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USING SPATIAL MODELS TO PREDICT AREAS OF ENDEMISM AND GAPS IN THE PROTECTION OF ANDEAN SLOPE BIRDS

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Abstract.—Seeking more precise knowledge of avian endemism on the east slope of the Andes in Peru and Bolivia, one of the most diverse faunal regions on Earth, we used distribution models based on locality records and 10–12 uncorrelated environmental variables to map the distributions of 115 species. Both maximum-entropy and deductive models reveal three areas of endemism, broadly supporting previous assessments of endemism in the region but showing much more detail. Regions such as the southwestern Cordillera de Vilcabamba and the Río Mapacho-Yavero valley in Cusco, Peru, and the Cordillera de Apolobamba in western Bolivia support a greater richness of endemic species than has been recognized, a result likely attributable to the ability of predictive models to partially control for biases in survey effort. National-level protected areas cover ≥1,000 km^2 of the ranges, or four-fifths of the ranges of species with distributions <1,000 km^2, of 77% of the endemic species. However, an analysis of summed irreplaceability, which emphasizes the locations of the most narrowly distributed endemics, showed that only 18% of these critical areas are currently protected. The fine-scale maps of endemic areas are suitable for regional and local-scale conservation planning, activities that can fill current gaps in protection of many species. *Received 15 August 2008, accepted 25 January 2009.*

Key words: Andes, distribution mapping, diversity, endemism, maximum entropy, protected areas, summed irreplaceability.

Usando Modelos Espaciales para Predecir Áreas de Endemismo y Vacíos de Conservación de Aves de las Vertientes Andinas

Resumen.—Con el fin de mejorar la precisión de nuestro conocimiento de las áreas de endemismo para aves en la vertiente oriental de los Andes en Perú y Bolivia, una de las regiones faunísticas más diversas del mundo, utilizamos modelos de distribución basados en registros de localidad y 10–12 variables ambientales no-correlacionadas para mapear las distribuciones de 115 especies. Los resultados, derivados del algoritmo de entropía máxima y de modelos deductivos, muestran tres áreas de endemismo que respaldan en general las evaluaciones anteriores de endemismo hechas en la región, pero con mucho más detalle. Las regiones como el sur-occidente de la Cordillera de Vilcabamba y el valle del Río Mapacho-Yavero en Cusco, Perú, y la Cordillera de Apolobamba en el occidente de Bolivia albergan una diversidad de especies endémicas más alta de lo que se ha reconocido anteriormente. Este resultado probablemente se debe a la característica de los modelos predictivos de controlar, en parte, el sesgo por esfuerzo de muestreo. Las áreas protegidas al nivel nacional cubren por lo menos 1.000 km^2 de las distribuciones, o cuatro quintos de las distribuciones de las especies con rangos de menos de 1.000 km^2, del 77% de las especies endémicas. No obstante, un análisis de la irreemplazabilidad total, que da énfasis a las localidades de las especies con los rangos más reducidos, demostró que solamente el 18% de estas áreas críticas están protegidas en la actualidad. Los mapas de escala fina de las áreas de endemismo pueden permitir la planificación de la conservación tanto al nivel local como al nivel regional, actividades que pueden llenar los vacíos de protección actuales de muchas especies.

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Understanding patterns of endemism in Andean birds has challenged biogeographers for some time (Müller 1973, Terborgh and Winter 1983, Cracraft 1985). Our knowledge about the distributions of Neotropical birds continues to improve, as do the spatial methods available for analyzing the growing body of distributional information. The field has progressed from hand-drawn range maps (Cracraft 1985, Ridgely and Tudor 1989) to documenting and interpolating species' presence in quarter-degree grids (Fjeldså et al. 1999, 2005). Today, algorithms for predicting species' distributions on the basis of suites of environmental variables are increasing in sophistication and prediction accuracy and can even perform satisfactorily for species known from few localities (Elith et al. 2006, Hernandez et al. 2006). These new techniques have the potential to provide a fresh look at avian areas of endemism and application of this knowledge to fields such as conservation.

Cracraft (1985) defined "areas of endemism" as places where species' ranges are congruent and identified 33 such areas in South America, including 6 in the Andes. At that time, distributional information was too fragmentary to describe finer-scale divisions, other than to suggest that the Apurímac and Marañón rivers in Peru may serve as barriers to dispersal and delimit areas of endemism. A few years later, Ridgely and Tudor (1989) mapped areas of endemism for South American birds with circumscriptions similar to those used by Cracraft (1985). A subsequent effort defined "endemic bird areas" as places that encompass the complete ranges of at least two species with restricted ranges (<50,000 km^2; Stattersfield et al. 1998). These researchers collated locality records for range-restricted birds from the literature and from a network of field workers and then used the extent of relevant habitats or geographic features such as elevational contours, rivers, or coastlines to develop distribution maps for each species. The resulting endemic areas are delineated at a finer scale than in previous analyses, with 18 such areas mapped along the length of the Andes. The most recent effort used published records and field data to score the presence of each species in a quarter-degree grid placed over a map of the Andes (Fjeldså et al. 1999, 2005). Scoring the numbers of species in each cell provides a picture of the richness of either all species or the species with the smallest ranges, defined as those in the lower quartile of ranked range sizes.

Species distribution models have the potential to improve our ability to identify and protect areas of endemism. These models estimate the relation between a species and its environment and then predict a distribution based on the occurrence of the identified suite of environmental variables across the landscape under study (Guisan and Thuiller 2005). Although sometimes these models may not account for interspecific interactions that can modify species' ranges, they have nonetheless proved powerful in a variety of applications, including study of the possible effects of climate change, prediction of potential distributions of invasive species, and identification of areas that may harbor undescribed endemic species (Peterson and Vieglais 2001, Raxworthy et al. 2003, Araújo et al. 2005). Recently, researchers have begun using the results of distribution models in conservation applications such as identification of protection needs and calculation of risk status for organisms ranging from plants to dung beetles (Chefaoui et al. 2005, Pawar et al. 2007, Peralvo et al. 2007, Solano and Feria 2007).

Here, we describe a large-scale effort to use modeled ranges of Andean birds to address the question of where areas of endemism are located and how well they are protected. We focus on birds endemic to the east slope of the Andes and adjacent lowlands in Peru and Bolivia (to ~18°S latitude), a region recognized as among the most diverse anywhere for birds (Orme et al. 2005). The models include vegetation variables derived from remotely sensed data to enhance prediction accuracy (Buermann et al. 2008). Because modeled ranges predict areas of suitable habitat independent of the locations of field surveys, we ask how our results differ from previous efforts that may have been more influenced by where field work was conducted. The fine scale of the distributions generated is more useful for local conservation planning than the results of previous continental or global analyses, which allows us to address how well existing systems of protected areas cover areas of avian endemism (Fjeldså and Rahbek 1997, Loiselle et al. 2003, Rodrigues et al. 2004). Throughout, we define "areas of endemism" as places where multiple species endemic to the study area co-occur.

Methods

Study area.—The study area covers the lowlands and adjacent mountain slopes as high as the upper extent of closed-canopy forest on the eastern versant of the Andes in Peru and Bolivia (Fig. 1). The habitats include forest dominated by trees in the genus *Polylepis*, Yungas forest, dry forest, seasonally flooded savannas, and lowland rainforest (for a more detailed description, see Josse et al. 2007). This area encompasses 1,249,282 km^2. Because ecological boundaries are rarely as sharp as they appear on a vegetation map, and to avoid edge effects, the extent of most of our analyses included a 100-km buffer around the study area. For example, many isolated patches of woodlands dominated by *Polylepis* occur in montane regions to the west of and just outside our study area.

Focal species.—We included all species that are endemic to our study area that had been formally described by 2006. English and scientific names of all species in the study are listed in the Appendix. We also included a new species of flycatcher, the Yungas Tyrannulet, for which a description was in press during the study (Herzog et al. 2008), and species that are largely endemic to the study area but also occur in (but not beyond) the 100-km buffer. To determine species for inclusion, we applied the following criteria. First, we identified all species with ranges entirely within the analysis extent (study area buffered by 100 km). From the resulting list of species, we eliminated all that were restricted to the buffer area and, therefore, did not occur in the study area *sensu stricto*. For the species occurring in both the buffer area and the study area, we eliminated all that were restricted to habitat types such as puna that did not occur in substantial amounts within the study area. Additionally, for species in humid forests on the northern and eastern boundaries of the study area, we eliminated those for which most known localities lie outside the study area. We eliminated one species, the Coppery Thorntail (*Discosura letitiae*), because both known records are too vague to georeference accurately. In sum, 115 species fulfilled these criteria.

Compilation of locality records.—We requested specimen locality information for the target species from major in-country natural-history museums and from all North American museums

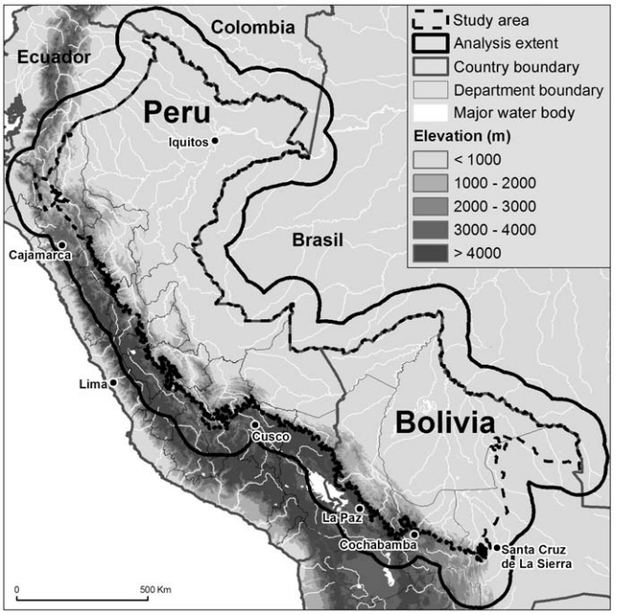


FIG. 1. Map of the study area showing elevational relief and major cities. Heavy black line delimits the analysis extent, which includes the study area (dashed line) buffered by 100 km.

with significant holdings of specimens from South America (see Acknowledgments for list of contributors). We georeferenced all localities for which the specimen labels did not include geographic coordinates, using gazetteers (Stephens and Traylor 1983), topographic maps produced by national cartographic institutes, and 1:250,000 digital databases (Programa Nacional de Informática y Comunicaciones de Naciones Unidas 1998) available for the study area. For more complete coverage, we added records from the literature by searching the *Zoological Record* and other sources for target species and their synonyms. We also included observational and sound-recording records compiled by S.K.H., A. B. Hennessey, J. Fjeldså, D. F. Lane, S. Mayer, J. P. O'Neil, and T.V. To ensure the accuracy of the coordinates assigned to each locality, S.K.H., I.F., D. F. Lane, J. P. O'Neil, and T.V.—all field ornithologists who have extensive experience with these species—reviewed maps displaying the localities for each species. Before running models, we filtered the data to include only unique localities (only one record per species per 1-km^2 grid cell, our unit of analysis).

Environmental data layers.—We relied on layers describing climatic, topographic, and vegetative cover conditions within our study area to develop species distribution models (Table 1). To remove redundant information, we performed a correlation analysis to identify a subset of climatic variables that were not correlated with each other (correlation coefficient <0.7) and also not correlated with elevation. This analysis was performed separately for the montane region (>800 m elevation) and the lowland region (Table 1).

To account for current habitat availability, we used three variables derived from the Moderate Resolution Imaging Spectroradiometer (MODIS) set of data. One variable was the percent tree cover layer for South America from the Vegetation Continuous Fields collection (Hansen et al. 2003). The other two variables were the first two axes of a principal component analysis of the Enhanced Vegetation Index (EVI) data for 16-day periods from 2001 to 2003. Principal component analysis is a commonly used data-reduction technique of multitemporal remotely sensed imagery. The first two axes can be interpreted to represent vegetative structure and temporal dynamics (which accounts for annual variation), respectively (Hirosawa et al. 1996). Persistent cloud cover can complicate this sort of analysis, though using

TABLE 1. Climatic, topographic, and vegetative variables used for the models.

Variable	Source
Climate	
Annual mean temperature [a]	Worldclim bioclimatic database (Hijmans et al. 2005)
Isothermality [a]	
Maximum temperature of warmest month [a]	
Temperature seasonality [a]	
Mean diurnal range [b]	
Precipitation in wettest month	
Precipitation in driest month [b]	
Precipitation seasonality	
Topography	
Elevation	Hole-filled seamless Shuttle Radar Topographic Mission (SRTM) 90-m digital elevation data, version 2 (see Acknowledgments). Slope calculated as the maximum rate of change in elevation from each pixel to its neighbors. Topographic position index calculated by determining the difference between the mean elevation within a neighborhood of pixels and the center pixel (Zimmermann 2000).
Slope	
Topographic position index	
Vegetation	
Percent tree cover	Moderate Resolution Imaging Spectroradiometer (MODIS) 500-m Global Vegetation Continuous Fields (Hansen et al. 2003).
Enhanced vegetation index (EVI) 1	MODIS/Terra Vegetation Indices 16-day L3 global, 1 km. EVI 1 and EVI 2 are the first and second principal components from a correlation matrix of EVI geotif images.
EVI 2	

[a] Used for lowland species (<800 m) only.
[b] Used for montane species (>800 m) only.

images that summarize data for a number of days helps alleviate the problem. Even 16-day periods can be affected by cloud cover, but areas with continuous cloud cover may have similar vegetative characteristics. We chose the EVI instead of the traditional Normalized Difference Vegetation Index (NDVI) because EVI has proved less prone to saturation in humid forested areas (Huete et al. 2002) and, therefore, more sensitive to canopy variation.

A spatial mismatch between the low precision of the species locality data and the high precision of the MODIS satellite data may reduce the utility of the MODIS data for predicting the distribution of our endemic species. For example, a small georeferencing error could assign a bird collected just inside a forest with coordinates that correspond to a nearby pasture. In an attempt to compensate for this potential mismatch, we summarized each MODIS layer within moving windows 2 km and 5 km in diameter. Further summarizing vegetative-cover data in this fashion may be more ecologically relevant as well, because factors that influence habitat selection often include the conditions of the surrounding landscape (Mazerolle and Villard 1999, Pearce et al. 2001, Johnson et al. 2002).

Distribution modeling.—We attempted inductive models for species known from multiple localities and used a deductive method for species known from single localities and for those in which inductive methods failed to produce a realistic model. Inductive methods use the environmental conditions at points of known occurrence in a statistical analysis to construct a definition of the species' relationship with its environment, whereas deductive methods rely on knowledge about the species' biology to quantify the species–environment relationship. We used maximum entropy in MAXENT (see Acknowledgments), a statistical mechanics approach, as our inductive model (Phillips et al. 2004, 2006). Previous comparative studies have demonstrated that MAXENT yields robust predictions even with few locality records (Elith et al. 2006; Hernandez et al. 2006, 2008; Phillips et al. 2006). Like other modeling algorithms, MAXENT uses the environmental characteristics of areas where a species has been recorded to predict its distribution.

For each species modeled with MAXENT, we ran four models (using default settings for MAXENT 2.1, except that we considered only linear and quadratic features because of small numbers of localities available) varying in the use of the MODIS data: no MODIS data, MODIS data unsummarized, MODIS data summarized by 2 km, and MODIS data summarized by 5 km. To evaluate the models, we could not partition the data into training and evaluation records because of the scarcity and low spatial precision of available locality data. In this situation, review by specialists familiar with the species is often the best way to determine the modeling procedure that produces the most realistic range prediction (Hernandez et al. 2008, Kremen et al. 2008, Loiselle et al. 2008). Three of us (I.F., S.K.H., and T.V.) who are familiar with the study area and species reviewed the output. These reviewers determined whether any of the MAXENT models produced maps that accurately depicted known areas of occurrence and, if they did, whether they identified the model and threshold (from the 0–1 scale of Maxent output depicting how well the variables in each pixel match those found where the species has been recorded) that produced the most reasonable map for the species according to our present understanding of its distribution and habitat availability. The reviewers also eliminated predicted areas of distribution where the species is known not to occur, such as those separated by geographic barriers from verified records.

For most cases in which the MAXENT results were unsatisfactory, we used deductive models based on elevational ranges to depict distributions. We generated predictions by defining the maximum and minimum elevations where the species has been recorded, buffered by 100–200 m. For species that occur in lowland areas, and those for which reliable elevation information was unavailable, we buffered known localities by 5–15 km, depending on the presumed dispersal ability of the genus of the species being modeled (for example, we buffered localities by shorter distances for tapaculos [*Scytalopus* spp.] than for tanagers [*Tangara* spp.]). In two cases, we reran MAXENT with a reduced number of environmental variables to improve the predictions. Three species, the Scarlet-banded Barbet, Vilcabamba Tapaculo, and Sira Tanager, are known from single localities. We modeled their distributions using the elevational range where the species have been recorded at these localities. In a few cases, the best approach was to use hybrid models with MAXENT results for one part of the range and deductive results for a separate, spatially discrete portion of the range.

Identification of areas of endemism.—We calculated the following two indices by using the predicted distribution data to identify areas of endemism. First, we calculated "endemic species richness" as the number of species considered endemic to the study area that are predicted to occur in each analysis pixel (Müller 1973). We defined "areas of endemism" as those pixels that contained at least two-thirds of the maximum number of overlapping endemic species anywhere. To examine how our criteria for defining "endemic species" differed from those of previous studies that used range-size cutoffs to identify restricted-range species (e.g., Fjeldså et al. 1999), we mapped a subset of the focal species that have restricted ranges. We defined "restricted-range species" as those falling in the first quartile of range size of resident, nonmarine South American birds, calculated from available digital range maps (Ridgely et al. 2005). The cutoff range size was 76,096 km^2. The pattern of species richness did not differ, so we present the results only for the full suite of endemic species.

Second, we calculated summed irreplaceability as the likelihood that an analysis pixel must be protected to achieve a specified conservation target for the study area (Pressey et al. 1994, Pressey 1999, Ferrier et al. 2000). Modeling with C-PLAN conservation planning software (Pressey et al. 2005), we used 10-km^2 analysis pixels and set 25 of these pixels for each species as a conservation target. Although this target is somewhat arbitrary, spatial patterns of irreplaceability are typically robust to target level (Rissler et al. 2006). If a species occurs in <25 of the 10-km^2 pixels, we set the target as the number of pixels in which the species occurs. For each species, irreplaceability for each pixel ranges from 0 to 1. Low numbers indicate that a species occurs in many pixels, whereas values close to 1 reflect the existence of species with very restricted ranges. Summed irreplaceability sums the irreplaceability values for all species occurring at each pixel, drawing attention to the sites (pixels) with the greatest numbers of narrow-ranging species. Summed irreplaceability incorporates the concept that the species with the smallest ranges offer the fewest options for conservation,

just as weighted endemism (the sum of the inverse of each species' range that overlaps each pixel, also known as "range-size rarity"; Knapp 2002) does, but additionally incorporates the complementarity of sites for protecting suites of species. To summarize the results, we divided pixels into six classes of irreplaceability using natural breaks (Jenk's optimization).

Protected areas coverage.—To assess the completeness of protected areas in preserving habitat for endemic birds, we overlaid maps of national-level parks and reserves on the modeled distributions of the focal species within the unbuffered study area. We included all protected areas that correspond to World Conservation Union (IUCN) scores I–VI (IUCN 1994), as well as those that have not been scored against the IUCN criteria. Birds also are protected in private and municipal reserves, but currently most protected lands in the study area are managed by national governments. We considered species with "at least minimum protection" as those with ≥1,000 km^2 of their ranges within protected areas. We considered species with ranges <1,000 km^2 to have minimum protection if 80% of their range occurred within a protected area. In addition, we calculated the percentage of each endemic area covered by protected areas.

Results

Distribution modeling.—We compiled a total of 2,437 unique locality records for the 115 endemic bird species (Appendix). Sample sizes of localities per species ranged up to 94 (for Rufous-naped Brush-Finch) and averaged 21.2. Thirty-seven species (32% of the total) had ≥25 unique localities, and 76 species (66%) had ≥10 unique localities. Reviewers selected MAXENT models for 99 species (86%), hybrid models for 6 species (5%), and deductive models for 10 species (9%). Reviewers most frequently chose MAXENT results incorporating MODIS data generalized to 5 km (74 species, or 70%), followed by runs using MODIS data generalized to 2 km for 17% of the inductively modeled species. The other models, either not using MODIS data or using ungeneralized MODIS data, were chosen for just 10% of species. The range sizes of the resulting distribution maps varied from 78 km^2 (Vilcabamba Tapaculo) to 309,168 km^2 (Elusive Antpitta), with an average of 33,544 km^2. (Maps for all species are posted online; see Acknowledgments.)

Endemic species richness.—Superimposing the modeled ranges of all species revealed three areas of endemism with 25–38 bird species per 1-km^2 grid cell (Fig. 2). These areas are (1) Southern Huánuco, the portion of the east slope of the Peruvian Andes in the southern half of the department of Huánuco, including the Carpish Hills area along the road to Tingo María and extending south to the northwest corner of the Yanachaga-Chemillén National Park in Pasco Department; (2) Central Cusco, the region extending from the east bank of the Río Apurímac east to the Yungas of Megantoni National Sanctuary and Manú National Park, including the southwestern Cordillera de Vilcabamba, Machu Picchu, and the valleys of Ocobamba, Yanatile, and Mapacho-Yavero; and (3) the Upper Yungas of northern Bolivia, an extended segment of the upper portion of the study area from the Cordillera de Apolobamba, the portion of the east slope of the Andes in Bolivia just south of the Peruvian border in Madidi National Park, along the Cordillera de La Paz (also known as the Cordillera Real, near the city of La Paz), and southeast to the Cordillera de Cocapata-Tiraque, near the city of Cochabamba. These three regions cover a total of 23,625 km^2. All occur along the upper elevational limit of the study area on the east slope of the Andes, at an average elevation of 2,533 m. Typically, less than five endemic species occurred anywhere in the study area below 1,500 m elevation.

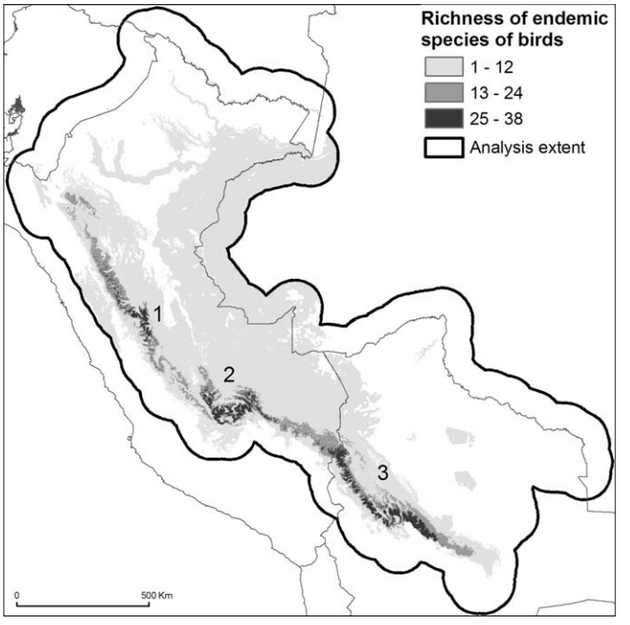


Fig. 2. Richness of endemic bird species on the eastern versant of the Andes in Peru and Bolivia. Heavy black line delimits the analysis extent. Numbered areas of endemism: 1 = Southern Huánuco, 2 = Central Cusco, and 3 = Upper Yungas of northern Bolivia.

Summed irreplaceability.—Summed irreplaceability analysis highlighted 10 areas important for narrow-ranging endemics (representative species given for each): (1) white-sands forests near Iquitos (Ancient Antwren and Allpahuayo Antbird); (2) Rio Morona (White-masked Antbird); (3) Cordillera de Colán and the Alto Mayo region (Long-whiskered Owlet, Marvelous Spatuletail, Speckle-chested Piculet, Ochre-fronted Antpitta, and Johnson's Tody-Tyrant); (4) southeastern La Libertad Department (Yellow-browed Toucanet and Golden-backed Mountain-Tanager); (5) Tingo María-Carpish Hills (White-tufted Sunbeam, Bay Antpitta, and Tschudi's Tapaculo); (6) southwestern Cordillera de Vilcabamba (Vilcabamba Tapaculo, Inca Wren, and Vilcabamba Brush-Finch); (7) Cordillera de Urubamba (White-browed Tit-Spinetail); (8) Valle de Pilcopata (Fine-barred Piculet and Black-backed Tody-Flycatcher); (9) upper Consata watershed (Yungas Tyrannulet and Green-capped Tanager); and (10) Cordillera Muñecas (Berlepsch's Canastero) (Fig. 3).

Coverage of protected areas.—Currently, 44 national-level protected areas have been designated in the study area, covering 240,125 km^2, or 19% of the study area. Eighty-nine species (77%) satisfied the criteria for having minimal protection. Five species—Blue-throated Macaw, Berlepsch's Canastero, Masked Antpitta, Black-spectacled Brush-Finch, and Vilcabamba Brush-Finch—occur completely outside of protected areas. All

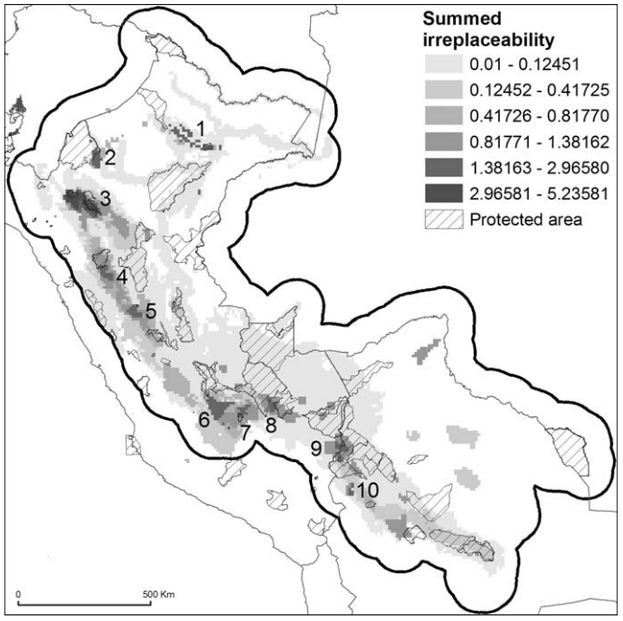


FIG. 3. Summed irreplaceability analysis highlighting areas with the greatest numbers of narrow-ranging species in the study area and locations of national-level protected areas. Numbered areas of high irreplaceability: 1 = Iquitos, 2 = Rio Morona, 3 = Cordillera de Colán–Alto Mayo, 4 = southeastern La Libertad Department, 5 = Tingo María-Carpish Hills, 6 = southwestern Cordillera de Vilcabamba, 7 = Cordillera de Urubamba, 8 = Valle de Pilcopata, 9 = upper Consata watershed, and 10 = Cordillera Muñecas.

three areas of endemism identified in the species-richness analysis have portions of their extensions included within protected areas, with 22% of the total area protected. Eighteen percent of the area identified as highly irreplaceable is currently protected, but three areas (Tingo María-Carpish Hills, southwestern Cordillera de Vilcabamba, and Cordillera de Muñecas) currently are not covered by any national-level protected areas (Fig. 3).

DISCUSSION

Use of distribution models produced highly detailed maps of where 115 species endemic to the tropical eastern Andean slope and adjacent lowlands in Peru and Bolivia are most likely to occur. The distributions of most of these species are concentrated on the upper slopes, within ~1,000 m in elevation below the tree line. Overlaying the distribution maps highlighted three distinct regions of sympatry of large numbers of endemic species. Even more valuable in a conservation context, summed irreplaceability analysis revealed 10 areas with especially narrowly distributed species. The results point out areas most in need of protection as a means of achieving minimal conservation goals of preserving habitat for all endemic birds.

Modeling success.—Inductive distribution models yielded successful results for most of the bird species endemic to the study area. MAXENT produced favorable results for 91% of the species. The adequate sample of localities available and the tendency for most of the target species to distribute themselves in elevational bands may have contributed to this result. Typically, inductive modeling methods work better for specialist than for generalist species (Thuiller et al. 2004, Hernandez et al. 2006).

Rare lowland species such as the Selva Cacique were difficult to model with the environmental data available. This species is known from just six scattered localities and may be restricted to microhabitat types, such as canebreaks occurring along river margins (Gerhart 2004), that are not distinguishable in the 1-km-scale vegetation data available from MODIS imagery. The Blue-throated Macaw was another lowland species that was difficult to model. The MAXENT model showed a much wider distribution than is presently known for this critically endangered species, which is currently subject to intensive monitoring. The area of overprediction may indicate potential habitat for the species, but persecution for the pet trade and other threats may have extirpated the species from these areas. Grugru Palm (*Acrocomia totai*; known locally as "Totai") and Motacú Palm (*Attalea phalerata*), which produce important fruits in the Blue-throated Macaw's diet (Juniper and Parr 1998), are widespread in the area and, therefore, do not appear to limit distribution. Because of the inability of available environmental variables to depict microhabitats, because of human exploitation, or for an as-yet-unidentified reason, models for lowland species produced with the methods employed here required judicious review by ornithologists familiar with the species to eliminate areas of overprediction.

The distribution maps developed in the present study likely suffer fewer biases caused by uneven observation efforts than might be the case in our study area for more poorly studied and microendemic taxa, such as amphibians or plants (Nelson et al. 1990, Young 2007). Sample sizes of localities and ranges were sufficient to interpolate ranges between localities; we thereby avoided results showing concentrations of endemics near cities or along roads or rivers where field efforts have been focused. Nonetheless, two of the areas of endemism occur near the accessible regions of Cusco, Peru, and Cochabamba, Bolivia. Intense study in the cordilleras near these cities may have led to recording more endemic species there than elsewhere. Conversely, the Cordillera de Apolobamba, another area that supports large numbers of endemic species, has only recently been the subject of bird surveys (Vogel et al. 2001, Vogel 2002, Hennessey and Gómez 2003). The paucity of locality data here suggests that the distribution models are working as they were intended—serving as proxies for more intensive survey effort.

Congruence of modeled with previously recognized areas of endemism.—Stattersfield et al.'s (1998) analysis of endemic bird areas showed that most of the upper portion of the study area occurs in an endemic bird area (Figs. 4, 5). Thus, in a broad sense, our results, produced by a more detailed process to identify species' ranges (but using a different definition of endemism), support the conclusions of Stattersfield et al. (1998). Because of the fine resolution of the results presented here, we can identify which portions of a particular endemic bird area likely harbor the most endemic species. For example, the Bolivian and Peruvian lower Yungas endemic bird area probably has many more sympatric endemic species in Cochabamba than in La Paz (Fig. 5).

An important contribution of the present study is the identification of endemic areas that were previously overlooked. The two

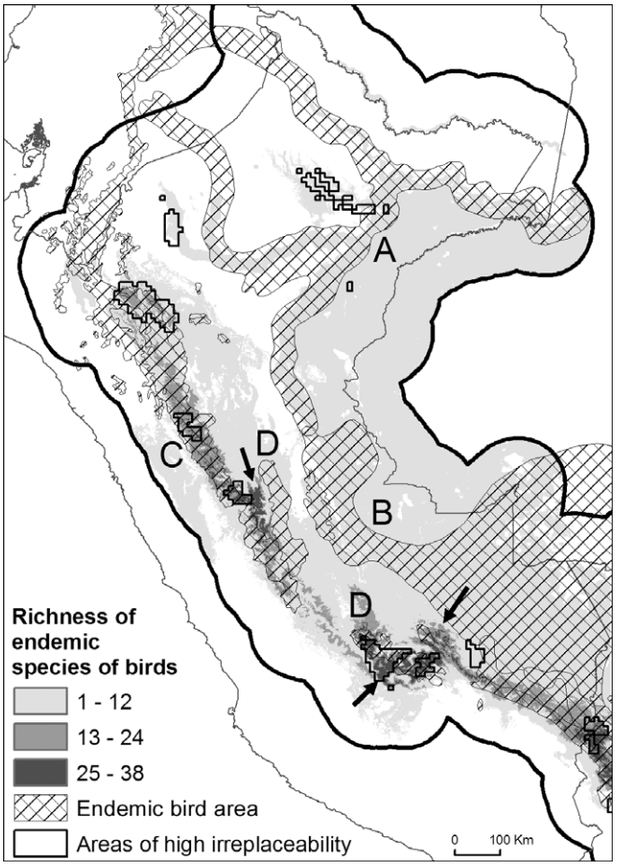


Fig. 4. Overlap of endemic species richness, areas of high irreplaceability, and endemic bird areas (Stattersfield et al. 1998) in Peru. Endemic bird areas are indicated by letters: A = upper Amazon–Napo lowlands, B = southeast Peruvian lowlands, C = northeast Peruvian cordilleras, and D = Peruvian east Andean foothills. Arrows highlight potential areas of endemism identified for the first time in the present study.

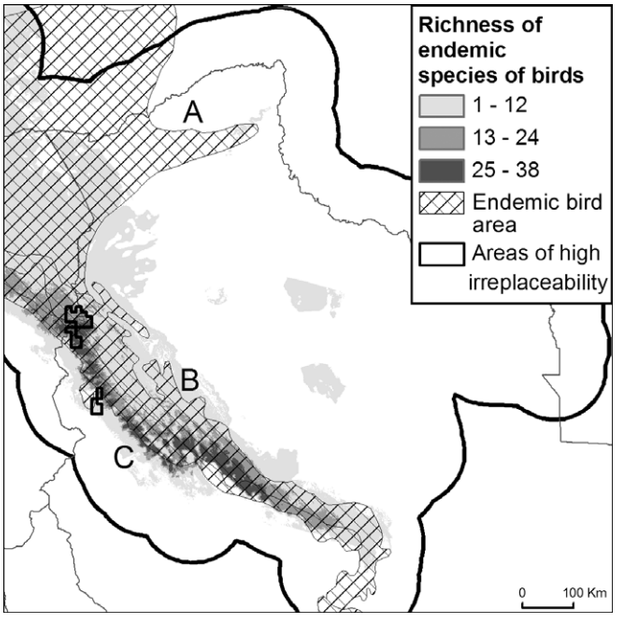


Fig. 5. Overlap of endemic species richness, areas of high irreplaceability, and endemic bird areas (Stattersfield et al. 1998) in Bolivia. Endemic bird areas are indicated by letters: A = southeast Peruvian lowlands, B = Bolivian and Peruvian lower Yungas, and C = Bolivian and Peruvian upper Yungas.

Peruvian endemic areas we identified were only partially included in endemic bird areas. Much of the southern Huánuco region occurs between endemic bird areas in the northeast cordilleras and east Andean foothills in Peru (Fig. 4). The central Cusco region is somewhat covered by the Peruvian East Andean foothills endemic bird area (Stattersfield et al. 1998), but the southwestern Cordillera de Vilcabamba, between the Río Apurímac and Cerro Pumasillo, and the region along the Río Mapacho-Yavero east of Cusco are not (Fig. 4). These remote regions have received little attention from ornithologists, as measured by the number of specimens collected there, and, therefore may have been overlooked by previous studies that relied on recorded observations, but not by the modeling approach we employed.

Stattersfield et al. (1998) reported two lowland endemic bird areas in the study area, the Upper Amazon–Napo lowlands and the southeast Peruvian lowlands. Neither of these areas is highlighted in our study, for two reasons. First, our criterion for defining an area of endemism emphasizes regions with many endemic species, a phenomenon restricted to higher-elevation sites. Also, the two lowland endemic bird areas include species that range into Amazonian Ecuador, Colombia, and Brazil and are not treated here. Interestingly, the Iquitos area of high irreplaceability identified in the present study (Figs. 3 and 4) falls outside the lowland endemic bird areas. The concentration of species with small ranges there may warrant extension of the upper Amazon–Napo lowland endemic bird area.

Our results also generally agree with the patterns of endemic species richness described by Fjeldså et al. (2005), with only slight differences. Fjeldså et al. (2005) highlighted the La Paz region more, and the Cordillera de Apolobamba less, than the present study. In the Cusco region, Fjeldså et al.'s (2005) results are similar to those for endemic bird areas, showing the greatest abundance of endemic species in central Cusco near Machu Picchu. Our results suggest that regions both east and west of there may have nearly as many of these species. The differences may have resulted from our use of predicted ranges in an attempt to control for the collecting bias that has occurred in places such as the Machu Picchu and La Paz regions. Alternatively, the area of high endemic richness east of Machu Picchu may result from model overprediction. This area, with few records of target species, is more exposed to cold southern winds than elsewhere in the Cusco region and could prove to have fewer endemics than predicted.

Value for conservation.—The distribution maps generated in the present study provide useful guidance for conservationists. Summed irreplaceability analyses pinpoint areas of greatest importance for protecting narrowly distributed species. Predictions of the

previously under-recognized areas of endemism are also valuable. Land near cities, where previous studies have pinpointed endemic areas, tends to be more costly because of its development potential. Creating protected areas in these places is often complicated further by competing economic interests and consequent lack of support by local communities. Identification of remote areas that are just as important for biodiversity allows conservationists to locate protected areas where costs are lower and conflicts are fewer.

Our analysis demonstrates that although the governments of Peru and Bolivia have set aside a significant portion (19%) of the study area in protected areas, the locations of existing reserves do not cover the habitat needs of all endemic birds. Five endemic species occur entirely outside of reserves, and more than three-fourths of the extent of areas of endemism identified is unprotected. The summed irreplaceability analysis confirms that endemics are incompletely protected on the east slope of the Andes in Peru and Bolivia. More than four-fifths of the study area that is highly irreplaceable because it contains narrowly distributed endemics is unprotected. Local governmental and private efforts (e.g., Angulo et al. 2007) that complement national reserve systems will be necessary to fully protect species with very restricted ranges.

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APPENDIX. Endemic species modeled, with numbers of unique localities and sizes of predicted ranges (km^2) for each.

Family	Species	Number of unique localities	Size of predicted range
Tinamidae	Hooded Tinamou (*Nothocercus nigrocapillus*)	26	78,903
Cracidae	Horned Curassow (*Pauxi unicornis*)	15	8,647
Odontophoridae	Stripe-faced Wood-Quail (*Odontophorus balliviani*)	26	46,443
Psittacidae	Blue-throated Macaw (*Ara glaucogularis*)	23	8,914
	Amazonian Parrotlet (*Nannopsittaca dachilleae*)	15	101,517
	Black-winged Parrot (*Hapalopsittaca melanotis*)	35	20,210
Strigidae	Cloud-forest Screech-Owl (*Megascops marshalli*)	6	12,709
	Long-whiskered Owlet (*Xenoglaux loweryi*)	5	3,016
Trochilidae	Koepcke's Hermit (*Phaethornis koepckeae*)	23	42,113
	White-browed Hermit (*P. stuarti*)	31	52,064
	Green-and-white Hummingbird (*Leucippus viridicauda*)	10	19,770
	Peruvian Piedtail (*Phlogophilus harterti*)	14	18,036
	Rufous-webbed Brilliant (*Heliodoxa branickii*)	15	86,582
	White-tufted Sunbeam (*Aglaeactis castelnaudii*)	18	9,102
	Coppery Metaltail (*Metallura theresiae*)	16	20,699
	Fire-throated Metaltail (*M. eupogon*)	12	14,306
	Scaled Metaltail (*M. aeneocauda*)	41	28,690
	Marvelous Spatuletail (*Loddigesia mirabilis*)	6	3,054
Capitonidae	Scarlet-banded Barbet (*Capito wallacei*)	1	139
Ramphastidae	Versicolored Barbet (*Eubucco versicolor*)	88	170,959
	Yellow-browed Toucanet (*Aulacorhynchus huallagae*)	3	4,810
	Hooded Mountain-Toucan (*Andigena cucullata*)	38	31,107
Picidae	Speckle-chested Piculet (*Picumnus steindachneri*)	7	5,616
	Plain-breasted Piculet (*P. castelnau*)	8	21,837
	Fine-barred Piculet (*P. subtilis*)	8	18,026
Furnariidae	Royal Cinclodes (*Cinclodes aricomae*)	14	5,641
	White-browed Tit-Spinetail (*Leptasthenura xenothorax*)	10	3,948
	Puna Thistletail (*Schizoeaca helleri*)	8	24,629
	Black-throated Thistletail (*S. harterti*)	26	11,312
	Cabanis's Spinetail (*S. cabanisi*)	50	77,703
	Marcapata Spinetail (*Cranioleuca marcapatae*)	14	13,220
	Light-crowned Spinetail (*C. albiceps*)	33	28,748
	Bolivian Spinetail (*C. henricae*)	12	2,239
	Russet-mantled Softtail (*Thripophaga berlepschi*)	7	5,779
	Line-fronted Canastero (*Asthenes urubambensis*)	29	35,023
	Berlepsch's Canastero (*A. berlepschi*)	10	473
	Bolivian Recurvebill (*Simoxenops striatus*)	22	37,130
	Rufous-backed Treehunter (*Thripadectes scrutator*)	25	69,519
Thamnophilidae	Upland Antshrike (*Thamnophilus aroyae*)	34	24,723
	Ashy Antwren (*Myrmotherula grisea*)	21	29,755
	Creamy-bellied Antwren (*Herpsilochmus motacilloides*)	10	48,064

(*Continued*)

APPENDIX. Continued.

Family	Species	Number of unique localities	Size of predicted range
	Ash-throated Antwren (*H. parkeri*)	2	4,971
	Ancient Antwren (*H. gentryi*)	11	2,208
	Yellow-rumped Antwren (*Terenura sharpei*)	5	26,064
	Black-tailed Antbird (*Myrmoborus melanurus*)	8	59,279
	Allpahuayo Antbird (*Percnostola arenarum*)	11	11,045
	White-masked Antbird (*Pithys castaneus*)	3	1,894
Formicariidae	Rufous-fronted Antthrush (*Formicarius rufifrons*)	6	83,184
	Elusive Antpitta (*Grallaria eludens*)	5	309,168
	Pale-billed Antpitta (*G. carrikeri*)	5	19,418
	Rusty-tinged Antpitta (*G. przewalskii*)	12	6,376
	Bay Antpitta (*G. capitalis*)	8	6,439
	Red-and-white Antpitta (*G. erythroleuca*)	11	17,462
	Chestnut Antpitta (*G. blakei*)	7	3,832
	Rufous-faced Antpitta (*G. erythrotis*)	45	22,754
	Masked Antpitta (*Hylopezus auricularis*)	5	1,098
	Ochre-fronted Antpitta (*Grallaricula ochraceifrons*)	3	2,086
Rhinocryptidae	Trilling Tapaculo (*Scytalopus parvirostris*)	63	78,423
	Large-footed Tapaculo (*S. macropus*)	12	10,129
	Rufous-vented Tapaculo (*S. femoralis*)	21	49,171
	Neblina Tapaculo (*S. altirostris*)	5	10,044
	Tschudi's Tapaculo (*S. acutirostris*)	2	6,218
	Vilcabamba Tapaculo (*S. urubambae*)	1	78
	Diademed Tapaculo (*S. schulenbergi*)	19	12,922
Tyrannidae	Inca Flycatcher (*Leptopogon taczanowskii*)	29	38,206
	Unstreaked Tit-Tyrant (*Anairetes agraphia*)	16	38,401
	Ash-breasted Tit-Tyrant (*A. alpinus*)	17	42,821
	Cinnamon-faced Tyrannulet (*Phylloscartes parkeri*)	9	38,579
	Yungas Tyrannulet (*Phyllomyias weedeni*)	9	3,012
	Bolivian Tyrannulet (*Zimmerius bolivianus*)	54	56,428
	Mishana Tyrannulet (*Z. villarejoi*)	3	2,416
	Peruvian Tyrannulet (*Z. viridiflavus*)	27	41,361
	Hazel-fronted Pygmy-Tyrant (*Pseudotriccus simplex*)	17	43,356
	White-bellied Pygmy-Tyrant (*Myiornis albiventris*)	43	67,211
	Yungas Tody-Tyrant (*Hemitriccus spodiops*)	33	41,720
	Johnson's Tody-Tyrant (*Poecilotriccus luluae*)	8	3,950
	White-cheeked Tody-Tyrant (*P. albifacies*)	16	2,924
	Black-backed Tody-Flycatcher (*P. pulchellus*)	5	3,506
	Unadorned Flycatcher (*Myiophobus inornatus*)	15	21,416
	Rufous-bellied Bush-Tyrant (*Myiotheretes fuscorufus*)	28	45,346
Cotingidae	Bay-vented Cotinga (*Doliornis sclateri*)	12	19,922
	Band-tailed Fruiteater (*Pipreola intermedia*)	52	52,226
	Masked Fruiteater (*P. pulchra*)	15	41,514
	Scimitar-winged Piha (*Lipaugus uropygialis*)	16	15,436
Pipridae	Cerulean-capped Manakin (*Lepidothrix coeruleocapilla*)	36	95,078
Corvidae	White-collared Jay (*Cyanolyca viridicyanus*)	62	133,484
Troglodytidae	Incan Wren (*Thryothorus eisenmanni*)	8	3,010
	Peruvian Wren (*Cinnycerthia peruana*)	33	45,002
	Fulvous Wren (*C. fulva*)	32	59,861
Turdidae	White-eared Solitaire (*Entomodestes leucotis*)	73	121,073
Thraupidae	Slaty Tanager (*Creurgops dentatus*)	18	46,287
	Peruvian Black-capped Hemispingus (*Hemispingus auricularis*)	37	49,342
	Orange-browed Hemispingus (*H. calophrys*)	19	13,246
	Parodi's Tanager (*H. parodii*)	3	7,634
	Rufous-browed Hemispingus (*H. rufosuperciliaris*)	13	23,017
	Drab Hemispingus (*H. xanthophthalmus*)	26	52,308
	Three-striped Hemispingus (*H. trifasciatus*)	35	39,400
	Pardusco (*Nephelornis oneilli*)	12	15,913
	Black-bellied Tanager (*Ramphocelus melanogaster*)	19	41,659
	Golden-backed Mountain-Tanager (*Buthraupis aureodorsalis*)	4	2,737

(*Continued*)

APPENDIX. Continued.

Family	Species	Number of unique localities	Size of predicted range
	Chestnut-bellied Mountain-Tanager (*Delothraupis castaneoventris*)	83	66,053
	Golden-collared Tanager (*Iridosornis jelskii*)	40	68,438
	Yellow-scarfed Tanager (*I. reinhardti*)	31	34,933
	Green-capped Tanager (*Tangara meyerdeschauenseei*)	5	2,734
	Sira Tanager (*T. phillipsi*)	1	117
	White-browed Conebill (*Conirostrum ferrugineiventre*)	49	79,553
Emberizidae	Rufous-naped Brush-Finch (*Atlapetes rufinucha*)	94	23,426
	Apurimac Brush-Finch (*A. forbesi*)	8	10,083
	Cuzco Brush-Finch (*A. canigenis*)	7	13,915
	Black-spectacled Brush-Finch (*A. melanopsis*)	4	4,170
	Black-faced Brush-Finch (*A. melanolaemus*)	20	19,466
	Vilcabamba Brush-Finch (*A. terborghi*)	4	1,581
Icteridae	Selva Cacique (*Cacicus koepckeae*)	6	21,075
	Southern Mountain-Cacique (*C. chrysonotus*)	43	58,121
	Dusky-green Oropendola (*Psarocolius atrovirens*)	88	71,706