 228997) is typical for *P. coraya*, with dark throughout the auriculars, malar, and lateral throat stripe and rich chestnut coloration on the flanks and belly. The 4 individuals from Preferida on the east bank (left to right: LSUMZ 228994, 228992, 228996, 228988) show variation in their facial patterns, including in the degree of white streaking in the auriculars and the extent to which a white malar divides the auriculars from the dark lateral throat stripe. The color of the flanks also varies, but interestingly does not seem to correspond with the face pattern: the individual with the most *coraya*-like face pattern (LSUMZ 228994) has among the lightest and least extensive chestnut coloration on the underparts.

feathers, dark orbital skin, and dusky bill east of the Ucayali River and a Black-headed Parrot (AMNH 237774) with rusty orange on the forecrown whose date of collection (5 August

1927) suggests it was east of the Ucayali River (see Wiley 2010). Some of the specimens we collected showed similar morphological intermedicity. In our series of 10 adult White-bellied

Parrot-like individuals from Preferida, we found that 6 had variable but substantial amounts of black feathering on the hind-crown and 4 had essentially pure, rusty orange crowns. Three individuals from this series displayed particularly dark orbital skin and 6 had noticeably dusky coloration on their bills, but these traits were quite variable. Some individuals (e.g., LSUMZ 228727 and 228729) also had a few scattered green feathers in the lores. Also at our Preferida camp, we collected an 11th *Pionites* that appeared more like an adult Black-headed Parrot (LSUMZ 228725) with a fully black crown, bill, and orbital skin, yet with very limited greenish in the lores. In our series of 7 adult Black-headed Parrot-like individuals from Tournavista, we also observed variable amounts of black feathering on the crown, with several individuals having a fully black crown and several showing extensive rusty orange on the forecrown. This suggests introgression with White-bellied Parrot, a species that remains undocumented west of the middle Ucayali River. A recent photograph in an eBird report indicates presence of some White-bellied Parrot-like individuals west of the lower Ucayali (Rowland 2018; ML216708631), and Harvey et al. (2014b) documented White-bellied Parrot west of the upper Ucayali. Although we currently lack confirmatory genetic data, we suggest that the phenotypes of birds sampled here are indicative of substantial introgression not just around the Ucayali avulsion, but more widely in the middle Ucayali Valley. The observation that adult White-bellied Parrots can have scattered black feathers on the crown up to nearly 500 km southeast of the Amazon River in northeastern Pará, Brazil (Novaes 1981), may suggest either that introgression occurs far from zones of potential contact, or that phenotypic variation within White-bellied Parrot is complex. Further collections and high-quality photographs of *Pionites* are greatly needed to assess plumage variation in and away from contact zones.

Second, we found that Coraya Wren (*Pheugopedius coraya*) and Moustached Wren appear to hybridize across the middle Ucayali River (Fig. 2b). Previous studies suggested this might be the case: O'Neill and Pearson (1974) noted both species at Yarinacocha and Schulenberg et al. (2010) noted intergradation in plumage features of birds on the west bank of the Ucayali. At our Preferida site, on the east bank, we collected a

series of 9 *Pheugopedius* wrens that exhibit substantial variation in the extent of white streaking on the auriculars (mostly like Moustached Wren but in some individuals approaching the mostly black auriculars of the Coraya Wren phenotype). In this series, variation was also notable in the extent of the white malar stripe directly above (and which highlights) the black lateral throat stripe characteristic of Moustached Wren. In some cases, the white malar stripe was essentially absent or faint, which resulted in nearly continuous black feathering from the lateral throat stripe to the auriculars in several individuals. These intermediate plumage features in the Preferida series suggest hybridization. The single individual of Coraya Wren that we collected at Tournavista (LSUMZ 228997) shows the expected limited white streaking in the auriculars and lacks the white malar stripe. Vocal evidence also suggests hybridization between Coraya and Moustached wrens on the left bank of the Ucayali River. The populations of Coraya Wren in lowland Amazonia (*P. c. amazonicus*) and foothills of San Martín (*P. c. albiventris*) west of the Ucayali River and south of the Marañón River give the *djeer djeer* call (e.g., ML190519 and P. Boesman recording XC230995) that is typical of Moustached Wren and is lacking in Coraya Wren populations (e.g., *P. c. griseiventris* and *P. c. coraya*) north of the Marañón and Amazon Rivers and farther east (DFL, pers. obs.). This shared call between taxa across the Ucayali River seems most plausibly explained by a scenario of extensive gene flow, although, because call learning has been documented in oscine passerines (Löhr 1963, Bertram 1970, Munding 1979, Zann 1985), it is conceivable that this pattern is due to a shared and learned dialect.

### Notable distributional records

We documented first regional records of 28 bird species across the Ucayali (18), Huánuco (3), and Junín (7) regions (Table 2) and numerous other geographic range extensions with implications for patterns of avian diversity and taxonomy (see Supplemental Appendix). Many of these notable records derive from our sampling of poorly known habitats in the area, particularly blackwater wetland systems, *Guadua* bamboo tracts, and riverine islands. Both blackwater systems and

**Table 2.** Summary of first regional records in the central Amazon of Peru in 2015, 2018, and 2019. Abbreviations: S = specimen, M = media (audio recording and/or photograph in Macaulay Library), X = only detected visually and/or aurally.

Common name	Scientific name	Region	Habitat type	Documentation
Band-tailed Nighthawk	<i>Nyctiprogne leucopyga</i>	Ucayali	Blackwater wetland	S, M
White-chinned Swift	<i>Cypseloides cryptus</i>	Ucayali, Huánuco	Aerial	M
Green-tailed Goldenthrout	<i>Polytmus theresiae</i>	Ucayali	Blackwater wetland	S, M
Wire-crested Thorntail	<i>Discosura popelairii</i>	Ucayali	Foothill forest	X
Semipalmated Plover	<i>Charadrius semipalmatus</i>	Ucayali	Riverine marsh/beach	X
Killdeer	<i>Charadrius vociferus</i>	Ucayali	Riverine marsh/beach	X
Wilson's Phalarope	<i>Phalaropus tricolor</i>	Ucayali	Riverine marsh/beach	S, M
Franklin's Gull	<i>Leucophaeus pipixcan</i>	Ucayali	Ucayali River	X
Bamboo Antshrike	<i>Cymbilaemus sanctaemariae</i>	Ucayali	<i>Terra firme</i> forest	S, M
Yellow-breasted Antwren	<i>Herpsilochmus axillaris</i>	Ucayali	Foothill forest	S, M
Dot-backed Antbird	<i>Hylophylax punctulatus</i>	Ucayali	Blackwater wetland	S
Yellow-chinned Spinetail	<i>Certhiaxis cinnamomeus</i>	Ucayali	Blackwater wetland, river island	S, M
Brownish Elaenia	<i>Elaenia pelzelni</i>	Ucayali	River island	S, M
Torrent Tyrannulet	<i>Serpophaga cinerea</i>	Ucayali	Foothill stream	X
Blackish Pewee	<i>Contopus nigrescens</i>	Ucayali	Foothill forest	S, M
Amazonian Black-Tyrant	<i>Knipolegus poecilocercus</i>	Ucayali	Blackwater wetland	S
Gray-chested Greenlet	<i>Hylophilus semicinereus</i>	Ucayali	Blackwater wetland	S, M
Southern Martin	<i>Progne elegans</i>	Ucayali	Aerial	M
Needle-billed Hermit	<i>Phaethornis philippii</i>	Huánuco	<i>Terra firme</i> forest	X
Variiegated Flycatcher	<i>Empidonomus varius</i>	Huánuco	<i>Terra firme</i> forest edge	M
Black-and-white Hawk-Eagle	<i>Spizaetus melanoleucus</i>	Junín	Foothill forest	M
Undulated Antshrike	<i>Frederickena unduliger</i>	Junín	<i>Terra firme</i> forest	M
Manu Antbird	<i>Cercomacra manu</i>	Junín	<i>Guadua</i> bamboo	S
Brown-rumped Foliage-gleaner	<i>Automolus melanopezus</i>	Junín	<i>Guadua</i> bamboo	S, M
Striolated Manakin	<i>Machaeropterus striolatus</i>	Junín	Foothill forest	S, M
Black-backed Tody-Flycatcher	<i>Poecilatriccus pulchellus</i>	Junín	Dense, second-growth forest	S
Shiny Cowbird	<i>Molothrus bonariensis</i>	Junín	Marsh	M

riverine islands have been extensively surveyed north of our study area along the lower Ucayali and upper Amazon rivers in the Loreto Region (Remsen and Parker 1983, Rosenberg 1990, Begazo and Valqui 1998, O'Shea et al. 2015, Socolar et al. 2018). Thus, the range extensions for birds in these habitats were all southward (~230–600 km). In contrast, our surveys in *Guadua* bamboo extended the known ranges of several specialists north and/or west from sites in the Cuzco and Madre de Dios regions (Kratzer 1997, Parker et al. 1997, Lebbin 2007, Harvey et al. 2014a) and from Balta in far eastern Ucayali (O'Neill 1974, 2003).

## Discussion

Our surveys in the central Amazon of Peru highlight a remarkably diverse avifauna and provide new information about how this diversity is partitioned across habitats and biogeographic

barriers. We found that, despite a long history of ornithological work in the area, visits to under-surveyed habitats revealed many species not previously detected. These results emphasize the importance of habitat specialization to Amazonian birds and the need for greater attention to the characteristics of surveyed habitats, including soil conditions, which have a key but underappreciated influence on avian distributions (Whitney and Alvarez 1998). Our results also refine the locations of range limits and contact zones with respect to rivers and the Cerros del Sira, pointing to additional geographic sampling priorities and revealing preliminary evidence of some biogeographic stability even in a dynamic landscape.

Our surveys were the most extensive to date in blackwater wetland systems, *Guadua* bamboo tracts, and riverine islands in the central Peruvian Amazon. However, these were still insufficient to develop a complete picture of the avian diversity of these habitats. Future surveys in blackwater

systems should target species such as Masked Duck (*Nomonyx dominicus*), Zigzag Heron (*Zenaidura macroura*), Rufous Potoo (*Nyctibius bracteatus*), Three-striped Flycatcher (*Conopias trivirgatus*), Sulphur-bellied Tyrant-Manakin (*Neopelma sulphureiventer*), and Orange-crowned Manakin (*Heterocercus aurantiivertex*) that are as yet unrecorded or are very poorly known in the area. The blackwater systems within the Área de Conservación Regional Imiría are even more extensive than the ones we visited and are a high priority for future surveys. The 4 obligate riverine island species still unrecorded in Peru's central Amazon are Ash-breasted Antbird (*Myrmoborus lugubris*), Leaden Antwren (*Myrmotherula assimilis*), Pale-billed Hornero (*Furnarius torridus*), and Pearly-breasted Conebill (*Conirostrum margaritae*), and they should be searched for especially on larger islands near Pucallpa. Zimmer's Woodcreeper (*Dendroplex kienerii*) is also found on riverine islands in northern Peru (Moncrieff et al. 2019) and should be looked for farther south. Similarly, *Guadua* bamboo tracts likely hold several species not yet documented or very poorly known in the area such as Ihering's Antwren (*Myrmotherula iheringi*), Slate-colored Seedeater (*Sporophila schistacea*), and the newly described Acre Tody-Tyrant (*Hemitriccus cohnhaffti*; Zimmer et al. 2013), a species only recently documented for Peru in the Madre de Dios Region (Harvey et al. 2014a). Stunted white-sand forests, a habitat type we did not visit during this fieldwork, remain a glaring gap for avifaunal surveys throughout most of the central Peruvian Amazon. The only surveys of this habitat in the area so far are along the Cohengua River (Harvey et al. 2014b), where records of Zimmer's Tody-Tyrant (*Hemitriccus minimus*), "Campina" Fuscous Flycatcher (*Cnemotriccus fuscatus duidae*), Yellow-throated Flycatcher (*Conopias parvus*), and Black Manakin (*Xenopipo atronitens*) remain over 200 km from the nearest records in Acre, Brazil (Whittaker and Oren 1999, Guilherme and Borges 2011).

In addition to its close association with habitat diversity, avian diversity in the study area is tied to landscape features, particularly the Ucayali River. We found that patterns of species replacement across the Ucayali were generally consistent with those observed previously (Harvey et al. 2014b), but the apparent presence of 2 subspecies on the "wrong" bank and hybridization in 2 species pairs

along the middle Ucayali suggests more complicated biogeographic histories in some species. Events such as the Ucayali avulsion of the 18th century have likely occurred regularly over the history of the river drainage (Pärssinen et al. 1996), passively transferring populations of birds to the "wrong" bank of the river. Despite the recent transfer of ~2,000 km<sup>2</sup> of land, including *terra firme* forest, to the east side of the river during the Ucayali avulsion, we found that most avian populations within this landmass morphologically matched the east bank species. This suggests that patterns of avian replacements around river barriers can recalibrate even after large-scale barrier adjustments. We suspect that the small populations of west bank birds that were passively transferred during the Ucayali avulsion quickly died out or were genetically swamped by the large populations of east bank birds. Future genetic work may provide additional clues about the fate of those populations and reveal insight into the impacts of landscape dynamics on populations.

Our knowledge of how habitat diversity and landscape features influence patterns of avian diversity helps to predict patterns in unsurveyed areas, but we emphasize that sometimes expected species simply do not occur at apparently suitable sites. Given our current limited data, it is often impossible to distinguish between true species absence and insufficient sampling. For example, our targeted surveys for Blue-crowned Manakins in *terra firme* at multiple localities in the Tambo-Urubamba interfluvium failed to detect any individuals, but we hesitate to suggest species absence from such a large area. A single specimen (AMNH 240618) collected by the Olalla brothers in 1927 from "Boca Rio Urubamba" appears to indicate presence of the species in the interfluvium, but modern verification is highly desirable. A second specimen from the same locality (AMNH 407206) appears to be from the problematic Harvey Bassler collection in which locality information is of dubious origin (see Wiley 2010). As we continue to conduct surveys, we ultimately hope to confidently identify distribution gaps and limits. In addition to species absence, species turnover away from rivers generally remains a mystery. For example, many pairs of related taxa including Red-billed/Rufous-vented Ground-Cuckoo (*Neomorphus pucheranii/N. geoffroyi*), Needle-billed/Straight-billed Hummingbird (*Phaethornis philip-*

*pii/P. bourcierii*), Rusty-breasted/Fulvous-chinned Nunlet (*Nonnula rubecula/N. sclateri*), Saturnine/Dusky-throated Antshrike (*Thamnomanes saturninus/T. ardesiacus*), White-eared/Purus Jacamar (*Galbalcyrhynchus leucotis/G. purusianus*), and Rufous-backed/Rio Madeira Stipplethroat (*Epinecrophylla haematonota/E. amazonica*) appear to turn over in continuous forest of central Peru east of the Ucayali River (Schulenberg et al. 2006, Del-Rio et al. 2021, Johnson et al. 2021), highlighting the need for finer resolution data to further investigate these biogeographic patterns.

Despite the high diversity and comparatively pristine condition of the central Peruvian Amazon, serious conservation issues plague the area. The most notable center of habitat loss is around the city of Pucallpa and along the Federico Basadre Highway (ruta nacional PE-18 C), a road established in the 1940s and a major determinant of regional deforestation patterns (Ichikawa et al. 2014, Bax et al. 2016). Perhaps foremost among the emerging threats to regional biodiversity is the rapid expansion of oil palm plantation monocultures in Peru (Vijay et al. 2018), which have been documented to hold depauperate bird communities around Pucallpa and farther abroad in Amazonia (Lees et al. 2015, Srinivas and Koh 2016). Although more focused in its effect, Pucallpa's thriving illegal animal trade also poses a conservation threat to numerous species of birds—primarily parrots (Gastañaga et al. 2011, Daut et al. 2015). Even now, the biggest asset for conservation of the central Peruvian Amazon is the very remoteness that has limited ornithological work. As this remoteness ebbs, efforts to avert catastrophic loss of avian diversity will benefit from a more complete understanding of regional avian diversity, habitat associations, and biogeography.

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