Habitat Specialization by Birds in Western Amazonian White-sand Forests

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ABSTRACT

In the Peruvian Amazon, white-sand forests are patchily distributed and restricted to a few localities in the North. Although recent studies have documented patterns of habitat specialization by plants in these unique forests, very few studies of the fauna of these habitats have been conducted. The species composition of the avifauna of the white-sand forests at six localities in the region was sampled by conducting transects and point counts. Surrounding habitats were also sampled to compare avifaunal communities and to determine the degree of restriction of bird species to white-sand habitats. Non-metric multidimensional scaling analysis showed that bird communities of white-sand forests were more similar to each other than they were to *terra firme* or flooded forest communities. Sites on either side of the Amazon-Marañón barrier were the most similar within habitat type consistent with the hypothesis that these rivers represent a major biogeographic barrier. Twenty-six species, belonging to 13 families, were to some degree specialized to white-sand forests. This is the first comprehensive ornithological assessment carried out on these habitats in Peru. The high degree of habitat specialization found in these 26 bird species highlights the need for conservation and management measures that will protect white-sand forests.

Abstract in Spanish is available in the online version of this article.

Key words: avian biogeography; edaphic specialists; Peruvian Amazonia; river barriers, specialized avifauna; tropical conservation; varillal.

WESTERN AMAZONIA IS KNOWN FOR ITS EXCEPTIONAL SPECIES RICHNESS OF MANY TAXA. It is thought that habitat heterogeneity created by different edaphic and ecological conditions contributes strongly to this high species richness (Remsen & Parker 1983, Terborgh 1985, Gentry 1986, Tuomisto *et al.* 1995, Fine *et al.* 2010). White-sand forests (hereafter WSFs) on nutrient-poor soils are a conspicuous component of the edaphic heterogeneity in Amazonia. WSFs have several distinguishing characteristics that usually include distinctive vegetation with stunted, unbuttressed trees, characterized by pronounced sclerophylly, low diversity, high endemism, high density of trees, and scarce large emergent trees, large lianas, and herbs (Anderson 1981, Medina *et al.* 1990). In northern Amazonia, WSFs are known from Venezuela, Surinam, Guyana, Brazil, and Colombia (Anderson 1981, Duivenvoorden 1996). Locally known in Peruvian Amazonia as 'varillales', WSFs are also called 'bana', 'wallaba', 'campina', 'campinarana' and 'Amazon caatinga' in Amazonia.

Few studies of the birds of WSFs have been conducted in Peru or elsewhere, beyond rapid inventories (*i.e.*, Vriesendorp *et al.* 2006, 2007). Stotz *et al.* (1996), in their comprehensive analysis of Neotropical birds, listed 20 species of birds as 'indicators' (*i.e.*, more or less specialized on this habitat) of WSFs in northern Amazonia. Borges (2004) conducted a detailed survey of the WSF avifauna of Jaú National Park in Brazil and found 14 species that were completely restricted to WSF there. In Acre Brazil, Guilherme and Borges (2011) described six specialist birds found

in a small patch of WSF. Recently, several bird species new to science and to Peru have been discovered in WSFs (Whitney & Álvarez Alonso 1998, Isler *et al.* 2001, Álvarez Alonso & Whitney 2003). There have been no studies, however, evaluating the habitat specialization of WSF birds to test whether these habitats harbor a unique bird fauna. Here, we present data from surveys of six geographically distinct localities of WSFs and compare these data with surveys from neighboring forest types to address three main objectives: (1) evaluate the bird diversity of WSFs and the degree to which the bird community found in WSFs is restricted to this unique and rare forest type or are also found in other, more common forest types; (2) evaluate the biogeography of WSFs, and, in particular, test whether the Amazon/Marañón rivers act as a barrier that prevents dispersal among WSF patches; and (3) test which bird species are significantly associated with WSF and can be classified as a habitat specialist. This study represents the first comprehensive assessment of the avifauna of the WSFs in Peruvian Amazonia.

METHODS

STUDY AREA.—The Department of Loreto is covered with humid rain forest with average canopy height of about 30–35 m, and elevation varying from 110 to 180 m asl. The terrain is flat or gently undulating *terra firme*—with seasonally or permanently flooded habitats along rivers, lakes, and swamps. River levels generally are highest from April to June (with another period of elevated levels from October to November), and lowest July through September. Annual precipitation in Iquitos has never

been recorded at < 2500 mm (average 3087 mm), with a mean annual temperature of 24°C (maximum annual means between 28 and 30°C and minimum means of 17–20°C). As in most areas near the Equator in western Amazonia, there is no marked seasonal climatic pattern, nor a clearly defined 'dry' and 'wet' season in Loreto.

The study area is characterized by an exceptionally diverse mosaic of soil types. In particular, *terra firme* soils vary considerably in origin, age, texture, and geochemistry as a result of millions of years of Andean orogeny, weathering, and fluvial disturbances (*e.g.*, Räsänen *et al.* 1987, Puhakka *et al.* 1992, Räsänen 1993). Phytogeographic patterns are closely correlated with edaphic properties (Gentry 1986, Tuomisto *et al.* 1995, Fine *et al.* 2010). Differences between vegetation of WSFs, mixed forest (which include *terra firme* forests on brown sand (terrace) and clay soils) (hereafter MF) and seasonally flooded vegetation here referred to as várzea forests (hereafter VF) are obvious due to the differences in forest structure (height of the canopy, diameter of the trees) and surface soils as well as the very different species composition of the plants (Fine *et al.* 2010).

Because patches of WSFs, with their specialized flora and fauna, occur in a matrix of other forest types, WSFs function as 'islands' in terms of their biogeography and isolation. Although the WSF islands in Amazonia occur at the same elevations as surrounding habitats, they reflect depositional conditions different from the morphogenetic and hydrological systems prevailing in lowland Amazonia today (Ab'Sáber 1982). The WSF islands usually occur on areas of tectonic uplift, or 'anticlinal emerging arches', where very ancient lacustrine and fluvial sediments from the late Tertiary, originally covered by Quaternary fluvial deposits, appear in the surface because of intensive erosion. They are typically surrounded by younger, more extensive, and nutrient-rich Quaternary fluvial sediments (Räsänen *et al.* 1987, Räsänen 1993). In the Peruvian Amazon, unlike the larger and more contiguous patches of WSFs found in Brazil, the WSF patches are more like archipelagoes, more or less clumped or connected according to geological formations, and are clustered in four areas (Fig. S1). Two of these areas (Jeberos and Morona) are relatively close to the foothills of the Andes, and their creation was probably related to the uplifting of these mountains in the late Miocene, and again in the Quaternary (Dőaz *et al.* 1998). The other two areas in the Nanay (AM Reserve and upper Nanay) and Ucayali (Tamshiyacu & Jenaro Herrera) river basins are both related to the 'Iquitos Arch', a Tertiary anticlinal emerging arch among more modern Quaternary sediments (Räsänen 1993).

Anderson (1981) attempted to standardize the different terms used to describe different kinds of WSFs. Following his terminology, in the Peruvian Amazon, there is Amazonian Caatinga Woodland (known as *chamizal* in Peru) with tree canopies reaching 5–20 m and Amazonian Caatinga Forest (known as *varillal* in Peru) with tree canopies from 20 to 30 m, whereas Amazonian Caatinga Savanna and Amazonian Caatinga Scrub (both with areas of bare ground) are absent in Peru except in areas recently disturbed by humans. In Peru, *varillales* and *chamizales* can be further differentiated by their drainage (hydromorphic or non-hydromorphic according to Anderson 1981), depending on whether the water table stays within a meter of the surface for most of the year. This is referred to as wet or dry (*húmedo* or *seco*) *varillal* or *chamizal*. Finally, some people use the terms high and low (*alto* y *bajo*) to further differentiate higher and lower canopy *chamizales* and *varillales*, giving a maximum of eight different categories of white-sand forest occurring in Peru. It is important to note that these forest type differences refer to the structure of the forest (average canopy height, density, and thickness of tree trunks) rather than any particular vegetation assemblage. While there are a few plants that specialize on hydromorphic versus non-hydromorphic soils, many of the white-sand specialist trees occur on all these eight categories (Fine *et al.* 2010).

For this study, surveys of birds were conducted in WSFs and MF on clay and loamy soils at six localities, and in VF in three of the six localities (Table 1). The six localities (Fig. S1 and Table 1) are described as follows:

North of the Amazon and Marañón rivers:

1. The Reserva Nacional Allpahuayo-Mishana (hereafter 'AM Reserve'), a 58,600-ha reserve 25 km southwest of Iquitos, located in the lower Nanay River basin. In this reserve are concentrated almost fifty patches of WSF grouped in an archipelago within the area of the reserve, covering in total 2500–3000 ha. The largest patches extend a kilometer in diameter and the smallest less than 100 m. The white-sand forests of Allpahuayo-Mishana are the most diverse in terms of their structure (canopy height), drainage and characteristic vegetation, with eight different types of WSF listed by Garcia-Villacorta *et al.* (2003).

2. Upper Nanay River, near the village of Alvarenga. The forest structure of the white-sand patches in the Upper Nanay is similar to those in the AM Reserve, but, instead of small island-like patches, the WSFs here are distributed more continuously in contour lines close to the Nanay River. The biggest concentration of WSFs occur closest to Alvarenga where we have found WSFs of 4–5 km in length by 1.5 km in width. We estimate that, all told, there are 4000–6000 ha of WSF in the Upper Nanay.

3. The village of Tierra Blanca on the lower Morona River close to the confluence with the Mayuriaga River (hereafter 'Morona'). These WSFs are the most extensive (from satellite maps, we would estimate they cover 10,000–15,000 ha) and least fragmented of Loreto, occupying a continuous area between the western bank of the Morona River to the northern bank of the Marañon River and its first tributaries on the Cordillera of Campanquis. Here, there is only one type of WSF (poorly drained, high-canopy Amazonian caatinga forest or *varillal alto húmedo*).

South of the Amazon and Marañón rivers:

1. The village of Jeberos, in the Aypena–Huallaga rivers interfluvium; This very isolated area of WSFs covering approximately 1000–1200 ha is located far away from the major rivers of Loreto, found halfway between the lower Huallaga and the lower Marañón. We found four types of WSF here.

TABLE 1. *Localities, period of study, number of bird species found in each habitat type, and number of point counts, sites where transects were conducted, and total number of transects per habitat per study site. The mean (SD) number of individuals and species per transect is also indicated for each habitat type at a locality.*

LOCALITY	Habitat	Species Observed	No. Point Counts	No of Sites (Total No. Transects)	Transects Average No. Individuals	Average No. Species
Upper Nanay (2000–2001)	WSF	69	26	1 (7)	39.43 (12.69)	25.86 (6.79)
03°43′87″ S						
74°07′20″ W						
AMR (1999–2002)	MF	236	94	3 (20)	58.95 (16.37)	41.6 (11.8)
03° 57′5″ S	VF	142	53	2 (11)	73.36 (13.71)	50.45 (5.85)
73°24′31″ W	WSF	168	246	6 (42)	37.24 (11.03)	24.48 (6.52)
Morona (May-June 2001)	MF	227	29	1 (7)	41.29 (23.92)	27.29 (15.45)
04° 16′51″S	VF	242	24	1 (8)	66.62 (17.06)	38.38 (6.46)
77°14′17″ W	WSF	74	38	1 (11)	42.55 (13.69)	23.82 (6.54)
Jeberos (July 2011)	MF	205	23	1 (7)	51.57 (5.06)	30.71 (2.69)
05°18′46″ S	WSF	67	42	2 (13)	39.08 (14.2)	19.31 (5.06)
76°16′26″ W						
Jenaro Herrara (Dec 2001)	MF	168	16	1 (0)		
04°51′55″ S	VF	80	8	1 (0)		
73°36′29″ W	WSF	111	44	1 (0)		
Tamshiyacu (May 2002)	MF	95	12	1 (0)		
3°59′ S 73°04′ W	WSF	83	49	1 (0)		

2. The village Jenaro Herrera, east of the Ucayali River. This locality includes the smallest concentration of white-sand patches, located on the Eastern side of the Ucayali River, close to the village of Jenaro Herrera. There are around six small and medium size WSFs (10–60 ha) and they are well-dispersed with more than 10 km separating each patch, including a total area of 400–600 ha of WSF. Here we have found 2–3 types of WSF, all with poorly drained soils.

3. The village of Tamshiyacu, south of the Amazon. Here the white-sand forests consist of only half a dozen patches, and, among these, there are three bigger pieces that are more than 4–5 km in length. All the WSF patches together cover about 500–700 ha and are clustered, with distances among them not exceeding 3 km. These white-sand forests are south of the Amazon river and more than 10 km from any riverbank. They include four types of vegetation, the most common of which corresponds to well-drained soils and high-canopy WSF (*varillal alto seco*).

To census birds, 'point counts' and 'line transects' were conducted by the first author. Point counts were conducted to sample smaller patches of habitats that are diverse and that occur in small pockets, as is the case with WSFs. Transects were used to sample larger areas and thus many more individuals and species are recorded. In total, 126 transects and 705 point counts were taken (Table 1). Birds were surveyed along trails from 0515 to 1100 h using binoculars (8 × 40) for visual detections and a professional-grade tape-recorder (Sony TCM 5000, Tokyo, Japan) with directional microphone (Sennheiser, Mod. ME88, Old Lyme,

CT, USA) to lure in birds with unfamiliar voices. Locations were recorded with a GPS unit.

To ensure that the species recorded was in a specific habitat, *i.e.*, white-sand forest versus non- white-sand forest, birds were recorded only if observed by sight or heard within 50 m of the sample point. Birds were counted for 10 min at each point; these were separated from other stops by at least 250 m to reduce the possibility of counting the same individual twice. To make point counts statistically independent, we discarded from the analysis potentially duplicated individuals, *i.e.*, those moving in the direction of the next point. For WSF patches that had a minimum diameter of 1200 m, we conducted line transects that were 1200 m long, located randomly, and surveyed once a day for 3.2–4.1 h. A transect survey consisted of walking the line at a slow pace (0.3–0.5 km/h) as silently as possible and identifying and recording the position of all birds detected, by sight or sound within 50 m along of the trail.

BIRD COMMUNITY ANALYSES.—Transect data within study sites at the six localities were combined (three sites in Morona, 11 sites in AMR, one site in Upper Nanay, and three sites in Jeberos) or point count data were merged (three sites at Jenaro Herrera and two Tamshiyacu sites) to obtain presence/absence matrices of 341 bird species for 23 study sites. Similarities in species composition were examined among sites and habitat types using non-metric multidimensional scaling (NMDS) and Jaccard dissimilarity matrices. Two dimensions were used in the ordination after performing multiple ordinations with random starts and assessing a

scree plot of the stress values versus dimensions of each ordination (McCune & Grace 2002). We excluded one Jeberos transect from the analyses because this was the only *chamizal bajo* (canopy height < 5 m) WSF transect included in the study (the other *chamizales bajos* visited in this study were surveyed with point counts because they covered too small an area to conduct transects), and the community composition of this site was species poor that was an outlier that obscured other site differences in the ordination. When interpreting the NMDS graphs, each point represents a study site (N = 22), and those sites that are close to each other in the ordination configuration have similar composition of bird species, whereas those that are far from each other differ greatly in their species composition. We also tested whether habitat type, geographic region, or the interaction of the two was a significant determinant of bird community composition using a factorial analysis of variance (also called permutational or nonparametric manova) (McArdle & Anderson 2001).

HABITAT ASSOCIATION ANALYSES.—We used the point count data to test for habitat association because there were many more observations and these were more evenly distributed across habitat types. Because WSF sites are spatially autocorrelated, to test whether a species was significantly associated with WSFs, we subjected the point count data to two-tailed Fisher's Exact tests, making a two-by-two matrix of the number of point counts in WSFs where a species was recorded, the number of point counts in WSFs that a species was absent, the number of non-WSF point counts a species was recorded, and the number of non-WSF point counts the species was absent (Zar 1999). Fisher's Exact tests treat each point count as if it is independent, which is not exactly the case (since some points were closer together in space than others). Nevertheless, each of the birds counted represents an independent observation, as special care was made to ensure that the same individuals were not counted more than once.

RESULTS

WSFs in the six sites averaged 94.4 species, about 50 percent lower than the average species diversity from the six MF sites (186.2 species) (Table 1). There were more transects and point counts conducted in WSF than the other habitat types; hence, this disparity in species richness is not related to sampling effort. Besides lower diversity, WSF supports unique species composition of its bird communities (Fig. 1). The NMDS figure is rotated to principal components so that the first axis captures the largest dimension of variation. The ordination depicts strong differences in community composition among habitats that is consistent for each geographic region (Fig. 1). Soil type and location relative to the Amazon-Marañón rivers were both important predictors of bird community composition, with habitat type (along NMDS axis 1) explaining slightly more of the variation among study sites than whether sites were north or south of the Amazon-Marañón rivers (along axis 2). The results are consistent with the hypothesis that the Amazon-Marañón rivers act as a geographic barrier
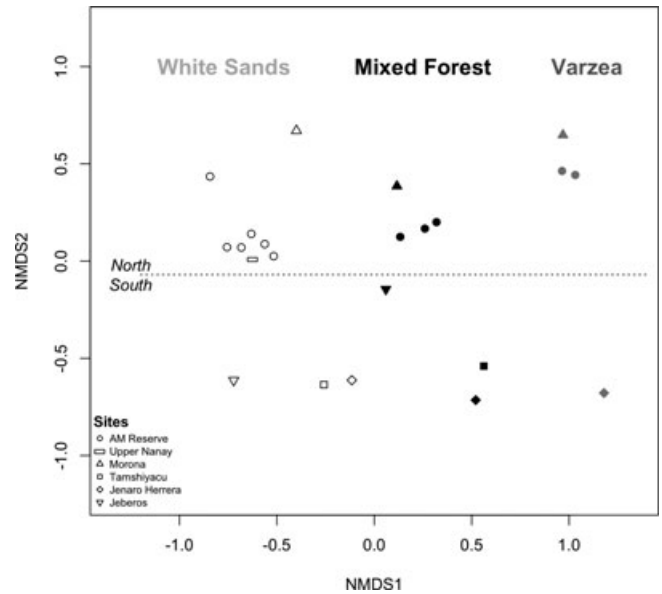

FIGURE 1. Turnover of bird communities with forest type and region. Results of a two-dimensional NMDS ordination (stress = 0.12) of bird presence/absence data for 22 study sites. Within the same geographic region, communities are most similar to other communities from the same soil type. WSFs are open symbols, MF sites are black symbols, and VF are gray. The geographic locations (see Fig. S1 and Table 1) are listed in the legend, with closed and open symbols denoting sample sites that are north and south, respectively, of the Amazon-Marañón rivers. The ordination is rotated to principal components so the first axis represents the maximum variation and demonstrates species turnover with soil type. Species turnover along the second NMDS axis supports the hypothesis that the Amazon-Marañón rivers are an important geographic barrier to bird communities for all three habitat types. Turnover with geographic distance (east to west, see Figure S1), is not an important determinant of species composition.

that structures the composition of bird communities. Both habitat type (F = 15.94, P = 0.001), sampling region (F = 5.50, P = 0.001), and their interaction (F = 2.17, P = 0.003), were significant predicators of bird community composition, explaining 39.0, 33.7, and 18.6 percent of the variance, respectively. Where there were multiple transects within a sampling region, avifaunal communities clustered together by soil type and not geographic distance within or among sampling regions (Fig. 1).

Of the 178 bird species found in WS forest point counts, 26 species were significantly associated with WSF using Fisher's Exact tests (Table S1). The majority of these 26 species were associated with WSF in the Nanay river basin (Table S1).

DISCUSSION

WSFs in the Peruvian Amazon have low species diversity compared to other forest types (Table 1), but harbor a unique community of avifauna (Fig. 1), including 26–39 habitat specialists (Table S1). The contribution of floristics and vegetation structure to habitat specialization and diversity in birds has already been

shown in other cases in the Amazon basin by Borges (2004) in WSFs of Jaú National Park, Brazil, by Remsen & Parker (1983) in riverine floodplain habitats, by Rosenberg (1990) in river islands, by Kratter (1997) in bamboo-dominated forests, by Borges and Carvalhaes (2000) in black-water inundated forests, and by Pomara *et al.* (2012) in sandy versus clayey upland forests (MF). This relationship is also very clear in Peruvian WSFs, which exhibit distinctive bird communities (Fig. 1), including at least 26 habitat-specialist bird species that are rarely, or never found in other forest types. The existence of a community of birds specialized for WSFs is evidence that habitat specialization is one of the factors contributing strongly to the high regional species richness in the Neotropics (Terborgh 1985, Cohn-Haft *et al.* 1997). The Iquitos region is famous for high levels of both alpha and beta biodiversity, especially in plants and some vertebrate groups. With respect to the avifauna, within a radius of 200–300 km at 100–200 m altitude around Iquitos, 778 bird species can be found (Wiley 1999).

Both forest type and geography influence the similarity of bird communities (Fig. 1). Pomara *et al.* (2012) showed that bird communities were correlated with edaphic variables (and plant community composition) in sandy and clay upland forests in the same region. In our study, in each of the six sampling localities, WSF, MF, and VF clustered in similar ways in the ordination, lending support that WSF, MF, and VF each harbor their own bird communities that change with increasing geographic distance and with respect to geographic boundaries, which appear to be circumscribed by major rivers. River barriers play an important role, as spatially close-together but cross-Amazon sites, such as Tamshiyacu and the AM Reserve, exhibited very different bird communities. Both of these locations are geologically part of the 'Iquitos Arch', however, had closer affinities with sites that were much further away, but on the same side of the Amazon-Marañón barrier, which has been previously described as a major biogeographical boundary for Amazonian avifauna (Cracraft 1985).

The present study has allowed the formation of a preliminary list of specialist WSF birds (Table S1). We found that 26 birds exhibited statistically significant associations with WSF. In addition to the systematic surveys of bird communities in WSFs, MF and VF in the six localities cited above, we compared our results with those found in other well-studied sites from the northern Peruvian Amazon. These studies, mostly unpublished reports (in the 'gray literature'), were made in the same geographical areas, but were conducted in TF and VF, but not in WSFs (Table S1).

The list of WSF specialists generated here can be divided into three categories. First, there are species that have been found only in WSF and no other habitat in the study region (strict specialists). Second, there are other species that appear to be completely restricted to WSF, but only in part of their range (local specialists). For example, *Myrmeciza castanea* occurs only in WSF in the AM Reserve, whereas at the Jeberos site, it was more abundant in clay-soil forest than in white-sand forest. Such species may have different patterns of specialization at different sites, either because of different patterns of habitat heterogeneity in different regions, or because of interactions with other bird species. These species, while recorded in other habitats besides WSF, are usually restricted to other oligotrophic forest growing on nutrient-poor, deeply weathered soils. For example, *Heterocercus aurantiivertex* and *Attila citriniventris* are found occasionally in oligotrophic black-water swamps and seasonally flooded forests (igapó). Finally, there are other bird species which could be classified as facultative white-sand users, because although they are more common in WSFs than in other habitats they are not either statistically significant, and/or commonly found in habitats other than WSFs in this study or from previous studies by the first author.

The Nanay River basin contains the highest diversity of WSF specialists, with 25 species. Only *Pithys castaneus* and *Epinecrophylla leucophthalma* subsp. nov. are absent from the Nanay basin; both are restricted to the Morona WSFs. The reasons for these patterns could be historical (age and origin of the white-sand formations), ecological (habitat heterogeneity, extension, and clumping of the white-sand patches), and/or geographical processes (distance and isolation from the presumed center of origin, the Guianan and Brazilian Shields). Island biogeography theory states that the area of an island and its distance from the mainland accounts for most variation in species numbers in islands (MacArthur & Wilson 1967), and Oren (1982) found in Brazilian WSF that the avifaunal diversity patterns followed these predictions. Oren (1982) did not emphasize other factors, however, that can influence the presence of bird species in a given WSF, such as habitat quality and heterogeneity, individual history, and origin of each patch. The WSFs of Morona cover perhaps the largest total area in Peru, however, they do not rival the species diversity of the AMR WSFs, indicating that WSF patch size is likely not the only important variable explaining bird diversity.

WSF communities on the southern side of the Marañón/Amazon are depauperate (Table 1) compared to the northern side, and this barrier appears to strongly influence community composition (Fig. 1). We propose that the size of individual WSF patches may not be as important for determining the composition of species as the size of the 'WSF archipelago', age and history, distance from the 'mainland' -the Guianan Shield-, and habitat heterogeneity. It is difficult to isolate these variables; however, because the oldest and most heterogeneous WSF patches also cover a large area.

EVOLUTION AND DISPERSAL OF THE WHITE-SAND SPECIALIST BIOTA.—Many Peruvian WSF specialist bird species are shared with the Guianan Shield in Brazil, Colombia, and Venezuela (Stotz *et al.* 1996, Álvarez Alonso & Whitney 2003, Table S1). This ancient geological formation (and related areas of the Brazilian Shield south of the Amazon) has been hypothesized as being not only the original source-pool of the white-sand specialized biota found in northwestern Amazonia (Hershkovitz 1963, Whitney & Álvarez Alonso 1998), but also the original source of the same white-sand sediments of the Nanay basin area (Räsänen 1993).

Many WSF bird species may have colonized the Nanay basin, and subsequently other WSF islands, via long-distance dispersal from populations from the Brazilian and Guianan Shield.

Macedo and Prance (1978) found that about 76 percent of the plant species in campinas have the potential for long-distance dispersal, of which about 60 percent are bird-dispersed. This tendency towards long-distance dispersal, and especially towards ornithochory, is characteristic of oceanic islands, and we also find this pattern in habitat-islands like WSFs. If WSFs are thus often filled with trees that produce bird-dispersed fruit, this could also influence bird behavior, perhaps selecting for birds to increase their dispersal range and seek out WSF patches. However, long-distance dispersal seems less likely for understory or terrestrial bird species, which rarely cross 'open areas' a few dozens of meters wide and are known to have different taxa on both sides of rivers, such as the Napo and the Amazon (Capparella 1991).

An alternative explanation of the presence of the same WSF specialist bird communities on geographically separated WSFs in Peru is that the WSF patches may be relicts of a formerly more widespread habitat, as proposed for WSF plants in northern Brazil (Prance 1982). Some authors have even postulated that the Guianan and Brazilian shields may have been the region of origin for many *terra firme* bird species in western Amazonia, not just WSF species (Aleixo & Rossetti 2007), meaning that biogeographical connections with the eastern part of the continent may be a more general phenomenon. Nevertheless, WSFs may have been more extensive in the past in Brazilian Amazonia, at least during the Pleistocene (Ab'Saber 1982, Oren 1982).

Finally, some of the white-sand specialists may have speciated *in situ* in Western Amazonian WSFs. In other words, some WSF specialists may be recently derived sister taxa of bird species associated with non-WSF habitat types, in accordance with the gradient hypothesis (ecological speciation) (Moritz *et al.* 2000). The way to test these theories is to examine the phylogenetic relationships of the Western Amazonian endemic WSF species and their closest relatives and compare the geographic distributions and habitat preferences of the putative sister taxa. At least two of the species in these groups (*Percnostola arenarum* and *Polioptila clementsi*) have sister species in the Guianan Shield area, from which both presumably originated (*Percnostola rufifrons* and *Polioptila guianensis,* respectively; Whitney and Álvarez Alonso 2005, Isler *et al.* 2001). Three other specialists (*Zimmerius villarejoi*, *Pithys castaneus,* and *Myrmeciza castanea*) all have putative sister taxa with widespread distributions (including Western Amazonia), but are found in habitats other than white-sand forests. The Morona–Pastaza area harbors *Pithys castaneus,* of which only one specimen collected more than 70 years ago was known prior to this study from the middle-upper Pastaza River, relatively close to the Morona WSFs (Lane *et al.* 2006). Populations of two other birds also occur in this region and probably represent undescribed new species or subspecies (pending detailed studies; preliminarily designated *Epinecrophylla leucophthalma* and *Percnostola arenarum*).

Phylogenetic studies of these genera using molecular-based characters will be invaluable for untangling the biogeographical history of these white-sand endemics, and to better understand the contribution of habitat heterogeneity and biogeographic barriers to the evolution of the diverse avifauna of the Amazon basin.

In addition, population genetic and phylogeographic studies of these isolated WSF populations and phenotypic indicators of genetic differences (or lack thereof), such as subtle differences in color, measurements, voice, etc., are required to estimate gene flow among the individual WSF patches, as well as among the six WSF 'archipelagoes' we studied in northern Peruvian Amazonia. These types of studies together with analysis of the characteristics of their resource and habitat use (*e.g.,* canopy vs. undergrowth, frugivore/nectarivore vs. insectivore, and other indirect measures of potential dispersal ability or persistence) would provide important clues for understanding the origin and to explain the patterns of distribution of this unique avifauna.

Conservation implications and conclusions.—In response to the discovery near the city of Iquitos of about a dozen species of birds new to Peru, including some new to science, the Reserva Nacional Allpahuayo-Mishana (AM Reserve) was proposed and created (Álvarez Alonso 2007, Salo & Pyhälä 2007) for the protection of these birds and the entire community of unique plant and animal species that are restricted to white-sand forests. Many WSF specialists are extremely rare and with tenuous prospects for continued survival. For example, fewer than 25 individuals are known of the newly described gnatcatcher *Polioptila clementsi* and all live in two different WSF in and near the AM Reserve (Whitney & Alvarez 2005). This species is classified as 'Critically Endangered' by the IUCN. Today there are three areas in Peru with WSF that are conservation areas, the AM Reserve (58,069 ha), the Reserva Nacional Matsés (420,635 ha) (Vriesendorp *et al.* 2006), and the Regional Conservation Area Alto Nanay-Pintuyacu-Chambira (954,635 ha) (Vriesendorp *et al.* 2007). Despite the legal status of the AM Reserve, deforestation continues, and local government officials are often reluctant to enforce the law, because of strong social and political pressures. There are few economic alternatives to clearing forest, and the local people have to some extent continued with their traditional activities of shifting agriculture and extraction of resources from the forest to make a living. Although the long-term impact of these activities on the unique fauna and flora are not known, the short-term impact appears highly destructive. Continued logging activities in these kinds of forests could put at risk long-term survival of those species.

It is important to study and protect these forests not only because they are biologically unique and home to a rich community of rare and range-restricted species, but also because they are so fragile that once disturbed, they may require hundreds or thousands of years to recover (Uhl *et al.* 1982). Many WSF specialists may never recolonize regenerated white-sand forest patches especially if they are separated from intact forest by open areas. Some animals, especially the obligate white-sand specialists, may be affected by minor disturbances of the forest, disturbances such as that caused by the selective timber extraction. More studies are required to precisely define habitat requirements of WSF species and to assess threats that various habitat changes would have on them.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

FIGURE S1. Study area, with location of study sites in northern Peruvian Amazonia. See Table 1 for latitude and longitude data.

TABLE S1. *Preliminary list of white-sand specialist birds in the Peruvian Amazon.*

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