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Are Mixed-Species Bird Flocks Stable through Two Decades?

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ABSTRACT: The stability of tropical systems has been hypothesized to explain the evolution of complex behavioral interactions among species. We evaluate the degree to which one highly evolved social system, mixed-species flocks, are stable in space and time in French Guiana, where flocks were characterized 17 years apart. These flocks are led by alarm-calling "sentinels," which may benefit from food flushed by other "beater" species. Using null models, we found that flock roost sites, home range overlap, and composition were more similar than expected by chance; home ranges were nearly identical between the two time periods. Such extremely stable conditions may be essential for the evolution and maintenance of the sentinel-beater system that appears to characterize some flocks. These results may reflect an evolutionarily stable strategy among potentially interdependent species within mixed-species flocks, where home ranges contribute to stability by being far larger than the most common local disturbances in the forest.

Keywords: mixed-species bird flocks, long-term stability, Nouragues biological station, home range, evolutionarily stable strategy.

Introduction

Ecologists have hypothesized that constant environmental conditions through evolutionary time, such as those presumed to exist in the tropics, explain both high diversity and the maintenance of stable biological communities (Dobzhansky 1950; Pianka 1966). Despite this perception, studies of community stability (i.e., persistence in species composition and community structure through time) have mainly focused on nontropical ecosystems (Ives and Carpenter 2007). The limited number of studies from the tropics has reported varying degrees of stability. Furthermore, most studies in the tropics focus on sessile plants and animals, presumably because they are easier to monitor through longer periods of time (Collins 1995; Condit 1995; Connell et al. 1997).

Studies of stability in mobile tropical animal communities are scarce, logistically challenging, and rarely include

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data from more than a few years. Early studies of tropical bird communities suggested stability in bird diversity, abundance, and spatial distribution (Orians 1969; MacArthur 1972; Ricklefs 1973; Munn 1985; Murray 1985; Greenberg and Gradwohl 1986). However, studies using mist nets have documented high variation in species composition and abundance over a 3- to 8-year period (Karr 1976, 1982; Martin and Karr 1985; Loiselle and Blake 1992). Therefore, the stability of highly mobile tropical bird communities remains poorly understood.

Mixed-species flocks are among the most fascinating natural history features of Neotropical bird communities. Specifically, these flocks form socially complex aggregations that exhibit year-round multispecies territoriality and partitioning of ecological roles, including alarm calls and defense. These flocks occur throughout the Neotropics (Amazonia: Munn and Terborgh 1979; Munn 1985; Atlantic Forest of Brazil: Stotz 1993; Central America: Powell 1979; Greenberg and Gradwohl 1986; Guiana Shield: Jullien and Thiollay 1998) and are among the most cohesive multispecies groups found in terrestrial vertebrates (Munn 1985). Amazonian flocks, for example, usually consist of a permanent group of 5–10 species pairs or family groups of insectivores that defend a joint home range (Munn 1985). They are usually led by one or two "sentinel species" from the antbird genus *Thamnomanes* (Munn and Terborgh 1979; Jullien and Thiollay 1998). Sentinels, which appear to lead the flock as it moves, constantly vocalize and sound "alarm calls" in the presence of predators. Other members of the flock remain within several meters of the sentinels and take advantage of alarm calls. Other members are usually perch-gleaning insectivores, many in the antwren genus *Myrmotherula*, that spend most of their time myopically searching for insects, often while probing their entire head into suspended, curled dead leaves and other dense clusters of leaves. Sentinels have been hypothesized to benefit from flushed insects and to possibly steal large prey items while distracting them with the use of "false" alarm calls (Munn 1986). Up to 65 other species join these flocks throughout the day within single-forest bird com-

munities, which means that they play a central role in the ecology of a large fraction of the resident bird community of Neotropical forests (Munn and Terborgh 1979; Munn 1985; Jullien and Thiollay 1998).

Stability of the flocks in space and time may allow for the rise of evolutionarily stable strategies, such as the interdependence of flock members that flush insects and the flycatcher foraging behavior of the "sentinels" that benefit from catching flushed prey (Munn 1986). Only one study, however, has documented the territorial stability of mixed-species flocks. Greenberg and Gradwohl (1986) found that flocks in central Panama were stable in terms of territory occupancy and species composition over an 8-year period. Apart from this study, most information on the stability of mixed-species flocks is largely anecdotal; opportunities to measure stable territories or home ranges and species composition over multiple generations would be useful in documenting the extent to which stability is widespread in this community module.

Jullien and Thiollay (1998) reported the home ranges and roosting sites of 11 flocks occurring in the Nouragues field station (Inselberg camp) in French Guiana in 1994. These flocks were located in a ~130-ha trail system of lowland tierra firme forest. Almost 20 years after Jullien and Thiollay (1998) originally mapped the home ranges and roosting sites of these flocks, the Nouragues station has maintained an environment free of human impact. Nevertheless, the forest is highly dynamic, with tree-fall gaps opening frequently but closing in short periods of about 5 years (P. M. Forget, personal communication). This suggests that the forest has a stable landscape composition free of large-scale disturbances but retains the gap-phase dynamics typical of tropical forest communities (Brokaw 1985; Denslow 1987). The 20-year interval between the first study and this study is likely to comprise more than one generation of birds (Brawn et al. 1985; Blake and Loiselle 2008), giving us a unique opportunity to test whether flock features outlive the individuals that form them. Given that selection acts on individuals, the retention of the characteristics through different generations would allow us to make inferences about the evolution of flocking behavior. Thus, Nouragues is an ideal site to document the stability of flock characteristics over a 20-year interval.

In this study, we quantify patterns of home range stability and spatial distribution of mixed-species flocks by comparing samples of home ranges, location and spatial distribution of roosting sites, and species composition of flocks from 1994 and 2011. We compared observed values of home range overlap, distance between roosting sites, dispersion between roosting sites, and species similarity between the flocks in 1994 and 2011. We further constructed several null models to determine whether such results are in fact the result of true community stability or random expectation. Quantifying such patterns will allow us to better understand the stability and distribution of tropical rain forest communities and to understand the conditions under which such complex multispecies associations might have evolved.

Methods

In October 2011, based on the home range and gathering site map by Jullien and Thiollay (1998), we located each of the 11 flocks by visiting grid locations where roosting sites were originally reported. We use the term "roosting site" instead of "gathering site" because we believe that species do not gather but actually spend the night in close proximity to one another at the site. Every day we found a flock at a roosting site, most of the species were close together, and we did not find evidence that species started to gather as the "sentinel" species started calling. Although *Thamnomanes* antshrikes often sang first, most species started singing at nearly the same time, and in some cases we located the flock by the call of a core species other than the sentinel. We arrived at sites reported on the map before dawn and located flocks by song identification of sentinel species. If the flock was located using the song of other core species, we waited until we made visual contact with flock members to identify the sentinels and subsequently marked the coordinate locations of the flock roosting sites using a Garmin 60CSx GPS unit. Next, we followed the flock as closely as possible and recorded its location every 10 min and its species composition over 30-min intervals in the same day. We repeated this with each of the 11 flocks based on roosting site locations established in the original study (Jullien and Thiollay 1998). We usually started the first interval at 6:30 a.m. and followed the flock continuously until 5:00 p.m. We followed seven flocks for 11 h, one flock for 10.5 h, two flocks for 10 h, and one flock for 9.5 h, for a total of 117 h. Jullien and Thiollay (1998) followed the flocks for 937 h. Color-banded individuals, as in the original study, would have helped us identify individual flocks, allowing us to follow them for more than 1 day. Because we did not have marked individuals, however, we restricted our sampling effort to 1 day per flock. However, we believe this has little effect on our study, because we were testing for position of roosting site and flock territory and not territory size. To look at species occurrence, we recorded the percent of the 11 flocks in which each species occurred. Birds were considered part of the flock if they were seen moving and feeding within 15 m of other birds for at least 15 min (see Jullien and Thiollay 1998).

Data analysis. Using ArcGIS version 9.3 (ESRI 2011), we digitized the map reported in the original paper (fig.

8 in Jullien and Thiollay 1998) and georeferenced it using our own data points from trail intersections and a grid layer provided by the Centre National de la Recherche Scientifique. We further enhanced the figure, creating a digital map of roosting sites and flock territories. This allowed us to compare distances between 1994 and 2011 roosting sites, the average nearest neighbor distance, and the percent overlap of territories in 1994 and 2011. To determine the statistical significance of each comparison, we constructed four null models: one for the distance between the 1994 and 2011 roosting sites, one for the average nearest neighbor at 1994 and 2011, and two different null models for the percentage overlap of territories. All of the following analyses regarding null models were constructed using ArcGIS, except where noted. The P value of all randomization tests was calculated by dividing the rank of the observed value in the null distribution by the number of randomizations made.

Null model of roosting sites. To establish whether the roosting sites we observed in 2011 were closer than expected to those observed in 1994 by chance, we first calculated the distance from the roosting site reported in the original map (Jullien and Thiollay 1998) to the one recorded in 2011. We then built a null model in which we reconstructed 1,000 random roosting sites within the 1994 flock home range and calculated the distance between each of these 1,000 random roosting sites and the observed 1994 roosting site and built a null distribution of distance values. If smaller than expected by chance, then the observed distance would be smaller than most distances from the random distribution.

Null models of overlap of home range points. In this case, we were confronted with biologically realistic null models that were either too relaxed or too restrictive. As a result, we include both models here.

Null model 1 (relaxed). First, we constructed polygons that matched the size of the home range of each flock in the 1-day samples of 2011. Then, we constructed a polygon the size of the combined 11 flock home ranges of 1994. Next, we randomly placed each of the constructed 2011 polygons 1,000 times within the bigger polygon and calculated the amount of overlap between each flock in 1994 and the 2011 random polygons. This resulted in a distribution of percent overlap between the 1994 and the 1,000 2011 randomly placed polygons. We were interested in testing whether the amount of observed overlap was greater than expected by chance; thus, we expected the observed value to be greater than the majority of overlaps generated randomly.

Null model 2 (restrictive). For this null model, we used the same concept as in the previous one, but this time we randomly placed 1,000 points within the 1994 home range of each flock and used those points as the centroid of

1,000 polygons based on the size of the 2011 1-day sample. This null model might be more realistic than the first one because our searching for flocks was not random throughout the grid of the station but was systematically targeted to the home range that each flock occupied in 1994. However, it is also much more restrictive in that all the randomly placed polygons will be biased to have high degrees of overlap.

Nearest neighbor ratio (NNR) analysis. We used roosting sites from both 1994 and 2011 to test the hypothesis that flocks were evenly distributed in the space available. Roosting sites were spread over two habitat types that clearly influenced home range size (see Jullien and Thiollay 1998 and our own results below); thus, for this analysis, we only used eight of the roosting sites that were located in high mature-forest habitat (see Jullien and Thiollay 1998) to remove this bias. We used the Average Nearest Neighbor distance tool in ArcGIS to compare the average nearest neighbor distances between the roosting sites of the eight flocks. This analysis calculated the distance between each point in the data set and its nearest neighbor and determined whether the points were clustered, random, or overdispersed in a given space. It is based on the ratio between observed and random average distance. A ratio greater than 1 means that points are more dispersed in space than expected by chance, which is the result we predicted. We set the area to which the points could be randomly placed to be the area of the grid that the eight flocks occupied. We further calculated the standardized effect size of the NNR (SES.NNR) and associated P values to test whether flocks were overdispersed within the Nouragues station grid.

Comparison of community composition of flocks. We used the Bray-Curtis (BC) dissimilarity index to compare community composition between the flocks in 1994 and 2011. The BC index ranges from 0 (similar) to 1 (dissimilar) and measures similarity between two sets of samples (Krebs 1989). We then randomized the community matrix for each time period 1,000 times, keeping the number of species present in each period of time constant, thus generating a null distribution of dissimilarity indexes. We compared the observed dissimilarity index with the randomly generated distribution of values and calculated a P value in the same way as previous null models. The randomizations were constructed using the picante package (Kembel et al. 2010) for R (R Development Core Team 2011), and the Bray-Curtis index was calculated using the vegan package (Oksanen et al. 2011).

Results

Change in roosting sites. Seven out of 11 roosting sites observed in 2011 were statistically identical to those ob-
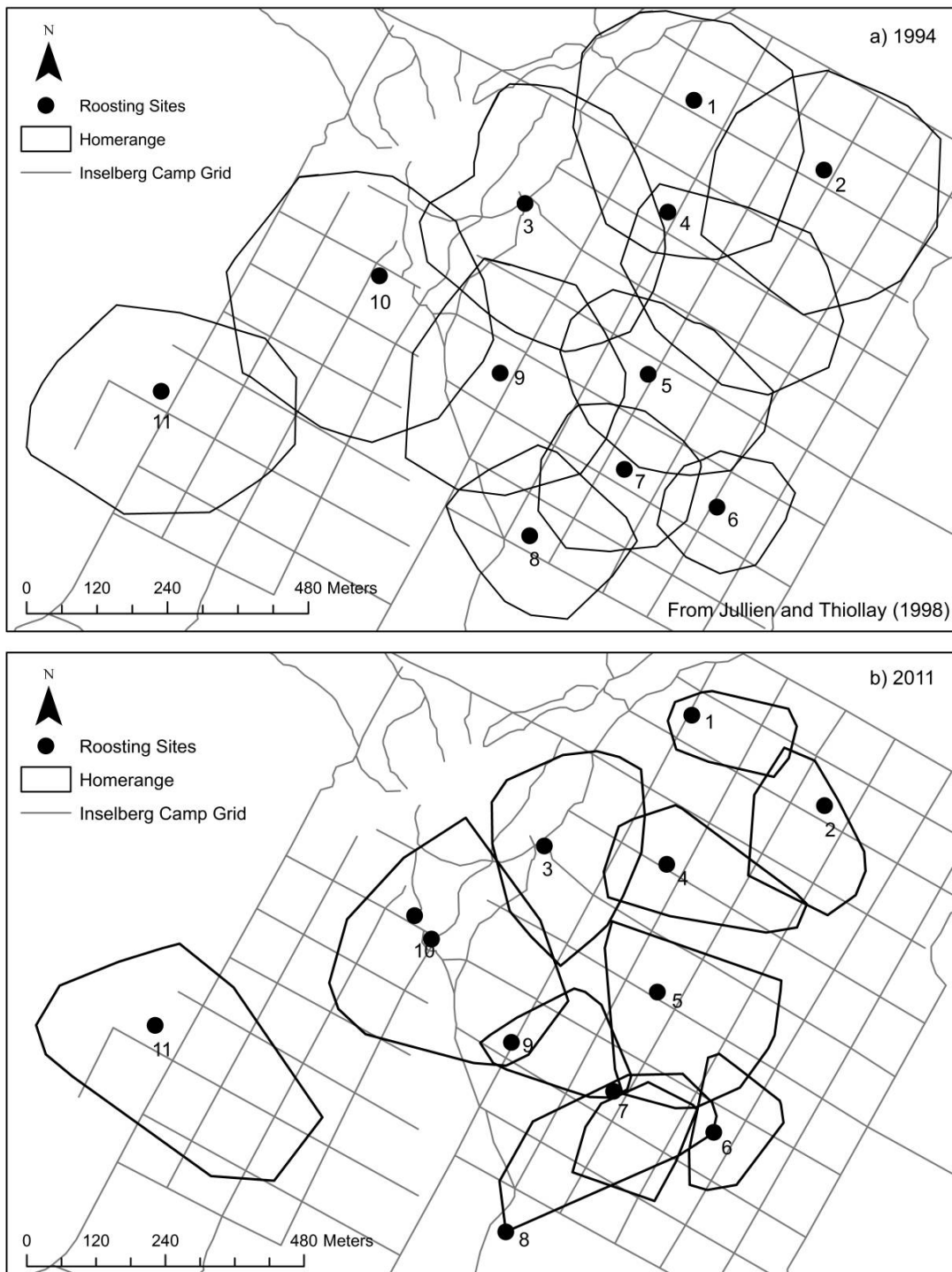
Figure 1: Maps showing the distribution of flocks and roosting sites in 1994 (*a*) and 2011 (*b*).

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Table 1: Observed and expected values for roosting sites and home range for 1994 and 2011

Flock	Roosting site distance observed	Roosting site distance null model			Overlap observed (%)	Overlap null model 1 (%)			Overlap null model 2 (%)		
		Mean	SD	P value		Mean	SD	P value	Mean	SD	P value
1	54.56	147.99	61.18	.076	100.00	11.80	20.96	**<.0001**	81.98	18.60	**0**
2	29.66	140.21	51.16	**.016**	100.00	13.12	23.75	**<.0001**	76.53	19.42	**0**
3	14.38	150.45	56.83	**.007**	99.10	14.00	22.14	**<.0001**	68.42	18.23	.054
4	28.18	192.35	95.74	**.030**	65.60	10.42	19.90	**.038**	70.67	17.89	.546
5	50.07	112.16	46.93	.110	88.70	7.89	17.36	**<.0001**	60.95	15.25	.051
6	50.31	70.76	27.49	.233	72.60	2.64	11.46	**.007**	65.68	17.18	.332
7	60.51	93.12	35.06	**.006**	100.00	5.33	14.96	**<.0001**	70.29	18.73	**0**
8	99.27	95.84	36.29	.504	71.20	4.97	15.62	**.014**	61.18	15.63	.268
9	38.23	131.67	48.60	**.038**	96.80	11.43	20.37	**<.0001**	77.53	19.26	.297
10	46.02	160.84	63.00	**.034**	62.30	13.91	23.09	.066	64.32	16.81	.49
11	29.46	139.05	55.85	**.026**	69.80	9.95	21.31	**.028**	59.84	15.21	.267

Note: Boldface indicates *P* values <.05.

served in 1994 (fig. 1; table 1). Of the other four roosting sites, flock 8 was the only flock where the roosting site was not closer or farther than expected by chance from the 1994 sites (see *P* values in table 1).

Home range overlap. Visually, the single-day sample of home ranges observed in 2011 appeared to overlap greatly with the original home ranges from 1994 (fig. 1). This was confirmed using null model 1, where 10 of the 11 flocks had a higher overlap than expected by chance (table 1). However, null model 2, which is more restrictive, suggested that only three of the single-day samples in 2011 had a significantly higher overlap with the original home ranges observed in 1994 than expected by chance, along with two more showing a strong tendency in the same direction (table 1). The other six flocks showed results in the direction of greater stability in space (higher overlap than expected), but their overlap could not be distinguished from a random expectation.

Roosting site distribution. The results from the NNR analysis suggest that distribution of roosting sites was nonrandom for both periods of time (1994 and 2011). For 1994 and 2011, the NNR was higher than 1, suggesting that roosting sites were overdispersed in the Nouragues station grid (NNR 1994 = 1.7; NNR 2011 = 1.71). In fact, SES.NNR was positive and significant, also suggesting the overdispersion in space of the roosting sites (SES.NNR 1994 = 3.79, $P < .001$; SES.NNR 2011 = 3.85, $P < .001$).

Community composition. Species composition was more similar than expected by chance when comparing samples from 1994 with 2011, suggesting that flocks are mainly composed of the same species in the two time periods (observed BC index = 0.26, mean null BC index = 0.61, null BC standard deviation = 0.047, $P < .001$, fig. 2; appendix, available online).

Discussion

To our knowledge, our study provides evidence for the longest period of stability in space and composition documented for a Neotropical animal community. The strikingly similar position of territory and roosting sites in 1994 and 2011 (fig. 1) was corroborated by statistical tests of these patterns against null models (table 1). This stability almost certainly occurred across multiple generations of flocking species, which generally are thought to live 2–4
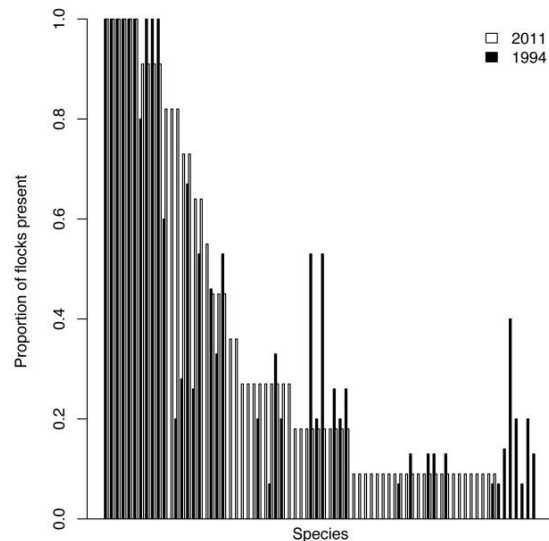

Figure 2: Bar plot showing the similarity in the abundance of species that compose the flocks in 1994 and 2011.

years (Brawn et al. 1985; Blake and Loiselle 2008). At the Nouragues field site, many of the birds that participated in the original flocks in 1994 were banded (Jullien and Thiollay 1998). However, in our sampling from 2011, none of the birds were banded, suggesting that all of the almost identical home ranges and roosting sites were being used by different individuals. Thus, our study provides evidence of community stability through more than one generation, a limitation of most studies addressing these types of questions (Connell and Sousa 1983).

Theoretical models suggest that long-term environmental stability is required for the selection of traits that lead to evolutionarily stable strategies (Maynard Smith and Price 1973). However, environmental stability may be altered in the forest by large- and local-scale disturbances that could potentially perturb animal communities in different ways. In humid lowland Amazonian rain forests, natural disturbances manifest themselves primarily as tree-fall gaps within the forest matrix (Brokaw 1985; Denslow 1987). However, while gaps occur throughout the forest across a number of bird home ranges, they are generated in random fashion and on smaller scales than the home ranges of flocks. The average home range size of flocks at the Nouragues station is 10.3 ha, and tree-fall gaps in Amazonian forests have been reported to vary between 0.001 and 0.4 ha (Uhl et al. 1988). Flock home ranges, therefore, may be large enough that they need not change in response to the most common form of disturbance. Because they are larger than tree-fall disturbances generated by gap-phase dynamics, home ranges would naturally provide a constant environment and, thus, the conditions necessary for stability in territory position and species composition of the multispecies flocks.

At the same time, stability might have strong implications for the evolution of characteristics of birds in mixed-species flocks, such as "sentinel" alarm systems and kleptoparasitism. The flycatcher foraging strategy of sentinels potentially allows them to be more vigilant and emit alarm calls in case of predation threat (Munn 1985; Sridhar et al. 2009; Martínez and Zenil 2012). In return, "sentinels" might take advantage of the alarm systems by sounding false calls to steal prey items from other flock members (i.e., kleptoparasitism; Munn 1986; A. E. Martínez and J. P. Gomez, personal observation). The evolution of these complex behaviors and strong interdependence between sentinels and other members of the flock can happen only in a scenario of long-term stability, in which the signal of selection for these behaviors is strong and constant during long periods of time (Futuyma and Moreno 1988).

The stability in composition of mixed flocks is consistent with results of several plant studies that report compositional stability in large plots throughout the Neotropics (see Condit 1995 for review). Evidence suggests that the Nouragues station shares this plant community stability with other large plots in the Neotropics (Sarthou et al. 2010). Thus, it is possible that flock stability evidenced here results from long-term stability in plant communities, reflecting resource stability throughout the forest. In fact, the maintenance of overdispersed roosting sites through time might suggest that resources are not only evenly distributed but stable through a period of time of almost 20 years.

Finally, this study hints that at least some tropical animal communities might have high stability through long periods of time. Nevertheless, questions about the mechanisms that drive this stability remain to be answered. Documenting the degree to which various systems might be stable despite environmental variation may provide insight into how communities may respond to human-induced environmental change.

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Myrmotherula axillaris. Photo credit: Judit Ungvari-Martin.