Avoiding Pitfalls of Using Species Distribution Models in Conservation Planning

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Abstract: *Museum records have great potential to provide valuable insights into the vulnerability, historic distribution, and conservation of species, especially when coupled with species-distribution models used to predict species' ranges. Yet, the increasing dependence on species-distribution models in identifying conservation priorities calls for a more critical evaluation of model robustness. We used 11 bird species of conservation concern in Brazil's highly fragmented Atlantic Forest and data on environmental conditions in the region to predict species distributions. These predictions were repeated for five different model types for each of the 11 bird species. We then combined these species distributions for each model separately and applied a reserve-selection algorithm to identify priority sites. We compared the potential outcomes from the reserve selection among the models. Although similarity in identification of conservation reserve networks occurred among models, models differed markedly in geographic scope and flexibility of reserve networks. It is essential for planners to evaluate the conservation implications of false-positive and false-negative errors for their specific management scenario before beginning the modeling process. Reserve networks selected by models that minimized false-positive errors provided a better match with priority areas identified by specialists. Thus, we urge caution in the use of models that overestimate species' occurrences because they may misdirect conservation action. Our approach further demonstrates the great potential value of museum records to biodiversity studies and the utility of species-distribution models to conservation decision-making. Our results also demonstrate, however, that these models must be applied critically and cautiously.*

Evitando Dificultades Resultantes del Uso de Modelos de Distribución de Especies en Planeación de Conservación

Resumen: *Los registros de museos tienen un gran valor potencial al proporcionar entendimiento sobre la vulnerabilidad, distribución histórica y conservación de especies, especialmente cuando se combinan con modelos de distribución de especies utilizados para predecir los rangos de distribución de las especies. No obstante, la mayor dependencia sobre los modelos de distribución de especies para la identificación de prioridades de conservación requiere una evaluación crítica de la robustez del modelo. Utilizamos 11 especies de aves de interés para la conservación en el muy fragmentado Bosque Atlántico en Brasil así como datos de condiciones ambientales en la región para predecir la distribución de las especies. Estas predicciones fueron repetidas para cinco tipos diferentes de modelos para cada una de las 11 especies de aves. Luego combinamos estas distribuciones de especies para cada modelo por separado y aplicamos un algoritmo de selección de reservas para identificar sitios prioritarios. Comparamos los resultados potenciales de la selección de reservas*

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entre modelos. Aunque hubo similitud entre los modelos en la identificación de redes de reservas, los modelos difirieron marcadamente en el alcance geográfico y la flexibilidad de las redes de reservas. Es de importancia fundamental para los planificadores evaluar las implicaciones sobre la conservación de errores falsos positivos y falsos negativos para su escenario de manejo específico antes de comenzar el proceso de modelado. Las redes de reservas seleccionadas por modelos que minimizaron los errores falsos positivos proporcionaron mejor correspondencia con las áreas prioritarias identificadas por especialistas. Por lo tanto, instamos a tener precaución con el uso de modelos que sobreestiman la ocurrencia de especies porque pueden desviar las acciones de conservación. Nuestro método demuestra además el gran potencial de los registros de museos en estudios de biodiversidad y la utilidad de los modelos de distribución de especies para la toma de decisiones de conservación. Sin embargo, nuestros resultados demuestran que estos modelos deben ser aplicados crítica y cuidadosamente.

Introduction

Museum records have great potential to provide insights into the vulnerability, historical distribution, and conservation of species (e.g., Davis 1996; Ponder et al. 2001). Knowledge of the historic distribution of a species is necessary to assess changes relative to the current distribution. For example "hotspots" are areas with high species richness coupled with habitat loss exceeding 70% (Myers et al. 2000). Species-distribution models (SDMs) are powerful tools for converting individual point-locality data, such as museum collection records, into the hypothetical distributional range of a species (Corsi et al. 2000; da Fonseca et al. 2000) or predicted ranges following global climate change (e.g., Polansky et al. 2000; Peterson et al. 2002). Thus, SDMs have great potential utility to conservation, especially because conservation biologists are often pressed to make recommendations about conserving biodiversity based on limited species-distribution data (da Fonseca et al. 2000; Peterson et al. 2000). However, the variety of existing SDM algorithms could produce different species distributions and hence different recommendations to conservation planners. Little attention has been paid to how robust these different species-distribution models (SDMs) are and whether the use of these models in reserve-selection processes lead conservation policymakers to different outcomes (e.g., Elith 2000). Discrepancies between individual SDMs used for conservation planning and actual organismal distributions may have profound effects on conservation (Smith & Catanzaro 1996).

We produced hypothetical distributional ranges based on historic museum record data for 11 threatened or endangered cotingids (BirdLife International 2000) (Aves) in the Atlantic Forest region of Brazil (Fig. 1). We selected the Atlantic Forest region because it is a biodiversity hotspot and one of the most endangered regions of the world, with >90% forest loss (Mittermeier et al. 1998; Myers et al. 2000). To test the sensitivity of reserve selection to underlying SDMs, we first produced species distributions from five model types for all 11 cotingid species. We quantitatively compared prediction errors and examined the degree of spatial overlap among a subset of the models. To determine whether the different model types result in similar recommendations to conservation-reserve planners, we compared the number and location of minimum sites needed to conserve all species and the flexibility of potential reserve sites. Flexibility occurs when multiple localities capture the same essential set of species, and thereby provides options for negotiating and establishing reserve networks (Williams et al. 1996). We also compared reserve-selection results from different models with "key areas" identified by experts from BirdLife

Figure 1. Original extent of the Atlantic forest region (shaded) in Brazil and its proximity to select densely populated cities. Codes for state names: RN, Rio Grande do Norte; PB, Paraíba; PE, Pernambuco; AL, Alagoas; SE, Sergipe; BA, Bahia; MG, Minas Gerais; ES, Espírito Santo; RJ, Rio de Janeiro; SP, São Paulo; PA, Parana; SC, Santa Catarina; RS, Rio Grande do Sul.

International (Wege & Long 1995). Our approach adds to the increasing awareness of the value of museum data to biodiversity studies and the great utility of SDMs to conservation decision-making when applied appropriately and cautiously.

Methods

In the following sections we describe the four-step process that was necessary to evaluate the impact of different SDMs on conservation planning. These steps included (1) acquiring bird locality data from museums, (2) overlaying bird locality data with environmental layers to produce species distributions using different models, (3) combining SDMs to produce a composite map in which identities of bird species occurring in each pixel of the map are known, and (4) selecting the conservation reserve network based on the species-richness maps and a complementarity algorithm. Step three also allowed for creation of species-richness maps, which provided some graphical indication of the differences among the models.

Specimen Data and Study Species

We compiled data on known species occurrences from museums and private collections in North America and Brazil and from verified records from BirdLife International for 11 species of Cotingidae that occur in the Atlantic Forest of Brazil (step 1). Three study species are considered critically endangered (*Cotinga maculata, Xipholena atropurpurea, Iodopleura pipra*), three are vulnerable (*Laniisoma elegans, Carpornis melanocephalus, Lipaugus lanioides*), four are near threatened (*Phibalura flavirostris, Tijuca atra, Procnias nudicollis, Carpornis cucullatus*), and the remaining species is of "special conservation concern" (*Pyroderus scutatus*) (The Nature Conservancy 1999; BirdLife International 2000). Two species of cotingids of conservation concern (*Calyptura cristata*, *Tijuca condita*) were not included because of the paucity of historical records. Although historical records with specific locality information date back to the last decade of the nineteenth century; the majority came from 1920–1970. Most museum specimens were examined to verify identifications. Specimen data came from 276 spatially referenced localities well distributed throughout the Atlantic Forest of Brazil. Verified records of occurrence represent presence data.

The number of presence records used in model development generally ranged from 24 to 71; *Tijuca atra* models, however, had only four independent locality records. Because the primary focus of this project was to compare outcomes from SDMs for conservation planning, we included all museum presence records in generation of SDMs. Museum, herbarium, and other locality data sets provide only presence data; extensive plot or census data are required for reliable absence data. In our case, reliable plot or census data were not available over a large number of sites in the Atlantic Forests, and we therefore needed to generate absence data. We assigned species-specific absence based on a subset of relatively well-collected localities (>3 independent [in time] collections of cotingids; $n = 150$ localities of the original 276) within the zoogeographic region(s) of each species (Parker et al. 1996). Our assumption was that if multiple expeditions did not result in a collection, then the species was likely absent. Given that we were dealing with mostly range-restricted species from the same family, we believe individuals, if encountered, would most likely have been collected and not passed over by the collectors. We used absence data for logistic-regression models and for later validation of all models. An alternative would have been to use random points for model validation and as absence points in logistic-regression models. Both methods of selecting localities undoubtedly include areas where either the species is present and unrecorded or the habitat is suitable but the species is not present. We believed, however, that the former method was more likely to identify sites that represent true absences than the latter. Having both true absence and presence sites are key for evaluating model performance (e.g., Fielding & Bell 1997).

Environmental Data Layers and Species-Distribution Modeling

To produce hypothetical species distributions we needed to combine museum records and environmental data layers (step 2). Environmental layers (seven total) came from existing digital data sets and new data digitized from published sources. The soils map was produced by Empresa Brasileira de Pesquisa Agropecuária (EMBRAPA) in Brazil and digitized at EROS Data Center, in Sioux Falls, South Dakota. The vegetation map, which represents historical vegetation cover, was produced by Ministério da Agricultura at the Instituto Brasileiro de Desenvolvimento Florestal (IBDF) and was digitized by the Fundação Instituto Brasileiro da Geografia e Estatística (IBGE). Both soils and vegetation map closely approximated those found within Atlas Nacional do Brasil (IBGE 1992). This atlas was the data source for geology, effective humidity, and elevation coverages. Mean annual precipitation and temperature were digitized from climate maps produced in 1975 by the United Nations Agency for Education, Science and Culture.

The SDMs we compared varied from simple sets of rules based on overlays of environmental and species occurrence data (e.g., Bioclim [Nix 1986; Busby 1991] and Simple Overlay), to sophisticated multivariate analyses (e.g., Domain [Carpenter et al. 1993] and logistic regression [Pereira & Itami 1991]), to artificial intelligence techniques using rule-based sets of algorithms (e.g., GARP [Stockwell 1999; Godown & Peterson 2000]). The SDMs

we used cover most of the methods used most commonly in the literature. The logistic, Domain, and GARP models each had three variants. Logistic-regression model variants include 50%, 85%, and 95% probability of occurrence (LOG50, LOG85, LOG95), and Domain model variants have cut-offs of 85%, 90%, and 95% (DOM85, DOM90, DOM95). The GARP SDM produced a potentially different distribution model during each run, so we ran the model five times and randomly chose the results of one model (GARP1). The GARP4 model represents the range of a species for which at least four GARP models selected cells as suitable; GARP5 included cells for which all five runs of GARP selected the cell as suitable. The Simple model included as areas of occupancy only those sites in which all seven environmental conditions were suitable as indicated by overlays between known locations of birds and environmental layers.

All models had the same historic museum locality data and environmental data layers; scale of analysis was 4 × 4 km raster cells. All models included species presence data, and the logistic-regression model also included absence data. For comparison, we included maps based on the extent of occurrence for each taxon from published accounts (Ridgley & Tudor 1994). The extent of occurrence reflects the range over which a species is found and is usually shown as a single area or polygon unless there is some notable disjunction in occurrence. In the latter case, the extent may be shown from two up to a few areas.

Species-Richness Maps and Complementarity Analyses

We created composite maps (step 3) by combining the SDMs from all 11 species; any location on the map could have species richness ranging from 0 to 11. In addition, bird distributions based on extent-of-occurrence maps (i.e., those from Ridgley & Tudor 1994) were combined to generate a composite map. Prior to producing the composite maps, we scaled the SDMs for individual species up to a 15-minute resolution (i.e., approximately 26 × 26 km) to better reflect the area from which conservation reserves might be selected across a region like the Atlantic Forest (step 4). To scale up, we converted the 4 × 4 km raster into a vector polygon coverage by using ARC/INFO (version 8.1, Environmental Systems Research Institute, Redlands, California) and then converted the polygon coverage back into a raster with a cell size of 15 minutes on a side by using majority rules (i.e., if >50% of the grid cell has a polygon value of 1, indicating presence, then the cell receives a value of 1). These composite maps serve two purposes. First, for each pixel on the map, we know the identity of all species predicted to occur there. This step is necessary for selection of reserve sites (step 4). Second, we can produce a species-richness map from each of the SDMs, which provides a graphical indication of differences among the SDMs.

The use of quantitative methods, such as complementarity, for selecting and prioritizing areas within a conservation-reserve network is now well established (Williams et al. 1996; Margules & Pressey 2000; Myers et al. 2000; Peterson et al. 2000). We chose complementarity (Pressey et al. 1993; Williams et al. 1996) to select reserve networks because of its efficiency in "capturing" species. We used complementarity rules in Worldmap to identify the minimum number of "cells" (i.e., 15-minute grid cells) that "captured" all 11 species (near-minimum set) from composite maps (step 4). Cells were then reordered and ranked by complementary richness into conservation-reserve sets. Each "set" contains the grid cells that represent one or more "goal-essential species" (Williams et al. 1996; Williams 1999*a*). However, any set of goal-essential species justifying selection of a set may occur together elsewhere within the geographic region. Cells that contain the same combination of goal-essential species are identified as fully flexible alternative cells. Here we also map all fully flexible grid cells as "options" for each selected reserve set presented to conservation decision-makers. This set of fully flexible sites should be viewed as an upper bound that may overestimate the options available.

Statistical Analyses

The accuracy of SDMs requires independent testing and validation. Models can be accurate in two ways and inaccurate in two ways. Ideally, a model should correctly predict both species absence and presence. In practice, however, incorrect classification occurs when a model predicts either that a species should be at a location when in fact it is not (i.e., false-positive error or Type I error; often termed *commission*) or that a species should not be at a location when in fact it is (i.e., false-negative error or Type II error, often termed *omission*) (Fielding & Bell 1997). An overall index of the performance of a species-distribution model is given by its Kappa value (Fielding & Bell 1997). Kappa is given by the formula

$$\frac{[(a+d)-(((a+c)(a+b)+(b+d)(c+d))/N)}{[N-(((a+c)(a+b)+(b+d)(c+d))/N)]},$$

where a is the number of times when both model and observations predict occurrence, b is the number of times when observations indicate absence and model predicts occurrence, c is the number of times observations predict occurrence and model absence, and d is the number of times when both model and observations predict absence. We used Kappa because it incorporates all four ways in which a model's predictions reflect observations. Here we calculated the average percentage of false-positive and false-negative errors by using existing presence/absence data from museum records and Kappa values for each species-distribution model we generated. We tested for significant differences in Kappa values

across the models with one-way analysis of variance. Individual species were the replicates in the statistical model.

We used regression analyses to identify general "rules" that emerged to guide conservation decision-making by determining whether model characteristics (Kappa, false-positive or false-negative errors) predicted the flexibility of reserve set selection. In this case, we determined the average number of fully flexible sites (i.e., cells) selected within the first two minimum reserve sets determined by complementarity analyses. In these regressions the response variable was the average number of fully flexible sites, and the predictor variable was either the average value of Kappa, false-positive error, or false-negative error. These latter values were averaged over all 11 bird species for each model type. We used only the first two reserve sets identified by complementarity analysis because at least two minimum sets were identified by all models. Some models required a third or fourth set to capture remaining species, but because of the small number of species in this study ($n = 11$), these third or fourth sets often included only one species. Consequently, the number of fully flexible sites for these latter sets that captured only one species equals the number of 15-minute grid cells in which that species occurred. This greatly increased the variation in the average flexibility for a model and obscured what we believe are meaningful relationships.

Results

Species-richness maps created by combining SDMs across species were consistent among models in predicting the greatest concentration of species along the coast of southeast Brazil (Fig. 2). Pockets of species richness for Cotingidae extended north into Bahia and south into Parana. In nearly all models, inland areas within Minas Gerais were also modeled to contain areas of high species richness. These species-richness maps provided an indication of how the 11 SDMs models varied in their predictions of species occurrences (Fig. 2). For example, species richness produced by the extent of occurrence maps as well as some models encompassed broad regions (e.g., Simple, Bioclim, LOG50, DOM80, GARP1), whereas other models encompassed narrower regions (LOG95, DOM95).

We determined whether models differed consistently among species in the relative area predicted to be occupied by any one species using a randomized-block analysis of variance. In this model, we divided the predicted area for each model by the maximum area predicted by any one model for each species separately. This provided the proportional area relative to the maximum for each model, with values ranging from 0 to 1 (proportional area was the dependent variable in the model). The main effect was model type and blocks were the bird species. Significant differences occurred among models in the proportional area predicted to be occupied by a species ($F_{10,100} = 16.4$, $p < 0.001$). The models with consistently low proportional areas of occupancy were DOM95, LOG95, and GARP5, whereas Bioclim and LOG50 had consistently high proportional areas of occupancy (Table 1). These differences reflect the degree to which the individual SDM's area of predicted occupancy fills the extent of occurrence (Maurer 1994). The extent of occurrence generally encompasses a continuous area over which a species' records are known and are typically shown as range maps in field guides. Areas of occupancy, on the other hand, only include those areas within the extent to which the species is known (or modeled) to occur. In these models, the average percentage of the full range extent occupied by a species varied from 20% (DOM95) to 78% (LOG50). Further, when the percent overlap among models was examined, on average 96% of the area predicted to be occupied by DOM95 was encompassed by the LOG50 predictive models. Compared with the Simple SDM, an intermediate model in terms of proportional area occupied, average overlap was 86% and 79% with LOG50 and DOM95, respectively. These results emphasize that some models appear to be consistently conservative and may underestimate range and area occupied, whereas other models potentially overestimate species distributions. Moreover, the species-richness maps (Fig. 2) and our examination of individual SDMs demonstrate that models differed in the degree to which the species' range periphery was included.

We used complementarity rules in Worldmap to select hypothetical conservation reserve networks based on the composite maps derived from the 11 SDMs and extent-of-occurrence maps (see Fig. 2 for representation of species richness from these maps). Conservation decision-makers would receive different answers regarding priorities for reserve area selection with the different composite maps (Fig. 3). From two to four reserve areas (minimum sets) were necessary to represent all 11 bird species in the Atlantic Forest of Brazil, depending on the species-distribution model used, but these two to four areas do not necessarily overlap geographically (Table 2, Fig. 3). Nearly all outputs from complementarity analyses selected areas near Rio de Janeiro and farther north along the coast in northern Espírito Santo or southern Bahia. Reserve-selection networks differed in their propensity to include the more southern and northern sectors of the Atlantic Forest. Selected networks also differed in the flexibility of the areas selected (Table 2, Fig. 3). The number of flexible alternatives for any reserve network depended on the range extent of the most restricted taxa captured by that set and on the frequency of co-occurrence of the goal-essential taxa elsewhere in the region (Table 2). Reserve sets that appeared to have high flexibility generally

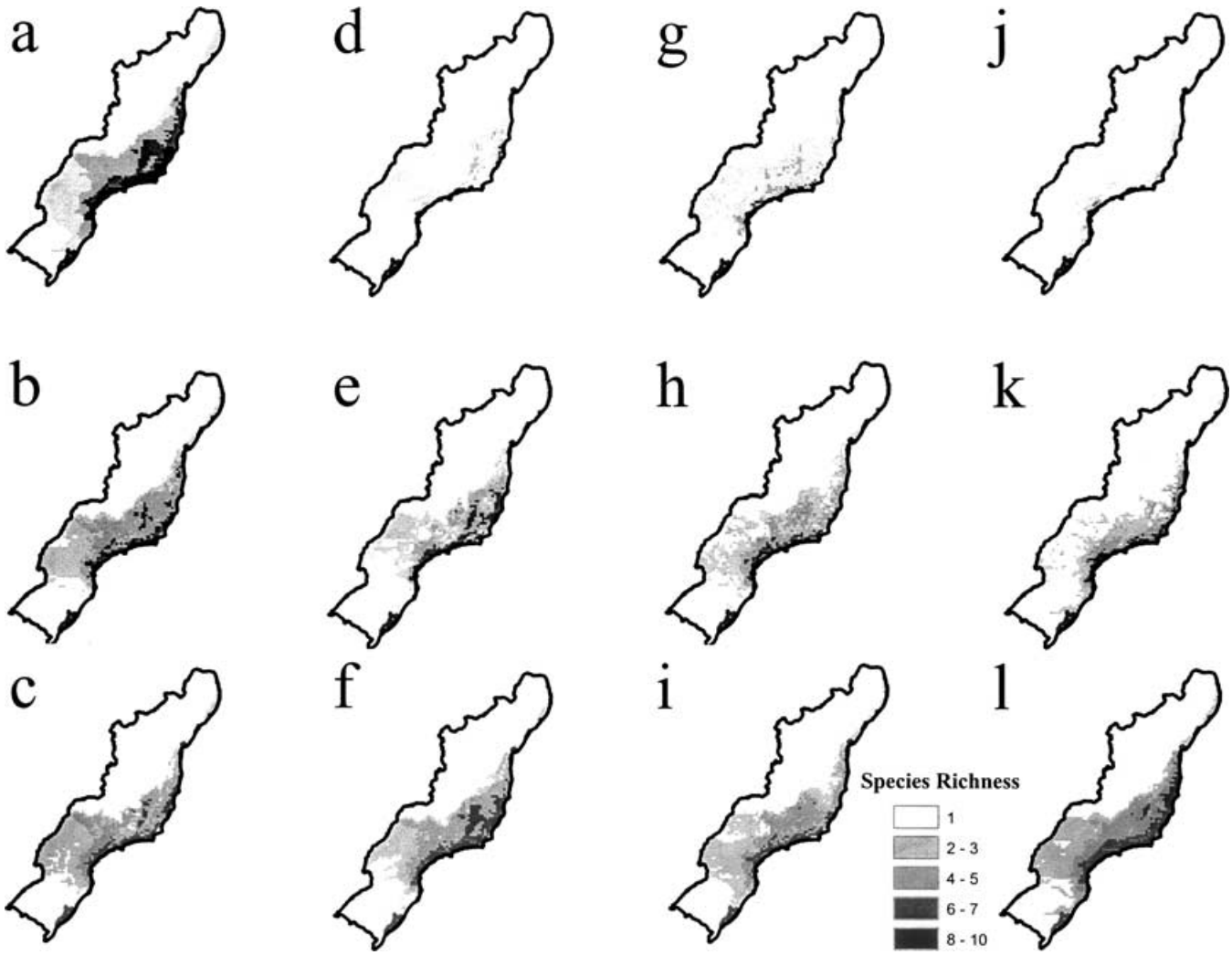

Figure 2. Species-richness maps (result of step 3) of Cotingidae based on predicted occurrences derived from species-distribution models. Species richness values can range from 0 to 11. The figures correspond to the species-distribution models used to predict occurrence: (a) extent of occurrence, (b) Bioclim, (c) Simple, (d) DOM95, (e) DOM90, (f) DOM85, (g) GARP5, (h) GARP4, (i) GARP1,(j) LOG95, (k) LOG80, (l) LOG50. Darker colors represent cells containing greater number of species.

captured only one to two goal-essential species of the 11 taxa (e.g., see ellipse 3 in Fig. 3d; Table 2).

Models differed in the degree to which they made false-positive and false-negative errors and in their overall performance as measured by Kappa ($F_{10,110} = 5.6, p < 0.001$; Fig. 4). We found a significant negative correlation between false-positive and false-negative errors ($r = -0.62$, $n = 11, p < 0.05$), although DOM95 tended to minimize both errors and thus had the highest Kappa value. Only Kappa values for DOM95 approached 0.6, a value recommended as representing a "good" model by Fielding and Bell (1997). Neither Kappa nor false-negative errors were related to the average flexibility of sets selected by reserve algorithms. There was a significant relationship, however, between false-positive errors and average flexibility of the first two reserve sets selected ($r^2 = 0.64$, df = 8, $F = 7.13$, $p < 0.02$; Fig. 5). As false-positive errors increased, reserve sets contained increasingly more fully flexible sites on average, thus apparently offering a greater number of choices for decision-makers.

The models we developed naturally should be followed with field validation, although this is problematic given the dramatic habitat loss in the region. To provide an indication of how well our models reflect current conditions and priorities, we compared the overlap between reserve-network areas selected by the models (Fig. 4) with BirdLife International's "key areas" for the same set of threatened cotingid species in the Atlantic Forest region (Wege & Long 1995). Models with low false-positive errors (DOM95, GARP5, LOG95) included the greatest number of key areas in selected reserve networks (50–62.5% of 40 key areas included), whereas four of five models with

Table 1. Mean proportional area (and standard error, SE) occupied by a species as a function of the species-distribution model type.*

Model	*Mean proportional area*	*SE*
DOM95	0.23a	0.040
LOG95	0.27a	0.068
GARP5	0.46a,b	0.048
DOM90	0.54b,c	0.063
LOG80	0.62b,c,d	0.064
Simple	0.66b,c,d	0.057
GARP4	0.69b,c,d	0.054
GARP1	0.76c,d,e	0.056
DOM85	0.80c,d,e	0.070
Bioclim	0.83d,e	0.089
LOG50	0.96e	0.042

**Values can range from 0 to 1. See text for description of models and how proportional area was calculated. The replicates were the 11 species of Cotingidae. Different letters (a–e) indicate a significant difference in a post-hoc Tukey comparison.*

the highest percentage of false-positive errors (extent of occurrence, LOG50, DOM85, Bioclim) included only 10–37.5% of key areas. The GARP1 was an exception in that this model, with high false-positive errors, included 30 key areas. However, species distribution models based on GARP produced a different prediction during every run. We randomly selected one of the five GARP runs for this analysis. If we were to repeat the analysis, we would expect the new GARP1 to include a different number of key areas.

Discussion

Given the significant negative correlation between false-positive and false-negative errors within models, conservationists may wish to use models that minimize one or the other error. Type I errors may lead to failure to conserve a species because sites selected as reserves do not contain the target taxa. A Type I error does not necessarily mean the reserve is unsuitable for occupancy; the area could be suitable but, by chance, the species is not presently found there. Type II errors, on the other hand, potentially result in sites not being selected even though target taxa may be present. In the latter case, one may fail to select sites that are of importance to the overall survival of a species, such as those that represent viable populations or unique genotypes. Conservation decision-makers must decide which error is more "dangerous." A prudent solution would be to select SDMs that minimize false-positive errors because of the danger that conservationists may identify reserve areas that do not actually contain the target taxa. It is true that species might be able to occur there at a later time through dispersal or range expansion, but this assumes that such opportunities exist. Moreover, if models with high false-positive errors overestimate species' ranges, then high species richness may appear to occur because of overlap among species at range peripheries. Thus, areas selected first for reserve sites based on complementarity may not be ideal because some species are represented from the edge of their ranges instead of the center. This problem may be reduced by using the probability of persistence (Williams 1999*b*; Williams & Araújo 2000) or probability of occurrence (Polansky et al. 2000) directly from individual species-distribution models. The former down-weights marginal habitats, whereas the latter quantifies the uncertainty of a species' occurrence at a location. The two are not necessarily correlated because greater population densities can be found in areas where fitness values are lower (e.g., van Horne 1983). Reliable persistence or probability estimates, however, require considerable information on species occurrences or densities. Such data are especially difficult to obtain for rare taxa, the species of highest conservation concern.

When a species is not present at a location predicted by the model, uncertainty exists as to whether the model prediction is in error or whether the absence reflects low population size, random or patchy distribution of organisms, or natural variation in occurrence (e.g., seasonal or temporal variation in distribution). Assigning probabilities of occurrence is one treatment for this kind of ecological uncertainty (Regan et al. 2002). Estimates of the probability of occurrence can be obtained from certain models (e.g., logistic regression; Margules & Nicholls 1987; Margules & Stein 1989), and reserve-selection algorithms have been adapted to deal with probability rather than presence/absence data (Polansky et al. 2000). Compared with presence/absence data, efforts to maximize species richness resulted in different sites being selected by probabilistic occurrence data. These differences were more pronounced when uncertainty was higher (i.e., probability values farther from 0 or 1). Thus, incorporating uncertainty may lead to different recommendations in conservation planning. The application of these algorithms that use probability-of-occurrence data are somewhat limited, however, due to the computational time necessary to find optimal solutions (Polansky et al. 2000). Continued efforts to design reserve-selection algorithms that maximize expected occurrence (or persistence) of species and provide some method for error estimation, especially in cases where error can be accumulated across models, would greatly facilitate decision-making processes in conservation.

Our approach further demonstrates the great potential of using museum records for biodiversity studies. Although our findings do not provide guidance for reserve selection in the Atlantic Forest of Brazil because they represent only a subset of the threatened taxa and are based on historic specimen data, they do demonstrate inherent differences among SDMs and the dangers in identifying priorities for reserve selection based on these models if

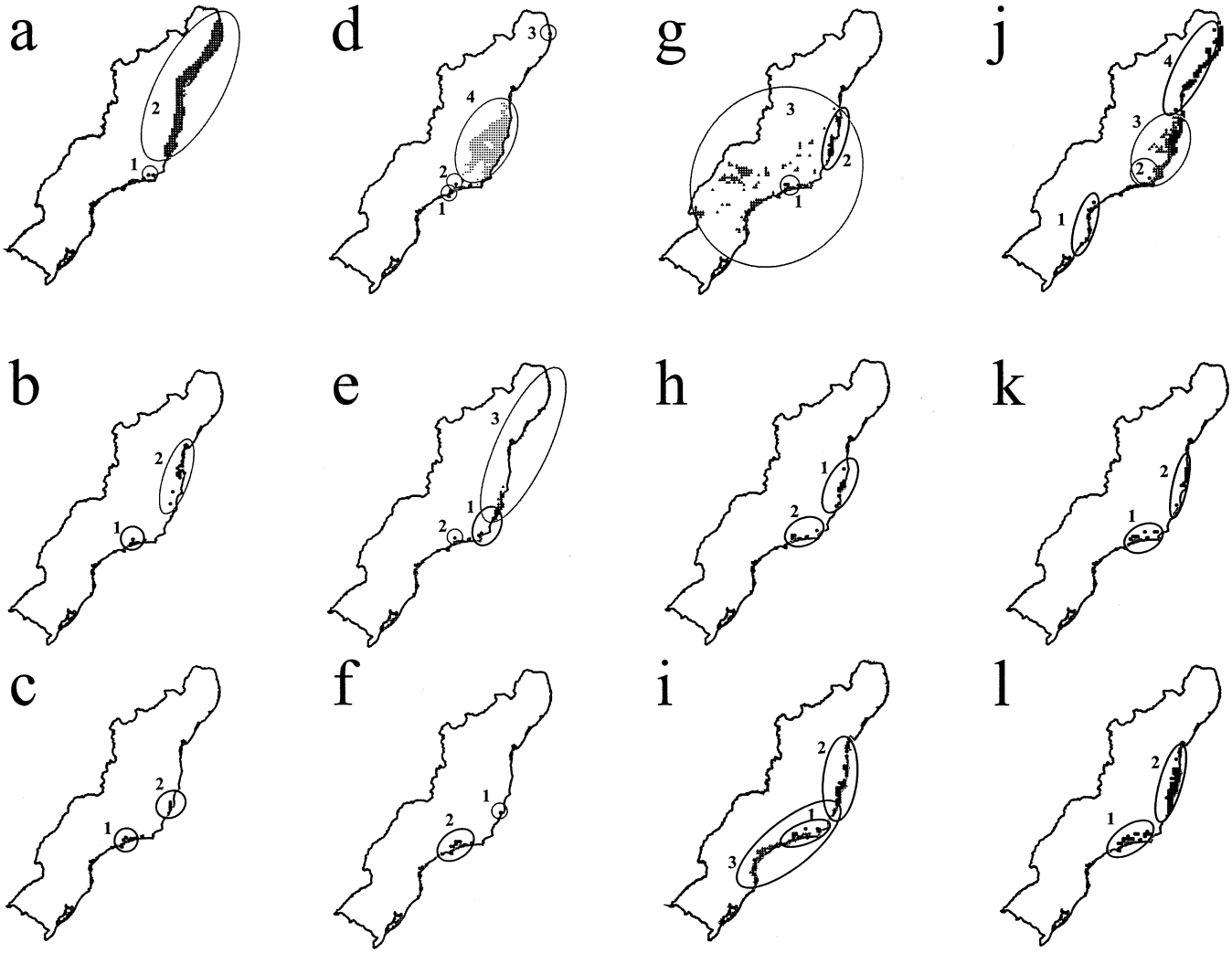

Figure 3. Reserve-network hypotheses (result of step 4; from Worldmap) based on extent of occurrence and species-distribution models as lettered in Fig. 2. Cells with the same shading represent a reserve set that captures the same combination of goal-essential species, and individual cells represent fully flexible sites within that reserve set. Ellipses are drawn around reserve sets to aid in identification.

Table 2. Number of reserve sets selected by complementarity analyses when applied to the composite of species distribution maps.*

		Set 1		*Set 2*		*Set 3*		*Set 4*	
Model	*Number of reserve sets*	*sites*	*species*	*sites*	*species*	*sites*	*species*	*sites*	*species*
Bioclim	2	1	8	15	3	—	—	—	—
DOM85	2	1	8	6	3	—	—	—	—
DOM90	3	6	9	2	1	32	1	—	—
DOM95	4	1	7	1	2	1	1	254	1
GARP1	3	5	7	30	2	45	2	—	—
GARP4	2	4	7	12	4	—	—	—	—
GARP5	3	2	6	15	3	150	2	—	—
LOG50	2	16	8	49	3	—	—	—	—
LOG80	2	7	6	11	5	—	—	—	—
LOG95	4	4	6	1	2	85	2	91	1
Simple	2	2	8	4	3	—	—	—	—

**Model refers to the species-distribution model used to derive predictions about each individual species distribution. Also shown are number of fully flexible sites (sites) and number of goal-essential species (species) captured for each reserve set.*

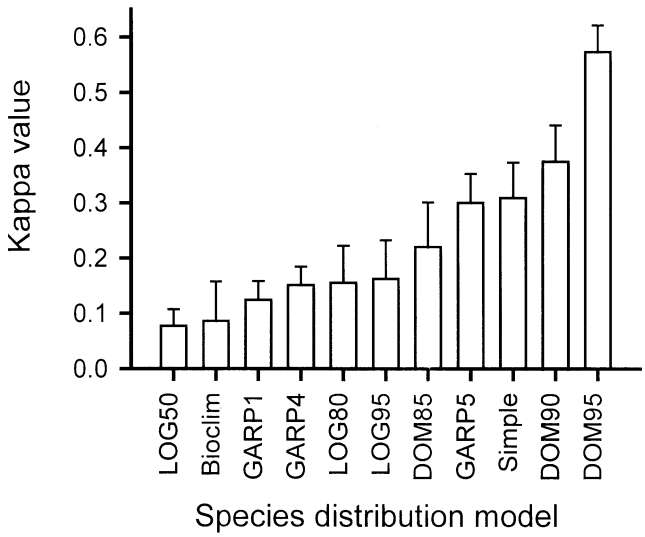

Figure 4. Kappa values for the 11 species-distribution models. Kappa values could not be calculated for extent-of-occurrence maps. Intuitively, extent-of-occurrence maps have maximum false-positive errors and minimum false-negative errors when compared with species-distribution models. Kappa values typically range from 0 to 1, where values approaching 1 have fewer overall errors.

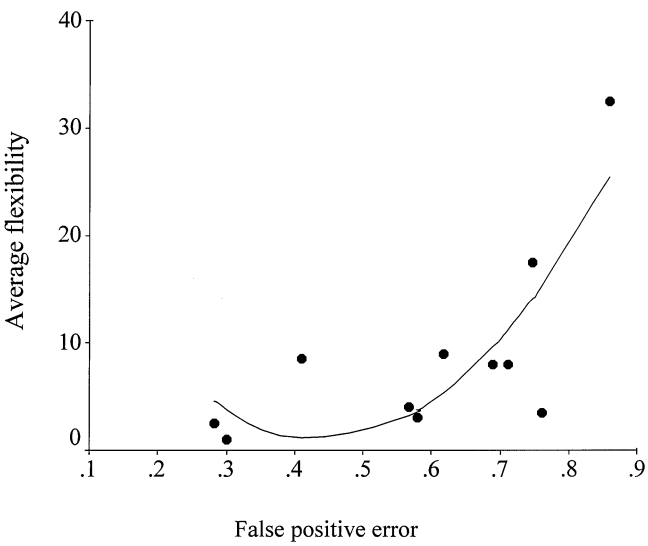

Figure 5. Relationship between mean false-positive errors and average flexibility for the first two reserve sets selected by the reserve algorithm. Mean false-positive errors were calculated by averaging false-positive error scores across species for each species-distribution model. The number of fully flexible sites for each reserve set is given in Table 2. A quadratic equation provided the best fit for the regression model ($y = -24.12x + 140.61x^2 + 28.36$).

they are applied uncritically. The appearance of quantitative tools and spatial models in the conservationists' tool box is a significant step forward, yet major challenges remain in ensuring that these tools are applied wisely in a management context (Smith & Catanzaro 1996; Prendergast et al. 1999; Myers et al. 2000; Williams & Araújo 2000). It is essential for planners to evaluate the conservation implications of false-positive and false-negative errors for their specific management scenario before beginning the modeling process. Well-intentioned but overgenerous models (with high commission or false-positive errors), when combined with optimizing selection techniques, could misdirect conservation action and policy (Smith & Catanzaro 1996). Conservation decisions are ultimately based on a combination of biological and nonbiological factors, and many decisions may be highly constrained by present-day realities. The consequences of decisions made today are not likely to be felt until decades in the future (Pimm & Raven 2000).

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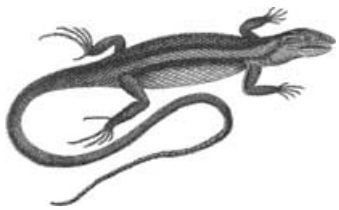
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