Noteworthy bird records from northeastern Peru reveal connectivity and isolation in the western Amazonian avifauna

Author(s): Jacob B. Socolar, Juan Díaz-Alván, Percy Saboya Del Castillo, Lars Y. Pomara, Brian J. O'Shea, Susana Cubas Poclin, Douglas Stotz, Fabrice Schmitt, Devon Graham, Blaine H. Carnes, and Ernesto Ruelas Inzunza
Source: The Wilson Journal of Ornithology, 130(1):94-111.
Published By: The Wilson Ornithological Society
https://doi.org/10.1676/16-082.1
URL: http://www.bioone.org/doi/full/10.1676/16-082.1

The Wilson Journal of Ornithology 130(1):94–111, 2018

Noteworthy bird records from northeastern Peru reveal connectivity and isolation in the western Amazonian avifauna

Jacob B. Socolar,[1,2]* Juan Díaz-Alván,[3] Percy Saboya Del Castillo,[3] Lars Y. Pomara,[4]
Brian J. O'Shea,[5] Susana Cubas Poclin,[3] Douglas Stotz,[6] Fabrice Schmitt,[7] Devon Graham,[8]
Blaine H. Carnes,[9] and Ernesto Ruelas Inzunza[10]

ABSTRACT—Amazonian bird species often have patchy spatial distributions, and previous work has attributed this pattern to habitat specialization and dispersal limitation; however, we know comparatively little about the origins and maintenance of the isolated populations that constitute a patchy distribution. In this study, we ask whether patchy populations are interconnected by dispersal. We formulated 2 alternative hypotheses: (1) patchy populations are relicts of ancient connectivity or dispersal; and (2) patchy populations are centers of local abundance embedded in a matrix of contemporary dispersal or diffuse intervening populations. We confronted these hypotheses with circumstantial evidence derived from a unique suite of noteworthy bird records and geological observations from northeastern Peru. We found support for both hypotheses in different species, and sometimes within single species at different spatial scales. Phenotypically differentiated populations in relictual habitat patches provide strong support for the first hypothesis, whereas populations in recently created, ephemeral habitat patches provide strong support for the second. Colonizations of anthropogenic habitats are further examples of the second process, and they indicate ongoing changes in the porous connectivity of upper Amazonia. These results highlight the need for a conservation approach that accounts for metapopulation dynamics across patchy species ranges. *Received 27 May 2016. Accepted 7 February 2017.*

Key words: Amazon, avian biogeography, connectivity, dispersal, peatlands, relictual distribution.

Registros notables de aves en el noreste del Perú revelan conectividad y aislamiento en la avifauna de la Amazonía occidental

RESUMEN (Spanish)—En la Amazonía, especies de aves amazónicas a menudo tienen distribuciones espaciales irregulares en parches. Estudios previos han atribuido este patrón a la especialización del hábitat y la limitación de la dispersión, pero se sabe comparativamente poco sobre los orígenes y el mantenimiento de las poblaciones aisladas que constituyen una distribución en parches. En este estudio, preguntamos si las poblaciones en parches están interconectadas por dispersión. Formulamos dos hipótesis alternativas: (1) las poblaciones fragmentadas son relictos de conectividad o dispersión antigua; y (2) las poblaciones fragmentadas son centros de abundancia local integrados en una matriz de dispersión contemporánea o poblaciones intermedias difusas. Evaluamos estas hipótesis usando evidencia circunstancial derivada de un conjunto de registros de aves y observaciones geológicas del noreste de Perú. Encontramos apoyo para ambas hipótesis en diferentes especies, y algunas veces dentro de especies individuales a diferentes escalas espaciales. Poblaciones diferenciadas fenotípicamente en parches de hábitat relictual apoyan la primera hipótesis, mientras que las poblaciones en parches de hábitat efímeros de reciente creación apoyan la segunda. Las colonizaciones de hábitats antropogénicos también son ejemplos de segundo proceso, e indican que la conectividad porosa de la alta Amazonía está cambiando. Estos resultados resaltan la necesidad de un enfoque de conservación que tenga en cuenta las dinámicas de metapoblaciones de especies con rangos en parches.

Palabras clave: Amazonía, biogeografía aviar, conectividad, dispersión, distribución relictual, turberas.

More than 40 years ago, James Karr and Jared Diamond independently observed that tropical birds often have patchy distribution patterns (Karr 1971, Diamond 1973) resulting from a variety of factors. Some tropical bird species are habitat specialists that tightly track the patchy distribution of forest microhabitats (Marra and Remsen 1997). Extreme dispersal limitation (Moore et al. 2008) might prevent a species from colonizing otherwise suitable habitat or from recolonizing such areas after local extinctions fragment formerly widespread populations (Diamond 1973). And some species characteristically occur at densities so low that substantial areas of suitable habitat are necessarily unoccupied (Willis 1974, Thiollay 1994). Thus, our notion of patchiness subsumes

---

[1] Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ, USA.
[2] Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT, USA.
[3] Universidad Nacional de la Amazonía Peruana (UNAP), Iquitos, Perú.
[4] US Forest Service, Southern Research Station, Asheville, NC, USA.
[5] Research and Collections, North Carolina Museum of Natural Sciences, Raleigh, NC, USA.
[6] Keller Science Action Center, The Field Museum, Chicago, IL, USA.
[7] Wings Birding Tours, Tucson, AZ, USA.
[8] Project Amazonas Inc., Ft Lauderdale, FL, USA.
[9] No current address.
[10] Universidad Veracruzana, Instituto de Biotecnología y Ecología Aplicada, Xalapa, Veracruz, México.
* Corresponding author: jacob.socolar@gmail.com

patterns related to habitat requirements, dispersal patterns, and population dynamics.

In western Amazonian bird communities, these factors all contribute to patchiness. These communities attain extraordinary alpha diversity with unexceptional densities of individuals, so Amazonian birds necessarily have low population densities on average (Terborgh et al. 1990). Some species occur over large geographic areas in densities so low they are hardly ever detected (Haffer 1976, Thiollay 1989). At the same time, habitat heterogeneity drives variation in the bird communities of spatially proximate forest plots (Robinson et al. 1990, Pomara et al. 2012), and numerous specialist species occur exclusively in particular forest formations (Remsen and Parker 1983, Rosenberg 1990, Kratter 1997, Álvarez Alonso et al. 2013). Many of these formations have patchy spatial distributions (Fine et al. 2010, de Carvalho et al. 2013). Dispersal limitation prevents some species from crossing rivers and other unsuitable habitats, and doubtless prevents them from accessing some patches of suitable habitat (Cracraft 1985, Pomara et al. 2014).

If additional fieldwork finds populations spanning supposed gaps in a distribution, it can falsify the perception that the distribution is patchy (Diamond 1972, Beehler et al. 1986). Recent Amazonian fieldwork, however, reinforces rather than tempers the idea that western Amazonian bird populations are frequently maintained in patchy isolation (Álvarez Alonso and Whitney 2003, Harvey et al. 2014b, Díaz-Alván et al. 2017). The avifauna of numerous sites is now sufficiently characterized to robustly conclude that certain species are absent or vanishingly rare (Álvarez Alonso et al. 2012, Pomara et al. 2012). Furthermore, discoveries of new isolated populations have continued unabated. White-sands forests provide a spectacular example: following the discovery of numerous Guianan taxa on white-sand patches near Iquitos (Álvarez Alonso and Whitney 2003), surveys of additional white-sand enclaves encountered many of these species across western Amazonia (Lane et al. 2006, Guilherme and Borges 2011, Harvey et al. 2014b). Similar discoveries have also come from bamboo forests (Lane et al. 2007, Harvey et al. 2014a), swamps (Begazo and Valqui 1998), deforested areas (Piana et al. 2012, Harvey et al. 2014a), and seemingly unexceptional forest (Stotz and Díaz-Alván 2007, Díaz-Alván et al. 2017).

Although numerous Amazonian bird species have unequivocal patchy distributions, the biogeographic mechanisms for the origin and maintenance of these populations have not received systematic consideration. In particular, the extent of recent connectivity and its role in maintaining patchy populations is poorly understood. One possibility is that patchy distributions are relictual, reflecting ancient connectivity or dispersal that has long since abated. Alternatively, patchy distributions might involve local centers of abundance interconnected by dispersal or extremely diffuse intervening populations. In addition to representing different historical possibilities for the development and maintenance of patchy Amazonian bird distributions, these alternatives carry different implications for conservation. In particular, patchy distributions interconnected by dispersal might necessitate a metapopulation approach to conservation across vast spatial scales if ongoing connectivity is important for the long-term maintenance of local populations.

Circumstantial evidence derived from contemporary species distributions can provide a strong test of these alternatives. For example, numerous bamboo-specialist birds have patchy distributions, reflecting the distribution of bamboo. But bamboo patches are dynamic; they grow, flower, and die on characteristic timescales of <30 years, and bamboo-specialist birds colonize and vacate patches over the course of this cycle (Socolar et al. 2013). This pattern robustly implies that existing populations are not relictual and are connected by contemporary dispersal.

This study extends the approach of circumstantial inference to a suite of bird records collected in Loreto Department, Peru. These records involve species outside their previously known distributions. Therefore, if records involve established populations, they are either H1: isolated relictual populations (i.e., products of ancient connectivity or dispersal not ongoing) or H2: semi-isolated centers of local abundance connected by ongoing dispersal or extremely diffuse intervening populations. Otherwise, H3 records involve vagrant individuals or low-density nonbreeding (e.g., overwintering) populations rather than established breeding populations. Hypotheses H1–H3 are not mutually exclusive because different processes

Table 1. A framework for understanding records of birds of patchy distributions in Western Amazonia: circumstantial evidence to confront hypotheses H1–H3.

	Falsified by	Disfavored by	Favored by
H1	**a** Occurrence in recently created habitat patches	**b** Records in the matrix between known populations	**c** Distribution confined to known or suspected relictual habitat patches **d** Population divergence between patches
H2		**c** Distribution confined to known or suspected relictual habitat patches **d** Population divergence between patches	**a** Occurrence in recently formed habitat patches
H3	**3a** Repeated records of multiple individuals through time	**3b** Repeated records through time **3c** Records of multiple individuals **3d** Local territoriality/breeding **3e** Pattern of discovery at similar sites **3f** Evidence of dispersal limitation	**3g** Migratory species with seasonal pattern of occurrence

H1: Patchy populations are isolated relicts of formerly widespread populations or ancient dispersal.
H2: Patchy populations are centers of local abundance connected by contemporary dispersal or very diffuse intervening populations.
H3: No population exists, and isolated records are of vagrant individuals or low-density migrants in the nonbreeding range.

may act on different species or even on single species at different times, places, or spatial scales. Each hypothesis makes unique predictions about the circumstances surrounding a given record, and in some cases these predictions can be leveraged for strong tests of the alternative hypotheses H1–H3 (see methods and Table 1).

Loreto's geology is well understood (Salo et al. 1986, Räsänen et al. 1990, Hoorn et al. 2010) and provides unique opportunities to test these hypotheses. In particular, Loreto contains a variety of habitats known to be recently created (Roucoux et al. 2013) and habitats known to be relictual (Räsänen et al. 1990, Higgins et al. 2011). Here, we review existing distributional data on species with patchy distributions as well as new records from recent fieldwork. We find support for all 3 hypotheses, with widespread support for H2 (ongoing connectivity). We discuss the implications of this pattern for biogeography and conservation.

Methods

Study region

In northeastern Peru, Loreto department stretches west from the Brazilian border to the first outlying Andean ridges (e.g., Cordillera Azul, Cordillera Escalera). This study focused on lowland Loreto (excluding the western ridges). Our fieldwork was loosely concentrated in the vicinity of Iquitos (03°45′S, 73°15′W), with reduced effort at progressively greater distances. The climate is uniformly hot and wet, with mean annual temperature 26.5 °C and rainfall 2,400–3,100 mm at Iquitos (Marengo 1998). Viewed from the air, the region is almost completely covered by tropical forest, broken by rivers and sparse deforestation.

The uniform climate and forest cover belies a dynamic and heterogeneous landscape. Seasons are marked by dramatic changes in river levels (~10 m at Iquitos) driven by upstream rainfall. Beginning in January, rivers spread across their floodplains, inundating a tremendous area of forest (called várzea forest) until waters peak in April or May (Espinoza et al. 2013). Rivers retreat to the confines of their banks by the end of June and continue to recede, exposing extensive mudflats and sandbars.

The rivers contribute substantially to the heterogeneity of forest habitats in Loreto, and roughly 15% of the nonaquatic avifauna is restricted to river-created habitats (Remsen and Parker 1983). In addition to the várzea, these habitats include permanent swamps (Begazo and Valqui 1998, Pitman et al. 2014) and a variety of successional habitats created by recent erosional–depositional processes on point-bars, river islands, and floodplains (Salo et al. 1986, Rosenberg 1990, Robinson and Terborgh 1997). The mightiest rivers also serve as important biogeographic barriers, and numerous bird species are range-restricted to one bank of the Amazon or the other (Cracraft 1985, Pomara et al. 2014).

Additional forest heterogeneity derives from edaphic variation in both uplands and seasonally flooded forests (Tuomisto et al. 1995, 2003; Higgins et al. 2011; Pomara et al. 2012). The most striking example involves the white-sands forests, where extremely poor soils stunt tree growth and give rise to a structurally and floristically distinctive forest type (Fine et al. 2010) and an associated avifauna with Guianan affinities (Álvarez Alonso and Whitney 2003).

Relictual habitats

The inference presented in this paper is based on comparing patterns of bird distribution across habitats suspected to be relictual and other habitats known to be of recent origin. The main relictual habitat in our study is the poor-soil Nauta Formation, which probably once formed part of a vast region of nutrient-poor soils that stretched north to the Guiana Shield. In Ecuador and northern Peru, fluvial erosion has removed the nutrient-poor alluvial sediments of the Nauta Formation and re-exposed the richer underlying sediments of the Pebas Formation across vast areas, thereby disconnecting the nutrient-poor forests of Loreto west of the Napo River from those of the Guiana Shield (Higgins et al. 2011). Thus, the main relicutal habitats in our system were isolated during the Pliocene or Pleistocene (Räsänen et al. 1990, Higgins 2011).

Rivers can create and then fragment patches of floodplain habitat, such as meander scrolls fragmented by subsequent erosion or marshes that become isolated in oxbow lakes. The present-day distribution of Loreto's blackwater swamps may also be relictual, fragmented by the establishment of the present-day drainage of major whitewater rivers. We are unaware of any historical reconstruction of the distribution of blackwater habitats in Loreto's geologic past, however, so the idea that they are remnants of formerly connected blackwater regions is purely speculative. Dynamism of the Ucayali and Marañón channels has fragmented the swamps of the Ucamara Depression (the Tigre-Pastaza interfluvium, Pacaya-Samiria Basin, and Ucayali-Tapiche basin) in new ways during the Holocene (Dumont 1991); however, extensive swamps divided by narrow dynamic channels do not fit the typical notion of a patchy distribution.

Novel habitats

Recently created habitats in Loreto take several important forms and are most common on dynamic river floodplains and in the Ucamara Depression. We treated habitats as recent if evidence indicates they arose during the Holocene. Bird species that occur in these habitats must have arrived there by dispersing across similar forest formations to those that exist today and therefore provide evidence of contemporary connectivity. In fact, all of the habitats we discuss originated considerably more recently than the dawn of the Holocene, within the last several thousand years at most.

Peatland pole forests are stunted forests with white-sand affinities that grow on isolated peatlands across the Ucamara Depression (Fig. 1b, Supplemental Fig. S2; Draper et al. 2014). Radiocarbon dates for the onset of peat accumulation indicate these formations are geologically quite young, with basal dates <10,000 years before present (Lähteenoja et al. 2012, Roucoux et al. 2013). Pole forest forms only after peat accumulation rises above the flood level, and these formations are likely centuries or at most a few millennia old (F. Draper, Carnegie Inst. Sci., 2015, pers. comm.). A few birds typical of white-sands forest have been reported from one peatland (Lähteenoja et al. 2009), but otherwise the birdlife of the peatland pole forests is unsurveyed.

Peatlands across the Ucamara Depression also support isolated patches of savanna (Draper et al. 2014). We surveyed one such savanna in the Tapiche-Blanco interfluvium on clay soils overlain by a thick layer of peat (05°48′S, 73°52′W). The habitat was characterized by a low herbaceous layer dominated by *Scleria* sp. (Cyperaceae), isolated islands of trees and shrubs <5 m tall, and scattered *Mauritiella armata* palms (Fig. 1c, Supplemental Fig. S3; Torres Montenegro et al. 2015). Like pole forests, contemporary peatland savannas probably formed within the last several thousand years; however, the Tapiche-Blanco savanna we visited is adjacent to extremely stunted white-sands forest that might have harbored relictual populations of savanna species.

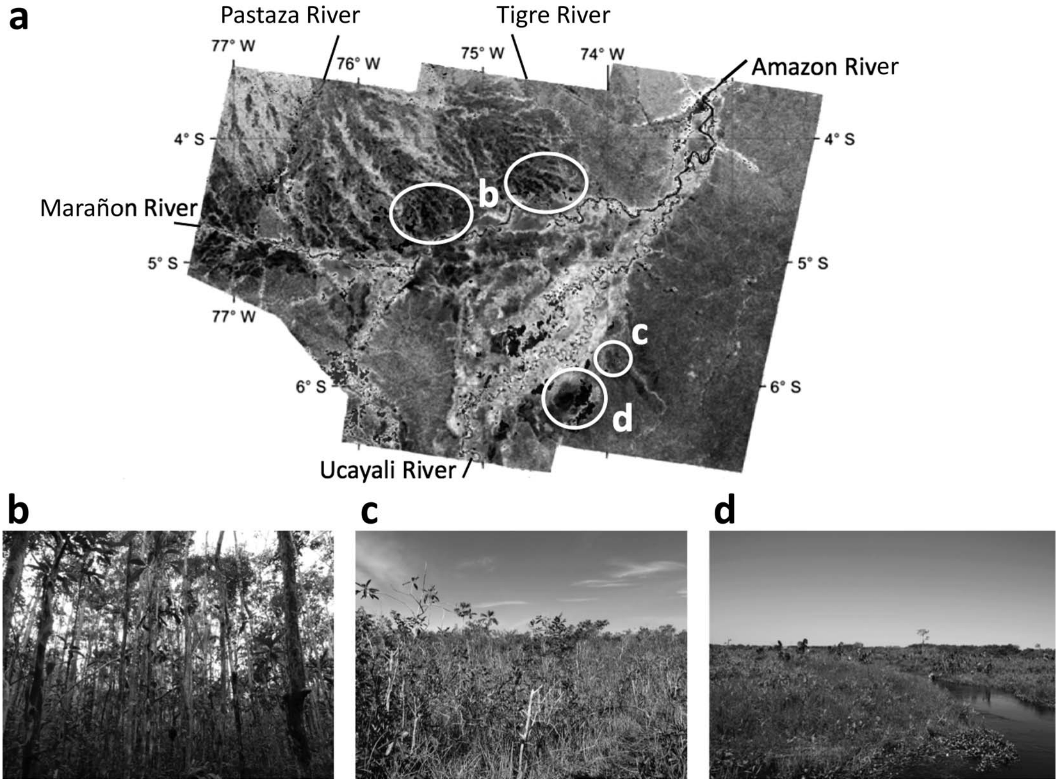

Figure 1. The subsiding Ucamara Depression contains a wide variety of unusual floodplain habitats that appear as (a) a variety of textures in false-color Landsat imagery adapted from Draper et al. 2014). The most interesting of these appear as various textures of dark coloration on the Landsat image, including (b) peatland pole forest (image courtesy of F. Draper), (c) peatland savanna, and (d) the Tapiche wetland complex. See Supplemental Fig. S1–S4 for full-color versions.

Many river-created habitats are even younger. The upper Amazon probably recycles its entire floodplain within 5,000 years (Mertes et al. 1996), and successional processes in old river channels and oxbows take place much faster, creating isolated and transitory patches of blackwater scrub. Along river channels, sediment deposition on bars and levees creates patches of habitat that rapidly succeed from grasses to *Gynerium* cane, *Tesseria*/*Salix* scrub, *Cecropia* woodland, and finally to more diverse forest. The location of these habitat patches changes rapidly depending on where the river happens to be depositing new sediment (Terborgh and Petren 1991, Dunne et al. 1998).

A large treeless wetland (Fig. 1d) covers >500 km^2 on both banks of the Tapiche River south of Santa Elena (06°08′S, 74°08′W). The entire treeless area formed subsequent to land subsidence that began in 1927 (Dumont and Garcia 1991). Today, the area is a vast complex of seasonally flooded marshes, including grassy areas and extensive stands of *Montrichardia* sp. Gallery forest grows on narrow levees on either side of the Tapiche itself, and in places the inland side of the levees supports stunted forest dominated by *Ficus* spp. (Fig. 1d, Supplemental Fig. S4). Large lakes north of the main treeless area also contain extensive marshes. The formation of this wetland is uniquely rapid, recent, and well documented among similarly extensive natural habitat formations in western Amazonia.

Finally, extensive patches of anthropogenic habitat have arisen in the past several decades. These habitats include pastures, cultivations, and secondary forests, often intermingled in mosaic fashion (Supplemental Fig. S5). Although a long history of human settlement exists along the banks of the major rivers in Peru, today's extensive clearings are a recent phenomenon (McMichael et al. 2014).

Observations

The bird records presented here result primarily from our own fieldwork in Loreto over the past decade. This paper includes records that represent previously unpublished range extensions beyond the maps presented by Schulenberg et al. (2010). We sought photographs or sound recordings of noteworthy species wherever possible. Photographs are provided in the supplemental material, and audio materials are deposited either in the Xeno-Canto sound library (www.xeno-canto.org) or with the Macaulay Library (www.macaulaylibrary.org; Supplemental Material part 3).

Additional records came to our attention via Project eBird, a global initiative that allows citizen-scientists to upload bird observations to a public database (Sullivan et al. 2009). Data quality is maintained using filters to automatically flag noteworthy records for evaluation by expert reviewers who may contact the observer to obtain confirmatory details. Because one of the authors (JBS) is the principal reviewer for Loreto, these records came to our direct attention, and we have assessed all available details pertaining to each record. Some ornithologists working in Peru routinely upload noteworthy records to eBird that they themselves intend to publish, so we personally contacted each observer to obtain explicit permission to publish every record presented in this paper.

Inferences based on field records

We applied the evidentiary criteria outlined in Table 1 to evaluate hypotheses H1–H3 with respect to every species reported in this paper. First, we assessed evidence for and against H3 (no established population). Where evidence suggested that records involve nonbreeding migrants or vagrants (see Table 1), we attributed the pattern to H3. Where no evidence existed with respect to population establishment, we attributed the pattern to unknown origin. Where evidence existed to disfavor or falsify H3, we then considered whether the population was likely connected to other conspecific populations over recent timescales (thousands of years or shorter). If no criteria were met to favor, disfavor, or falsify either hypothesis H1 or H2 (see Table 1), we attributed the pattern to unknown origin. Otherwise, we attributed the pattern to whichever hypothesis (H1 or H2) received support. If simultaneous evidence existed to favor both hypotheses, we attributed the pattern to both. We never recorded simultaneous evidence for both H1 and H2 within a species at the same spatial scale. Instead, simultaneous support for H1 and H2 always suggested connectivity at fine scales and relictual distributions at larger scales.

Because the species accounts that follow focus on species recorded beyond the ranges mapped by Schulenberg et al. (2010), our accounts do not include some species known to have patchy distributions in the western Amazon. For example, a broad disjunction exists in the Amazonian range of the Brown-rumped Foliage-gleaner (*Automolus melanopezus*), but we obtained no records of this species outside the previously known range and therefore do not include an account for that species. This method of selecting focal species could potentially bias our inference about the relative importance of relictual distributions and connectivity in the western Amazonian avifauna. Except for a few species discussed below, however, we are unaware of evidence to resolve between hypotheses H1 and H2 for the vast majority of these species. We provide an annotated list of species with disjunct Amazonian ranges (as mapped by Schulenberg et al. 2010; Supplemental Material part 4) that occur in Loreto but are not included in the species accounts that follow.

Results

Avifaunas of noteworthy study sites

Tigre River peatland pole forests—These forests support an avifauna with white-sands affinities. Two patches along the lower Tigre River are described more fully by Díaz-Alván et al. (2017). These patches yielded records of numerous nutrient-poor forest specialists sensu Pomara et al. (2012) and Álvarez Alonso et al. (2013), including Mishana Tyrannulet (*Zimmerius villarejoi*) as well as Brown-banded Puffbird (*Notharchus ordii*), Zimmer's Tody-Tyrant (*Hemitriccus minimus*), Cinnamon Manakin-Tyrant (*Neopipo cinnamomea*), and Yellow-throated Flycatcher (*Conopias parvus*). Otherwise, these forests harbor an eclectic mix of species typical of terra firme and várzea forest. For example, these areas contain typical floodplain species like Scarlet-crowned Barbet (*Capito aurovirens*) and White-chinned Jacamar (*Galbula tombacea*), but also typical upland species like Rednecked Woodpecker (*Campephilus rubricollis*) and Rufous-capped Antthrush (*Formicarius colma*).

Tapiche-Blanco savanna—The Tapiche-Blanco savanna contained several species with limited distributions in Peru, including Green-tailed Goldenthroat (*Polytmus theresiae*), Cherrie's Antwren (*Myrmotherula cherriei*), Swainson's Flycatcher (*Myiarchus swainsoni*), and Black Manakin (*Xenopipo atronitens*; see Species Accounts). In this sense, the avifauna is comparable to other isolated savannas in Loreto and elsewhere in Amazonia (O'Shea et al. 2015).

Tapiche wetland complex—The birdlife of the Tapiche wetlands consists largely of typical species of open habitats, deforested areas, and wetlands; however, Yellow-chinned Spinetail (*Certhiaxis cinnamomea*), which was previously known in Peru only from the lowermost Peruvian reach of the Amazon River, was among the most common passerines. The avifauna also includes a plethora of waterbirds; of these, we encountered the most interesting species, Least Bittern (*Ixobrychus exilis*) and Azure Gallinule (*Porphyrio flavirostris*), in the grassy margins of a large lake north of the main treeless area (05°37′S, 74°01′W).

Species accounts

In the species accounts that follow, every record is associated with the observers via their initials (observers' full names are in Supplemental Material part 1). The bolded letters **P** or **A** are given alongside species names to indicate photo or audio documentation, organized by species (Supplemental Material part 3). Each species is assigned to 1 or 2 of hypotheses H1–H3 (or is assigned "unknown" if no hypothesis is given). Following the hypothesis assignment, we enumerate the evidentiary basis for our treatment using the codes given in Table 1. We then summarize our conclusions for each species (Table 2).

*Barred Tinamou (*Crypturellus casiquiare*)* **A**—We encountered one individual in white-sands forest near Pucaurco (PSC and JBS, 27 Jan 2016; 03°49′S, 74°06′W). The species is additionally known in Peru from one specimen and one sighting in white-sands on nearby sections of the Tigre River (Álvarez Alonso and Whitney 2003), where locals report that it uses widespread poor-soil forest habitats (J. Álvarez, Ministerio del Ambiente del Perú, 2016, pers. comm.). Reexposed Pebas sediments isolate this population from conspecifics in Guianan sandy-belt forests, suggesting the pattern is relictual (H1; c+3a).

*Least Grebe (*Tachybaptus dominicus*)*—Two adults with 2 downy young were observed at the Santa Cruz Forest Reserve near Mazán (AB, 14 May 2012; 03°30′S, 73°10′W). Additionally, 2 adults were found on a manmade fishpond in deforested country along the Iquitos-Nauta highway (JBS, 28 Aug 2013; 04°24′S, 73°34′W). This species is rare or absent across most of Loreto. Although vagrant *T. dominicus* individuals sometimes breed (e.g., in the southwestern United States; McMurry and Monson 1947), local breeding suggests an establishing population. Presence on a manmade pond cannot be relictual, and so we attribute this pattern to contemporary connectivity (H2; a+3d).

*White-cheeked Pintail (*Anas bahamensis*)* **P**—Two individuals photographed on Rimachi Lake represent the first documented record from lowland Peruvian Amazonia (FS and others, 6 Jun 2013; 04°25′S, 76°41′W). The birds were found during the high-water period in the middle of the lake, far from the shore and vegetation. The lack of additional records of this conspicuous strong flier suggests vagrancy (H3; 3g–h).

*Bare-faced Ibis (*Phimosus infuscatus*)* **P**—On 4 May and 12 June 2014, DeG photographed one individual at a marshy water-buffalo pasture at Yanamono (03°27′S, 72°51′W), constituting the first record for this species in Peru. Because no evidence exists of an established population, we treat this record as a vagrant (H3; 3h). Additional records have been subsequently obtained from northernmost Peru, where a population is established in deforested areas across the Colombian border (O. Janni, 2006, pers. comm.).

*Least Bittern (*Ixobrychus exilis*)* **P**—An individual photographed on a large lake between the middle Tapiche and Ucayali rivers is apparently the first Loreto record away from the immediate vicinity of the largest rivers (JBS and SS, 27 Jul 2014; 05°37′S, 74°01′W). The Tapiche wetland complex provides ideal habitat for a population, but we cannot rule out vagrancy (unknown).

*Paint-billed Crake (*Mustelirallus erythrops*)* **A**—On 21 September 2014, JBS flushed one individual from an overgrown field near Requena (05°03′S, 73°52′W). Voice recordings obtained the following day provide the first record and

Table 2. Noteworthy species described in this paper and hypotheses favored by circumstantial inference. Plus-signs indicate that multiple hypotheses are favored at different times, places, or spatial scales; "unknown" indicates that no hypothesis receives noteworthy circumstantial support.

Birds found in natural habitat	Hypotheses	Birds found in anthropogenic habitat	Hypotheses
Crypturellus casiquiare	H1	*Tachybaptus dominicus*	H2
Anas bahamensis	H3	*Phimosus infuscatus*	H3
Ixobrychus exilis	unknown	*Mustelirallus erythrops*	H3
Porphyrio flavirostris	H2	*Gallinula galeata*	H2
Heliodoxa schriebersii	unknown	*Vanellus chilensis*	H2
Polytmus theresiae	H1+H2	*Caracara plancus*	H2
Geotrygon saphirina	unknown	*Nannopsittaca dachilleae*	unknown
Nyctibius leucopterus	H1+H2	*Synallaxis albescens*	unknown
Notharchus ordii	H1+H2	*Capsiempis flaveola*	H2
Malacoptila rufa	unknown	*Muscisaxicola fluviatilis*	H3
Nonnula sclateri	unknown	*Tachyphonus rufus*	unknown
Certhiaxis cinnamomea	H2	*Conirostrum bicolor*	H2
Myrmotherula cherriei	H1+H2	*Sporophila schistacea*	H3
Myrmotherula longicauda	H2	*Sturnella militaris*	H2
Percnostola arenarum	H1+H2		
Phlegopsis nigromaculata	unknown		
Zimmerius villarejoi	H1+H2		
Ramphotrigon fuscicauda	H2		
Ramphotrigon megacephalum	H2		
Conopias trivirgatus	unknown		
Myiarchus swainsoni phaeonotus	unknown		
Neopelma sulphureiventer	H2		
Xenopipo atronitens	H1		
Xipholena punicea	H1+H2		
Polioptila clementsi	H1+H2		
Dacnis albiventris	unknown		
Euphonia plumbea	unknown		

H1: Patchy populations are isolated relicts of formerly widespread populations or ancient dispersal.
H2: Patchy populations are centers of local abundance connected by contemporary dispersal or very diffuse intervening populations.
H3: No population exists, and isolated records are of vagrant individuals.

documentation of *M. erythrops* from Loreto. The site is underwater during April–May, suggesting seasonal movements. The closest known populations are near Pucallpa (Schulenberg et al. 2010) and in the Mayo valley. This species might be spreading in deforested areas (Harvey et al. 2014a), but accidental occurrence seems likely in this vagrancy-prone rail (H3; 3h; Arnold 1978).

*Azure Gallinule (*Porphyrio flavirostris*)* **P**—MR and DC suspect this species is resident on a large lake near the middle Tapiche Rivers based on repeated sightings over several years (05°37′S, 74°01′W). On 27 July 2014, JBS and SS encountered 3 individuals at the same location. BS encountered this species here the following year (26 Aug 2015). On 11 October 2007, DS encountered one at Redondococha (00°33′S, 75°13′W). Previously, the species was presumed a scarce migrant to the region during January–June (Remsen and Parker 1990, Schulenberg et al. 2010). The occurrence in recently created floodplain habitats suggests ongoing connectivity (H2; a+3b).

*Common Gallinule (*Gallinula galeata*)*—On 12 December 2013, JBS observed 2 individuals on a manmade pond near Iquitos (03°56′S, 73°23′W). On 12 October 2014, MG found 5 adults and 1 chick on a nearby pond (03°54′S, 73°21′W). Up to 3 individuals have been repeatedly observed near the mouth of the Nanay River at Iquitos (JDA, 7 and 13 Aug 2016; DeG, 11 Nov 2016 and 5 Jan 2017; 03°42′S, 73°16′W). Few records of this species exist from northeast Peru. Occurrence on manmade ponds cannot be relictual, and we attribute this pattern to ongoing connectivity (H2; a+3d).

*Southern Lapwing (*Vanellus chilensis*)* **P**—This species is rapidly colonizing deforested areas of

Amazonia. It is established on pastures at Jenaro Herrera (DS and JBS, 25 Feb 2010 and 14–16 Sep 2014; 04°54′S, 73°40′W) and Oran (up to 6 individuals; AB, LYP, DFL, BMW, and JBS, 8 Nov 2010, 26–30 July 2013, and 27–31 Aug 2015; 03°29′S, 72°40′W). We have also observed this species near the Iquitos-Nauta highway (SCP, 20 Dec 2013; 03°50′S, 73°19′W; and JBS, 17 Aug 2014; 03°53′S, 73°21′W), near Yanamono (KR, 7 Jul 2005; 03°27′S, 72°51′W), and on the middle Putumayo River (DS, 23 Feb 2016; 02°27′S, 72°40′W). We attribute this pattern to ongoing connectivity (H2; a+3a).

*Southern Caracara (*Caracara plancus*)*—This species is rapidly colonizing deforested areas and is established along the Iquitos-Nauta highway (Piana et al. 2012). One individual on an island near Iquitos (JBS, 22 Nov 2013; 03°40′S, 73°14′W) and 2 individuals on islands in the lower Ucayali (JDA, Mar 2014; 04°41′S, 73°37′W) are apparently the first records from river-island habitats in Loreto. Additional recent records include 2 individuals at Jenaro Herrera (DS, 1 Mar 2010; 04°54′S, 73°40′W), individuals including a juvenile near Tamshiyacu (JDA, Feb 2015; 03°51′S, 73°12′W), and 2 individuals at Oran (JBS, 31 Aug 2015; 03°29′S, 72°40′W). We attribute this pattern to ongoing connectivity (H2; a+3a).

*Black-throated Brilliant (*Heliodoxa schriebersii*)*—LYP encountered individuals twice in terra firme forest south of the Amazon River, on 6 August 2007 near the Tamshiyacu River (04°07′S, 72°55′W) and on 7 July 2004 at Estación Biológica Quebrada Blanco (04°22′S, 73°09′W). These are apparently the first records of this species from south of the Amazon and east of the Ucayali River. We have no evidence to determine whether these records indicate an established population or how this population originated (unknown).

*Green-tailed Goldenthroat (*Polytmus theresiae*)*—On 10–11 October 2014, BJO, PSC, ERI, and DS encountered this species on the left bank of the Blanco River (05°48′S, 73°52′W), where it was uncommon in savanna. In Loreto, this species is also known from savanna habitat near Jeberos (Schulenberg et al. 2010) and from deforested areas near San Lorenzo on the north bank of the Marañón (Schmitt et al. 2017). The occurrence in isolated savannas might be relictual (H1; c+3c,e), but the presence in deforested areas at San Lorenzo suggests contemporary connectivity (H2; a+3c,e). Such connectivity must be limited because the species is absent from deforested areas on the lower Tapiche River near the Blanco River population.

*Amazonian Parrotlet (*Nannopsittaca dachilleae*)* **P**—This species is best known from southeastern Peru and adjacent Bolivia and Brazil, well south of the type locality in central Peru (O'Neill et al. 1991). A few additional records exist from the vicinity of Iquitos (Schulenberg et al. 2010). On 9 December 2015 and 29 January 2016, PSC and JBS recorded a small flock visiting a flowering coconut palm at San Juan de Ungurahual (03°54′S, 73°49′W), roughly 40 km west of previous records in Loreto. Interestingly, all Loreto records have come from deforested or heavily degraded areas; however, this species might be overlooked even where it is present (Schulenberg et al. 2010). Therefore, there is neither strong indication that the species does not occur more widely in natural forests nor strong evidence that populations do not span the gap between Iquitos and known populations further south (unknown).

*Sapphire Quail-Dove (*Geotrygon saphirina*)*—This species apparently occurs disjunctly in northernmost Loreto and south of the Amazon (Stotz and Díaz-Alván 2007, Schulenberg et al. 2010, Díaz-Alván et al. 2017). Consistent with this pattern, we obtained 2 records in terra firme forest in the Arabela drainage (JDA and DS, Aug 2006; 02°08′S, 75°08′W; and JDA, May 2008; 01°47′S, 75°36′W), and one record near the Tamshiyacu River (LYP, 8 Sep 2006; 04°09′S, 73°05′W). We have no evidence to determine whether the distribution is relictual or connected (unknown).

*White-winged Potoo (*Nyctibius leucopterus*)* **P, A**—We recorded this species 7 times from 5 widely separated poor-soil locations on both banks of the Amazon: near the Algodoncillo River (JDA, 26 Oct 2009; 02°47′S, 72°55′W); north of the lower Napo (DaG, 12 Aug 2012; 03°15′S, 72°55′W); at Estación Biológica Quebrada Blanco (JBS, 14–15 Oct 2014; 04°22′S, 73°09′W); at 2 white-sands sites near the Blanco River (PSC, BJO, ERI, and DS, 16–25 Oct 2014; 60°15′S, 73°54′W and 05°58′S, 73°46′W), and at 2 white-sands sites on the upper Nanay River (PSC and JBS, 13 Dec 2015; 03°40′S, 74°14′W; and PSC, JBS, and BaW, 21 Jan 2016; 03°29′S, 74°29′W).

These observations reveal that this species, formerly known from a single white-sands mass (Álvarez Alonso and Whitney 2003), is widespread on poor-soil formations that connect the white-sands masses where it is most common (H2; b+3c–e). Peruvian and Guianan populations might be disjunct, which would evidence a large-scale relictual distribution.

*Brown-banded Puffbird (*Notharchus ordii*)* **A**—We recorded this species numerous times at poor-soil sites without white-sand, including at Estación Biológica Quebrada Blanco (LYP and JBS, multiple dates 2004–2014; 04°22′S, 73°09′W) in tall forest on a weathered clay terrace; similar habitats in the Tigre, Tapiche, and Orosa drainages (Pomara et al. 2012, O'Shea et al. 2015, Díaz-Alván et al. 2017); and peatland pole forest in the Tigre basin (Díaz-Alván et al. 2017). Occurrence on widespread poor-soil forests between white-sands and colonization of peatlands suggests ongoing connectivity (H2; a,b+3c–e). At a larger scale, Loreto populations might be relicts of ancient connectivity with the Guiana Shield (H1; c).

*Rufous-necked Puffbird (*Malacoptila rufa*)* **P**—This species has been observed several times in floodplain forest on the middle Tapiche River (MR and DC, 05°38′S, 73°58′W). The nearest records east of the Ucayali are ~150 km farther north. This record indicates a previously undocumented band of overlap at least 100 km wide between *M. rufa* and Semicollared Puffbird (*M. semicincta*) on the east bank of the Ucayali River. We lack evidence to assess whether this pattern is relictual, and additional surveys east of the lower Ucayali River are required to confirm that the distribution is truly patchy.

*Fulvous-chinned Nunlet (*Nonnula sclateri*)*—JDA and JAA encountered this species in white-sands forest at Jenaro-Herrera (Dec 2001; 04°51′S, 73°36′W), and DS subsequently observed it at the same location. These are the first records for Loreto, a range extension of roughly 300 km from the middle Ucayali. The species was not found in the intervening white-sands of the Tapiche-Blanco (O'Shea et al. 2015). A nunlet with red orbital skin from the Tahuayo River may be this species or *N. brunnea* (R. Ahlman, 2015, pers. comm.; audio recording). We do not attribute the pattern to any hypothesis at this time (unknown).

*Yellow-chinned Spinetail (*Certhiaxis cinnamomea*)* **P**—This species is common in the Tapiche wetland complex (JBS and SS, 29–30 Jul 2014; 06°09′S, 74°09′W). Additionally, it occurs on the lower Yanayacu River (JDA, multiple dates; 04°18′S, 73°17′W), at Lucero Pata (DBa and others, Jan 2015 and Jan–Feb 2016; 04°07′S, 73°20′W), and near the mouth of the Nanay River at Iquitos (JDA, 7 and 13 Aug 2016; 03°42′S, 73°16′W). Aside from one record in Madre de Dios, these are the only Peruvian records away from the lower Amazon River (below the mouth of the Napo). We attribute these disjunct populations in highly dynamic river floodplains, including the Tapiche wetland complex, which never connected to a major whitewater river, to ongoing connectivity (H2; a+3a–e).

*Pale-breasted Spinetail (*Synallaxis albescens*)*—On 25 July 1979, PC encountered one individual at Caballococha (03°55′S, 70°31′W) in a field of waist-high grass. This record came to light via Project eBird, and convincing written details were provided. *S. albescens* is known from adjacent Colombia, but this record is the first for Loreto. We lack evidence to determine whether this record involves a vagrant (unknown).

*Cherrie's Antwren (*Myrmotherula cherriei*)* **A**—On 10–12 October 2014, BJO, PSC, ERI, and DS encountered at least 8 individuals in semi-flooded scrubby savanna near the Blanco River (05°48′S, 73°52′W). Otherwise, the species is known in Loreto only from white-sand scrub (chamizal) along the upper Nanay River and chamizal-like blackwater scrub on the middle Tigre River near white-sands areas (Álvarez Alonso and Whitney 2003). The distribution on widely isolated white-sands with extensive chamizal, and the disjunction between Peruvian populations and larger populations in Brazil, suggest a relictual distribution (H1; c+3a). At a finer scale, occurrence in blackwater chamizal along the Tigre (likely a peatland formation) may reflect recent connectivity to nearby white-sands (H2; a).

*Stripe-chested Antwren (*Myrmotherula longicauda*)* **P, A**—We encountered this species in 2 locations east of the Ucayali River, where it was previously unknown. Our records come from seasonally flooded forest with patches of secondary forest at San José de Vinuya (JDA, Jul 2005; 07°51′S, 74°40′W) and from seasonally flooded bamboo scrub near the Tapiche River (Supplemental Fig. S6), where it is fairly common (PSC and JBS, 6 Nov 2012; 05°25′S, 73°57′W). *M. longicauda* is primarily an Andean species, but an isolated population occurs in blackwater scrub in the Pacaya-Samiria basin (Begazo and Valqui 1998). Our records, together with a recent record from terra firme bamboo in Madre de Dios (Harvey et al. 2014a), suggest that this species is widespread along both banks of the Ucayali in habitats similar to those used by *Neopelma sulphureiventer*. These records in patchy successional habitats indicate ongoing connectivity (H2; a+3a–e).

*Allpahuayo Antbird (*Percnostola arenarum*)* **A**—We encountered this species several times in hilly, poor-soil forest near Nauta where we heard territorial countersinging (LYP, 3–15 Oct 2005; 04°27′S, 73°35′W; and JBS, 22 Aug 2013; 04°22′S, 73°37′W). These are the southernmost records for this species globally. This species was previously known primarily from a few isolated white-sands masses, but these observations, together with observations from similar habitat in an arc fringing the Pastaza-Marañón Basin (Díaz-Alván et al. 2017), reveal that low-density populations are widespread on intervening poor-soil forest formations (H2; b+3c–f). At larger scales, the disjunction from large populations of its sister species, Black-headed Antbird (*Percnostola rufifrons*) on the Guiana Shield, may be relictual (H1; c,d).

*Black-spotted Bare-eye (*Phlegopsis nigromaculata*)* **P**—On 15 June 2013, FS photographed 3 individuals on an army ant swarm in white-sand forest at Cocha Caña, on the west bank of the Morona River (04°17′S, 77°14′W). One presumed juvenile had a gray orbital skin while the other 2 had bright red orbital skins, indicating a probable family group. This is the first documented record north of the Marañón River and west of the Tigre River. Reddish-winged Bare-eye (*Phlegopsis erythroptera*) occurred in the same area. We cannot determine whether this population is likely to be relictual or connected to other populations (unknown).

*Mishana Tyrannulet (*Zimmerius villarejoi*)* **A**—Díaz-Alván et al. (2017) encountered this species at 2 new locations: weathered clay terraces in the Tigre/Pucacuro drainage, and peatland pole forest along the lower Tigre River. An audio recording from the peatland pole forest (JBS, 31 Aug 2013; 04°25′S, 74°04′W) documents a voice similar to the populations in the Nanay basin. These are the first records of Nanay-type birds away from white-sands in the Nanay basin. The occurrence on peatlands indicates recent dispersal between habitat patches at small spatial scales (H2; a+3d), whereas differentiation from its sister taxon in the Mayo Valley (Whitney et al. 2013) suggests these 2 populations originated from ancient long-distance colonization or vicariance (H1; d).

*Yellow Tyrannulet (*Capsiempis flaveola*)* **A**—On 8 December 2013, JBS encountered one territorial individual in regenerating scrub on nutrient-poor soil near Sabalillo (03°21′S, 72°18′W). *C. flaveola* is known from successional habitats on the south bank of the Amazon River in Loreto, but to our knowledge this is the first record from the north bank. Occurrence in anthropogenic scrub indicates ongoing connectivity (H2; a+3d).

*Dusky-tailed Flatbill (*Ramphotrigon fuscicauda*)* **A**—On 31 July 2014, JBS recorded the territorial loudsong of one individual from swampy tangles on the middle Tapiche River (05°38′S, 73°58′W). Our record bridges a large gap between the Orosa River (H. Wiley, Univ. North Carolina, 2014, pers. comm.) and the upper Ucayali (Harvey et al. 2014b). This observation of a territorial bird in ephemeral floodplain habitat between known populations suggests ongoing connectivity (H2; a+3d).

*Large-headed Flatbill (*Ramphotrigon megacephalum*)* **A**—On 28 July 2009, JDS recorded the territorial loudsong of one individual from flooded scrub on the middle Maquia River (06°29′S, 74°48′W). We are aware of only one previous Loreto record, from the Matsés National Reserve. The observation of a territorial bird from ephemeral habitat suggests ongoing connectivity (H2; a+3d).

*Little Ground-Tyrant (*Muscisaxicola fluviatilis*)* **P**—Occasional records suggest this species is an austral migrant as far north as the Amazon River during the low water period (Schulenberg et al. 2010). We observed individuals at Iquitos (03°45′S, 73°14′W) on multiple occasions (DS, 2–7 Nov 2010; and JBS, 4 Oct 2012 and 2 Dec 2015). Additionally, we observed 2 near Explor-Napo Lodge (DB, 23 Sep 2008; 03°15′S, 72°55′W), one at Jenaro Herrera (JDA, Nov 2009; 04°54′S, 73°41′W), and one at Contamanía (JBS, 22 Sep 2014; 05°03′S, 73°52′W). The seasonal pattern in these records indicates that the species is a nonbreeding migrant (H3; 3g).

*Three-striped Flycatcher (*Conopias trivirgatus*)*—JDA observed one individual in April 2012 along the lower Ucayali River in the Pacaya-Samiria buffer zone and another in August 2012 in floodplain forest along the Yanayacu Pucate River, also in the Pacaya-Samiria National Reserve. These records reinforce a pattern of occurrence near Pacaya-Samiria (Schulenberg et al. 2010, Díaz-Alván et al. 2017, Schmitt et al. 2017). We do not know enough about this species' distribution or habitat preferences to suggest whether the distribution might be connected or relictual (unknown).

*Swainson's Flycatcher (*Myiarchus swainsoni phaeonotus*)* **P**—In the Tapiche-Blanco savannas, we encountered several dark-mandibled *Myiarchus swainsoni* that appeared to be territorial and in pairs (O'Shea et al. 2015). *M. swainsoni* is known in Amazonian Peru as a widespread austral migrant (Schulenberg et al. 2010), but the dark-mandibled *phaeonotus*, which breeds in stunted blackwater forest in Brazil, Ecuador, and the Guianas, was previously unknown in Peru. The Tapiche-Blanco population might be connected to Ecuador across the unsurveyed peatlands of the Ucamara Depression, or it could be a relict of Pleistocene savannas (unknown).

*Sulphur-bellied Tyrant-Manakin (*Neopelma sulphureiventer*)* **P, A**—We recorded this species several times east of the Ucayali River, where it was previously unknown. Our records include a pair in seasonally flooded tangles near the middle Maquia River (JDA, 28 Jul 2009; 06°29′S, 74°48′W), an individual in seasonally flooded scrub near the Tahuayo River (DaG, 2 Aug 2011; 04°19′S, 73°14′W), and 4 individuals in seasonally flooded bamboo adjacent the Tapiche River (PSC and JBS, 6 Nov 2012; 05°25′S, 73°57′W). These are the first Loreto records away from the Pacaya-Samiria basin, and they indicate a widespread but sparse distribution in patches of seasonally flooded successional tangles on both banks of the Ucayali, suggesting ongoing connectivity (H2; a+3a–d).

*Black Manakin (*Xenopipo atronitens*)* **P**—This species is common in semi-flooded scrubby habitats along the Blanco River (BJO, PSC, ERI, and DS, 10–12 Oct 2014; 05°48′S, 73°52′W). Nearby, we also encountered it in extremely stunted forest, where it was much less common (21–25 Oct 2014, 05°59′S, 73°46′W). While *X. atronitens* occurs in numerous white-sands enclaves farther east in Amazonia (Capurucho et al. 2013), previous Loreto records exist only from savanna-scrub at Jeberos, ~300 km to the west. This species was also recently discovered in highly stunted forest in Acre and Ucayali (Guilherme and Borges 2011, Harvey et al. 2014b). This distribution is likely a relict of formerly more widespread savanna habitats during the Pleistocene, and genetic data provide support for a model of Pleistocene connectivity and subsequent isolation (H1; c+3c–e; Capurucho et al. 2013).

*Pompadour Cotinga (*Xipholena punicea*)*—On 12 October 2014, BJO observed one male in flight over the Blanco River (05°47′S, 73°51′W), the first Peruvian record south of the Amazon River. On 14 October 2005, LYP observed an apparent family group of at least 4 individuals, including 2 adults and 1 juvenile, in hilly poor-soil forest near Nauta (04°27′S, 73°35′W). The species also occurs in similar habitat in the Tigre/Pucacuro drainage >200 km to the northwest (Díaz-Alván et al. 2017). These observations reveal that this species, formerly known only from white-sands, occurs in low density across the poor-soil forest formations between the main white-sands masses (H2; b+3b–c). At a larger scale, populations on the poor soils of the Nauta Formation may be relicts of earlier connectivity with the Guiana Shield (H1; c+3a).

*Iquitos Gnatcatcher (*Polioptila clementsi*)*—On 7 December 2011, BHC encountered 2 individuals in white-sands forest near El Porvenir in the Allpahuayo-Mishana National Reserve (03°54′S, 73°33′W), ~7 km from the closest known location for this critically endangered species (Álvarez Alonso et al. 2012). Phenotypic differentiation between *P. clementsi* and its Guianan sister taxon *P. guianensis* indicates that the entire distribution of *P. clementsi* is likely relictual (H1; c,d+3a), but the fact that only 1–2 pairs occupy any given white-sands patch suggests that the population must be connected by inter-patch dispersal through terra firme forest (H2).

*White-lined Tanager (*Tachyphonus rufus*)*—We encountered an adult male in banana cultivations and regenerating scrub near the town of Indiana on the Amazon River (JBS, 9 Sep 2014; 03°30′S, 73°02′W) and one individual in secondary habitats along the lower Ucayali (JDA). This species otherwise is known in Loreto only from scrubby habitat at Jeberos (Schulenberg et al. 2010) and San Lorenzo (Schmitt et al. 2017). We lack evidence to determine whether these records are vagrants (unknown).

*Bicolored Conebill (*Conirostrum bicolor*)*—In Peru, this species is known primarily from river islands in the Amazon, Marañón, and Napo rivers. We encountered an adult and juvenile in a stand of *Cecropia* between the Ucayali River and the mouth of the Tapiche (JBS, 21 Sep 2014; 05°03′S, 73°52′W). This record is apparently the southernmost for this species in Peru. Additional eBird records exist from the lower Ucayali. This species specializes on ephemeral habitats on river islands, so populations are presumably connected (H2; a+3c,e).

*Slate-colored Seedeater (*Sporophila schistacea*)*—On 7 December 2013, JBS observed one adult male in a patchwork of hedgerows and cultivations in terra firme near the Orosa River (03°38′S, 72°16′W). Previous Loreto records are of territorial birds from seeding bamboo and secondary forest along the Tigre River (Álvarez Alonso and Whitney 2003). The single Orosa record of this species may be a vagrant (H3; 3h), but this species' appearance in seeding bamboo along the Tigre River suggests opportunistic nomadism across vast spatial scales, blurring the line between connectivity and vagrancy.

*White-bellied Dacnis (*Dacnis albiventris*)* **A**—We recorded this species several times in poor-soil forest, especially at degraded sites. The species is regular in mature poor-soil forest at Estación Biológica Quebrada Blanco (LYP and JBS, 2004–2014; 04°22′S, 73°09′W). Additional records from mature poor-soil forest include 3 individuals with a mixed flock on white-sands at Jenaro Herrera (JDA, DS, and PSC, Feb 2010; 04°54′S, 73°38′W), one individual with a mixed flock near the mouth of the Orosa River (LYP, 27 Nov 2006; 03°30′S, 72°02′W), and one individual in poor-soil forest canopy in Reserva Nacional Allpahuayo Mishana (LYP, 16 Sep 2005). Several records exist from fruiting Melastomes along the canopy walkway at the ACTS field station (03°15′S, 72°54′W; L. Pando, deceased, 2015, pers. comm.). Our observations in degraded poor-soil habitats include 2 individuals at hilly forest edge near the Ecuadorian border (JDA, Jun 2008; 01°43′S, 75°36′W), individuals at degraded forest edge at 2 locations in the Allpahuayo-Mishana National Reserve (PSC, Sep 2012, 03°53′S, 73°26′W; JBS, Oct 2012, 03°54′S, 73°29′W), 5 individuals at a fruiting Melastome in secondary scrub near Picuroyacu (JBS, 6 Aug 2013; 03°37′S, 73°16′W), and several individuals in a fruiting tree in mixed agricultural lands at Oran (LYP, DFL, and BMW, 24 Jul 2013; 03°29′S, 72°30′W). This species' widespread distribution suggests connectivity, but we are uncertain whether the distribution is patchy.

*Red-breasted Meadowlark (*Sturnella militaris*)*—On 30 August 2015, JBS observed 3 individuals on a cattle pasture at Oran (03°29′S, 72°30′W). This species is well established at Iquitos, but few records exist from elsewhere in Loreto. Recent colonization of disturbed habitats suggests connectivity (H2; a+3c,e).

*Plumbeous Euphonia (*Euphonia plumbea*)*—On 29 November and 6 December 2011, BHC encountered a male-female pair along forest edge near a blackwater stream on a trail between the village of El Porvenir (03°54′S, 73°33′W) and the Nanay River. These conform to a pattern of sight-records in the Allpahuayo-Mishana National Reserve. The Peruvian distribution is similar to *Zimmerius villarejoi* (including the Mayo Valley sister taxon) and thus might be relictual, but it does not meet any of our outlined evidentiary criteria (unknown).

Discussion

Our results add 5 species to the avifauna of lowland Loreto, including the first record of *Phimosus infuscatus* for Peru. Ongoing discoveries of large range extensions, novel habitat associations, and entirely unsurveyed habitat types highlight the incomplete knowledge of bird distributions in the region. We frame these records in terms of 3 tractable hypotheses about the origins and maintenance of disjunct and patchy distributions. Using the records presented here and elsewhere, we can compile evidence for and against specific hypotheses in particular cases. Support for each hypothesis follows.

H1: Records represent isolated relicts of formerly widespread populations

We interpret as relictual 10 of the distributions considered here. All are specialized to nutrient-poor habitats, and 8 occur in poor-soil forest and might be relicts of poor-soil habitats that were once more extensive and well-connected. Geologic evidence is consistent with this hypothesis operating on multiple nutrient-poor specialist species (not just those treated in this paper). Nutrient-poor late Miocene deposits (e.g., the Nauta/Içá formation) were once widespread through the region but have subsequently eroded to expose nutrient-rich Pebas/Solimões sediments across large areas. Thus, contemporary nutrient-poor terra firme forests are patchily distributed in Loreto and in some cases are relicts of formerly more extensive forests (Räsänen et al. 1990, Higgins et al. 2011). Additional fluvial-geomorphological processes and weathering of ancient soils also explain some patchily distributed nutrient-poor soils in the region, however, and long-distance colonization from the Guiana Shield cannot be ruled out as a possible origin for associated bird populations. Yet in some cases (e.g., *Crypturellus casiquiare*), long-distance dispersal seems improbable.

The remaining 2 species (*Polytmus theresiae* and *Xenopipo atronitens*) are distributed in scrubby dystrophic savannas. These distributions might be relicts of Pleistocene savannas, and these species may have colonized the area from the south ("around Amazonia") rather than the north (Capurucho et al. 2013). Both species occur in southern Amazonian savannas, including Pampas del Heath.

Our records show that many nutrient-poor specialists, including species that near Iquitos occur only on white-sands, are actually more broadly distributed on nutrient-poor soils elsewhere in the region, especially on the Nauta Formation. At a regional scale, these populations might connect contemporary centers of abundance on white-sands (see H2 discussion). At larger spatial scales, the differentiation of *Polioptila clementsi*, Ancient Antwren (*Herpsilochmus gentryi*), and *Percnostola arenarum* from sister taxa on the Guiana Shield is strong evidence that at least some populations have been truly isolated over evolutionary timescales, whether by vicariance induced by ancient range fragmentation or by colonization of western Amazonia via ancient dispersal.

We do not interpret taxa distributed primarily in blackwater areas as relictual, but we cannot discount this possibility. Our records do not include several species with massively disjunct distributions in Loreto: Red-fan Parrot (*Deroptyus accipitrinus*), Rufous-vented Ground-Cuckoo (*Neomorphus geoffroyi*), Brown-rumped Foliage-gleaner (*Automolus melanopezus*), Ornate Antwren (*Epinecrophylla ornata*), and Variegated Antpitta (*Grallaria varia*). Dispersal is unlikely to span these massive disjunctions, and these populations are probably relictual.

H2: Records represent patchy populations founded and connected by dispersal or by intervening populations so diffuse as to be below the threshold for detection

This hypothesis finds strong support in a diverse suite of 21 species that occur patchily in geologically young habitats, 5 of which occur in patchy habitats on dynamic river floodplains, including wetlands, early successional scrub, and peatlands. For example, a large population of *Certhiaxis cinnamomea* inhabits the Tapiche wetland complex, which is less than a century old, and *Myrmotherula longicauda* and *Neopelma sulphureiventer* inhabit isolated patches of successional floodplain scrub.

Eleven nutrient-poor specialist species, including 8 not treated in detail here (Díaz-Alván et al. 2017), occur on peatland pole forests less than a few thousand years old or in peat-associated blackwater scrub (e.g., *Myrmotherula cherriei*). These records demonstrate recent connectivity between isolated nutrient-poor forest patches and a possible mechanism for connectivity between the white-sands of the Tigre/Upper Nanay, Jeberos, and the Tapiche-Blanco. Further support for fine-scale connectivity between patches of poor-soil forest comes from 5 species we recorded for the first time in the poor-soil matrix between white-sands patches, and from species like *Polioptila clementsi* and "Campina" Fuscous Flycatcher (*Cnemotriccus fuscatus duidae*) that maintain tiny populations in any given white-sand patch. For example, a tiny chamizal in the Allpahuayo-Mishana National Reserve supports exactly one pair of *C. fuscatus duidae* (Álvarez Alonso et al. 2012), clearly not a self-sustaining population. These species are interpreted as having contemporary connectivity between patches of poor-soil forest but relictual distributions at broader spatial scales, based on the gap between populations on the Nauta Formation and the Guiana Shield.

Finally, 9 species (including the nutrient-poor specialist *Polytmus theresiae*) have recently colonized human-created habitats. Species like *Caracara plancus* have encountered highly isolated patches of extensive pasture at Iquitos, Jenaro Herrera, and Oran, perhaps representing the most straightforward demonstration of ongoing connectivity.

H3: Records represent vagrant individuals

We attribute 5 of the patterns presented here as probable cases of vagrancy, mostly based on known or inferred migratory behavior, or single records of species with good dispersal ability. For example, *Muscisaxicola fluviatilis* occurs exclusively during the low-water period in locations inundated at other times of year, whereas *Phimosus infuscatus*, a strong flier, has occurred just once in the Yanamono area. In 3 other species (e.g., *Ixobrychus exilis*), we found little evidence to rule out vagrancy, although established populations seem equally possible.

All our other noteworthy records had at least one of the following characteristics that argue against vagrancy, however: presence of multiple individuals, repeated detections through time in a particular area, territorial behavior, or an ongoing history of discovery in similar habitat. Furthermore, extreme dispersal limitation severely restricts the movement of some Neotropical birds (Stouffer and Bierregaard 1995, Moore et al. 2008, Smith et al. 2014), whose distributions are often constrained by persistent dispersal barriers such as rivers (Cracraft 1985, Burney and Brumfield 2009, Pomara et al. 2014). Vagrancy seems unlikely in such species.

Implications

Overall, our findings suggest that recent connectivity is frequently observed in patchily distributed birds in the Amazon, a feature not widely recognized previously (Álvarez Alonso et al. 2013). The view that patchy Amazonian bird populations are interconnected by gene flow and/or dispersal successfully explains several key features of Amazonian bird distributions, including the presence and persistence of certain species in tiny patches of appropriate habitat, the appearance of appropriately adapted species in newly created habitat patches, and the detection of species in low densities between known population centers. This view has manifest consequences for biogeography and conservation.

Consistent with findings of new genetic analyses (Smith et al. 2014), this view suggests that physiogeographic barriers like rivers and mountains are of paramount importance in restricting dispersal and structuring populations. Barriers imposed by variation in forest habitats seem to be somewhat permeable, at least over moderate distances.

From a conservation perspective, this view highlights the need for a metapopulation approach to Amazonian conservation. Small populations in tiny habitat enclaves might not be self-sustaining, especially true of specialists on dynamic or ephemeral habitats. If such species require a forested matrix for dispersal between habitat patches, population persistence may depend on the conservation of large blocks of forest (Areta and Cockle 2012). The rapid colonization of Loreto by open-country species indicates that the connectivity of upper Amazonia has already changed to the benefit of some species (and possibly the detriment of others), despite high remaining forest cover.

Acknowledgments

We gratefully acknowledge logistical support from Juan-Carlos Palomino Bernt, Eckhard Heymann, Murilo Reis, Deborah Chen, Project Amazonas, Explorama Tours, Otorongo Expeditions, and Judit Ungvari-Martin. Funding for fieldwork came from sources including The Field Museum, American Ornithologists' Union, American Museum of Natural History, American Philosophical Society, High Meadows Foundation, Wildlife Conservation Society, and National Science Foundation. Scientific fieldwork was undertaken with the permission of the Peruvian protected areas authority SERNANP and the agriculture ministry MINAG. We thank Bret M. Whitney for sharing his expertise in Amazonian birdlife, Bruce Beehler for valuable comments on patchy tropical bird distributions, Freddie Draper for valuable comments on the distribution and origins of several habitats in Loreto, and David Wilcove for help and advice at every stage of the project. The following observers contributed bird records: Alex Bernzweig, Ben Schweinhart, Barry Walker, Cristophe Gouraud, David Barton, David Beadle, Deborah Chen, David Geale, Fernando Díaz, José Álvarez, Ken Rosenberg, Mary Gustafson, Murilo Reis, Peter Colasanti, Raphaël Sané, Rodrigo Barros, Roger Ahlman, and Sam Sheline.

Literature cited

Álvarez Alonso J, Díaz-Alván J, Shany N. 2012. Avifauna de la Reserva Nacional Allpahuayo Mishana, Loreto, Perú [Avifauna of the Allpahuayo Mishana National Reserve, Loreto, Peru]. Cotinga. 34:132–152.

Álvarez Alonso J, Metz MR, Fine PV. 2013. Habitat specialization by birds in western Amazonian white-sand forests. Biotropica. 45:365–372.

Álvarez Alonso J, Whitney BM. 2003. New distributional records of birds from white-sand forests of the northern Peruvian Amazon, with implications for biogeography of northern South America. Condor. 105:552–566.

Areta JI, Cockle KL. 2012. A theoretical framework for understanding the ecology and conservation of bamboo-specialist birds. Journal of Ornithology. 153:163–170.

Arnold KA. 1978. First United States record of Paint-billed Crake (*Neocrex erythrops*). Auk. 95:745–746.

Beehler BM, Pratt TK, Zimmerman DA. 1986. Birds of New Guinea. Princeton (NJ): Princeton University Press.

Begazo AJ, Valqui TH. 1998. Birds of Pacaya-Samiria National Reserve with a new population (*Myrmotherula longicauda*) and a new record for Peru (*Hylophilus semicinereus*). Bulletin of the British Ornithologists Club. 118:159–166.

Burney CW, Brumfield RT. 2009. Ecology predicts levels of genetic differentiation in Neotropical birds. American Naturalist. 174:358–368.

Capurucho JMG, Cornelius C, Borges SH, Cohn Haft M, Aleixo A, et al. 2013. Combining phylogeography and landscape genetics of *Xenopipo atronitens* (Aves: Pipridae), a white sand campina specialist, to understand Pleistocene landscape evolution in Amazonia. Biological Journal of the Linnean Society. 110:60–76.

Cracraft J. 1985. Historical biogeography and patterns of differentiation within the South American avifauna: areas of endemism. Ornithological Monographs. 36:49–84.

de Carvalho AL, Nelson BW, Bianchini MC, Plagnoi D, Kuplich TM, Daly DC. 2013. Bamboo-dominated forests of the southwest Amazon: detection, spatial extent, life cycle length and flowering waves. PLOS ONE 8:e54852.

Diamond JM. 1972. Avifauna of the Eastern Highlands of New Guinea. Cambridge (MA): Nuttall Ornithological Club.

Diamond JM. 1973. Distributional ecology of New Guinea birds: recent ecological and biogeographical theories can be tested on the bird communities of New Guinea. Science. 179:759–769.

Díaz-Alván J, Socolar JB, Álvarez Alonso J. 2017. The avifauna of the Río Tigre basin, northern Perú. Ornitologia Neotropical. 28:11–21.

Draper FC, Roucoux KH, Lawson IT, Mitchard ETA, Coronado ENH, et al. 2014. The distribution and amount of carbon in the largest peatland complex in Amazonia. Environmental Research Letters. 9:1–12.

Dumont JF. 1991. Fluvial shifting in the Ucamara Depression as related to the neotectonics of the Andean foreland Brazilian Craton Border (Peru). Géodynamique. 6:9–20.

Dumont JF, Garcia F. 1991. Active subsidence controlled by basement structures in the Marañón Basin of northeastern Peru. Land subsidence: Proceedings of the Fourth International Symposium on Land Subsidence, May 1991. IAHS Publication number 200; p. 343–350.

Dunne T, Mertes L, Meade RH, Richey JE, Forsberg BR. 1998. Exchanges of sediment between the flood plain and channel of the Amazon River in Brazil. GSA Bulletin. 110:450–467.

Espinoza JC, Ronchail J, Frappart F, Lavado W, Santini W, Guyot JL. 2013. The major floods in the Amazonas River and tributaries (Western Amazon Basin) during the 1970–2012 period: a focus on the 2012 flood. Journal of Hydrometeorology. 14:1000–1008.

Fine PVA, García-Villacorta R, Pitman NCA, Mesones I, Kembel SW. 2010. A floristic study of the white-sand forests of Peru 1. Annals of the Missouri Botanical Garden. 97:283–305.

Guilherme E, Borges SH. 2011. Ornithological records from a campina/campinarana enclave on the upper Juruá River, Acre, Brazil. Wilson Journal of Ornithology. 123:24–32.

Haffer J. 1976. A systematic review of the Neotropical ground cuckoos (Aves, Neomorphus). Bonner Zoologische Beiträge. 28:48–76.

Harvey MG, Lane DF, Hite J, Terrill RS, Ramírez SF, et al. 2014a. Notes on the bird species in bamboo in northern Madre de Dios, Peru, including the first Peruvian record of Acre Tody-Tyrant (*Hemitriccus cohnhafti*). Occasional Papers of the LSU Museum of Natural Science. 81:1–38.

Harvey MG, Seeholzer GF, Cáceres D, Winger ABM, Tello JG, et al. 2014b. The avian biogeography of an Amazonian headwater: the Upper Ucayali River, Peru. Wilson Journal of Ornithology. 126:179–191.

Higgins MA, Ruokolainen K, Tuomisto H, Llerena N, Cardenas G, et al. 2011. Geological control of floristic composition in Amazonian forests. Journal of Biogeography. 38:2136–2149.

Hoorn C, Wesselingh FP, Ter Steege H, Bermudez MA, Mora A, et al. 2010. Amazonia through time: Andean uplift, climate change, landscape evolution, and biodiversity. Science. 330:927–931.

Karr JR. 1971. Structure of avian communities in selected Panama and Illinois habitats. Ecological Monographs. 41:207–231.

Kratter AW. 1997. Bamboo specialization by Amazonian birds. Biotropica. 29:100–110.

Lähteenoja O, Reátegui YR, Räsänen M, Torres DDC, Oinonen M, Page S. 2012. The large Amazonian peatland carbon sink in the subsiding Pastaza-Marañón foreland basin, Peru. Global Change Biology. 18:164–178.

Lähteenoja O, Ruokolainen K, Schulman L, Álvarez Alonso J. 2009. Amazonian floodplains harbour minerotrophic and ombrotrophic peatlands. Catena. 79:140–145.

Lane DF, Servat GP, Valqui T, Lambert FR. 2007. A distinctive new species of tyrant flycatcher (Passeriformes: Tyrannidae: *Cnipodectes*) from southeastern Peru. Auk. 124:762–772.

Lane DF, Valqui T, Álvarez Alonso J, Armenta J, Eckhardt K. 2006. The rediscovery and natural history of the

White-masked Antbird (*Pithys castaneus*). Wilson Journal of Ornithology. 118:13–22.

Marengo J. 1998. Climatología de la zona de Iquitos, Perú [Climatology of the Iquitos area, Peru]. In: Kalliola R, Flores Paitán S, editors. Geoecología y Desarrollo Amazónico: estudio integrado en la zona de Iquitos, Perú. Analles Universitatis Turkuensis Series A II. 114:35–57. Turku.

Marra PP, Remsen JV Jr. 1997. Insights into the maintenance of high species diversity in the Neotropics: habitat selection and foraging behavior in understory birds of tropical and temperate forests. Ornithological Monographs. 48:445–483.

McMichael CH, Palace MW, Bush MB, Braswell B, Hagen S, et al. 2014. Predicting pre-Columbian anthropogenic soils in Amazonia. Proceedings of the Royal Society B: Biological Sciences. 281:20132475–20132475.

McMurry FB, Monson G. 1947. Least Grebe breeding in California. Condor. 49:125–126.

Mertes L, Dunne T, Martinelli LA. 1996. Channel-floodplain geomorphology along the Solimões-Amazon river, Brazil. GSA Bulletin. 108:1089–1107.

Moore RP, Robinson WD, Lovette IJ, Robinson TR. 2008. Experimental evidence for extreme dispersal limitation in tropical forest birds. Ecology Letters. 11:960–968.

O'Neill JP, Munn CA, Franke I. 1991. *Nannopsittaca dachilleae,* a new species of parrotlet from eastern Peru. Auk. 108:225–229.

O'Shea BJ, Stotz DF, Saboya del Castillo P, Ruelas Inzunza E. 2015. Birds. In: Pitman N, Vriesendorp C, Rivera Chavez L, Wachter T, Alvira Reyes D, et al., editors. Perú: Tapiche-Blanco. Rapid biological inventories Rep. 27. Chicago (IL): Field Museum of Natural History.

Piana RP, Díaz-Alván J, Chalco Luna JJ, Sevillano CS, Saboya del Castillo P, Cubas Poclín S. 2012. El Caracara Carancho (*Caracara plancus*) estaría expandiendo su rango de distribución hacia el norte y oeste de la Amazonía peruana [The Southern Caracara is expanding its distribution north and west in the Peruvian Amazon]. Boletín Informativo UNOP. 7:5–11.

Pitman NCA, Andino JEG, Aulestia M, Cerón CE, Neill DA, et al. 2014. Distribution and abundance of tree species in swamp forests of Amazonian Ecuador. Ecography. 37:902–915.

Pomara LY, Ruokolainen K, Tuomisto H, Young KR. 2012. Avian composition co-varies with floristic composition and soil nutrient concentration in Amazonian upland forests. Biotropica. 44:545–553.

Pomara LY, Ruokolainen K, Young KR. 2014. Avian species composition across the Amazon River: the roles of dispersal limitation and environmental heterogeneity. Journal of Biogeography. 41:784–796.

Räsänen ME, Salo JS, Jungner H, Pittman LR. 1990. Evolution of the western Amazonian lowland relief: impact of Andean foreland dynamics. Terra Nova. 2:320–332.

Remsen JV Jr, Parker TA III. 1983. Contribution of river-created habitats to bird species richness in Amazonia. Biotropica. 15:223–231.

Remsen JV Jr, Parker TA III. 1990. Seasonal distribution of the Azure Gallinule (*Porphyrula flavirostris*), with comments on vagrancy in rails and gallinules. Wilson Bulletin. 102:380–399.

Robinson SK, Terborgh J, Munn CA. 1990. Lowland tropical forest bird communities of a site in Western Amazonia. In: Keast A, editor. Biogeography and ecology of forest bird communities. Hague (Netherlands): SPB Academic Publishing; p. 229–258.

Robinson SK, Terborgh J. 1997. Bird community dynamics along primary successional gradients of an Amazonian whitewater river. Ornithological Monographs. 48:641–672.

Rosenberg GH. 1990. Habitat specialization and foraging behavior by birds of Amazonian river islands in northeastern Peru. Condor. 92:427–443.

Roucoux KH, Lawson IT, Jones TD, Baker TR, Coronado ENH, et al. 2013. Vegetation development in an Amazonian peatland. Palaeogeography, Palaeoclimatology, Palaeoecology. 374:242–255.

Salo J, Kalliola R, Häkkinen I, Mäkinen Y, Niemelä P, et al. 1986. River dynamics and the diversity of Amazon lowland forest. Nature. 322:254–258.

Schmitt F, Sané R, Thibault M, Vásquez G. [online] 2017. New locality for White-masked Antbird (*Pithys castaneus*) and other bird range extensions for Department of Loreto, Peru. Queensland (Australia): Cotinga; 39. http://www.neotropicalbirdclub.org/cotinga/C39_online/Schmitt%20et%20al.pdf

Schulenberg TS, Stotz DF, Lane DF, O'Neill JP, Parker TA III. 2010. Birds of Peru. Princeton (NJ): Princeton University Press.

Smith BT, McCormack JE, Cuervo AM, Hickerson MJ, Aleixo A, et al. 2014. The drivers of tropical speciation. Nature. 515:406–409.

Socolar J, Robinson SK, Terborgh JW. 2013. Bird diversity and occurrence of bamboo specialists in two bamboo die-offs in southeastern Peru. Condor. 115:253–262.

Stotz DF, Díaz-Alván J. 2007. Aves/Birds. In: Vriesendorp C, Álvarez J, Barbagelata N, Alverson WS, Moskovits DK, editors. Perú: Nanay, Mazán, Arabela. Rapid Biological Inventories Rep. 18. Chicago (IL): Field Museum of Natural History.

Stouffer PC, Bierregaard RO Jr. 1995. Use of Amazonian forest fragments by understory insectivorous birds. Ecology. 76:2429–2445.

Sullivan BL, Wood CL, Iliff MJ, Bonney RE, Fink D, Kelling S. 2009. eBird: a citizen-based bird observation network in the biological sciences. Biological Conservation. 142:2282–2292.

Terborgh J, Petren K. 1991. Development of habitat structure through succession in an Amazonian floodplain forest. In: Habitat structure. Netherlands: Springer; p. 28–46.

Terborgh J, Robinson SK, Parker TA III, Munn CA, Pierpont N. 1990. Structure and organization of an Amazonian forest bird community. Ecological Monographs. 60:213–238.

Thiollay J-M. 1989. Area requirements for the conservation of rain forest raptors and game birds in French Guiana. Conservation Biology. 3:128–137.

Thiollay J-M. 1994. Structure, density and rarity in an Amazonian rainforest bird community. Journal of Tropical Ecology. 10:449–481.

Torres Montenegro L, Mori Vargas T, Pitman N, Ríos Paredes M, Vriesendorp C, Johnston M. 2015. Vegetation and flora. In: Pitman N, Vriesendorp C, Rivera Chavez L, Wachter T, Alvira Reyes D, et al., editors. Perú: Tapiche-Blanco. Rapid biological inventories Rep. 27. Chicago (IL): Field Museum of Natural History.

Tuomisto H, Ruokolainen K, Kalliola R, Linna A, Danjoy W, Rodriguez Z. 1995. Dissecting Amazonian biodiversity. Science. 269:63–66.

Tuomisto H, Ruokolainen D, Yli-Halla M. 2003. Dispersal, environment, and floristic variation of western Amazonian forests. Science. 299:241–244.

Whitney BM, Schunck F, Rêgo MA, Silveira LF. 2013. A new species of *Zimmerius* tyrannulet from the upper Madeira-Tapajos interfluvium in central Amazonian Brazil: birds don’t always occur where they “should.” In: del Hoyo J, Elliott A, Sargatal J, Christie DA, editors. Handbook of the birds of the world. Special volume: new species and global index. Barcelona (Spain): Lynx Edicions; p. 286–291.

Willis EO. 1974. Populations and local extinctions of birds on Barro Colorado Island, Panama. Ecological Monographs. 44:153.