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RESEARCH ARTICLE

Understanding the distribution of a threatened bird at multiple levels: A hierarchical analysis of the ecological niche of the Santa Marta Bush-Tyrant (*Myiotheretes pernix*)

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ABSTRACT

An understanding of the ecological factors determining bird species' distributions is essential for making informed conservation decisions. These data are especially important for range-restricted species, such as the Santa Marta Bush-Tyrant (*Myiotheretes pernix*), a threatened endemic of the Sierra Nevada de Santa Marta (SNSM) in Colombia. Here we adopt a novel hierarchical analysis to describe the bush-tyrant's ecological niche and infer the regional and local determinants of its limited distribution. We first describe habitat selection based on local habitat use and microhabitats used for foraging. We then use a geoprocessing modeling algorithm to combine habitat selection data with a climatic niche model. The resulting model produced an index of habitat suitability, which we converted into a predicted geographic distribution. Santa Marta Bush-Tyrants showed no clear habitat preferences, but favored forested and secondary growth habitats over open areas, at elevations between 2,100 and 3,300 m. The species' predicted distribution was restricted to the northern flanks of the SNSM, with an estimated extent of ~352 km^2. This estimate is more restricted than previous estimates (570 km^2), but does not alter the species' status as Endangered based on IUCN criteria. The model predicted that the presence of Santa Marta Bush-Tyrants was regionally dependent on cold and humid climates, with low annual variation in temperature and precipitation. Locally, the species' presence was determined by the availability of habitat edges between forests and open areas. Conservation actions should aim to reduce rates of forest loss, while maintaining the presence of areas with good light and exposed perches, microhabitat conditions typically found in habitat edges or areas of natural disturbance. An explicit integration of quantitative data on habitat use and foraging patterns into niche models would help to obtain more realistic and detailed projections of the occupied distribution of range-restricted birds.

Keywords: Colombia, distribution, foraging ecology, habitat use, microhabitat, Sierra Nevada de Santa Marta

Entendiendo la distribución de un ave amenazada a múltiples escalas: un análisis jerárquico del nicho ecológico del *Myiotheretes pernix*

RESUMEN

Una comprensión básica de los determinantes ecológicos de la distribución de la avifauna es esencial para fundamentar decisiones sobre su manejo y conservación. Esta información es especialmente relevante para especies de distribución restringida, como el *Myiotheretes pernix*, una especie amenazada y endémica a la Sierra Nevada de Santa Marta (SNSM) en Colombia. Utilizamos un análisis jerárquico para incrementar la información del nicho ecológico de este atrapamoscas, permitiéndonos inferir las determinantes regionales y locales de su limitada presencia. Primero, analizamos información sobre el micro-hábitat y hábitat local en sus zonas de forrajeo. Luego, empleando un algoritmo de geo-procesamiento, combinamos esta información con un modelo de nicho climático. El modelo resultante generó un índice de idoneidad de hábitat que se usó para proyectar la distribución geográfica de la especie. El *Myiotheretes pernix* no mostró claras preferencias en el uso del hábitat, pero seleccionó zonas boscosas y crecimiento secundario sobre áreas abiertas, entre los 2,100 y 3,300 m de altitud. La distribución predicha para la especie se restringe a los flancos del norte de la SNSM, extendiéndose por ca. 352 km^2. Dicha estimación es más restringida que los estimados previos (570 km^2), pero no alteraría su estatus En peligro de acuerdo a los criterios de la UICN. El modelo predijo que su presencia dependería regionalmente de climas fríos y húmedos, donde la estacionalidad de la temperatura y la precipitación es baja. Localmente, la especie dependería de la disponibilidad de bordes entre hábitats boscosos y áreas abiertas. Las acciones de conservación deberán enfocarse en el control de la deforestación, siempre y cuando se mantengan áreas con buenas condiciones de luz y perchas expuestas, características típicas de los bordes de hábitat o áreas perturbadas (natural). La integración explícita de información sobre uso del hábitat y patrones de forrajeo con modelos de nicho permitirán obtener proyecciones más realistas y detalladas del área ocupada por las especies de distribución restringida.

Palabras clave: Colombia, distribución, ecología de forrajeo, micro-hábitat, uso de hábitat, Sierra Nevada de Santa Marta

INTRODUCTION

Conservation planning and habitat management for species in peril presuppose some knowledge of a species' ecological requirements (Garshelis 2000, Sutherland et al. 2004), which is why ecological studies have been considered vital for devising effective conservation strategies for threatened birds (e.g., Renjifo et al. 2002, 2014, Boyla and Estrada 2005). An understanding of the main factors determining the presence or absence of a bird species will assist conservation stakeholders in prioritizing actions and increasing the efficacy of any applied strategy (Sutherland et al. 2004). However, for numerous threatened bird species in the Neotropics, there is still a lack of basic ecological information, particularly for some of the most vulnerable species, including those with restricted geographical ranges in areas threatened by habitat degradation and loss (Renjifo et al. 2002). Valuable insights into the conservation needs of these birds can be achieved by combining geographical distribution models with behavioral and ecological data (e.g., Botero-Delgadillo et al. 2015). Here we present data on the habitat use and distribution of the threatened Santa Marta Bush-Tyrant (*Myiotheretes pernix*), and assess the regional and local factors explaining its spatial occurrence.

The Santa Marta Bush-Tyrant is endemic to the Sierra Nevada de Santa Marta (SNSM), an isolated coastal mountain range in northern Colombia with exceptional levels of endemism (Krabbe 2008). The species occurs only in montane ecosystems and is currently listed as Endangered (EN) by Birdlife International, as it is believed to have undergone a moderate population decline and has been subject to a high rate of habitat loss (BirdLife International 2014). Agricultural expansion, small-scale logging, and afforestation with nonnative trees are the most important ongoing threats (BirdLife International 2014, Botero-Delgadillo and Olaciregui In press). Although forest fragmentation is thought to pose a threat to this species, birds are commonly seen in scrub and secondary growth, although they are less common in pine plantations and open areas with scattered trees (BirdLife International 2014, Botero-Delgadillo and Olaciregui In press).

The currently proposed ecological requirements and geographical distribution of the species (e.g., BirdLife International 2014) are based on very few records, and do not include a quantitative relationship with regional climatic conditions or vegetation. Two recent studies describe in some detail the species' foraging behavior and microhabitat use (Botero-Delgadillo 2011, Botero-Delgadillo and Bayly 2012), but without discussing explicitly the consequences for conservation. A compilatory analysis of all available information, linking ecological data at multiple scales, could help to accurately describe the species' ecological requirements and explain its apparently narrow geographical range, while simultaneously providing a model for improving our knowledge of other threatened species for which there is a paucity of information.

This study aimed to collate all published and unpublished data on the Santa Marta Bush-Tyrant in order to provide a quantitative assessment of its ecological niche at the regional, local, and microhabitat levels. First, we used historical and recent geographical records to identify the elevational and regional climatic patterns associated with the species' presence. Second, we quantitatively described the bird's foraging areas and documented patterns of habitat and microhabitat use to determine the main correlates of habitat selection, using geographic information system (GIS) tools. Finally, we combined all of this information to build a model of the species' occupied distribution, enabling us to infer the regional and local environmental variables that best explain its occurrence. Based on the resulting model, we discuss the current conservation status of the Santa Marta Bush-Tyrant.

METHODS

Regional Analyses: Elevational and Climatic Patterns

Geographical records for the Santa Marta Bush-Tyrant were obtained from museum specimens, the literature (Todd and Carriker 1922, Renjifo et al. 2002, Strewe and Navarro 2004), public databases including Global Biodiversity Information Facility (GBIF; http://www.gbif.org) and eBird (eBird 2012), and the authors' unpublished records (see http://ebird.org/content/ebird/). An initial dataset of 41 records was subjected to data cleaning by removing spatial replicates (e.g., records located within 1 km of each other) and geographical outliers (see Chapman 2005), and by discarding data points with less than 1 km precision. The remaining 15 localities (Figure 1A) were used to describe the elevational and climatic patterns associated with the species' presence.

Elevations between the 10^{th} and 90^{th} percentile of the presence dataset (between 1 and 2 SD around the mean value, or 80% of the data) were taken to represent the boundaries of the bush-tyrant's core elevational range. A

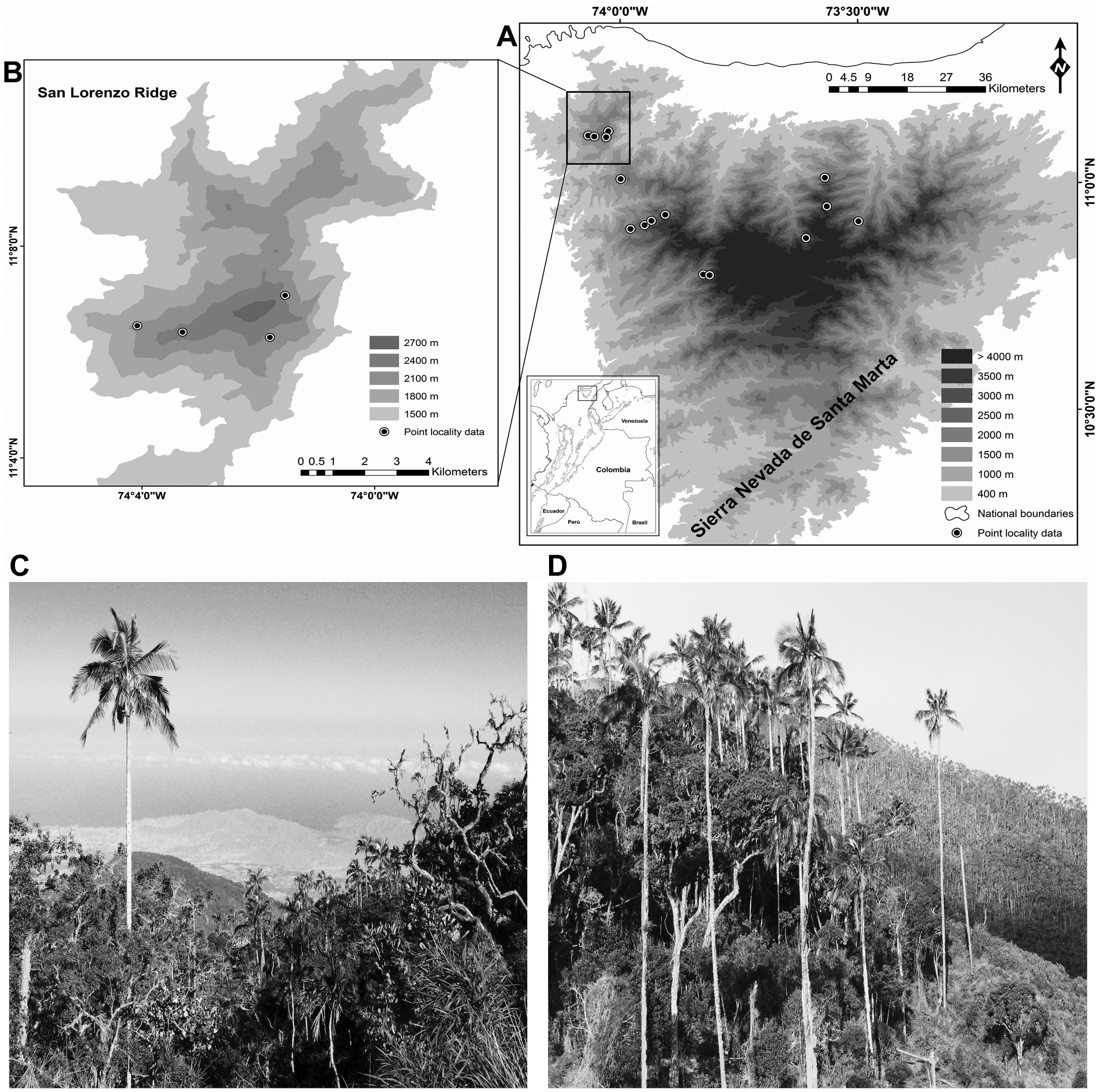

FIGURE 1. Geographical records of the Santa Marta Bush-Tyrant in the Sierra Nevada de Santa Marta (SNSM), northern Colombia. For regional analyses, 15 localities were used (**A**), while habitat and microhabitat analyses were based on records from the San Lorenzo Ridge, located on the northwestern flank of the SNSM (**B**). The San Lorenzo Ridge has extensive areas of mature and secondary forest (**C**), as well as edges between forested areas and open–transitional zones (**D**).

similar approach was used to quantify the core environmental space where most geographical records were located, using 3 uncorrelated climatic variables extracted from the 19 variables of the WorldClim database (http://www.worldclim.org/) at 1 km^2 resolution (see below). The 3 climatic variables were extracted by first constructing a correlation matrix for the 19 variables based on Spearman's correlation coefficients (r_s), and removing those variables with coefficients >0.85 (see Kamilar and Muldoon 2010). The remaining 8 variables were then subjected to a principal components analysis (PCA correlation matrix; Digby and Kempton 1987) to select the variables with the highest loading for each of the first 3 components; together these components explained 91% of the environmental variability associated with species presence points and 1,000 randomly generated points throughout the SNSM. The PCA was also useful for exploring the main climatic correlates determining the presence of the species throughout the SNSM in a multivariate space, since the 1,000 random points were representative of the environmental diversity available: Rarefaction curves showed that 800–1,000 points were needed to represent ~95% of the spatial diversity of the climatic variables. The same variable set used for the PCA was also employed for modeling the bush-tyrant's climatic niche. We used a modeling algorithm that allowed us to identify the climatic variables that contributed the most to the model and best explained the species' regional distribution (see details below).

Random point generation and data extraction for all points were carried out in ArcGIS 9.3 (ESRI, Redlands, California, USA). Statistical analyses were performed in R 2.15.2 (R Development Core Team 2012).

Local (Habitat) and Microhabitat Analyses

Habitat and microhabitat analyses were based on descriptions of foraging areas used by the Santa Marta Bush-Tyrant on the San Lorenzo Ridge, located on the northwestern slope of the SNSM (Figures 1B, 1C, 1D). This is the most accessible locality within the species' range and the source of the majority of information on its ecology. The dataset ($n = 35$) combined 22 foraging observations taken from Botero-Delgadillo (2011) and 13 subsequent observations made by E. Botero-Delgadillo. Habitat and microhabitat features were recorded each time a bird was observed performing a foraging bout, along two 2-km transects that were sampled twice a day during 4 nonconsecutive days per month from February to September 2008 (Botero-Delgadillo 2011) and in March 2009. Both transects reached the maximum elevation of the San Lorenzo Ridge, covering an altitudinal gradient from 1,600 to 2,700 m. To reduce spatiotemporal dependence among data (Noon and Block 1990), we marked all foraging spots to prevent future record collection at the same site.

Using a digital recorder, the following information about each bird's foraging habitat and microhabitat was recorded: vegetation type following the CORINE Land Cover Methodology for Colombia, 2008 (IDEAM 2008); the bird's position relative to the edge of the habitat type, defined as (i) edge, when the observed bird occurred <50 m from any edge (including clearings within forest patches), and (ii) interior, when the bird was >50 m from any edge (see Paton 1994, Murcia 1995); a visual estimate of the bird's height from the ground (m); a visual estimate of the vertical distance from the bird's position to the forest canopy or top of the tree or bush (m); the horizontal position of the bird relative to the center of the tree or bush (Remsen and Robinson 1990), defined as 1 of 4 categories (1: center; 2: near the center; 3: mid-portion outward; 4: outer branches); and the percentage of vegetation cover (i.e. foliage density; see details in Remsen and Robinson 1990) in an imaginary sphere of 50-cm radius around the bird's position. Estimation of all distances was aided by using a GPS (habitat scale) or a laser rangefinder (microhabitat scale).

Analyses of habitat use and selection followed a Type I design (i.e. pooling all individual data for a single analysis at the population level; Garshelis 2000) to compare the observed and expected frequencies of use of each vegetation type present on the San Lorenzo ridge. Five habitat categories were identified within the study area and we estimated the total area of each one in ArcGIS 9.3 using a geographical layer of vegetation cover based on the CORINE Land Cover Methodology for 2008 at 1:25,000 scale. Habitat types with <5 records were lumped before estimating the habitat use proportions and the confidence intervals around them (Neu et al. 1974, Cherry 1996); confidence intervals were then compared to expected proportions through a chi-square goodness-of-fit test (see Garshelis 2000). Expected values by habitat were obtained by dividing the total number of records (35) by the proportion of San Lorenzo Ridge covered by each habitat (habitat extents estimated from 1,800 m upwards; see Figure 1B). We also calculated the Neu's selection ratio (the ratio of observed to expected frequencies) for each habitat.

To summarize the microhabitat features associated with the foraging sites, we estimated the interquartile range (IQR; Q_3–Q_1), the 10^{th} and 90^{th} percentiles, and the minimum and maximum values for continuous variables (height above ground, distance from the canopy or top of a tree or bush, foliage density), while for discrete variables (horizontal position) we calculated the percentage for each category. A multivariate approximation to the microhabitat selection of the Santa Marta Bush-Tyrant was based on a PCA, in order to explore the microhabitat features present both in areas used by the species and in the areas never used during the study period (see Garshelis 2000). Microhabitat features for areas used by the species were based on data from 35 foraging spots. Data for unused areas (i.e. available areas) were based on 350 foraging spots arising from observations of 10 distinct individuals per species per site that were recorded foraging near to where a bush-tyrant had recently completed a foraging bout. The species recorded included members of 11 passerine families: Rhinocryptidae, Furnariidae, Tyrannidae, Tityridae, Vireonidae, Troglodytidae, Turdidae, Thraupidae, Emberizidae, Parulidae, and Fringillidae.

The areal extents of habitats were calculated in ArcGIS 9.3. Descriptive and multivariate analyses were performed in R 2.15.2.

Climatic Niche Modeling and Environmental Correlates

Climatic niche modeling was performed with the MaxEnt algorithm (Phillips 2010) using 15 locality data points (Figure 1A) and 8 WorldClim variables previously extracted from a correlation analysis (see above; see also results for the variable list). We used the MaxEnt algorithm because of its higher performance compared with many other algorithms (Elith et al. 2006), even with limited datasets (e.g., Pearson et al. 2007). We combined this algorithm with resampling techniques (see below) in order to avoid overfitting (Elith et al. 2011), and because of their good performance when used for analysis for other Neotropical birds lacking large datasets (e.g., Botero-Delgadillo et al. 2012, 2015).

In accordance with our limited sample size, 9 distinct combinations of regularization constants (0.2, 0.5, and 0.8) and modeling features (linear, quadratic, and linear + quadratic) were utilized (Phillips and Dudík 2008). The best model was selected with the software ENMTools 1.3 (Warren et al. 2010) using Akaike's Information Criterion corrected for small samples (AIC_c). This model was subsequently evaluated using a 5-fold cross-validation technique (Hastie et al. 2001, Peterson et al. 2011). Four runs of the cross-validation procedure were obtained through data reshuffling (Efron 1987), generating a total of 20 model replicates to assess uncertainty around estimates of model performance and significance (see Botero-Delgadillo et al. 2015). Model performance was evaluated by using the mean values and standard deviations of the regularized training gains and the threshold-based omission error rates on training and test data; model significance was tested by means of the threshold-dependent binomial probability tests applied in each replicate (Pearson et al. 2007, Phillips and Dudík 2008). In order to avoid using arbitrary thresholds with poor ecological meaning (see Peterson et al. 2011), we applied the Minimum Training Presence Threshold (Phillips et al. 2006, Pearson et al. 2007), a presence-only method used to minimize the inclusion of commission error in model testing (Fielding and Bell 1997). Model calibration for all replicates used a 1,000-sample point background to reduce the chance of overfitting given the spatial resolution of climatic data and the complex topography and reduced extent of the study area (restricted to the SNSM). For projecting the climatic niche and further analyses we used the model calibrated with all 15 data points (Peterson et al. 2011).

The resulting modeling output was projected into geographical space with 1 km^2 resolution using ArcGIS 9.3. The Minimum Training Presence Threshold was then applied to obtain a binary spatial projection of environmental suitability (i.e. a spatial projection of the species' climatic niche; see Peterson et al. 2011).

To identify the environmental variables that could be limiting the species' distribution at the regional scale, we assessed the explanatory power of each climatic variable used for modeling. Jackknife replicates allowed us to estimate the percentage contribution of each variable to the model and to infer the response of the species to spatial variation in climate.

Occupied Distribution Modeling

We used the projection of the Santa Marta Bush-Tyrant's climatic niche to delimit the starting area within which the occupied distributional area (sensu Peterson et al. 2011) would be modeled. Thereafter, we combined the model with rasterized layers of habitat types across the region using a geoprocessing algorithm to assign a value for habitat suitability to each cell within a 0.02 km^2 grid. The explicit incorporation of land-use and habitat layers in analyses of ecological niches is now common and has yielded accurate predictions when modeling and estimating the geographical distribution and extinction risk of bird species (e.g., Rojas-Soto et al. 2003, 2008). To calculate habitat suitability, an index was created using the following function:

$$SIndex_i = Clim_i \times [(0.6 \times Hab_i) + (0.4 \times Bor_i)],$$

where $SIndex_i$ represents the index estimate (from 0 to 1) in cell i; $Clim_i$ represents the environmental suitability of the climatic niche model in each cell; and Hab_i and Bor_i are values assigned according to the vegetation cover found in each cell (habitat and microhabitat features, and the presence or absence of edges, respectively) and the relative use of such features by the bush-tyrant. The coefficients for these variables were weighted constants defined by using available information and after averaging the values assigned by 5 experts on the species or related taxa (see Acknowledgments). Elevation was not considered in the model, given that its correlation with the species' occurrence is a result of its correlation with variables that more directly affect the species' presence (e.g., climatic variables; Peterson et al. 2011).

Spatial information on habitat types and habitat edges was based on a vegetation layer from the CORINE Land Cover Methodology for Colombia, 2012, at 1:25,000 scale (IDEAM 2012). Given that raster resolution differed among layers, we resampled the climatic niche projection to set cell size at 0.02 km^2 (i.e. the native resolution for vegetation cover), assigning the new subdivided cells the same suitability value as the original 1 km^2 cell. Clipping of habitat edges, raster analyses and resampling, and model building were performed in the Spatial Analyst and Geostatistical tools available in ArcGIS 9.3.

Prior to the modeling process, values for vegetation cover were transformed into discrete variables within categories, each one with a corresponding score or value. Habitat types were assigned to 4 categories depending on the birds' proportional use (see results): (i) habitats with proportional use $\geq$25% (i.e. at least 8 out of 35 records) were assigned a score of 1.0; (ii) habitats with proportional use between 10% and 24% (i.e. at least 4 records) were scored as 0.7; (iii) habitats with $<$10% use were assigned a value of 0.5; and (iv) unused habitats were assigned a score

TABLE 1. Principal components analyses of climatic and microhabitat features shaping the ecological niche of the Santa Marta Bush-Tyrant. (**A**) Climatic variables used to describe environmental features at 15 presence localities in the Sierra Nevada de Santa Marta (SNSM), northern Colombia. (**B**) Microhabitat variables describing the dominant features at 35 foraging spots on the San Lorenzo Ridge, SNSM. The variable Horizontal position (1–4) represents the horizontal position of the bird relative to the center of the tree or bush (Remsen and Robinson 1990), defined as 1 of 4 categories (1: center; 2: near the center; 3: mid-portion outward; 4: outer branches).

	Components loadings		
Eigenvectors	PC1	PC2	PC3
A. Climatic analysis			
Max. temp. warmest month (°C)	0.97	0.07	−0.15
Precip. driest quarter (mm)	−0.93	0.15	0.19
Precip. seasonality (CV)	0.88	0.21	−0.28
Temperature seasonality (SD)	−0.85	−0.32	−0.22
Isothermality (%)	0.82	0.51	0.05
Temp. annual range (°C)	0.71	−0.53	0.15
Precip. wettest quarter (mm)	−0.41	0.86	0.19
Precip. coldest quarter (mm)	0.38	−0.16	0.86
B. Microhabitat analysis			
Vegetation cover (%)	−0.83	−0.23	0.19
Horizontal position (1–4)	0.75	0.51	−0.08
Distance to canopy (m)	−0.49	0.73	0.43
Height above ground (m)	0.63	−0.33	0.70

of 0.0. Also, considering their relative use by the species (see results), habitat edges were modeled as a binary variable, with 0 vs. 1 values depending on the absence vs. presence of birds detected in edges.

The resulting output raster with suitability values ranging from 0 to 1 was used as a geographical projection of the species' occupied distributional area; a total count of cells with values ≥0.1 was used to estimate the areal extent of the bush-tyrant's distribution.

RESULTS

Ecological Niche at the Regional Level

Eight climatic variables were retained for further analyses: isothermality (%), temperature seasonality (SD), maximum temperature of the warmest month (°C), temperature annual range, precipitation seasonality (CV), precipitation of the driest quarter of the year (mm), precipitation of the wettest quarter (mm), and precipitation of the coldest quarter (mm). According to the loadings for the first 3 components extracted from the PCA (Table 1A), the most influential variables were the maximum temperature of the warmest month, precipitation of the wettest quarter, and precipitation of the coldest quarter.

All spatial records for the Santa Marta Bush-Tyrant came from the northern and northwestern slopes of the SNSM (Figure 1A), covering an elevational range from 2,035 to 3,583 m, but primarily between 2,100 and 3,300 m (core elevational range; Figure 2A). Maximum temperatures at these localities varied between 13.6 °C and 20.8°C, and never exceeded 21°C (Figure 2B), while precipitation varied from 172 mm to 206 mm during the coldest quarter of the year and from 926 mm to 1,107 mm during the wettest quarter (Figures 2C, 2D). In general, the species occurred where mean annual temperature did not exceed 15°C and annual precipitation was always between 2,220 and 2,580 mm.

The PCA suggested that the species' climatic niche was shaped to a greater extent by the degree of seasonality and extreme variation in temperature and precipitation. The species occurred at sites where precipitation was moderate to high, even during the driest periods of the year, and where temperature neither exceeded 20°C nor fluctuated drastically during the year (PC1 in Figure 2E; see components loadings in Table 1A).

The jackknife heuristic estimates of the relative contribution of each variable to the climatic niche model (see below for modeling results) also supported the finding that the maximum temperature of the warmest month was an important determinant of the species' presence (Table 2). The 4 variables with the highest predictive power, as identified through jackknife tests on the regularized training gain during model calibration, were the maximum temperature of the warmest month, temperature annual range, precipitation seasonality, and precipitation of the driest quarter (Table 2). After modeling environmental suitability as a function of these 4 variables, it was evident that the species' distribution was limited to where monthly temperatures did not exceed 25°C (Figure 3A) and did not fluctuate by more than 13°C (Figure 3B), and where the coefficient of variation (CV) of monthly precipitation did not exceed 70% (Figure 3D).

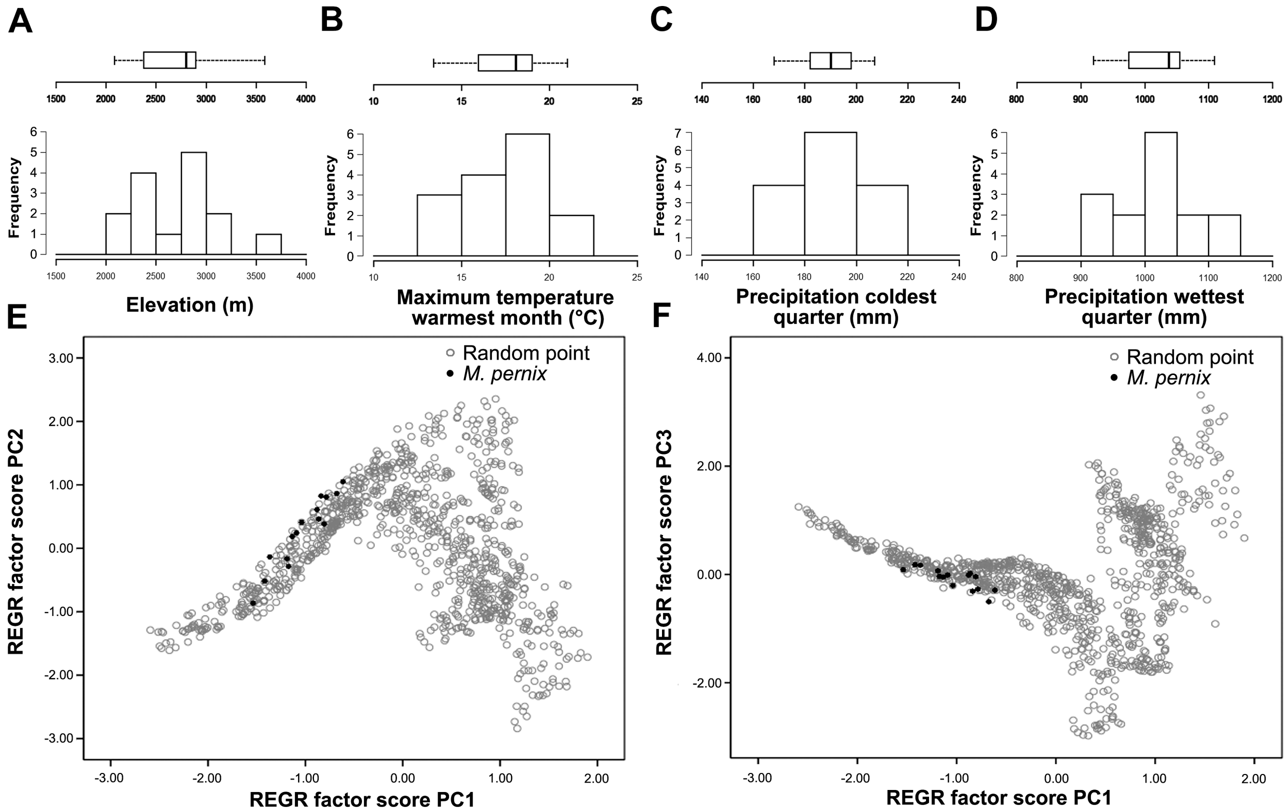

FIGURE 2. Descriptive and multivariate analyses of the ecological niche of the Santa Marta Bush-Tyrant (*Myiotheretes pernix*) at a regional level in the Sierra Nevada de Santa Marta, northern Colombia. (**A–D**) Frequency distributions depict the variation in elevation and in 3 climatic variables (maximum temperature of the warmest month, precipitation in the coldest quarter, and precipitation in the wettest quarter) associated with site localities for the species. (**E**, **F**) A principal components analysis was used to compare the dominant climatic features between confirmed presence localities and random locations in the Sierra Nevada de Santa Marta.

The Ecological Niche at the Local and Microhabitat Levels

There were 5 dominant habitat types on the San Lorenzo Ridge: mature forest, secondary vegetation, mixed areas of agricultural and native vegetation, pastures, and coffee plantations. Mature forest (57%) and secondary vegetation (29%) were the habitats most frequented by the bush-tyrant, whereas coffee plantations were never used (Table 3A). Secondary vegetation and mature forest had the highest values in Neu's selection index (1.5 and 1.1, respectively) compared with the remaining habitats (lumped together in the category of mixed natural and

TABLE 2. Heuristic estimates of the relative contribution and relative performance of 8 climatic variables to modeling the climatic niche of the Santa Marta Bush-Tyrant in the Sierra Nevada de Santa Marta, northern Colombia.

Environmental variable	Mean contribution (SD) [a]	Training gain without [b]	Training gain with only [c]
Precip. seasonality	12.19 (1.76)	1.92 (0.11)	0.24 (0.02)
Precip. of driest quarter	3.21 (1.78)	1.94 (0.11)	0.10 (0.01)
Precip. of wettest quarter	1.92 (1.92)	1.95 (0.11)	0.29 (0.02)
Precip. of coldest quarter	0.21 (0.11)	1.93 (0.11)	0.18 (0.01)
Isothermality	0.15 (0.35)	1.94 (0.11)	0.20 (0.02)
Temp. seasonality	0.26 (0.30)	1.94 (0.11)	0.34 (0.03)
Max. temp. of warmest month	52.40 (4.24)	1.26 (0.10)	0.85 (0.05)
Temp. range	29.63 (5.50)	1.48 (0.07)	0.88 (0.08)

[a] Values represent each variable's mean percent contribution (%).
[b] Values represent the model's training gain achieved with all but the regarded variable.
[c] Values represent the model's training gain achieved with only the regarded variable and excluding the remaining seven.

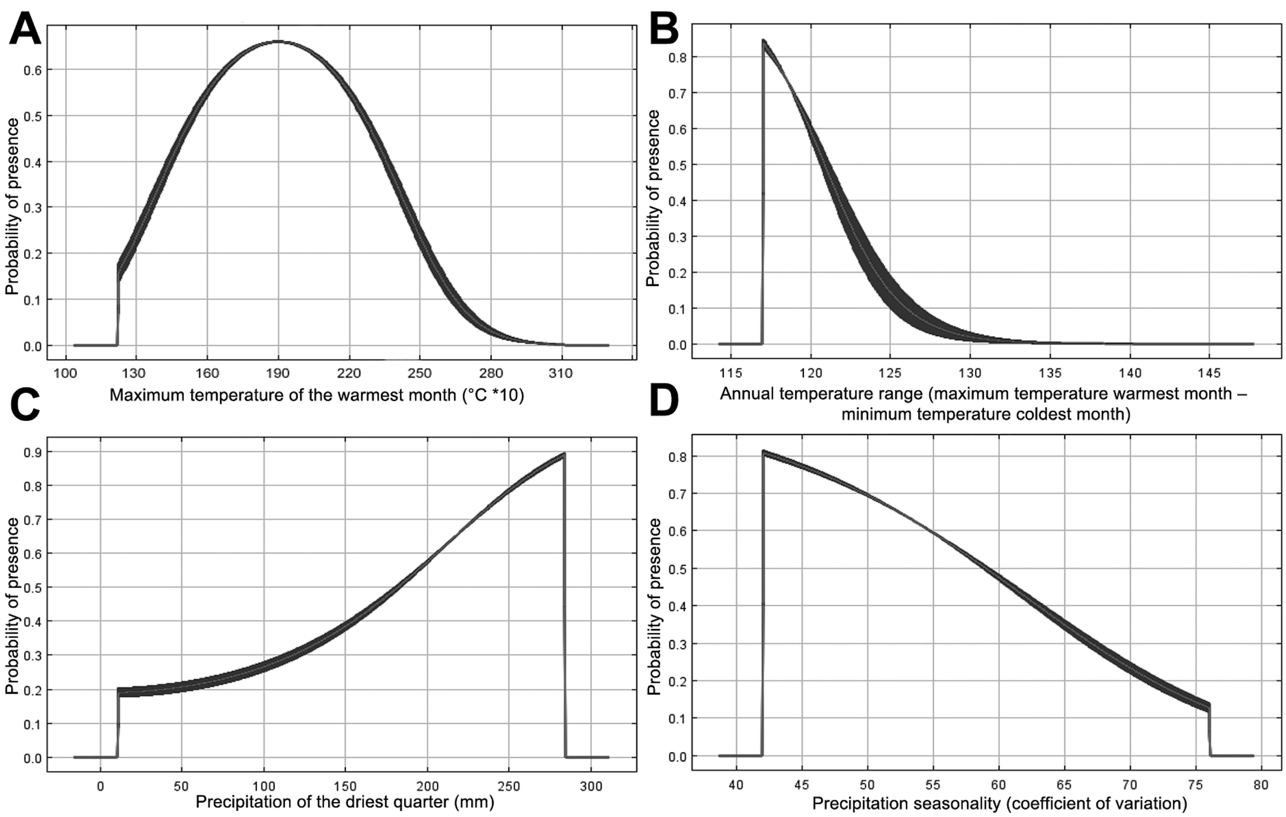

FIGURE 3. The probability of presence of the Santa Marta Bush-Tyrant in relation to spatial variation in (**A**) the maximum temperature of the warmest month; (**B**) annual temperature range; (**C**) precipitation in the driest quarter of the year; and (**D**) precipitation seasonality in the Sierra Nevada de Santa Marta, northern Colombia.

modified areas; Table 3B). Despite having the highest values in the selection index, neither habitat was used more frequently than expected given its areal extent on the San Lorenzo ridge ($\chi^2_2 = 2.80$, $P = 0.25$). Repeating this analysis with each habitat's area above 1,900 m alone did not alter this result ($\chi^2_2 = 2.62$, $P = 0.21$). However, when we grouped all habitats into only 2 categories, we found that bush-tyrants positively selected forested areas (selection index = 1.2) over the remaining vegetation types (selection index = 0.4; $\chi^2_1 = 4.1$, $P = 0.04$). Most records

TABLE 3. Description of the ecological niche of the Santa Marta Bush-Tyrant at the local level based on 35 records from the San Lorenzo Ridge, Sierra Nevada de Santa Marta, northern Colombia. (**A**) Habitat use patterns were inferred from proportional use of the 5 main habitats found on the San Lorenzo Ridge, whereas (**B**) habitat selection patterns were based on the 3 main categories.

A. Habitat use analysis Neu's habitat proportions	Observed count	Proportional use (%)		
Mature forest	20	56		
Secondary vegetation	10	29		
Mixed areas	3	9		
Pastures	2	6		
Coffee plantations	0	0		
B. Habitat selection analysis Neu's habitat proportions	Observed count	Proportional use (%)	Expected count	Selection index
Mature forest	20	53	18	1.1
Secondary vegetation	10	28	7	1.5
Natural + disturbed areas	5	19	10	0.5

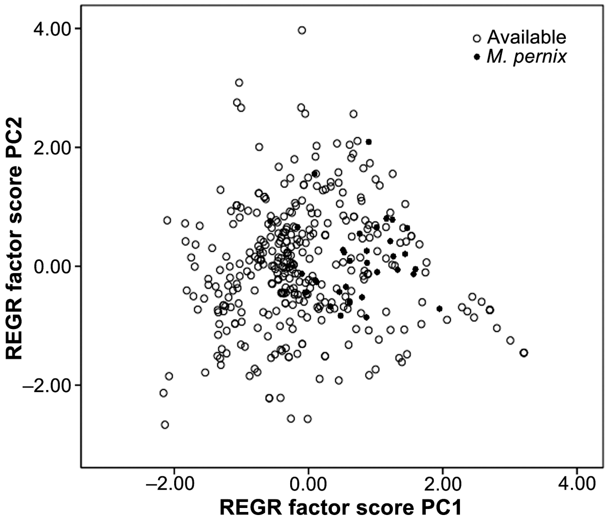

FIGURE 4. Principal components analysis comparing the microhabitat features of 35 foraging spots used by the Santa Marta Bush-Tyrant (*M. pernix*) and 350 unused spots (available) on the San Lorenzo Ridge, Sierra Nevada de Santa Marta, northern Colombia.

from mature forest (18 of 20) and secondary vegetation (9 of 10) were obtained at edges, and assuming that the probability of use of a habitat's edge and interior is equivalent to availability (spatial extent of forest interior: edge = 29.8 km^2:3.2 km^2; secondary vegetation interior: edge = 7.4 km^2:2.7 km^2), our data suggest that birds used edges more frequently than expected (one-tailed exact binomial tests, $P < 0.001$; $P < 0.001$). All records from mixed areas were obtained in edges near forested habitat (e.g., Figure 1D), whereas observations in pastures came from birds perched on scattered trees far from any edge.

Santa Marta Bush-Tyrants were frequently observed 4.5–6.5 m above the ground (IQR), but birds could be seen perching from 3.5 to 9.0 m. Birds used intermediate-height perches, usually at a distance of 2–4 m from the canopy or top of the vegetation (IQR). While foraging, birds used relatively exposed perches; they were always observed in the mid-portion outward (57%) or outer branches (43%), and foliage density around the perch was largely between 20% and 35%, and never exceeded 50%. The PCA showed that despite the availability of foraging spots with highly variable microhabitat features, bush-tyrants used more exposed spots with little foliage cover compared with other passerines (PC1 in Figure 4), and tended to perch in intermediate positions relative to canopy height (PC2 in Figure 4; components loadings in Table 1B). Of the 3 extracted components, the first 2 explained 72% of the variability in the data.

Climatic Niche Modeling

According to the AIC_c values, the best model of the 9 evaluated used quadratic features and a regularization constant (i.e. beta-multiplier) of 0.5 (Table 4). The mean regularized training gain (1.96 $\pm$ 0.11; $n = 20$) and the mean values of the threshold-based training omission error rates (0.08 $\pm$ 0.01; $n = 20$) and test omission error rates (0.16 $\pm$ 0.23; $n = 20$) confirmed that the model performed well. All cross-validation replicates were statistically significant according to the threshold-dependent binomial test (all $P < 0.02$; $n = 15$).

The area predicted by the projection of the threshold climatic niche was equivalent to 1% of the modeling background, while the most frequent probability values were between 0.6 and 0.8 (Figure 5A). We obtained a 95% confidence interval around the extent of the predicted climatic niche from the 20 modeling replicates (see above), which suggested that the climatically suitable area for the bush-tyrant could cover between 833 km^2 and 978 km^2, concentrated on the northern and northwestern slopes of the SNSM (Figure 5B). Nearly 80% of the species' climatic niche was predicted to occur between 2,000 and 3,000 m; the remaining niche area was above 3,000 m (Figure 5B). Nearly

TABLE 4. Model set for modeling the climatic niche of the Santa Marta Bush-Tyrant in the Sierra Nevada de Santa Marta, northern Colombia, containing different combinations of coefficient features (L: linear; Q: Quadratic; L + Q: linear + quadratic) and regularization constants (0.2, 0.5, 0.8). Models were ranked based on the difference from the top model in Akaike's Information Criterion corrected for small sample sizes (ΔAIC_c). *K* is the number of model parameters, $-2\ln L$ is the maximized log-likelihood, and w_i is the Akaike weight.

Model	*K*	$-2\ln L$	ΔAIC_c	w_i
Q (0.5)	4	222.15	0.00 [a]	0.3953
L + Q (0.2)	6	213.12	1.47	0.1892
Q (0.2)	6	213.51	1.86	0.1559
L + Q (0.5)	5	219.95	2.47	0.1149
Q (0.8)	4	225.31	3.17	0.0811
L + Q (0.8)	4	225.81	3.66	0.0633
L (0.2)	6	227.46	15.81	0.0001
L (0.5)	5	234.75	17.27	0.0001
L (0.8)	5	242.31	24.83	0.0000

[a] The AIC_c value of the top model = 234.15.

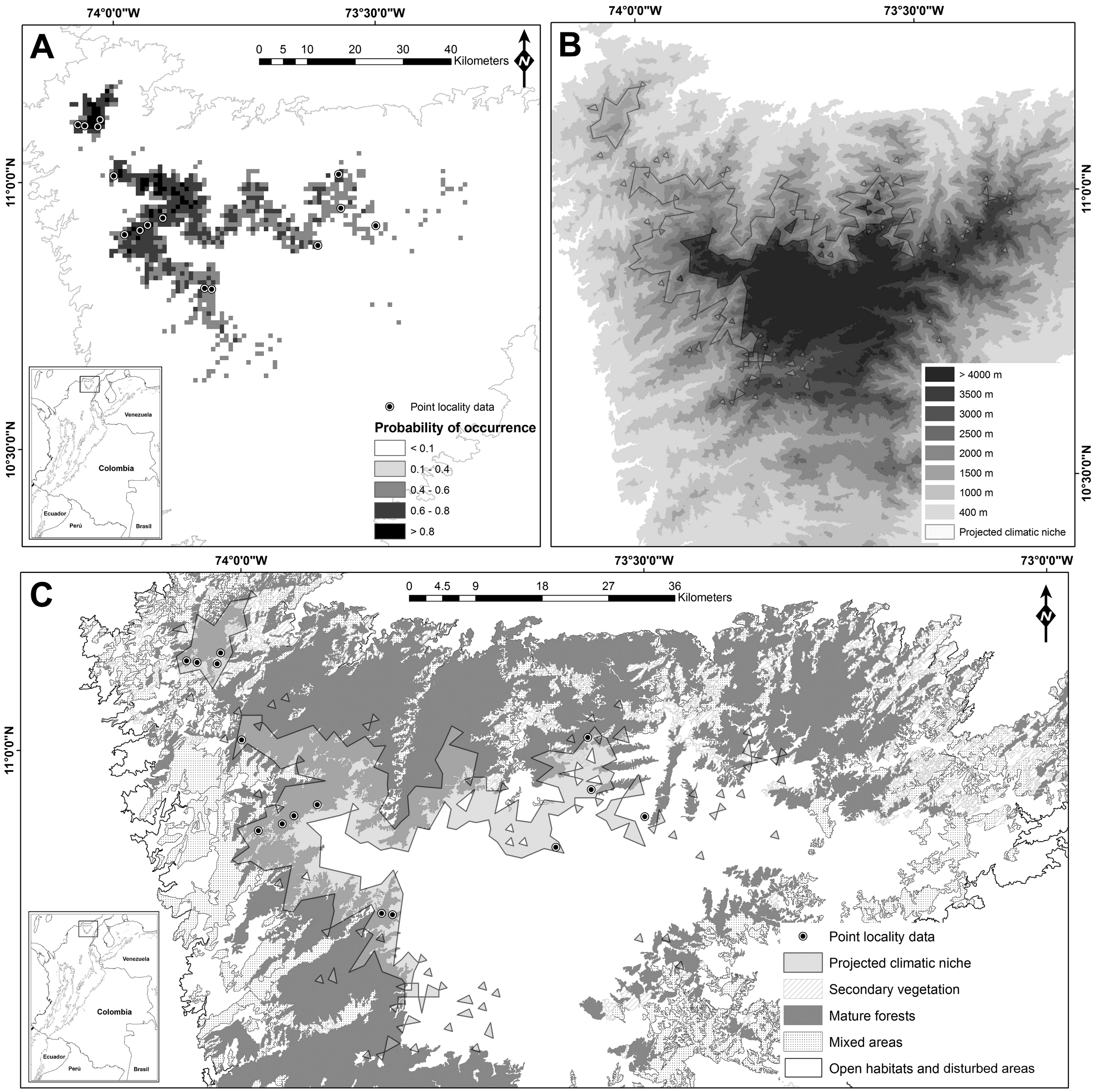

FIGURE 5. Projected climatic niche of the Santa Marta Bush-Tyrant in the Sierra Nevada de Santa Marta, northern Colombia. (**A**) Climatic suitability values across space (i.e. probability values); and the location of the projected niche in relation to (**B**) the elevational gradient, and (**C**) the main landscape components throughout the study region.

40% of this climatically suitable area overlapped areas of open vegetation or heavily disturbed areas (Figure 5C).

Summarizing Multiscale Correlates: The Occupied Distributional Area

The geoprocessing modeling results showed that 50% of the suitability index (*SIndex*) values were between 0.21 and 0.60 (IQR), and that the mean value corresponded to 0.45 (n = 4,930). The predicted occupied distributional area extended 352 km^2 (Figure 6). The highest ecological suitability was predicted to be between 2,500 and 3,000 m and where edges between mature forests and secondary vegetation–mixed areas occurred (Figure 6). The model's omission rate was low (0.2), since only 3 of all the data points were not included within the predicted distribution (Figure 6).

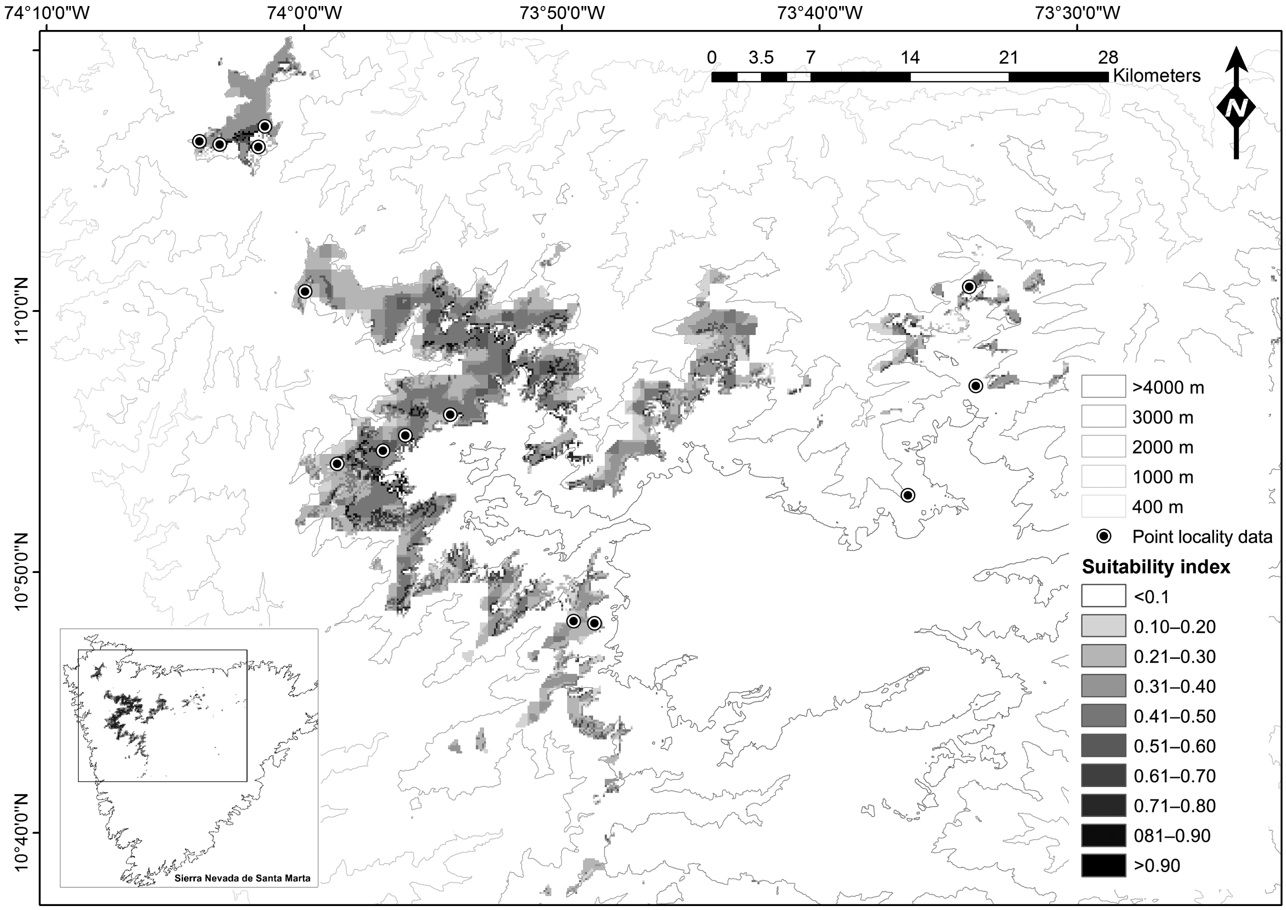

FIGURE 6. Predicted occupied distributional area for the Santa Marta Bush-Tyrant in the Sierra Nevada de Santa Marta, northern Colombia, based on a combination of climatic niche modeling and data on habitat use. The occupied distribution and the suitability values are based on a habitat suitability model at 1:25,000 resolution.

DISCUSSION

The information currently available on the Santa Marta Bush-Tyrant (e.g., Salaman et al. 2002, BirdLife International 2014), although valuable, is largely based on isolated and anecdotal observations that are not suitable for inferring general patterns about the species' ecology. The results presented here suggest that the species is likely restricted to the humid northern and northwestern slopes of the SNSM, being absent from the other flanks, especially where the climate varies markedly with the time of year. Although the species frequently uses forested areas and secondary growth, our data indicate that this bird is much more closely associated with habitat edges than previously documented.

Climatic Determinants at the Regional Level

The analyses presented here show that the Santa Marta Bush-Tyrant has been recorded in areas with low mean annual temperatures and where annual precipitation is >2,000 mm. However, the most important environmental factors determining presence appear to be the absence of extreme fluctuations in temperature and precipitation during the warmest, coldest, and wettest periods of the year (Figures 2, 3). The maximum temperature reached during the warmest month of the year also seems to have an important influence on the species' presence. Conversely, the species is expected to be absent where temperature and precipitation are highly seasonal, or where precipitation is relatively high during dry periods but does not reach extreme levels during the wettest season.

Relatively constant precipitation and low variability in temperature are typical features of montane (1,800–2,400 m) and high montane forests (2,500–3,100 m) on the northwestern and northern flanks of the SNSM (Fundación Pro Sierra Nevada de Santa Marta 1998), where our climatic niche model predicted presence of the bush-tyrant (Figure 5). The species' apparent dependence on such climatic conditions could be a consequence of either a predictable and constant food supply (i.e. insects) associated with the constant environmental conditions, or a high rate of decay of trees in the humid environment, leading to the formation of gaps and edge microhabitats where insects tend to be abundant. Disentangling these causes is beyond the scope of this study, but this dependency on cold, humid, and constant environments is a common feature shared by multiple SNSM endemics, including several bird species, as well as other vertebrates, invertebrates, and plants (Fundación Pro Sierra Nevada de Santa Marta 1998). Indeed, the northern slopes of the SNSM have the highest levels of endemism of the entire massif, as well as being where the greatest number of threatened bird taxa co-occur (Fundación Pro Sierra Nevada de Santa Marta 1998, Renjifo et al. 2002).

The Santa Marta Bush-Tyrant has been considered to occur between 2,100 and 2,900 m (Salaman et al. 2002, Fitzpatrick 2004), but our climatic niche model suggested that areas above 3,000 m are environmentally suitable (Figure 5), and the occupied area model also predicted presence above this elevation (Figure 6). Despite the paucity of records above 3,000 m, it is probable that the species occurs at this elevation (or above) more frequently than has been described, and may occupy the habitat edges found in the transition zone between high montane forests and páramo (montane grassland). More observations from other localities in the SNSM between 3,000 and 3,500 m are needed to test the predictions of both models. Based on the data analyzed here, however, bush-tyrants occur between 2,100 and 3,300 m, but are more likely to be present between 2,500 and 3,000 m (Figures 2, 6).

The Ecological Niche at the Local and Microhabitat Levels

There was no evidence that the Santa Marta Bush-Tyrant preferentially selected any of the individual habitat types encountered on the San Lorenzo Ridge, but there was support for the species favoring forested habitats over open and disturbed areas. Indeed, the species has been observed in mature forests, secondary growth, scrub, open areas with scattered trees, and plantations of exotic trees such as *Eucalyptus* spp. or *Cupressus* spp. (Salaman et al. 2002, Fitzpatrick 2004, Botero-Delgadillo 2011), but bush-tyrants tended to use the first 2 habitats more frequently than expected given their extent. Further, our results indicated that bush-tyrants used edges more than expected, implying that edges between woodland and open areas, or areas of natural disturbance within the forest, could be more important than any other habitat (e.g., Figure 1D). Microhabitat analyses favored this conclusion, as birds frequently used zones with good light, such as exposed perches or the tops of trees, features typical of forest edges or clearings.

Species in the genus *Myiotheretes* are considered montane forest generalists (Traylor and Fitzpatrick 1982, Fitzpatrick 2004), but Botero-Delgadillo (2011) suggested that the Santa Marta Bush-Tyrant should be viewed as a behaviorally stereotyped bird—a sit-and-wait predator that captures its prey almost exclusively through aerial hawking maneuvers. This behavior is typical of birds that forage in open microhabitats (Botero-Delgadillo 2011), where they search for social insects or other kinds of patchily distributed prey (Sherry 1984, Traylor and Fitzpatrick 1982). Furthermore, the species' relatively short tarsi, long wings, and long bill are typical of flycatcher taxa that frequently perform aerial hawking or sally-strike maneuvers in open areas or habitat edges (Fitzpatrick 1980, 1985, Botero-Delgadillo and Bayly 2012). The ecomorphological evidence and the results presented here point to the Santa Marta Bush-Tyrant being an edge specialist that selects mature forests and secondary vegetation over other vegetation types. However, the species can behave as a habitat opportunist, using modified areas and plantations, as long as microhabitat features attract potential prey.

Two potential limitations regarding our analyses at the local and microhabitat scales must be addressed: (i) potential bias in observer effort between behavioral observations in habitat edge vs. habitat interior; and (ii) the possibility that the scope of our results could be limited by the ecological conditions present between 2,000 and 2,700 m. We tried to minimize observer bias by spreading effort equally across all habitat and microhabitat types, having previously defined types and an appropriate sampling design. The potential for the elevations sampled to introduce bias is difficult to quantify, but in the absence of evidence to the contrary, it seems reasonable to expect that habitat selection patterns are similar in other localities and across elevations.

Distributional Patterns and Conservation Issues

Our analyses of the Santa Marta Bush-Tyrant's occupied distribution incorporated both recent and unpublished data, and we therefore expected to find differences between our estimates and previous ones. The species' distribution was first calculated at 856 km^2 (Salaman et al. 2002), while a subsequent refinement estimated it at 570 km^2 (BirdLife International 2014), both higher than our estimate (352 km^2). However, there is a noticeable similarity between our proposed distribution and that of BirdLife International (2014), supporting the hypothesis that the species is currently restricted to the northern slopes of the SNSM. The lower value of our estimate is best explained by the incorporation of habitat selection criteria in our model.

Since the IUCN criteria define a species' area of occupancy (AOO) as the suitable habitats within its extent of occurrence (IUCN 2011), our occupied distribution estimate could be taken as an estimate of the bush-tyrant's AOO. Following this logic, our estimate for the AOO supports the species categorization as Endangered (EN) following criterion B2 (BirdLife International 2014). Although our climatic niche model predicted a larger geographical range, the ~500 km^2 difference relative to our estimated area of occupancy (AOO) was a result of large-scale habitat modification within the species' potential range.

The Santa Marta Bush-Tyrant is one of the most threatened taxa in the SNSM, but there is still limited knowledge of other important aspects of its spatial and trophic ecology, and aspects such as its reproductive biology and population ecology and status are completely unknown (Botero-Delgadillo and Olaciregui In press). The use of a larger dataset to better estimate its geographical range and rates of habitat loss will be possible only if a more extensive and representative exploration of additional areas is made, highlighting the urgency of confirming the species' presence in other localities (BirdLife International 2014). That said, the approach adopted here, i.e. combining limited site locality records, climatic niche modeling, and observational data in a geoprocessing model, has improved our knowledge of the species and its occupied range, and provides an example of how to maximize limited data to provide key baseline information for designing conservation measures. The explicit incorporation of local patterns of habitat and microhabitat use into models provides a realistic representation of the hierarchical process of habitat selection in birds (Cody 1985), and can therefore help to identify the factors limiting spatial occurrence at different levels. Explicit geoprocessing algorithms encompassing such multiscale approaches could be valuable for further studies on other endemic and/or threatened taxa requiring urgent action.

While most of the bush-tyrant's range is currently located within the SNSM National Park, logging and agricultural expansion is suspected to occur in some portions of its distribution. However, our results suggest that small-scale logging or localized exotic plantations may not pose a significant threat (but see Salaman et al. 2002), since they could favor the creation of small areas of secondary growth or generate transitional zones and habitat edges, respectively. If logging and exotic plantations are essential for local communities, conservation planning should integrate participative education and habitat management strategies such as selective logging, allowing control over rates of habitat loss while maintaining the presence of habitat and microhabitat features selected by the Santa Marta Bush-Tyrant. Climate change is another issue that deserves further study, and it should be considered in management plans, given the species' apparent intolerance of high variability in temperature and precipitation.

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Ethics statement: This study involved only observations of bird behavior and the collation of geographical records gathered previously or during the development of this work. Therefore, we did not need to follow any ethics protocols regarding manipulation of wild birds.

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