Birds of a palm-dominated *terra firme* forest: the contribution of habitat heterogeneity to regional avian diversity

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Aquí yo documento las diferencias entre las comunidades de aves de dos tipos del bosque terra firme que ocurre en typos de suelos differentes adyacente uno al otro en el valle por el río Pauya superior, dpto. Loreto, Perú. Durante julio y agosto de 2000, yo usé redes y inspecciones visuales y auditivos para probar las comunidades de aves de un bosque terra firme típico y un otro bosque que no es típico pero las palmeras dominan abajo de dosel del bosque. La diversidad de especies y complejidad estructurales de la vegetación eran más bajas en el bosque dominado de las palmeras que en el bosque terra firme típico. El bosque dominado de las palmeras sostuvo menos especies de aves y menos individuales de aves que el bosque terra firme típico, y había la superposición pequeña en la composición de la especies de las dos comunidades de aves. Aves que comen insectos o insectos y jugos eran notablemente menos abundante en el bosque dominado de palmeras. Sin embargo, unas especies tuven densidades de poblaciones mas alto en el bosque dominado de la palmeras, sugerir la importancia de la segregación de la escala de la multa a lo largo de declives del habitat, determinaron por los typos de suelos y acentuar la necesidad para conservar todos de los tipos de habitates dentro de una región.

Many historical hypotheses (see references in Haffer[7]) and ecological hypotheses (see references in Marra & Remsen[12]), have been suggested to explain the origin and maintenance of high avian diversity in the Neotropics, and many factors contribute to the maintenance of Neotropical biodiversity, but there is increasing recognition of the importance of habitat heterogeneity[5,11,13,17]. Edaphic conditions generate fine-scale habitat heterogeneity within Amazonian *terra firme* forests that were previously considered essentially homogeneous[18], affecting the diversity and composition of avian communities[1,8].

Scientific teams from the Field Museum of Natural History, the Louisiana State University Museum of Natural Science (LSUMNS), and the Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos catalogued the flora and fauna of the upper río Pauya, Peru, during summer 2000 as part of a Rapid Biological Inventory[2] preliminary to the establishment of a new national park (Parque Nacional Cordillera Azul), which was created in May 2001. The drainage of the upper río Pauya lacks a well-developed floodplain forest, but is characterised by two distinct types of unflooded lowland forest (*terra firme*), growing on different soil types, below 600 m elevation: 1) an unusual palm-dominated forest occurring on alluvial fans along the river, and 2) a more typical *terra firme* forest on hills and alluvial terraces further from the river.

The palm-dominated forest appeared to possess a significantly depauperate avifauna compared to the typical *terra firme* forest, with fewer avian species and fewer individual birds than the typical forest. In addition, there seemed to be little overlap in the composition and structure of the two avian communities. I quantified these apparent differences in the vegetation structure and avian communities of the two forest types.

Study area

The study was conducted in July–August 2000 in the headwaters of the río Pauya, c.170 km north-west of Pucallpa, in dpto. Loreto, Peru (c.73º05'S 75º56'W). The río Pauya arises in the Cordillera Azul, a range of low sandstone mountains between the valleys of the ríos Huallaga and Ucayali. The río Pauya drains into the río Cushabatay, which in turn is a tributary of the Ucayali. Within the upper río Pauya drainage, two types of unflooded lowland forest (*terra firme*), occurring on different soil types, can be recognised on slopes below 600 m. At c.350–400 m, a unique palm-dominated forest grows on the sandy soils of alluvial fans formed by landslides from the slopes of the Cordillera Azul. Broadleaf trees (including many deciduous species) dominate the canopy of this forest, but the dense subcanopy is dominated almost exclusively by tall, widely spaced palms (mostly *Attalea* and *Astrocaryum*). Relatively few shrubs, saplings or herbaceous plants grow in the low light beneath the palms, resulting in a very open forest floor. Further from the river, at c.400–600 m, a more typical *terra firme* forest grows on the rocky soils of hills and ancient alluvial terraces. This forest type is characterised by a more complex vegetation structure and greater diversity of plant species than the palm-dominated forest. In the typical *terra firme* forest, vegetation is very dense throughout all strata, from the herbaceous layer to the canopy. The vegetative communities of the río Pauya are described in greater detail in Alverson[2].

Methods

I established two 1-km transects (one in each forest type) along a trail running parallel to a small stream (Quebrada John) that flows into the río Pauya. The elevation of the transect in palm-dominated forest ranged from 380 m to 395 m, and the transect in typical *terra firme* forest, c.1 km distant, was at 480–555 m. I sampled vegetation at ten 5-m radius plots spaced 100 m apart along each transect (in the middle of each 100-m section). Vegetation plots were centred 7.5 m from the transect to avoid sampling disturbed vegetation along the trail, and neighbouring plots were located on alternate sides of the transect. Within each vegetation plot, I collected the data on the structural complexity and vegetative diversity of the habitat (Table 1).

I surveyed birds along each transect on five different days. Surveys were alternated between transects from one day to the next, and each transect was surveyed in alternating directions from one visit to the next. All birds were recorded, although observer bias may have favoured detection of understorey and terrestrial birds over canopy birds. Surveys were conducted by slowly walking along the transect during the first three hours after dawn. I also sampled birds using 2 x 12 m mist-nets with a 30-mm mesh. Five mist-nets were placed 200 m apart along each transect, and 5–10 m from the transect to avoid disturbed vegetation along the trail; neighbouring mist-nets were set on alternate sides of the transect. Each net was opened for extended periods (generally eight hours) during five days, for totals of 192 net hours in the typical *terra firme* forest and 208 net hours in the palm-dominated forest. Nets along the two transects were opened on alternate days.

I used multivariate analysis of variance to compare structural complexity and vegetative diversity of the two forest types. I then tested individual habitat variables for significant differences between forest types, using a sequential Bonferonni correction. Variables that did not meet the assumption of normality were log transformed prior to analysis; other variables could not be normalised by any transformation, but non-parametric Wilcoxon tests performed on these variables yielded the same results as the parametric tests. I used analysis of variance to compare avian species richness and individual abundance between the two forest types, using a sequential Bonferonni correction. To further assess differences in the structure of the avian communities of the two forest types, I used data from foraging observations made at the site and from the literature to assign all bird species to one of four foraging guilds (frugivores, frugivore/insectivores, insectivores and miscellaneous). The miscellaneous category includes several guilds (nectarivores, granivores, omnivores and piscivores) that were too rare to be analysed separately. I performed a G-test on the data to test the null hypothesis that the distribution of species between forest types is independent of guild membership. A significant result would suggest that different guilds respond differently to the habitat heterogeneity between forest types. All statistical tests were performed using SAS 8.01.

Results

Both the structural complexity and species diversity of the vegetation were lower in the palm-dominated forest than in the typical *terra firme* forest (Wilk's Lambda for MANOVA=0.0009) (Table 1). There was a significantly higher density of palm fronds in the shrub layer of the palm-dominated forest, whilst woody plant stems were significantly more frequent in the typical *terra firme* forest, which also supported a significantly greater diversity of plant species ≥2.5cm dbh. The palm-dominated forest had significantly less leaf litter and fallen logs than the typical *terra firme* forest. The paucity of leaf litter in the palm-dominated forest resulted in significantly more

Table 1. Structural complexity and diversity of the vegetation is lower in the palm-dominated forest than in the typical *terra firme* forest (Wilk's Lambda for MANOVA=0.0009). Results indicate mean ± one SD.

variable	palm forest	typical forest	p-value
ground cover (%)			
rocks	10.0 ± 11.8	0.0 ± 0.0	0.0090[d]
leaf litter and logs	60.0 ± 11.6	76.0 ± 9.2	0.0045[d]
live plants	30.0 ± 12.4	24.0 ± 9.2	0.3274
vegetation density[a]			
woody plants			
upper	2.0 ± 2.4	5.3 ± 3.2	0.0289
lower	2.2 ± 3.4	3.1 ± 2.9	0.3365
palms			
upper	1.4 ± 0.9	0.0 ± 0.0	0.0002[d]
lower	0.6 ± 0.9	0.1 ± 0.3	0.1373
# woody plant stems[b]	3.4 ± 2.2	11.8 ± 3.9	0.0001[d]
# palm stems[b]	2.0 ± 2.0	1.2 ± 2.0	0.4174
canopy height (m)	30.8 ± 6.2	30.5 ± 6.2	0.8974
number of plant OTUs[c]	2.8 ± 1.2	5.5 ± 0.8	0.0001[d]

[a] number of leaves (for woody plants) or fronds (for palms) passing through the upper and lower halves of a 2 m^2 plane (2 m long and 0.5–2.5 m above ground)

[b] number of woody plant and palm stems ≥ 2.5cm dbh

[c] number of operational taxonomic units (OTUs) for woody plants and palms; OTUs, defined by leaf and bark morphology, were used because of the difficulty of identifying many rainforest plants

[d] individual variables that differ significantly between forest types

Table 2. The palm-dominated forest supports fewer avian species and fewer individual birds than the typical *terra firme* forest. All variables differ significantly between forest types. Results for survey data indicate mean ± one SD species or individuals per survey. Results for mist-net data indicate mean ± one SD species or individuals per 100 net hours.

variable	palm forest	typical forest	*P*-value
survey data			
number of species	12.6 ± 1.0	22.8 ± 1.8	0.0001
number individuals	28.0 ± 4.7	37.8 ± 2.3	0.0059
mist-net data			
number of species	0.7 ± 0.8	2.4 ± 0.8	0.0237
number individuals	0.7 ± 0.8	2.6 ± 0.8	0.0150

Table 3. There is little overlap in the species composition of the avian communities of the two forest types, and the two avian communities differ in guild structure. Results indicate number of species of each guild in each forest type, with percentage of guild members (species) found in a given forest type in parentheses.

		forest types		
guild	palm forest	typical forest	both forests	totals
frugivores	1 (10%)	7 (60%)	3 (30%)	11
insectivore/frugivore	1 (10%)	10 (90%)	0 (0%)	11
insectivores	6 (30%)	17 (70%)	0 (0%)	23
miscellaneous[a]	4 (40%)	3 (30%)	2 (20%)	9
totals	12 (22%)	37 (69%)	5 (9%)	54

[a] see Methods section for definition of miscellaneous guild

exposed rocks on the ground than in the typical *terra firme* forest, but this is misleading, because the palm-dominated forest grew on generally sandy soil, whereas the typical *terra firme* forest was on better-developed, though rocky, soil.

I recorded 54 avian species (Appendix). A more complete list of the avifauna of the two forest types, based on more extensive but less systematic sampling, is presented by Alverson[2]. The systematic samples reported here were roughly equal between forest types, so the results should reflect real differences in the relative species diversity and individual abundance of birds of the two forest types. Both transect surveys and mist-netting indicated that the palm-dominated forest supports a lower diversity of avian species and fewer individual birds than the typical forest (Table 2). There was little overlap in species composition of the avian communities of the two forest types (Table 3). Of the 54 avian species recorded during the study, 37 (69%) were recorded exclusively in the typical *terra firme* forest, 12 (22%) exclusively in the palm-dominated forest, and only five species (9%) in both forest types. The G-test for the null hypothesis that the distribution of species between the two forest types is independent of guild membership was not quite significant (2=6.1002, df=3, P=0.1068), but the avian communities of the two forest types did differ in guild structure (Table 3). Whilst all guilds were represented by more species in the typical *terra firme* forest (except for the miscellaneous category), the insectivore/frugivore and insectivore guilds were noticeably depauperate in the palm-dominated forest.

Discussion

The palm-dominated and typical *terra firme* forests differ significantly in vegetation structure and diversity, probably due to edaphic conditions. The palm-dominated forest has a simplified vegetative structure characterised by a low density of vegetation below the understorey, and it exhibits decreased plant species richness in all vegetative strata. A dense understorey of *Attalea* and *Astrocaryum* palms develops on sandy soils along the río Pauya, preventing the development of a complex shrub or herbaceous layer and inhibiting the growth of canopy tree saplings. Herds of White-lipped *Tayassu pecari* and Collared Peccaries *T. tajacu*, attracted by palm fruit, may also contribute to the reduction of ground-level vegetation.

The significant differences in vegetation structure and diversity between the two forest types results in differences in their avian communities. Species richness and individual abundance of birds are significantly lower in the palm-dominated forest than in the typical *terra firme* forest. Differences between the avian communities of the two forest types vary by feeding guild, with the insectivore/frugivore and insectivore guilds being especially depauperate in the palm-dominated forest. Low vegetative complexity and low plant species diversity limit diversity and abundance of arthropods and the diversity of foraging substrates[8,9,16], and a lack of suitable foraging substrates is probably the most significant limiting factor for many insectivores[8]. At the río Pauya study site, insectivores that forage in vine tangles and other low, dense vegetation (e.g. Buff-throated Foliage-gleaner *Automolus ochrolaemus*, Fasciated Antshrike *Cymbiliamus lineatus* and Mouse-coloured Antshrike *Thamnophilus murinus*) are absent from or occur at very low abundances in the palm-dominated forest, because of the scarcity of their preferred foraging substrates. These results are preliminary and further research is needed, particularly as to whether the differences between the avian communities of the two forest types are seasonal or stable year-round. Although the phenology of flowering and fruiting in Neotropical palms is poorly documented compared to that of other plant taxa, there appears to be seasonal variability in the availability of palm fruit in the Neotropics[6,14].

There is relatively little overlap in the species composition of the avian communities in the two forest types. Whilst the palm-dominated forest has a relatively depauperate avifauna, it nonetheless supports high densities of several species that were less common in the typical *terra firme* forest. Avian communities of forests growing on nutrient-poor white sands are characterised by low diversity but high endemism in both Peru[19] and Brazil[4]. Edaphically-determined habitat heterogeneity contributes significantly to the diversity and composition of avian communities in Amazonia, suggesting that adequate protection of regional biodiversity requires that nature reserves encompass the entire range of habitat heterogeneity within the landscape mosaic[1,3,10,15]. Reserves such as the newly created Parque Nacional Cordillera Azul, which protects the entire watershed of the upper río Pauya, are particularly effective because they preserve an intact series of habitat types along a regionally important environmental gradient.

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References

1. Alvarez Alonso, J. & Whitney, B. M. (2001) A new *Zimmerius* tyrannulet (Aves: Tyrannidae) from white sand forests of northern Amazonian Peru. *Wilson Bull*. 113: 1–9.
2. Alverson, W. S., Rodriquez, L. O. & Moskovits, D. K. (eds.) (2001) *Rapid biological inventories 02: Peru: Biabo Cordillera Azul*. Chicago: The Field Museum.
3. Blake, J. G. & Loiselle, B. A. (2000) Diversity of birds along an elevational gradient in the Cordillera Central, Costa Rica. *Auk* 117: 663–686.
4. Borges, S. H. (2004) Species poor but distinct: bird assemblages in white sand vegetation in Jaú National Park, Brazilian Amazon. *Ibis* 146: 114–124.
5. Cohn-Haft, M., Whittaker, A. & Stouffer, P. C. (1997) A new look at the "species-poor" Central Amazon: the avifauna north of Manaus, Brazil. *Orn. Monogr*. 48: 205–236.
6. Foster, R. B. (1982) The seasonal rhythm of fruitfall on Barro Colorado Island. In: Leigh, E. G., Rand, A. S. & Windsor, D. M. (eds.) *The ecology of a tropical forest: seasonal rhythms and long-term changes*. Washington DC: Smithsonian Institution Press.
7. Haffer, J. (1997) Alternative models of vertebrate speciation in Amazonia: an overview. *Biodiv. & Conserv*. 6: 451–476.
8. Holmes, R. T., Bonney, R. E. & Pacala, S. W. (1979) Guild structure of the Hubbard Brook bird community: a multivariate approach. *Ecology* 60: 512–520.
9. Holmes, R. T. & Recher, H. F. (1986) Determinants of guild structure in forest bird communities: an intercontinental comparison. *Condor* 88: 427–439.
10. Karr, J. R. & Freemark, K. E. (1983) Habitat selection and environmental gradients: dynamics in the "stable" tropics. *Ecology* 64: 1481–1494.
11. Kratter, A. W. (1997) Bamboo specialization by Amazonian birds. *Biotropica* 29: 100–110.
12. Marra, P. P. & Remsen, J. V. (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. *Orn. Monogr*. 48: 445–483.
13. Salo, J., Kalliola, R., Hakkinen, O., Makinen, Y., Niemela, P., Puhakka, M. & Coley, P. D. (1986) River dynamics and the diversity of Amazonian lowland forest. *Nature* 322: 254–258.
14. Scariot, A., Lleras, E. & Hay, J. D. (1995) Flowering and fruiting phenologies of the palm *Acrocomia aculeata*: patterns and consequences. *Biotropica* 27: 168–173.
15. Stotz, D. F., Fitzpatrick, J. W., Parker, T. A. & Moskovits, D. K. (1996) *Neotropical birds: ecology and conservation*. Chicago: University of Chicago Press.
16. Terborgh, J. (1977) Bird species diversity on an Andean elevational gradient. *Ecology* 58: 1007–1019.
17. Tuomisto, H. & Ruokolainen, K. (1997) The role of ecological knowledge in explaining biogeography and biodiversity in Amazonia. *Biodiv. & Conserv*. 6: 347–357.
18. Tuomisto, H., Ruokolainen, K., Kalliola, A., Linna, W., Danjoy, W. & Rodriguez, Z. (1995) Dissecting Amazonian biodiversity. *Science* 269: 63–66.
19. Whitney, B. M. & Alvarez Alonso, J. (1998) A new *Herpsilochmus* antwren (Aves: Thamnophilidae) from northern Amazonian Peru and adjacent Ecuador: the role of edaphic heterogeneity of *terra firme* forest. *Auk* 115: 559–576.

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Appendix. Species lists for typical *terra firme* forest (*n*=42) and palm-dominated forest (*n*=17). Results are based on transect surveys, mist-netting and opportunistic sightings. Species in bold were recorded in both forest types. Taxonomy follows Stotz *et al.*[15].

Key:
Guild: F = frugivore; I/F = insectivore/frugivore;
I = insectivore; M = micellaneous.

Status: C = common; FC = fairly common;
U = uncommon; R = rare.

Evidence: T = visual or auditory detection during transect survey; N = captured in mist-net; O = opportunistic sighting (not during transect survey).

Species		Status		
	Guild	Typical forest	Palm forest	Evidence
CRACIDAE				
Ortalis motmot	M	R	O	
ODONTOPHORIDAE				
Odontophorus stellatus	M	R	O	
COLUMBIDAE				
Columba plumbea	F	R	U	T
Geotrygon montana	F	FC	N, T	
PSITTACIDAE				
Ara sp.	F	C	T	
***Aratinga* sp.**	F	C	C	T
Pionus menstruus	F	FC		T
TROCHILIDAE				
Phaethornis superciliosus	M	C	R	N, T
Phaethornis longuemaeris	M	R		N
Campylopteris largipennis	M		R	N
TROGONIDAE				
Trogon viridis		F	U	R T
Trogon collaris	F	C		T
ALCEDINIDAE				
Chloraceryle sp.	M		U	T
GALBULIDAE				
Galbula cyanescens	I		R	O
BUCCONIDAE				
Monasa morphoeus	M	C		T
Monasa nigrifrons	M		C	T
CAPITONIDAE				
Capito niger	I /F	R		T
RAMPHASTIDAE				
Selenidera reinwardtii	F	R		O
Ramphastos tucanus	F		C	T
PICIDAE				
Celeus elegans	I		R	T
Celeus flavus	I	U		T
FURNARIIDAE				
Automolus ochrolaemus	I	R		N
Sclerurus caudacutus	I	R		N
DENDROCOLAPTIDAE				
Dendrocincla fuliginosa	I	R		N
Dendrocincla merula	I		FC	N
Deconychura stictolaema	I		R	N
Xiphorhynchus guttatus	I	R		N
THAMNOPHILIDAE				
Cymbilaimus lineatus	I	R		O
Thamnophilus murinus	I	FC		N
Thamnomanes ardesiacus	I	U		T
Thamnomanes caesius	I	R		N
Mymotherula obscura	I	U		T
Cercomarca cinerascens	I	R		T
Pithys albifrons	I	R		N
Hylophylax naevia	I		C	T
Phlegopsis nigromaculatus	I	FC		T
Myrmeciza fortis	I	R		N
TYRANNIDAE				
Mionectes oleagineus	I		R	N
Pachyramphus minor	F	R		T
PIPRIDAE				
Pipra coronata	I/F	FC		N
Pipra fasciicauda	I/F	FC		N
COTINGIDAE				
Lipaugus vociferans	I/F	C		T
Querula purpurata	I/F	R		O
TROGLODYTIDAE				
Microcerclus marginatus	I	R		N
TURDIDAE				
Turdus albicollis	I/F	R		N
THRAUPIDAE				
Cissopis leveriania	I/F	R		T
Chlorothraupis carmioli	I/F	U		T
Tachyphonus rufiventer	I/F	U		T
Euphonia sp.	I/F		U	T
Tangara chilensis	I/F	R		O
VIREONIDAE				
Hylophilus hypoxanthus	I	U		T
Hylophilus ochraceiceps	I	U		N, T
ICTERIDAE				
Cacicus cela	M	C	C	T
Psarocolius bifasciatus	F	C		T