



Elevational changes in the avian community of a Mesoamerican cloud forest park

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ABSTRACT

Harboring many range-restricted and specialized species, high elevation tropical cloud forests are diverse habitats represented in many protected areas. Despite this, many such areas receive little practical protection from deforestation and land conversion. Moreover, montane species may be more sensitive to climate change owing to various factors affecting community assembly across elevational gradients. Few studies have used annual monitoring to assess how biological communities in cloud forests may be shifting in response to habitat or climate change or assessed the efficacy of protected areas in buffering these effects. We analyzed avifaunal community trends in a 10-yr dataset of constant-effort bird point-count data in a cloud forest national park in Honduras, Central America. We found that species richness and diversity increased at higher elevations, but decreased at lower elevations. Abundances of most dietary and forest-dependency groups exhibited similar trends, and many key cloud forest species shifted upslope and/or increased in abundance. Taken together, our results suggest that the avian community is moving upslope and species composition is changing. Results for species richness and diversity were similar when only nondegraded transects were considered, suggesting the role of climate change as an important driver. At lower elevations, however, many species may be negatively affected by increased habitat degradation, favoring species with low forest dependency. Continued habitat conversion and climate change could push the cloud forest bird community further upslope, potentially resulting in increased competition, mortality, and even extirpation of some species. Increased protection is unlikely to mitigate the effects of climate change.

Abstract in Spanish is available with online material.

Key words: bird diversity; climate change; conservation biology; functional group; Honduras; indicator species; land-use change; protected area; range shifts; tropical mountains.

THE WORLD'S TROPICAL FORESTS ARE AT INCREASING RISK FROM THE TWIN THREATS OF CLIMATE CHANGE AND HABITAT DEGRADATION (Malhi *et al.* 2008, Şekercioğlu *et al.* 2012, Hansen *et al.* 2013). Large portions of lowland and foothill tropical forest continue to be converted to agricultural land (Hansen *et al.* 2013, Achard *et al.* 2014). Meanwhile, incremental changes in temperature and precipitation could lead to increased extinction risk and upward elevational shifts for tropical species as they track their climatic and habitat niches (Şekercioğlu *et al.* 2008). It is crucial to understand climate change induced changes in tropical ecosystems. These systems are underrepresented in the literature (Harris *et al.* 2011, Feeley *et al.* 2016) and yet contain the majority of the world's species, many of which are extinction prone due to their high specialization (Belmaker *et al.* 2011, Şekercioğlu 2011) and low dispersal ability (Moore *et al.* 2008, Salisbury *et al.* 2012). Birds are an especially important taxon within the tropics where

they provide diverse ecosystem functions (Şekercioğlu *et al.* 2016). Birds are also relatively easy to survey (Şekercioğlu 2012b), indicate the health of the ecosystem (Schulze *et al.* 2004, Wormworth & Şekercioğlu 2011), and are charismatic species that can act as flagships for conservation (Veríssimo *et al.* 2009).

The tropical forests of Mesoamerica comprise one of 36 global biodiversity hotspots (CEPF 2017) and support 2800 tetrapod species, of which 31.1 percent are endemic to the hotspot (CEPF 2017). Of particular concern are the cloud forests of this region, high elevational forests defined by the persistence of clouds and mist where lush vegetation captures moisture from the air (Bubb *et al.* 2004). Cloud forests may be relatively small in area yet they are important centers of endemism across taxonomic groups (Renjifo *et al.* 1997, Anderson & Ashe 2000, Wilson & McCranie 2004). Furthermore, range-restricted montane species are typically low in abundance (Jankowski & Rabenold 2007), highly specialized (Jankowski *et al.* 2009, Pigot *et al.* 2016), and subject to various ecological constraints that determine their elevational ranges, including narrow thermal tolerance (Janzen 1967, McCain 2009b),

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ecotones (Terborgh 1985), and interspecific competition (Jankowski *et al.* 2010, Jankowski 2012, Freeman *et al.* 2016). This renders them especially sensitive to environmental and habitat change (Harris *et al.* 2011).

Central American forests are under great threat from habitat conversion, with high rates of deforestation (Redo *et al.* 2012). In particular, burgeoning human populations and infrastructure are putting increasing pressure on Mesoamerica's highland areas (Aldrich *et al.* 1997). In response, 91 protected areas have been established in Honduras (Vreugdenhil *et al.* 2002), including 37 in montane cloud forest. 'Buffer zones' around the parks provide protection for the inner 'core zones', allowing some human activity such as agriculture and resource extraction. One such protected area in northwest Honduras is Cusuco National Park (CNP), designated as one of 137 irreplaceable protected areas in the world (Le Saout *et al.* 2013). Despite its designation, the actual protection of CNP is nominal, earning it the moniker 'paper park' (Martin & Blackburn 2009). Paper parks are typically understaffed and undermanaged, lacking the financial investment and enforcement required to successfully maintain and protect the forest from deforestation and resource extraction (Peres & Terborgh 1995, Greve & Svenning 2011, Blackman *et al.* 2015). In the case of CNP, the park boundaries are still debated by different parties and military patrols are restricted to infrequent visits to the lower-lying camps. Deforestation continues at the park's boundaries, hunting occurs in the remaining forest, and there is little to prevent further encroachment into the core zone. Other Honduran parks have varying degrees of realized protection, but the paper park phenomenon is unlikely to be limited to CNP and may even be worse for some, given the international attention that CNP receives (Le Saout *et al.* 2013).

To truly understand and track the effects of habitat degradation and climate change on species communities in the tropics, long-term monitoring is required (Struhsaker *et al.* 2005, Grosbois *et al.* 2008, Şekercioglu *et al.* 2012). This can be difficult to achieve because monitoring projects are costly, labor-intensive and time-consuming, especially in the tropics where study sites are often remote and challenging to access and operate within. Most monitoring programs are in temperate regions despite the fact that the need to understand community dynamics in the face of anthropogenic change is probably greater in the tropics (Rosenzweig *et al.* 2008, Harris *et al.* 2011, Feeley *et al.* 2016). One option for conservation monitoring programs is 'research tourism' or 'volunteer tourism' (Ellis 2003, Benson 2005, Cousins 2007). Operation Wallacea (hereafter OpWall) is a conservation-and-research organization funded by volunteers who help researchers gather data on a range of taxa in 14 countries around the world, with a particular focus on the tropics. OpWall's goal is primarily biodiversity monitoring, but they also form extensive collaborations with biologists with specific research questions. Their model is a potentially successful way of maintaining both income and labor to facilitate accurate long-term monitoring.

Since 2006, OpWall has conducted annual expeditions in CNP. Previously, Martin and Blackburn (2009) investigated the

spatial variation in avifaunal communities within CNP, providing one of the first assessments of paper park efficacy based on community metrics of a particular taxon. However, their study used community data from only one field season. Thus, little is known about community dynamics in such protected areas over time. Further, owing to limited published data, the value of conservation organizations initiating and maintaining long-term robust monitoring programs under the funding model outlined remains infrequently validated, despite this model's distinct place in the conservation-volunteer market (Ellis 2003, Cousins 2007). Hereafter, we analyze a 10-yr dataset of avian point-count data to assess the presence and extent of changes to CNP's avifauna. Specifically, we assess to what extent species richness, diversity, and community composition have changed over 10 yr and how this change relates to elevation. We also examine abundance changes in guilds based on diet and forest specialization. Finally, we assess abundance and elevational changes in a selection of common cloud forest species. Because we expect communities to shift up-slope due to climate change and habitat degradation, we hypothesize an increase in species richness and diversity at higher elevations. As a result, we also expect increases in abundance at higher elevations for species groups with high affinities for cloud forest habitat (*e.g.*, insectivores and highly forest-dependent species). Groups such as granivores or species with low forest dependency would be more likely to increase at low elevations in response to habitat change.

METHODS

STUDY SITE.—Fieldwork was conducted in Cusuco National Park, Cortés, NW Honduras (15°29'–15°32' N, 88°13'–88°26' W; Fig. S1). The park is 24,195 ha in size, with a central core zone of 7325 ha peaking at 2243 m asl, and a surrounding buffer zone of 16,870 ha. Annual precipitation is *ca.* 2500 mm, with a wet season between May and November. Forest types present are predominantly mixed broadleaf and pine, including many species within the genera *Quercus* (Fagaceae), *Liquidambar* (Altingiaceae), and *Pinus* (Pinaceae). At the highest elevations, stunted elfin forest is found on more exposed mountain ridges. The buffer zone, which allows human settlement, features many anthropogenic landscapes including secondary forest, cattle pastures, and coffee plantations, used by the 38 communities (up to 40,000 people) living within the park borders. Encroachment into and resource extraction from the core zone is not allowed, but is observed increasingly each year, particularly on the western side. Surveying in CNP is conducted over a network of 26 transects spanning an elevational range from 679 to 2183 m asl, accessible from seven satellite camps. Each transect consists of two-to-eight fixed survey sites (total 132), spaced at least 200 m apart (typically *ca.* 400 m) for sampling independence. For the purposes of later analyses, we identified a subset of transects that had experienced no deforestation during the study period. The resident avifaunal diversity of the park has been comprehensively inventoried and comprises *ca.* 280 species.

BIRD SURVEYS.—Since 2007, fieldwork has been conducted annually for 8 wk between 6 June and 14 August. Every transect was surveyed in its entirety at least three times per field season, giving temporal replicates that were generally at least 1 wk apart. At least one replicate per transect was surveyed in reverse order to balance against potential diel temporal bias. Every transect replicate was conducted over the course of a morning between 0530 h (dawn) and 0930 h, when birds are most vocally active and detectable, but surveys were not conducted in windy conditions, heavy rain, or mist. For every transect replicate, a point count was conducted at every survey site. Each point count consisted of one minute settlement period followed by ten minutes of surveying during which the number and identity of each species detected was recorded (Gregory *et al.* 2004). A ten-minute point count reduces the probability of inflated abundance estimates due to re-detection, while still allowing more than 80 percent of present species to be detected (Lynch 1995). Counts had an unlimited radius because we wanted to maximize detection of scarcer birds or birds that avoid proximity to humans while reducing variation introduced by distance estimation (Ralph *et al.* 1995). Additionally, we found no elevational trend in detection distance (Poisson regression: $t = 0.04$, $P = 0.97$). Ornithologists carrying out the surveys were hired by OpWall and chosen based on their appreciable bird identification skills (especially auditory) and field experience. Pre-season, they received comprehensive bird lists and vocalizations to learn. Once on-site, the ornithologists received extensive training for at least a week to verify their ability to identify local species (Kosmala *et al.* 2016). Variation in skill level is inherent to any project with multiple surveyors. However, this variation is effectively randomized across the park in terms of elevation and throughout the 10-yr study duration and also minimized by the rigors of the hiring and training process.

STATISTICAL ANALYSIS.—Community metrics (species richness, etc.) were calculated based on combined unlimited-radius point counts for each transect replicate. Occasionally, one or two sites were not surveyed on a given transect replicate (for a variety of logistical reasons) and this affected our ability to compare transect replicates across years in the analyses. Thus, we trimmed the data so that every replicate of a given transect consisted of the same effort, across years. This involved either removing from a given transect the sites that were not surveyed every year (transect shortening) or removing transect replicates that did not survey every site (replicate removal). Whether we used transect shortening or replicate removal depended on which would minimize data loss in each instance. Thus, we used data from 115 survey sites from 25 transects (679 to 2178 m asl) and each replicate of a given transect was of a fixed length and survey duration (although different transects varied in length). Due to a military coup in Honduras, which limited the number of ornithologists available for field surveys, the 2009 data were insufficient and were removed from the analyses.

To assess general avifaunal change over time, we calculated species richness and Shannon diversity for each transect replicate. To determine community composition changes, we created a

Bray-Curtis dissimilarity matrix based on the combined unlimited-radius counts of each species during each transect replicate. We used a Principal Coordinate Analysis (PCoA) to ordinate the dissimilarity matrix and extract the greatest axes of variation. This provided compositional scores for each replicate along each axis of the PCoA. To assess changes in different guilds, we classified the bird species into six dietary guilds (insectivore, frugivore, nectarivore, granivore, omnivore, and carnivore) and three levels of forest dependency (high, medium, and low; Birdlife International 2017), and analyzed abundance changes in each group. Diet data were obtained from a comprehensive bird-ecology database covering all the bird species of the world (see Burin *et al.* 2016 for details).

For each avifaunal metric, we analyzed changes in relation to year, elevation, and the interaction between the two. These relationships were modeled using linear mixed models (for diversity and species composition) and generalized linear mixed models with Poissons errors (for species richness and abundances). As mixed effects in the models, we accounted for the nesting of replicates within each transect and transect within camp, and we included the effects of the elevational range of each transect and the number of observers completing the point counts. To try and separate the potential effects of habitat and climate change, we also separated transects into closed-canopy and open-canopy transects and re-ran the models for diversity and species richness. The former have experienced no deforestation and little-to-no habitat degradation over the 10-yr survey period (13 transects, 65 sites, 1197–2178 m asl; Fig. S1), while the latter have experienced varying degrees of deforestation (12 transects, 50 sites, 679–1650 m asl).

Finally, we analyzed abundance changes per transect and mean elevation changes in a subset of 18 selected cloud forest species (Table S1). This subset comprises some of the most common and easily identified species in the park that are indicative of montane cloud forest across dietary niches. Furthermore, with a high volume of recordings, they present the highest power to detect changes at the species level (hereafter, referred to as cloud forest indicator species). As points of comparison, two additional species (*Henicorbina leucosticta* and *Ramphastos sulfuratus*), found at lower elevations than their parapatric confamilials (*Henicorbina leucophrys* and *Aulacorhynchus prasinus*), were added to the subset. Species abundances for each transect replicate were calculated as the sum of unlimited-radius detections across sites. Abundance changes were analyzed using GLMMs with year as an explanatory variable and the same random effects as listed above. Elevational change over time was analyzed with linear models of year against detection elevation for every individual bird. Analyses were carried out in R (version 3.1.2; R Core Team 2017) using the packages VEGAN (Dixon 2003), APE (Paradis *et al.* 2004), and lme4 (Bates *et al.* 2015) for diversity/community composition, PCoA, and mixed models, respectively.

RESULTS

Across 3147 point-count surveys, we detected 207 bird species. We found a significant effect of year, elevation, and a

year*elevation interaction on per-transect species richness and diversity (Table 1). Both species richness (Fig. 1A) and diversity (Fig. 1B) increased at higher elevations and decreased at lower elevations. When only non-disturbed closed-canopy transects were considered, which tended to be at higher elevations, the results showed similar increases in species richness and diversity. When only disturbed transects, with variably open canopies, were considered, the decrease in species richness and diversity at lower elevations was slightly more pronounced. Species composition changed significantly over time (Fig. 2), indicated by the first and second axes of the PCoA.

Of the six dietary guilds, five significantly changed in abundance per transect over time (Table 1) and four of these showed an interaction of year and elevation (Fig. 3A-E). All forest-dependency groups also showed a year*elevation interaction effect in their abundance (Fig. 3F-H). Insectivores, granivores, and both high and medium forest-dependency species increased in abundance at higher elevations, but decreased at lower elevations (Fig. 3A,D,F,G). Frugivores, nectarivores, and omnivores showed decreases in abundance at lower elevations (Fig. 3B,C,E). Low forest-dependency species increased in abundance at lower

elevations (Fig. 3G). Carnivores increased in abundance over time (not pictured due to the absence of an effect of elevation).

Of the 18 cloud forest indicator species, 13 significantly changed in abundance per transect (Table 2). Eleven species increased in abundance over time (Fig. S2A-K; *Arremon brunneinucha*, *Catharus mexicanus*, *Chlorophonia occipitalis*, *Cyanolyca cucullata*, *Empidonax flavescens*, *Pharomacrus mocinno*, *Trogon collaris*, *Vireo leucophrys*, *Xiphorhynchus erythropygius*, *Piranga bidentata*, and *Zentrygon albifacies*), while only two species declined (Fig. S2L-M; *Chlorospingus flavopectus* and *Myadestes unicolor*). Overall, the indicator species shifted upslope by 1.58 m per year. Ten species were detected at significantly different elevations over time. Eight of these species moved upslope by an average of 7.33 m per year (Fig. S3A-H; *Catharus mexicanus*, *Chlorospingus flavopectus*, *Empidonax flavescens*, *Henicorbina leucophrys*, *Ramphastos sulfuratus*, *Vireo leucophrys*, *Piranga bidentata*, and *Zentrygon albifacies*), while only two species moved downslope by an average of 9.50 m per year (Fig. S2I-J); *Aulacorhynchus prasinus* and *Pharomacrus mocinno*. Four species showed no change in abundance or elevation (*Anabacerthia variegaticeps*, *Henicorbina leucosticta*, *Myioborus miniatus*, and *Penelopina nigra*).

TABLE 1. Model results showing the effect of year and elevation on the avifauna of a Honduran cloud forest park.

	Year		Elevation		Year*Elevation	
	Z/t	P	Z/t	P	Z/t	P
Species richness						
All transects	-4.61	<0.0001***	-4.45	<0.0001***	5.97	<0.0001***
Closed-canopy	-2.35	0.019*	-4.26	<0.001***	3.42	0.001***
Open-canopy	-3.53	<0.001***	-2.11	0.035*	4.02	<0.0001***
Shannon diversity						
All transects	-2.54	0.011*	-5.23	<0.001***	3.91	<0.001***
Closed-canopy	-1.27	0.203	-4.12	0.020*	2.36	0.018*
Open-canopy	-1.76	0.080	-2.38	0.060	2.26	0.025*
Species composition						
PCoA Axis 1	-3.46	0.001***	5.63	<0.0001***	3.21	0.001**
PCoA Axis 2	-3.29	0.001**	2.90	0.024*	-1.76	0.079
PCoA Axis 3	14.31	<0.0001***	-1.49	0.119	1.62	0.107
Dietary guild abundance						
Carnivores	-2.42	0.015*	1.29	0.196	-1.73	0.084
Frugivores	-6.22	<0.0001***	-3.69	<0.001***	6.51	<0.0001***
Granivores	-5.16	<0.0001***	2.06	0.040*	5.02	<0.0001***
Insectivores	-9.48	<0.0001***	-1.08	0.279	11.81	<0.0001***
Nectarivores	-5.00	<0.0001***	-3.68	<0.001***	3.07	0.002**
Omnivores	-6.71	<0.0001***	-4.01	<0.0001***	7.09	<0.0001***
Forest-dependency abundance						
High	-7.33	<0.0001***	0.63	0.532	9.36	<0.0001***
Medium	-13.01	<0.0001***	-3.87	<0.001***	14.41	<0.0001***
Low	7.60	<0.0001***	-0.56	0.579	-9.17	<0.0001***

Generalized linear mixed models were used for species richness and the abundance of six dietary guilds and three forest-dependency groups. For species richness and diversity, the models were re-ran considering undisturbed, closed-canopy transects separately from open-canopy transects which have experienced varying degrees of deforestation. Linear mixed models were used for Shannon diversity and community composition based on a PCoA of a Bray-Curtis community dissimilarity matrix. Asterisks denote significance level (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$).

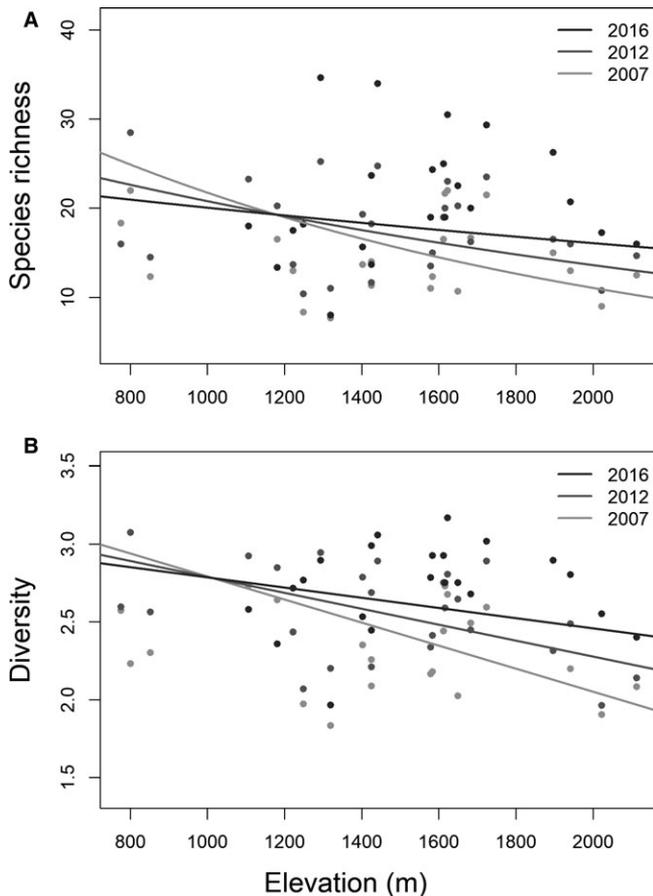


FIGURE 1. The effect of year and elevation on (A) species richness and (B) diversity per transect of the bird community in a Honduran cloud forest park from point counts spanning 2007 through 2016. We represent the effect of elevation on species richness/diversity at three time points: 2007 (light gray), 2012 (median year, medium gray), and 2016 (dark gray). The points are the mean values for each of those years at each transect, colored as per the lines.

DISCUSSION

Over a 10-year period, we found general increases in avian species richness and diversity at mid-to-high elevations (>1200 m), but declines at low elevations. This suggests upslope shifts in the community with lowland biotic attrition (Colwell *et al.* 2008), whereby mid-to-high elevation forest gains species from lower elevations, while retaining, to some degree, the montane avifauna it already had. Indeed, there were significant changes in species composition over the 10-year, with higher elevations (1500 m or more) featuring more cloud forest species (as represented by the cloud forest indicator species subset) and mid-elevations becoming more similar to lower elevations. Insectivores, the most speciose dietary group, showed a similar trend to that of diversity and species richness, with increasing abundance at higher elevations and declines at lower elevations. Species with high-to-medium forest dependency exhibited similar trends. Frugivores, nectarivores, and omnivores also showed declines in abundance at lower elevations, while granivores increased at higher

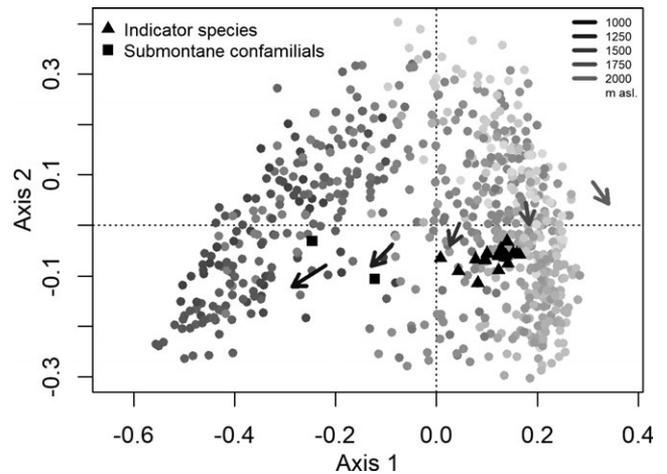


FIGURE 2. Ordination plot of the first two axes of a PCoA of the bird community composition per transect in a Honduran cloud forest park over 25 transects from 2007 to 2016, based on a Bray-Curtis dissimilarity matrix. Proximity of points represents the similarity in species composition. Transect replicates are colored by elevation where the highest elevation transects (2113 m asl) are light gray and the lowest (775 m asl) are dark gray. Triangles represent the weighted mean contributions of the 18 indicator species to the community composition, the two squares represent the submontane confamilials. Arrows indicate the vector change in community composition over ten years based on linear mixed models, with the trend at five different elevations shown: 1000, 1250, 1500, 1750, and 2000 m asl.

elevations. The congruence in trends across groups further supports an upslope shift in the bird community, with the core of the park becoming increasingly suitable for cloud forest birds over time. Indeed, many of the cloud forest indicator species increased in abundance and/or moved upslope, while few exhibited the opposite trend.

Two potential drivers behind an upslope shift in the community are climate change and habitat loss. Climate change is predicted to cause upslope shifts in bird communities as species track their climate envelopes (Şekercioğlu *et al.* 2008, La Sorte & Jetz 2010). This is especially true in the tropics where altitudinal gradients in environmental variables are far more acute than latitudinal gradients (Janzen 1967, Colwell *et al.* 2008). Along humid mountains, bird diversity tends to decline with elevation (McCain 2009a, Quintero & Jetz 2018), and if climate change were to shift whole communities upslope, one would expect increases in diversity at higher elevations. This could favor some species in the short term as they move into more protected areas of the park. We know empirically that area declines with elevation in CNP (Elsen & Tingley 2015), so if individuals are moving upslope one would expect higher densities at higher elevations. Short-term high densities could be unsustainable, potentially resulting in long-term population declines (Jackson & Sax 2010), reflected demographically by decreased survivorship (Korfanta *et al.* 2012).

While some studies have shown upslope community shifts over multi-decadal periods (Peh 2007, Forero-Medina *et al.* 2011, Harris *et al.* 2012, Freeman & Class Freeman 2014, Rosselli *et al.*

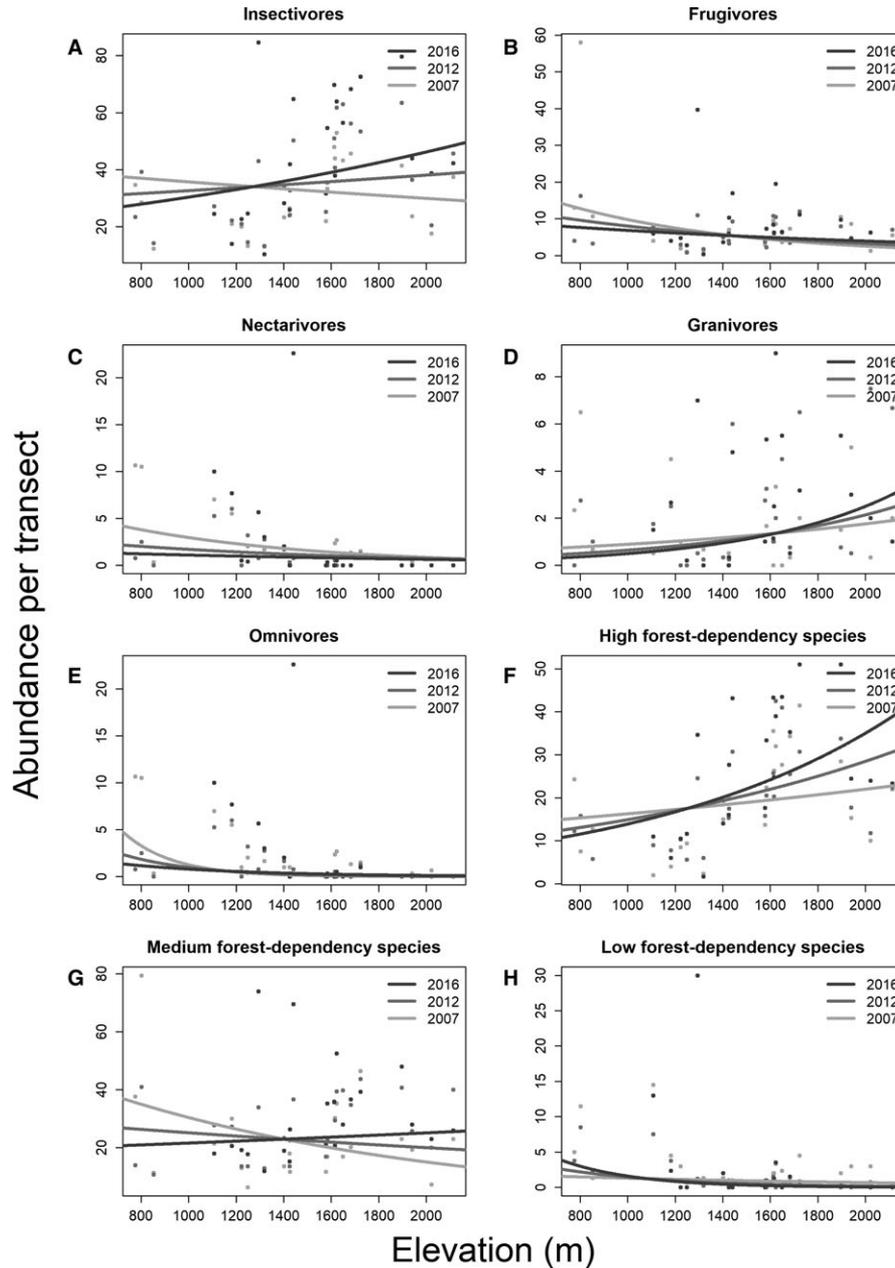


FIGURE 3. The effect of year and elevation on the abundance per transect of dietary guilds and habitat-dependency groups in a Honduran cloud forest park from point counts spanning 2007 through 2016. (A) insectivores, (B) frugivores, (C) nectarivores, (D) granivores, (E) omnivores, (F) high forest dependency, (G) medium forest dependency, and (H) low forest dependency species. We represent the effect of elevation on abundance at three timepoints: 2007 (light gray), 2012 (median year, medium gray) and 2016 (dark gray). The points are the mean values for each of those years at each transect, colored as per the lines.

2017), no studies have provided high temporal resolution for these shifts. Furthermore, how or why species might track their climatic niches remains unclear and has seen limited support in recent mechanistic physiological studies (Freeman 2016, Londoño *et al.* 2016). A more important factor determining elevational distributions could be habitat associations, and elevational shifts may be constrained by the speed of habitat change (Forero-Medina *et al.* 2011, Jankowski *et al.* 2013, Rosselli *et al.* 2017). Species even have the potential to move downslope due to competitor

release or favorable changes in climatic variables other than temperature (Lenoir *et al.* 2010, Tingley *et al.* 2012, Freeman & Class Freeman 2014). Thus, a greater understanding of the mechanistic determinants of species elevational ranges coupled with long-term monitoring of communities as a whole are needed to accurately project how climate change may negatively affect species along elevational gradients in the tropics.

The other possible mechanism explaining diversity reductions at lower elevations is habitat change. In particular, we

TABLE 2. Model results showing the separate effects of year and elevation on the transect abundance of 20 indicator species from a Honduran cloud forest park.

Indicator species	Abundance				Elevation			
	Estimate	SE	Z	P	Estimate	SE	t	P
<i>Anabacerthia variegaticeps</i>	0.025	0.013	1.91	0.056	-1.38	2.23	-0.62	0.538
<i>Arremon brunneinucha</i>	0.171	0.013	13.49	<0.0001***	0.86	3.23	0.27	0.790
<i>Aulacorhynchus prasinus</i>	0.013	0.015	0.86	0.388	-8.09	3.23	-2.50	0.013*
<i>Catharus mexicanus</i>	0.068	0.009	7.42	<0.0001***	3.69	1.50	2.47	0.014*
<i>Chlorophonia occipitalis</i>	0.066	0.021	3.19	0.001**	-3.67	4.87	-0.75	0.452
<i>Chlorospingus flavopectus</i>	-0.040	0.006	-6.59	<0.0001***	2.93	1.29	2.27	0.023*
<i>Cyanolyca cucullata</i>	0.111	0.021	5.35	<0.0001***	-3.47	3.28	-1.06	0.291
<i>Empidonax flavescens</i>	0.071	0.011	6.61	<0.0001***	5.48	2.30	2.39	0.017*
<i>Henicorbina leucophrys</i>	0.012	0.008	1.44	0.151	3.83	1.53	2.51	0.012*
<i>Myadestes unicolor</i>	-0.024	0.006	-4.11	<0.0001***	0.57	1.22	0.47	0.640
<i>Myioborus miniatus</i>	-0.005	0.011	-0.45	0.655	-0.16	2.09	-0.08	0.939
<i>Penelopina nigra</i>	-0.019	0.014	-1.35	0.178	0.84	2.50	0.34	0.737
<i>Pharomacrus mocinno</i>	0.049	0.017	2.80	0.005**	-10.92	2.73	-4.00	<0.0001***
<i>Trogon collaris</i>	0.075	0.015	4.96	<0.0001***	1.61	3.19	0.50	0.615
<i>Vireo leucophrys</i>	0.052	0.017	3.05	0.002**	8.55	2.93	2.92	0.004**
<i>Xipborhynchus erythropygius</i>	0.131	0.014	9.18	<0.0001***	5.16	3.34	1.55	0.123
<i>Piranga bidentata</i>	0.171	0.022	7.96	<0.0001***	14.42	4.76	3.03	0.003**
<i>Zentrygon albifacies</i>	0.140	0.022	6.44	<0.0001***	9.51	4.17	2.28	0.023*
Foothill Confamilials								
<i>Henicorbina leucosticta</i>	-0.004	0.020	-0.20	0.839	-8.34	5.15	-1.62	0.107
<i>Ramphastos sulfuratus</i>	0.029	0.017	1.67	0.095	10.19	3.93	2.59	0.001**

General linear-mixed models with Poisson errors were used to model species abundance over time. Linear models were used to test for species' changes in elevation over time. Asterisks denote significance level (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$).

Nomenclature after International Ornithological Congress World Bird List v 7.1; Gill & Donsker 2017.

observed declines in high and medium forest-dependency species, but increases in low forest-dependency species. Deforestation can negatively impact forest interior specialists both through the direct loss of habitat and via edge effects on remaining forests (Laurance 2004, Banks-Leite *et al.* 2010). Forest edges and agropastoral mosaics do have the potential to harbor reasonable amounts of bird diversity (Ricketts *et al.* 2001, Şekercioğlu *et al.* 2007, Neate-Clegg *et al.* 2016). However, more species in general are lost than gained through habitat conversion in the tropics (Waltert *et al.* 2004, Mahood *et al.* 2012), resulting in lower species turnover (Moura *et al.* 2013, de Castro Solar *et al.* 2015) particularly along elevational gradients (Sreekar *et al.* 2017). In montane parks such as CNP, the buffer zone is both more accessible to local communities and more suitable for agricultural use. Every year, new areas of the park, including the core zone, are deforested. The loss of primary forest in CNP is thus a likely driver of the differential responses of the forest-dependency groups. The fact that no dietary guild increased at lower elevations in the park is surprising, as more disturbed habitats have the potential to support higher abundances of nectarivores, granivores, and omnivores (Waltert *et al.* 2005, Barlow *et al.* 2007, Burivalova *et al.* 2015).

It is difficult to separate the effects of climate change from the concurrent effects of land-use change on tropical montane communities and rarely is it possible to study sites free from disturbance (Harris *et al.* 2012). Instead, we attempted to look for an un-confounded signal of climate change by separately analyzing closed- and open-canopy transects. Closed-canopy transects demonstrated increasing diversity and species richness above 1200 m, suggesting that habitat change is not directly responsible for changes at mid-to-high elevations. However, we cannot rule out more cryptic disturbance such as edge effects or hunting. Yet, the latter is only likely to affect tinamous or scarce terrestrial galliformes (*e.g.*, *Crax rubra*), while the arboreal *Penelopina nigra* showed no change in abundance. The fact that low forest-dependency species were the only group to increase in abundance while overall diversity declined (particularly in disturbed-canopy forest) suggests an additional role of habitat change, perhaps exacerbating climate effects. Harris *et al.* (2014) found that climate change affected birds more at higher elevations, while deforestation was a greater influence at mid-elevations and our results seem to corroborate this. Future elevational studies should aim to disentangle the effects of climate and habitat change by taking accurate, comprehensive measurements of abiotic and biotic variables at survey sites across time.

In the short term, increases in diversity and species richness at higher elevations may appear positive for the cloud forest bird community. However, if the drivers persist and the community continues to move upslope, cloud forest species could be pushed toward the elevational limits of the park, leading potentially to extirpation. Species that inhabit high-elevation elfin forest (*e.g.*, *Catharus frantzii*, *Atthis ellioti*, *Turdus plebejus*) are at greater immediate risk because such habitat only exists in very narrow bands on the highest ridges of the park. Additionally, for species at the upper elevational limits of their range, a negative effect of a warming climate may be exacerbated by competitively dominant lowland congeners (Jankowski *et al.* 2010, Jankowski 2012, Freeman *et al.* 2016). While we did observe an upslope shift in *Henricborina leucophrys*, we did not observe a concomitant shift in its submontane congener *H. leucosticta* and the prevalence of competitive constraints remains poorly known (Pasch *et al.* 2013). Two species (*Pharomacrus mocinno* and *Aulacorhynchus prasinus*) actually moved downslope by an average of 9.5 m per year. As larger-bodied frugivores, they are predicted to respond negatively to habitat change (Şekercioğlu 2012a, Newbold *et al.* 2013, Bregman *et al.* 2014). It is possible that large, more volant species are able to use more patchily distributed resources where smaller species are reluctant to cross gaps (Lees & Peres 2009). Additionally, *P. mocinno* is known to undergo seasonal migrations to lower elevations from August to October at other locations (Powell & Bjork 1995). If their phenology were to shift to earlier in the year, it is possible that we might observe more quetzals at lower elevations in our June-to-August sampling period.

If climate change is the primary driver of upslope community shifts, there is little a protected area can do to prevent future elevational movements. One option when designating protected areas is to choose land which encompasses the greatest continuous elevational range. By contrast, protected areas do have an important role to play in mitigating direct land-use change. This is an issue for CNP as it receives little enforced protection. Local guides do form small patrols, but military presence is infrequent. Contraction of the remaining cloud forest continues (at least in the accessible regions of the park), and this could further exacerbate the effects of climate change. Ideally CNP would receive more concrete protection to address these issues. Additionally, more sustainable land-use practices and community outreach could help reduce anthropogenic change, for example, by encouraging the cultivation of shade coffee instead of sun coffee (Buechley *et al.* 2015). No comparison has yet been made with an unprotected cloud forest system, so the nominal protection this park receives may still have some conservation benefit (Bruner *et al.* 2001, Struhsaker *et al.* 2005, Martin & Blackburn 2009). Moreover, the visitation to the park each year by hundreds of volunteers and conservation biologists in addition to tourists helps to raise awareness of the park's status (Le Saout *et al.* 2013) and is likely to improve its protection (Laurance 2013). Elevational study systems are needed elsewhere in the tropics to compare different regions and habitats and areas with differing degrees of protection. In particular, quantifying demographic changes at the species level

could provide a mechanistic insight into observed community shifts (Korfanta *et al.* 2012).

The collection of long-term data with fine temporal resolution is vital if we are to understand how avian communities are responding to climate and land-use change along elevational gradients, inside and outside protected areas (Newmark 2006, Grosbois *et al.* 2008, Şekercioğlu *et al.* 2012). We have demonstrated that conservation research organizations have the potential to use 'research tourism' (Benson 2005) to initiate, maintain, and fund long-term monitoring programs. Furthermore, research tourism provides invaluable field experience to the volunteers who fund it, helping to ensure the education and inspiration of the next generation of scientists both locally and internationally. However, we encourage continued discussion of the benefits and limitations of this model of data collection. One potential issue with this study is variability in observer skill which is inherent when multiple observers are employed over time. We aimed to minimize any inter-observer variability through the comprehensive hiring and training process and by randomizing the placement of observers across the park over each field season. Although it is possible that observer skill increased over the study period such that more species are detected in later years, this would not be biased toward higher elevations because observer survey coverage at different areas of the park is random. Moreover, the fact that trends were observed in the majority of cloud forest indicator species, which are easier for observers to identify regardless of skill, suggests the results are not an artifact. If conservation research organizations are to provide high-quality data and contribute to the scientific community, they must be well-organized and minimize bias with strict protocols and standardization (Kosmala *et al.* 2016). When conducted appropriately, long-term monitoring programs can provide critical information on how tropical communities are responding to anthropogenic change.

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AUTHOR CONTRIBUTIONS

MHCNC and SEIJ conceived and designed the study. SEIJ collected much of the data (since 2012). MJ and OB maintained

survey design and data. MHCNC conducted the analysis and wrote the manuscript with large input from SEIJ. MHCNC created the graphs and OB the map. CHS coordinated intellectual concepts. All authors reviewed drafts of the manuscript and provided intellectual insight.

DATA AVAILABILITY

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.b025kp0> (Neate-Clegg *et al.* 2018).

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

TABLE S1. *Selected cloud forest indicator species.*

FIGURE S1. Maps of Cusuco National Park, Cortés, NW Honduras.

FIGURE S2. Statistically significant changes in abundance per transect over ten years for 13 indicator species in a Honduran cloud forest park, as estimated by generalized linear models.

FIGURE S3. Statistically significant changes in elevation over ten years for ten indicator species in a Honduran cloud forest park, as estimated by linear models.

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