

NESTEDNESS AND PATCH SIZE OF BAMBOO-SPECIALIST BIRD COMMUNITIES IN SOUTHEASTERN PERU

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Abstract. In 2003 and 2004 I investigated the relationship between patch area and number of avian bamboo specialists among 13 patches of *Guadua* bamboo habitat in southeastern Peru. In these patches, specialists were sensitive to area at local spatial scales. The structure of communities of bamboo specialists was nested, meaning species present in depauperate patches were almost always present in richer patches. Richness of specialist species was positively correlated with the size of the patch. My results indicate that prior estimates of populations of bamboo specialists based on remotely sensed images of vegetation may be underestimates because several specialists were present in small patches difficult to detect in remotely sensed images.

Key words: Amazon, area sensitivity, bamboo specialist, bird communities, *Guadua*, nestedness, patch size, Peru.

Anidamiento y Tamaño de Parche en Comunidades de Aves Especialistas de Bambú en el Sudeste de Perú

Resumen. En 2003 y 2004, investigué la relación entre área y número de aves especialistas de bambú en 13 parches de hábitat del bambú *Guadua* en el sudeste de Perú. En estos parches, los especialistas fueron sensibles al área a escalas espaciales locales. La estructura de las comunidades de especialistas de bambú fue anidada, lo que significa que las especies presentes en los parches pobres estuvieron casi siempre presentes en los parches más ricos. La riqueza de especies especialistas estuvo positivamente correlacionada con el tamaño de parche. Mis resultados indican que las estimaciones previas de las poblaciones de especialistas de bambú basadas en imágenes de vegetación obtenidas por sensores remotos pueden brindar subestimaciones debido a que muchos especialistas estuvieron presentes en pequeños parches difíciles de detectar en imágenes de sensores remotos.

INTRODUCTION

Global richness of bird species reaches its peak in the western Amazon basin (Stotz et al. 1996, Rahbek and Graves 2001). Such a diversity of birds coexists here in part because of resource partitioning among different habitats (Remsen and Parker 1983, Robinson and Terborgh 1995, 1997). In the Amazon of southeastern Peru, mature forests characterized by a high diversity of trees and a canopy 35–50 m tall with a layer of emergents dominate the lowlands (Salo et al. 1986, Terborgh and Petren 1991). Patches dominated by single plant species occur within this matrix of diverse forest, presenting distinct habitats on which birds specialize. Patches of *Guadua* bamboo are one example and support a community of specialized insectivorous birds richer than those of other nearby habitats dominated by single species, such as *Mauritia* palm swamps, *Gynerium* canebrakes, and groves of *Tessaria* (Kratte 1997, Lebbin 2007).

Guadua bamboo patches typically grow within forest gaps 30–200 m in diameter (0.07–12.6 ha; Saatchi et al. 2000), but they can also cover larger areas. The southwestern

Amazon in Brazil, Peru, and Bolivia contains 12–18 million ha dominated by *Guadua* bamboo, more than any other portion of the Amazon basin (Nelson 1994, Nelson and Irmão 1998, Saatchi et al. 2000, Silman et al. 2003). Habitats that cover greater areas tend to support greater numbers of species because of species–area relationships (Arrhenius 1921, MacArthur and Wilson 1967, Gotelli 1995). In this study, I investigated whether the number of avian specialists in a *Guadua* bamboo patch decreases with decreasing patch size and, if so, whether the individual specialists drop out of the community in a predictable fashion. I also discuss the importance of these findings for estimating the sizes of populations of bamboo specialists.

METHODS

STUDY AREA

I visited patches of *Guadua* bamboo at forested research sites along the Manu (Terborgh et al. 1984, Gentry 1990, Robinson and Terborgh 1997), Amigos (Pitman 2006), and

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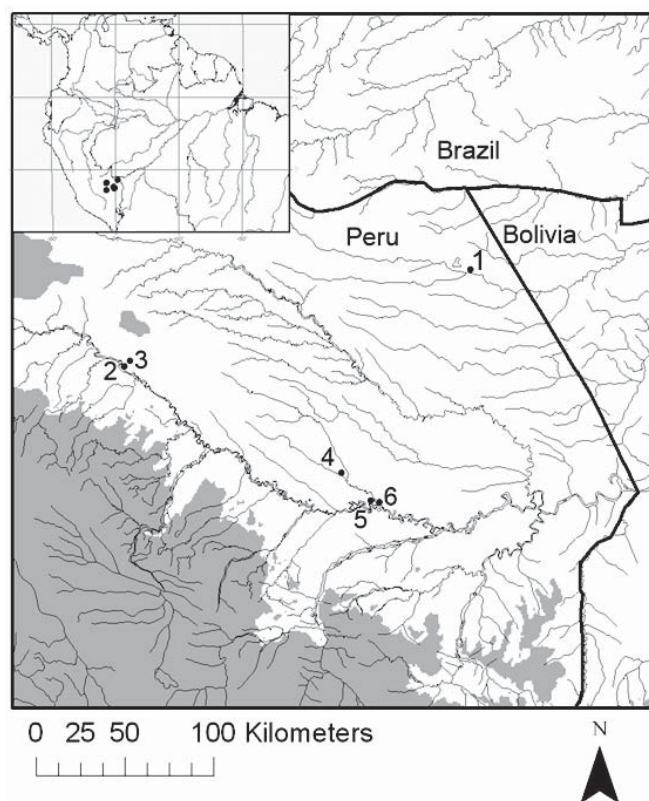


FIGURE 1. Map of study areas in lowland southeastern Peru. Areas above 500 m elevation are shaded gray, and research sites are referenced as closed circles. Numbered sites are Oceania (1; 11° 23' S, 69° 32' W), Cocha Cashu Biological Station (2; 11° 85' S, 71° 32' W), Playa Bonita (3; 11° 50' 19' S, 71° 23' 07' W), La Vieja bush camp along the Río Amiguillos (4; 12° 26' S, 70° 16' W), CICRA (5; 12° 34' S, 70° 05' W), and CM1 (6; 12° 34' S, 70° 04' W), which ranged in elevation from 270 to 350 m above sea level.

Tahuamanu (Alverson et al. 2000) rivers of southeastern Peru (Fig. 1). Bamboo patches consisted of *G. sarcocarpa* and/or *G. weberbaueri*, which I did not usually distinguish. My study took place at the Centro de Investigación y Capacitación Río Los Amigos (CICRA), managed by the Asociación para la Conservación de la Cuenca Amazónica (ACCA) and located between the Río Madre de Dios and Río Amigos, at the CM1 ranger station at the mouth of the Río Amigos, and at a bush camp on the Río Amiguillos. I worked at Los Amigos 27–30 July 2002, 11 June–3 August 2003, 16 February–21 April 2004, 1–23 June 2004, 20 July–15 September 2004, and 1 October–10 November 2004. More information concerning the research stations, climate, habitats, and natural history of Los Amigos can be found at the ACCA's website (<http://www.amazonconservation.org>) and in Pitman (2006).

Inside Manu National Park along the Río Manu, I worked from 26 June to 19 July 2004 at Estación Biológica Cocha Cashu and at Playa Bonita, located approximately

6 km north of Cocha Cashu. Habitats included mature floodplain forests and *Guadua* bamboo patches, described in more detail by Terborgh et al. (1990), Silman et al. (2003), and Patterson et al. (2006).

Between 8 and 18 October 2004, I visited a large patch of *G. weberbaueri* bordered by mature *terra firme* forest and cleared pasture along the north bank of the Río Tahuamanu at Oceania, Departamento Madre de Dios, Peru, 6 km west of Iberia, roughly 130 km north of Puerto Maldonado on the road to Iñapari, a frontier town on the border with Acre, Brazil. This site is further described by Tobias et al. (2007).

FIELD METHODS

I surveyed the bird communities of 13 bamboo patches or patch clusters ranging in size from less than 0.5 ha to 48.3 ha (mean = 11.1 ha, SD = 13.7) at Los Amigos, Manu National Park, and along the Río Tahuamanu (Fig. 1). I did point counts and spot-mapping along transects and supplemented these observations with mist-net captures. Patch clusters consisted of multiple imperfectly distinct bamboo patches close enough (<100 m) together that I suspected specialists would treat them as a single patch, and therefore I analyzed them as a single patch. Sampling within the 13 patches totaled 140.4 hr over 77 days. Alone, I sampled along transects marked every 25 m, between dawn and no later than 10:00 (and usually ending before 09:00). I recorded all birds seen or heard while walking and while stationary during 8-min point counts spaced no farther than ~150 m apart along transects. In 11 of these same bamboo patches, I also captured 134 species of birds in mist nets (1096 captures in 36 953.5 net-m hr over 53 days). I also estimated the areas of these 13 bamboo patches by using a geographic information system in ArcMap 9.1 (ESRI 2005). Patch area, and net capture, and census effort for each patch are summarized in Table 1. I believe this search effort was more than sufficient to detect almost all bamboo specialists in these patches, as I also spent much additional time recording other kinds of data or camped in these patches without detecting species undetected during censuses or mist netting.

From these surveys, I created a presence-absence matrix to summarize use of each patch by bamboo specialists (Table 2). On the basis of a literature review and surveys of other adjacent habitats, I categorized *Guadua* bamboo specialists according to their degree of habitat specialization, with "obligate" specialists restricted to bamboo throughout their ranges, "near-obligate" specialists only occasionally found outside bamboo, and "facultative" or "potentially facultative" specialists having at least a local habitat preference for bamboo (Kratter 1997, Lebbin 2007).

STATISTICAL ANALYSES

Nestedness is a measure of order within a set of communities (Atmar and Patterson 1993). In a perfectly nested system, no species found within a depauperate community (island or

TABLE 1. Location, name, area, and mist-net and survey effort (rounded to nearest hour) expended to sample the bird communities of 13 patches of *Guadua* bamboo, southeastern Peru. The numbers of bamboo specialists detected in each patch are apportioned by the number of total specialists and of obligate and near-obligate specialists (facultative specialists excluded). The final column presents the nestedness rank of each patch when only obligate and near-obligate specialists are analyzed. Patches with the bird communities most nested within the matrix have the highest nestedness rankings. Patches 2 and 4 were likely larger prior to this study, but recent clearing for agriculture had reduced the extent of patch 2, and within 2 years bamboo died off naturally in large areas adjacent to patch 4. Patch 11 bordered an airstrip and may have been larger many years prior to this study. Less search effort was required and expended in smaller patchers. In patch 12, the total sampling time includes a single ~1-hr survey in the late afternoon (all other patches were censused during the morning only).

Patch	Location: patch name	Patch area (ha)	Net effort			Census effort		Total specialists (<i>n</i>)	Obligate and near-obligate specialists (<i>n</i>)	Obligate nestedness rank
			Net-m hr	Days	Months/ years	Hours/ days	Months/ years			
1	CICRA: CICRA cluster	19.02	7462.9	12	Jun–Jul 2003, Jul 2004	29 hr, 8 days	Jul 2003, Aug 2004	32	15	3.5
2	Oceania	22.21	4843.5	6	Oct 2004	17 hr, 6 days	Oct 2004	31	17	1.0
3	La Vieja	18.90	6708.9	10	Jul 2003	27 hr, 8 days	Jul 2003	30	16	2.0
4	EBCC: Playa Bonita	9.63	4077.0	6	Jun–Jul 2004	7 hr, 7 days	Jun–Jul 2004	29	15	3.5
5	CM1	48.33	4125.6	4	Aug–Sep 2004	22 hr, 6 days	Sep 2004	25	13	5.0
6	CICRA: Palmeras	6.04	2925.9	5	Jun 2004	8 hr, 5 days	Aug 2004	23	12	6.0
7	CICRA: Huangana	11.43	2850.6	4	Jun–Jul 2003	7 hr, 5 days	Jul 2003	22	10	7.5
8	CICRA: Pacal	0.86	813.6	2	Jun 2003	4 hr, 5 days	Jul 2003	20	10	7.5
9	CICRA: Toledo	1.41	1023.0	2	Aug 2004	6 hr, 6 days	Aug 2004	14	8	9.0
10	CICRA: Luisa cluster	1.19	2122.5	2	Sep 2004	4 hr, 5 days	Aug 2004	11	3	10.5
11	CICRA: Avioneta	0.46	—	—	—	3 hr, 4 days	Aug 2004	9	3	10.5
12	EBCC: Cocha Cashu cluster	4.21	—	—	—	6 hr, 4 days	Jul 2004	8	4	12.0
13	CICRA: Salchicha	0.15	—	—	—	2 hr, 3 days	Aug 2004	1	0	13.0

habitat patch) is absent from a more species-rich community. I used Atmar and Patterson's (1995) Nestedness Calculator to determine the degree of nestedness of these bamboo-specialist communities. The Nestedness Calculator generates a measure, referred to as the "temperature" (T), from a presence-absence matrix and compares the observed temperature to those of 5000 matrices created by randomly rearranging the original matrix. The temperature can range from zero to 100° with zero being perfectly nested and low temperatures representing ordered systems with little "heat of disorder" and high temperatures reflecting highly disordered, un-nested systems (Atmar and Patterson 1993). I used one-tailed Spearman ρ correlation tests to investigate correlations between area of

the bamboo patch, nestedness rank, and species richness of bamboo specialists.

RESULTS

Within the 13 *Guadua* bamboo patches, I detected 38 bird species of some degree of specialization, including 20 classified as obligate or near-obligate specialists and 18 classified as facultative or potentially facultative specialists. Communities of bamboo specialists were significantly nested, whether the analysis was restricted to obligate and near-obligate specialists ($T = 12.26^\circ$, $P = 2.19 \times 10^{-19}$) or included all specialists ($T = 10.08^\circ$, $P = 4.98 \times 10^{-29}$). Nestedness rank of

TABLE 2. Presence-absence matrix of bamboo specialists (0 = absent, 1 = present) in 13 patches of *Guadua* bamboo surveyed in south-eastern Peru. Values of 1 are shaded in gray to make the nestedness easier to recognize. The subset of obligate and near-obligate specialists is highlighted in boldface and considered separately as an additional presence-absence matrix. Species not in bold are facultative bamboo specialists or potentially facultative bamboo specialists. Bamboo patch numbers correspond with those in Table 1.

Species	Bamboo patch												
	1	2	3	4	5	6	7	8	9	10	11	12	13
<i>Myrmeciza hemimelaena</i>	1	1	1	1	1	1	1	1	0	1	1	1	1
<i>Campylorhamphus trochilirostris</i>	1	1	1	1	1	1	1	1	1	1	1	1	0
<i>Microrhopias quixensis</i>	1	1	1	1	1	1	1	1	1	1	1	1	0
<i>Pheugopedius genibarbis</i>	1	1	1	1	1	1	1	1	1	1	1	1	0
<i>Drymophila devillei</i>	1	1	1	1	1	1	1	1	1	0	1	1	0
<i>Hemitriccus flammeatus</i>	1	1	1	0	1	1	1	1	1	1	1	0	0
<i>Automolus melanopezus</i>	1	1	1	1	1	1	1	1	1	1	0	0	0
<i>Epinecrophylla ornata</i>	1	1	1	1	1	1	1	1	1	1	0	0	0
<i>Ramphotrigon fuscicauda</i>	1	1	1	1	1	1	1	1	1	1	0	0	0
<i>Myrmeciza goeldii</i>	1	1	1	1	1	1	1	1	1	0	0	1	0
<i>Percnostola lophotes</i>	1	1	1	1	1	1	1	1	1	0	0	1	0
<i>Hypocnemis subflava collinsi</i>	1	1	1	1	1	1	1	1	1	0	1	0	0
<i>Myrmoborus leucophrys</i>	1	1	1	1	1	1	1	1	0	0	1	0	0
<i>Leptopogon amaurocephalus</i>	1	1	1	1	1	1	1	1	0	1	0	0	0
<i>Lophotriccus eulophotes</i>	1	0	1	1	0	1	1	1	1	1	1	0	0
<i>Simoxenops ucayalae</i>	1	1	1	1	1	1	1	1	0	0	0	0	0
<i>Ramphotrigon megacephala</i>	1	1	1	1	1	1	1	1	0	0	0	0	0
<i>Machaeropterus pyrocephalus</i>	1	1	1	1	1	1	1	1	0	0	0	0	0
<i>Cymbilaimus sanctaemariae</i>	1	1	1	1	1	1	0	1	1	0	0	0	0
<i>Lathrotriccus euleri</i>	1	0	1	1	1	1	1	0	1	0	0	0	0
<i>Nonnula ruficapilla</i>	1	1	1	1	0	1	1	0	0	0	0	0	0
<i>Automolus rufipileatus</i>	1	1	1	1	1	0	1	0	0	0	0	0	0
<i>Dromococcyx pavoninus</i>	1	1	1	1	1	0	0	0	0	0	0	0	0
<i>Myrmotherula iheringi</i>	1	1	1	1	1	0	0	0	0	0	0	0	0
<i>Picumnus rufiventris</i>	1	1	1	1	0	0	1	0	0	0	0	0	0
<i>Monasa flavirostris</i>	1	0	1	0	1	1	0	0	0	0	0	0	0
<i>Celeus spectabilis</i>	1	1	0	1	0	0	0	0	0	0	0	1	0
<i>Synallaxis rutilans</i>	1	1	0	0	0	0	0	1	0	1	0	0	0
<i>Ramphocaenus melanurus</i>	1	1	1	1	0	0	0	0	0	0	0	0	0
<i>Cercomacra manu</i>	1	1	0	1	0	0	0	0	0	0	0	0	0
<i>Poecilatriccus albifacies</i>	0	1	1	0	1	0	0	0	0	0	0	0	0
<i>Bucco macrodactylus</i>	1	1	0	0	0	0	0	0	0	0	0	0	0
<i>Neotantes niger</i>	1	0	0	0	0	1	0	0	0	0	0	0	0
<i>Anabazenops dorsalis</i>	0	0	1	1	0	0	0	0	0	0	0	0	0
<i>Neotantes niger</i>	1	0	0	0	0	1	0	0	0	0	0	0	0
<i>Neopelma sulphureiventer</i>	0	1	1	0	0	0	0	0	0	0	0	0	0
<i>Synallaxis cabanisi</i>	0	0	0	0	1	0	0	0	0	0	0	0	0
<i>Synallaxis cherriei</i>	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>Cnipodectes superrufus</i>	0	1	0	0	0	0	0	0	0	0	0	0	0

bamboo patches (Table 1) was negatively correlated with patch size ($r_s = -0.82$, $P < 0.001$, $n = 13$, facultative specialists excluded; $r_s = -0.85$, $P < 0.001$, $n = 13$, all specialists included), meaning that smaller patches were used primarily by a subset of the species found in larger patches. Richness of specialist species was positively correlated with size of bamboo patches ($r_s = 0.85$, $P < 0.001$, $n = 13$, facultative specialists excluded; $r_s = 0.85$, $P < 0.001$, $n = 13$, all specialists included).

DISCUSSION

PATCH SIZE AND NESTEDNESS

Communities of bamboo specialists were nested and highly sensitive to patch area at the local scale. As patch size declined, specialist species dropped out of the community in a nonrandom, nested fashion. Small bamboo patches may still support a diversity of specialists, and I found 10 species of near-obligate and obligate bamboo specialists in a 0.86-ha

patch (number 8) near CICRA. These included the Peruvian Recurvebill (*Simoxenops ucayalae*), not detected in the slightly larger patches 9 and 12.

No obligate specialists and only a single facultative specialist, the Chestnut-tailed Antbird (*Myrmeciza hemimelaena*), were present in the smallest bamboo patch (patch 13, 0.15 ha), suggesting that 0.15 ha is below the minimum patch size most specialists require. The Peruvian Warbling-Antbird (*Hypocnemis peruviana peruviana*), also detected in this tiny bamboo patch, is closely related to the bamboo specialist Yellow-bellied Warbling-Antbird (*Hypocnemis subflava collinsi*). The Peruvian Warbling-Antbird was likely using dense forest along a stream nearby as well as the bamboo patch, potentially offering a glimpse of the transition that presumably occurs when forest species colonize bamboo patches in the early stages of the process of specialization for bamboo habitat.

PATCH SIZE, OCCURRENCE OF SPECIALISTS, AND POPULATION ESTIMATES

I found bamboo specialists in small patches, indicating that they may occur at higher densities and have larger populations than previously estimated. My results indicate that occurrence of specialists may differ from that assumed in prior studies.

Of 19 specialists (Table 3) compared, I detected 14 (74%) in patches smaller than territory sizes estimated by Kratter (1997) and Lloyd (2004). This likely indicates that these species' territories can be smaller than previously estimated on the basis of a small sample of bamboo patches; however the influence of a history of shrinking patch size or species incorporating adjacent forest into their territory can not be completely ruled out. Four of the 14 species (29%) were facultative specialists, possibly defending territories larger than the smallest bamboo patch within which they were detected. The remaining ten species were obligate and near-obligate specialists, less likely to use adjacent forest habitats. I detected all nine of these obligate and near-obligate specialists in at least two patches smaller than their previously estimated territory sizes. I found the Striated Antbird (*Drymophila devillei*) in three smaller patches, the Rufous-headed Woodpecker (*Celeus spectabilis*) and Peruvian Recurvebill in four smaller patches, the Flammulated Pygmy-Tyrant (*Hemitriccus flammulatus*) in five smaller patches, and the Brown-rumped Foliage-Gleaner (*Automolus melanopezus*) and Dusky-tailed Flatbill (*Ramphotrigon fuscicauda*) in six smaller patches. Although it is possible that these species incorporated both forest and bamboo into their territories or that these bamboo patches were larger prior to this study, it seems

TABLE 3. Density and size of territories of *Guadua* bamboo specialists from Kratter (1997) and Lloyd (2004) and the size of the smallest patch in which specialists were detected in this study. Territory size was estimated by dividing 100 ha by the number of territories or density of birds per 100 ha, under the assumption the entire area was saturated or included in a territory.

Bamboo specialist	Territories (100 ha ⁻¹) (Kratter 1997)	Densities (100 ha ⁻¹) (Lloyd 2004)	Estimated territory size (ha)	Size of smallest patch in which detected in this study (ha)
<i>Picumnus rufiventris</i>	4.7	—	21.3	9.63
<i>Celeus spectabilis</i>	—	1.9 pairs	52.6	4.21
<i>Campylorhamphus trochilirostris</i>	17.6	—	5.7	0.46
<i>Synallaxis cabanisi</i>	2.7	—	37.0 ^a	48.33
<i>Simoxenops ucayalae</i>	5.4	4.7–7.7	13.0–21.3	0.86
<i>Anabazenops dorsalis</i>	15.5	—	6.5	9.63
<i>Automolus melanopezus</i>	7.4	—	13.5	0.86
<i>Cymbilaimus sanctaemariae</i>	27.0	—	3.7	0.86
<i>Epinecrophylla ornata</i>	15.5	—	6.5	0.86
<i>Myrmotherula iheringi</i>	15.5	—	6.5	9.63
<i>Microrhopias quixensis</i>	18.9	—	5.3	0.46
<i>Drymophila devillei</i>	25.0	—	4.0	0.46
<i>Pernostola lophotes</i>	35.1	—	2.8	0.86
<i>Myrmeciza goeldii</i>	24.3	—	4.1	0.86
<i>Cercomacra manu</i> ^b	25.0	3.7 pairs	4.0–27.0 ^a	9.63
<i>Hemitriccus flammulatus</i>	14.9	—	6.7	0.86
<i>Poecilatriccus albifacies</i>	14.2	4.4	7.0–22.7 ^a	18.90
<i>Ramphotrigon megacephala</i>	21.6	—	4.6	0.86
<i>Ramphotrigon fuscicauda</i>	6.1	—	16.4	0.86

^aTerritory size likely inflated, species not using all of or saturating bamboo patches surveyed.

^bZimmer and Isler (2003) reported territory sizes of 0.5–1.0 ha in Bolivia, and of 0.2–0.5 ha in Brazil, which are both smaller than extrapolated from Kratter (1997) or Lloyd (2004).

just as or more likely that they can use territories smaller than previous thought. Small bamboo patches are often undetected in remotely sensed images. Individual birds inhabiting small bamboo patches or a combination of small bamboo patches and bits of adjacent forest will not be counted in population estimates, and actual sizes of populations of these specialists may be underestimated.

Other factors may influence the presence of bamboo specialists within a patch, such as proximity to rivers that may serve as dispersal routes for certain species. I encountered the Manu Antbird (*Cercomacra manu*) in only three of the 13 patches I surveyed, all of which were within a few hundred meters of rivers. The Manu Antbird is also closely related to the Jet Antbird (*C. nigricans*), Rio Branco Antbird (*C. carbonaria*), Mato Grosso Antbird (*C. melanaria*), and Bananal Antbird (*C. ferdinandi*), of which the latter three are also closely associated with riparian habitats (Zimmer and Isler 2003). If the Manu Antbird requires proximity to rivers for dispersal or other reasons, then it may be absent from vast areas of bamboo far from large streams in *terra firme*, resulting in an overestimate of its population based on the extent of bamboo.

Specialists may also be absent from suitable habitat because of interspecific competition. In no patch I sampled did I find more than two of the three specialist tody-tyrants or more than one of the three *Synallaxis* spinetails. Interspecific competition among these ecologically similar tody-tyrants may prevent all three tody-tyrants, the Long-crested Pygmy-Tyrant (*Lophotriccus eulophotes*), Flammulated Pygmy-Tyrant, and White-cheeked Tody-Flycatcher (*Poecilatriccus albifacies*), or even two of three spinetails, the Ruddy Spinetail (*S. rutilans*), Chestnut-throated Spinetail (*S. cherriei*), and Cabanis's Spinetail (*S. cabanisi*) from co-occurring in a single patch. Therefore, the White-cheeked Tody-Flycatcher may be absent from much suitable habitat (e.g., *terra firme* bamboo patches) because of the presence of the Flammulated Pygmy-Tyrant and Long-crested Pygmy-Tyrant. Additional sampling of the specialist bird community of bamboo patches deep within *terra firme* would help clarify these patterns of these species' co-occurrence and would clarify whether the Manu Antbird is as scarce away from rivers as my study suggests.

My data come from areas of relatively intact and unfragmented forests so may not be applicable to isolated bamboo patches in landscapes heavily altered by people. Regional development proposals, such as the paved "Trans-Oceanica" highway, likely will increase human settlement, habitat destruction, and regrowth of bamboo within human-altered landscapes (Nepstad et al. 2001, Conover 2003). Conditions under which specialists are present or absent in bamboo patches regenerating from human disturbances may be a worthy study for future researchers. I have seen many specialists, such as the Chestnut-capped Puffbird (*Bucco macrorhynchus*), Cabanis's Spinetail, Bamboo Antshrike (*Cymbilaimus sanctaemariae*), and Yellow Tyrannulet (*Capsiempis flaveola*) during brief visits to patches of bamboo

growing in clearings along the Manu Road that are contiguous with areas of natural bamboo and forest, and I have seen the Long-crested Pygmy-Tyrant on territories at the edge of treefall gaps and forest edges created by loggers at Los Amigos and along the road to Iberia. Bamboo that invades roadsides and pastures, however, may not support specialists if the quantity or quality of the surrounding habitats is difficult for specialists to disperse through, and I have not encountered any bamboo specialists during short visits to such isolated bamboo patches along roads near Puerto Maldonado. Therefore, I am doubtful that regrowth of bamboo in isolated, human-disturbed areas will increase the habitat available for bamboo specialists of conservation concern until data suggesting otherwise become available.

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LITERATURE CITED

- ALVERSON, W. S., D. K. MOSKOVITS, AND J. M. SHOPLAND [EDS.]. 2000. Bolivia: Pando, Rio Tahuamanu. Rapid Biological Inventories Report 1. Field Museum, Chicago.
- ARRHENIUS, O. 1921. Species and area. *Journal of Ecology* 9:95–99.
- ATMAR, W., AND B. D. PATTERSON. 1993. The measure of order and disorder in the distribution of species in fragmented habitats. *Oecologia* 96:373–382.
- ATMAR, W., AND B. D. PATTERSON. 1995. The nestedness calculator: a visual basic program, including 294 presence-absence matrices. AICS Research, Inc., University Park, NM.
- CONOVER, T. 2003. Peru's long haul: highway to riches or ruin. *National Geographic*, p. 80–111.
- ESRI. 2005. ArcMap 9.1. ESRI, Inc., Redlands, CA.
- GENTRY, A. H. [ED.] 1990. Four neotropical rainforests. Yale University Press, New Haven, CT.
- GOTELLI, N. J. 1995. A primer of ecology. Sinauer Associates, Sunderland, MA.
- KRATTER, A. W. 1997. Bamboo specialization by Amazonian birds. *Biotropica* 29:100–110.
- LEBBIN, D. J. 2007. Habitat specialization among Amazonian birds: why are there so many *Guadua* bamboo specialists? Ph.D. dissertation, Cornell University, Ithaca, NY.
- LLOYD, H. 2004. Habitat and population estimates of some threatened lowland forest bird species in Tambopata, south-east Peru. *Bird Conservation International* 14:261–277.
- MACARTHUR, R. H. AND E. O. WILSON. 1967. The theory of island biogeography. Princeton University Press, Princeton, NJ.

- NELSON, B. W. 1994. Natural forest disturbance and change in the Brazilian Amazon. *Remote Sensing Reviews* 10:105–125.
- NELSON, B. W., AND M. N. IRMÃO. 1998. Fire penetration in standing Amazon forest. *Proceedings of the Ninth Brazilian Remote Sensing Symposium*, 19–12 September 1998, Santos, Brazil.
- NEPSTAD, D., G. CARVALHO, A. BARROS, A. ALENCAR, J. CAPOBIANCA, J. BISHOP, P. MOUTINHO, P. LEFEBVRE, S. U. LOPES, AND E. PRINS. 2001. Road paving, fire regime feedbacks, and the future of Amazon forests. *Forest Ecology and Management* 154:395–407.
- PATTERSON, B. D., D. F. STOTZ, AND S. SOLARI. 2006. Biological surveys and inventories in Manu. *Fieldiana* 110:3–12.
- PITMAN, N. C. A. 2006. An overview of the Los Amigos watershed, Madre de Dios, southeastern Peru. June 2006 version of an unpublished report available from its author at npitman@amazonconservation.org.
- RAHBK, C., AND G. R. GRAVES. 2001. Multiscale assessment of patterns of avian species richness. *Proceedings of the National Academy of Sciences USA* 98:4534–4539.
- REMSEN, J. V. JR., AND T. A. PARKER III. 1983. Contribution of river-created habitats to bird species richness in Amazonia. *Biotropica* 15:223–231.
- ROBINSON, S. K., AND J. TERBORGH. 1995. Interspecific aggression and habitat selection by Amazonian birds. *Journal of Animal Ecology* 64:1–11.
- ROBINSON, S. K., AND J. TERBORGH. 1997. Bird community dynamics along primary successional gradients of an Amazonian whitewater river. *Ornithological Monographs* 48:641–672.
- SAATCHI, S. S., B. NELSON, E. PODEST, AND J. HOLT. 2000. Mapping land cover types in the Amazon Basin using 1 km JERS-1 mosaic. *International Journal of Remote Sensing* 21:1201–1234.
- SALO, J., R. KALLIOLA, I. HÄKKINEN, Y. MÄKINEN, P. NIEMELÄ, M. PUHAKKA, AND P. D. COLEY. 1986. River dynamics and the diversity of Amazon lowland forest. *Nature* 322:254–258.
- SILMAN, M. R., E. J. ANCAYA, AND J. BRINSON. 2003. Los bosques de bambú en la Amazonía occidental, p. 63–74. *In* R. Leite Pitman, N. Pitman, and P. Álvarez [EDS.], *Alto Purús: biodiversidad, conservación y manejo*. Center for Tropical Conservation, Lima.
- STOTZ, D. F., J. W. FITZPATRICK, T. A. PARKER III, AND D. K. MOSKOVITS. 1996. *Neotropical birds: ecology and conservation*. University of Chicago Press, Chicago.
- TERBORGH, J. W., J. W. FITZPATRICK, AND L. EMMONS. 1984. Annotated checklist of bird and mammal species of Cocha Cashu Biological Station, Manu National Park, Peru. *Fieldiana* 21:1–29.
- TERBORGH, J., AND K. PETREN. 1991. Development of habitat structure through succession in an Amazonian floodplain forest, p. 28–46. *In* S. S. Bell, E. D. McCoy, and H. R. Mushinsky [EDS.], *Habitat structure: the physical arrangement of objects in space*. Chapman and Hall, London.
- TERBORGH, J., S. K. ROBINSON, T. A. PARKER III, C. A. MUNN, AND N. PIERPONT. 1990. Structure and organization of an Amazonian forest bird community. *Ecological Monographs* 60:213–238.
- TOBIAS, J. A., D. J. LEBBIN, A. ALEIXO, M. J. ANDERSEN, E. GUILHERME, P. A. HOSNER, AND N. SEDDON. 2007. Distribution, behavior, and conservation status of the Rufous Twistwing *Cnipodectes superrufus*. *Wilson Journal of Ornithology* 120:38–49.
- ZIMMER, K. J., AND M. L. ISLER. 2003. Family Thamnophilidae (typical antbirds), p. 448–681. *In* J. del Hoyo, A. Elliott, and D. A. Christie [EDS.], *Handbook of the Birds of the World*, vol. 8: broadbills to tapaculos. Lynx Edicions, Barcelona.