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BIRD DIVERSITY AND OCCURRENCE OF BAMBOO SPECIALISTS IN TWO BAMBOO DIE-OFFS IN SOUTHEASTERN PERU

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Abstract. A post-flowering die-off of bamboo in an established bird-census plot afforded us an opportunity to investigate the response of bamboo-dwelling birds to a natural transformation of their habitat. In 1984 and 1985 SR and JT generated spot maps for an 80-ha plot in *terra firme* forest near the Cocha Cashu Biological Station, Manu National Park, Peru. Two mapped bamboo patches in the plot totaled approximately 30 ha. In 2001 and 2002, the bamboo flowered and died. In 2009, JS revisited the plot and generated spot maps for the former bamboo patches and adjacent forest. By 2009, trees had grown up in the erstwhile bamboo patches, creating stands of second growth surrounded by mature forest. Twelve species of bamboo specialists were no longer present but almost no new species had invaded. We conclude that the maintenance of high bird diversity in western Amazonian forests does not depend on the spatial heterogeneity caused by dying off of bamboo. This result contrasts with, but does not contradict, previous research demonstrating the importance of some disturbances such as treefalls opening gaps to avian biodiversity in neotropical forests. A few bamboo specialists, including the Brown-rumped Foliage-Gleaner (*Automolus melanopezus*), Goeldi's Antbird (*Myrmeciza goeldii*), Flammulated Pygmy-Tyrant (*Hemitriccus flammulatus*), and Dusky-tailed Flatbill (*Ramphotrigon fuscicauda*), persisted in the die-offs. Their choices of microsites suggested that vegetation structure rather than plant-species composition is an important determinant of habitat suitability for these specialists.

Key words: bamboo, bird communities, disturbance, diversity, Guadua*, habitat specialization.*

Diversidad de Aves y Ocurrencia de Especialistas de Bambú en Dos Áreas de Bambú Muertas en el Sudeste de Perú

Resumen. La muerte del bambú posterior a la floración en una parcela establecida de muestreo de aves nos dio la oportunidad de investigar la respuesta de las aves que habitan el bambú a la transformación natural de su hábitat. En 1984 y 1985 SR y JT generaron mapas de ubicación para una parcela de 80 ha en bosques de *terra firme* cerca de la Estación Biológica de Cocha Cashu, en el Parque Nacional Manu, Perú. Dos parches de bambú mapeados en la parcela totalizaron aproximadamente 30 ha. En 2001 y 2002, el bambú floreció y murió. En 2009, JS revisitó la parcela y generó mapas de ubicación para los parches originales de bambú y el bosque adyacente. Para 2009, los árboles habían crecido en los antiguos parches de bambú, creando stands de crecimiento secundario rodeados de bosque maduro. Doce especies de especialistas de bambú yo no estuvieron presentes pero casi ninguna nueva especie había invadido. Concluimos que el mantenimiento de una alta diversidad de especies en los bosques amazónicos del oeste no depende de la heterogeneidad espacial causada por la muerte del bambú. Este resultado contrasta con, pero no contradice, investigaciones previas que demuestran la importancia de algunos disturbios como los claros causados por la caída de árboles para la diversidad de aves en los bosques neotropicales. Unos pocos especialistas de bambú, incluyendo a *Automolus melanopezus*, *Myrmeciza goeldii*, *Hemitriccus flammulatus* y *Ramphotrigon fuscicauda*, permanecieron en las áreas muertas. Sus elecciones de micro sitios sugieren que la estructura de la vegetación más que la composición de especies de plantas es un determinante importante de la calidad del hábitat para estos especialistas.

INTRODUCTION

The lowland tropical forests of southeastern Peru are home to one of the most diverse avifaunas on the planet (Walker et al. 2006). The diversity is maintained in part by the extraordinary heterogeneity of habitats in the region. These include not only widespread forest types such as floodplain forest and *terra firme* but also highly localized habitats such as early-successional stands of the tree *Tessaria integrefolia*, *Gynerium* canebrakes, *Mauritia* palm swamps, and *Guadua* bamboo forests, each with an attendant community of specialist birds (Robinson et al. 1990). These habitats are created by

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characteristic disturbance regimes. Floodplain forest grows in the alluvial belt of meanderings of the Manu River and is subject to rare, brief floods, whereas *terra firme* remains dry year round. Successional communities, including stands of *Tessaria* and *Gynerium*, form on points on sandbars in loops of rivers and contribute greatly to the bird diversity of the region (Robinson and Terborgh 1997). The bamboo *Guadua* colonizes disturbed areas such as treefall gaps or landslides. Clones then expand over many years, forming large pure stands of spiny bamboo that harbor an especially diverse group of specialists (Kratter 1997, Lebbin 2007).

We investigated the response of bird communities to natural die-offs of *Guadua*, comparing bird censuses before and after the die-offs to examine the effect of the die-offs on bird species richness. We analyzed the responses of the bamboo specialists to understand the factors influencing their habitat selection. In this paper, we ask which bamboo specialists persisted and which disappeared from the die-offs and which disturbance-dependent species colonized the regenerating patches of even-aged forest (dominated by *Inga thibaudiana*) that sprang up after the die-offs.

Birds specializing in *Guadua* are insectivores that generally forage along the culms or amid the dense foliage. Kratter (1997) classified 19 species as obligate, near-obligate, or facultative specialists depending on the observed extent of their restriction to bamboo habitats in southeastern Peru. He classified an additional eight species as apparent bamboo specialists, having data insufficient to confirm the relationship.

A peculiar challenge faced by sedentary specialists in *Guadua* is the periodic disappearance of their habitat. Like many bamboos, *Guadua* propagates vegetatively to form large clonal patches, excluding trees by resource competition and through physical damage to trees' canopies (Griscom and Ashton 2006). The patches are monocarpic, dying en masse after long-delayed flowering. *Guadua sarcocarpa* flowers at roughly 30-year intervals (Griscom and Ashton 2003). After the bamboo dies, numerous early-successional plant species, sometimes including a new generation of bamboo, rapidly revegetate the site. In some cases, generally in small (several hundred hectares or less) patches, very little bamboo returns, and the site becomes dominated by early-successional forest. Thus bamboo specialist species must cope with a habitat that is not only spatially fragmented and patchy but also temporally unstable.

Depending on the timescale of analysis, bamboo die-offs may have different effects (possibly in opposite directions) on bird diversity in a habitat mosaic. Taking a short view, we might expect a priori that bird diversity should decline when habitat for bamboo specialists vanishes. On the longer timescale of an entire bamboo cycle, however, we might expect that the habitat heterogeneity created by the die-off should promote diversity beyond that of undisturbed primary forest lacking bamboo by creating habitat for birds of gaps and successional habitats.

A die-off of two bamboo patches in an established bird-census plot in Manu National Park, Peru, afforded us an opportunity to obtain information about the response of the avifauna to the die-offs. Comparisons of spot maps of the bird communities prior to and following the die-offs provided a direct test of the responses of specialist species and whole-community richness to the changed habitat. We hypothesized that following the die-off, true bamboo specialists would disappear from the plots and that these species would be replaced by species characteristic of early-successional habitats, possibly resulting in little overall change in species richness. We further hypothesized that Kratter's (1997) classification of the degree of specialization would roughly predict which specialists persisted and which disappeared.

METHODS

STUDY SITE

The study site, an 80-ha bird-census plot, was established in the 1984 as part of a larger effort to characterize the bird communities in the vicinity of the Cocha Cashu Biological Station, Manu National Park, Peru (Terborgh et al. 1990, Robinson et al. 1990). Manu National Park protects approximately 1.9 million ha of lowland and montane forests along the eastern flank of the Andes Mountains in southern Peru. The Cocha Cashu Biological Station is situated near the Manu River at 380 m above sea level (11° 55′ S, 77° 18′ W), and its bird communities have been well characterized (Terborgh 1985, Terborgh et al. 1990, Robinson et al. 1990). Species richness is greatest in the *terra firme* forest of upland terraces, formed by the uplift of an ancient floodplain and dissected by numerous ravines (Terborgh 1985). The census plot is situated on such a terrace at the edge of the floodplain of the Manu River.

The site was suitable for the present study because a major die-off of bamboo occurred in the plot after the initial sampling. When the plot was first surveyed in 1984 and 1985, its habitats were mapped in detail with a compass and tape measure. Bamboo forests totaling approximately 30 ha grew in two patches separated by approximately 150 m and a ravine.

These patches flowered simultaneously in 2001, and the bamboo subsequently died and disappeared. The plot was re-censused in 2009. We used the mapped extent of bamboo in 1985 as a proxy for the extent of the die-off during the second census. By 2009, trees had quickly reclaimed the die-offs, forming 8-year-old even-aged stands dominated by *Inga* spp. and surrounded by mature forest. Very little bamboo was present. In 2009 we did not analyze the vegetation in detail but identified several of the most common tree species (see Table 1), and assessed the vegetation structure qualitatively.

BIRD CENSUSES

To census the bird community prior to and following the die-off, we spot-mapped the entire community in 1984–1985 and again in 2009. For the initial census, the plot was sampled

TABLE 1. Common plant species of the bamboo die-offs (identified from leaves by Varun Swamy). All species grew as trees unless noted.

Taxon	Notes
Cecropia sp.	Fairly common in southern die-off
Croton matourensis	Locally common in southern die-off
Fabaceae (*Tachigali* sp.?)	Primarily in northern die-off
Inga coruscans	With *I. thibaudiana*, the commonest tree in southern die-off
Inga thibaudiana	With *I. coruscans*, the commonest tree in southern die-off
Inga sp.	Dominant tree in swampy areas of southern die-off
Pourouma minor	Moderately common, mainly in southern die-off
Psychotria poeppigiana	Abundant shrub (<2 m tall), especially in southern die-off and gaps
Socratea sp.	Significant in both die-offs, but nowhere abundant

via four trails cut 200 m apart from one another and three connecting trails. On each census day, August–November, observers walked a route of between 1.5 and 2.0 km, beginning at least 15 min before first light and continuing until at least 3 hr after sunrise. Locations of birds detected aurally or visually were noted on a map of the census plot. For comparison, we use 1984–1985 data only from a 50-ha subplot surveyed in 2009.

In July and August 2009, we spot-mapped birds in a 50-ha subplot of roughly 700 × 700 m designed to concentrate on the bird communities of the bamboo die-offs. Within this subplot, observer effort was concentrated in the bamboo die-off areas. Census routes were walked beginning at least 15 min before first light, and the location of the starting point was rotated in order that birds singing in the dawn chorus be detected throughout the subplot. To detect participants in the dusk chorus, we occasionally censused in the afternoon. Birds encountered opportunistically in the vicinity of a campsite within the subplot were also spot-mapped.

STATISTICAL ANALYSES

Estimation of bird species richness. Analysis of the diversity dynamics of the entire bird community was complicated by the truncation of the 2009 census, which surveyed only 50 ha over two months and was not sufficient to produce complete spot maps for many species that were well represented by the initial census. To facilitate comparisons of species richness in the subplot before and after the bamboo die-off, we estimated the total species richness in the subplot with Chao's richness estimator (Chao 1987) in the software package EstimateS (Colwell 2009). Chao's estimator predicts the total richness present from presence/absence data in multiple samples. It is an appropriate estimator for use with sparse data such as ours, where many species were sampled only a few times (Herzog et al. 2002). To obtain samples, we used spatial quadrats to subsample the spot maps from both censuses. We laid well-spaced quadrats of uniform size over the spot maps and recorded the presence or absence of each species detected on the census in each quadrat. Incomplete spot maps provide precisely the sort of incidence data used by Chao's richness estimator, but the spot maps must be partitioned into multiple (ideally independent) samples.

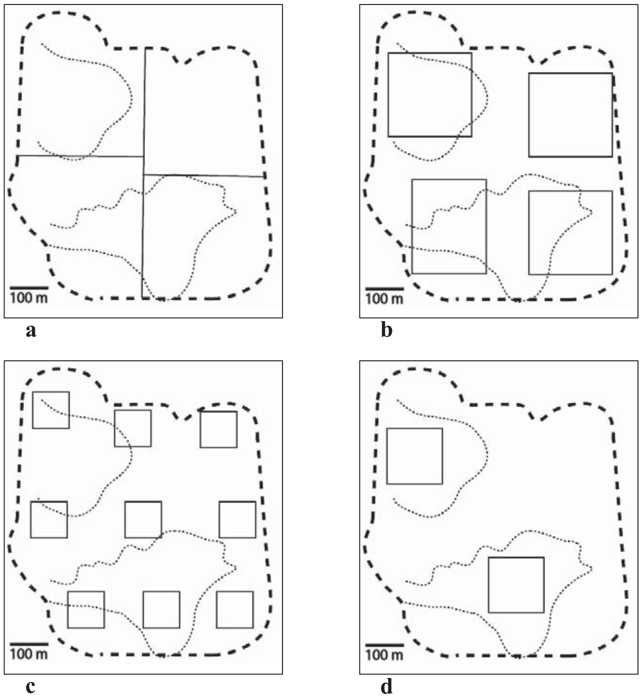


FIGURE 1. Configurations of quadrats for subsampling the spot maps. Rectangles represent the quadrats, thick dashed lines represent the limits of the census plot, and thin dashed lines delineate the edges of the bamboo areas. (a) Four large quadrats of 12 ha each that share borders, covering the entire census plot. (b) Four medium quadrats of 5 ha each separated from one another by at least 100 m. (c) Nine small quadrats of 1 ha each separated from one another by at least 100 m. (d) Two quadrats of 2.25 ha each centered in the bamboo patches and separated from one another by 225 m.

In order to develop robust estimates for the total richness in the plot, we used several different spatial configurations of quadrats (Fig. 1). Although the statistical independence of the samples is compromised by the fact that many species hold territories large enough to include portions of two or more quadrats, the estimator produced reasonable results with broad agreement across different configurations of quadrats, and there is precedent in the literature for violating assumptions of independence in similar analyses (Herzog et al 2002, Wang and Dodson 2006).

We employed a similar strategy to estimate the total richness of bird species within the patches and die-offs of bamboo (collectively, the "bamboo areas"). We defined a

2.25-ha quadrat near the center of each bamboo area. The two quadrats were separated by 225 m (Fig. 1d). To estimate the total richness of species in the bamboo areas, we used presence/absence data for the quadrats, as above. For all four quadrat configurations, we defined a difference between censuses in species richness as significant at a Bonferroni-corrected α level of 0.0125. We calculated P for these comparisons by the log-normal confidence intervals outlined by Chao (1987).

The use of Chao's estimator is complicated by the availability of a bias correction that is appropriate to use only some of the time. We have followed the suggestions of EstimateS (Colwell 2009) and avoided the bias correction in two cases where it was not appropriate: for the medium and small whole-plot quadrat configurations of the final census. We note that in each of these cases, our results do not differ qualitatively regardless of whether the bias correction is used, and the decision not to perform the bias correction has not altered our conclusions whatsoever.

Assessment of the association of birds with bamboo die-offs. To evaluate the importance of the bamboo die-offs to the bird diversity of the plot, we devised a metric to assess whether in 2009 birds had a significant association with the die-offs or with the surrounding forest. For the 102 species recorded with at least three separate detections in 2009, we calculated a "die-off fraction" as the ratio of detections that were within the bamboo die-off to all detections in the census plot. As the precision of the spot maps was approximately 15 m, we ignored detections within 15 m of the forest/die-off interface did not count them toward the minimum of three detections required for a species to be included for analysis. We compared the die-off fractions of persisting specialists to those of all other species, using a Mann–Whitney U-test (Mann and Whitney 1947) in the statistical package JMP (SAS 2007). This analysis is valid even when there are habitat-specific and species-specific differences in the probability of detection of individual birds, but the analysis fails if there are species-by-habitat interactions that shape idiosyncratic detection probabilities. Therefore, we repeated the analysis, first including only the persisting bamboo specialists and their families (Thamnophilidae and Tyrannidae) and then only the bamboo specialists and their congeners (*Myrmeciza*, *Hemitriccus*, and *Ramphotrigon*). We expect probabilities of detection of closely related species to be similar and to change similarly across the mature forest/die-off boundary.

To investigate the potential significance of bamboo die-offs for the occurrence of other bird species, we relaxed the requirement that species be represented by at least three detections and analyzed all species except for a few boreal and austral migrants (these would have been preferentially detected by the initial and final censuses, respectively). We computed die-off fractions for all species detected. These fractions give an imprecise indication of whether a species uses the die-off preferentially. We considered species undetected in 1984–1985 but with high die-off fractions in 2009 to be likely candidates for species whose presence in 2009 was a result of the habitat created by the die-offs.

Abundance estimation for bamboo specialists. For all specialists with sufficiently complete spot maps, we ascertained the number of territories in the census subplot from the spot map. When bamboo specialists were confined to bamboo areas on both censuses, their changes in abundance could be calculated exactly, provided that the spot-map censuses were complete. Because the bamboo areas are spatially bounded, the sampling covered the entire potential extent of local occurrence for these species, and fluctuations in the number of territories in the plot cannot merely reflect random rearrangement of territories in the larger forest. The exact density of territories is simply the number of territories in the plot divided by the 30 ha of bamboo in the census plot. We performed this analysis for seven species that we believe to have complete spot maps with the caveat that the results are sensitive to any errors in our interpretation of spot-map data.

RESULTS

BIRD-DIVERSITY DYNAMICS

The 2009 census recorded 205 bird species, including seven bamboo specialists, represented by 1643 individual spots. The 1984–1985 census recorded 270 bird species, represented by 7155 individual spots. Eighteen of those species were bamboo specialists (Table 2) or apparent bamboo specialists (Kratter 1997).

The decrease in the number of species recorded is partly or entirely an effect of the reduced sampling effort of 2009. Chao's richness estimator, computed from the quadrat samples, indicates that a comparable number of species occupied the plot before and after the bamboo die-off, although the large uncertainties may mask an effect (Fig. 2). These estimates also agree with the species total detected in the full 80-ha census plot during the initial sampling, a total assumed to approximate the true richness of birds using the area (Robinson et al. 1990).

Richness estimates computed from the bamboo quadrats indicate that fewer bird species used the die-offs than used the bamboo (88 vs. 155 spp.; $P < 0.001$; Fig. 2). In total, the bamboo-area quadrats sampled 71 species in 2009. Thus the estimate suggests that approximately 17 species (95% confidence interval 8–38 species) used the quadrats but escaped detection. Some of these species likely occurred in the die-offs but outside the quadrats.

We investigated the possibility that bamboo die-offs contribute to the bird species richness of the forest by harboring unique species that would otherwise be absent by considering species that used the bamboo die-offs but not the surrounding forest. The persisting bamboo specialists are prime candidates

TABLE 2. Bamboo specialists recorded in the 50-ha census subplot, 1984–1985 and 2009.

Category of specialization[a]	Approximate number of territories 1984–1985	Approximate number of territories 2009	Density change (individuals ha^{-1})[b]
Obligate			
Drymophila devillei	4	0	—
Hemitriccus flammulatus	3	5	+0.13
Poecilotriccus albifacies	2	0	–0.13
Near-obligate			
Simoxenops ucayalae	3	0	–0.20
Anabazenops dorsalis	2	0	–0.13
Automolus melanopezus	4	0.5	—
Cymbilaimus sanctaemariae	1	0	–0.07
Percnostola lophotes	5	0	—
Myrmeciza goeldii	2	2–3	—
Ramphotrigon megacephala	2	0	–0.13
Ramphotrigon fuscicauda	2	4	+0.13
Facultative			
Picumnus rufiventris	present[c]	present[c]	—
Campylorhamphus trochilirostris	1.5	0	—
Myrmotherula ornata	present[c]	0	—
Myrmotherula iheringi	3	0	—
Myrmotherula quixensis	3.5	present[c]	—
Apparent			
Dromococcyx pavoninus	0	present[c]	—
Nonnula ruficapilla	present[c]	0	—
Automolus rubiginosus	1	0	—

[a] According to Kratter (1997).

[b] Calculated only when the population density in bamboo areas can be calculated exactly for both censuses. This is possible when the species is completely confined to bamboo areas, and the density of adults is given exactly by twice the number of territories divided by 30 ha, reflecting the assumption that each territory contains exactly one pair of adult birds.

[c] Recorded in the census plot, but detections insufficient to define the territorial boundaries.

for such species. Among the 102 species with at least three detections, the die-off fractions of the specialists clustered above those of all other species, confirming their association with the die-offs (Mann–Whitney $U = 20$, $n_1 = 99$, $n_2 = 3$, $P = 0.009$; Fig. 3). This analysis requires no assumptions about the expected size or shape of bird territories, nor does it assume that equal observer effort was invested in the bamboo die-offs and surrounding forest. The results were robust when we restricted the taxonomic scope of the analysis. The result remained significant when only thamnophilids and tyrannids were analyzed (Mann–Whitney $U = 48$, $n_1 = 16$, $n_2 = 3$, $P = 0.002$) and was nearly significant when only *Myrmeciza*, *Hemitriccus*, and *Ramphotrigon* were analyzed (Mann–Whitney $U = 9$, $n_1 = 3$, $n_2 = 3$, $P = 0.10$). At the sample size available for the test of congeners only, it is statistically impossible to produce a significant result at the 0.05 level, and our result is the most extreme P-value possible.

Twenty-one species were recorded in 2009 but not on the initial census. These are candidates for species whose presence in the plot in 2009 results from habitat created by the die-offs. For only six of these species, however, was the die-off fraction 0.8 or above, and all six were represented by only one or two detections each, precluding any genuine conclusions about the importance of the die-offs to their occurrence in the plot (Table 3).

OCCURRENCE OF BAMBOO SPECIALISTS IN BAMBOO DIE-OFFS

Of the seven bamboo specialists (sensu Kratter 1997) detected in 2009, one species, the Pavonine Cuckoo (*Dromococcyx pavoninus*), was not recorded on the original census, though it was detected in 1984 outside the regular census period. Three species, the Pavonine Cuckoo, Rufous-breasted Piculet (*Picumnus rufiventris*), and Dot-winged Antwren (*Microrhopias quixensis*), were represented on the 2009 census by only one detection each. The remaining four species were detected enough times for their territorial boundaries and abundances in 2009 to be quantified (Table 2).

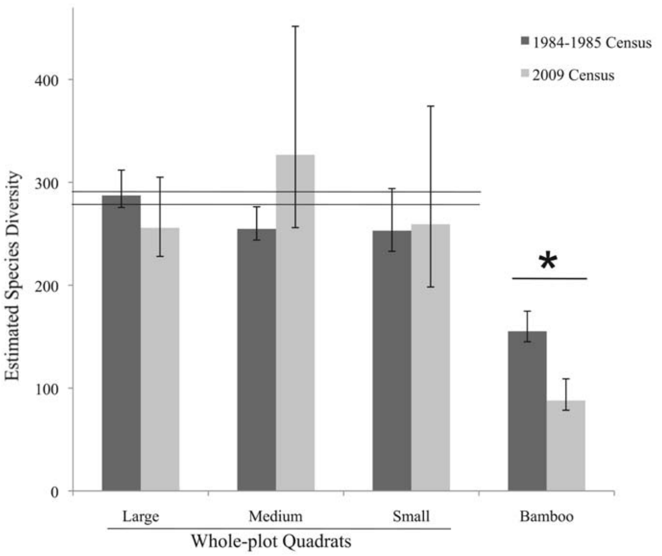
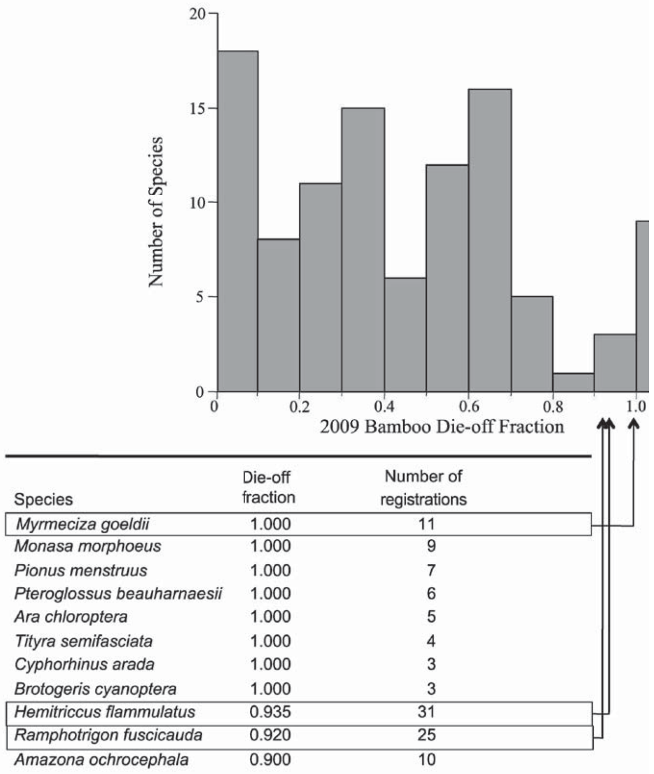


FIGURE 2. Significantly fewer bird species used the bamboo die-offs in 2009 than used the bamboo in 1984 and 1985. The columns show Chao's richness estimator for bird species richness in the census plot based on quadrat sampling (the Chao2 statistic in EstimateS). See Figure 1 for sizes and configurations of the four quadrat types. Following Colwell (2009), the 2009 estimates based on medium and small quadrats are given by Chao's classic statistic, while all other values are given by Chao's bias-corrected statistic. Error bars show 95% confidence intervals calculated in EstimateS (Colwell 2009). The asterisk (*) indicates statistical significance under Bonferroni correction ($P < 0.001$). The horizontal lines correspond to the number of bird species found on the 1984–1985 census in the 50-ha subplot (lower line) and in the entire 80-ha census plot (upper line).

Specialists such as the Flammulated Pygmy-Tyrant (*Hemitriccus flammulatus*) and Dusky-tailed Flatbill (*Ramphotrigon fuscicauda*) were confined largely to bamboo in 1984 and 1985. In 2009, when no bamboo was present, there was less reason to expect that these species would still be confined to the areas previously occupied by bamboo patches. The spot maps from 2009, however, suggested that the specialists' occurrence remained strongly associated with the bamboo die-offs (Fig. 4). The trend was confirmed by analysis of the die-off fractions for the persisting specialists (Fig. 3), permitting the direct calculation of the 2009 abundance of these species. The Flammulated Pygmy-Tyrant, classified by Kratter as an obligate bamboo specialist, increased in abundance after the die-off, as did the near-obligate specialist Dusky-tailed Flatbill (Table 2). The trends for the Brown-rumped Foliage-Gleaner (*Automolus melanopezus*) and Goeldi's Antbird (*Myrmeciza goeldii*) are harder to determine because these species were not confined to bamboo on the initial census. Though it might be expected that facultative specialists (sensu Kratter 1997) persist better in die-offs than obligate specialists, we observed no such trend (Fig. 5).



Species	Die-off fraction	Number of registrations
Myrmeciza goeldii	1.000	11
Monasa morphoeus	1.000	9
Pionus menstruus	1.000	7
Pteroglossus beauharnaesii	1.000	6
Ara chloroptera	1.000	5
Tityra semifasciata	1.000	4
Cyphorhinus arada	1.000	3
Brotogeris cyanoptera	1.000	3
Hemitriccus flammulatus	0.935	31
Ramphotrigon fuscicauda	0.920	25
Amazona ochrocephala	0.900	10

FIGURE 3. Ignoring detections within 15 m of the border of a die-off, we calculated a "die-off fraction" as the ratio of detections in bamboo die-offs to all detections in the census subplot for each species recorded at least three times on the 2009 census. The histogram groups the die-off fractions by bins of 0.1 and displays the count for each bin ($n = 102$). The table shows all species with die-off fractions of at least 0.9, which include all three bamboo specialists (boxed) that met the criteria for analysis. The die-off fractions of specialists were significantly higher than those of all other species as a group (Mann-Whitney $U = 20$, $n_1 = 99$, $n_2 = 3$, $P = 0.009$). Furthermore, of species detected more than ten times in 2009, the bamboo specialists had the three highest die-off fractions of all species.

A better predictor of bamboo specialists' ability to persist in bamboo die-offs was provided by Lebbin (2013), who demonstrated that the communities of bamboo specialists found in different bamboo patches form nested subsets of one another in a highly significant fashion. In our study, the four specialist species that persisted in the bamboo die-offs, being recorded multiple times, were among the least nested species in Lebbin's analysis (Mann–Whitney $U = 10$, $n_1 = 4$, $n_2 = 10$, $P = 0.038$).

Preliminary assessments of the vegetation in the bamboo die-offs revealed a young and structurally simple plant community. Predominant trees included representatives of *Inga* and *Cecropia*, genera characteristic of early successional habitats in Amazonia (Table 1). The structure of the vegetation was not uniform. In the southern die-off, the two major vegetation layers consisted of a low canopy of young trees roughly 10 m in height and a dense layer of

TABLE 3. Bird species associated to bamboo die-offs in 2009 and undetected 1984–1985, with the total number of detections and the fraction thereof in bamboo die-offs.

Species	Die-off fraction	Number of detections
Dromococcyx pavoninus	1.0	1
Nyctibius aethereus	1.0	1
Camptostoma obsoletum	1.0	1
Tyrannopsis sulphurea	1.0	1
Myiarchus ferox/ tuberculifer	1.0	1
Chlorophonia cyanea	1.0	2[a]

[a] Although *Chlorophonia cyanea* was detected twice on the census, one detection was at the border of the die-off and so was not used in the calculation of the proportion of sightings that were in bamboo.

shrubs 1–3 m tall. These layers were often blurred or connected by viny thickets (Fig. 6a). In the northern die-off, a layer of widely spaced emergent trees (many of them 30 m tall or more) partially shaded the layer of regrowth. While the low closed canopy of young trees resembled that of the southern die-off, the shrub layer was virtually absent (Fig. 6b). Though we did not quantify it, the difference was stark. Sight lines were much longer in the northern die-off, and two researchers working together could make a trail at approximately five times the rate possible in the southern die-off. However, dense viny tangles ringed a massive treefall gap in the northern die-off (Fig. 6c). This gap, which involved four large treefalls, created an island of dense habitat similar to that of the southern die-off.

The spatial variation in plant cover permitted a test of the importance of vegetation architecture in determining habitat suitability for the persisting bamboo specialist birds. All four specialists for which territories could be defined in 2009 were confined to the southern die-off and the vicinity of the treefall gap in the northern die-off (Fig. 4).

DISCUSSION

Our results only partially confirmed our predictions generated from the hypothesis that bamboo die-offs have a neutral effect on avian biodiversity through the simultaneous loss of

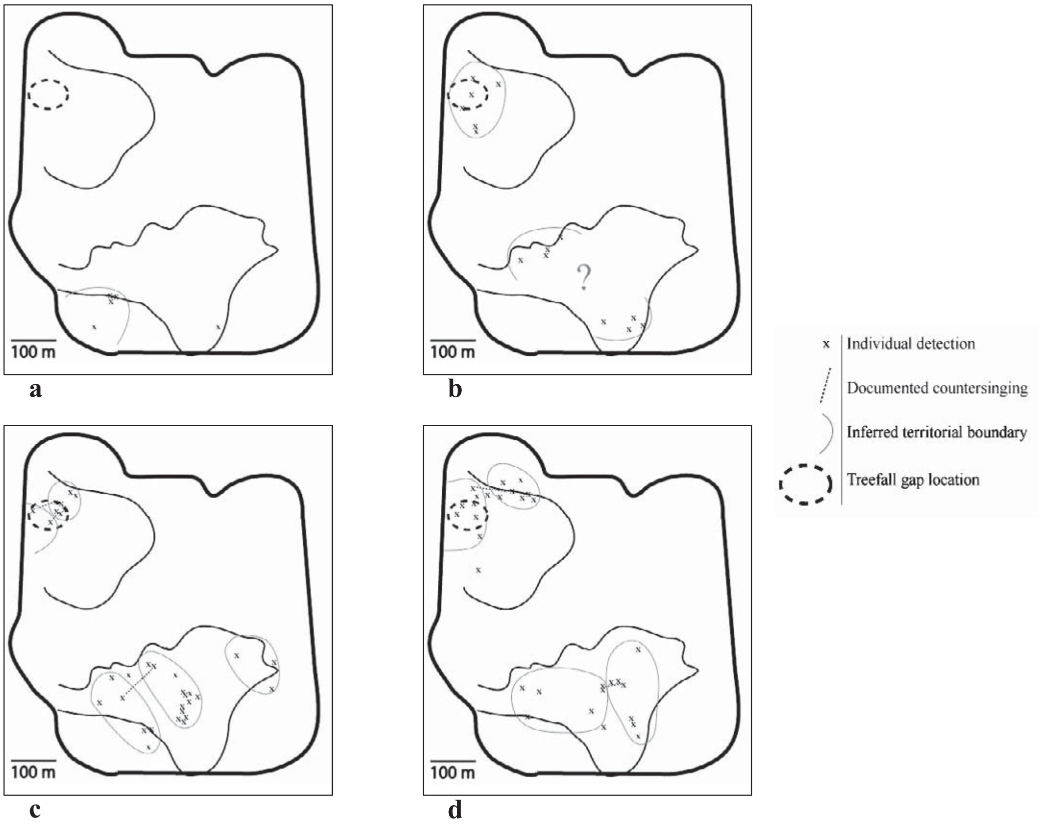


FIGURE 4. Spot maps for all persisting bamboo specialists detected multiple times in 2009. Thick black lines indicate the boundary of the 50-ha subplot; thin black lines indicate the borders of the bamboo die-off. (a) *Automolus melanopezus*; (b) *Myrmeciza goeldii;* (c) *Hemitriccus flammulatus;* (d) *Ramphotrigon fuscicauda*. Every persisting specialist was encountered in the southern die-off, and the treefall gap was the epicenter of detections for every specialist encountered in the northern die-off. Countersinging individuals of *H. flammulatus* and *R. fuscicauda* were encountered in both die-offs.

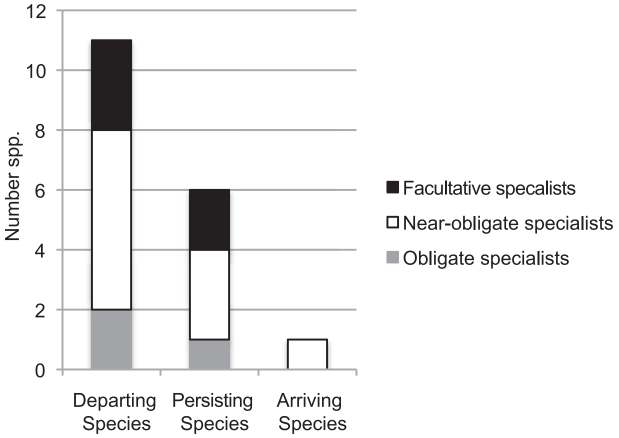


FIGURE 5. Patterns of departure and persistence of obligate, near-obligate, and facultative bamboo specialists in the bamboo die-offs. Following Lebbin (2007), we treat *Dromococcyx pavoninus* and *Nonnula ruficapilla*, classified as apparent bamboo specialists by Kratter (1997), as near-obligate specialists. *Automolus rubiginosus*, also an apparent specialist sensu Kratter (1997), departed the census plot but is omitted from this figure, again following Lebbin (2007).

FIGURE 6. Habitats of the bamboo die-offs. (a) The impenetrable viny understory of the southern bamboo patch. (b) The relatively open understory of the northern bamboo patch. (c) Dense viny tangles ringing a treefall gap within the northern bamboo patch.

bamboo specialists and the gain of early-successional species that colonize the newly regenerating patches of forest in the gaps created by the die-offs. Many of the species previously considered to be bamboo specialists (Kratter 1997) disappeared as predicted from the loss of their distinctive plant community. Several species, however, persisted long after the die-off in the complete absence of bamboo, which suggests that they may not be true bamboo specialists but may instead be responding to some other aspect of vegetation structure. Contrary to our predictions, we detected no species characteristic of early-successional vegetation that had invaded the gaps, even though some areas contained the kind of dense shrub/sapling layer that characterizes early-successional habitats. Within the bamboo areas, bird species richness was far lower after the die-offs than it was when bamboo was present. Nevertheless, the species richness in the entire plot before and after the die-off remained largely the same, suggesting that bamboo die-offs may have less effect on local species composition than we predicted. In the remainder of this discussion we explore the implications of these results for Amazonian community structure.

BIRD SPECIES RICHNESS AND BAMBOO CYCLES

Despite comparable richness at the level of the whole plot, the quadrat sampling suggests that the bird species richness within the bamboo die-offs was far less than in the intact bamboo. The low richness of the bird community of the die-offs resulted mainly from the loss of bamboo specialists and the lack of newly colonizing species restricted to the die-offs. Only six species that were not found on the initial census had die-off fractions greater than 0.8, and each of the six was represented by only one or two detections. The paucity of detections of these species means that even if the detections were distributed at random in the forest, they may have appeared only in the bamboo die-offs. Among the six species, the Pavonine Cuckoo, a near-obligate bamboo specialist, is likely to be genuinely restricted to the die-off; its appearance in 2009 following its absence in 1984 was not mediated by the disappearance of the bamboo and establishment of early-successional habitats. It was detected in 1984 but only outside the census period. It may have passed undetected on the census because it sings primarily at night. A similar situation applies to the nocturnal Long-tailed Potoo (*Nyctibius aethereus*); the song of this species was not known to JT or SR at the time of the1984–85 censuses. The Blue-naped Chlorophonia (*Chlorophonia cyanea*) is a rare altitudinal migrant (Merkord 2010) that has been detected in the vicinity of Cocha Cashu only a handful of times, and its presence in the census plot in 2009 may have had little to do with the bamboo die-off.

The remaining three species added to the plot list following the die-off may have occurred in the plot as a direct consequence of the die-off. *Tyrannopsis sulphurea* is a near-obligate specialist on *Mauritia flexuosa* palm swamps but also occurs at forest edges (Lebbin 2007, del Hoyo et al. 2004). A *Myiarchus* flycatcher was left unidentified as the Dusky-capped (*M. tuberculifer*) or Short-crested (*M. ferox*), but the latter, along with the Southern Beardless-Tyrannulet (*Camptostoma obsoletum*), are typical birds of edge habitats and are absent from mature *terra firme* forest (Terborgh et al. 1990, Robinson and Terborgh 1997).

Conspicuously absent were numerous specialists of early-successional riverine habitats at Cocha Cashu (see Lebbin 2007, Robinson et al. 1990). Some of these, such as the Barred Antshrike (*Thamnophilus doliatus*), are widespread inhabitants of second growth and might be expected to occur in the bamboo die-offs, especially as the northern die-off is a mere 300 m from the nearest loop of the Manu River. Second growth supports many species characteristic of riverine successional vegetation, and such species are capable of dispersing into isolated patches of second growth (Terborgh and Weske 1969, Borges 2007). Furthermore, in 1984 and 1985, a few riverine species, such as the Silver-beaked Tanager (*Ramphocelus carbo*), occurred in early-successional vegetation on a landslide in the plot, confirming their ability to disperse to the area. In 2009, several early-successional species were frequently encountered along the riverside access trail for the census plot but never observed on the plot itself.

BAMBOO SPECIALISTS AND BAMBOO DIE-OFFS

The responses of bamboo specialists to the die-off ranged from complete disappearance to actual increases in the abundance of the Flammulated Pygmy-Tyrant and Dusky-tailed Flatbill, two species Kratter (1997) considered to be obligate bamboo specialists. When the persisting specialists are placed in the context of Lebbin's (2013) nestedness matrix, it is clear that those species with the strictest requirements for large and/or high-quality bamboo patches do not occur in bamboo die-offs, whereas species that are able to use small or marginal bamboo patches tend to use the die-offs also.

Determining why some specialists are able to use marginal habitats whereas others cannot requires data on their ecology and the mechanisms underlying their dependence on bamboo. Factors influencing habitat selection by Amazonian birds include physical habitat structure, food resources, nest sites, and interspecific competition (Terborgh 1985). Previous studies have suggested that vegetation architecture and habitat structure may be an important driver of bamboo specialization. When bamboo specialists occur outside of bamboo, they are most often found in viny tangles, dense vegetation with low canopies, edge habitats, and stands of *Gynerium* cane. Sympatric congeners of several bamboo specialists characteristically occur in these same habitats (Kratter 1997). Each of these habitats bears a structural resemblance to *Guadua* bamboo, with dense foliage, a low canopy, and simplified vertical structure. The patterns of specialists' persistence in the bamboo die-offs suggest that vegetation architecture rather than plant species composition may be driving the persisting specialists' association with bamboo patches. All seven persisting specialists forage among the foliage in the canopy and subcanopy of bamboo patches, and all of these specialists except the Dot-winged Antwren were confined to the densest and structurally simplest areas of the bamboo die-offs. We recorded the Dot-winged Antwren only once in 2009, in dense vegetation in a ravine outside of the bamboo die-offs, and the species regularly occurs outside of bamboo in floodplain forest (Terborgh et al. 1990). The two specialists detected in 1984 that forage on bamboo culms, the Red-billed Scythebill (*Campyloramphus trochilirostris*) and Peruvian Recurvebill (*Simoxenops ucayalae*), had departed the plot. In the Cocha Cashu area, the scythebill often uses successional stands dominated by *Gynerium* cane, but the vegetation of the bamboo die-offs did not approximate the morphology of the stems that these specialists use.

Our study furnished no evidence of a role for interspecific competition in mediating habitat selection by bamboo specialists. Many specialist taxa left the area despite a lack of invading species to displace them. In general, the bamboo die-off was not invaded by congeners of the departing specialists, suggesting that direct competition does not play an important role in comparison to that of structural features of the habitat in mediating specialists' habitat selection. For example, although the Fasciated Antshrike (*Cymbiliamus lineatus*) did not appear to invade the bamboo die-off, the specialist Bamboo Antshrike (*C. sanctaemariae*) departed the plot. Interestingly, playback experiments testing for interspecific responses between congeners inhabiting bamboo and *terra firme* forest revealed no instances of interspecific aggression (SR and JT, unpubl. data), a further suggestion that interference competition in the form of interspecific territoriality may not exclude congeners from either habitat. The low alpha diversity of birds in the bamboo die-offs suggests that diffuse competition (see Terborgh 1971) was similarly insignificant in driving the departure of the specialists.

The responses of bamboo specialist birds to bamboo die-offs have implications for conservation planning. Because single bamboo patches do not provide long-term habitat for most specialists, these species may require intact landscapes at the vast spatial scales on which bamboo cycles operate. This point that has been made by Areta and Cockle (2012) in the context of nomadic granivorous bamboo specialists that follow the masting of bamboo, and it is equally true of the sedentary insectivores. The disappearance of most taxa after a die-off confirms the importance of successful dispersal for the viability of these species. Few other habitats in the world disappear as frequently or abruptly, and populations of specialists may depend on intact landscapes at spatial scales that encompass numerous bamboo patches as they develop and disappear. It is fortunate that large protected areas such as the Manu National Park and adjoining conservation areas preserve landscapes on such scales.

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