

Ecological Niche Modeling as a New Paradigm for Large-Scale Investigations of Diversity and Distribution of Birds¹

A. Townsend Peterson^{2,3} and Daniel A. Kluza²

Introduction

Large-scale assessments of the distribution and diversity of birds have been challenged by the need for a robust methodology for summarizing or predicting species' geographic distributions (e.g. Beard et al. 1999, Manel et al. 1999, Saveraid et al. 2001). Methodologies used in such studies have at times been inappropriate, or even more frequently limited in their analytical scope and predictive properties (Peterson et al. 2002c). A new set of methodologies focus on modeling the dimensions of species' ecological niches, and offer considerably improved analytical and predictive possibilities. The purpose of this brief contribution is to summarize these new methodologies, and to discuss several possible applications of this new approach.

Ecological Niche Modeling

Grinnell was first to propose an ecological niche concept (Grinnell 1917)—the range of ecological conditions within which a species can maintain populations. Later investigators focused niche concepts increasingly on the role of a species in an ecological community, and the two foci were eventually integrated and made more quantitative by MacArthur (1972). In the Grinnellian and MacArthurian views, the ecological niche is the quantity that governs the limits of geographic distributions of species.

To maximize applicability of these new techniques, we focus on techniques that relate point occurrence data to geographic information about the ecological and environmental characteristics of a landscape to produce a hypothesis of the dimensions of the species' niche. This ecological niche model can then be projected onto a landscape to identify geographic regions that have conditions inside and outside of the species' niche, producing a hypothesis of a potential geographic distribution for the species. It is important to distinguish this sort of approach (two steps: model the niche in ecolo-

gical space, and project onto a landscape in geographic space) from other, simpler approaches that do not distinguish between ecological and geographic spaces (Peterson et al. 2002c): see e.g., Scott et al. (1996).

A particularly promising tool for ecological niche modeling is the Genetic Algorithm for Rule-set Prediction (GARP), a software application⁴ that includes several inferential tools in an iterative, artificial-intelligence-based approach (Stockwell and Noble 1992, Stockwell 1999, Stockwell and Peters 1999). Occurrence points are divided evenly into training and test data sets. GARP works in an iterative process of rule selection, evaluation, testing, and incorporation or rejection: first, an inferential tool is chosen from a set of possibilities (e.g., logistic regression, bioclimatic rules), and then is applied to the training data and a rule developed; a rule is an IF...THEN statement that describes the conditions under which a species may be present (or absent). Rules are evolved by a number of means (e.g., truncation, point changes, crossing-over among rules) to maximize predictivity. Predictive accuracy is evaluated based on the test data and an equivalent number of points sampled randomly from the study region as a whole. The change in predictive accuracy from one iteration to the next is used to evaluate whether a particular rule should be incorporated into the model, and the algorithm runs either 1000 iterations or until convergence.

GARP models provide an efficient means of modeling species' ecological niches, and for projecting those models onto geography in the form of maps, which are testable hypotheses of distributional potential. The present implementation—for a stand-alone PC workstation—is able to process approximately 1000 models per 24 hr, and allows a rich environment for hypothesis-testing. The methodology has now seen numerous tests of predictive ability, including simple distributional prediction, prediction of community composition, and prediction of species invasions (Peterson et al. 1999; Peterson 2001; Peterson and Vieglais 2001; Anderson et al. 2002a, 2002b; Fera and Peterson 2002; Peterson et al. 2002a, 2002c). The particulars of the method and its sensitivities have been tested and assessed with care (Peterson and Cohoon 1999; Stockwell and Peterson 2002a, 2002b; Anderson et al. 2003).

¹A version of this paper was presented at the **Third International Partners in Flight Conference, March 20-24, 2002, Asilomar Conference Grounds, California.**

²Natural History Museum and Biodiversity Research Center, The University of Kansas, Lawrence, Kansas 66045 USA.

³Corresponding author. E-mail: town@ku.edu

⁴Available for download at <http://beta.lifemapper.org/desktopgarp/>.

New Analytical Functionalities

Predicting and Summarizing Distributions

The principal focus of ecological niche modeling (e.g., GARP) is on predicting species' geographic distributions. GARP offers a highly predictive methodology to this end: limited numbers of known occurrence points (Stockwell and Peterson 2002) can be combined with limited numbers of ecological-environmental coverages (Peterson and Cohoon 1999) to produce models that are highly predictive of species' broader geographic distributions (Peterson et al. 1999; Peterson 2001; Feria and Peterson 2002; Peterson et al. 2002a, 2002c; Anderson et al. 2003).

One typical distribution-related challenge to which GARP models can speak powerfully is the vertebrate distributional models that are the core of Gap Analysis (Scott et al. 1996). The U.S. National Gap Analysis program and its proponents pioneered many of the early applications of distributional modeling and prediction, but too often stayed with earlier habitat-modeling techniques that offer considerably less predictive power. The essential difference between these older techniques and those being developed and explored presently is that the older approaches do not develop a quantitative model of an ecological niche. Too often, the distributional models used in Gap Analysis are static summaries of known distributions that cannot predict new knowledge. A head-to-head test of common Gap methodologies against ecological niche modeling techniques demonstrated considerably better predictive power in the latter approaches (Peterson and Kluza 2003).

Conservation Assessments

With the ability to predict species' distributions with statistical confidence, broader assessments of distributional patterns across entire biotas become feasible. For example, one study assessed the distributional patterns of endangered species in the United States (Godown and Peterson 2000), another examined threatened and endangered species in China (Chen and Peterson 2000, 2002), and another the distributions of endemic species in eastern Mexico (Egbert et al. 1998, Peterson et al. 2000).

The general approach in these studies is that of (1) identifying a universe of species to be examined, (2) modeling and predicting their distributions, and (3) prioritizing areas for conservation based on patterns of richness and complementarity among areas. In each case yet examined, the ecological niche modeling approach has been able to identify key additions to protected areas systems via addition of critical suites of species to the reserve system.

Invasions and Reintroductions

An early observation indicated that species' ecological niches are constraints on potential geographic distributions of species (Peterson et al. 2002c), and are often quite conservative over evolutionary time periods (Peterson et al. 1999). If such is the case, then niches can be good predictors of species' potential geographic distributions, even in completely different geographic scenarios. Application of this idea to the challenge of predicting the geographic dimensions of species' invasions revealed rich predictivity (Peterson and Vieglais 2001), now confirmed in a series of subsequent studies (Peterson et al. submitted).

Although invasive species may seem a topic relatively removed from conservation concerns for birds, such is not the case. For example, the Barred Owl (*Strix varia*), an invasive species in the Pacific Northwest, may pose a significant threat to the survival of its endangered congener, the Spotted Owl (*S. occidentalis*; Dark et al. 1998). Also, invasion of certain plant species can literally threaten entire ecosystems via conversion of landscapes into areas not as hospitable for bird species (Blossey et al. 2001).

Invasive potential and its prediction can also be turned to the positive. One frequent concern is that of where to attempt reintroduction programs for endangered species. Although for some species and regions the answer is straightforward (e.g., wherever there is forest!), in other cases it is not at all clear. A preliminary exploration of this functionality focused on the Mexican Wolf (*Canis lupus*; E. Martínez-Meyer et al. in prep.), and managed to identify areas both hospitable and not, the latter including the prime site that had previously been identified for reintroduction efforts.

Change Scenarios

Finally, ecological niche modeling has the special advantage of permitting prediction of distributional potential across scenarios of environmental change. Particularly relevant at present is the challenge of understanding the effects that ongoing human-caused global climate change will have on biodiversity. Application of ecological niche modeling techniques to this challenge produced a preliminary analysis (Peterson et al. 2001), and a broad survey over 1800+ species (Peterson et al. 2002b).

Completely unexplored, however, are the interactions between these climate change effects on biodiversity and conservation practice. Future applications must begin to evaluate which sorts of protected areas will be particularly vulnerable or particularly robust to climate change effects. Further development of scenarios of vegetation change and human land use change in

concert with climate change will also greatly enrich and educate these early-generation models.

Conclusions

The broadest result of this symposium should be the realization that new geographic tools have the potential to enable research in bird conservation biology greatly. GIS, in the first place, offers a first view of broad geographic patterns of geographic distribution. Ecological niche modeling then provides layers of interpolated distributional ecology (beyond just known occurrence points to likely occurrence across the landscape), as well as new capabilities of predictions across novel or changing conditions. Exploration of these tools and their potential applications is in its infancy, but already rich rewards are becoming apparent.

Acknowledgments

Thanks to T. Will for the invitation to participate in this symposium, and to B. Loiselle and C. Moore for their comments on the manuscript.

Literature Cited

- Anderson, R. P., M. Laverde, and A. T. Peterson. 2002a. **Geographical distributions of spiny pocket mice in South America: Insights from predictive models.** *Global Ecology and Biogeography* 11: 131-141.
- Anderson, R. P., M. Laverde, and A. T. Peterson. 2002b. **Using niche-based GIS modeling to test geographic predictions of competitive exclusion and competitive release in South American pocket mice.** *Oikos* 93: 3-16.
- Anderson, R. P., D. Lew, and A. T. Peterson. 2003. **Evaluating predictive models of species' distributions: Criteria for selecting optimal models.** *Ecological Modelling* 162: 211-232.
- Beard, K. H., N. Hengartner, and D. K. Skelly. 1999. **Effectiveness of predicting breeding bird distributions using probabilistic models.** *Conservation Biology* 13: 1108-1116.
- Blossey, B., L.C. Skinner, and J. Taylor. 2001. **Impact and management of purple loosestrife (*Lythrum salicaria*) in North America.** *Biodiversity and Conservation* 10: 1787-1807.
- Chen, G. and A. T. Peterson. 2000. **A new technique for predicting distributions of terrestrial vertebrates using inferential modeling.** *Zoological Research* 21:231-237.
- Chen, G., and A. T. Peterson. 2002. **Prioritization of areas in China for biodiversity conservation based on the distribution of endangered bird species.** *Bird Conservation International* 12: 197-209.
- Dark, S. J., R. J. Gutierrez, and G. I. Gould, Jr. 1998. **The barred owl (*Strix varia*) invasion in California.** *Auk* 115: 50-56.
- Egbert, S. L., A. T. Peterson, V. Sanchez-Cordero, and K. P. Price. 1998. **Modeling conservation priorities in Veracruz, Mexico.** In: S. Morain, editor. *GIS in natural resource management: Balancing the technical-political equation.* Santa Fe, NM: High Mountain Press; 141-150.
- Feria, T. P., and A. T. Peterson. 2002. **Prediction of bird community composition based on point-occurrence data and inferential algorithms: a valuable tool in biodiversity assessment.** *Diversity and Distributions* 8: 49-56.
- Godown, M. E., and A. T. Peterson. 2000. **Preliminary distributional analysis of U.S. endangered bird species.** *Biodiversity and Conservation* 9: 1313-1322.
- Grinnell, J. 1917. **Field tests of theories concerning distributional control.** *American Naturalist* 51: 115-128.
- MacArthur, R. 1972. **Geographical Ecology.** Princeton, NJ: Princeton University Press.
- Manel, S., J. M. Dias, and S. J. Ormerod. 1999. **Comparing discriminant analysis, neural networks and logistic regression for predicting species distributions: a case study with a Himalayan river bird.** *Ecological Modeling* 120: 337-347.
- Peterson, A. T. 2001. **Predicting species' geographic distributions based on ecological niche modeling.** *Condor* 103: 599-605.
- Peterson, A. T., L. G. Ball, and K. C. Cohoon. 2002a. **Predicting distributions of tropical birds.** *Ibis* 144: e27-e32.
- Peterson, A. T., and K. C. Cohoon. 1999. **Sensitivity of distributional prediction algorithms to geographic data completeness.** *Ecological Modeling* 117: 159-164.
- Peterson, A. T., S. L. Egbert, V. Sanchez-Cordero, and K. P. Price. 2000. **Geographic analysis of conservation priorities using distributional modeling and complementarity: Endemic birds and mammals in Veracruz, Mexico.** *Biological Conservation* 93: 85-94.
- Peterson, A. T., and D. A. Kluza. 2003. **New distributional modeling approaches for gap analysis.** *Animal Conservation* 6: 47-54.
- Peterson, A. T., M. A. Ortega-Huerta, J. Bartley, V. Sanchez-Cordero, J. Soberon, R. H. Buddemeier, and D. R. B. Stockwell. 2002b. **Future projections for Mexican faunas under global climate change scenarios.** *Nature* 416: 626-629.
- Peterson, A. T., V. Sanchez-Cordero, J. Soberon, J. Bartley, R. H. Buddemeier, and A. G. Navarro-Siguenza. 2001. **Effects of global climate change on geographic distributions of Mexican Cracidae.** *Ecological Modelling* 144: 21-30.
- Peterson, A. T., R. Scachetti-Pereira, and W. W. Hargrove. Submitted. **Potential distribution of Asian longhorned beetles (*Anoplophora glabripennis*) in North America.** *Journal of Economic Entomology*.

Ecological Niche Modeling – Peterson and Kluza

- Peterson, A. T., J. Soberon, and V. Sanchez-Cordero. 1999. **Conservatism of ecological niches in evolutionary time.** *Science* 285: 1265-1267.
- Peterson, A. T., D. R. B. Stockwell, and D. A. Kluza. 2002c. **Distributional prediction based on ecological niche modeling of primary occurrence data.** In: J. M. Scott, P. J. Heglund, M. Morrison, J. B. Haufler, M. G. Raphael, W. A. Wall and F. B. Samson, editors. *Predicting species occurrences: Issues of scale and accuracy.* Washington, DC: Island Press; 617-623.
- Peterson, A. T., and D. A. Vieglais. 2001. **Predicting species invasions using ecological niche modeling.** *BioScience* 51: 363-371.
- Saveraid, E. H., D. M. Debinski, K. Kindscher, and M. E. Jakubauskas. 2001. **A comparison of satellite data and landscape variables in predicting bird species occurrences in the Greater Yellowstone ecosystem, USA.** *Landscape Ecology* 16: 71-83.
- Scott, J. M., T. H. Tear, and F. W. Davis, editors. 1996. **Gap Analysis: A landscape approach to biodiversity planning.** Bethesda, Maryland: American Society for Photogrammetry and Remote Sensing; 320 p.
- Stockwell, D. R. B. 1999. **Genetic algorithms II.** In: A. H. Fielding, editor. *Machine learning methods for ecological applications.* Boston, MA: Kluwer Academic Publishers; 123-144.
- Stockwell, D. R. B., and I. R. Noble. 1992. **Induction of sets of rules from animal distribution data: A robust and informative method of analysis.** *Mathematics and Computers in Simulation* 33: 385-390.
- Stockwell, D. R. B., and D. P. Peters. 1999. **The GARP modeling system: Problems and solutions to automated spatial prediction.** *International Journal of Geographic Information Systems* 13: 143-158.
- Stockwell, D. R. B. and A. T. Peterson. 2002a. **Controlling bias in biodiversity data.** In: J. M. Scott, P. J. Heglund, M. Morrison, J. B. Haufler, M. G. Raphael, W. A. Wall and F. B. Samson, editors. *Predicting Species Occurrences: Issues of Scale and Accuracy.* Washington, DC: Island Press; 537-546.
- Stockwell, D. R. B., and A. T. Peterson. 2002b. **Effects of sample size on accuracy of species distribution models.** *Ecological Modelling* 148: 1-13.