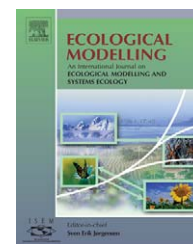


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Tracking population extirpations via melding ecological niche modeling with land-cover information

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ARTICLE INFO

Article history:

Received 24 December 2004

Received in revised form 12 August 2005

Accepted 15 November 2005

Published on line 10 January 2006

Keywords:

Endemic species

Extinction

Land use change

Jays

Geographic distribution

ABSTRACT

We explored a new approach to tracking population losses in poorly known species across broad spatial scales, based on integration of tools from ecological niche modeling with data resources derived from remotely sensed land-cover information. Ecological niches were modeled based on known occurrences of species (natural history museum specimen data) and environmental dimensions including topography, climate and original vegetation; these niche models were then projected onto land use/land-cover maps (with classes equivalent to those in the original vegetation dataset) based on air photography and Landsat imagery from 1976, 1993 and 2000, to track loss of potential distributional area over two decades. As an illustration, we analyzed 11 endemic Corvidae (jays) in Mexico; the method is applicable to any species for which distributional information exists and any region for which multi-temporal land-cover information has been developed. We envisage this approach evolving into a “population loss meter”, permitting monitoring of losses of species-specific combinations of environmental and landscape features.

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1. Introduction

The ‘biodiversity crisis’ recognized in the past 2–3 decades has as its central concept the idea that increasing human pressure on landscapes and natural habitats is resulting in population extirpation and even species extinction at unprecedented rates (Diamond, 1987; Wilson, 1988; Manne et al., 1999). In spite of intense research in this area, and a great number of investigators focusing on questions of biodiversity conservation, however, surprisingly little advance has been made in characterizing where population loss is occurring and how much has been lost (Herkert, 1996; Sánchez-Cordero et al., 2005).

The problem is clearly one of spatial scale—when an investigator examines a species in sufficient detail to be able to detect population declines, he or she usually loses the range-wide perspective. Quite simply, one rarely can maximize both detail and scope simultaneously. Just as clearly, studying single populations or circumscribed regions is much more feasible in general than broad-scale views of species’ population status (Ricklefs and Schluter, 1993).

This paper represents an exploration of a means of deriving a range-wide view of population loss in species. The approach is founded on the ideas of ecological niche modeling—that ecological niches can be inferred from simple occurrence

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0304-3800/\$ – see front matter © 2005 Published by Elsevier B.V.
doi:10.1016/j.ecolmodel.2005.11.020

information combined with environmental data that characterize an ‘ecological landscape’ available to the species, and that these niche models have significant predictive power regarding the geographic and ecological potential of the species. The approach consists of modeling ecological niches, and projecting the rule-sets describing the niches onto land-cover information from distinct time periods to detect likely population losses or gains between time periods.

2. Methods

2.1. Input data

The method explored herein requires three distinct data streams: primary species occurrence information (records placing a particular species in a particular location), ecological and environmental data characterizing landscape features and land-cover data sets for multiple time periods. Because of the particular land-cover data sets employed herein, we limit application to species that use primary (not disturbed) habitats principally. The conjunction of these three sets of information permits the novel ‘population extirpation tracking’ capabilities explored in this paper, which can be applied generally to any taxon and region for which such information is available.

Species occurrence information was drawn from the *Atlas of Mexican Bird Distributions* database, a compendium of bird specimens from Mexico, drawn from data associated with specimens from 57 natural history museum collections worldwide (see Acknowledgments). Although not available for public consultation because of data use agreements with institutions, the dataset is nevertheless a comprehensive (about 450,000 records from 39,000 localities) view of bird distributions in the country (Peterson et al., 1998; Navarro-Sigüenza et al., 2002, 2003). Point occurrence data were georeferenced to the nearest 0.1' of latitude and longitude based on diverse map series for Mexico. All species' names were modernized to a taxonomic revision of the Mexican avifauna by two of the authors (Navarro-Sigüenza and Peterson, 2004). For the purposes of illustration, we analyze herein the species of the family with the greatest number of endemic species in Mexico—the 13 endemic species of Corvidae; as the method is most applicable to species of primary habitats, we omitted from consideration the two endemic crows of northern Mexico (*Corvus imparatus*, *C. sinaloae*), leaving 11 species for analysis.

Data sets (raster GIS layers) describing the ecological landscape of Mexico were drawn from a variety of sources. For topographic information, we used the Hydro-1K data set,¹ which includes elevation, slope, aspect and an index of tendency to pool water, all at a native resolution of 30 arc seconds (about 1 km). For climatic data, we used data sets describing minimum, mean and maximum annual temperatures; annual mean precipitation and soil humidity, all available from the Comisión Nacional para el Uso y Conocimiento de la Biodiversidad (CONABIO²) data facility (vector coverages, 1:1,000,000).

All GIS data sets were resampled to a 0.02° grid for analysis using a nearest-neighbor approach.

Data sets summarizing land-cover across Mexico were assembled (Fig. 1), also in the form of raster GIS grids. For a picture of land-cover that coincides temporally with the specimen data used to generate the niche models, we used an ‘original vegetation’ map originally developed in hard-copy form (Rzedowski, 1978), and now served publicly in electronic format (also on the CONABIO site). This data layer attempts to reconstruct pre-human vegetation type distributions (a very difficult challenge), but quite adequately reflects the vegetation types that would be available to species using primary habitats in the nineteenth and twentieth centuries; this allowed us to key known occurrences of species using primary habitats from the past two centuries to particular land-cover classes. To summarize land-cover shifts over recent decades (Fig. 1), we used the land-cover classifications, which were developed based on aerial photography from 1973 to 1979, and based on Landsat imagery for 1993 and 2000 (Velázquez et al., 2002). These land-cover data sets were then generalized to make them parallel and compatible with the original vegetation map: categories were combined to make the categories in the modern land-cover maps match those in the original vegetation map (Table 1).

2.2. Modeling ecological niches and reconstructing population losses

Species' ecological requirements can be conceptualized via the idea of an ecological niche—among the various definitions of this idea that exist (MacArthur, 1972), the most appropriate to a coarse-scale approach such as this one is that of Grinnell (1917, 1924)—the set of conditions under which a species can maintain populations without immigrational input (Hutchinson, 1957). A series of efforts over the past decade has focused on developing computational approaches to approximating this ecological niche, based on known occurrences of species (Austin et al., 1990)—this work has demonstrated that ecological niches of species as modeled in this framework (1) are highly predictive of distributional phenomena (Peterson, 2001; Peterson et al., 2002a,b), (2) permit visualization of distributions in ecological and geographic dimensions (Austin et al., 1990; Costa et al., 2002; Martínez-Meyer et al., 2004), (3) are highly conserved over ecological and evolutionary time periods (Peterson et al., 1999) and (4) provide a long-term constraint on the geographic potential of species (Peterson, 2003).

Ecological niches were modeled using the Genetic Algorithm for Rule-set Prediction (GARP) (Stockwell and Noble, 1992), now available for public download.³ This algorithm has seen extensive testing for predictions of species' geographic distributions (Peterson and Cohoon, 1999; Egbert et al., 2002; Stockwell and Peterson, 2002a,b; Anderson et al., 2003; Peterson and Shaw, 2003; Stockwell and Peterson, 2003; Peterson et al., 2004). In GARP, occurrence points are divided evenly into training and testing data sets. GARP works in

¹ <http://edcdaac.usgs.gov/gtopo30/hydro/index.asp>.

² <http://www.conabio.gob.mx/>.

³ <http://www.lifemapper.org/desktopgarp>.

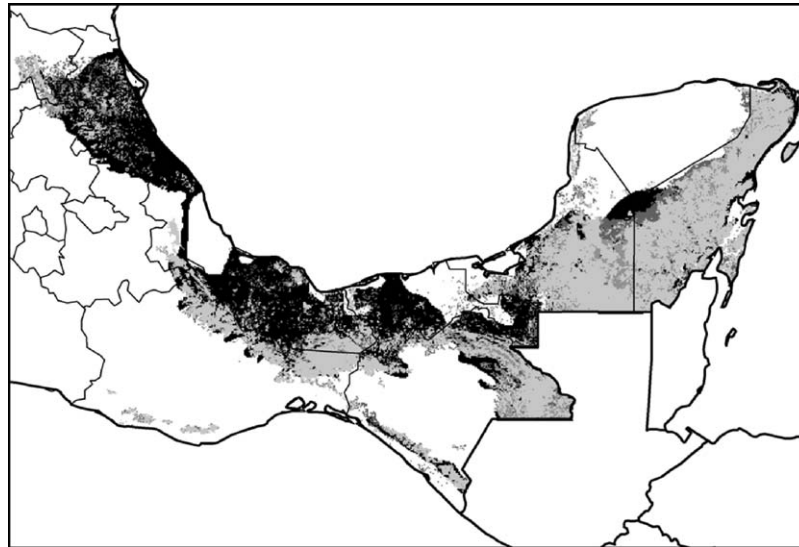


Fig. 1 – Example comparison of extent of evergreen rain forest or near-evergreen rain forest according to the land use/land-cover maps used in this study. Black, ‘original’ extent (Rzedowski, 1978); dark gray, 1976 extent; medium gray, 1993 extent and light gray, 2000 extent. With the more recent maps on top in this visualization, areas in light gray represent remaining areas of evergreen rain forest as of 2000, whereas areas in black represent rain forest areas that have been converted to other land-cover types.

an iterative process of rule selection, evaluation, testing and incorporation or rejection: a method is chosen from a set of possibilities (e.g., logistic regression, bioclimatic rules) and applied to the training data to develop or evolve a rule. Predictive accuracy is evaluated based on the testing data. Rules may evolve in ways that mimic DNA evolution (e.g., point mutations, deletions). Change in predictive accuracy between iterations is used to evaluate whether particular rules should be incorporated into the model; the algorithm runs 1000 iterations or until convergence.

To optimize model performance, we developed 100 replicate models of ecological niches for each species. We chose a ‘best subset’ of these models based on optimal error distributions for individual replicate models (Anderson et al., 2003): we chose the 20 models with least omission error, and then retained the 10 of these models with predicted

area closest to the median area predicted among the 20 low-omission models. The geographic predictions of these 10 models were summed to provide a summary of potential geographic distributions. Model predictivity was assessed and validated via the coincidence of random 50% subsets of available information withheld from model building and the geographic predictions—this coincidence was evaluated using a χ^2 statistic that summarizes the predictive performance of the model above and beyond that expected at random (Peterson, 2001). Finally, given that niche model results represent potential distributional areas, and can include disjunct areas not actually inhabited for historical reasons, it was necessary to remove such disjunct areas of overprediction; we assumed that species’ distributions were well-sampled at the level of biogeographic regions (CONABIO website), and used known occurrences to select polygons in the ecoregions data layer,

Table 1 – Vegetation types of Mexico used in our analyses, following Rzedowski (1978) ‘original vegetation’ classification

Rzedowski	Land use maps 1970–1990
Dry scrub	Dry scrub
Coniferous or oak forest	Coniferous forest, mixed coniferous and broadleaved forest, broadleaved forest
Grassland	Natural grassland
Thorn scrub	Mesquite scrub
Bodies of water	Bodies of water
Deciduous tropical scrub or semideciduous tropical forest	Deciduous/semideciduous tropical scrub/forest
Cloud forest	Cloud forest
Aquatic vegetation	Hydrophilous vegetation
Evergreen rain forest	Evergreen and near-evergreen forest
Other	Other vegetation types, areas without vegetation, introduced and cultivated grassland, seasonal agriculture, irrigated agriculture, forestry plantation, human settlement

The land use maps result from satellite imagery taken in 1976, 1993 and 2000, and were reclassified to match Rzedowski’s scheme as indicated.

and used those polygons to mask biogeographic regions not known to hold populations of the particular species.

Models were developed based on the original vegetation coverage, and rule sets resulting from modeling were then used to identify appropriate potential distributional areas on the 1970, 1980 and 1990 maps. In this way, it was possible to capture the essence of species-specific associations with multidimensional ecological suites of conditions—a species may use a particular land-cover type under particular climatic conditions or in particular topographic circumstances, and not under others. This flexible, species-specific approach thus allows a view of the effects of land-cover change from the perspective of maintenance of populations of particular species, much better than could be achieved than simply by tracking loss of primary habitats independent of species' particular ecological needs.

3. Results

The geographic distributions of the 11 bird species examined in this study were all predicted with an accuracy well above that expected at random (χ^2 tests, all $P < 0.05$). This test is based on occurrence information independent of that used to build models, so the models and maps that serve as the basis for this study appear to have significant predictive ability regarding the distributions of each species involved.

Projections of models onto the three actual land use data layers indicated losses of distributional area in each species. Fig. 2 permits a before-and-after visualization of land use change effects on distributions of each of the 11 species in the study. Summarizing this result as percentages of original range remaining habitable (Fig. 2), modeled effects on species' distributions range from essentially nil (*Cyanocorax sanblasianus*) to drastic (35% loss by 1990 in *C. beecheii*; Fig. 3). Three species showed essentially minimal changes in distributional area, whereas the remainder showed loss of potential distributional area through time.

Summing range retractions across species provides a view of the spatial distribution of corvid range loss and population extirpation in Mexico (Fig. 4). A clear focus of population loss is on the southern slopes of the Transvolcanic Belt, and another along the Pacific Coast in Sinaloa and Nayarit.

4. Discussion

In this study, we have explored a novel integration of diverse data streams describing occurrences of species, climate, topography and land-cover and its change over time. Assembling these three data suites permits a view into patterns of probable population loss across a species' geographic distribution. Although preliminary and exploratory, this application provides a new view of complex biodiversity phenomena.

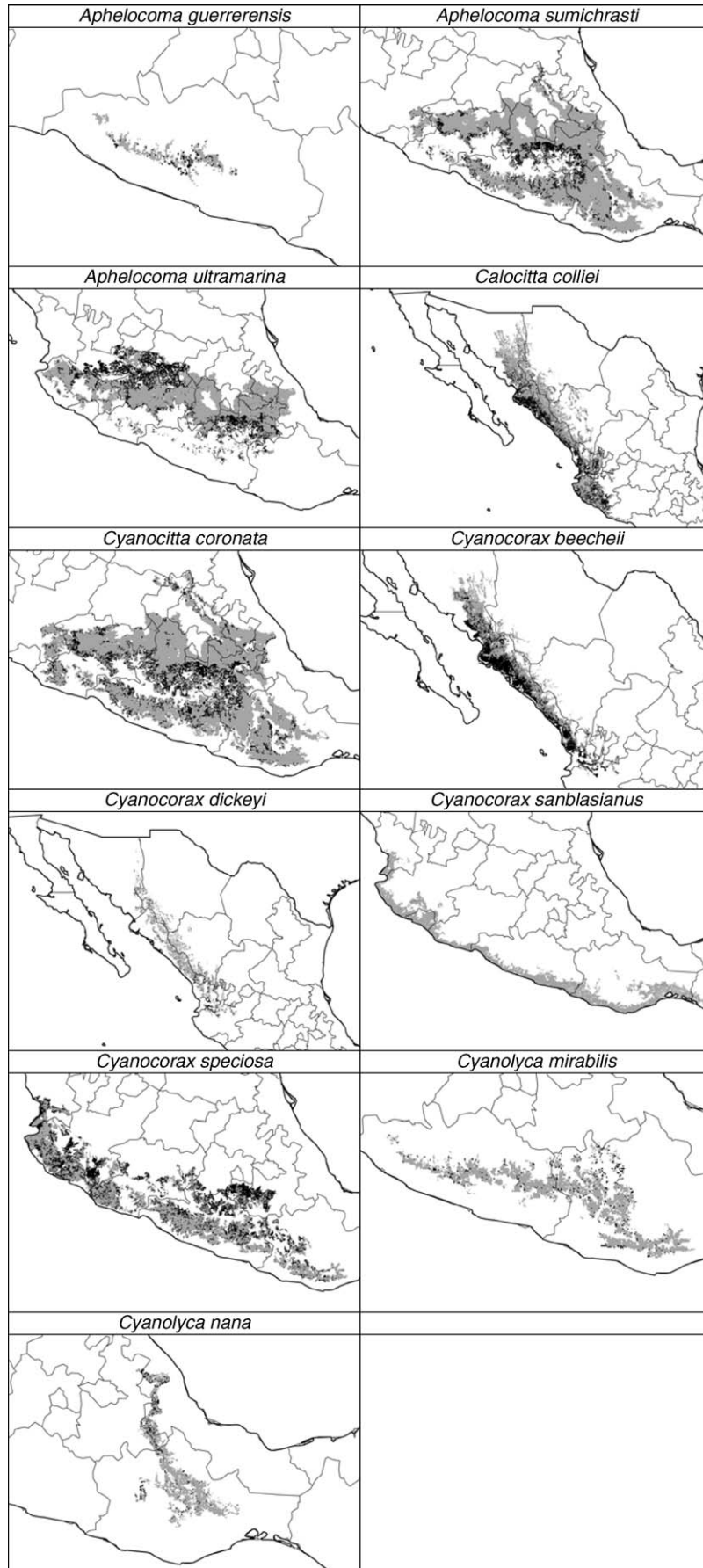
The biological reality of the predictions and projections presented herein nevertheless depend on a number of points—assumptions that together may limit the basis for our inferences—as follows. (1) Ecological niches are assumed to be modeled in the appropriate suite of dimensions, and are assumed not to be limited significantly in other suites of dimensions (which would make the actual distributional areas smaller than those reconstructed herein). (2) The resolution of the land-cover data sets employed (1 km × 1 km resolution) is assumed to be sufficiently fine as to represent real population presence or absence (i.e., that population units sufficiently smaller than 1 km² in extent are neglected in these projections). (3) We assume that the land-cover classifications employed herein are developed in a consistent, parallel manner that permits extrapolation and comparison between time periods. The above are the assumptions for which we have no good evidence one way or another, and so are presented as assumptions subject to modification.

The methodology outlined and demonstrated herein offers some clear advantages over previous approaches (Patterson, 1987; McDonald and Brown, 1992; Lomolino and Channell, 1995; Brooks et al., 1997; Bergman et al., 2004), although many methodological alternatives exist and should be explored for actually creating the ecological niche models. The basic challenge is one of converting the potential distributional areas generated by the ecological niche modeling algorithm into actual distributions based on fine-grained land use/land-cover information (Sánchez-Cordero et al., 2005). Previous workers (Scott et al., 1993, 1996; Krohn et al., 1998; Cully et al., 2003) have generally assumed a one-to-one correspondence between presence of a species and particular land-cover types, an assumption that will prove quite limiting (Peterson et al., 2002b; Peterson and Kluza, 2003; Peterson, 2005), whereas the truth is likely rather that considerable regional variation exists in the degree to which a particular species is able to use different land-cover types. Our methodology removes the need for this assumption of direct correspondence—the regional variation in land-cover type use that characterizes the 'original' (pre-disturbance) distribution of the species also characterizes the post-disturbance projections.

The result of this exploration is a first picture of region-wide population loss and extirpation. The picture is one of focused loss along much of the coastal slopes of Sinaloa and Nayarit, as well as in a narrow band across Morelos and southern Puebla, touching into northwestern Oaxaca. These regions effectively are the areas characterized by high diversity of endemic corvids and intensive human pressure on landscapes. Previous studies of Mexican biodiversity loss and conservation have generally been regional in scope from the outset, and have generally focused on the tropical southeastern lowlands (Dirzo and García, 1992; Bojorquez-Tapia et al., 1995).

Our result, of course, is based only on 11 species of corvids, and so is not readily generalizable to the broader biota. Nevertheless, the picture created is one of where two phenomena collide—rich biodiversity and human modification of natural

Fig. 2 – Summary of geographic patterns of population loss reconstructed for 11 corvid species endemic to Mexico in this study. Black, 'original' range extent (Rzedowski, 1978); gray, projected 2000 range extent. With gray on top of black in this visualization, areas in gray are likely range areas retained, whereas black areas are range areas lost.



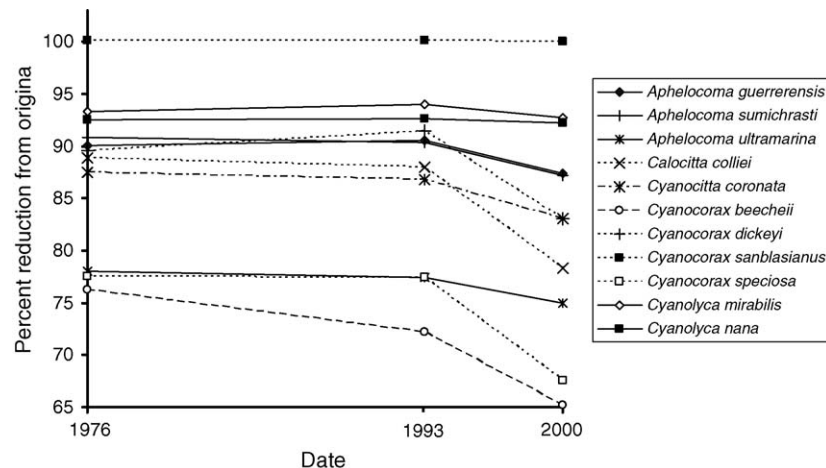


Fig. 3 – Summary of projected percent loss of distributional area for each of the 11 endemic species treated in this study.

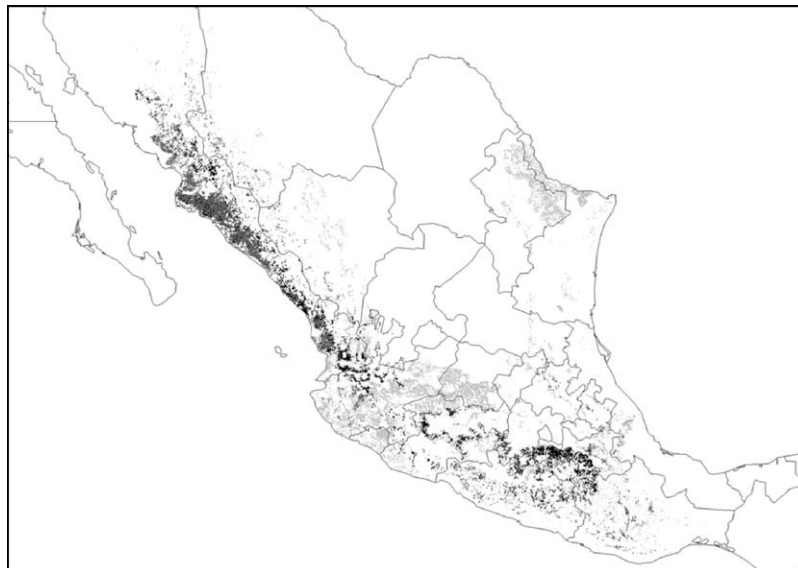


Fig. 4 – Geographic foci of population losses across 11 endemic species of Mexican corvids, as reconstructed in this study. Light gray, 1 species lost; medium gray, 2 species lost; black, 3–4 species lost.

habitats. This result has much to offer to studies of biodiversity conservation worldwide, and the methodology is applicable in any region for which such multitemporal land-cover data sets exist or can be developed. Linking land-cover monitoring via remote sensing with biodiversity status monitoring on the ground may provide fertile future advances for biodiversity conservation.

Acknowledgements

We thank the staff of the numerous natural history museums around the world that provided information and access critical to this study: Moore Laboratory of Zoology, Occidental College; Museum of Comparative Zoology, Harvard University; Instituto de Biología, Universidad Nacional Autónoma de México (UNAM); British Museum (Natural History); Louisiana State University Museum of Natural Science; Delaware Museum of Natural History; American Museum of Natural History;

University of Michigan Museum of Zoology; Western Foundation of Vertebrate Zoology; Field Museum of Natural History; Bell Museum of Natural History, University of Minnesota; Museo de Zoología, Facultad de Ciencias, UNAM; Museum of Vertebrate Zoology, University of California; University of Kansas Museum of Natural History; United States National Museum of Natural History; Universidad Michoacana San Nicolás de Hidalgo; Carnegie Museum of Natural History; California Academy of Sciences; San Diego Natural History Museum; University of California, Los Angeles; Cornell University Laboratory of Ornithology; Canadian Museum of Nature; Peabody Museum, Yale University; Muséum Nationale d'Histoire Naturelle, Paris; Los Angeles County Museum of Natural History; Florida Museum of Natural History; Royal Ontario Museum; Academy of Natural Sciences, Philadelphia; University of British Columbia Museum of Zoology; University of Arizona; Texas Cooperative Wildlife Collections; Forschungsinstitut Senckenberg, Frankfurt; Museum für Naturkunde, Berlin; Museo de la Biodiversidad Maya,

Campeche; Übersee-Museum, Bremen; Denver Museum of Natural History; Museo Regionale di Scienze Naturali, Torino; Burke Museum, University of Washington, Seattle; Staatliches Museum für Naturkunde, Stuttgart; Museo Nacional de Ciencias Naturales, Madrid; Natuurhistorische Museum, Leiden; Muséum Nationale d'Histoire Naturelle, Genève; Museum Koenig, Bonn; Museo della Specola, Università di Firenze; Museum Mensch und Natur, Munich; Museo di Storia Naturale, Genova; Russian Academy of Sciences, St. Petersburg; University Museum of Zoology, Cambridge; Fort Hays State College, Kansas; Manchester Museum, Manchester; Nebraska State Museum; Museo Civico di Storia Naturale, Milano; Iowa State University, Ames; Moscow State University Museum; Darwin Museum, Moscow; and Museo Federico Craveri, Bra. Special thanks to Alejandro Gordillo for georeferencing data. We also thank our valued colleagues David Stockwell, David Vieglais, and Ricardo Pereira, for their many contributions of novel technology and analytical capability. This work was supported by grants from the U.S. National Science Foundation and Mexico's Consejo Nacional para la Ciencia y Tecnología.

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