

REPORT

Niche differentiation in Mexican birds: using point occurrences to detect ecological innovation

A. Townsend Peterson¹ and
Robert D. Holt^{2*}†

¹Natural History Museum, The
University of Kansas, Lawrence,
KS 66045, USA

²Department of Zoology,
University of Florida,
Gainesville, FL 32611, USA

*Correspondence: E-mail:
rdholt@zoo.ufl.edu

†Both authors contributed
equally to this paper.

Abstract

The development of quantitative models of species' distributions has largely ignored the potential for intraspecific variation in species' niche requirements. Application of such models may nevertheless provide a rich, untapped opportunity to address the basic issue of niche conservatism vs. evolution. We illustrate this potential using genetic algorithms coupled with geographical information systems, which provide a powerful and novel approach to characterizing species' ecological niches and geographical distributions. Our example consists of several species of Mexican birds with recognized subspecies, and associated climatic and vegetation data. Our basic protocol is to develop an ecological niche model for each subspecies, and use this model to predict distributions of other subspecies. In some cases, the ecological niche model inferred for one subspecies provides an excellent descriptor of other subspecies' ranges, whereas in other cases the prediction is rather poor. We suggest that the latter may reveal the potential existence of evolved, intraspecific niche differentiation. We discuss alternative, non-evolutionary explanations, and point out potential implications of our results for predictive models of species' invasions.

Keywords

Genetic algorithms, Mexican birds, niche evolution, predictive distributional models.

Ecology Letters (2003) 6: 774–782

INTRODUCTION

All species have limited spatial distributions. Understanding factors that shape species' ranges is a question central in both ecology (e.g. Lawton *et al.* 1994; Maurer & Taper 2002) and evolutionary biology (e.g. Graham *et al.* 1996). A species' range clearly should be influenced by its ecological niche – here defined as that set of environmental conditions, resources, and so on, that permit local populations to persist without immigration (i.e. a 'Grinnellian' vs. 'Eltonian' perspective on the niche; James *et al.* 1984; Schoener 1989). In recent years, great interest has been manifested in developing quantitative models of species' niches and species–environment relationships to characterize species' distributions (e.g. papers in Scott *et al.* 2002, and *Ecological Modelling* 157, issue 2–3, 2002), using a wide range of techniques such as generalized linear models, Gaussian models, generalized additive models, and genetic algorithms. An issue that has remained largely unexplored in this literature is the consequences of intraspecific evolution leading to shifts in ecological niches among populations. This issue has implications for the development and

refinement of distribution models in the first place (e.g. as in the need for spatial data partitioning in model development, Osborne & Suarez-Seoane 2002). We suggest that the potential for intraspecific niche evolution leading to geographical variation in species–environment relationships also provides a significant problem to which this wide range of techniques in distributional ecology could be fruitfully applied.

Understanding geographical variation has been a classic issue in evolutionary biology. Gould & Johnston (1972) stated that 'the foundation of most evolutionary theory rests upon inferences drawn from geographical variation'. Most studies of intraspecific geographical variation have examined spatial variation patterns in concrete attributes of organisms, such as morphological characters or gene frequencies (e.g. Endler 1977; Avise 2000). Our focus is on geographical variation in a more abstract character, namely the ecological niche. The fundamental niche of a species encapsulates the population-level implications of entire suites of organismal traits. Operationally, conditions at a particular point in space are within a species' niche if its numbers can potentially increase when it is rare relative to its carrying capacity

(Holt & Gaines 1992). Hence, an introduced species placed at a location with environmental conditions within its niche is expected to increase exponentially initially, unless prevented from doing so by interspecific interactions such as competition. If, by contrast, conditions at the site of introduction are outside the niche, the populations should decline towards extinction; indeed, many introductions fail owing to mismatches between local conditions and species' niche requirements.

In some situations intraspecific niche differentiation may be insignificant. Analyses of historical biogeography (e.g. Bradshaw 1991; Peterson *et al.* 1999) and predictive models of invasions (Peterson & Vieglais 2001) suggest that species' niches can be relatively conservative. Theoretical studies of evolution in heterogeneous environments (Holt & Gaines 1992; Kawecki 1995, 2000; Holt 1996, 2003; Holt & Gomulkiewicz 1997; Kirkpatrick & Barton 1997; Tufto 2001; Kawecki & Holt 2002; Proulx 2002) provide a framework for understanding how niche conservatism can reflect the interplay of dispersal, selection, and demographical asymmetries (e.g. spatial variation in abundance). For instance, along steep environmental gradients in carrying capacity, gene flow can readily swamp selection and lead to evolutionarily conserved species' ranges (Kirkpatrick & Barton 1997), particularly when competitors are present (Case & Taper 2000). Recent analyses using new tools from biodiversity informatics and quantitative geography have found that conservatism appears to be a dominant theme in birds, mammals, and butterflies in southern Mexico (Peterson *et al.* 1999) and elsewhere (Peterson & Vieglais 2001; Anderson *et al.* 2002; Iguchi *et al.* 2003; Papes & Peterson 2003).

Nevertheless, species' niches clearly do evolve, and range limits shift as a result of such evolution. If such were not the case, all species would have identical niches, which they do not! Hence, over some evolutionary time scale, niche evolution and ecological innovation have taken place. In some cases, niche evolution can be rapid and dramatic, as in adaptive radiations (Schluter 2000), and a growing number of examples demonstrate evolutionary shifts in range limits in rapidly changing environments (e.g. Davis & Shaw 2001; Thomas *et al.* 2001). Indeed, the theoretical framework noted above predicting niche conservatism in many circumstances also predicts niche evolution in others (Holt 1996; Holt & Gomulkiewicz 1997; Gomulkiewicz *et al.* 1999).

Here we examine patterns of niche variation within species using predictive models of ecological niches and geographical distributions. Our focus is on demonstrating that one can identify potential candidates for both niche conservatism and intraspecific evolution in ecological niche dimensions. We use as an example a particular class of distributional model (based on genetic algorithms) applied to several species of Mexican birds. Our purpose in

presenting this demonstration is not to compare in detail this type of model against other classes of distributional models, nor even to attempt full characterization of the niches of the species we examine, but rather to develop a demonstration that highlights the potential use of distributional and ecological niche modelling applied to the issue of niche evolution.

The above observations provide a rationale for applications of a flexible analytic tool recently developed for the study of species' distributions [Genetic Algorithm for Rule-set Prediction (GARP); Stockwell & Noble 1992; Stockwell & Peters 1999; Stockwell 1999]. The basic idea is that by comparing environmental states associated with a species' occurrences with environmental states where it is absent, species' ecological niche requirements (or environmental correlates of these requirements) can be ascertained. To a first approximation, organisms tend to occupy sites matching their niche, and are absent in sites with conditions outside the niche (for exceptions because of source-sink dynamics, see Pulliam 2000; these complicating effects are most likely to arise at the level of local landscapes, rather than over entire continental ranges). In effect, quantitative distributional data provide a kind of niche 'bioassay,' and distributional data aggregated from numerous sites can thus permit a quantitative assessment of presumptive niche requirements.

As described below in more detail, this approach begins with distributional records, overlays them on sets of environmental data, and uses machine-learning procedures to arrive at a rule set – a predictive model that characterizes the species' potential distribution in the variables of an environmental/ecological space. At local scales, species are expected to occupy sites within their realized niches (Hutchinson 1978), defined in part by the action of competitors and natural enemies. Given spatial variation in community composition, by examining distributions at broad geographical scales, we suggest that niche relationships that can be discerned are likely to be closer to the fundamental niche of the species.

If geographical variation exists in a species' ecological niche, it should be reflected in models (e.g. rule sets) that define its niche; such variation can arise to different degrees and at different spatial scales among populations. Consider the distribution of a hypothetical montane bird found in two disjunct regions (for simplicity, we refer to these two areas as distinct 'populations'). At one extreme (Fig. 1a), the two populations have not diverged, so that each population's niche is nearly coextensive with that of the entire species. Were empty habitat available within the region 1, propagules introduced from region 2 should potentially be able to establish. At the other extreme (Fig. 1c), the two populations have diverged ecologically to the point that their niches are non-overlapping, so reciprocal introductions

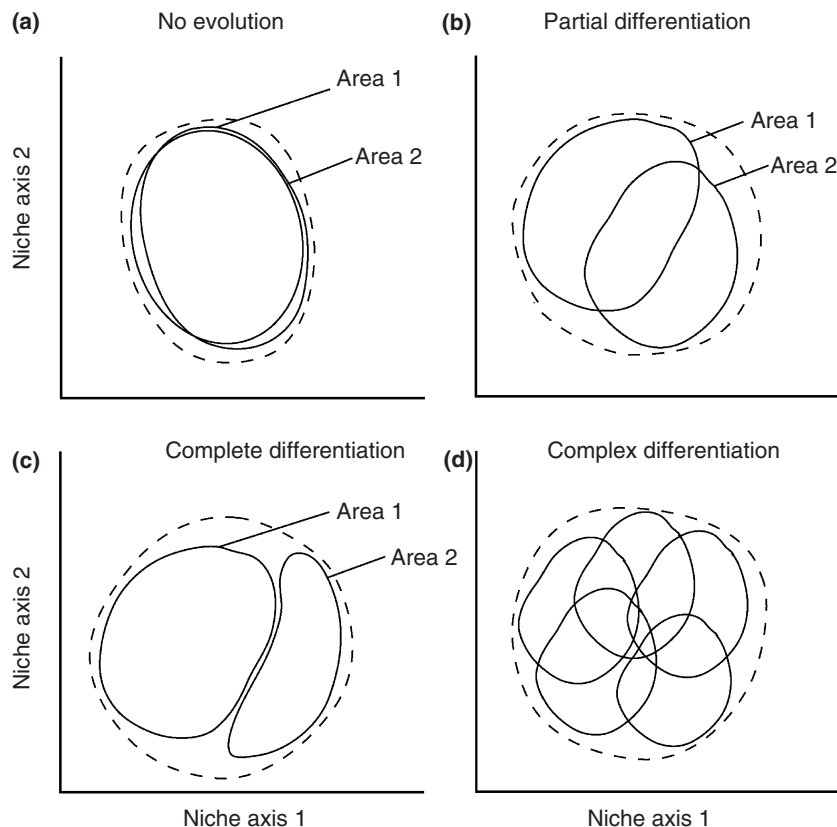


Figure 1 Schematic depiction of intraspecific variation in ecological niches. Niches can be represented pictorially as domains of environmental axes (e.g. temperature, humidity), within which populations of species can persist, and outside which they are likely to go extinct (Hutchinson 1978). The dotted line denotes the species' niche as a whole; the solid lines indicate the niche of locally adapted populations in distinct geographical regions. Genetically distinct populations occupying different areas may have essentially identical niches (1a), or be partially (1b) or completely (1c) differentiated. These entail different expectations about the likely success of reciprocal introductions. In reality, species are likely to exhibit all these patterns in intraspecific niche differentiation, as well as much more complex spatial patterns (1d).

would fail. Recognition of evolved niche differences as extreme as this might in practice lead to the recognition of allopatric species, each with its own unique niche requirements. In general, less extreme divergence might be expected (Fig. 1b). In this case, the success of reciprocal introductions would be highly variable. Within a continuous range, clinal or more complex patterns of niche variation might also exist (Fig. 1d). Moreover, one might observe an 'included niche' pattern (not shown), in which one population has niche requirements that are more specialized (and included within) the requirements of the other population.

It seems reasonable to hypothesize that intraspecific niche variation arising from microevolutionary processes might be most evident when sought over the entirety of a species' range, and should be more likely when geographical variation with a genetic basis is known to exist. One pragmatic difficulty is that at these broad spatial scales, it is difficult to find systems in which detailed local analyses of species' niche requirements have been conducted at enough localities to permit sensible comparisons. Systematists have long used morphological variation to recognize subspecies, representing major patterns of geographical variation within species. In this paper, we explore the utility of GARP analyses for characterizing coarse-scale intraspecific niche variation among previously named avian subspecies. For

each named subspecies or subspecies group of four widespread Mexican bird species, we develop GARP niche models, and test whether or not these models retain their predictive power when applied to other sectors of the species' overall distribution. High predictability across a species' range would indicate minimal niche differentiation, whereas low cross-range predictability is consistent with (though not conclusive proof of) the evolution of niche characteristics within a species. In the discussion, we briefly examine alternative, non-evolutionary explanations for apparent geographical variation in species' niches. For instance, patterns of correlation between species and abiotic environmental factors can be altered by antagonistic interspecific interactions (Hutchinson's distinction between a species' 'realized' and 'fundamental' niches), so that what appears to be geographical variation in niches may arise from variation in community structure instead.

METHODS

Natural history of study species

Species were chosen for analysis based on prior field experience (ATP) and on the literature (Peterson & Varajas 1993; Howell & Webb 1995). We selected two species that

are apparently relatively conservative in known ecological traits, showing little phenotypic variation (e.g. in body size and plumage) across their geographical distributions (*Ptilonys cinereus* and *Dryocopus lineatus*) and two species that are less conservative, with more marked geographical and ecological variation across their distributional areas (*Abelocoma californica* and *Melanerpes aurifrons*). Point-occurrence data ($n = 148, 231, 206,$ and $529,$ respectively) were drawn from the *Distributional Atlas of the Birds of Mexico* database (Peterson *et al.* 1998) under development by ATP and A. G. Navarro-Sigüenza (Acknowledgments). Subsets of point data were compiled corresponding to named subspecies; in the case of *A. californica* and *M. aurifrons*, owing to large numbers of subspecies, subsets were at the level of somewhat more inclusive regional divisions identified in previous genetic studies (Peterson 1992; A.G. Navarro-Sigüenza, unpubl. data) that comprise non-overlapping spatial units.

The geographically variable species (*A. californica* and *M. aurifrons*) both include geographical representatives near the species level (Peterson & Navarro-Sigüenza 1999). *Abelocoma californica* in Mexico includes three parapatric forms that differ in plumage, size, and genetic characters (Pitelka 1951; Peterson 1991, 1992, 1993). *Melanerpes aurifrons* includes forms ranging from Texas to northeastern and central Mexico; southeastern Mexico, the Yucatan Peninsula, and northern Chiapas; southeastern Oaxaca to southern Chiapas; and, southeastern Chiapas to Nicaragua (A.G. Navarro-Sigüenza *et al.*, unpubl. data), with differences principally in plumage characters (no genetic data are available).

Ecological niche modelling

Distributional data for each subset of each species were submitted to the GARP algorithm to produce ecological niche models (the conjunction of ecological conditions within which a species is observed to maintain populations) (Stockwell & Noble 1992). In GARP, available distributional points are divided into datasets for rule generation (training data) and model testing (test data). GARP works via a random-walk, iterative process of rule selection, evaluation, testing, and incorporation or rejection: first, a method is chosen from a set of possibilities (e.g. logistic regression, bioclimatic range rules), applied to the training data, and a rule developed; rules may be spliced, truncated, or otherwise adjusted. Predictive accuracy is evaluated using 1250 points resampled randomly, with replacement, from the test data, and 1250 points sampled randomly, with replacement, from the entire study region. Change in predictive accuracy in successive iterations is used to evaluate whether a particular rule should be incorporated into the model; the algorithm runs either 1000 iterations or until convergence. As GARP's processing is intended to be a broad, random review of

solution space, the algorithm may use any combination of rule types, may apply a rule to particular subregions in detail, etc.; options that were user-determined include the number of points used for resampling, and the relative sizes of training presence and pseudoabsence points in resampled data sets. (The recent release of a desktop version of GARP makes much of the function of the algorithm accessible, and includes a user's manual; <http://www.lifemapper.org/desktopgarp/>.) The measure of predictive success is the proportional area predicted to be occupied, compared against the number of test points that would be occupied were a species distributed randomly (assessed by a chi-square statistic).

Geographical data for Mexico were entered into the GARP algorithm in the form of digitized raster data coverages. Geographical data layers used included annual mean temperature, annual mean precipitation, elevation, and potential vegetation, at a pixel resolution of 7×7 km (distributional records are aggregated to presence/absence at this scale). Potential vegetation is defined as the vegetation expected to be present in a pixel, not including effects of humans. At a mechanistic level, these four variables clearly do not describe all relevant aspects of species' niches, but prior work (cited above) has shown that they do encapsulate important aspects of species–environment correlations. Moreover, for these taxa and at the spatial scale and degree of resolution considered here, these data are available and considerably more reliable than other niche parameters (e.g. direct measures of resource availability). By using pixels that are large relative to individual home ranges, aggregated over large geographical regions, it is less likely that source-sink dynamics will cloud basic species–environment relationships. These digital data, based upon maps produced by the Instituto Nacional de Estadística, Geografía e Informática (INEGI), were kindly provided by the Comisión Nacional para el Concimiento y Uso de la Biodiversidad (CONABIO).

The models based on ecological characteristics of each geographical subset of each species were used to predict the geographical distribution of other geographical subsets. For each species, this information regarding accuracy of cross-predictions (percentage of points correctly predicted) was organized in a n subsets \times n subsets square matrix. The diagonal elements (e.g. subset A predicts subset A) we term *autopredictions*, whereas off-diagonal elements (e.g. A predicts B) are *allopredictions*. We use the ratio of mean alloprediction rate to mean autoprediction rate as an inverse measure of intraspecific niche differentiation; the greater this quantity, the less the apparent magnitude among subspecies of geographical variation in a species' niche. (As noted by a reviewer, local geographical differentiation could also exist within subspecies, which would lower levels of auto-prediction.)

RESULTS

The four species varied in their degree of apparent geographical variation. *Ptilogonys cinereus* exhibited high levels of interpredictivity among subspecies (Fig. 2): autopredictions averaged 94% successful, whereas allopredictions averaged 79%. The allo-to-autoprediction ratio was 83.9%. In other words, predicting a different subspecies' range was only 16.1% less accurate than predicting the same subspecies' range. Two other species, *D. lineatus* and *M. aurifrons*, showed moderate levels of interpredictivity, with an allo-to-autoprediction ratio around 50%. These species thus showed some degree of consistency in niche requirements over broad geographical area; in *M. aurifrons*, this moderate level of conservatism contrasts with dramatic geographical variation in plumage. It is interesting that in several cases, allopredictions are markedly asymmetric, consistent with an 'included niche' pattern.

The fourth species, *A. californica*, showed much lower interpredictivity (Fig. 3). Autoprediction averaged 94%, whereas alloprediction ranged no higher than 24%, and averaged 9%, for an allo-to-autoprediction ratio of 9.9%. Indeed predictions from the *californica* group within this complex misses all occurrences of the *woodhouseii* and *sumichrasti* groups (Fig. 3), suggesting that the groups use strikingly different environments. We suggest that of the four species considered, this species is the best candidate for harbouring substantial evolved, intraspecific variation in the niche. Conclusively supporting this hypothesis requires much more detailed work (both in direct field studies of niche requirements, and in development of more refined niche models) than is reported here.

DISCUSSION

Aphelocoma californica was by far the most clearly ecologically differentiated from one region to the next of the four species in this study. However, surprisingly, not *M. aurifrons* but *D. lineatus* was the next most ecologically differentiated species. Although *M. aurifrons* shows marked geographical variation in morphological phenotype (as recognized by named subspecies), that differentiation is apparently not strongly manifested in ecological dimensions, compared with other co-occurring species. Hence, a discrepancy between classical phenotypic markers of geographical variation (e.g. plumage coloration, morphometrics) and ecological niche characteristics seems to be present: marked morphological differentiation can exist without sharp ecological differences.

We should stress that non-evolutionary explanations for the effects we have documented should be considered in tandem with evolutionary explanations. Among these possibilities are: (1) complexities because of biases in sampling, (2) differences in ecological characteristics of landscapes across Mexico, and (3) geographical expressions of unmeasured ecological variables, including species' interactions. These alternative explanations could yield apparent niche differentiation and conceivably account for the observed patterns.

Sampling biases arise if particular environments are by chance better represented, and others not represented well or at all, across the observed distributions (Stockwell & Peterson 2002a, b). Sampling biases within our geographically defined units could thus produce spurious niche differentiation. However, such biases are most likely when

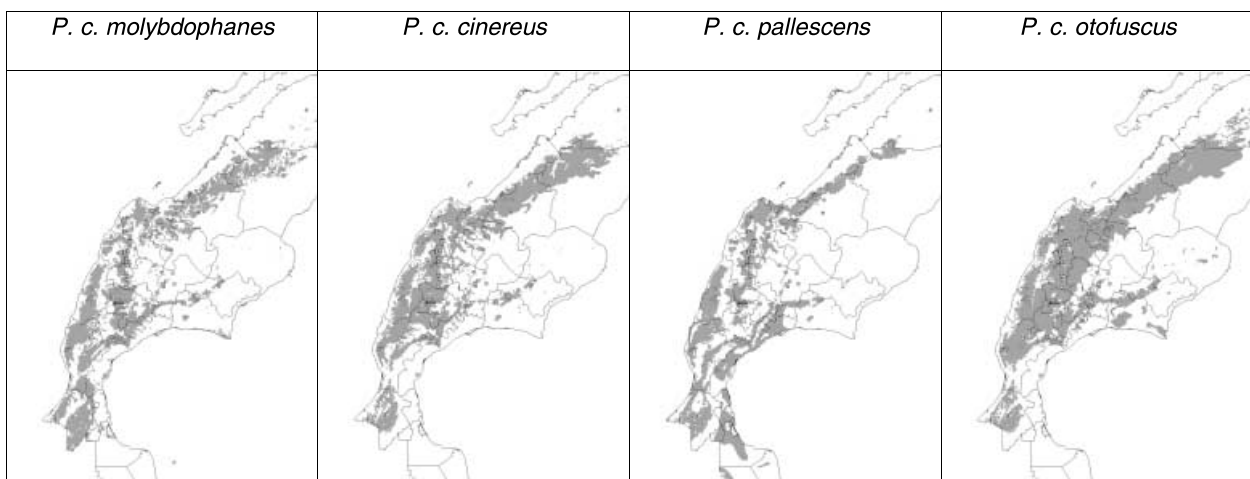


Figure 2 Interprediction example for *Ptilogonys cinereus*, showing known occurrence points for all subspecies overlain on the distributional predictions modelled for each subspecies: pcpal (dotted circle), pccin (dotted square), pcmol (dotted triangle), and pcoto (crossed circle) (see Table 1 for subspecies labels).

Table 1 Summary of predictive tests among populations of four species of Mexican birds

Predictor species	Predicted species				<i>n</i>	Autoprediction average	Alloprediction average	Niche differentiation index
<i>Aphelocoma coerulescens</i>								
	accal	acwoo	acsum					
accal	0.96	0.04	0		62	0.93	0.09	9.9
acwoo	0.03	0.86	0.24		77			
acsum	0.07	0.16	0.96		67			
<i>Ptilonotus cinereus</i>								
	pcoto	pcpal	pccin	pcmol				
pcoto	0.86	0.80	0.84	1.00	14	0.94	0.79	83.9
pcpal	0.5	1.00	0.60	1.00	10			
pccin	0.71	0.90	0.91	0.8	109			
pcmol	0.64	0.90	0.78	1.00	15			
<i>Dryocopus lineatus</i>								
	dlsim	dlpet	dlsca	dlobs				
dlsim	0.92	0.62	0.93	0.38	122	0.95	0.47	49.4
dlpet	0.32	0.90	0.72	0.56	39			
dlsca	0.48	0.18	1.00	0.44	54			
dlobs	0.16	0.51	0.37	1.00	16			
<i>Melanerpes aurifrons</i>								
	mepol	meaur	megra	mesan				
mepol	1.00	0.41	0.67	0.64	67	0.88	0.45	51.6
meaur	0.73	0.76	0.65	0.43	359			
megra	0.60	0.24	0.89	0.43	89			
mesan	0.21	0.17	0.25	0.86	14			

Subspecies designators are given as five-letter codes, as follows: *Aphelocoma californica*: accal = *A. c. californica*, acwoo = *A. c. woodhousei*, acsum = *A. c. sumichrasti*; and *Ptilonotus cinereus*: pcoto = *P. c. otofuscus*, pcpal = *P. c. pallescens*, pccin = *P. c. cinereus*, pcmol = *P. c. molybdophanes*; *Dryocopus lineatus*: dlsim = *D. l. similis*, dlpet = *D. l. petersi*, dlsca = *D. l. scapularis*, dlobs = *D. l. obsoletus*; and *Melanerpes aurifrons*: mepol = *M. e. polygrammus*, meaur = *M. e. aurifrons*, megra = *M. e. grateloupensis*, and mesan = *M. e. santacruzi*.

sampling is relatively sparse – GARP appears robust to minor biases in sampling regimes (Stockwell & Peterson 2002a, b), and tests under diverse conditions suggest that such biases are not in practice common (Peterson *et al.* 1999, 2002a, b, c; Anderson *et al.* 2002).

Geographical differences in ecological landscapes present a greater challenge to uncovering evolved geographical variation in species' niches. Imagine that models are built in region A where temperatures span 20–30 °C, and projected onto a region B with a temperature range of 20–40 °C. If the region A model includes a rule that says 'if temperature >25 °C, species is present', what does this rule imply about region B? It could mean that presence is predicted only in the range 25–30 °C, or that presence is predicted at any temperature above 25 °C. Based on region A, one cannot discriminate between these alternatives (the algorithm presently interprets in the latter manner).

A more refined characterization of the niches of the species we have examined would require detailed and spatially extensive field studies and doubtless include variables beyond the climatic and vegetation variables we

have included in our analyses (e.g. measures of nest site and food availability). Geographical differences in the correlation structure of this suite of niche variables could potentially lead to different predictive models, without evolved differences between populations' niches. Spatial variation within the pixel resolution used for our analyses (7 × 7 km) may also cloud the adequacy of our measures of potential niche axes. Nevertheless, the results of this study, with one species showing strong regional differentiation, and the other three not, suggest that this complication is not pervasive, as the four species are codistributed across much of Mexico.

Species' interactions are yet another potential non-evolutionary reason for apparent geographical variation in niches. Geographical variation in the community can lead to spatial variation in the realized ecological niche (*sensu* Hutchinson 1978). Indeed, GARP models can be used to assess hypotheses of competition between species at coarse geographical scales (Anderson *et al.* 2002). However, detecting such interactions without prior knowledge of their existence presents a greater challenge: species' distributions can be exclusive, or inverse in the pattern of their occurrences

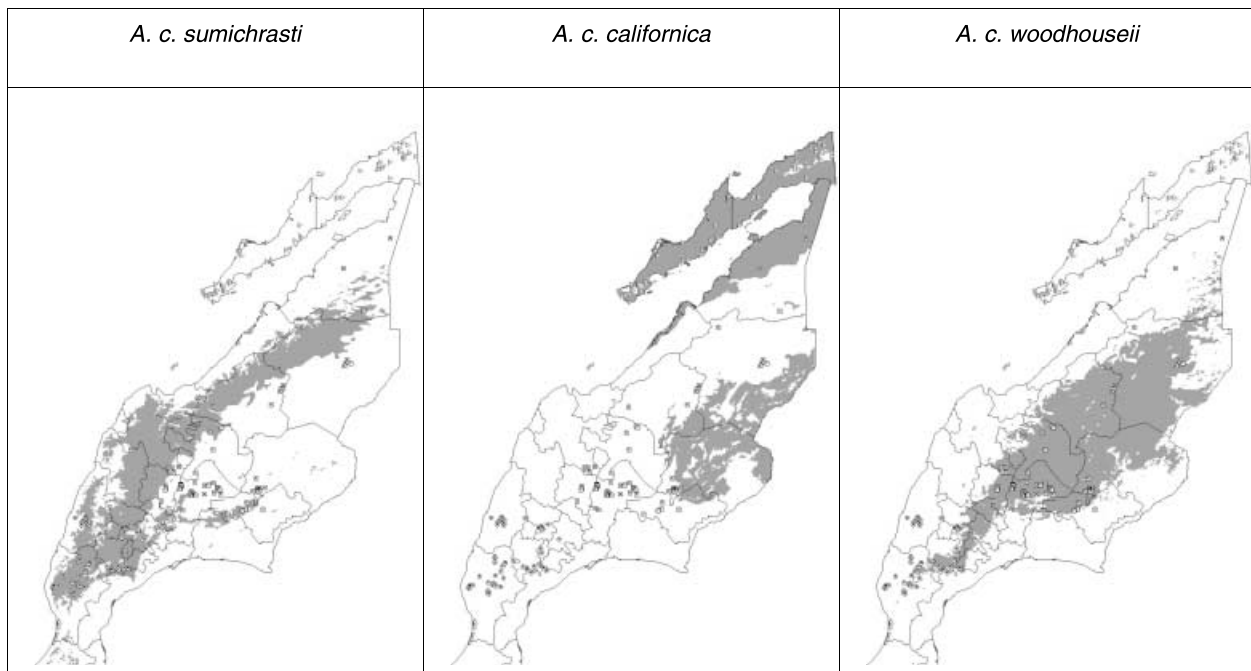


Figure 3 Interprediction example for *Apbelocoma californica*, showing known occurrence points for all subspecies groups overlain on the distributional predictions modelled for each subspecies group: accal (dotted triangle), acwoo (dotted square), and acum (dotted circle) (see Table 1 for subspecies labels).

for a wide range of reasons. For example, the sister species pairs analysed in a recent paper (Peterson *et al.* 1999), which arose from vicariant speciation (Escalante-Pleigo *et al.* 1993), have distributions that could be mistakenly interpreted as reflecting competitive exclusion. Deep analysis of this possible source of intraspecific geographical variation requires more complex analyses that integrate models of interspecific interactions with distributional models.

Finally, a reviewer has pointed out that geographical variation may also arise from phenotypic plasticity (facultative habitat use), rather than evolutionary innovation. For instance, habitat selection behaviour may be sensitive to the array of habitats (Boyce *et al.* 2002; Osborne & Suarez-Seoane 2002), with rare habitats being selectively ignored. Our suspicion is that this is not a major effect at the coarse spatial scales of entire subspecies and species distributions, where one is concerned with the ability of a species to persist within spatial units large enough to harbour entire populations inhabiting complex landscapes.

Implications for studies of invasions

Predictive models of species' distributions have many uses. One use of practical importance is to predict the likely success of new invasions. GARP models have been applied to several invasions with high predictive power (Peterson & Vieglais 2001; Iguchi *et al.* 2003; Papes & Peterson 2003,

Peterson *et al.* 2003). Understanding intraspecific niche evolution pertains to gauging the likely utility of predictive models in invasion biology, for two distinct reasons (one leading to overprediction, and the other to underprediction).

First, assume a predictive model has been developed using a species' entire distribution, but that substantial genetic differentiation in niche requirements exists within that range. If propagules are drawn from a particular location in the ancestral range, their ecological potential will be but a subset of that modelled, and many introductions should fail. In other words, overprediction should be frequent if substantial prior geographical differentiation in the niche exists.

Second, the existence of niche variation may imply that the niche is labile. If introduced propagules can adapt rapidly, niche traits may emerge in the region of introduction differing from those describing range limits in the ancestral distribution. Introductions may succeed owing to rapid microevolution leading to divergence between the niches of ancestral and introduced populations. In other words, for species with labile ecological requirements, models developed based on the native range of the species could underpredict the success and pattern of spread of invasions. In future work, identifying instances of underprediction could be valuable, as they may provide testing grounds for assessing theoretical expectations about niche conservation, vs. rapid niche evolution.

More broadly, rather than viewing deviations in extrapolating niche and distributional models at broad scales as solely reflecting 'errors' in model-building and testing, we suggest that such variation may reflect genuine underlying evolved variation in species' basic ecological niches.

ACKNOWLEDGEMENTS

We thank Brian Maurer and three reviewers for insightful comments, and Dr A.G. Navarro-Sigüenza for his ever-helpful advice and suggestions. Distributional information and access to specimens was provided by Academy of Natural Sciences of Philadelphia, American Museum of Natural History, Bell Museum of Natural History, California Academy of Sciences, Carnegie Museum of Natural History, Cornell University, Delaware Museum of Natural History, Field Museum of Natural History, Los Angeles County Museum of Natural History, Louisiana State University Museum of Natural Science, Moore Laboratory of Zoology, Museo de Zoología of the Facultad de Ciencias (UNAM), Muséum Nationale d'Histoire Naturelle of Paris, Museum of Comparative Zoology of Harvard University, Museum of Vertebrate Zoology, Museum of Zoology of the University of California at Los Angeles, Natural History Museum (Tring) (BMNH), Natuurhistorische Museum of Leiden, Royal Ontario Museum, Southwestern College, Texas Cooperative Wildlife Collections, U.S. National Museum of Natural History, Universidad Autónoma del Estado de Morelos, Universidad Michoacana San Nicolás de Hidalgo, University of Kansas Natural History Museum, University of Michigan Museum of Zoology, Naturhistorisches Museum of Vienna, Western Foundation of Vertebrate Zoology, and Yale Peabody Museum. This work was supported by the National Science Foundation, US Environmental Protection Agency, and the University of Florida Foundation.

REFERENCES

- Anderson, R.P., Laverde, M. & Peterson, A.T. (2002). Niche-based models of species' potential macrodistributions suggest competition and competitive release in spiny pocket mice. *Oikos*, 93, 3–16.
- Avise, J.C. (2000). *Phylogeography: The History and Formation of Species*. Harvard University Press, Cambridge, MA.
- Boyce, M.S., Vernier, P.R., Nielsen, S.E. & Schmiegelow, F.K.A. (2002). Evaluating resource selection functions. *Ecol. Model.* 157, 281–300.
- Bradshaw, A.D. (1991). Genostasis and the limits to evolution. *Philos. Trans. R. Soc. Lond. B Biol. Sci.*, 333, 289–305.
- Case, T.J. & Taper, M.L. (2000). Interspecific competition, environmental gradients, gene flow, and the coevolution of species' borders. *Am. Nat.* 155, 583–605.
- Davis, M.B. & Shaw, R.G. (2001). Range shifts and adaptive responses to Quaternary climate change. *Science* 292, 673–679.
- Endler, J.A. (1977). *Geographic Variation, Speciation, and Clines*. Princeton University Press, Princeton, NJ.
- Escalante-Pleigo, P., Navarro-Sigüenza, A.G. & Peterson, A.T. (1993). A geographic, historical, and ecological analysis of avian diversity in Mexico. In: *Biological Diversity of Mexico: Origins and Distribution* (eds Ramamoorthy, T.P., Bye, R., Lot, A. & Fa, J.). Oxford University Press, New York, pp. 281–307.
- Gomulkiewicz, R., Holt, R.D. & Barfield, M. (1999). The effects of density dependence and immigration on local adaptation and niche evolution in a black-hole sink environment. *Theor. Popul. Biol.* 55, 283–296.
- Gould, S.J. & Johnston, R.F. (1972). Geographic variation. *Annu. Rev. Ecol. Syst.* 3, 457–498.
- Graham, R.W., Lundelius, E.L., Graham, M.A., Schroeder, E.K., Toomey, R.S., Anderson, E., Barnosky, A.D., Burns, J.A., Churcher, C.S., Grayson, D.K., Guthrie, R.D., Harington, C.R., Jefferson, G.T., Martin, L.D., McDonald, H.G., Morlan, R.E., Semken, H.A., Webb, S.D., Werdelin, L. & Wilson, M.C. (1996). Spatial response of mammals to late quaternary environmental fluctuations. *Science* 272, 1601–1606.
- Holt, R.D. (1996). Demographic constraints in evolution: towards unifying the evolutionary theories of senescence and niche conservatism. *Evol. Ecol.* 10, 1–11.
- Holt, R.D. (2003). On the evolutionary ecology of species' ranges. *Evol. Ecol. Lett.* 5, 159–178.
- Holt, R.D. & Gaines, M.S. (1992). Analysis of adaptation in heterogeneous landscapes – implications for the evolution of fundamental niches. *Evol. Ecol.* 6, 433–447.
- Holt, R.D. & Gomulkiewicz, R. (1997). The evolution of species' niches: a population dynamic perspective. In: *Case Studies in Mathematical Modelling* (eds Othmer, H., Adler, F., Lewis, M. & Dallon, I.). Prentice-Hall, Englewood Cliffs, NJ, pp. 25–50.
- Howell, S.N.G. & Webb, S. (1995). *A Guide to the Birds of Mexico and Northern Central America*. Oxford University Press, Oxford.
- Hutchinson, G.E. (1978). *An Introduction to Population Ecology*. Yale University Press, New Haven, CT.
- Iguchi, K., Matsuura, K., McKyset, K., Peterson, A.T., Scachetti-Pereira, R., Vieglais, D.A., Wiley, E.O. & Yodo, T. (2003). Predicting invasions of bass in Japan. *Trans. Am. Fish. Soc.*, in press.
- James, F.C., Johnston, R.F., Wamer, N.O., Niemi, G.J. & Boecklen, W.J. (1984). The Grinnellian niche of the Wood Thrush. *Am. Nat.* 124, 17–30.
- Kawecki, T.J. (1995). Demography of source-sink populations and the evolution of ecological niches. *Evol. Ecol.* 9, 38–44.
- Kawecki, T.J. (2000). Adaptation to marginal habitats: contrasting influence of the dispersal rate on the fate of alleles with small and large effects. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 267, 1315–1320.
- Kawecki, T.J. & Holt, R.D. (2002). Evolutionary consequences of asymmetric dispersal rates. *Am. Nat.* 160, 333–347.
- Kirkpatrick, M. & Barton, N.H. (1997). Evolution of a species' range. *Am. Nat.* 150, 1–23.
- Lawton, J.H., Nee, S., Letcher, A.J. & Harvey, P.H. (1994). Animal distributions: patterns and processes. In: *Large Scale Ecology and Conservation Biology* (ed. Edwards, P.J., May, R.M. & Webb, N.R.). Blackwell, London, pp. 41–58.
- Maurer, B. A. & Taper, M.L. (2002). Connecting geographic distributions with population processes. *Ecol. Lett.* 5, 223–231.

- Osborne, P.E. & Suarez-Seoane, S. (2002). Should data be partitioned spatially before building large-scale distribution models? *Ecol. Model.* 157:249–259.
- Papes, M. & Peterson, A.T. (2003). Predictions of the geographic course of the invasion of *Ageratina adenophora* in China. *J. Wubian Bot. Res.*, in press.
- Peterson, A.T. (1991). Gene flow in scrub jays (*Apbelocoma californica*): frequency and direction of movement. *Condor* 93, 926–934.
- Peterson, A.T. (1992). Phylogeny and rates of molecular evolution in the jays of the genus *Aphelocoma* (Corvidae). *Auk* 109, 134–148.
- Peterson, A.T. (1993). Adaptive geographic variation of beak shape in Scrub Jays (*Apbelocoma californica*). *Am. Nat.* 142, 508–527.
- Peterson, A.T. & Navarro-Sigüenza, A.G. (1999). Alternate species concepts as bases for determining priority conservation areas. *Con. Biol.* 13, 427–431.
- Peterson, A.T. & Varajas, N. (1993). Ecological diversity in Scrub Jays, *Apbelocoma coerulescens*. In: *Biological Diversity of Mexico: Origins and Distribution* (eds Ramamoorthy, T.P., Bye, R., Lot, A. & Fa, J.). Oxford University Press, New York.
- Peterson, A.T. & Vieglais, D.A. (2001). Predicting species invasions using ecological niche modeling: New approaches for bioinformatics attack a pressing problem. *Bioscience* 51, 363–371.
- Peterson, A.T., Navarro-Sigüenza, A.G. & Benítez-Díaz, H. (1998). The need for continued scientific collecting; a geographic analysis of Mexican bird specimens. *Ibis* 140, 288–294.
- Peterson, A. T., Soberón, J. & Sánchez-Cordero, V. (1999). Conservatism of ecological niches in evolutionary time. *Science* 285, 1265–1267.
- Peterson, A.T., Ball, L.G. & Cohoon, K.P. (2002a). Predicting distributions of tropical birds. *Ibis* 144, e27–e32.
- Peterson, A.T., Ortega-Huerta, M.A., Bartley, J., Sánchez-Cordero, V., Soberón, J., Buddemeier, R.H. & Stockwell, D.R.B. (2002b). Future projections for Mexican faunas under global climate change scenarios. *Nature* 416, 626–629.
- Peterson, A. T., Stockwell, D.R.B. & Kluza, D.A. (2002c). Distributional prediction based on ecological niche modeling of primary occurrence data. In: *Predicting Species Occurrences: Issues of Scale and Accuracy* (eds Scott, J.M., Heglund, P.J. & Morrison, M.L.). Island Press, Washington, DC, pp. 617–623.
- Peterson, A.T., Scachetti-Pereira, R. & Hargrove, W.W. (2003). Potential distribution of Asian longhorned beetles (*Anoplophora glabripennis*) in North America. *J. Econ. Entomol.*, in press.
- Pitelka, F.A. (1951). Speciation and ecologic distribution in American jays of the genus *Apbelocoma*. *Ucal. Pub. Zool.* 50, 195–464.
- Proulx, S.R. (2002). Niche shifts and expansion due to sexual selection. *Evol. Ecol. Res.* 4, 351–369.
- Pulliam, H.R. (2000). On the relationship between niche and distribution. *Ecol. Lett.* 3, 349–361.
- Schluter, D. (2000). Ecological character displacement in adaptive radiation. *Am. Nat.* 156, S4–S16.
- Schoener, A. (1989). The ecological niche. In: *Ecological Concepts* (ed. Chernet, J.M.). Blackwell Science, Oxford, UK, pp. 79–114.
- Scott, J.M., Heglund, P.J., Samson, F., Haufler, J., Morrison, M., Raphael, M., Wall, B. (eds) (2002). *Predicting Species Occurrences: Issues of Accuracy and Scale*. Island Press, Covelo, CA.
- Stockwell, D.R.B. (1999). Genetic algorithms II. In: *Machine Learning Methods for Ecological Applications* (ed. Fielding, A.H.). Kluwer Academic Publishers, Boston, pp. 123–144.
- Stockwell, D.R.B. & Noble, I.R. (1992). Induction of sets of rules from animal distribution data – a robust and informative method of data-analysis. *Math. Comp. Sim.* 33, 385–390.
- Stockwell, D.R.B. & Peters, D.P. (1999). The GARP modelling system: problems and solutions to automated spatial prediction. *Int. J. Geo. Inform. Sys.* 13, 143–158.
- Stockwell, D.R.B. & Peterson, A.T. (2002a). Controlling bias in biodiversity data. In: *Predicting Species Occurrences: Issues of Scale and Accuracy* (eds Scott, J.M., Heglund, P.J. & Morrison, M.L.). Island Press, Washington, DC, pp. 537–546.
- Stockwell, D.R.B. & Peterson, A.T. (2002b). Effects of sample size on accuracy of species distribution models. *Ecol. Model.* 148, 1–13.
- Thomas, C.D., Bodsworth, E.J., Wilson, R.J., Simmons, A.D., Davies, Z.G., Musche, M. & Conradt, L. (2001). Ecological and evolutionary processes at expanding range margins. *Nature* 411, 577–581.
- Tufto, J. (2001). Effects of releasing maladapted individuals: a demographic-evolutionary model. *Am. Nat.* 158, 331–340.

Editor, Brian Maurer

Manuscript received 12 March 2003

First decision made 18 April 2003

Manuscript accepted 13 June 2003