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Title Paper UC1656: Modeling the South American Range of the Cerulean Warbler

Coauthors:

Members of El Grupo Cerúleo: Barker, S., Benítez, S., Baldy, J., Cisneros Heredia, D., Colorado Zuluaga, G., Cuesta, F., Davidson, I., Díaz, D., Ganzenmueller, A., García, S., Girvan, M. K., Guevara, E., Hamel, P., Hennessey, A. B., Hernández, O. L., Herzog, S., Mehlman, D., Moreno, M. I., Ozdenerol, E., Ramoni-Perazzi, P., Romero, M., Romo, D., Salaman, P., Santander, T., Tovar, C., Welton, M., Will, T., Pedraza, C., Galindo, G.

Abstract

Successful conservation of rare species requires detailed knowledge of the species' distribution. Modeling spatial distribution is an efficient means of locating potential habitats. Cerulean Warbler (*Dendroica cerulea*, Parulidae) was listed as a Vulnerable Species by the International Union for the Conservation of Nature and Natural Resources in 2004. These neotropical migratory birds breed in eastern North America. The entire population migrates to the northern Andes in South America to spend the nonbreeding period. As part of a larger international conservation effort, we developed spatial hypotheses of the bird's occurrence in South America. We summarized physical, climatic, and recent land-cover data for the northern Andes using ESRI software, ArcGIS. We developed five hypothetical distributions based on Mahalanobis D, GARP, Biomapper, MAXENT, and Domain models. Combining results of the different models on the same map allowed us to design a rigorous strategy to ground-truth the map and thus to identify sites for protection of the species in South America.

Introduction

Successful conservation of rare species requires detailed knowledge of the species' distribution. Often the decline of a species' population occurs with a particular geographical pattern (Maurer 1994). This pattern of decline may represent changes affecting the entire range which are expressed more severely in one part of the range, resulting disappearance from one portion of the range. The spatial pattern of decline may also represent changes affecting only a portion of the range and causing the species to become restricted there (Smith *et al.* 1996). Understanding the spatial distribution of change is a key to inferring the causal factors. Conservation requires redress of those causes.

A variety of approaches to spatial modeling of species distributions has been summarized by Elith *et al.* (2006). Expressing a range in a spatially explicit way provides interested persons with a means to visualize the range in relation to external factors and to relate changes in the range to potential causal factors. When data on distribution of the species are scarce, for whatever reason, the range is difficult to present on a map, to visualize, and to relate to changes in causal factors. Using known occurrences in combination with ambient variables to model spatial distribution is an efficient means of locating potential habitats in unsurveyed areas; this is especially true where existing distributional data are scarce or biased in some way. For declining species of migratory North American birds (Terborgh 1989), mapping the nonbreeding distributions in Central and South America and the Caribbean typically involves surmounting a wider variety of data constraints than does mapping the breeding range in North America.

The Cerulean Warbler (*Dendroica cerulea*, Parulidae) was listed as a Vulnerable Species by the International Union for the Conservation of Nature and Natural Resources in 2004 (Birdlife International 2004, 2006). These nearctic/neotropical migratory birds breed in eastern North America (Hamel 2000b). Breeding habitat consists of a variety of deciduous forests (Rosenberg *et al.* 2000), including especially tall trees of large diameter from which the breeding males sing, as well as more modest-sized trees in which the females place their nests (Hamel 2005). The entire population migrates to the northern Andes of South America to spend the nonbreeding period (Hilty and Brown 1986).

Two different verbal descriptions of the nonbreeding habitat of the species follow. Hilty and Brown (1986) was arguably the most authoritative source of information on birds in the northern Andes when it was published. These authors indicate that the species was a very uncommon resident during the nonbreeding period in Colombia, that most of the birds were south of that country during the October-March period, and identified the range as forests and forest borders primarily west of the Andes, from elevations of 500 to 2000 m. Robbins *et al*. (1992) identified primary forest as important nonbreeding habitat. More recently, Hamel (2000b) extended the description of Hilty and Brown (1986) and Robbins *et al*. (1992) to include canopy and borders of broadleaved, evergreen forests and woodland at middle and lower elevations on the east slopes of the Andes from Colombia to Peru and possibly Bolivia, as well as premontane forests and the tepui region of Venezuela, at elevations typically from 500-1500 m, reaching higher in the northern portion of the range than in the south. Jones *et al*. (2002) determined that the birds use shade coffee plantations as nonbreeding habitat. Questions currently being investigated by several groups include whether habitat must be primary forest or secondary forest and the value of some anthropogenic habitats such as shade coffee plantations. Deforestation and other changes to habitats in this range have been and continue to be extensive (Armenteras *et al.* 2005). Unfortunately, much of the information on the distribution of the species within this range has been the incidental result of birdwatchers visiting areas favored for reasons of access or for presence of desired resident species.

The breeding population of this species has been declining steadily throughout the period of quantitative population assessment (Link and Sauer 2002) by our only measurement tool, the North American Breeding Bird Survey (Robbins *et al.* 1986). An early evaluation of these data and others (Robbins *et al.* 1992) identified a number of potential threats to the population of the species, including those acting on breeding, migration, and nonbreeding residency periods of the annual cycle. An estimate of total population of approximately 560,000 individuals ±50%, with a conservation goal of doubling the population, has been presented in the North American Landbird Conservation Plan (Rich *et al.* 2004). Jones *et al*. (2004) showed that one population commonly believed to be reproducing well might not be maintaining its numbers. Concern for the species has been expressed through legal recognition of status in numerous US states and Canadian provinces (Committee on the Status of Endangered Wildlife in Canada 2003, Hamel 2000a, Hamel 2000b), as well as by a petition to list the species as Threatened under the US Endangered Species Act (Ruley 2000).

Extensive interest in the conservation of this species led to formation of an *ad hoc* association of interested parties, the Cerulean Warbler Technical Group (CWTG; Hamel *et al.* 2004). CWTG as a whole, as well as its subcommittee concerned with nonbreeding season activities, El Grupo Cerúleo, conducted a series of exercises to prioritize issues to address. In each case, issues regarding the paucity of information concerning the extent, condition, and changes in habitats in the nonbreeding range of the species have been identified as paramount to the future conservation of the species.

The situation is thus ripe for a lack of data to mislead us into overgeneralizing or overspecifying the nonbreeding range. Against the background of a strong conservation need for this species, and because of its overlap with a wide array of resident species of birds and other groups of conservation concern in this area of great biodiversity (Renjifo 1998), enormous implications to other species of conserving habitats for the Cerulean Warbler exist.

The current work responds to these identified needs. In a series of workshops and observer-directed field investigations, the members of El Grupo Cerúleo have identified and organized existing data on the nonbreeding distribution of the Cerulean Warbler. We here present the results of applying a series of spatial modeling algorithms to the very scarce existing data on the South American distribution of this species. Our objective in this work has been to develop a spatially explicit hypothesis of the distribution of the species that can be subjected to rigorous field tests.

Methods

Data Sets and Sources

Cerulean Warbler Modeling Data—We compiled a list of existing, georeferenced occurrence data for the species. Records included specimens from museum collections (D. Pashley, pers. comm.), as well as responses to a request for records sent to a wide variety of observers through online and other means, and published records summarized by Hamel (2000a). The dataset included 336 such observations. All of these observations and specimens constitute a convenience sampling frame for the occurrence of the species in South America during the October-March nonbreeding resident period, and represent historic and recent records dating from 1880-2005. The quality of georeferencing of these points also varied greatly, from GPS recordings to names of nearest town listed on specimen labels. We used a variety of gazetteers to infer coordinates from the available locality information.

Because of the number of repeat observations and because the scale of the climatic and other environmental variables was expressed at a pixel size of 1 km^2, data reduction was necessary prior to modeling the distribution. After elimination of duplicate localities and combining points that fell within the same 1 km^2, 185 unique localities remained (Figure 1). We separated the points for model construction and model verification in the ratio of 3:1 (training:test) by selecting at random 25% of the points for test points in the model runs. In this way we constructed five separate repetitions of the data for modeling.

Validation Data Points—Through a series of field projects funded by El Grupo Cerúleo in the nonbreeding periods of 2003-2004, 2004-2005, and 2005-2006, we were able to develop an independent set of validation data for the model predictions. These were all sight and capture records, georeferenced with GPS, and subject to the same convenience sampling constraint as the modeling data. Field collaborators contributed 113 such records, of which 50 constituted confirmed presence of the species (Figure 1).

Environmental Data—We gathered climatic, physical, and vegetation data from three primary sources available online to the public. Climate data consisted of 19 variables representing combinations of temperature and precipitation (Table 1) from WORLDCLIM (http://www.worldclim.org/, Hijmans *et al.* [no date], Hijmans *et al*. 2005). The data exist in a grid of 1 km^2 pixels. Physical data on slope, aspect, and elevation came from the digital elevation model available as GTOPO30 (US Geological Survey [no date]). These data were expressed also as a grid of 1 km^2 pixels. Vegetation data on percent bare ground, percent herbaceous cover, and percent tree cover came from Global land cover facility MODIS ([no date]). We accepted the value of 70% tree cover to indicate that the 500 m^2 pixels were forested. We transformed the vegetation cover data to 1 km^2 pixel size resolution for compatibility with the other data. We further transformed two of the environmental variables, Slope and Annual Precipitation, using Box-Cox procedures to remove nonnormality in these data (Sokal and Rohlf 1981).

Table 1. List of initial environmental, physical and land cover variables considered in the modeling process

Enviromental variable	Source	Original pixel scale	Used in final model
BIO1 = Annual Mean Temperature	WORLDCLIM	1000 m	
BIO2 = Mean Diurnal Temperature Range (Mean of monthly (max temp - min temp))	WORLDCLIM	1000 m	
BIO3 = Isothermality (P2/P7) (* 100)	WORLDCLIM	1000 m	**X**
BIO4 = Temperature Seasonality (standard deviation *100)	WORLDCLIM	1000 m	
BIO5 = Max Temperature of Warmest Month	WORLDCLIM	1000 m	
BIO6 = Min Temperature of Coldest Month	WORLDCLIM	1000 m	
BIO7 = Temperature Annual Range (P5-P6)	WORLDCLIM	1000 m	
BIO8 = Mean Temperature of Wettest Quarter	WORLDCLIM	1000 m	
BIO9 = Mean Temperature of Driest Quarter	WORLDCLIM	1000 m	
BIO10 = Mean Temperature of Warmest Quarter	WORLDCLIM	1000 m	
BIO11 = Mean Temperature of Coldest Quarter	WORLDCLIM	1000 m	
BIO12 = Mean Total Annual Precipitation	WORLDCLIM	1000 m	**X**

BIO13 = Precipitation of Wettest Month	WORLDCLIM	1000 m	
BIO14 = Precipitation of Driest Month	WORLDCLIM	1000 m	
BIO15 = Precipitation Seasonality (Coefficient of Variation of Mean Monthly Precipitation)	WORLDCLIM	1000 m	**X**
BIO16 = Precipitation of Wettest Quarter	WORLDCLIM	1000 m	
BIO17 = Precipitation of Driest Quarter	WORLDCLIM	1000 m	
BIO18 = Precipitation of Warmest Quarter	WORLDCLIM	1000 m	
BIO19 = Precipitation of Coldest Quarter	WORLDCLIM	1000 m	
Percent bare ground	MODIS	500 m	
Percent herbaceous cover	MODIS	500 m	
Percent tree cover	MODIS	500 m	**X**
Digital Elevation Model	GTOPO30	1000 m	**X**
Slope	GTOPO30	1000 m	**X**
Aspect	GTOPO30	1000 m	**X**

In order to remove multicollinearity from the environmental data, we subjected the combined data set of 25 environmental variables for 185 pixels in which Cerulean Warblers were present to a cluster analysis of the correlation matrix using the unweighted pair groups method with arithmetic mean (Sneath and Sokal 1973; Figure 2). The resulting graph of the tree was used to select one variable from each cluster with a similarity value greater than 0.65. From the resulting nine variables, we excluded two, percent bare ground and percent herbaceous cover, as not relevant to this species of the tree canopy. The remaining seven variables, elevation, aspect, slope, tree cover, isothermality as percent of mean annual temperature range experienced on a daily basis, mean annual precipitation, and seasonality of precipitation as coefficient of variation of mean monthly precipitation form the set of environmental variables used to construct the models.

Models Employed

We chose five modeling algorithms that utilize data such as ours to model spatial distributions of biological species based on values of environmental variables at known points of occurrence (Table 2): DOMAIN (Carpenter *et al.* 1993), GARP (Stockwell and Noble 1992, Stockwell and Peters 1999), MAXENT (Phillips *et al.* 2006), Mahalanobis distance (Jenness 2003), and Ecological Niche Factor Analysis (ENFA; Hirzel *et al.* 2002).

The application of these algorithms to ecological data such as ours is compared in detail by Elith *et al.* (2006), with the exception of ENFA, which is treated by Hirzel *et al.* (2002) and Mahalanobis by Jenness (2003). ENFA depends on the conceptual model of the ecological niche (Hutchinson 1957) as describing the distribution of a species in multidimensional environmental space, and uses only locations of known species presence. Two parameters are calculated in this space, marginality and specialization. Marginality of species distribution is defined as the difference between species mean values and study area wide mean values for a particular environmental variable standardized by the 95th percentile confidence interval on that area wide mean. Specialization of the species distribution is the ratio of the standard deviation of the global distribution to the standard deviation of the species distribution. High values of marginality indicate that the species niche is far from the norm in the study area, while high values of specialization indicate that the species niche is well-defined relative to the values available in the study area. Specific values for these indices are particular to each individual study. Over a number of environmental variables, vectors of marginality and specialization are subjected to multivariate factor analysis. This approach to modeling distribution has been implemented as Program Biomapper 3.0, which we used in our analysis here.

Table 2. Models used in exploring the range of the Cerulean Warbler

Model	Algorithm and Settings employed
MAXENT	Maximum Entropy Theory, single run of 1000 iterations
GARP	Genetics Algorithm for Rule Set Prediction, 50 runs of 1000 iterations, error rates at Omission=10%, Commission=40%, Convergence Limit of 0.01, Using 100% of training points
DOMAIN	Gower similarity index, single run, outliers established at 95th percentile
Mahalanobis	Mahalanobis D non-euclidean distance, single run
ENFA	Ecological Niche Factor Analysis, single run with 3 factors accommodating 85% of variation in the data

The Mahalanobis distance modeling utilizes pairwise differences between values of environmental variables to generate a distance matrix (Greenacre 1984). Several multivariate analytical procedures can use this parameter as a metric to evaluate differences between groups of data points. An example of its application to spatial modeling is Rotenberry *et al.* (2006), who used the procedure to estimate habitat and limiting factors for a rare bird, the California Gnatcatcher (*Polioptila californica*). We implemented our analysis using the Mahalanobis distances extension for ArcView 3.x (Jenness 2003).

Analysis

We conducted five separate analyses with each model, each using one of the five replicate data sets randomly selected to be 75% training - 25% test points. We calculated the AUC parameter for each of the runs, and computed mean and standard error of the AUC. AUC is the Area Under the Curve of Receiver Operating Characteristic Plots (Zweig and Campbell 1993, Fielding and Bell 1997). In this plot of commission error rate vs sensitivity, defined to be (1-omission error rate), a value of 1 represents the best the model could be, with 0 in the x axis (commission error) and 1 in the y axes (sensitivity). Any value below the diagonal in the plot is considered to be a random model, and the closer a model result is to upper left corner the better the model is considered to be.

We combined models by selecting for each an objective method of determining a threshold for predicting occurrence vs nonoccurrence. Such a method for each of the models; for MAXENT, we selected as threshold of 0.57023, because at this point the omission error rate is between 0.2 and 0.3. For ENFA, Mahalanobis distance and DOMAIN we used the Kappa Maximization approach widely used to determine thresholds for species distributions (Guisan et al. 1999), where the proportion of correctly predicted sites is calculated (Liu et al. 2005). The final values of threshold were: for Mahalanobis a d=245, for ENFA=35, Domain=91.4. For GARP, we decided to use the sum of the best subsets of each model and define the pixels where all eight best subsets are present as the area of potential distribution of the bird. We combined the resulting binary models after application of these thresholds for presence, and for each pixel in the five country study area calculated the number of models (from zero to five) that predicted presence.

We conducted a model validation test by intersecting coverage of the MAXENT map and the sum of binary maps of all models with the validation data points, and calculating a t-test of the MAXENT values for points indicating presence vs those indicating absence in the validation data set. We further intersected the binary maps of predicted habitat for all models and for the combination of ENFA, MAXENT, and Mahalanobis with the validation data set. Observed occurrences of Cerulean Warbler in the validation data set were examined visually. We conducted a χ^2 test to compare the distribution of observed absence and observed presence in the validation data set among categories defined by number of models predicting Cerulean Warbler presence at the validation data point.

Analyses of the occurrence data were carried out in the respective software packages indicated. All spatial analyses, selections, and evaluations were conducted in ArcGIS, with the exception of a small number which were carried out in ArcView.

Results

All models used in this project produced acceptable initial fit to the data, according to the AUC criterion of at least 0.5. Mean AUC values were considerably higher, though none was greater than 0.9 (Figure 3). The goodness of fit statistic suggests that the model produced by MAXENT has identified the signal in these data slightly better than the others and might be the one best suited to use with the training data set we have. Nevertheless, while the models individually represented decent fits to the data, they yielded substantially different results in terms of area predicted to be potential Cerulean Warbler habitat (Figure 4). Results of the ENFA model present two parameters, marginality=0.567 and specialization=0.640. The marginality value indicates that nonbreeding Cerulean Warbler occurrence in South America appears to be neither restricted to very well defined habitats, nor to be found in sites represented by average values of the measured variables. Similarly, the specialization value suggests that the species occurrence can be characterized neither as generalist nor specialist.

To better compare models and to combine them in single analyses, model-specific criteria were used to reduce the models to binary predictions of Presence vs Absence. The resulting maps reemphasize the differences among the models in area predicted as potential Cerulean Warbler habitat (Figure 5). The very large predicted areas of occurrence produced by Domain and GARP (Figure 5) suggest that these models are not especially useful in summarizing this dataset. Results of data reduction of ENFA, MAXENT, and Mahalanobis, after exclusion of Domain and GARP (Table 3) underscore the differences apparent visually (Figure 5). The much more conservative identification of area by MAXENT is evident (Table 3), reinforcing the suggestion from the goodness of fit test that this model may fit this data set better than the others. When these models are compared on the same map, a modest 200,000 km^2, 4.3% of the area of Venezuela, Colombia, Ecuador, Peru, and Bolivia, is predicted to be suitable for Cerulean Warbler occurrence (Table 4, Figure 6).

Distribution of validation data points indicating presence in the combined binary predictions of models ENFA, MAXENT, and Mahalanobis (Figure 7) and these plus Domain and GARP (Figure 8) show the distribution of recent records representing substantial effort in Colombia and Ecuador, and lesser effort among our field projects in Venezuela. The lack of presence in Peru is in part a result of a small amount of sampling and in part a result of absence of the birds from former range there and in Bolivia. In each case, the distribution of observed absences with confirmed occurrences of Cerulean Warbler differed from each other by χ^2 test (3 model combination, χ^2, 1 d.f. = 5.15, $P < 0.05$; 5 model combination, χ^2, 1 d.f. = 4.09, $P < 0.05$; Figure 9). In both cases the number of observed occurrences increased with the number of models predicting presence. Observed absences in the 3 model case declined with increasing number of models predicting presence; in the 5 model case the number of observed absences appeared to be independent of number of models predicting presence of Cerulean Warbler.

Validation data points were intersected with the results of the MAXENT model (Figure 10), and each validation data point assigned the probability of its pixel as predicted by MAXENT. Comparison of the group of observed absences (mean MAXENT probability = 0.09, N=63) to the group of observed presence (mean MAXENT probability = 0.12, N=50) with a t-test detected no difference in MAXENT probability between the two groups (t, 68 d.f., = -1.61, p=0.11).

Table 3. Realization of models with settings for binary predicted presence vs absence, based on cutoff values of statistics particular to each model: MAXENT, omission error rate between 0.2 and 0.3; Ecological Niche Factor Analysis (ENFA), K=35%; Mahalanobis d=245, DOMAIN K=91.3, GARP K=8.

MODEL	Number of pixels	Km^2	% of study area
ENFA	1201396	1,030,168	22
MAHALANOBIS	1781129	1,527,275	32
MAXENT	284333	243,809	5
DOMAIN	2165143	1,856,559	38
GARP	1514044	1,298,257	27

Table 4. Areas predicted differently by models as potential range of the Cerulean Warbler. Models employed in this exercise were ENFA, MAXENT, and Mahalanobis.

Number of models	Number of pixels	Km^2	% of study area
0	3,621,414	3,105,276	65.8
1	739,142	633,797	13.4
2	908,682	779,173	16.5
3	235,251	201,722	4.3
TOTAL	5,504,489	4,719,967	100

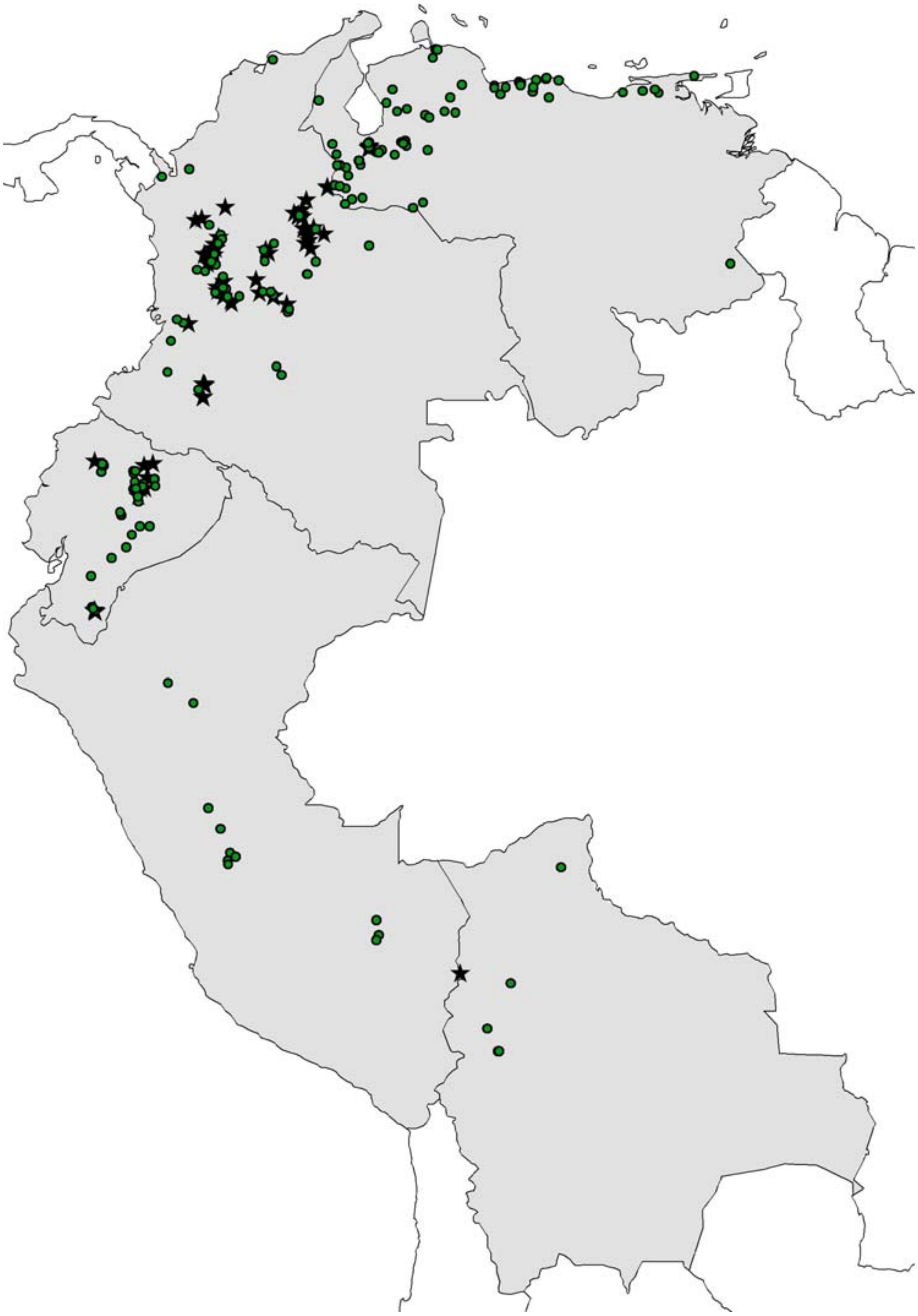


Figure 1. Records of Cerulean Warbler distribution in northern South America, October-March, used in Modeling (solid circles) and Validation data sets (stars).

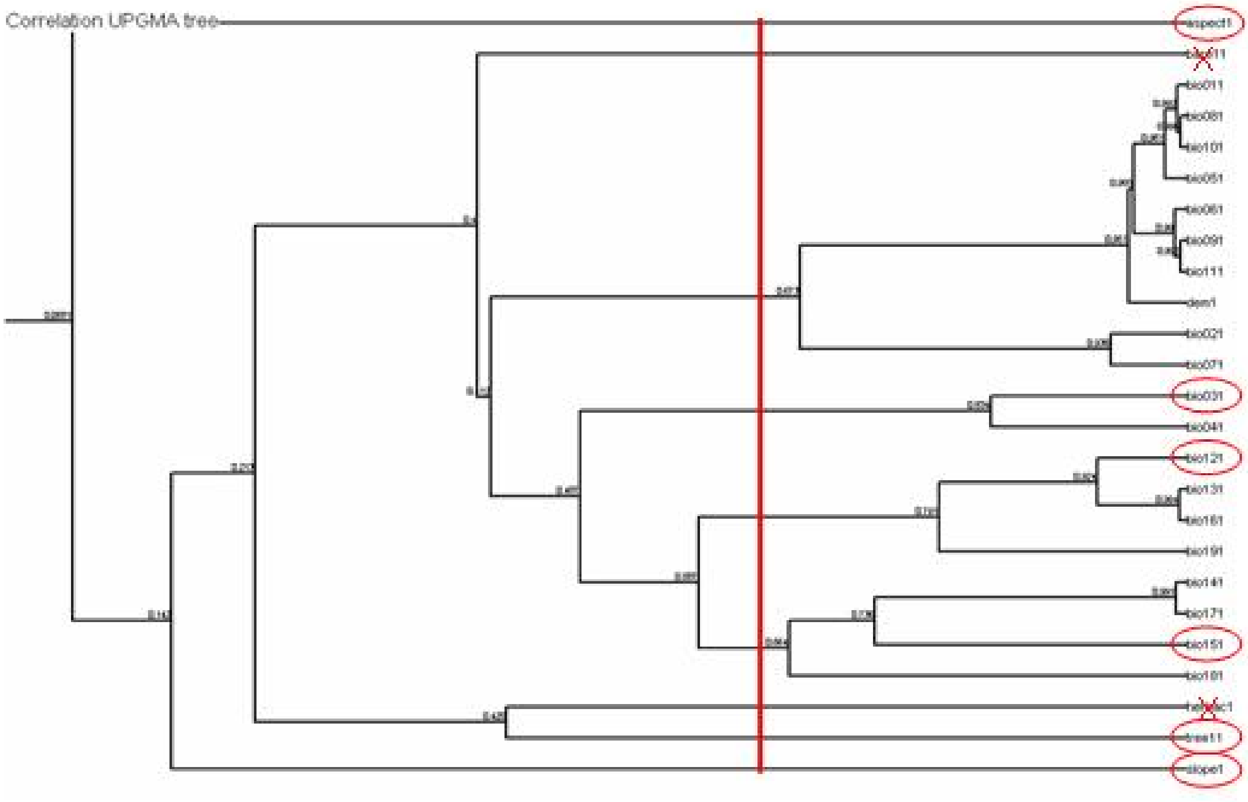


Figure 2. Cluster analysis of correlation matrix of 23 original variables measured on pixels within which Cerulean Warblers occurred in the modeling dataset. Red line indicates selection criterion of similarity values less than 0.65 (to the left), and greater than 0.65 (to the right). Selected variables circled in red as representative of their clusters, and variables excluded for lack of relevance to Cerulean Warbler biology marked with red X.

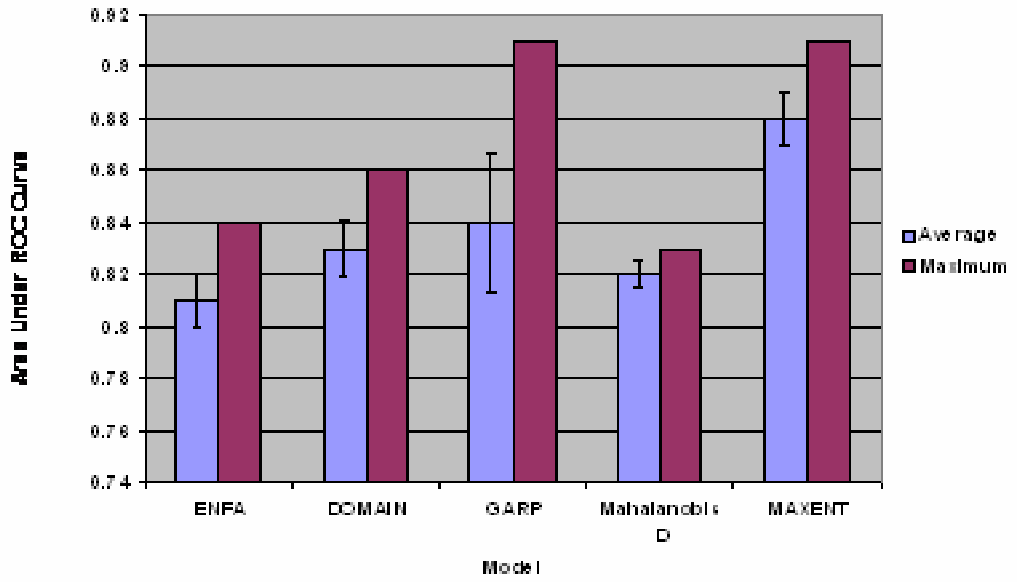
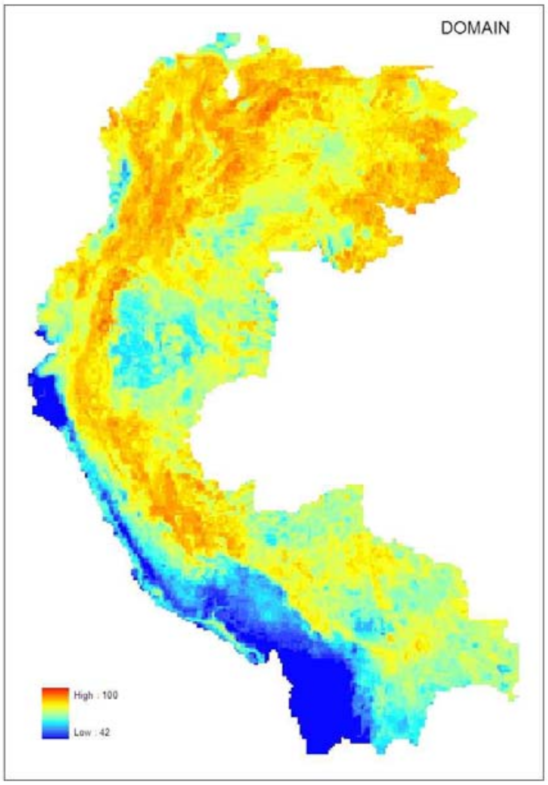
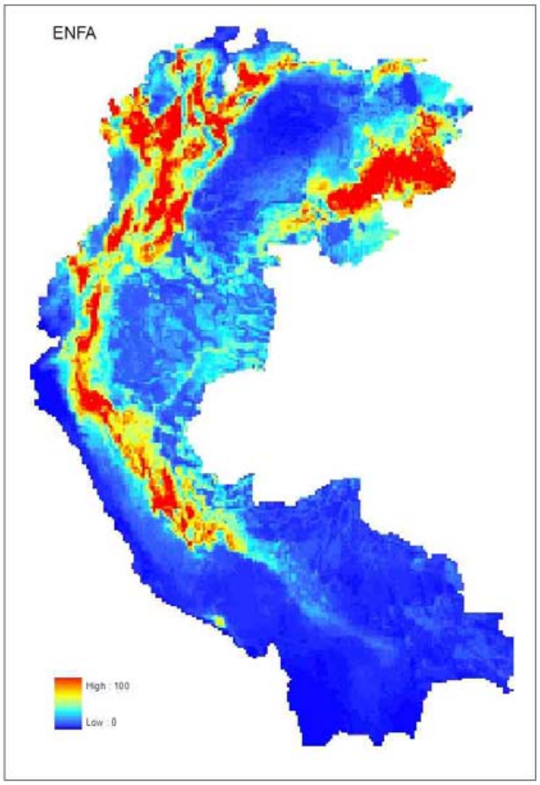


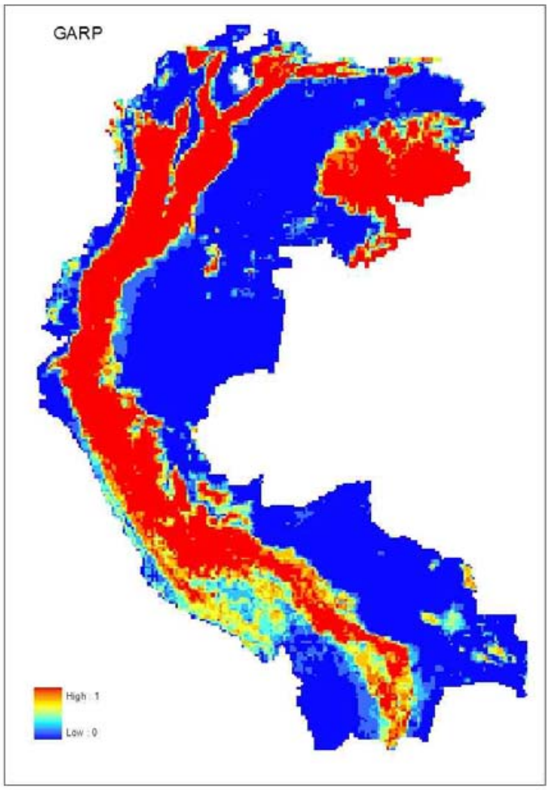
Figure 3. Goodness of fit of models used in exploring the range of the Cerulean Warbler, based on the Area Under the ROC Curve. Error bars indicate 1 s.e. based on 5 trials with random subsets of observations.


DOMAIN
High : 100
Low : 42

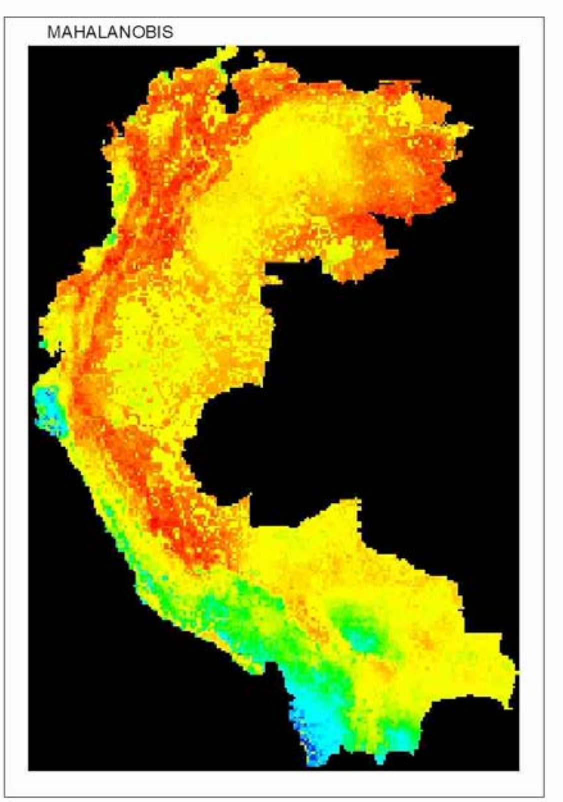
A


ENFA
High : 100
Low : 0

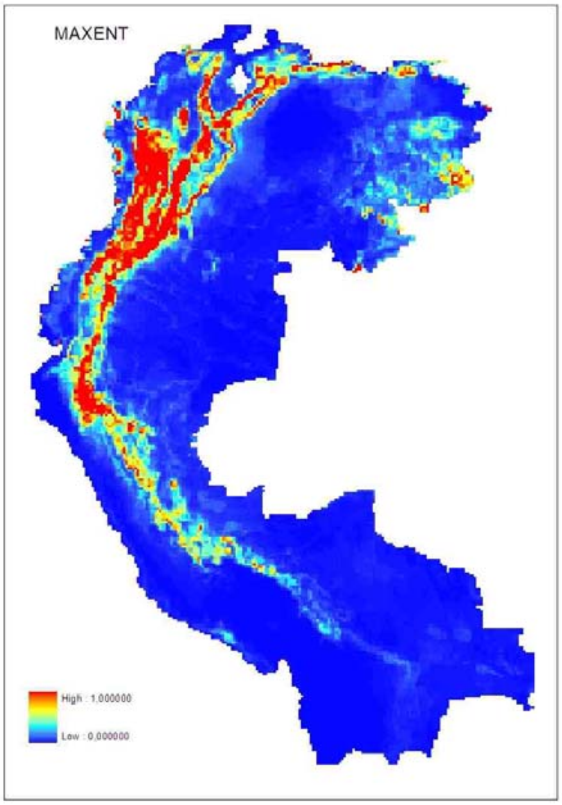
B


GARP
High : 1
Low : 0

C


MAHALANOBIS

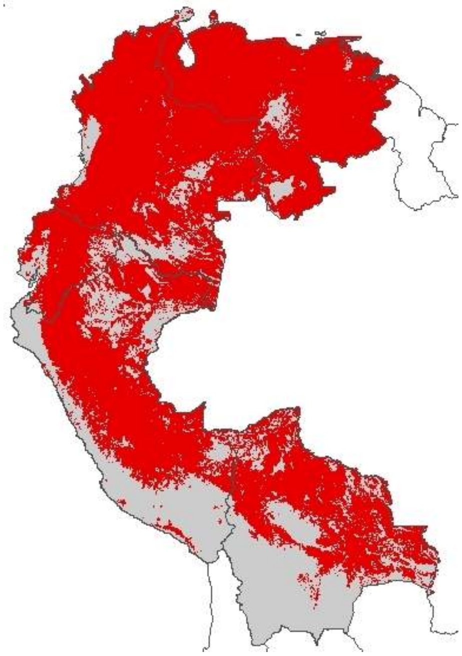
D



E

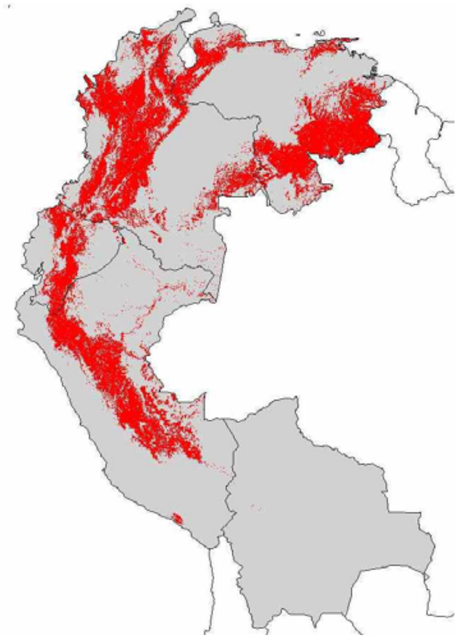
Figure 4. Potential nonbreeding range of Cerulean Warbler based on different algorithms.

Results from A – DOMAIN, B – ENFA, C – GARP, D – Mahalanobis, and E – MAXENT. In each case the expectation of presence in the model increases from the cool blues to the warm red colors.

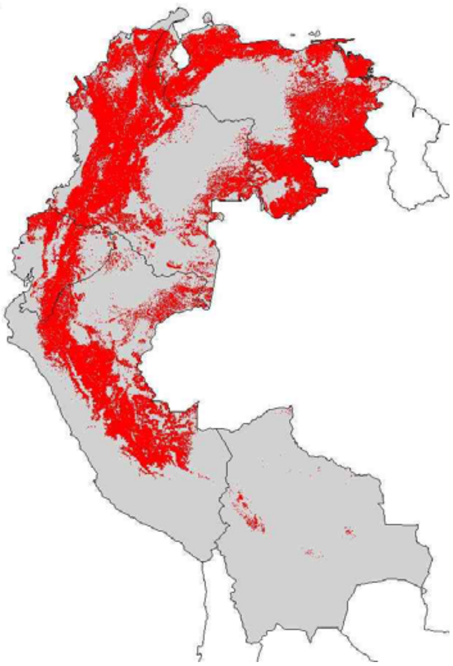


Domain

GARP



ENFA



Mahalanobis

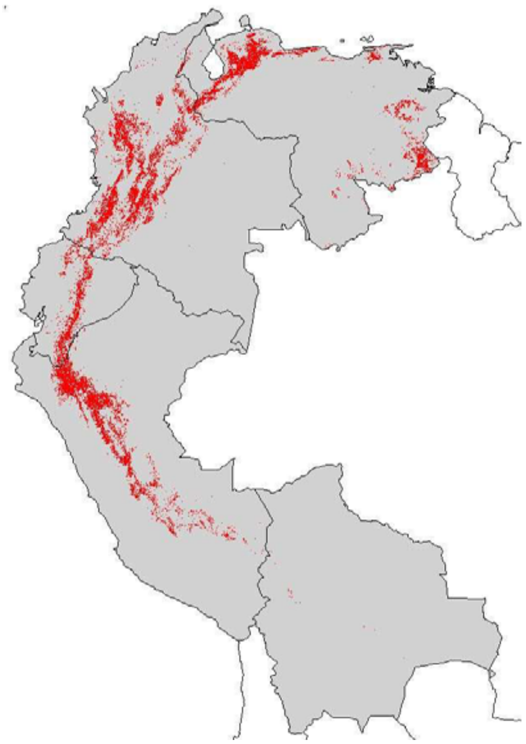


Figure 5. Results of reducing model output to binary predicted vs not predicted to be Cerulean Warbler habitat, using model-specific thresholds: MAXENT, 0.57023 where omission error rate was between 0.2 and 0.3; for GARP we used the union of pixels in the 8 best subsets of the model; Kappa Maximization approach identified threshold values for Ecological Niche Factor Analysis (ENFA)=35, Domain= 91.4, and Mahalanobis d=245.

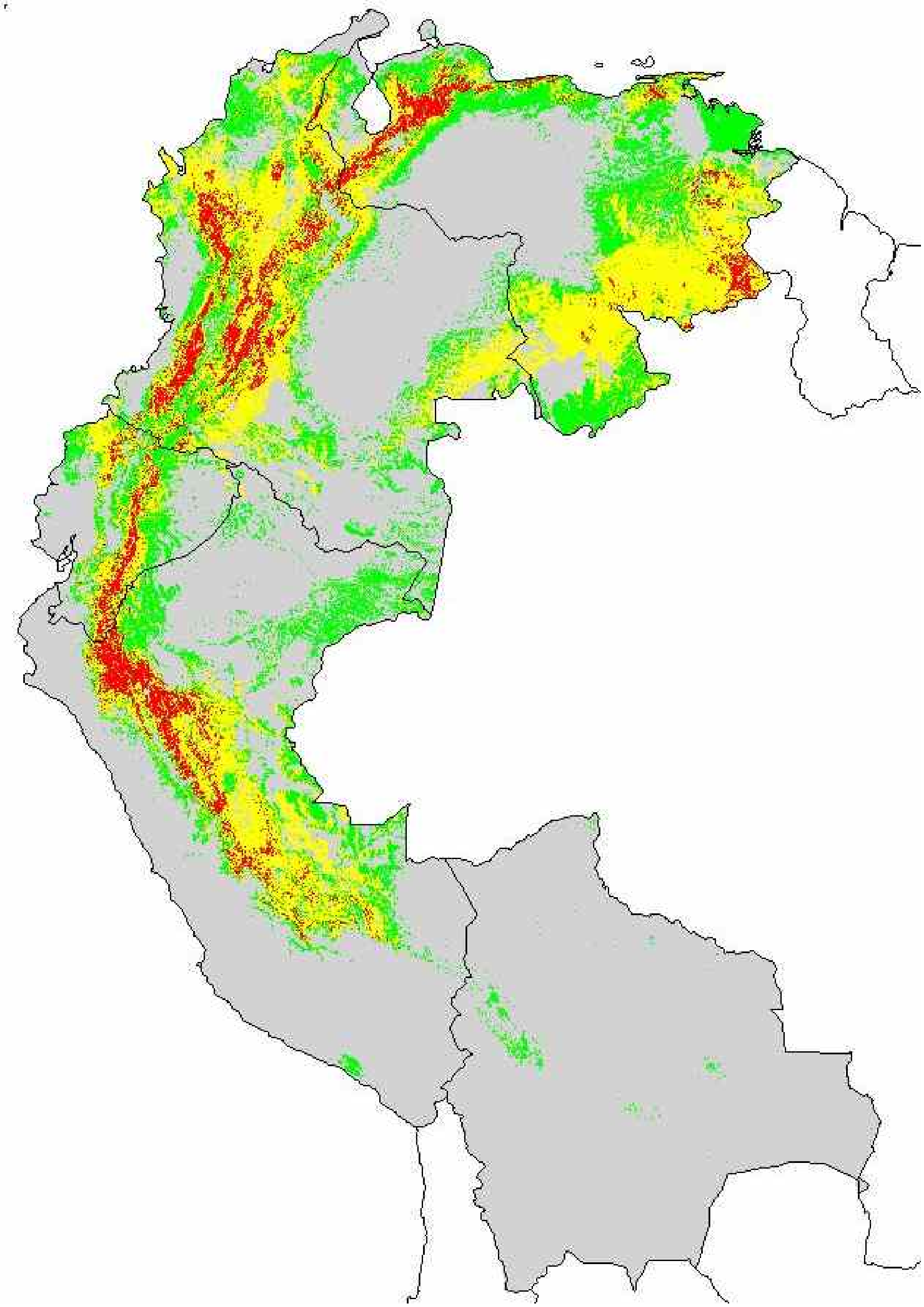


Figure 6. Combined map of binary results of ENFA, Mahalanobis, and MAXENT models. Areas in **gray** were predicted Cerulean Warbler range by none of the models, those in **green** were predicted by one model, those in **yellow** by two models, and those in **red** by all three models.

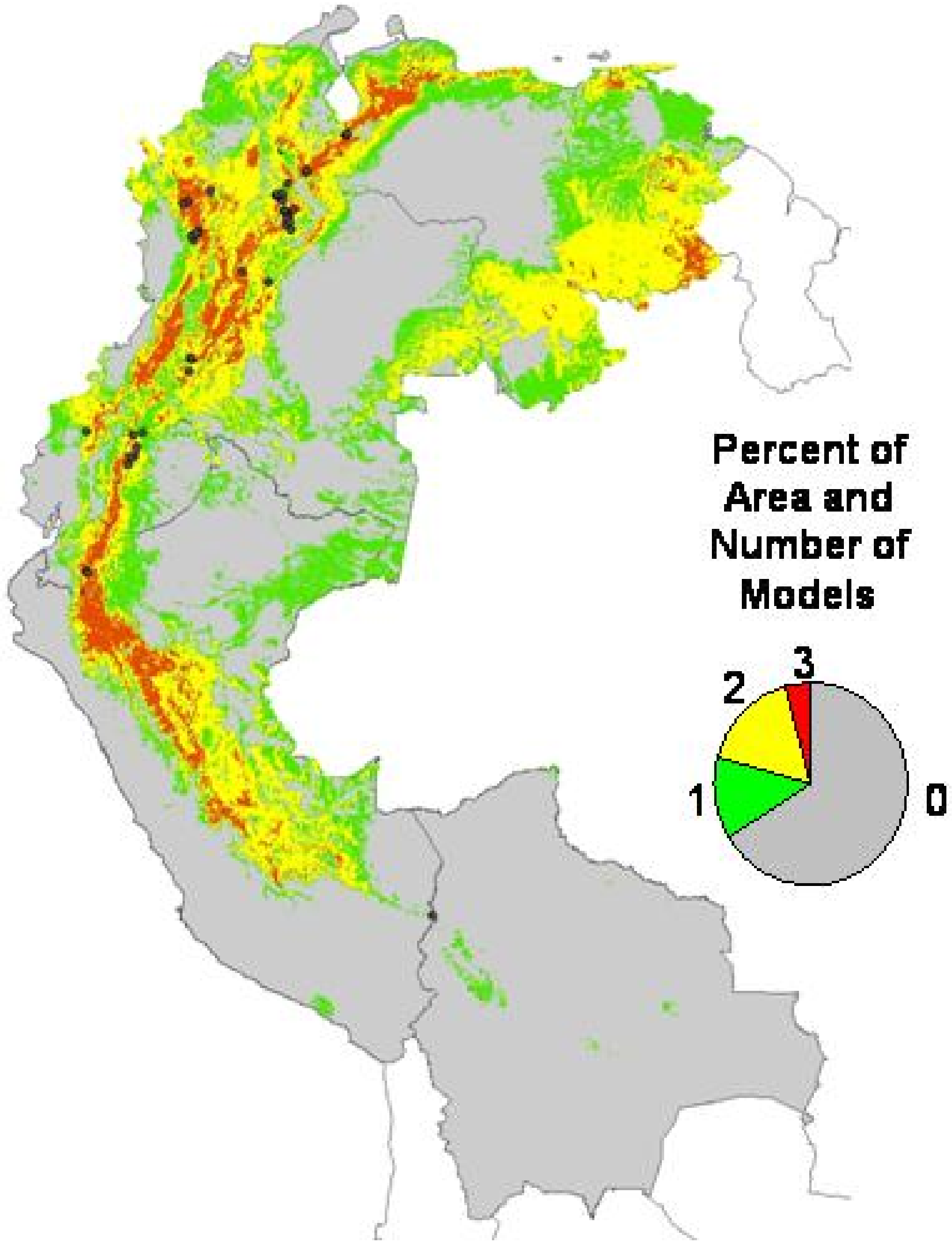


Figure 7. Intersection of Independent Cerulean Warbler Validation data set with combined map of Figure 6, including models ENFA, MAXENT, and Mahalanobis. Dark circles indicate validation points where Cerulean Warblers were found.

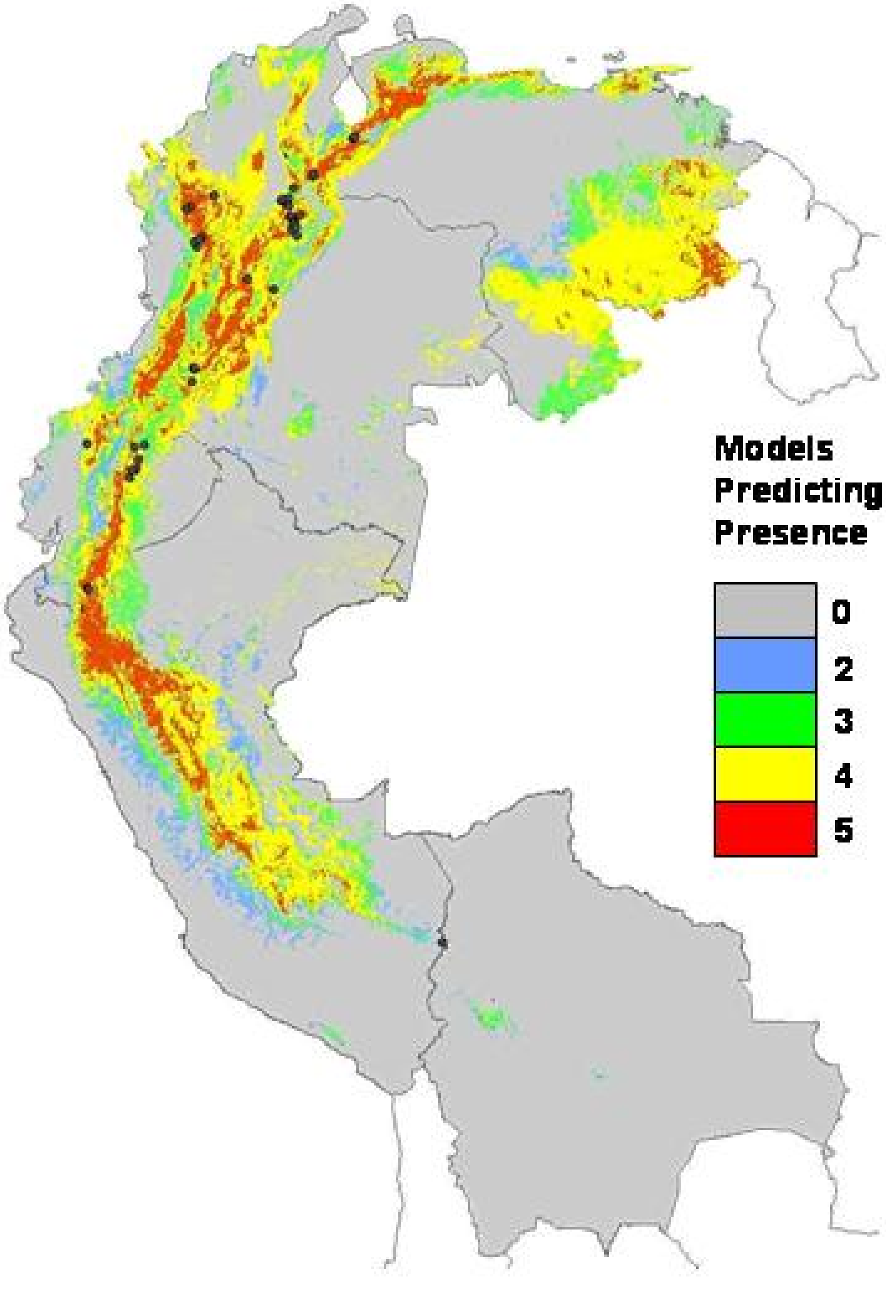


Figure 8. Intersection of Independent Cerulean Warbler Validation data set with combined binary results of all five models. Dark circles indicate validation points where Cerulean Warblers were found.

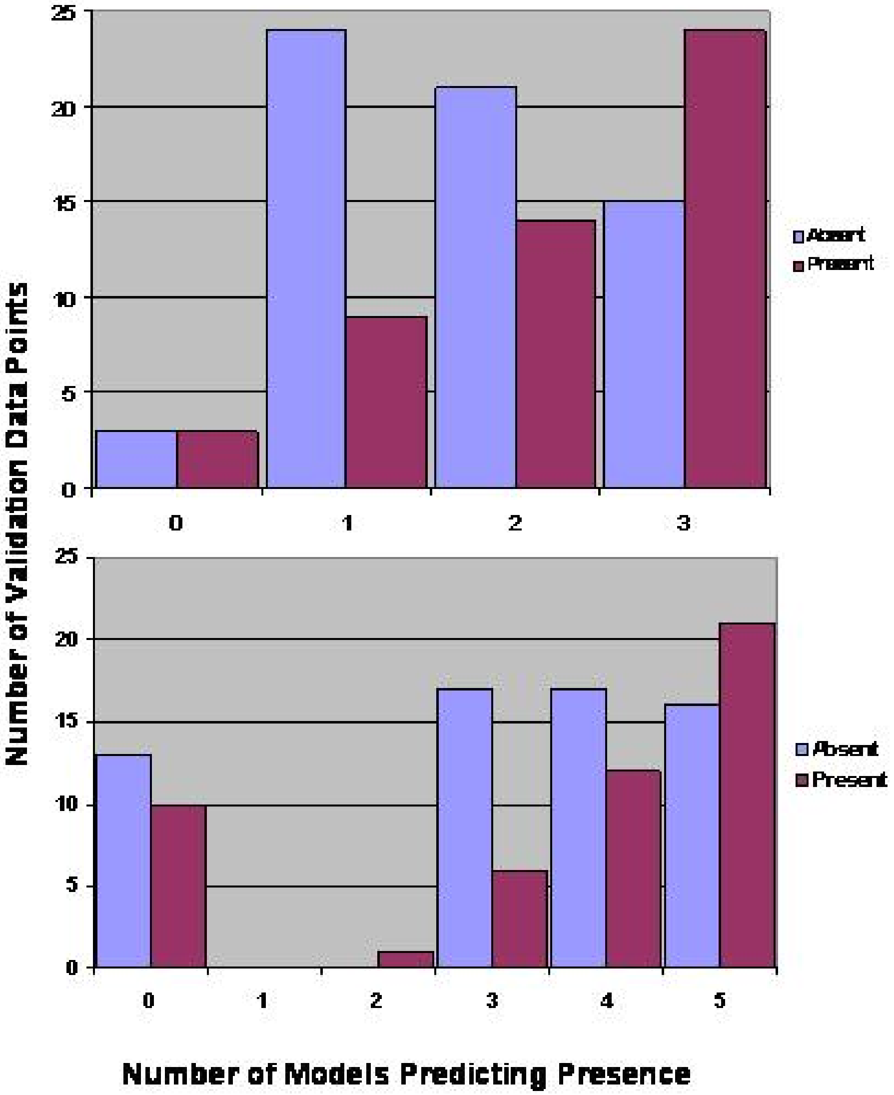


Figure 9. Distribution of Independent Cerulean Warbler Validation data points among model outputs displayed in Figures 7 and 8. Abscissa indicates the number of models predicting the point as an occurrence of Cerulean Warbler. Upper graph indicates results of ENFA, MAXENT, and Mahalanobis binary models. Lower graph indicates these three plus Domain and GARP. Blue bars indicate validation points where no Cerulean Warblers were found, purple bars indicate validation points where Cerulean Warblers were present.

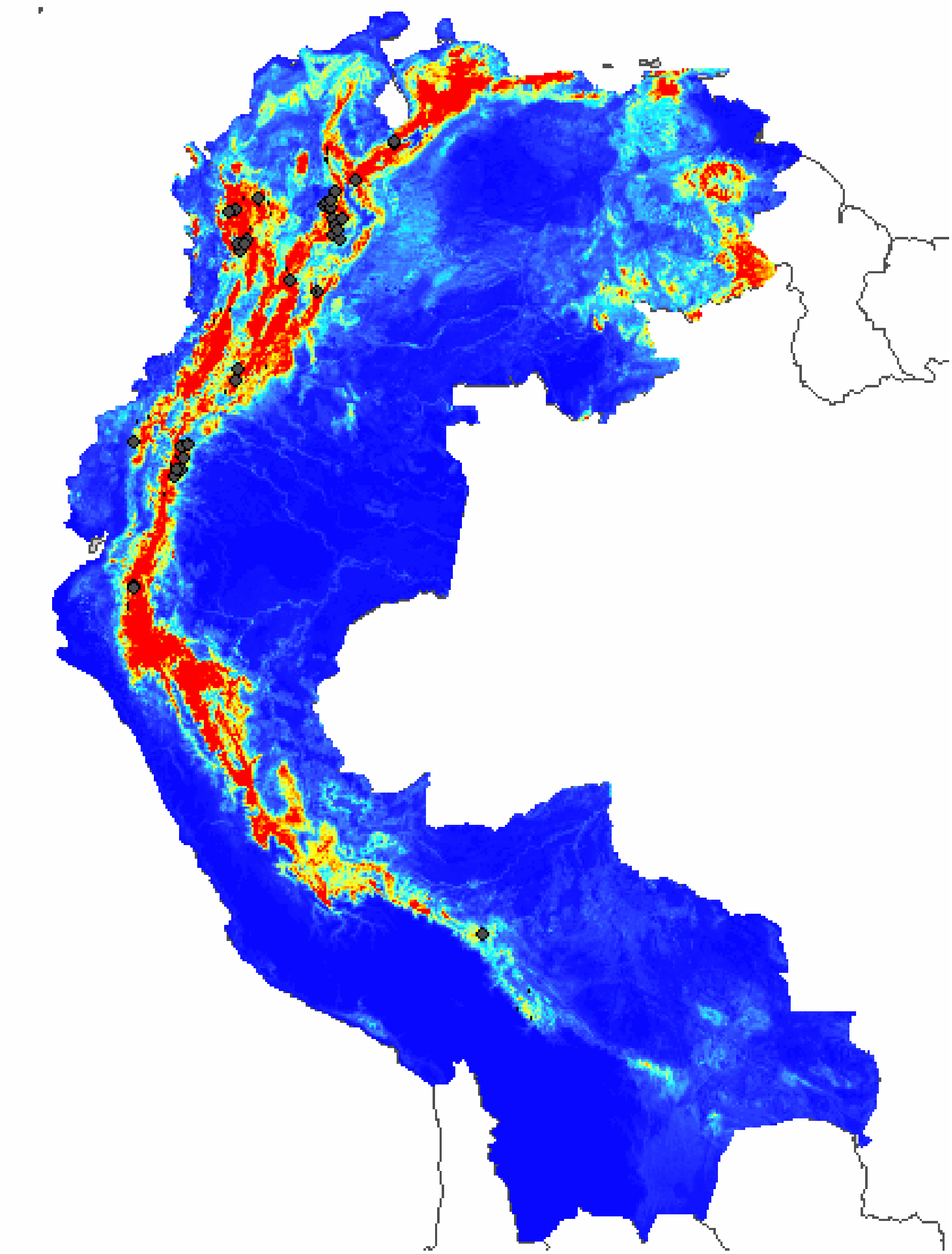


Figure 10. Intersection of Independent Cerulean Warbler Validation data set with output of MAXENT model. Dark circles indicate validation points where Cerulean Warblers were found.

Discussion

Modeling has produced a product that appears to be reasonably faithful to our existing understanding of the range. The strata suggested by the combined models form a convenient set from which we will select at random localities for field validation directed toward improving understanding of the range of the species, identifying heretofore unknown sites, and implementing conservation actions to improve the probability of long-term survival of the Cerulean Warbler.

Patterns of observed presence and observed absence in the independent validation data set indicate successful prediction of presence in the validation data set by at least one of the models in 40 of 50 cases in the combined result of the five models (Figure 9). The combined models thus included 20% false negatives, defined principally by the threshold value of omission errors of 20% for the most restrictive of the models, MAXENT. The counterpart of this result is the very high rate of false positives, as 50 of 63 absences occurred in areas in which the species was predicted to be present. Several interpretations of this finding are possible and merit attention.

First among these interpretations must be the difficulty of determining a true absence value. It is entirely possible that the birds were present in the areas but not detected, in which the absence is only a failure of detection, not a failure of prediction. Second, it is possible that these false positives result from limitations in the available data to determine what constitutes Cerulean Warbler habitat in this data set; in such a case, the birds may be more specialized to habitats than is suggested by the combined models, and these false positives are model failures to make accurate predictions. A third possibility is that these areas are equally good as potential sites for Cerulean Warblers as are those in which presence was both predicted and observed, but that the number of Cerulean Warblers is too low to be detected in them, or too few Cerulean Warblers are present to occupy these habitats. If this were the case, the suggestion is that unoccupied habitat exists for these birds in South America.

Some surprises are the results of predicted occurrence in portions of the tepui region of Venezuela, and possibly adjacent Brazil and Guyana outside the study area. Whether these areas truly constitute potential range for the species is uncertain, and may be the result of failures in the modeling and analysis process. Nevertheless, persistent occurrence of the species in certain accessible sites there suggests this may be a useful area for future field investigation. The combined model predicts considerable habitat in Colombia as well as in Ecuador and Peru.

Hilty and Brown (1986) suggested that the bulk of the Cerulean Warbler population spent the nonbreeding period south of Colombia. At that time, habitat was considered to consist of primary forest (Robbins *et al.* 1992). Recent data identified in this investigation and the experience of others, including both scientists, bird tour leaders, and independent birdwatchers, is that locating this species in Peru is increasingly difficult, that locations in Bolivia are vanishingly scarce, and that occurrence in some parts of Ecuador is more difficult to document than in the past. Current opinion thus is that the bulk of the existing Cerulean Warbler population is now found in Colombia and Venezuela during the nonbreeding period. Little primary forest exists in this range, and the birds have been repeatedly documented to use secondary forest such as shade coffee plantations (Jones *et al*. 2002). Indeed, their range in Colombia may coincide with the range of coffee cultivation.

Recent work analyzing stable isotopes in feathers suggests the existence of a recognizable migratory connectivity between breeding and nonbreeding residency sites (Girvan 2003).This raises an interesting and disturbing possibility. Breeding populations, particularly in the western and southern portions of the range, show steeper declines in BBS results, or have disappeared altogether, while populations in the central portion of the range and in the northern portion of the breeding range appear to be more stable, although not necessarily constituting source populations (Jones *et al.* 2004). The possibility is that some substantial habitat may exist in the southern portion of the nonbreeding range, and perhaps throughout, but the existing population is too small to exploit this habitat, or reduced to such low density as to be very difficult to encounter.

Biotic factors, such as potential competitors for food, or flock-forming species with which Cerulean Warblers associate on the nonbreeding grounds, present a further complication to inferring the nonbreeding distribution of the species entirely from these models. The scale of the percent tree cover is such that potentially important habitat patchiness or fragmentation are unavailable in the data that we used to construct our models. Should resident flock-forming species exhibit a negative response to fragmentation of habitat, resulting in failure of the mixed species flock resource on which Cerulean Warblers presumably depend, habitat that appears structurally appropriate to the Cerulean Warbler may not contain the appropriate complement of other species, and hence not attract Cerulean Warblers.

We suggest that the reader conduct a small test of this suggestion by considering two lines of questioning. The first comes from the existing population estimate (Rich *et al.* 2004) of 560,000. This is a top-down approach and addresses the question: Does sufficient habitat exist in South America to support the estimated population? The second begins with the results of the models here (Table 4) that indicate that 200,000 km^2 of potential habitat exists and uses an assumed nonbreeding density estimate of 1 bird/ha. This is a bottom-up approach and addresses the question: How many birds can existing habitats support?

In making such a calculation, the uncertainty in these data is substantial, and results from a number of sources, ornithological, computational, and spatial. Ornithological uncertainty concerns the rule of thumb that the observed density of 1 bird/ha might obtain over a considerable landscape. This is an unlikely occurrence. Additional ornithological uncertainty results from the assumptions inherent in the population estimate calculated by Rich *et al.* (2004), particularly the assumption that the species can dependably be detected out to distances as great as 125 m on BBS counts. This estimate is possibly as much as 50% too high (P. B. Hamel, unpublished data; J. Jones, pers. comm.), at least in forest conditions. A third source of ornithological uncertainty concerns the specificity of behavioral habitat selection by Cerulean Warblers in the nonbreeding season, which is especially poorly understood. All of these uncertainties are recognized by the ornithologists among the authors of this work.

Computational uncertainty derives from the great variety of methods used to identify locations and georeference the modeling data. Unfortunately, a relatively large number of the records were not georeferenced with surveying equipment or GPS, and hence are of unknown, but probably low, precision. Given the steep terrain in which these birds spend the nonbreeding period, errors in georeferencing might cause substantial variance into the calculations.

Spatial uncertainty in these predictions results from the need to project all the data sets to the same scale, which is to say to the coarsest one represented among the data layers to be analyzed. Thus, data on species presence have been generalized to the values obtaining over the 1 km^2 pixel in which the occurrence point was located. Local variation in topography, variation in forest cover, and other processes operative at finer scales cannot be inferred from these data because of the coarse scale necessary for completion of the analyses. These may be the features on which the birds base their habitat selection, however. In combination with the ornithological uncertainties, the computational and spatial uncertainties demand that readers and others interested in the obvious possible projections of these population and area estimates, using assumed density estimates, recognize that uncertainty is very great indeed, and leaves room for a variety of interpretations.

Perhaps the greatest uncertainty in our process is the nature of both the modeling and the validation data sets. Each is the result of convenience sampling and thus is subject to an unknowable amount of bias involved in the selection of areas for birdwatching.

The model of the Cerulean Warbler nonbreeding range produced by this project can be rigorously tested. Field testing of the model will enable use of data available at much finer scales, from the 500m pixel scale of the percent forest cover to the 90m scale of DEM. Some analyses may be conducted by examining the variance of these variables within the pixels in the current combination model (Figure 6). A more valuable result of applying finer scale resolution is that it will enable field observers more accurately to locate potential habitat and estimate its extent in the field with high quality georeferencing of the results.

These model predictions further lend themselves to test within the context of existing protected areas, in the public or private sector, including identified hot spots such as Important Bird Areas, and other locations of high conservation concern.

Conclusion

We have produced a stratified model of predicted occurrence of the Cerulean Warbler in its nonbreeding range in South America. Rigorous field testing of this model will hopefully lead to specific on the ground conservation activities likely to maintain habitat for the species at this critical time of the life cycle.

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Contact Information

Primary Author

Paul Hamel
USDA Forest Service
Center for Bottomlands Hardwoods Research, P.O. Box 227, 432 Stoneville Rd., Stoneville, MS 38776, USA
Phone (1) 662-686-3167

FAX   (1) 662-686-3195
Email phamel@fs.fed.us

Coauthors

Sara Barker
Cornell Lab of Ornithology
159 Sapsucker Woods Rd., Ithaca, NY 14850, USA
Phone (1) 607-254-2465
FAX   (1) 607-254-2104
Email sb65@cornell.edu

Silvia Benítez
The Nature Conservancy
Calle Los Naranjos N44-491 y Azucenas (Sector Monteserrin), Quito, Ecuador
Phone (593) 2-2257-138 / (593) 2-2258-113 / (593) 9-9723997 x 104
FAX   (593) 2-2257-138
Email sbenitez@tnc.org

Jennifer Baldy
University of Memphis
1228 Pallwood, Memphis, TN 38122, USA
Phone (1) 901-359-0584
FAX   (1) 901-678-2178
Email jenjoyb2002@yahoo.com

Diego Francisco Cisneros Heredia
Aves&Conservacion
Pasaje Joaquin Tinajero E3-05 y Calle Jorge Drom, Casilla Postal 17-17-906, Quito, Ecuador
Phone (593) 2-227-1800 / 09-980-6794
Email diegofrancisco_cisneros@yahoo.com

Gabriel Colorado Zuluaga
Universidad Nacional
Calle 52B #80-35, Apt. 402, Medellín, Colombia
Phone (57) 4-2345035
Email gjcolora@epm.net.co

Francisco Cuesta
Ecociencia
Francisco Salazar E14-34 y Av. La Coruna, P.O. Box 17-12-257, Quito, Ecuador
Phone (593) 2231-624, 2522-999, 2545-999
Email andes@ecociencia.org

Ian Davidson
BirdLife International
Vicente Cárdenas E5-75 y Japón, 3er Piso, C.P. / P.O.Box: 17-17-717, Quito, Ecuador
Phone (593) 2-245-3645, 227-7399, 227-7497
FAX   (593) 2-227-7059
Email ian.davidson@birdlife.org.ec

David Fco. Díaz Fernández
BirdLife International

Vicente Cárdenas E5-75 y Japón, 3er Piso, C.P. / P.O.Box: 17-17-717, Quito, Ecuador
Phone (593) 2-2277-497
FAX (593) 2-227-7059
Email david.diaz@birdlife.org.ec

Andrea Ganzenmueller
Ecociencia
Francisco Salazar E14-34 y Av. La Coruna, P.O. Box 17-12-257, Quito, Ecuador
Phone (593) 2231-624, 2522-999, 2545-999
Email andrea_ganzenmueller@yahoo.com

Santiago García
BirdLife International
Vicente Cárdenas E5-75 y Japón, 3er Piso, C.P. / P.O.Box: 17-17-717, Quito, Ecuador
Phone (593) 9-166-0320
Email santiago.llore@birdlife.org.ec

Kate Girvan
Queen's University
Norval Outdoor School, Box 226, Norval, Ontario, L0P 1K0, Canada
Phone (1) 905-877-2201
Email kgirvan16@hotmail.com

Esteban Guevara
Aves y Conservación
Florencia y Borramini 176, La Primavera, Cumbaya, Ecuador
Phone (593) 2-2891-553
Email esalguan@yahoo.com

A. Bennett Hennessey
Asociación Armonía – BirdLife International
Av. Lomas de Arena 400, Casilla 3566, Santa Cruz de la Sierra, Bolivia
Phone (591) 3-356-3636
Email abhennessey@armonia-bo.org

Olga Lucía Hernández
WWF Colombia
Carrera 35 #4A-25 San Fernando, Cali – Valle, Colombia
Phone (57) 2-5582577 x 110
Email olhernandez@wwf.org.co

Sebastian Herzog
Asociación Armonía – BirdLife International
Av. Lomas de Arena 400, Casilla 3566, Santa Cruz de la Sierra, Bolivia
Phone (591) 3-3568808
Email skherzog@armonia-bo.org

David Mehlman
The Nature Conservancy
1303 Rio Grande Blvd NW, Suite 5, Albuquerque, NM 87104, USA
Phone (1) 505-244-0535 x 24
FAX (1) 505-244-0512
Email dmehlman@tnc.org

María Isabel Moreno
Fundación ProAves
Carrera 20 Nº 36-61, Bogotá D. C, Colombia
Phone (57) 1-3403229/32/65
FAX (57) 1-3403285
Email mmoreno@proaves.org

Esra Ozdenerol
University of Memphis
Department of Earth Sciences, 236 Johnson Hall, 488 Patterson Street, Memphis, TN 38152, USA
Phone (1) 901-678-2787
FAX (1) 901-678-2178
Email eozdenrl@memphis.edu

Paolo Ramoni-Perazzi
Universidad de Los Andes
Facultad de Ciencias, Departamento de Biologia, Merida 5101, Venezuela
Phone (58) 274-240-1304
FAX (58) 74-40-12-86
Email rpaolo@ula.ve

Milton Romero
Instituto Humboldt
Calle 146A No. 40A – 18 Apt. 702 Bogotá, Colombia
Phone (57) 1-6086900 6335560
Email mhromero@humboldt.org.co

David Romo
Universidad San Francisco de Quito
Campus Cumbayá- Diego de Robles y Vía Interoceánica, P.O.BOX 17-1200-841, Quito, Ecuador
Phone (593) 2-297-1961
Email david@usfq.edu.ec

Paul Salaman
American Bird Conservancy
4249 Loudoun Avenue, PO Box 249, The Plains, VA 20198, USA
Phone (1) 540-253-5780
FAX (1) 540-253-5782
Email psalaman@abcbirds.org

Tatiana Santander
Aves y Conservación
Pasaje Joaquín Tinajero E3-05 y Jorge Drom, Quito, Ecuador
Phone (593) 2-227-1800
Email aves_proyectos@yahoo.com

Carolina Tovar Ingar
Centro de Datos para la Conservación, Universidad Nacional Agraria La Molina
Av. La Universidad s/n La Molina Lima-Perú
Phone (51) 1-349-6102

Email ctovar@lamolina.edu.pe

Melinda Welton
Gulf Coast Bird Observatory
5241 Old Harding, Franklin, TN 37064, USA
Phone (1) 615-799-8095
FAX (1) 615-799-2220
Email weltonmj@earthlink.net

Tom Will
U.S. Fish and Wildlife Service
Division of Migratory Birds, 1 Federal Drive — 6th Floor, Fort Snelling, MN 55111-4056, USA
Phone (1) 612-713-5362
FAX (1) 612-713-5393
Email tom_will@fws.gov

Carlos Pedraza
Instituto Humboldt
Calle 138 bis No. 25 – 37 Bogotá, Colombia
Phone (57) 1-6086900 6335560
Email cpedraza@humboldt.org.co

Gustavo Galindo
Instituto Humboldt
Calle 146A No. 40A – 18 Apt. 702 Bogotá, Colombia
Phone (57) 1-6086900 6335560
Email ggalindo@humboldt.org.co