

CLIMATE CHANGE EFFECTS ON NEOTROPICAL MANAKIN DIVERSITY BASED ON ECOLOGICAL NICHE MODELING

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Abstract. Assessing the nature and magnitude of potential effects of climate change on populations is important to anticipating effects on species diversity for conservation planning. We used ecological niche modeling to predict present and future distributions of 49 species of manakins (Pipridae) and allies. Predictions for present-day distributions were highly coincident with independent test data, suggesting good predictive ability. Assuming no dispersal, projections of potential distributions under four scenarios of climate change predicted that 20% of manakin species would likely go extinct from their current ranges, and that distributions would in general be reduced and fragmented, regardless of the area of present-day potential distribution or rarity. Predicted changes in potential distributions, spatial configuration of suitable habitats, and geographic position of species ranges were more dramatic for species inhabiting flatlands than for montane species. These results are an example of how ecological niche modeling techniques can anticipate the nature and magnitude of changes in biodiversity in response to climate change.

Key words: climate change, conservation, ecological niche, geographic distribution, manakin.

Efeitos de Mudanças Climáticas na Diversidade de Tangarás Neotropicais Estimados Através da Modelagem de Nicho Ecológico

Resumo. Conhecer a natureza e magnitude dos efeitos potenciais das mudanças climáticas em populações é importante em planos de conservação por antecipar os efeitos sobre a diversidade de espécies de uma região. Modelamos o nicho ecológico de 49 espécies de tangarás (Pipridae), e espécies aparentadas, para prever suas distribuições no presente e futuro. Estimativas para o presente foram altamente coincidentes com testes independentes, indicando boa previsibilidade dos modelos. As projeções de distribuições potenciais em quatro cenários de mudanças climáticas indicam que, na ausência de dispersão, 20% das espécies de tangarás irão se extinguir de suas localidades de ocorrência atuais, e que suas distribuições se tornarão reduzidas e fragmentadas, independentemente da área de distribuição potencial e raridade no presente. Mudanças previstas na distribuição potencial, disposição espacial de habitats propícios, e posição geográfica da distribuição de espécies foram maiores para espécies habitantes de baixadas que de regiões montanhosas. Estes resultados exemplificam o uso de modelagem de nicho ecológico para antecipar a natureza e magnitude de alterações na biodiversidade decorrentes de mudanças climáticas.

INTRODUCTION

Globally, climates are undergoing dramatic changes (Karl et al. 1996, Magnuson 2001), with demonstrable effects on the distribution of biodiversity, including both colonization of new areas and local extinctions (Brown et al. 1997, Parmesan et al. 1999, Xu and Yan 2001, Walther et al. 2002). Predictions of substantial further warming and reorganization of patterns

of precipitation for coming decades in Neotropical regions has generated concern about consequences for biodiversity across the region (Houghton et al. 2001), where numerous biodiversity hotspots are located (Myers et al. 2000). Thus, as future climate changes will likely affect the conservation status of many species (Peters and Darling 1985, Dobson et al. 1989, Peters and Myers 1991–1992, Chapin et al. 2000, Thomas et al. 2004), studies that anticipate the pattern and magnitude of effects of climate change on distributions of Neotropical species are urgently needed.

The geographic distributions of species are defined by autecological needs and tolerances, biotic interactions, and historical effects (So-

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berón and Peterson 2005). As such, climate change may affect the spatial manifestation of ecological niches (i.e., the set of environmental conditions within which a species is able to maintain populations without immigration; Grinnell 1917, 1924). When faced with changing ecological conditions, species may track appropriate conditions or adapt to the new conditions; failing both, populations will be extirpated (Holt 1990, Brown and Lomolino 1998). As both theoretical expectations and empirical studies suggest that ecological niches remain relatively constant over long time scales (Huntley et al. 1989, Kawecki and Stearns 1993, Holt 1996, Holt and Golmukiewicz 1996, Peterson et al. 1999, Rice et al. 2003, Martínez-Meyer et al. 2004), these ecological characteristics likely present long-term stable constraints on the geographic potential of species (Peterson 2003). As such, we make the provisional assumption in this analysis that evolution in ecological characteristics will be nil, and focus on anticipating spatial shifts in the position of appropriate conditions for species.

Ecological niche models can be based on present-day distributions with respect to environmental conditions (Soberón and Peterson 2005). Once models are built and validated in present-day conditions, their rule sets can be projected onto scenarios of change for anticipating potential distributional shifts and consequent changes in diversity (Pounds et al. 1999, Peterson et al. 2001, 2004, Root et al. 2003, Roura-Pascual et al. 2005). Although many studies modeling effects of climate change on potential species distributions have shown idiosyncratic and individualistic aspects of the likely responses of different species (Perry et al. 1990, Johnston and Schmitz 1997, Kadmon and Heller 1998, Price 2000, Peterson et al. 2001), some generalities are now emerging. For example, Peterson et al. (2001, 2002) and Peterson (2003) showed that species in flatlands regions experienced higher predicted distributional shifts and loss in habitable area than species in montane areas. Studies examining sufficient numbers of species to permit testing these predictions, however, are quite scarce.

The manakins (Aves: Pipridae) are a diverse clade of small frugivorous birds distributed across the Neotropics. The family includes about 45 species and is broadly distributed in Neotropical forests, inhabiting lowland rain

forests and other tropical forests. Additionally, manakins are easily collected, and so are well-represented in collections. Ecological niches are generally conserved among sister manakin species, suggesting ecological conservatism across lineages (MA and ATP, unpubl. data). The Neotropical manakins are therefore an ideal group for examining the consequences of predicted future climate changes on the distribution of Neotropical biodiversity. Here, we model ecological niches and predict future potential geography of Neotropical manakins in the face of changing climates over coming decades. We evaluate likely effects of regional topography on changes in predicted distributional area, geographic position of distributions, and fragmentation of species' ranges.

METHODS

Our approach to modeling future geographic distributions of manakin species consisted of two steps: (1) modeling ecological niches based on known occurrences and datasets summarizing present-day environmental features (climate and topography), and (2) projecting models onto environmental datasets summarizing climates predicted for future time periods (here, mid-21st century). The general methodology for modeling ecological niches and projecting effects of climate change on distributions is described in detail in Peterson et al. (2001).

INPUT DATA

Creation of an ecological niche model for projection across scenarios of change requires information on the occurrence of species of interest in the present day, digital raster GIS coverages summarizing climates for both time periods, and digital raster GIS coverages summarizing constant features of the landscape (e.g., topographic features, soil type). Occurrence information, in the form of unique geographic localities at which specimens of a particular species have been collected, was accumulated from data associated with natural history museum specimens for all manakin species and 10 species in closely related families (genera *Neopelma*, *Neopipo*, *Piprites*, and *Tyrannetes*). Specimen records were supplemented with data from the literature and field observations; complete lists of sources are available on request from the senior author. Sample sizes for eight species (five manakins and three from other

families) were insufficient for generating models; these species were omitted from analysis.

We used seven electronic map layers summarizing aspects of topography (slope, aspect, and topographic index, from the U.S. Geological Survey's Hydro 1k elevation derivation database <<http://edcdaac.usgs.gov/gtopo30/hydro/>>) and climate (annual mean precipitation, annual mean maximum monthly temperature, annual mean minimum monthly temperature, and mean annual temperature; Intergovernmental Panel on Climate Change <<http://www.ipcc.ch/>>). All environmental data sets were generalized to $0.1^\circ \times 0.1^\circ$ resolution (about 10×10 km) for an area including all of tropical America (34°N to 40°S). For refinement of modeled ecological niches, and because the aim of this study was to predict future distributions, we subdivided the study area into three subregions, based on the known distributions of most manakin species, within which models were developed (Amazon Basin, eastern South America, and northwestern Neotropics). Projections were made from these regional models to the whole study area.

SCENARIOS OF CLIMATE CHANGE

Ecological niches modeled for each species based on present-day occurrences and conditions were projected onto future climate data sets derived from two general circulation models: CGCM2, developed at the Canadian Centre for Climate Modelling and Analysis (Flato et al. 1999), and HadCM3, developed at the Hadley Centre for Climate Prediction and Research (Pope et al. 2000). For each circulation model, we averaged the results from two emissions scenarios, one conservative and one more severe set of assumptions for climates over the next 50 years: B2 assumes a 0.5% year⁻¹ CO₂ increase and incorporates sulphate aerosol forcing, and A2 assumes a 1% year⁻¹ CO₂ increase and does not take into account effects of sulphate aerosols (Nakicenovic and Swart 2000). Results are based on a 30-year average around 2055 (2040–2069), thus they do not consider potential effects of increased climate variability (El Niño events in particular) on species distributions.

As global circulation model data are provided at coarse spatial resolutions (Hadley: $2.5^\circ \times 3.75^\circ$; Canadian: $3.75^\circ \times 3.75^\circ$), we scaled all coverages down to $0.5^\circ \times 0.5^\circ$ resolution by

interpolation of expected changes in each climatic layer under each scenario. Although the scenarios are the same for both circulation models, implementing simulations under contrasting assumptions regarding emissions of greenhouse gases may give different predictions among the models and scenarios (Peterson et al. 2004). Because the goal of this study was an overall exploration of likely climate effects on manakin diversity, we present average estimates based on predictions from both models and both scenarios.

ECOLOGICAL NICHE MODELING

The ecological niche of a species can be defined as the conjunction of ecological conditions within which it is able to maintain populations without immigration (Grinnell 1917, Holt and Gaines 1992); as such, it is defined in multidimensional ecological and environmental space (MacArthur 1972). Several approaches have been used to approximate ecological niches (Nix 1986, Austin et al. 1990, Carpenter et al. 1993); that which has seen broadest application to questions of ecological niche evolution is the Genetic Algorithm for Rule-set Prediction (GARP), which includes several inferential approaches in an iterative optimization approach (Stockwell and Noble 1992, Stockwell 1999, Stockwell and Peters 1999).

All modeling in this study was carried out with a desktop implementation of GARP (<<http://www.lifemapper.org/desktopgarp/>>). Available occurrence points are divided evenly into "training" and "extrinsic test" data sets; the former is again divided evenly into true "training data" (for model rule development) and "intrinsic test data" (for model rule evaluation and refinement). When sample sizes were <20 unique localities, models were developed with intrinsic testing only. GARP is designed to use only presence data; absence information is included in the modeling via sampling of pseudoabsence points from the set of pixels where the species has not been detected. GARP works in an iterative process of rule selection, evaluation, testing, and incorporation or rejection. First, a method is chosen from a set of possibilities (e.g., logistic regression, bioclimatic rules) and is applied to the training data to develop a rule; rules may evolve by a number of means (e.g., truncation, point changes, crossing-over among rules) to

maximize predictive ability. Predictive accuracy of each rule (for use in model refinement) is then evaluated based on 1250 points resampled from the intrinsic test data set and 1250 points sampled randomly from the study region as a whole. The change in predictive accuracy from one iteration to the next is used to evaluate whether a particular rule should be incorporated into the model, and the algorithm runs either 1000 iterations or until convergence.

In all, 100 models were generated for each species, and the 10 best distribution models were selected using a best-practices procedure for identifying optimal models (Anderson et al. 2003) based on omission (leaving out true areas of occupation) and commission (including areas not potentially habitable) error statistics. Specifically, we used a soft omission threshold, focusing on the extreme 20% of the distribution of omission values across models. We then chose models presenting intermediate levels of commission (i.e., the central 50% of the commission index distribution). The 10 best models were summed in ArcView 3.2, and we took as a best and most conservative distribution estimate the areas in which a species was predicted to be present by all 10 of these best models. Finally, because species are often prevented from inhabiting the entire spatial extent of areas comprising their appropriate ecological niche by barriers to dispersal (Solerón and Peterson 2005), we reduced modeled distributions for the present to areas within or contiguous to known current distributions (Hellmayr 1924, Peters 1931, Hilty and Brown 1986, Sick 1993, Ridgely and Tudor 1994, Ridgely and Greenfield 2001, Hilty 2003). Given the small sample sizes available and prior experience with modeling such species in these regions (Peterson et al. 2002; MA and ATP, unpubl. data), we did not separate species data for independent model validation.

STATISTICAL ANALYSES

We evaluated expected effects of climate change on species distributions under a conservative assumption of no dispersal capabilities, which is likely appropriate for manakins, which tend to be habitat-restricted and sedentary. As such, we considered only the intersection of each species' predicted distribution after climate change with its present geographical distribution. This pro-

cedure identifies the portions of current potential distributions that will remain habitable for the species after modeled climate change.

Centroids of present-day and predicted future distributions under the assumption of no dispersal were calculated using the centroid option in ArcInfo 8.0. Pairwise distances between these centroids for each species were computed as Euclidian distances, where:

$$D = \sqrt{\sum (v_{iP} - v_{iF})^2},$$

and v_{iP} and v_{iF} are the values of the i^{th} geographical coordinate (latitude or longitude) at the centroid of the species' present and future distributions, respectively.

The overall predicted future distribution of manakin diversity was represented by the sum of final predicted future distribution maps across all species. To summarize this diversity regionally, we divided the study region into six ecoregions generally recognized to comprise specific groups of Neotropical birds and usually considered in conservation plans (Central America-Chocó and NW South America, Andes, Amazon, Guiana Region, Cerrado, and Atlantic Forest; Fig. 1) and estimated numbers of species predicted to be lost from each ecoregion. Geographical limits of ecoregions were compiled based on the World Wildlife Fund's maps of terrestrial biorealm (<http://www.worldwildlife.org/wildworld/profiles/>).

Effects of climate change on distributions were evaluated for montane and flatland species separately (species were classified as montane or flatland inhabitants based on the majority of their known ranges), and compared using nonparametric Mann-Whitney U -tests. We calculated levels of fragmentation for present and future distributions using the Patch and Proximity extensions in ArcView 3.2, estimating mean number of connected patches, patch sizes, distances to the nearest neighbor, and median isolation indices (according to index "PX₉₂"; Gustafson and Parker 1992) for each species. We used Wilcoxon matched-pairs tests to compare levels of fragmentation predicted for species distributions under present and future climates, and compared mean predicted changes in fragmentation level between present and future climates for flatland and montane species using Mann-Whitney U -tests.

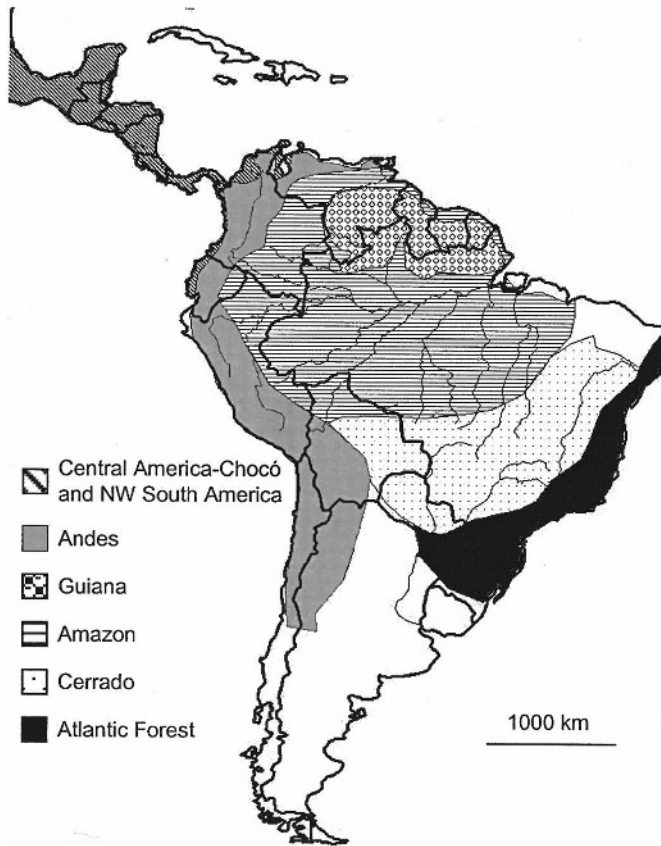


FIGURE 1. Geographical limits of ecoregions within the Neotropics used in this study.

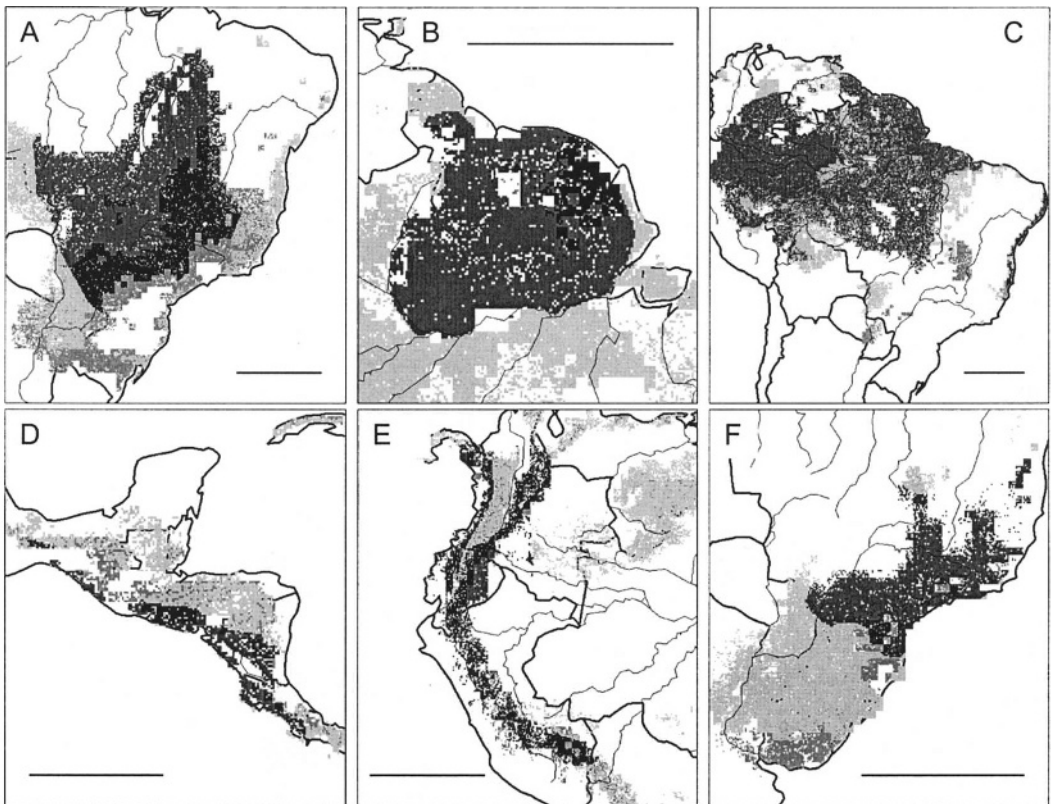
RESULTS

In a previous study (MA and ATP, unpubl. data), coincidence of predictions of present-day geographic distributions with independent test data was highly significantly better than random models for all species (chi-square tests, all $\chi^2 > 6.8$, all $P < 0.01$), suggesting good predictive power of models regarding the potential geographical distribution of each species. Based on this result, we were confident in continuing with further, extrapolative analyses.

Projections of niche models onto predicted future climate scenarios indicated moderate to extreme spatial changes in manakin distributions: under the assumption of no dispersal, areas of potential distributions were predicted to be reduced on average by 76% (range = 35% in the Blue-rumped Manakin [*Lepidothrix isidorei*] to 100% in the Yellow-crested Manakin

[*Heterocercus flavivertex*]) and dramatically reorganized, with range centroids shifting on average by 350 km in various directions (range = 6 km in the Pacific White-ruffed Manakin [*Corapipo heteroleuca*] to 1960 km in the Wing-barred Piprites [*Piprites chloris*]; Fig. 2). In general, about half the species were predicted to lose >80% of their modeled present-day distributions, and 11 species were predicted to retain <5% of their present suitable areas (Table 1). Consequent predicted changes in the distribution of manakin diversity include drastic reduction of species richness in forests in the Amazon Basin and a focusing of remaining species-rich areas along mountain ranges (Fig. 3).

Proportional reduction of habitable area was not correlated with modeled area of present-day distribution ($r^2 = 0.11$, $P > 0.05$). However, the ecological niche models predicted the effects of



■ = areas presently habitable that are projected to remain habitable within the known species range, ■ = areas presently habitable but not predicted to remain habitable within the known species range, ■ = areas predicted to be habitable at present but not predicted to remain habitable outside the known species range, ■ = areas outside the known species range predicted to become habitable under the scenario of climate change.

FIGURE 2. Examples of future projections of climate change effects (four climate change scenarios averaged) on the geographical distributions of three species of manakins from flatlands: (A) Helmeted Manakin (*Antilophia galeata*) in the Cerrado, (B) White-fronted Manakin (*Lepidothrix serena*) in the Guiana Region, and (C) Blue-backed Manakin (*Chiroxiphia pareola*) in the Amazon and Atlantic Forest; and three from montane regions: (D) Long-tailed Manakin (*Chiroxiphia linearis*) in Central America, (E) Green Manakin (*Chloropipo holochlora*) in the Andes, and (F) Pin-tailed Manakin (*Ilicura militaris*) in the Atlantic Forest. Areas outside the known distributional range represent overly extensive predictions owing to historical factors and their occupancy would represent historical range restriction. Black bars represent 1000 km.

climate change to be more severe for manakin species inhabiting flatlands than species in montane forests. Species inhabiting flatland forests in the Amazon and Cerrado ecoregions were predicted to lose ~80% of habitable area; indeed, ~20% of Cerrado manakin species would be potentially extinct from the biome under future climates (most of these species occur in other ecoregions). Predicted potential area loss and species extinction were lower in other ecoregions (16%–50% and 0%–5%, respectively), which are dominated by montane

landforms. Furthermore, larger proportions of present-day distributional areas were predicted to remain habitable in montane situations than in flatlands (Mann-Whitney $U = 110$, $P < 0.01$; Fig. 4), and flatlands species were predicted to experience larger spatial shifts in their modeled potential distributions than montane species (Mann-Whitney $U = 38.5$, $P < 0.01$; Fig. 4). Several examples are shown in Fig. 2.

In general, suitable habitats were predicted to become more fragmented under future climates (Wilcoxon matched-pair test, all $Z > 2.7$, all P

TABLE 1. Number of unique localities, areas of modeled present-day distribution, percent area loss and distance shifts of range centroids predicted under future climates, topography of inhabited area (m = montane, f = flatlands), and regions predicted to be habitable in the present day and to be lost through climate change for 49 species of Manakins and allies. Regions are: AF = Atlantic Forest, CE = Cerrado, AM = Amazon, AD = Andes, GU = Guiana Region, CC = Central America-Chocó and NW South America.

Species	Sample localities	Area		Distance shift (km)	Regions		
		Present (ha × 10 ⁻⁶)	% loss		Present	Future loss	Topography
Helmeted Manakin (<i>Antilophia galeata</i>)	40	162.4	67	316.7	AF; CE; AM	AM	f
Yungas Manakin (<i>Chiroxiphia boliviana</i>)	6	7.9	63	22.8	AD	–	m
Blue Manakin (<i>Chiroxiphia caudata</i>)	186	98.0	93	218.1	AF; CE	CE	m
Lance-tailed Manakin (<i>Chiroxiphia lanceolata</i>)	59	14.6	74	77.2	CC; AD	–	m
Long-tailed Manakin (<i>Chiroxiphia linearis</i>)	26	8.5	62	48.3	CC	–	m
Blue-backed Manakin (<i>Chiroxiphia pareola</i>)	79	344.2	100	1513.9	AF; GU; AD; AM; CE	CE	f
Green Manakin (<i>Chloropipo holochlora</i>)	48	40.2	50	177.5	CC; AD; AM	–	m
Jet Manakin (<i>Chloropipo unicolor</i>)	6	16.3	65	112.2	AD; AM	–	m
Olive Manakin (<i>Chloropipo uniformis</i>)	6	14.7	94	178.1	GU	–	m
Caribbean White-ruffed Manakin (<i>Corapipo altera</i>)	44	9.4	49	32.2	CC; AD	–	m
Pacific White-ruffed Manakin (<i>Corapipo heteroleuca</i>)	19	97.1	93	476.1	CC	–	m
White-throated Manakin (<i>Corapipo gutturalis</i>)	36	2.2	46	6.1	GU; AM	–	f
Colombian White-ruffed Manakin (<i>Corapipo leucorrhoea</i>)	27	18.7	52	13.5	CC; AD; AM	–	m
White-crowned Manakin (<i>Dixiphia pipra</i>)	118	401.3	92	774.1	AF; GU; CC; AD; AM	–	f
Yellow-crested Manakin (<i>Heterocercus flavivertex</i>)	13	26.0	100	441.3	GU; AM	–	f
Flame-crested Manakin (<i>Heterocercus linteatus</i>)	15	137.7	98	623.8	CE; AM	–	f
Pin-tailed Manakin (<i>Ilicura militaris</i>)	85	54.2	92	117.5	AF; CE	–	m
Cerulean-capped Manakin (<i>Lepidothrix caeruleocapilla</i>)	26	20.7	46	55.7	AD	–	m
Blue-crowned Manakin (<i>Lepidothrix coronata</i>)	115	251.6	52	298.2	GU; CC; AD; AM	–	f
Opal-crowned Manakin (<i>Lepidothrix iris</i>)	23	39.2	100	247.2	AM	–	f
Blue-rumped Manakin (<i>Lepidothrix isidorei</i>)	11	14.5	35	133.1	AD	–	m
Snow-capped Manakin (<i>Lepidothrix nattereri</i>)	21	70.0	73	239.3	AM	–	f
White-fronted Manakin (<i>Lepidothrix serena</i>)	10	63.6	87	303.4	GU; AM	–	f
Orange-bellied Manakin (<i>Lepidothrix suavisissima</i>)	11	28.5	70	60.2	GU; AM	–	m
Club-winged Manakin (<i>Machaeropterus deliciosus</i>)	20	4.5	55	132.0	AD	–	m

TABLE 1. Continued.

Species	Sample localities	Area		Distance shift (km)	Regions		Topography
		Present (ha × 10 ⁻⁶)	% loss		Present	Future loss	
Fiery-capped Manakin (<i>Machaeropterus pyrocephalus</i>)	39	118.4	97	1387.3	CE; AD; AM	–	f
Eastern Striped Manakin (<i>Machaeropterus regulus</i>)	19	12.3	68	89.8	AF	–	f
Western Striped Manakin (<i>Machaeropterus striolatus</i>)	38	169.2	74	374.1	AD; AM	–	m
Orange-collared Manakin (<i>Manacus aurantiacus</i>)	17	3.9	83	148.4	CC	–	f
White-collared Manakin (<i>Manacus candei</i>)	22	26.5	54	39.3	CC	–	f
White-bearded Manakin (<i>Manacus manacus</i>)	171	601.6	83	629.6	AF; CE; AM; GU; AD; CC	–	f
Milleri Bearded Manakin (<i>Manacus milleri</i>)	8	2.5	92	40.2	CC; AD	–	f
Lemon-throated Manakin (<i>Manacus viridiventris</i>)	6	9.6	54	188.2	CC; AD	–	f
Golden-collared Manakin (<i>Manacus vitellinus</i>)	17	10.9	77	79.3	CC; AD	–	f
Golden-winged Manakin (<i>Masius chrysopterus</i>)	91	45.0	36	303.4	AD	–	m
Crimson-hooded Manakin (<i>Pipra aureola</i>)	37	83.1	100	472.7	GU; AM	–	f
Round-tailed Manakin (<i>Pipra chloromeros</i>)	47	34.8	52	51.6	CE; AD; AM	–	m
Scarlet-horned Manakin (<i>Pipra cornuta</i>)	5	1.0	84	169.8	GU; AD; CC	–	m
Golden-headed Manakin (<i>Pipra erythrocephala</i>)	152	392.5	74	340.9	GU; CC; AD; AM	–	f
Band-tailed Manakin (<i>Pipra fasciicauda</i>)	57	348.8	82	912.7	AF; CE; AD; AM	–	f
Wire-tailed Manakin (<i>Pipra filiicauda</i>)	46	193.8	97	357.0	GU; AD; AM	–	f
Red-capped Manakin (<i>Pipra mentalis</i>)	49	36.1	49	112.9	CC; AD	–	f
Red-headed Manakin (<i>Pipra rubrocapilla</i>)	69	248.0	95	465.3	AF; AM	–	f
Black Manakin (<i>Xenopipo atronitens</i>)	28	291.5	98	1063.0	GU; AM	–	f
Wied's Tyrant-Manakin (<i>Neopelma aurifrons</i>)	8	53.3	73	206.7	AF	–	m
Pale-bellied Tyrant-Manakin (<i>Neopelma pallescens</i>)	15	178.0	91	601.5	AF; CE; AM; GU	AM; GU	f
Cinnamon Tyrant-Manakin (<i>Neopipo cinnamomea</i>)	12	223.8	96	517.5	AD; GU; AM	–	f
Wing-barred Piprites (<i>Piprites chloris</i>)	17	341.8	93	1964.6	AF; GU; AM; AD; CC	CC	f
Dwarf Tyrant-Manakin (<i>Tyrannneutes stoltzmanni</i>)	17	207.7	99	223.1	GU; AD; AM; CE	CE	f

< 0.01; Table 2), although flatland species were predicted to become confined to more highly reduced fragments in relation to present distributions than montane species (Mann-Whitney *U*-test, patch area: *U* = 156, *P* < 0.01; all other *U* > 176, all other *P* > 0.23). In addition,

predicted isolation indices showed that suitable habitat patches will be more isolated in the future only for flatland species (Wilcoxon matched-pair tests, flatland species: *Z* = 2.4, *P* < 0.05; montane species: *Z* = 0.3, *P* > 0.05; Table 2).

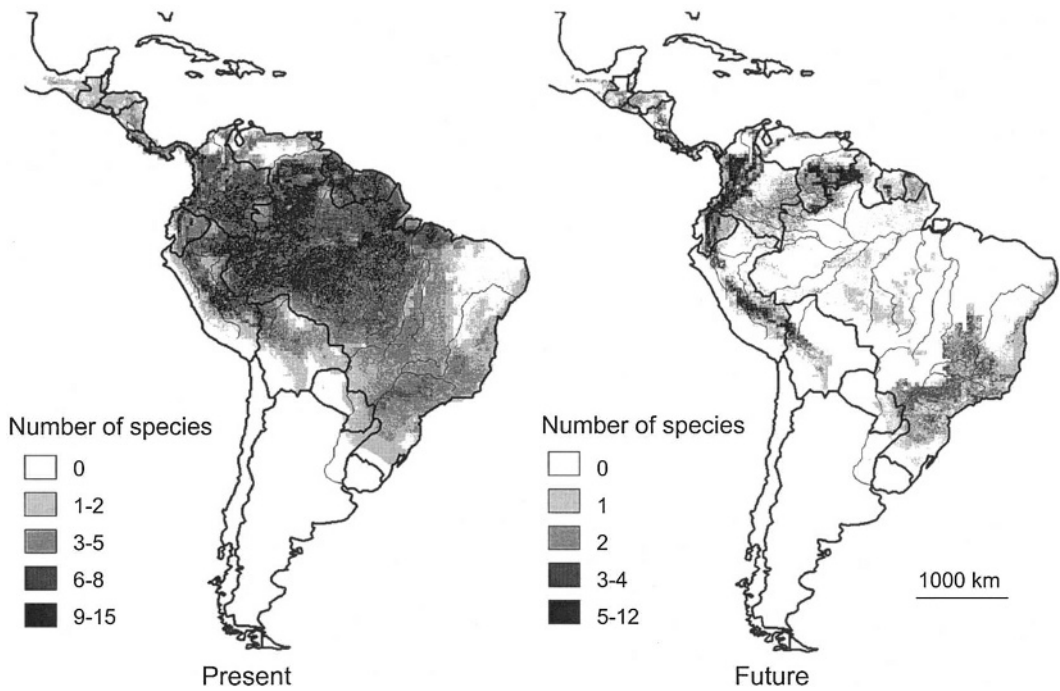


FIGURE 3. Species diversity of manakins across the Neotropics according to modeled geographic distributions for present and predicted future climates.

DISCUSSION

This study predicted considerable effects of future climate changes on the distribution and diversity of manakins throughout the Neotropics. Our approach focused on ecological niche modeling based solely on the responses of species to climatic and topographic variables, and did not evaluate effects of climate changes on forested habitats. Considering that climatic variables may often be surrogates for occurrence of plant species and vegetation types (Siqueira and Peterson 2003), and may not affect the persistence of bird species directly, other effects of future climates may affect distributions of manakins beyond those foreseen here. More dramatic effects would be expected if vegetation cover changes abruptly, or if potential effects on habitat parameters such as plant phenology and fruit availability are considered; conversely, effects might be less pronounced if habitat structure changes moderately in response to new climatic conditions. Nevertheless, we expect relatively minor variations from the species loss and distributional changes predicted here, as ecological niches

have defined species distributions accurately on both ecological and evolutionary timescales (Huntley et al. 1989, Peterson et al. 1999, Martinez-Meyer et al. 2004).

The Amazon and Cerrado regions are predicted to lose a large portion of their suitable manakin habitats, therefore a major reduction in diversity of these birds in flatland forests is expected. While manakin diversity is predicted to decrease dramatically in the Amazon region, overall species composition is not expected to be reduced greatly. In contrast, forested habitats in the Cerrado are predicted to face considerable loss of both habitable area and species. Although most manakins occurring in the Cerrado are not restricted to that region, generally inhabiting transitional zones to other biomes, Cerrado bird species diversity may be severely threatened, as previous assessments have shown drastic effects of future climates for Cerrado tree species (Siqueira and Peterson 2003). Predictions of vegetation cover and structure for these areas are, however, difficult to postulate. Although paleoclimatic reconstructions for the Amazon Basin indicated that

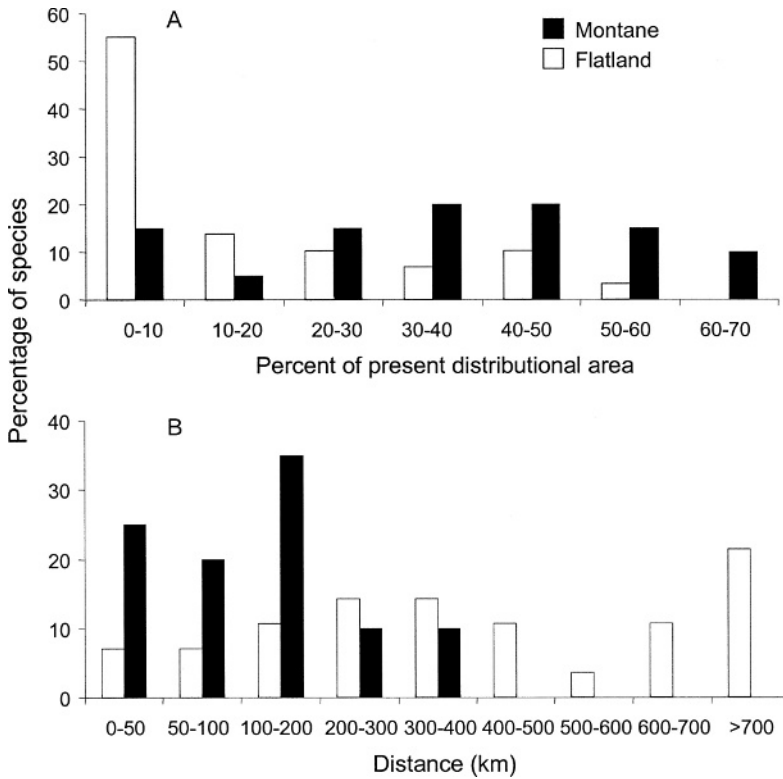


FIGURE 4. Percentage of manakin species in each category of projected change in (A) potential distributional areas (expressed as percent of present distributional area), and (B) projected distance that range centroids would shift, as a result of modeled climate change processes in montane and flatland habitats.

savanna formations did not expand in warmer interglacial periods during the Holocene (Hoorn 1997, Harbele and Maslin 1999, Colinvaux et al. 2000, Pennington et al. 2000, Bonnaccorso et al. 2006), some studies have shown that dry, sandy soil forests may have benefited from these climates (Prado and Gibbs

1993, Pennington et al. 2000, 2004) and may become more available in the future. In fact, the composition of biotas in the past indicates that climate changes affect individual species differently, and future biotas may not have contemporary analogues (Graham 1988, Hunter et al. 1988). Furthermore, the increase of 3.0–5.1°C

TABLE 2. Spatial statistics for modeled species distributions under present and future climates, for flatland and montane species. Comparisons are based on mean patch area and distance to the nearest neighbor (NN) and on a median isolation index (PX₉₂; Gustafson and Parker 1992). Future estimates differing significantly from present values are marked with * denoting $P < 0.05$ and ** denoting $P < 0.01$ (Wilcoxon matched pairs test).

Time period	Topography	Number of species ± SE	Number of patches ± SE	Patch area ± SE (km × 10 ⁻³)	NN ± SE (km × 10 ²)	PX ₉₂ × 10 ² ± SE
Present	All species	49	226.2 ± 37.1	11.0 ± 3.9	3.5 ± 0.4	0.1 ± 0.1
	Flatland	29	318.3 ± 55.0	13.3 ± 6.2	3.4 ± 0.4	0.0 ± 0.0
	Montane	20	92.6 ± 21.8	7.7 ± 3.5	3.8 ± 0.8	0.3 ± 0.3
Future	All species	49	136.1 ± 32.6	1.5 ± 0.3**	19.5 ± 8.9**	29.5 ± 21.7*
	Flatland	29	173.1 ± 52.9	1.3 ± 0.4**	27.7 ± 14.8**	41.0 ± 36.0*
	Montane	20	82.5 ± 18.4	2.0 ± 0.6**	7.6 ± 1.7**	12.8 ± 10.8

in temperature predicted for future decades largely exceeds records for oscillations of warm climates in the past (e.g., 1.7°C during the Eemian epoch, 130 000 bp; Sirocko et al. 2005).

In general, forested areas predicted to hold suitable habitats under future climates are of conservation importance for flatland faunas. However, predicted species losses should perhaps be regarded with some caution, as reactions to unknown climate combinations that species would likely experience under future climate regimes, to some degree at least, are unknown (Graham 1988, Hunter et al. 1988). Montane regions, on the other hand, appear to be crucial for conservation of Neotropical manakin species diversity. Montane forests are predicted to hold the highest local manakin diversity in coming decades and, although models predicted less severe effects of climate change in montane forests, montane species are nonetheless predicted to see significant reductions in distribution (>30%), and would likely also experience new climatic conditions under future climate regimens, with unknown effects on their persistence. Furthermore, the accelerated deforestation rates that some of these habitats are facing (da Fonseca et al. 2000, Myers et al. 2000) suggest that montane forests predicted to remain habitable in the future on climatic grounds should be assigned top priority for conservation action, as they may prove highly endangered on land-use considerations.

Flatland and montane topographies present different scenarios for changing distributions under future climates. The reduced horizontal shifts in suitable conditions in montane versus flatlands regions are instead associated with changes in distributional area along altitudinal gradients (Peterson 2003). This pattern probably results from the greater environmental heterogeneity found within grid squares in the more topographically diverse montane regions. Species inhabiting montane forests may also be more flexible regarding habitat requirements, as some species undergo altitudinal migrations among seasons (Rosselli 1994, Blake and Loiselle 2002; MA, unpubl. data). Altitudinal shifts may nevertheless make these species more vulnerable, as they may require lowland habitats for continuous fruit availability (Rosselli 1994). More accurate results will be possible once models of climate change become available at finer spatial scales, but the broad

responses of flatland and montane species to climate changes will likely be similar to the current results, given the variation in topography and spatial heterogeneity between these habitats.

Our assumption of no dispersal is unlikely to have influenced our results regarding effects of climate changes and topography on distributions of species. In the original publication outlining these effects (Peterson 2003), similar patterns were observed among North American birds when very liberal dispersal scenarios were considered, and dispersal ability affected only the distances by which geographic distributions shifted.

Although local manakin populations are usually not particularly sensitive to habitat fragmentation (Andrade 1999, Anciães and Marini 2000, Rosselli et al. 2002), effects of climate changes at regional scales (e.g., area loss and isolation, distributional shifts, metapopulation dynamics) may overcome local population processes. Under this scenario of accentuated isolation and reduction of habitable area, manakin species may indeed become threatened. Reduced patch size suggests increasing dependence of local populations on suitable habitats at regional scales to preserve metapopulation dynamics.

Niche modeling provides a useful means of exploring the effects of future climate change on biodiversity patterns. As such, it may prove helpful in identifying priority areas for conservation, i.e., areas where future climates will likely promote gain versus loss of biodiversity. Given the large predicted distributional shifts for flatlands species, their present-day ranges offer little information about future distributions. Thus, effective conservation of flatland species, in particular, depends on accurate predictive methods, as indicated here and in previous studies (Peterson et al. 2001, 2002, Peterson 2003). Conservation of montane species, on the other hand, requires techniques that are able to accurately locate remnant habitats that will likely remain habitable after climate change.

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