NEGATIVE TRENDS IN BIRD ABUNDANCE ARE STRONGLY CORRELATED TO RAINFALL DECLINE IN A CENTRAL AMERICAN TROPICAL FOREST

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ABSTRACT.— Climate change is considered one of the main factors threatening biodiversity. Weather is of major importance for bird population dynamics, but the implications of climate change have only recently begun to be addressed, especially for tropical birds. For Northern Central America, climate change scenarios for 2050 predict a reduction in precipitation across the region, with decreases ranging from 4–19% of current rainfall. In this work, we addressed the relationship between temporal changes in precipitation amount and bird community dynamics in eastern tropical Guatemala, for a time period of 18 years (1993–2010). Data consisted of yearly captures and recaptures in four sites, located at elevations between 100–750 masl, and analyses were carried out for total captures and for six foraging guilds. Statistical analyses consisted of Poisson regressions, where estimated abundance (taking into account recapture probability) was modelled as a function of wet-season, dry-season, and annual rainfall, and temporal trend. We detected strong declines in total abundance and in the abundance of nectarivores, omnivores, frugivores, and, to a lesser degree, foliage insectivores. These declines were strongly associated with declines in rainfall amount, generally during the rainy season. A more comprehensive understanding of the effects of climate change on animal abundance in tropical ecosystems is strongly needed to propose conservation and management actions in these biodiverse ecosystems.

KEY WORDS: *capture probability, climate change, community dynamics, feeding guilds, Guatemala, Poisson regression, tropical birds.*

RESUMEN. LAS TENDENCIAS NEGATIVAS EN LA ABUNDANCIA DE AVES ESTÁN FUERTEMENTE CORRELACIONADAS CON LA DISMINUCIÓN DE LAS PRECIPITACIONES EN UN BOSQUE TROPICAL CENTROAMERICANO.— El cambio climático es considerado uno de los principales factores que amenazan a la biodiversidad. El clima es de gran importancia para la dinámica poblacional de las aves, pero las consecuencias del cambio climático no han sido abordadas sino hasta recientemente, especialmente en aves tropicales. Para el norte de América Central, los escenarios de cambio climático para 2050 predicen una reducción en las precipitaciones, con disminuciones de 4–19% de las precipitaciones actuales. En este trabajo se evalúa la relación entre los cambios temporales en la cantidad de precipitaciones y la dinámica de la comunidad de aves en el este tropical de Guatemala para un período de 18 años (1993–2010). Los datos consistieron en capturas y recapturas anuales en cuatro sitios ubicados a altitudes entre 100–750 msnm, con análisis para las capturas totales y para seis gremios de alimentación. Los análisis estadísticos consistieron en regresiones de Poisson en las cuales la abundancia estimada (tomando en cuenta la probabilidad de recaptura) fue modelada en función de las precipitaciones (de la época lluviosa, de la época seca y la anual) y la tendencia temporal. Se detectaron fuertes declinaciones en la abundancia total y en la abundancia de las aves nectarívoras, omnívoras, frugívoras y, en menor grado, insectívoras de follaje. Estas declinaciones estuvieron fuertemente asociadas a la disminución en la cantidad de precipitaciones, principalmente de la época lluviosa. Se necesita un conocimiento más profundo de los efectos del cambio climático sobre la abundancia de animales en los ecosistemas tropicales, con el fin de proponer acciones de conservación y manejo en estos sistemas altamente diversos.

PALABRAS CLAVE: *aves tropicales, cambio climático, dinámica de comunidades, gremios de alimentación, Guatemala, probabilidad de captura, regresión de Poisson.*

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Climate change is considered one of the main factors threatening biodiversity (Root and Schneider 2002, Walther et al. 2002, Chen et al. 2004, Thomas et al. 2004) because species strongly depend on interannual fluctuations in precipitation, temperature, and extreme climatic events over ecological and evolutionary time scales (Chen et al. 2004, Parmesan 2006, Beever et al. 2011). Weather is of major importance for the population dynamics of bird populations, and there has thus been a recent, rising need to address the implications of climate change on these populations (Crick 2004, Wolfe and Ralph 2009, Sekercioglu et al. 2012, Faaborg et al. 2013, Foden et al. 2013, Blake and Loiselle 2015). Under the Millenium Ecosystem Assessment scenarios, Jetz et al. (2007) predicted that even under environmentally benign scenarios, at least 400 bird species are projected to suffer >50% range reductions by the year 2050. Also, multiple models based on the Intergovernmental Panel on Climate Change (IPCC) A2 Emissions Scenario predict tropical drying trends, particularly in the Caribbean and Central America region and equatorial South America (Neelin et al. 2006).

Climate-driven changes in abundance, phenology and changes in species range, among others, have been shown by recent studies, mainly for northern temperate latitudes, in general associated with rising temperatures (Root and Schneider 2002, Walther et al. 2002, Gordo and Sanz 2006, Parmesan 2006). However, due to the scarcity of long-term data sets in the tropics, biotic changes are relatively undocumented in the region (Harris et al. 2011), with some notable exceptions: in particular, a long-term study involving captures and observations in undisturbed lowland tropical forest, found that overall captures and observations declined by approximately 40 and 50%, respectively, from 2008 to 2014 (Blake and Loiselle 2015). Others have studied the effects of climate, mainly El Niño–Southern Oscillation (ENSO) effects, on tropical bird communities (Wolfe and Ralph 2009, Styrsky and Brawn 2011, Wolfe et al. 2015), but these studies have focused on one or a few bird species. Consequently, it is crucial to increase our basic knowledge in order to evaluate to what extent climate-driven changes have also occurred in the tropics, because: (1) climatic effects between biomes may be extremely different, and (2) we need to understand and eventually predict the impact of future climatic changes on all biotic communities and ecosystems, and particularly on the diverse tropical ecosystems.

Studies in northern latitudes have shown that insectivorous bird abundance and reproductive success are affected by insect food abundance, and both temperature and precipitation indirectly affect insect abundance and plant growth rates via leaf quality or budding (Sillett et al. 2000, Nott et al. 2002, Jones et al. 2003, Visser et al. 2004), suggesting that bird population dynamics are in turn indirectly driven by regional climate patterns, through their effects on plant and insect biomass. In the tropics, rainfall is the key factor determining the overall primary productivity and its temporal variability (Schloss et al. 1999), and it is positively associated with increases in plant and insect biomass (Schuur 2003, Cao et al. 2004, Cleland et al. 2007, Saatchi et al. 2007, for plants; Denlinger 1980, Lowman 1982, Frith and Frith 1985, Bonebrake et al. 2010, for insects). Likewise, the availability of food resources in Neotropical forests has been positively correlated with bird abundance for several feeding guilds, such as insectivores, frugivores, and nectarivores (Karr and Brawn 1990, Loiselle and Blake 1991, Poulin et al. 1992). Also, plant phenological cycles, in particular leaf flushing, fruiting and flowering periods, are associated (to different degrees) to the onset or end of the rainy season in the tropics (Frankie et al. 1974, Wolda 1978, van Schaik et al. 1993, Cattanio et al. 2004), and other studies from tropical sites have found that insect abundance was positively related to the peak of plant phenological activities (Wolda 1978, Lowman 1982). Because of these relationships between rainfall and plant and insect productivity, a positive association between the amount of rainfall during the rainy season and bird abundance could be expected (Powell et al. 2015). Alternatively, dry seasons are potential periods of scarce resources, resulting in "ecological bottlenecks" that limit species abundances and biotic interactions and processes, and may be important in structuring bird communities in variable ecosystems (Williams and Middleton 2008). Finally, rainfall in both seasons might have independent effects on tropical bird populations, because different demographic components that determine abundance might depend on either dry-season or wet-season rainfall. Thus, abundance might also be associated with total annual rainfall.

In this work, we addressed the relationship between temporal changes in precipitation and bird community dynamics in eastern tropical Guatemala, using mist-net data from the Bird Monitoring Program of the Caribbean Region of Guatemala, established in 1992 (Cerezo et al. 2012). We evaluated changes in total bird abundance and in the abundance of six foraging guilds, in relation to rainfall amount in the 1993–2010 period (18 years). Specific objectives were: (1) to evaluate if abundance was associated (positively or negatively) to the amount of rainfall in the previous year, either to wet-season rainfall, dry-season rainfall, a combination of these two, or to annual rainfall, and (2) to evaluate the existence of an increasing or decreasing trend in total abundance and of each feeding guild, that was independent of any potential relationship to the amount of rainfall.

METHODS

Study site, bird sampling, and rainfall data

The study was carried out in Cerro San Gil Watershed Protection Reserve, located in eastern tropical Guatemala (Fig. 1). The reserve is divided into three zones: a nuclear zone (full preservation zone, where only biological research and low-impact tourism activities are allowed), a buffer zone (its main objective is to mitigate possible impacts of surrounding human populations to the nuclear zone; only environmentally sustainable activities are allowed, e.g., reforestation, small-scale farming in established communities), and a multiple-use zone (extant economic activities are allowed, e.g., farming, cattle ranching, commercial plantations, as well as subsistence hunting and selective wood extraction). Large-scale deforestation is not allowed in either the multiple-use or buffer zones. The dominant vegetation type is tropical wet forest, with mean (± SD) annual temperature and precipitation of 26.6 ± 0.4 ºC and 3284.9 ± 596.5 mm, respectively, for the study period (INSIVUMEH 2012).

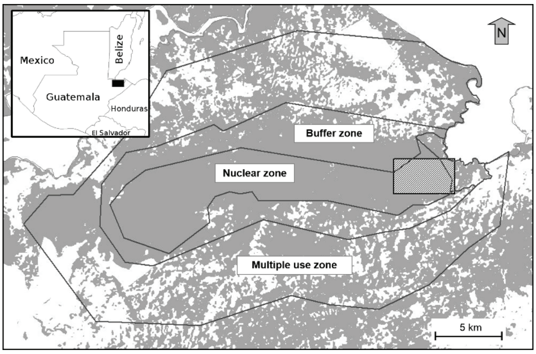

Figure 1. Study site (barred rectangle) located within Cerro San Gil Watershed Protection Reserve, eastern Guatemala. Grey shaded area is tropical wet forest.

Bird sampling was carried out in four sites, located approximately at 100, 200, 250 and 750 masl. All sites were located within the nuclear zone, in relatively undisturbed forest (i.e., with minimum human disturbance), and there have thus been no major habitat changes either in the immediate area or in the broader landscape. The 100 masl site was approximately 1 km away from sites at 200 and 250 masl, these two were very close together, approximately 200 m from each other, and the 750 masl site was approximately 3 km away from the 200 and 250 masl sites. Sampling consists of yearly constant-effort mist netting in each site throughout the duration of the study, between early February and mid-March. In each site, 16 mist nets (36 mm mesh size) were placed at the same net location every year, at an average distance of approximately 50 m from each other. Mist nets were only occasionally shifted a few meters as a result of tree falls. The understory bird community was sampled during three consecutive days, usually between 06:00–16:00 h, for an average (± SD) of 430.0 ± 60.6 net hours per site each year. During sampling periods, nets were occasionally closed because of heavy rain or human disturbances.

All captured birds were identified to the species level, and were banded with a serially-numbered aluminium ring, or note was taken of the ring number if it was a recaptured individual (i.e., a bird banded in a previous year to the current sampling period). For all individuals, we determined sex and age (if possible) with criteria described in Wolfe et al. (2009), measured wing length and weight, and took notes on moult and plumage condition. The Bander's Code of Ethics (North American Bird Banding Council 2001) was strictly followed during sampling. For the present analysis, we used data derived from the number of captured individuals per species. Taxonomy of birds is according to the North American Classification Committee checklist (American Ornithological Society 2016).

Precipitation data was taken from the nearest meteorological station of the Guatemalan Institute of Seismology, Vulcanology, Meteorology and Hydrology (INSIVUMEH 2012), located in the city of Puerto Barrios, approximately 3 km from the nearest of the four study sites. Other studies have evaluated the ENSO effects on different parameters of tropical bird communities and populations (Wolfe and Ralph 2009, Blake and Loiselle 2015, Wolfe et al. 2015). In the tropics, ENSO typically alters precipitation patterns (Holmgren et al. 2001, Mahli and Wright 2004), so we expected that our rainfall data would reflect abnormal rainfall conditions caused by ENSO, as well as the effects of such unusual conditions on bird abundance.

Statistical analysis

For statistical analyses, we only included species that had more than five captured individuals in at least three years. We considered that there would be a potential for bias in the results if these individuals were included in the analysis. We also excluded Nearctic migrants, because their population dynamics can be altered by other factors outside the wintering grounds. For species with captures in at least 9 of 18 years and more than 30 captures, we calculated a Pearson correlation coefficient as a descriptive measure of association between "year" and observed abundance (following Blake and Loiselle 2015), a negative association indicating a temporal decline in captures.

Because observed captures (i.e., captures that do not take into account capture or recapture probability) may provide biased counts of bird abundance (Pollock et al. 2002, Williams et al. 2002), we estimated yearly bird abundance using the estimator developed by Pollock and Otto (1983), using each one of the three sampling days per site as repeated sampling periods, which are necessary for the estimation process. Pollock and Otto's (1983) abundance estimator assumes heterogeneity among individuals in capture probability, and different capture probabilities for first and subsequent captures during the multiple sampling periods. Figure 2 provides graphs of capture and recapture rates, showing that the observed pattern of captures and recaptures conform to the assumptions of this model for estimating abundance (i.e., different capture and recapture probabilities). Estimated yearly abundance data were then expressed as capture rates per 100 net hours (net hours were transformed to vary between 0 and 1).

To analyse the relationship between bird abundance, rainfall variables and temporal trends in populations, we used Poisson regression, a special type of generalized linear model appropriate for the discrete, highly-skewed distribution of dependent variables that are counts (Vincent and Haworth 1983). Abundance was modelled as a function of: (1) total rainfall for the seven-month period prior to captures (July–January) comprising the rainy season and accounting on average for approximately 66% of total yearly rainfall, (2) total rainfall for the five-month period prior to cap-

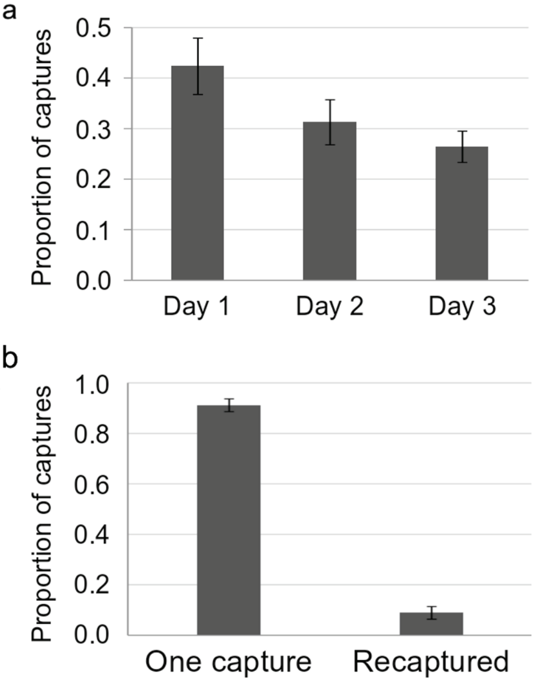

Figure 2. Decreasing proportion of captures with sampling day (a), and proportion of birds captured in only one day during each sample period ("One capture"), or recaptured in the second or third sampling day ("Recaptured") (b) in Cerro San Gil Watershed Protection Reserve, eastern Guatemala.

Table 1. Description of predictive variables in fitted models of bird abundance in Cerro San Gil Watershed Protection Reserve, eastern Guatemala.

Model	Predictive variables
Wet + Dry + Trend	Wet- and dry-season rainfall, and temporal trend
Wet + Trend	Wet-season rainfall and temporal trend
Dry + Trend	Dry-season rainfall and temporal trend
Annual + Trend	Annual rainfall and temporal trend
Trend	Temporal trend

tures (February–June) comprising the dry season and accounting on average for approximately 31% of total annual rainfall, (3) annual rainfall (the sum of wet- and dry-season rainfall), and (4) year or temporal trend. Poisson regression analyses were carried out for total abundance and for the abundance of six foraging guilds: frugivores, nectarivores, sallying insectivores, bark insectivores, foliage (gleaning/leaf-tossing) insectivores, and omnivores. Foraging guild classification was made according to Stiles and Skutch (1989) and Terborgh et al. (1990).

Models were compared using an information-theoretic framework. For total abundance and abundance of each foraging guild, we fitted five different models, with different combinations of wet-season, dry-season and annual rainfall, and temporal trend (Table 1). The second-order Akaike Information Criterion (*AICc*, recommended when $n/K < 40$, where n is sample size and K is the number of estimated parameters) and Akaike weights (w_i) were then used to choose the best-fitting models from the set of candidate models (Burnham and Anderson, 1998, 2001, Anderson et al. 2000). When differences between *AIC* values are small (< 2 *AIC* units), Akaike weights can be used as indicators of the strength of evidence for each model. The w_i is interpreted as the approximate probability that model i is the best model in the set of models being considered (Anderson et al. 2000). To compare the relative effects of the

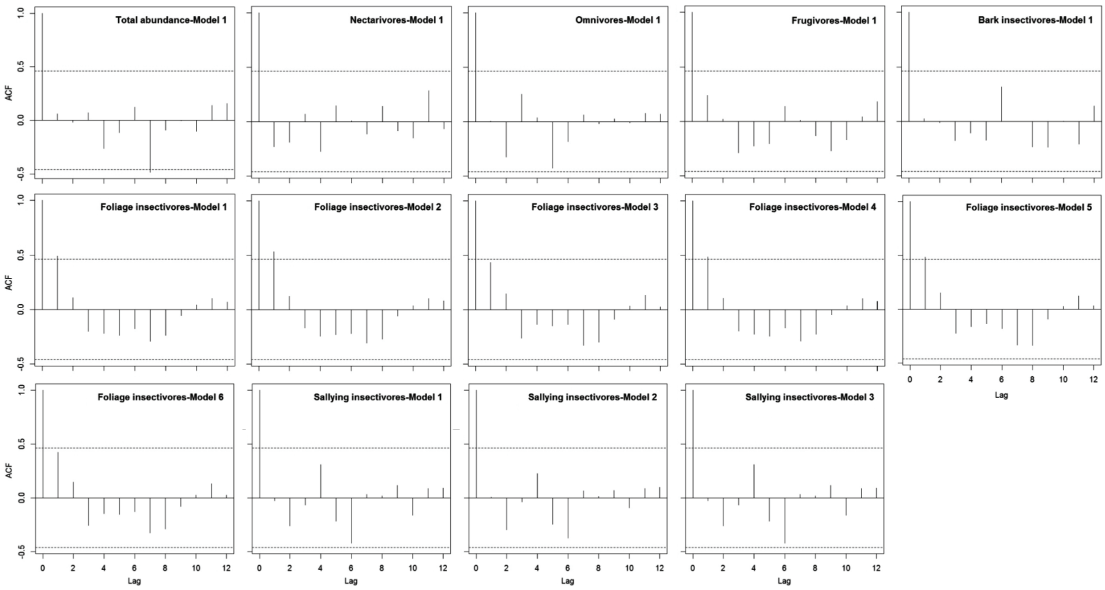

Figure 3. Plots of temporal autocorrelation function for residuals corresponding to fitted models of bird abundance in Cerro San Gil Watershed Protection Reserve, eastern Guatemala. Plots were produced for models in confidence sets, according to the Akaike weight.

three rainfall variables and linear trend, we used multi-model inference, or model averaging (Burnham and Anderson 1998). For each species group we obtained mean model coefficients for each effect, weighted by w_i.

Because rainfall variables were positively correlated, and rainfall variables and temporal trend were negatively correlated (to differing degrees; see *Results*), we used sequential regression (Graham 2003, Dormann et al. 2013) to avoid problems associated with multicollinearity in the estimation of regression parameters. Sequential regression consists in linearly regressing pairs of explanatory variables against each other, and then extracting the residuals for the regressed variable, thus producing a new explanatory variable that expresses variation that is completely independent of the other predictors (Dormann et al. 2013). In our study, we regressed "year" against "rainfall amount" to produce measures of temporal trend that were independent of rainfall amount. All variables were transformed to vary between 0 and 1, so that estimated model coefficients could be compared directly.

Finally, because we modelled a time series, we were possibly violating the statistical assumption of independence between model residuals, which can inflate type-I error rates (Zuur et al. 2009). For each model, we produced a plot of the temporal autocorrelation function for residuals, using the autocorrelation function ("acf") in R software (R Core Team 2014). The plot consists of a graph of the autocorrelation function of residuals for different time lags (in this case, of one year), and the horizontal dashed lines in graphs are lower and upper 95% confidence limits (Fig. 3). Values that fall within these limits correspond to the statistical hypothesis of no temporal autocorrelation in residuals (Zuur et al. 2009). Models did not show or showed very little autocorrelation (Fig. 3), and we proceeded with model formulations without autocorrelation structures.

RESULTS

In our study site, rainfall significantly decreased during the study period (Fig. 4). Estimated declines in rainfall were of -38.8 mm/year (-0.11 mm/day per year) for wet-season rainfall, -21.1 mm/year (-0.06 mm/day per year) for dry-season rainfall, and -59.9 mm/year (-0.16 mm/day per year) for annual rainfall. The declines were more evident for wet-season rainfall (r = 0.55; Fig. 2). The declines are much higher than those reported in other studies for tropical regions. Malhi and Wright (2004) reported declines in the tropics worldwide during the 1960–1998 period, with an estimated mean decrease of 22 mm/year (0.06 mm/day per year). Declines in rainfall have also been reported for more recent periods for Central America (-0.02 mm/day per year; IPCC 2014). In particular, Neelin et al. (2006) and Rauscher et al. (2008) have reported a significant drying trend in the Central America-Caribbean region. Neelin et al. (2006) report a 5–30% decline in rainfall from the mean values in 1979, and also report expected declines derived from climate models for the region of -0.005 to -0.01 mm/day per year in the next 100 years.

In total, 53 species were included in analyses (Table 2). Six species were classified as frugivores, 9 as nectarivores, 12 as sallying

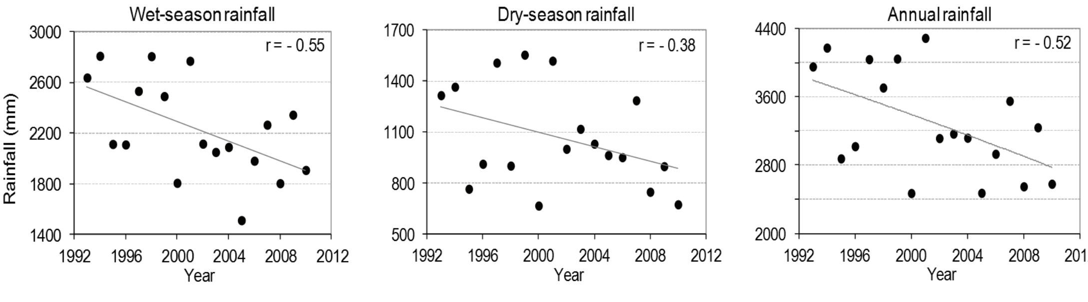

Figure 4. Temporal trends in wet-season, dry-season, and annual rainfall during the study period in Cerro San Gil Watershed Protection Reserve, eastern Guatemala. Pearson correlation coefficients between year and rainfall are shown.

Table 2. Bird species recorded in Cerro San Gil Watershed Protection Reserve (eastern Guatemala) included in the analysis. Foraging guild, total captures per year, Pearson correlation coefficient (*r*) as a descriptive measure of temporal change in captures, and number of individuals captured (with percentage between brackets) in each of the four sites (100, 200, 250 and 750 masl) are shown.

		Year (1993–2010)																			masl			
	Guild[a]	93	94	95	96	97	98	99	00	01	02	03	04	05	06	07	08	09	10	*r*	100	200	250	750
Leptotila cassinii	F	5		3	4	2	4	3	4	3	1	4	2	4	5	7	3	3	2	0.16	16 (27)	22 (37)	13 (22)	8 (14)
Geotrygon montana	F	9	2	9	5	5	12	4	16	2	5	13	9	10	12	6	3	10	2	0.00	40 (30)	18 (13)	69 (51)	7 (5)
Florisuga mellivora	N	3	2			1	1	6				1	1			1	1		1	-	8 (44)	6 (33)	2 (11)	2 (11)
Threnetes ruckeri	N	6	5	5	3	1	1	1	10	6	4	1		3	2	1				-0.54	3 (6)	19 (39)	25 (51)	2 (4)
Phaethornis longirostris	N	86	55	59	94	31	49	56	66	84	54	41	40	47	62	41	14	22	25	-0.66	312 (34)	199 (21)	293 (32)	122 (13)
Phaethornis striigularis	N	4	2	1	3	0	1	1	2	2	4	0	1	1	2	2	1	1	1	-	5 (17)	9 (31)	12 (41)	3 (10)
Campylopterus hemileucurus	N	104	39	9	76	10	57	30	17	45	14	11	6	9	14	13	1		11	-0.67	134 (29)	166 (36)	44 (9)	122 (26)
Eupherusa eximia	N	2	3	2	2	6	1	3	4	4	2	1	2	2	2	3	1	2	1	-0.34	-	1 (2)	1 (2)	41 (95)
Thalurania colombica	N	26	20	17	24	17	16	31	12	29	4	14	15	7	13	3	1	11	4	-0.71	69 (26)	61 (23)	45 (17)	89 (34)
Amazilia candida	N	8	10	9	11	2	9	11	3	7	3	6	3	3	1	2	1		3	-0.77	25 (27)	36 (39)	24 (26)	7 (8)
Amazilia tzacatl	N	1	1			1	2	4		2	2	2	1	3	5	1	1	1	1	-	16 (57)	9 (32)	3 (11)	-
Hylomanes momotula	SI	3							1	1			2	1		1		1		-	2 (20)	-	-	8 (80)
Momotus momota	SI	1		2	1	1	2	2	2	2	2	2	2	1	1			2	1	-	8 (33)	5 (21)	8 (33)	3 (13)
Malacoptila panamensis	SI	3			2		3			7	2	2	2		1		1	2	2	-	14 (52)	7 (26)	6 (22)	-
Picoides fumigatus	BI					2			5					1						-	-	2 (25)	4 (50)	2 (25)
Dysithamnus mentalis	FI	3	1	5	3	4	4	1	3	3	5	4	5	2	2	2	3	3	5	0.08	1 (2)	-	-	57 (98)
Myrmotherula schisticolor	FI	11	7	11	4	7	3	4	5	4	6	5	8	3	4	4	8	4	3	-0.49	1 (1)	4 (4)	10 (10)	86 (85)
Grallaria guatimalensis	FI			1	2			2	1		1									-	1 (14)	5 (71)	-	1 (14)
Formicarius analis	FI	4	4	6	6	7	6	2	5	3	7	2	4	4	4	2	1	2		-0.65	16 (23)	12 (17)	14 (20)	27 (39)
Sclerurus guatemalensis	FI	11	7	13	5	3	7	10	7	9	13	12	9	11	14	8	11	11	7	0.26	18 (11)	17 (10)	28 (17)	105 (63)
Sittasomus griseicapillus	BI							1	1	2		2			1			1	2	-	3 (30)	4 (40)	3 (30)	-
Dendrocincla anabatina	BI	30	23	13	11	32	23	21	14	28	20	12	38	16	18	12	11	14	8	-0.41	113 (33)	73 (21)	97 (28)	61 (18)
Dendrocincla homochroa	SI	12	11	3	1	8		1	2	11	1	5	2	2	1	5	3	6	7	-0.23	10 (12)	16 (20)	29 (36)	26 (32)
Glyphorynchus spirurus	BI	43	32	34	19	27	47	31	35	22	22	34	28	20	21	27	18	18	19	-0.63	134 (27)	67 (14)	234 (47)	61 (12)
Dendrocolaptes sanctithomae	BI	2	5		1	1	2		2	4	2		2	3	3	2	2	1	1	-0.05	11 (33)	7 (21)	15 (45)	-
Xiphorhynchus flavigaster	BI	1	3	5	4		9	6	9	8	3	6	1	2	6	2	5	2	4	-0.04	29 (38)	18 (24)	29 (38)	-
Xiphorhynchus erythropygius	BI			2						1				1		2	1			-	-	-	-	7 (100)

[a] F: frugivore, N: nectarivore, SI: sallying insectivore, BI: bark insectivore, FI: foliage insectivore, O: omnivore.

Table 2. Continuation.

		Year (1993–2010)																		masl			
	Guild[a]	93	94	95	96	97	98	99	00	01	02	03	04	05	06	07	08	09	10	*r*	100	200	250	750
Xenops minutus	FI	4	2	7	7	2	2	4	6	4	4	2	2	1	3	2	2	2	2	-0.52	7 (12)	17 (29)	9 (16)	25 (43)
Automolus ochrolaemus	FI	10	2	4	5	1	6	3	10	4	6	4	6	4	8	4	6	2	5	-0.05	-	5 (6)	2 (2)	83 (92)
Mionectes oleagineus	O	100	101	128	104	50	115	63	70	40	41	48	66	37	31	46	64	23	36	-0.78	416 (36)	397 (34)	222 (19)	128 (11)
Leptopogon amaurocephalus	SI	8	6	2		6	8	2	8	8	7	1	4	4	8	1	6	7	7	0.08	28 (30)	38 (41)	24 (26)	3 (3)
Oncostoma cinereigulare	SI	9	5	8	2		8	9	8	4	5	3	5	3	5	3	3	3	1	-0.49	9 (11)	52 (62)	13 (15)	10 (12)
Platyrinchus cancrominus	SI	13	10	17	14	14	14	13	14	11	10	7	7	11	11	5	9	13	10	-0.56	44 (22)	47 (23)	46 (23)	66 (33)
Onychorhynchus coronatus	SI	3	5	3		3	4	2	1	2		1	4	1	1	2	2		1	-0.49	20 (57)	9 (26)	4 (11)	2 (6)
Terenotriccus erythrurus	SI	9	6	5	6	7	3	4	5	6	7	3	8	4	8	5	6	5	2	-0.29	47 (47)	22 (22)	17 (17)	13 (13)
Myiobius sulphureipygius	SI	9	5	9	8	9	16	17	5	18	8	9	10	4	7	4	5	4	3	-0.42	44 (29)	14 (9)	35 (23)	57 (38)
Attila spadiceus	SI	5	3	3	7	13	7	7	7	10	14	4	5	8	3	2	5	5	2	-0.24	26 (24)	25 (23)	39 (35)	20 (18)
Ceratopipra mentalis	F	100	73	81	49	57	106	60	70	51	35	38	49	12	28	23	23	14	21	-0.85	258 (29)	335 (38)	203 (23)	94 (11)
Manacus candei	F	1		2	4	6	7	5	10	5	3	2	2	2	2	3	1			-0.31	5 (9)	34 (62)	14 (25)	2 (4)
Tunchiornis ochraceiceps	FI	29	16	17	24	18	35	27	21	23	15	11	18	10	11	14	13	4	16	-0.64	85 (26)	61 (19)	95 (30)	81 (25)
Microcerculus philomela	FI	1		2		1		1	2	1	2	1	1	1	2		1	1		-	-	2 (12)	1 (6)	14 (82)
Pheugopedius maculipectus	FI	2			1	2	4		3	4	5	2					2		1	-	-	11 (42)	11 (42)	4 (15)
Henicorhina leucosticta	FI	27	34	28	26	23	19	29	31	28	29	28	23	20	21	16	7	20	12	-0.71	93 (22)	64 (15)	92 (22)	172 (41)
Ramphocaenus melanurus	FI	2		2	5	2	4	1	4	4	2	1	1	1	2	2		1		-0.41	5 (15)	14 (41)	5 (15)	10 (29)
Myadestes unicolor	F	1	2	1	11	1	7			4		4			4				1	-0.33	12 (33)	7 (19)	6 (17)	11 (31)
Turdus assimilis	O	6	1	3	18		4	5	1	7		2	1	11	3	9	1	1	7	-0.07	16 (20)	8 (10)	25 (31)	31 (39)
Basileuterus culicivorus	FI		1	3	3	2	1	2	2	6	2	3	1	1		4		2	6	0.20	-	-	-	39 (100)
Lanio aurantius	SI	1	1	4	1		1			1	1	1	3					1		-	2 (13)	3 (20)	4 (27)	6 (40)
Arremon aurantiirostris	O	4		6	1					2	1	2	3	8	3		1	2		-0.03	12 (36)	10 (30)	11 (33)	-
Habia rubica	FI	4	4	5	5	9	12	2	7	2	6	9	6	4	4	2	4	3	6	-0.20	6 (6)	6 (6)	25 (27)	57 (61)
Habia fuscicauda	FI	4	5	6	3	1	2	8	11	13	8	9	10	7	2	8	1	4	1	-0.05	28 (27)	26 (25)	48 (47)	1 (1)
Cyanoloxia cyanoides	O	4	6	3	4	7	3	8	1	1	3		4	2		1	4	2	2	-0.50	20 (36)	26 (47)	9 (16)	-
Euphonia gouldi	F	60	18	26	49	31	50	27	40	34	19	16	17	24	27	14	6	25	19	-0.62	137 (27)	84 (17)	180 (36)	101 (20)

[a] F: frugivore, N: nectarivore, SI: sallying insectivore, BI: bark insectivore, FI: foliage insectivore, O: omnivore.

insectivores, 7 as bark insectivores, 15 as foliage insectivores, and 4 as omnivores. We captured a total of 8435 individuals for these 53 species. The foraging guild with the higher number of captures was the nectarivore guild (1915), followed by frugivores (1676), foliage insectivores (1607), omnivores (1331), bark insectivores (975), and sallying insectivores (931). Several guilds where dominated by one or a few species, omnivores being the most extreme case: 87% of captures were for a single species, the Ochre-bellied Flycatcher (*Mionectes oleagineus*). Frugivores were dominated by the Red-capped Manakin (*Ceratopipra mentalis*), with 53% of captures, and nectarivores were dominated by the Long-billed Hermit (*Phaethornis longirostris*), with 49% of captures. Bark insectivores were mostly represented by two species: Tawny-winged Woodcreeper (*Dendrocincla anabatina*) with 35% of captures, and the Wedge-billed Woodcreeper (*Glyphorynchus spirurus*), with

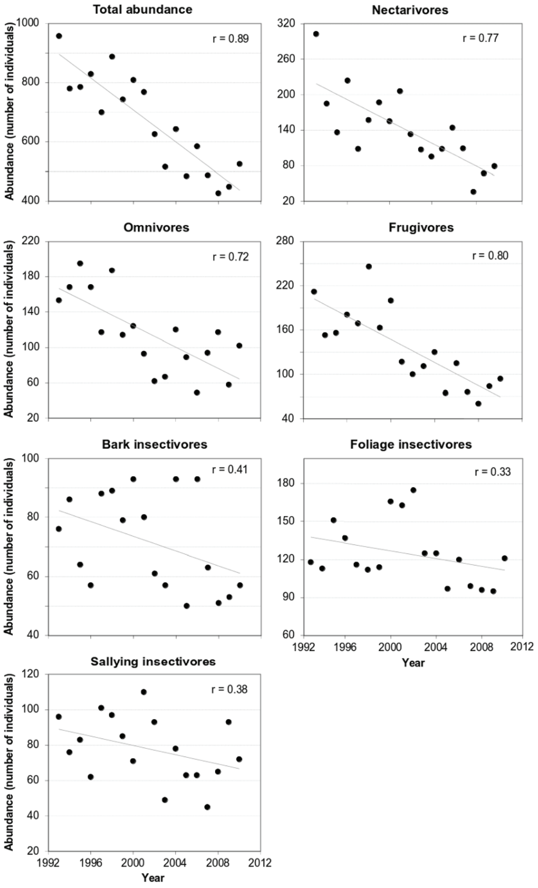

Figure 5. Temporal trends in total bird abundance and abundances for each foraging guild during the study period in Cerro San Gil Watershed Protection Reserve, eastern Guatemala. Pearson correlation coefficients between year and abundance are shown.

Table 3. Statistics for fitted models of bird abundance in Cerro San Gil Watershed Protection Reserve, eastern Guatemala. Predictive variables included in models are described in table 1.

	AICc	w_i
Total abundance		
Wet + Trend	215.3	0.60
Wet + Dry + Trend	216.1	0.40
Annual + Trend	295.9	0.00
Dry + Trend	379.7	0.00
Trend	379.8	0.00
Nectarivores		
Wet + Dry + Trend	236.4	0.99
Dry + Trend	246.4	0.01
Annual + Trend	277.7	0.00
Wet + Trend	336.3	0.00
Trend	346.2	0.00
Omnivores		
Wet + Dry + Trend	101.8	1.00
Wet + Trend	116.4	0.00
Dry + Trend	121.9	0.00
Trend	138.6	0.00
Annual + Trend	140.2	0.00
Frugivores		
Wet + Dry + Trend	141.4	0.99
Wet + Trend	150.3	0.01
Annual + Trend	180.1	0.00
Dry + Trend	215.3	0.00
Trend	226.3	0.00
Bark insectivores		
Wet + Trend	51.2	0.72
Wet + Dry + Trend	53.4	0.25
Annual + Trend	57.7	0.03
Trend	65.9	0.00
Dry + Trend	68.0	0.00
Foliage insectivores		
Annual + Trend	70.9	0.53
Trend	72.6	0.23
Dry + Trend	73.9	0.12
Wet + Trend	74.6	0.08
Wet + Dry + Trend	76.0	0.04
Sallying insectivores		
Wet + Trend	58.9	0.75
Wet + Dry + Trend	61.0	0.25
Trend	77.7	0.00
Annual + Trend	78.6	0.00
Dry + Trend	79.8	0.00

51% of captures. The other two guilds were more even in their distribution of individuals per species, although two or three species were significantly more abundant than other members of the guild.

When only considering the relationship between abundance and year (without considering rainfall effects), total abundance and the abundance of nectarivores, frugivores and omnivores showed significant, strong declines (Fig. 5). Fitted models of bird abundance with the highest support were those with wet-season rainfall, dry-season rainfall and temporal trend (average $w_i = 0.56$; Table 3), followed by the model containing wet-season rainfall and temporal trend (average $w_i = 0.31$). All other model types had average weights < 0.1 (Table 3). Upon consideration of weighted model averages, wet-season rainfall had the greatest positive effect on abundance, especially for total abundance and abundance of frugivores, followed by bark insectivores and sallying insectivores (Fig. 6). In other words, total abundance and abundance for these guilds increased with increasing wet-season rainfall in the previous year. Foliage insectivore abundance was positively related to annual rainfall, but this effect was weak (the 95% confidence interval includes 0; Fig. 6). Nectarivore abundance was mainly affected by dry-season rainfall. Also, dry-season effects where negatively related to omnivore and frugivore abundance (greater abundance when the previous dry season had less rain), but these effects where weak. Finally, once rainfall effects had been taken into account, total abundance and the abundance of several guilds still showed decreases in abundance that where independent of rainfall. This was the case for total abundance, nectarivores, omnivores, frugivores, and to a lesser degree, foliage insectivores (Fig. 6).

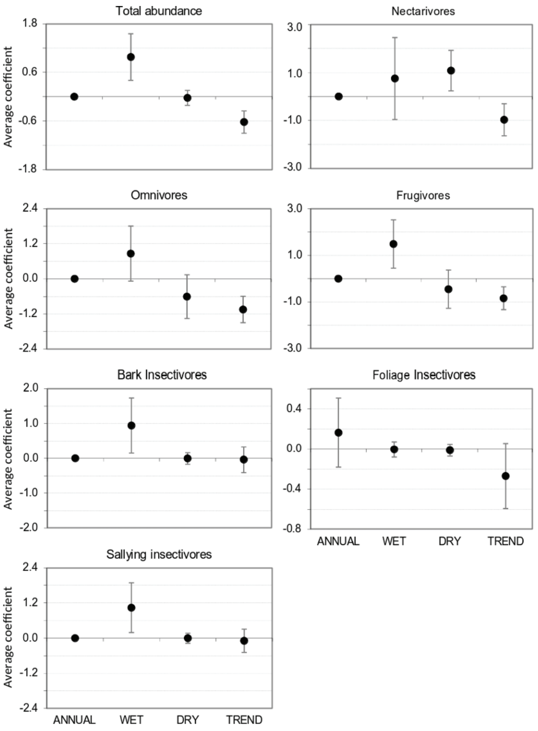

Figure 6. Average coefficients (weighted by Akaike weights) of fitted models of bird abundance in Cerro San Gil Watershed Protection Reserve, eastern Guatemala. Predictive variables included in models are described in table 1. Error bars show 95% confidence intervals.

DISCUSSION

In general, our results provide strong evidence of large, community-wide declines in bird abundance. More importantly, these declines were strongly associated with declines in rainfall amount. We hypothesized that precipitation has a direct effect on vegetation and insect productivity, and thus bird abundance is indirectly affected by rainfall amount, through its direct effects on bird resources (mainly food) (Powell et al. 2015). This hypothesis is consistent with the fact that most bird foraging guilds were strongly and negatively affected by decreases in rainfall amount, and thus the temporal decrease in rainfall is having an overall, community-wide effect. This result is also consistent with several, more species-focused studies in north temperate latitudes, which found direct evidence of a positive effect of rainfall amount on bird resources, and consequently on bird population dynamics (Sillett et al. 2000, Nott et al. 2002, Jones et al. 2003, Both and Visser 2005, Anders and Post 2006). In addition, in a Jamaican tropical dry forest, Brown and Sherry (2006) found that decreased precipitation associated with the dry season resulted in reduced arthropod activity at a time when migrants needed to accumulate fat in preparation for migration, causing a decrease in body condition of birds immediately prior to migration, which can in turn have demographic consequences on the breeding grounds

(Morrissette et al. 2010, Norris 2005, Norris and Taylor 2006).

In our study site in eastern tropical Guatemala, total abundance of birds and the abundance of most foraging guilds (except for nectarivores and foliage insectivores) were mainly affected by wet-season precipitation. Because fruiting periods and insect biomass both peak during the rainy season, it is consistent that frugivore abundance, and bark and sallying insectivore abundance were related to wet-season rainfall. Omnivore abundance, which mainly consisted of one species that feeds on fruits and insects, the Ochre-bellied Flycatcher, was also strongly and positively associated to wet-season rainfall. Note that the fact that the omnivore guild was mainly represented by one species is clearly a caveat of the guild approach, if a guild is excessively dominated by a single species. It would probably not be an exaggeration to say that results related to this guild in fact reflect what is happening to this particular species. Species-specific analyses for this flycatcher are then called for.

Of the insectivores, only the foliage insectivores did not follow the pattern of association to wet-season rainfall, being only weakly associated to annual rainfall. Although using the guild approach might provide hypotheses on the observed declines (because of the logical causal chains between rainfall, plant and insect biomass and bird abundance), it might also clearly mask species-specific patterns. Several species for this guild had strong negative associations with "year" (a negative Pearson correlation coefficient; Table 2), indicating a negative population trend. It is thus a possibility that the grouping of species under the "foliage insectivore" denomination might be masking important species-specific patterns. A revision of the grouping strategy may be called for, and for those species which in principle indicate strong declines, specific analyses are necessary for a clearer picture regarding their population status.

The nectarivores were the only guild to be associated with dry-season precipitation. In a study carried out in Costa Rica, Stiles (1992) found severe negative effects on the local population of the Long-billed Hermit due to an unusual drought that caused a severe flower shortage during the peak of the breeding season, which occurs during the drier months of the year. In our study site, this species is the most abundant understory hummingbird. It is thus plausible that the same mechanism that affected the Costa Rican population affected our local hummingbird population, given our result, thus providing some evidence for the bottle-neck hypothesis (Williams and Middleton 2008); i.e., that the amount of rainfall during the dry season, when flowering and hummingbird reproductive activity peaks, is a key driver of hummingbird populations.

Additional temporal decreases in abundance independent of rainfall amount in the previous year were detected for frugivores, nectarivores and omnivores. Evidently, the effects of the amount of rainfall may not only be limited to the rainy season immediately prior to captures, but to the amount of rainfall received in previous years. Time-lagged or carry-over effects are those effects of events that occur in one season but influence individual or population success in the following seasons, and recent empirical evidence suggests they may play an important role in bird population dynamics (Metcalfe and Monaghan 2001, Norris 2005, Brown and Sherry 2006, Norris and Marra 2007, Morrissette et al. 2010). For example, the reproductive success of long-distance migratory birds is influenced by the quality of habitat in their wintering grounds in the season prior to breeding (Norris et al. 2004, Norris and Taylor 2006). Additionally, because of delayed parental care and reproduction in tropical birds (Stutchbury and Morton 2001, 2008, Russell et al. 2004), these effects may be evidenced much later during the life cycles of birds. Consequently, the total decline may be associated with different environmental effects (such as a reduction in rainfall) affecting different components (i.e., age classes) in bird populations, at different points in time.

Beyond those effects of precipitation amount which directly impact bird resources, other indirect pathways may exist of the effects of changes in climatic regimes. For example, Chase et al. (2005) found that for Song Sparrows (*Melospiza melodia*), nest predation rates were lower in wetter years, and Martin (2001) describes similar indirect effects of weather on reproductive success: changes in weather caused four bird species to shift to microhabitats that yielded decreased nesting success. Biotic changes due to increasing temperature might also be expected: as climate warms, many types of vegetation and dependent organisms (including fruit trees and insects that many birds depend on) are expected to shift their distributions to track their preferred microclimates, possibly causing dispersal to higher altitudes (Sekercioglu et al. 2012). Thus, tropical lowland communities may experience net biotic attrition, as a result of the species moving to higher elevations not being replaced by other ones (Colwell et al. 2008, Harris et al. 2011, Sekercioglu et al. 2012). Lastly, synergies of climate change with other threats, such as habitat loss, emerging diseases, invasive species, and hunting may exacerbate the effects of climate change on tropical birds (Sekercioglu et al. 2012).

In conclusion, we detected strong, community-wide declines in species abundance, and these declines were strongly associated with declines in rainfall amount. Most importantly, the magnitude of the association between rainfall and bird abundance is large and not limited to a particular foraging guild, and we thus advocate a much greater effort to investigate current associations of animal abundance with weather, especially rainfall decline (and increase), in tropical regions. A more comprehensive understanding of the effects of climate change on the biotic abundance in tropical ecosystems is strongly needed to propose conservation actions for these diverse ecosystems.

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