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DISTRIBUTION OF NEARCTIC-NEOTROPICAL MIGRATORY BIRDS ALONG A SOUTH AMERICAN ELEVATION GRADIENT DURING SPRING MIGRATION

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ABSTRACT.—The Sierra Nevada de Santa Marta in northern Colombia has been identified as a critical spring stopover site for at least one Neotropical migratory bird species prior to crossing the Caribbean sea on migration. The strategic location of the Sierra suggests that other South American wintering migrants may stopover there, but no information is available on the migrant community during spring or how they distribute themselves between habitats and across the broad elevational gradient. Here, we present species richness and densities of migratory landbirds obtained through standardized census and captures along an elevation gradient (100–2,100 m) covering two habitats, forest and shade coffee, during two consecutive spring migrations. The migrant community (~39 species) showed a peak in species richness and abundance at mid elevations (700–1,700 m), mirroring the pattern often observed in communities of resident Neotropical birds. However, individually the abundance of the commonest species peaked at different elevations and showed high annual variability. We also found within-species differences in density between shade-coffee and forest at the same elevation, possibly reflecting differences in habitat quality for some species. Factors such as food availability and predation risk are expected to be critical in shaping the distribution of migrants during stopover, and further research is required to identify the drivers of the observed elevational patterns. This study contributes to our knowledge of the life histories of migrants during stopover and highlights the habitats and elevations where conservation measures would protect the highest number of species and individuals at a South American stopover site. *Received 31 January 2014. Accepted 5 September 2014.*

Key words: Colombia, density, habitat quality, montane tropical forest, shade-coffee, species richness, stopover.

Nearctic-Neotropical migrants have been intensively studied on their breeding grounds, and new technologies are rapidly increasing our understanding of the connections between the different stages of their life cycles (Bowlin et al. 2010, Robinson et al. 2010, McKinnon et al. 2013). However, basic yet important aspects of their life histories, particularly during migration and wintering periods in the Neotropics, are still poorly understood (Winker 1995, Jahn et al. 2004, Faaborg et al. 2010). For instance, we still lack comprehensive descriptions of non-breeding ranges, elevation preferences, and migration phenology for most migrants that stopover or winter in South America (Jahn et al. 2004, Faaborg et al. 2010, Gómez et al. 2011). Generating such information is vital if we are to understand the ecology of migratory species from a full life-cycle perspective and make informed decisions about how to conserve species experiencing population declines (Robbins et al. 1989, Faaborg et al. 2013, Sauer et al. 2013).

The way in which migratory birds are distributed across elevation gradients is a question of ecological and conservation importance (Merkord 2010, Sanders and Rahbek 2012, Jetz et al. 2012). Given that resident bird communities in the Neotropics have highly characteristic elevational distributions (Todd and Carriker 1922, Rahbek 1997, Stotz 1998, Kattan and Franco 2004, Herzog et al. 2005, Merkord 2010), the elevational distribution of migrants is expected to be non-uniform as well, likely reflecting the relative quality of habitats present and the environmental niche of individual species (Nakazawa et al. 2004, Gunnarsson et al. 2005). Indeed, the few studies that describe the elevational distribution of wintering Nearctic-Neotropical migrants have found non-uniform distributions (Young et al. 1998, Blake and Loiselle 2000, Ruelas-Inzunza et al. 2005). In Mexico, lower elevations held the highest species richness of wintering migrants (Ruelas-Inzunza et al. 2005), while in Costa Rica migrant richness and abundance was highest at mid-elevations (500–1,000 m) (Young et al. 1998, Blake and Loiselle 2000). Much less is known about what occurs in South America (Bosque and Lentino 1987, BirdLife International 2006, Colorado 2011, Gómez et al. 2013), but marked differences in geographical distribution between

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species (e.g., Andean vs. Amazonian), suggest that habitats at different elevations vary considerably in quality for migrants.

While some studies describe a decline in resident bird species richness with increasing elevation (Ruelas-Inzunza et al. 2005, Jankowski et al. 2013), most report what has been termed the 'mid elevation hump'—a peak in species richness at mid elevations (e.g., McCain 2009, Sanders and Rahbek 2012). Various explanations have been provided for this pattern, such as climate and productivity (Rahbek 1995, Jankowski et al. 2013) or the area of elevational belts (Kattan and Franco 2004, Karger et al. 2011). In the case of Nearctic-Neotropical migrants during stopover, maximizing food intake while minimizing predation risk, and possibly parasite exposure (e.g., Møller and Erritzøe 1998, Møller and Szép 2011), are probably the main drivers of habitat selection (Sapir et al. 2004, Buler et al. 2007, Hoye et al. 2012). Consequently, a non-uniform distribution of migrants by elevation will likely reflect food availability, as well as habitat preferences and availability for different species. Indeed, common South American wintering migrants, like the Blackburnian Warbler (*Setophaga fusca*) and Tennessee Warbler (*Oreothlypis peregrina*), are known to winter in Andean forests, while Gray-cheeked Thrush (*Catharus minimus*) and Red-eyed Vireo (*Vireo olivaceus*) largely winter in lowland Amazonian forest (Hilty and Brown 1986). These elevation preferences may be reflected in stopover habitat choice.

Habitat availability and its relative quality becomes particularly important when birds face ecological barriers during migration (Petit et al. 1995, Fusani et al. 2009). Indeed, resource availability at stopover sites prior to such barriers will affect rates of energy deposition and, in turn, the ability of migrants to store sufficient energy to cross barriers successfully (Alerstam et al. 2003, Newton 2006, Bayly et al. 2013). The Sierra Nevada de Santa Marta in northern Colombia is used by birds to store large energy reserves prior to crossing the Caribbean Sea (Bayly et al. 2013), a major ecological barrier for northward bound Nearctic-Neotropical migrants on spring migration (Gómez et al. 2013). However, as in all tropical mountains, habitats along the elevation gradient of the Sierra are not uniform (Janzen 1967, McCain 2009). Not only are there various types of native forests with distinct characteristics (Fundación Pro Sierra Nevada de Santa Marta 1998, Broxton et al. 2014) but also large expanses of agricultural land including pastures and shade-coffee plantations (Instituto de Hidrología, Meteorología y Estudios Ambientales 2010a). Understanding which migrants stopover in the Sierra prior to crossing the Caribbean Sea and how they are distributed within these habitats is the first step to defining conservation priorities.

Shade-coffee is widely regarded as a migratory bird-friendly agroecosystem (Jones et al. 2000, Wunderle and Latta 2000, BirdLife International 2006, Bakermans et al. 2009, Jha et al. 2014). However, few studies have directly compared migrant richness and density between shade coffee and natural forest in winter (Bakermans et al. 2009) and less so during stopover (but see Gómez et al. 2013). Given that migrants are expected to respond numerically to food availability during stopover (Buler et al. 2007, Buler and Moore 2011), comparing densities in shade coffee and forest may be an effective way of assessing relative habitat quality. Coffee is one of the major agricultural landscapes in the northern Andes of South America (Philpott et al. 2008, Jha et al. 2014), and it is essential to evaluate its quality for migratory birds with empirical evidence.

In this study, we describe how migratory species richness and density vary across an elevation gradient and between shade coffee and forest during spring migration in the Sierra Nevada de Santa Marta. We present the pattern of species richness and abundance by elevation for the entire migrant community, as well as density estimates by elevation and year for the four commonest species. We discuss these patterns in terms of the ecological pressures shaping tropical elevational distributions of migratory birds and the implications these variables have for inferring habitat quality and conservation priorities in a critical spring stopover region.

METHODS

Study Area and Sites.—This study took place in the Sierra Nevada de Santa Marta, an isolated coastal mountain range on the Caribbean coast of Colombia. We collected data at four sites representing different elevations and habitat types, on the north and north-western slope of the Sierra (Fig. 1): A. Lowland forest (100–200 m) in the Quebrada Valencia Nature Reserve (11° 14′ 10.48″ N, 73° 47′ 57.15″ W); B. Pre-montane forest and shade-coffee around the town of Minca (600–

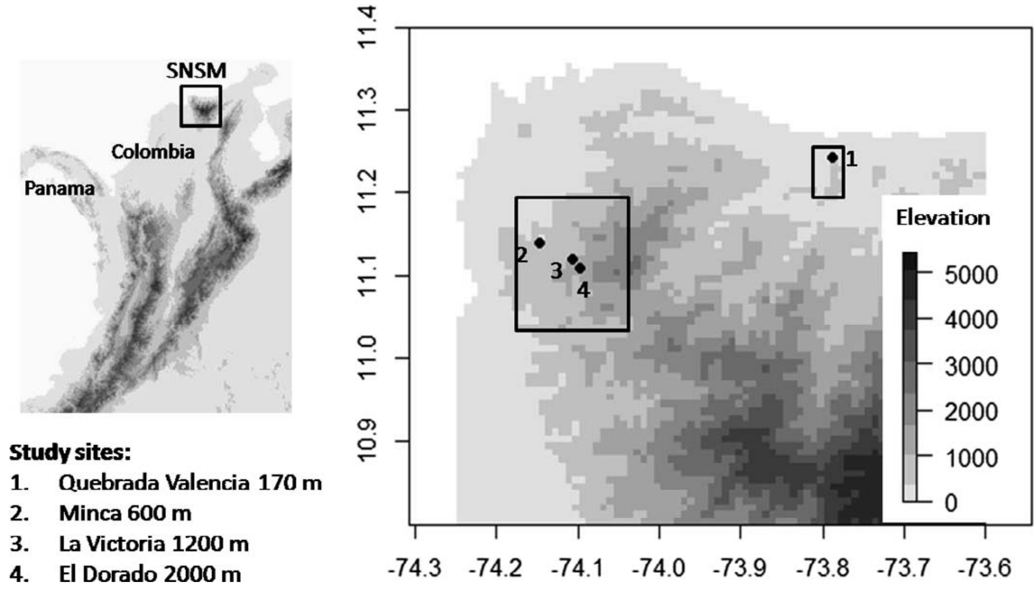

FIG. 1. Geographical location and elevation of study sites in the Sierra Nevada de Santa Marta in northern Colombia. Transects were located inside the two areas marked with a rectangle, and dots represent the capture stations at each site.

800 m) (11° 08′ 31.98″N, 74° 07′ 20.42″W); C. Pre-montane forest and shade-coffee in the Hacienda La Victoria (1,100–1,600 m) (11° 7′ 19.84″N, 74° 5′ 34.14″W); D. Montane forest (1,800–2,100 m) in El Dorado Nature Reserve (11° 06′ 66.88″N, 74° 04′ 15.15″W).

Sites B, C, and D were all located on the northwestern slope of the Sierra, while site A was in the northern foothills (Fig. 1). The lowland forest at site A was part of a 600 ha reserve representing one of the few remaining forest fragments at that elevation in the Sierra. The lowlands have mostly been transformed to pastures, cacao, and large scale banana cultivation (Fundación Pro Sierra Nevada de Santa Marta 1998 Instituto de Hidrología, Meteorología y Estudios Ambientales 2010b). The pre-montane and montane forest fragments at sites B and C were located in an area which has largely been transformed for shade-coffee cultivation between 600–1,200 m. However, there are still large remnants of forest, which are continuous with the higher elevation montane forests of site D. Canopy cover in the shade-coffee plantations ranged from 40–80%, and was provided primarily by two native tree species of the family Fabaceae (*Inga edulis* and *Enterolobium cyclocarpum*). The shade-coffee matrix dominated the landscape but was interspersed with riverine forests, secondary growth, small fields and gardens.

Data Collection.—Six experienced field observers carried out variable-distance transect counts during two spring migration seasons (Mar. to May 2010 and 2011). Given the timing of our sampling period, we likely recorded both migrating and wintering individuals of 10 species that wintered in the area (Hilty and Brown 1986, Gómez et al. 2013). However, as our sampling design covered the entire migration period, we assume that all individuals recorded were either actively migrating or initiated migration during the course of the study. We therefore only interpret our results in light of the migration period.

We established a total of 21 500-m long transects that followed existing trails or tracks at the four study sites (see Supplementary Table 1 for details and exceptions to the 500-m rule). The location of transects was chosen subjectively in order to have even coverage of the elevational gradient and to ensure that each transect was as uniform as possible, i.e. by making sure that at least 90% of the transect length was effectively within forest (at all sites) or within shade-coffee plantations (at sites B and C). Survey effort varied within sites and years (Table 1), but sampling dates were evenly distributed (every 3–5 days during 2 months) within the migration period in all cases (Banks-Leite et al. 2012, Gómez et al. 2013).

TABLE 1. Transect count effort, expressed in kilometers of transects walked, by year and elevational band (m) in the Sierra Nevada de Santa Marta, Colombia.

Year	0–500	500–1,000	1,000–1,500	1,500–2,000	2,000–2,500
2010	15.5	0	46.5	20	10
2011	3	22	39	9	0

Observers walked transects at a steady pace and recorded the perpendicular distance (to the nearest m) from the transect to all migratory birds detected. Perpendicular distances were estimated visually by tracing an imaginary line from the detected bird to the center of the transect (Bibby et al. 1993). No birds were recorded beyond 50 m. All observers were familiar with visual and sound identification of migratory species at the site and standardization sessions were carried out for distance estimation. Observers were also randomly assigned to transects on each sampling occasion.

In addition to the transect counts, three constant effort capture stations were set up at different elevations and were run between 14 March and 6 May in 2010 and 2011 (see Gómez et al. 2013). Stations were placed in lowland forest (175 m), pre-montane forest (1,150 m), shade-coffee (1,175 m), and montane forest (1,925 m) at the same study sites and were all in areas that overlapped with transects. Mist-nets were opened every day shortly before dawn and were operated for an average of 5 hrs. All birds captured were banded with uniquely numbered (Porzana made) metal bands.

Phenology of Migration.—To describe arrival and departure dates, the phenology of all species combined, and the phenology of individual species with >60 captures, capture data were averaged across 3-day periods. First, the total number of captures by day and by station were calculated including only captures from the first 4 hrs after dawn. We set the cut-off point at 4 hrs in order to avoid the need to correct for mist-net effort (Silkey 1999, Simons et al. 2004), taking into account that of the 134 days included in this analysis, effort was <4 hrs over just 7 days (5%). Daily totals were then averaged across 3-day periods, excluding days on which mist-netting did not take place, in order to account for the fact that mist-netting took place daily or on alternate days depending on the station.

Migrant Species Richness by Elevation.—Species richness by elevation was determined by calculating the total number of species recorded on transects at different elevations. Species accumulation curves were constructed for all transects to confirm that they had reached an asymptote regardless of differences in effort. To evaluate variation in species richness as a function of elevation, a generalized linear model framework was implemented in R (R Development Core Team 2013). We fitted linear, quadratic, and polynomial models and carried out model selection through AIC*c* (Burnham and Anderson 2002). Models were fit for both years combined and for each year separately.

Given that shade-coffee is only present within a relatively narrow elevation band in our study region (600–1,200 m), habitat could not be included as a covariate in the regression models that included transects across the complete elevation gradient. To test for differences between habitats, we first estimated mean species richness in coffee and forest between 600–1,200 m and then carried out a randomization test of the difference in means with 9,999 iterations using R (R Development Core Team 2013).

The area of each elevational band is known to be an important factor affecting species richness in elevation gradients (Rahbek 1995, Romdal and Grytnes 2007, Karger et al. 2011). To test for area effects within elevation bands in the Sierra (0–2,500 m, in 500 m intervals), the number of 0.5-km cells containing forest were estimated from a global land cover layer developed using MODIS data from the years 2000–2010 (Broxton et al. 2014). 'Forest cells' were defined as all the map cells classed as evergreen broadleaf forest, deciduous broadleaf forest, mixed forests, or closed shrubland (categories 2, 4, 5 and 6 in Broxton et al. 2014). Area calculations were carried out with the raster calculator in ArcMAP v10.0 (ESRI 2009). Species totals for each transect within the five 500-m elevation bands were averaged and linear models of species richness as a function of area were constructed with log-transformed variables (Rahbek 1995, Romdal and Grytnes 2007). The resulting slope was entered into the equation 'Corrected No. Spp

= Raw No. Spp / Area$^{(slope)}$', following the method proposed by Karger et al. (2011) to estimate area-corrected values of species richness by elevation.

Density of Migrants by Elevation.—Transect counts were used to estimate density by elevation for all migrant species combined and for the commonest species individually (those with at least 60 detections). Observations in forest and shade coffee were analysed separately both for all species combined and for individual species with enough detections. Densities of all species combined were estimated by transect; however, estimates of individual species were grouped by elevation bands of 500 m, because there were too few detections to estimate density by transect. The phenology of each species was used to determine the initial and final dates to include in the analyses, according to each species' passage period, in order to avoid underestimations of density by including transects conducted outside of passage periods.

Accounting for Imperfect Detection.—Transect data were analyzed using a multiple covariate distance sampling (MCDS) model approach in DISTANCE 6.0 (Marques and Buckland 2003, Marques et al. 2007, Thomas et al. 2010), with post-stratification by elevation and the inclusion of two categorical covariates to explain detection probability: year (2010, 2011) and observer (six field observers).

Initial examination of the raw detection histograms revealed some clumping at even-spaced distances, both for forest and for coffee, so raw observations were grouped in intervals of 2 m and truncated at 26 m. Only 1% of the observations were beyond 26 m. The resulting detection histograms were satisfactorily 'sigmoid-shaped' with the expected shoulder at short distances (0–5 m) (Fewster et al. 2005, Marques et al. 2007, Thomas et al. 2010), and they were used to estimate the global detection functions for forest and shade-coffee. The hazard rate and half normal key detection functions with cosine, simple polynomial, or hermite polynomial adjustment terms were tested for model fit (Marques et al. 2007). The best fit model was selected through AIC (Johnson and Omland 2004) and posteriorly used as a global detection function to estimate densities. Variance was assumed to be Poisson and a non-parametric bootstrap set to 999 re-sampling units was carried out to account for small sample sizes within elevation bands (Marques and Buckland 2003, Marques et al. 2007).

Density estimates in forest for individual species were used in a modeling framework to predict density as a function of elevation, with year as a factor. The resulting values were plotted to visualize variation in abundance by elevation for individual species.

RESULTS

Community Composition and Phenology of Migration.—We recorded 39 species of Nearctic-Neotropical migrants through transect counts and captures, during the spring migrations of 2010 and 2011 in the Sierra (Table 2). Ten species accounted for 90% of all observations and captures, with Tennessee Warbler, Red-eyed Vireo, Blackburnian Warbler and Gray-cheeked Thrush being the most abundant species.

The timing of spring passage for all species combined, estimated through captures, had an approximate duration of 1.5 months and showed a marked peak around 20 April (see Fig. 1S in supplementary material). Visual inspection of the phenology of individual species, revealed slight variation within this time period (see Fig. 2S in Supplementary Material). For example, Tennessee Warblers showed a peak in passage around 30 March while Red-eyed Vireos and Blackburnian Warblers peaked around 17 April. Gray-cheeked Thrush was the last species of the season to pass through, with passage peaking around 23 April. Of these species, Tennessee Warblers and Blackburnian Warblers also wintered in the Sierra; however, their dome shaped phenologies show that many more individuals passed through during migration than were present at the start of the study period and that almost all birds had departed prior to the end of the study (Fig. 2S in supplementary material).

Species Richness by Elevation.—Nearctic-Neotropical migratory species richness showed a mid-elevation hump with the greatest number of species occurring between 700–1,700 m (Fig. 2). Species richness was lower at high elevations (>2000 m) in comparison to low elevations (<500 m). In all cases (years combined and separate), the quadratic model of species richness as a function of elevation recieved more support from AIC*c* and had the highest r^2 values (Table 3). The randomization test showed that there was no significant difference in mean

TABLE 2. Number of observations of Nearctic-Neotropical migratory birds recorded during spring migration in 2010 and 2011 through transect surveys at different elevations in the Sierra Nevada de Santa Marta, Colombia. We present the number of observations per 10 km of transect, after correcting for transect length, as well as the raw number of observations in brackets.

	No. Observations (Ind/10 km) by Elevation (m)				
Species	0–500 m	500–1,000	1,000–1,500	1,500–2,000	2,000–2,500
Broad-winged Hawk (*Buteo platypterus*)		0.45 (1)	0.53 (5)		
Merlin (*Falco columbarius*)			0.10 (1)		
Peregrine Falcon (*Falco peregrinus*)			0.10 (1)		
Common Nighthawk (*Chordeiles minor*)	0.54 (1)		0.10 (1)		
Yellow-billed Cuckoo (*Coccyzus americanus*)	0.54 (1)	0.45 (1)	0.42 (4)		
Bank Swallow (*Riparia riparia*)	0.54 (1)				
Veery (*Catharus fuscescens*)	1.08 (2)				
Gray-cheeked Thrush (*Catharus minimus*)	3.78 (7)	40.45 (89)	8.24 (77)	12.61 (41)	0.83 (1)
Swainson's Thrush (*Catharus ustulatus*)		0.45 (1)	1.49 (14)	1.84 (6)	
Olive-sided Flycatcher (*Contopus cooperi*)	0.54 (1)	0.90 (2)	2.03 (19)	0.92 (3)	
Eastern Wood-Pewee (*Contopus virens*)	9.18 (17)	4.54 (10)	6.31 (59)	1.23 (4)	
''Trail's Flycatcher'' (*Empidonax traillí/alnorum*)		0.45 (1)			
Acadian Flycatcher (*Empidonax virescens*)		0.45 (1)	0.10 (1)		
Great Crested Flycatcher (*Myiarchus crinitus*)			0.21 (2)		
Sulphur-bellied Flycatcher (*Myiodynastes luteiventris*)		3.18 (7)	0.21 (2)		
Eastern Kingbird (*Tyrannus tyrannus*)		9.09 (20)	0.21 (2)		
Scarlet Tanager (*Piranga olivacea*)		1.36 (3)	5.46 (51)	1.23 (4)	
Summer Tanager (*Piranga rubra*)	1.62 (3)	0.90 (2)	2.56 (24)	1.53 (5)	
Indigo Bunting (*Passerina cyanea*)	0.54 (1)				
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)		1.81 (4)	10.81 (101)	2.15 (7)	
Yellow-green Vireo (*Vireo flavoviridis*)		0.90 (2)	0.10 (1)		
Red-eyed Vireo (*Vireo olivaceus*)	8.10 (15)	58.63 (129)	12.31 (115)	7.69 (25)	
Louisiana Waterthrush (*Parkesia motacilla*)		0.90 (2)	0.53 (5)		1.66 (2)
Northern Waterthrush (*Parkesia noveboracensis*)	7.02 (13)	3.18 (7)	2.14 (20)		
Black-and-white Warbler (*Mniotilta varia*)			0.96 (9)	3.07 (10)	
Prothonotary Warbler (*Protonotaria citrea*)	1.08 (2)		0.10 (1)	0.30 (1)	
Mourning Warbler (*Oporornis philadelphia*)	0.54 (1)	2.72 (6)	6.10 (57)	0.30 (1)	
Bay-breasted Warbler (*Setophaga castanea*)	0.54 (1)	0.45 (1)	0.21 (2)		
Cerulean Warbler (*Setophaga cerulea*)			0.10 (1)	0.30 (1)	
Blackburnian Warbler (*Setophaga fusca*)	2.16 (4)	5.90 (13)	39.93 (373)	51.38 (167)	37.5 (45)
Magnolia Warbler (*Setophaga magnolia*)			0.10 (1)		
Chestnut-sided Warbler (*Setophaga pensylvanica*)	1.08 (2)				
Yellow Warbler (*Setophaga petechia aestiva*)	1.08 (2)	3.18 (7)	0.10 (1)		
Black-throated Green Warbler (*Setophaga virens*)			0.21 (2)		
American Redstart (*Setophaga ruticilla*)	2.16 (4)	6.36 (14)	5.67 (53)	3.69 (12)	
Tennessee Warbler (*Oreothlypis peregrina*)	4.86 (9)	11.36 (25)	79.01 (738)	36.00 (117)	5.00 (6)
Golden-winged Warbler (*Vermivora chrysoptera*)			0.53 (5)	0.61 (2)	
Canada Warbler (*Cardellina canadensis*)	1.08 (2)				
Baltimore Oriole (*Icterus galbula*)			0.32 (3)		
Total No. Species by Elevation	**20**	**23**	**33**	**16**	**4**

species richness between shade-coffee and forest at the same elevation (9,999 iterations, $P = 0.35$).

The estimated area of forest decreased with elevation (Fig. 3) and log-transformed areas showed a relatively high correlation with log species richness (Linear model: No. Of Species = area*1.38 – 9.66; $r^2 = 0.60$, $P = 0.07$). However, correcting the number of species by area of forest available within the elevation bands did not change the hump-shaped pattern of species richness (Fig. 3). In fact, the correlation between the raw and corrected species richness values was high ($r^2 = 0.95$, $P < 0.01$).

Density of Migrants by Elevation.—The global detection functions which recieved the highest support from AIC were similar for coffee and forest in all cases but differed for the individual species: all species combined (half-normal with

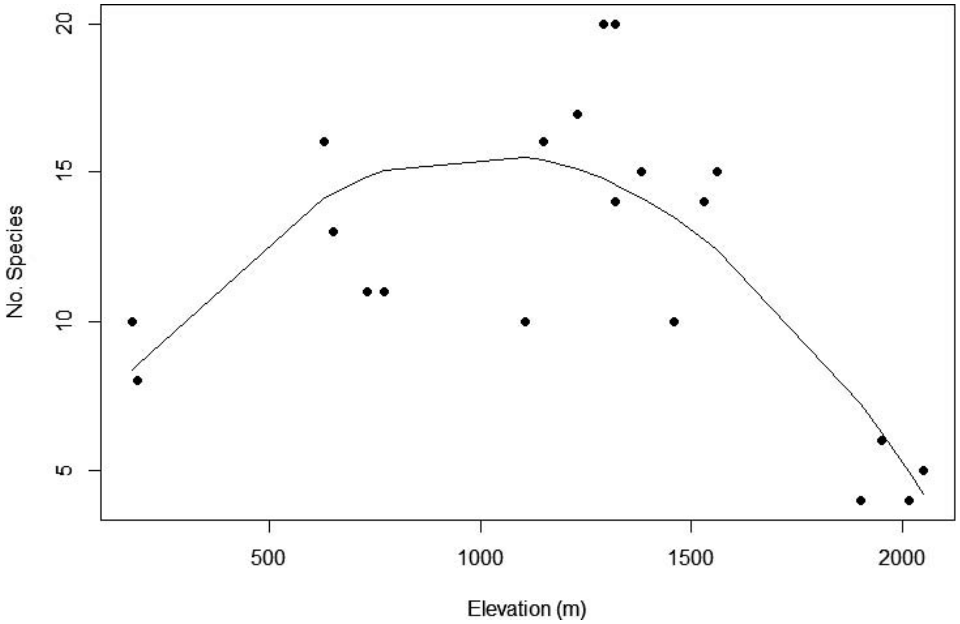

FIG. 2. Variation in species richness of Nearctic-Neotropical migratory landbirds as a function of elevation during spring migration 2010 and 2011 in the Sierra Nevada de Santa Marta. Points represent species richness for individual transects and the line shows the best AIC model for all years combined (quadratic model, $r^2 = 0.59$, $P < 0.01$).

cosine adjustments); Swainson's Thrush, Blackburnian Warbler and Red-eyed Vireo (half-normal key); Tennessee Warbler (hazard-rate with cosine adjustment).

Density estimates for all species combined showed a similar elevational pattern to that of species richness (Fig. 4), with higher densities of migrants at mid elevations. However, when examining the densities of the most abundant species individually, they each showed peaks at slightly different elevations (Table 4, Fig. 5).

The abundance of individual species also varied between years and habitats. Noteworthy was an increase in the number of birds of all species from 2010–2011 within the 1,000–1,500 m elevational band (Table 3, Fig. 5). Differences in abundance between forest and shade coffee at the same elevation were also evident (Table 3), with Tennessee Warblers, Red-eyed Vireos, and Gray-cheeked Thrushes being more abundant in forest than coffee, while Blackburnian Warblers showed similar numbers in both habitats at the same elevation.

DISCUSSION

Our findings suggest that Nearctic-Neotropical migratory landbirds have a unimodal distribution

TABLE 3. Results of models examining species richness as a function of elevation. In all cases, the model with the highest support was the quadratic function showing the mid elevation hump (also see Fig. 2).

	Model	AIC*c*	Δi	w_i	r^2	$P < 0.05$
All years	Quadratic	113.520	0.0	0.53	0.590	*
	Polynomial	113.768	0.2	0.47	0.630	*
	Linear	130.691	17.2	0.00	0.000	
2010	Quadratic	84.073	0.0	0.74	0.650	*
	Polynomial	86.165	2.1	0.26	0.670	*
	Linear	99.996	15.9	0.00	0.002	
2011	Quadratic	107.636	0.0	0.58	0.180	
	Linear	108.648	1.0	0.35	0.010	
	Polynomial	111.748	4.1	0.07	0.123	

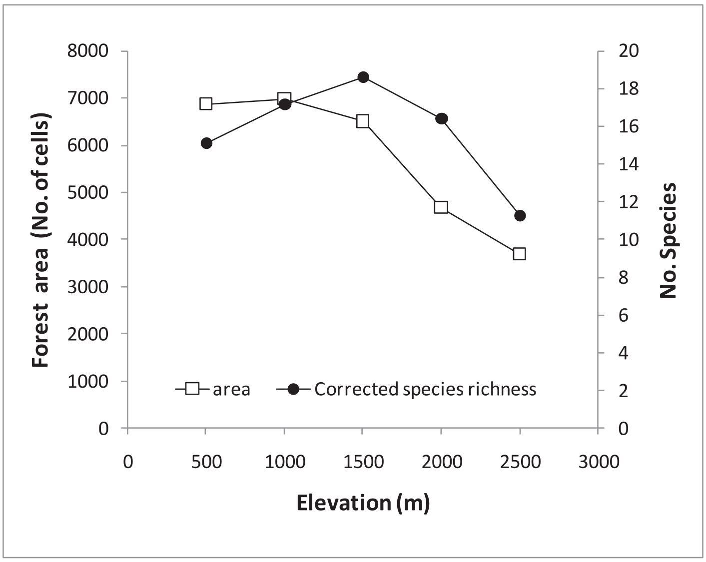

FIG. 3. Relationship between forest area within elevation bands and migratory species richness in the Sierra Nevada de Santa Marta. The hump-shaped distribution was maintained when correcting for area. Forest area was estimated from MODIS derived land cover data at 0.5-km resolution (Broxton et al. 2014), and the area-corrected species number was obtained from the equation 'Corr. Spp. No = Raw Spp. No / Area$^{(slope)}$' (Karger et al. 2011).

across an elevation gradient, when on stopover during spring migration in northern Colombia. As a community, migratory birds displayed a 'mid elevation hump' in both species richness and abundance, peaking between 700–1,700 m. This pattern held even after taking into account the area of forest available at different elevations (Romdal and Grytnes 2007, Karger et al. 2011). Individual species showed peaks in abundance at slightly different elevations, as well as large

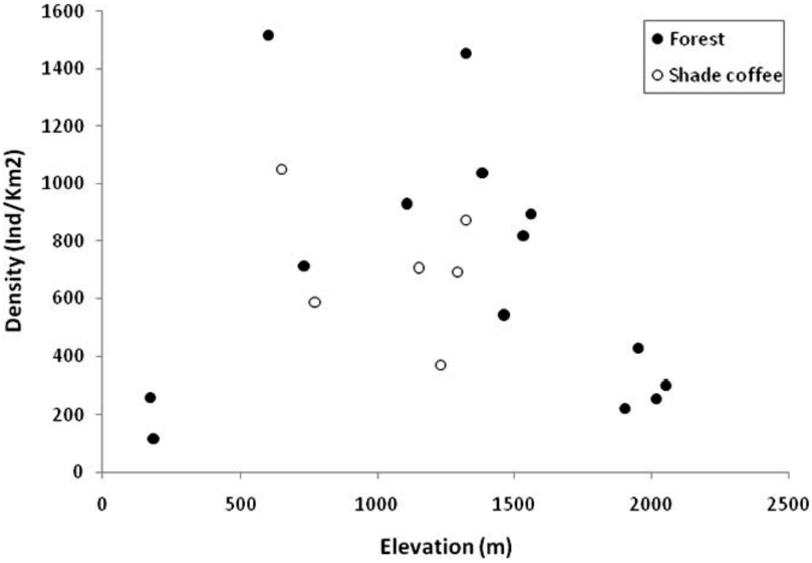

FIG. 4. Relationship between elevation and the density of all Nearctic-Neotropical migrant landbirds combined, in forest and shade coffee habitats in the Sierra Nevada de Santa Marta during spring migration 2010 and 2011. Points represent individual transects.

TABLE 4. Densities of the four most abundant species of Neotropical migratory birds along an elevation gradient during spring migration in the Sierra Nevada de Santa Marta. Values are expressed as individuals per km^2 ± SE. Blank spaces in the table represent elevations that were not sampled in either year.

		Forest		Shade coffee	
	Elevation	2010	2011	2010	2011
Gray-cheeked Thrush	0–500	42 ± 17	28 ± 19		
	500–1,000		266 ± 37		440 ± 67
	1,000–1,500	175 ± 34	119 ± 21	19 ± 4	69 ± 18
	1,500–2,000	84 ± 22	277 ± 47		
	2,000–2,500	36 ±18			
	Elevation	2010	2011	2010	2011
Tennessee Warbler	0–500	21 ± 7			
	500–1,000		47 ± 15		48 ± 15
	1,000–1,500	227 ± 25	1,126 ± 66	70 ± 13	231 ± 25
	1,500–2,000	146 ± 18	225 ± 38		
	2,000–2,500	24 ± 10			
	Elevation	2010	2011	2010	2011
Blackburnian Warbler	0–500	3 ± 2	0		
	500–1,000		21 ± 9		40 ± 13
	1,000–1,500	94 ± 14	138 ± 19	111 ± 11	246 ± 27
	1,500–2,000	189 ± 20	294 ± 43		
	2,000–2,500	159 ± 24			
	Elevation	2010	2011	2010	2011
Red-eyed Vireo	0–500	10 ± 5	92 ± 46		
	500–1,000		726 ± 83		186 ± 31
	1,000–1,500	136 ± 21	88 ± 18	30 ± 5	26 ± 7
	1,500–2,000	4 ± 2	0		
	2,000–2,500	0			

variations in abundance between years. This variation in species richness and abundance with elevation has not been previously documented for birds on migration in South America or elsewhere in the Neotropics, despite having considerable implications for their study and conservation (Faaborg et al. 2010). Indeed, our results imply that conservation measures directed towards mid-elevation forests in the Sierra would not only benefit the greatest number of species but also the greatest number of individuals. While some species would benefit less from such actions, it is noteworthy that species of conservation concern, such as the Cerulean Warbler (*Setophaga cerulea*), Golden-winged Warbler (*Vermivora chrysoptera*), and Olive-sided Flycatcher (*Contopus cooperi*) went almost undetected away from mid-elevations (Table 2).

Mid-elevation peaks in diversity are relatively common in resident communities along elevation gradients in the tropics (Terborgh 1977, Rahbek 1995, Kattan and Franco 2004, Herzog et al. 2005). Whether factors such as climate, predation risk, competition, habitat structure and heterogeneity, or pathogens determine variations in the elevational distribution of migrants, as they do for resident birds (Terborgh and Weske 1975, Terborgh 1977, Ricklefs and Schluter 1993, Kattan and Franco 2004), remains to be tested. Given that the Sierra is an important spring and fall stopover site for Nearctic-Neotropical migrants, where birds accumulate large energy reserves (Bayly et al. 2012, 2013; Gómez et al. 2013), we would expect food abundance to be the most critical factor shaping migrant distribution during that period, with predation risk and parasite exposure potentially playing a secondary role (Sapir et al. 2004; Pomeroy 2006a, b; Buler et al. 2007; Møller and Szép 2011). Previous research has shown that migrants are capable of detecting food abundance at a fine scale (McGrath et al. 2009, Wood et al. 2012), and a recent study showed that frugivorous migrants primarily used food abundance to select stopover habitats in Costa Rica, while insectivores

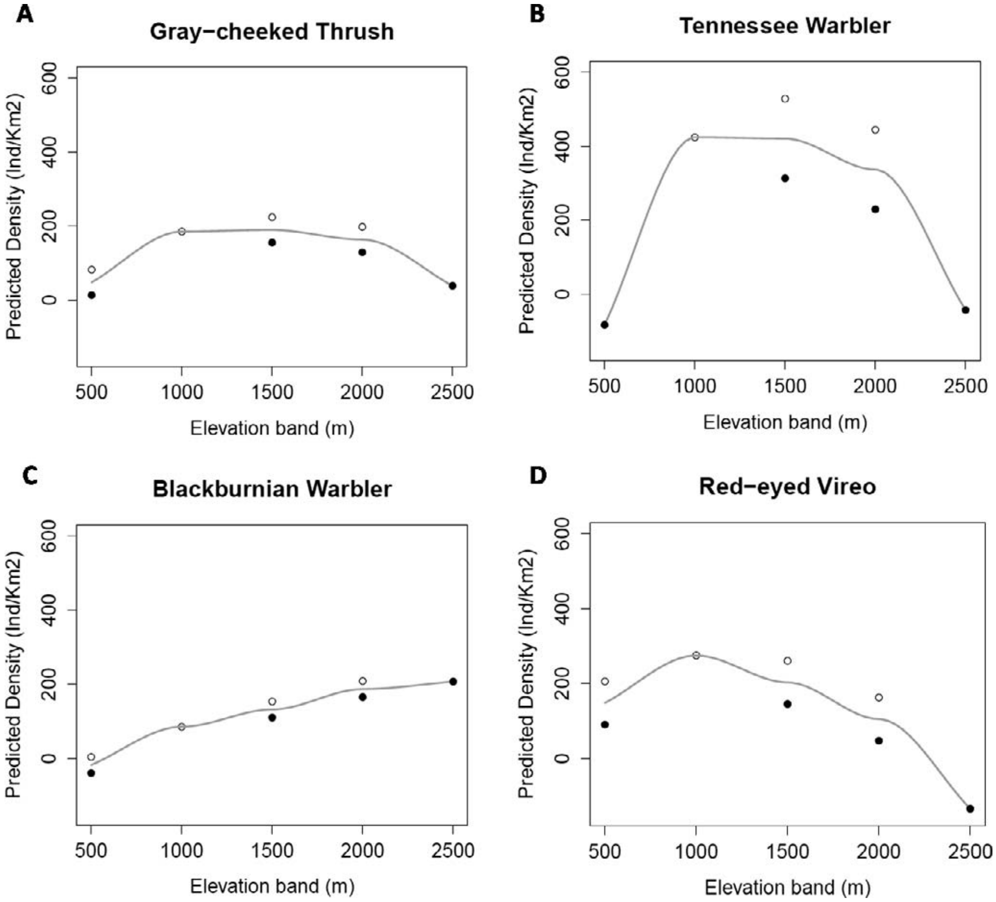

FIG. 5. Predicted density in forest of the four commonest species of migrants by elevation band. Fitted values were extracted from polynomial models of densities as a function of elevation and with year as a factor. A. Gray-cheeked Thrush (*Catharus minimus*), B. Tennessee Warbler (*Oreothlypis peregrina*), C. Blackburnian Warbler (*Setophaga fusca*), D. Red-eyed Vireo (*Vireo olivaceus*). Closed symbols represent model predictions for 2010 and open symbols for 2011.

used vegetation structure (Wolfe et al. 2014). Overall, this suggests that food availability could be shaping the distribution of migratory birds observed in the Sierra.

Although no information exists about predation risk for migrants along elevation gradients, the diversity and abundance of bird predators and pathogens are known to decrease with increasing elevation in the tropics (Martin 1995, Boyle 2008, Zamora-Vilchis et al. 2012). Moreover, migratory bird behavior during stopover has been documented to change specifically in response to predation risk (Schmaljohann and Dierschke 2004; Pomeroy 2006a, b). Regardless of the degree to which elevational variations in food abundance and predation risk determine the overall patterns observed, our results indicate that individual species respond differently to the factors present (Fig. 5). For instance, Blackburnian Warblers increased in abundance along the elevation gradient sampled, while Red-eyed Vireos peaked in abundance at lower elevations when compared to Gray-cheeked Thrushes or Tennessee Warblers. It is probable that Blackburnian Warblers would also show a hump-shaped distribution if higher elevations had been included in our sample. Indeed, general bird diversity and abundance decrease rapidly above 3,200 m in most Colombian mountains, and the vegetation structure at higher elevations becomes inappropriate for a canopy insectivore like the Blackburnian Warbler (Terborgh 1977, De La Zerda and Stauffer 1998, Kattan and Franco 2004). These individual patterns of abundance may well reflect habitat preferences and suitability for each species during migration (Sapir et al. 2004, Buler and Moore 2011), but it is interesting to note that they do not necesarily reflect winter habitat. For example, Gray-cheeked Thrushes and Red-eyed Vireos largely occupy lowland Amazonian forests in winter but show a mid-elevation peak in the Sierra.

The migrant community as a whole showed large annual variations in abundance, which might be attributed to varying food availability (Wolfe et al. 2014), weather patterns (Liechti 2006, Laughlin et al. 2013), annual variation in productivity (Rodenhouse et al. 2003, Hoye et al. 2012), or most likely a combination of all of these factors (Sillett and Holmes 2002, Mitchell et al. 2011). Individual species needs and preferences, as well as annual variation, must be taken into account when designing conservation and management strategies for Nearctic-Neotropical migrants during stopover (Sherry and Holmes 1996, Faaborg et al. 2010).

In addition to differences in distribution with elevation, we also found differences between shade-coffee and forest within the same elevation band. Although total species richness was not significantly different between the two habitats, frugivorous species like Gray-cheeked Thrushes and Red-eyed Vireos tended to be more abundant in forest relative to shade-coffee, while insectivores like Blackburnian Warblers were equally abundant in both habitats. This suggests that transformed habitats, like shade-coffee, may not fulfill the needs of all species during migration to the same degree as the native forests they have replaced (Petit et al. 1995, Shochat et al. 2002, Buler and Moore 2011, Wolfe et al. 2014). Despite the intuitiveness of this, there are no studies to date that compare fueling rates and general migratory performance between birds that stopover in coffee versus forest (Komar 2006).

The results of this study have conservation implications for migrants at the local and regional level, as well as underlining the need for future research. In the Sierra, as elsewhere in the Colombian Andes, habitats between 700–1,700 m have been subjected to high levels of deforestation and transformation (Fundación Pro Sierra Nevada de Santa Marta 1998, Instituto de Hidrología, Meteorología y Estudios Ambientales 2010a). Indeed, in Colombia the rate of deforestation has been estimated to be >320,000 ha/year (Instituto de Hidrología, Meteorología y Estudios Ambientales 2010a). Furthermore, forest remnants between 700–1,700 m in the Sierra are mostly outside of protected areas (Instituto de Hidrología, Meteorología y Estudios Ambientales 2010a, b), and much of the forest has already been transformed to shade-coffee plantations. Our finding that shade-coffee supports lower densities of certain species suggests that this habitat may be of lower quality, given that migratory birds are expected to respond numerically to food availability at stopover sites (Buler et al. 2007, Wolfe et al. 2014). This scenario of decreasing habitat availability and quality suggests an immediate need for the design of landscape-scale management strategies that take into account the patterns of species richness and abundance found here. Indeed, the densities of migratory birds recorded in mid-elevation forest in the Sierra are considerably higher (mean 914 birds/km^2) than those recorded in other stopover regions in the Americas, such as the Gulf Coast of North America (250 birds/km^2, max 612; Buler et al. 2007) or the Yucatan Peninsula (569–619 birds/km^2; Bayly and Gómez 2011), highlighting the importance of the Sierra.

The results presented here may have been affected in part by limitations in the study design, which led to variation in sampling effort, the differential coverage of the elevation gradient during the sampling period, and an incomplete coverage of the gradient in the study region (0–5,700 m). Consequently, it could be argued that a constant sampling effort and a wider coverage of the gradient might have resulted in different patterns of distribution than those reported; however, we argue to the contrary for the following reasons. First, all of our cumulative curves of species richness reached an asymptote regardless of differences in sampling effort between elevations and years. Second, the observed patterns of richness and abundance were consistent between the 2 years sampled, despite high annual variability in abundance. Finally, the inclusion of a wider elevation gradient is expected to strengthen the pattern we detected, as vegetation structure becomes simpler at higher elevations and its appropriatness for forest-dwelling migrants likely decreases.

To further our understanding of the needs of migratory birds, future research should evaluate the factors that have shaped elevational and habitat preferences, including an assessment of resource availability and use, and of predation risk for migrants along elevation gradients in the Neotropics. A comparison of fueling rates in a variety of species that stopover in forest versus transformed habitats should be a priority research topic, especially for species with pronounced population declines (Sauer et al. 2008, Faaborg et al. 2010). Finally, management measures such as increasing the diversity of shade trees in coffee plantations need to be evaluated (Philpott et al. 2008), as they might prove critical to enhancing the quality of this habitat for frugivorous migrants during stopover.

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