

Reconstructing the Pleistocene geography of the *Aphelocoma* jays (Corvidae)

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ABSTRACT

Understanding historical distributions of species and evolving lineages has been a topic of considerable interest, yet methods used to date have not provided detailed, quantitative distributional hypotheses. Here, we present a technique based on models of species' ecological niches and Pleistocene climate reconstructions that provides such hypotheses, providing the example of reconstructions for the *Aphelocoma* jays. We demonstrate in general a greater degree than expected of stability in jay species' distributional areas back through at least the most recent glaciation event, and that existing patterns of genetic differentiation may date to before the Late Pleistocene glaciations. More generally, the method offers the potential for reconstructing historical distributions of species or lineages, and providing a detailed geographic framework for addressing many biogeographic and systematic questions.

Keywords

Pleistocene distribution, potential distribution, speciation.

INTRODUCTION

The *Aphelocoma* jays represent one of the best-studied complex avian lineages in the world, with diverse systematic tools having been applied to understanding their geography and evolution. Morphometric studies and plumage comparisons have illuminated basic patterns of geographic variation and differentiation (Pitelka, 1951; Bardwell *et al.*, 2001); detailed field investigations have filled key holes in known distributions (Peterson, 1991c); focused inspections of specimen material have illuminated patterns of gene flow and ontogenetic variation among differentiated populations (Peterson, 1991a,b; Brown & Li, 1995); molecular genetic studies have revealed patterns of genetic identity and differentiation (Peterson, 1990b, 1992a); phylogenetic studies have revealed historical patterns of connection among lineages (Peterson, 1992b; de los Monteros & Cracraft, 1997; Saunders & Edwards, 2000; Rice *et al.*, 2003); and comparative molecular studies have illuminated more fine-scale genetic phenomena in the group (Peterson, 1992a; McDonald *et al.*, 1999). The genus has also served as an important model for studies of avian demography (Schoech *et al.*, 1996; Wcislo & Danforth, 1997; Breininger *et al.*, 1998; Breininger *et al.*, 1999; Breininger, 1999) and social behaviour (Bond *et al.*, 2003).

Several of these previous studies have focused on reconstructing the history of geography and ecology in the genus (Peterson, 1992b, 1993; Peterson & Holt, 2003; Rice *et al.*, 2003). These studies have assessed the geographic and ecological phenomena implied by morphological and phylogenetic patterns (Peterson, 1992b, 1993) using traditional systematic tools, but also have

begun to examine ecological variation in this group using quantitative ecological niche models based on a machine-learning approach (Peterson & Holt, 2003; Rice *et al.*, 2003).

In spite of such intense study, the Pleistocene geography of this group (and many others) has remained opaque. Although Pleistocene subfossil evidence indicates long-term residence in southern California (Miller, 1929), dating of the subfossil material is not sufficiently clear as to permit detailed inferences. Although application of molecular clock assumptions to genetic data reveals apparently quite old patterns of lineage-splitting, many reasons for caution exist, including wildly disparate rates of evolution in different *Aphelocoma* lineages (Peterson, 1992b). Moreover, broad-scale shifts of vegetation, as indicated by studies of palynology and packrat (*Neotoma* spp.) middens (Betancourt *et al.*, 1990; Rinehart & McFarlane, 1995; Smith & Betancourt, 1998; Smith *et al.*, 2000; Betancourt & Saavedra, 2002; Schmitt *et al.*, 2002; Smith & Betancourt, 2003), involve the Mojave and other south-western desert being invaded broadly by pinyon-juniper woodlands. These dramatic shifts suggest that the Pleistocene geography of *Aphelocoma* could have been dramatically different from the current distribution of the clade, but no quantitative evidence is available.

Here, we explore an alternative route to understanding *Aphelocoma* Pleistocene distributional patterns, the rudiments of which have been explored previously (Huntley *et al.*, 1989, 1995; Prentice & Webb, 1998; Hansen *et al.*, 2001; Hugall *et al.*, 2002; Hilbert *et al.*, 2004; Martínez-Meyer *et al.*, 2004); at difference from these first explorations, however, we incorporate local and regional variation in palaeoclimatic changes based on quantitative

models. Using the technique of ecological niche modelling (Peterson *et al.*, 2002c), we develop quantitative models of the ecological requirements of each species-level or near-species-level taxon (Peterson, 1990b) in the genus. Then, taking advantage of general circulation models of world climates that have been run 'backwards' to reconstruct climates 6000 and 21,000 BP (McFarlane *et al.*, 1992; Hewitt & Mitchell, 1996, 1997), we project our current ecological niche models onto past climates to reconstruct past potential geographic distributions for *Aphelocoma*. These reconstructions are then examined in light of current patterns of morphological and genetic differentiation.

METHODS

We follow the taxonomic arrangements for *Aphelocoma* suggested from the results of our previous work (Peterson, 1990b). Only partially adopted in recent regional checklists (AOU, 1998), this arrangement is certainly merited on Phylogenetic or Evolutionary Species Concept grounds (Wiley, 1978; McKittrick & Zink, 1988). That these groups are also recognizable under the biological species concept is quite defensible as well (Peterson, 1990b). Regardless, 10 such species-level subunits exist within the genus, including five within the traditional '*A. coerulescens*', three within the traditional '*A. ultramarina*', and at least two within the traditional '*A. unicolor*' (Fig. 1). Owing to its microscale distribution, results pertaining to *A. insularis* are not depicted in many of the figures.

We accumulated occurrence information in the form of unique latitude-longitude combinations for each of the species taxa in *Aphelocoma* based principally on a detailed compendium of specimen collection localities (Pitelka, 1951), and a few additional localities for taxa that were poorly known at the time of Pitelka's work (Peterson, 1991c). All localities were georeferenced (assigned decimal-degree geographic coordinates to the nearest 0.01°) using Internet-based gazetteer resources¹.

Ecological variation in the present and in the past was summarized in a series of GIS coverages ('layers') including aspects of climate and topography. The latter were derived from the USGS Hydro-1K data set, including slope, aspect, and tendency to pool water owing to landscape morphology, all of which are derived from a digital elevation model (elevation per se was excluded owing to the changing meaning of 'elevation' under different climates, but its derivatives listed above do not change in meaning). The former — climate data — were derived for present climates from the data provided for 1931–60 (to match modal age of *Aphelocoma* specimen collection dates) by the Intergovernmental Panel on Climate Change², and for past climates by the Palaeoclimate Modelling Intercomparison Project³. The past-climate data included time-slices representing 6000 and 21,000 BP, and — importantly, and at difference with previous such analyses (Hugall *et al.*, 2002; Hilbert *et al.*, 2004) — these data sets incorporate spatial variation in changes among time periods. To alleviate particularities

¹<http://www.calle.com>, <http://geonames.usgs.gov/pls/gnis/>.

²<http://www.ipcc.ch/>.

³<http://www-lsce.cea.fr/pmip/>.

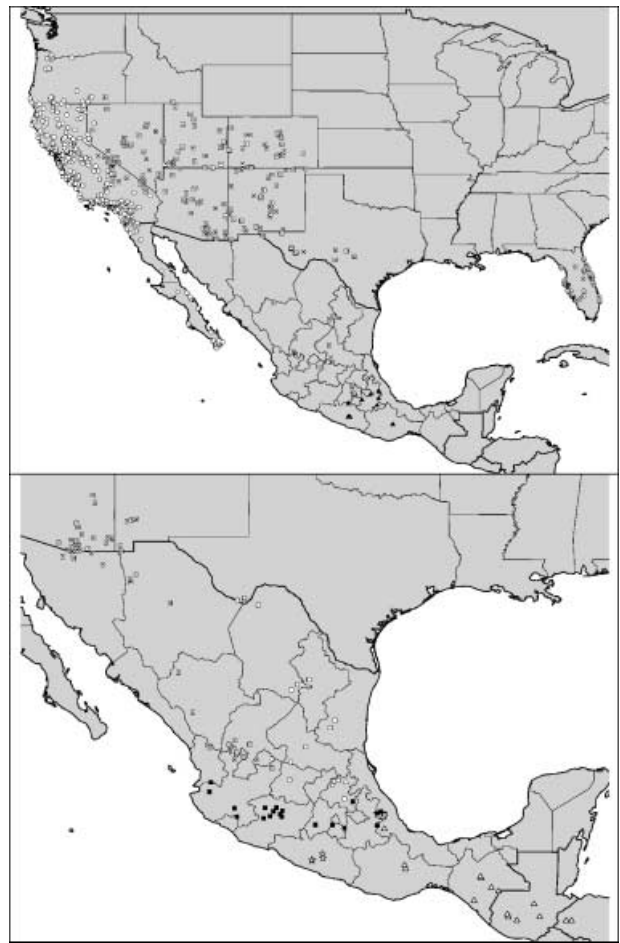


Figure 1 Present-day geography of species-level taxa in the genus *Aphelocoma*, as reflected by the point occurrences used in this study. Top: the *Aphelocoma* '*coerulescens*' complex, including *A. californica* (open circles), *A. woodhouseii* (dotted squares), *A. coerulescens* (dotted circles), *A. sumichrasti* (black triangles), and *A. insularis* (stars). Bottom: the remainder of *Aphelocoma*, including three forms within the present *A. 'ultramarina'* — *A. wollweberi* (dotted squares), *A. potosina* (open squares), and *A. ultramarina* (black squares), and two forms of *A. 'unicolor'* — *A. guerrerensis* (stars) and *A. unicolor* (open triangles). Note that this taxonomic treatment does not coincide with current dogma (AOU, 1998).

caused by the details of individual climate-model implementations, we included two independent modelling centres' (Hadley Centre and Canadian Climate Center) outputs (McFarlane *et al.*, 1992; Hewitt & Mitchell, 1996, 1997). Grids were resampled to 0.1° pixel resolution, and clipped to a region that included North America from the US-Canada border to the southern extreme of Nicaragua (matching the distribution of the genus).

Ecological niches were modelled and potential geographic distributions predicted using the *Genetic Algorithm for Rule-set Prediction* (GARP) (Stockwell & Noble, 1992; Stockwell & Peters, 1999; Stockwell, 1999). In general, the procedure focuses on modelling ecological niches (the conjunction of ecological conditions within which a species is able to maintain populations without immigration) (Grinnell, 1917). Specifically, GARP relates

ecological characteristics of known occurrence points to those of points randomly sampled from the rest of the study region, seeking to develop a series of decision rules that best summarize those factors associated with the species' presence; these decision rules can then be projected back onto geography to predict the geographic distribution of the species (Stockwell & Peters, 1999).

In GARP, 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: a method is chosen from a set of possibilities (e.g. logistic regression, bioclimatic rules), applied to the training data, and a rule is developed or evolved. Predictive accuracy is then evaluated based on 1250 points resampled from the test data and 1250 points sampled randomly from the study region as a whole. Rules may evolve by a number of means that mimic DNA evolution: point mutations, deletions, crossing over, etc. 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's predictive abilities have been tested and proven under diverse circumstances (Stockwell & Peters, 1999; Anderson *et al.*, 2002; Fera & Peterson, 2002; Stockwell & Peterson, 2002a,b; Anderson *et al.*, 2003; Peterson & Kluza, 2003; Stockwell & Peterson, in press). All modelling in this study was carried out on a desktop implementation of GARP available for public download⁴.

To optimize model performance, we developed 100 replicate models of species' ecological niche, based on random 50% subsets of available occurrence points (i.e. half of the occurrence points were used to build models, and the other half used to test their predictive ability). Unlike previous applications, which either used single models to predict species' distributions (Peterson *et al.*, 1999) or summed multiple models to incorporate model-to-model variation (Peterson *et al.* In press), we used a procedure (Anderson *et al.*, 2003) for choosing best subsets of models. The procedure is based on the observations that (1) models vary in quality (2) variation among models involves an inverse relationship between errors of omission (leaving out true distributional area) and commission (including areas not actually inhabited), and (3) best models (as judged by experts blind to error statistics in the original derivation of the method) are clustered in a region of minimum omission of independent test points and moderate area predicted (an axis which includes the commission error). The relative position of the cloud of points relative to the two error axes provides an assessment of the relative accuracy of each model. To choose best subsets of models, we (1) eliminated all but models that had negligible omission error based on the independent test points (2) calculated the median area predicted to be present among these low-omission models (% of the area analysed), and (3) identified the 10 models that were closest to the overall median extent for each species. The geographic manifestations of these models were summed to provide a best estimate of the potential geographic distribution of the particular group.

All present-day distributional models for taxa for which > 20 occurrence points were available were tested using random 50%

subsets of available distributional data — that is, models were built based on one-half of available information, and tested based on the other (independent) half of the occurrence data available. The number of test points \times the proportional area predicted present by a given model, provided an estimate of points expected to be predicted correctly if associations between predictions and test points were at random. These expectations and observed predictive success were then compared via a chi-square test (d.f. = 1). It should be noted that both correct prediction of known presence points and prediction of absence in areas from which presences are not recorded are taken into account in this test.

The projection of these 'best' 10 models for each species onto past climates (6000 and 21,000 BP, Hadley and Canadian models), in essence a spatial query for conditions fitting the modelled niche in each dimension, provides an estimate of past potential distributions. As with future projections (Peterson *et al.*, 2001), a key point is that of making assumptions regarding dispersal abilities of species — the degree to which a *potential* distribution is actually occupied is highly dependent on the ability of species to encounter and colonize those distributional areas. In this analysis, we made few explicit assumptions regarding dispersal; rather, we attempted to visualize distributional possibilities as generally as possible, considering the entire diversity of dispersal scenarios, from universal to non-existent. We do make the potentially tenuous assumption of no evolutionary change in niche characteristics in these evolving lineages, which may not be completely acceptable in the case of *Aphelocoma* (Peterson & Holt, 2003), although supported more generally (Peterson *et al.*, 1999).

RESULTS

Geographic distributions of *Aphelocoma* jays cover western North America (and peninsular Florida) from Oregon and Idaho south to Central America (Fig. 1). Our best-subset models were without exception statistically significant ($P < 0.001$) for independent test datasets (subsets of available distributional information), suggesting that model predictions were considerably better than random models. More importantly, this result indicates that our models — at least in the present day — suffice to provide a predictive understanding of distributional phenomena for each *Aphelocoma* species.

In general, projecting present-day models onto climate coverages for 6000 and 21,000 BP, *Aphelocoma* species were predicted to have retained a surprising amount of their present-day distributional areas at the Last Glacial Maximum (21,000 BP) (Figs 2 and 3). Most species retained > 90% of present distributional area as of 6000 year ago, and > 50% of present distributional area as of 21,000 BP (Fig. 4). Only three species are projected to have lost significant distributional areas during the Last Glacial Maximum: *A. coerulescens*, which retracted significantly southward in Florida; *A. wollweberi*, which is reconstructed to have shifted downslope and focused in north-western Mexico; and *A. guerrensis*, which is reconstructed to have had a highly fragmented relictual distribution in the past (Figs 2 and 3). This latter case, though, could result from underestimation of the species' niche

⁴<http://www.lifemapper.org/desktopgarp/>.

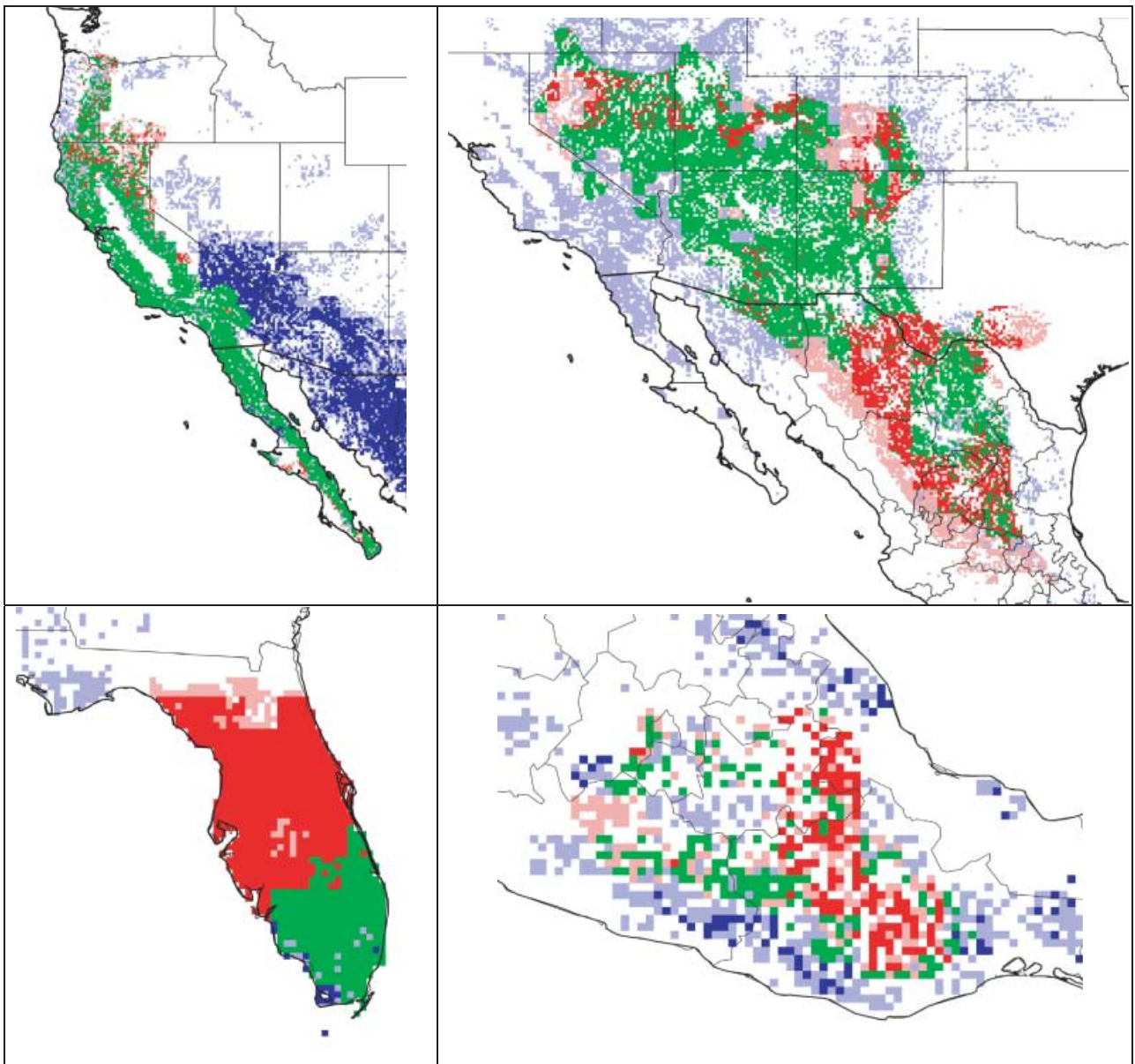


Figure 2 Present and past (21,000 BP) modelled ranges for members of the *Aphelocoma* 'coerulescens' group: top left *A. californica*, top right *A. woodhouseii*, bottom left *A. coerulescens*, bottom right *A. sumichrasti*. Green = areas that are stable, being inhabitable in both time periods; red = present distributional areas that are predicted not to have been habitable in the past; and blue = areas predicted to have been habitable in the past that are not presently habitable. Lighter shades of colours indicate prediction at lower levels of confidence.

resulting from the relatively few occurrence points available for input ($N = 5$). The Santa Cruz Island endemic *A. insularis* was reconstructed to have retained potential distributional areas across the island to which it is restricted.

DISCUSSION

Limitations of the approach

This paper is a first broad presentation of a methodology pioneered by one of the authors (Martínez-Meyer *et al.*, 2004); it improves on past approaches to the challenge (Hugall *et al.*,

2002; Hilbert *et al.*, 2004) via use of spatially explicit GCM results for input, rather than region-wide average change figures (e.g. temperature increases 2.3 °C, precipitation decreases 10.2 mm). Here, we take the original implementation (Martínez-Meyer *et al.*, 2004), and (1) generalize it to worldwide climate coverage sets (2) examine the implications of two distinct model scenarios, and (3) project models to two distinct points in the past (6000 and 21,000 BP). Although the results are intriguing, several limitations of this approach should be taken into account.

Development of ecological niche models that are genuinely *predictive* across time and space is a significant challenge. The robustness of this approach depends both on the approaches

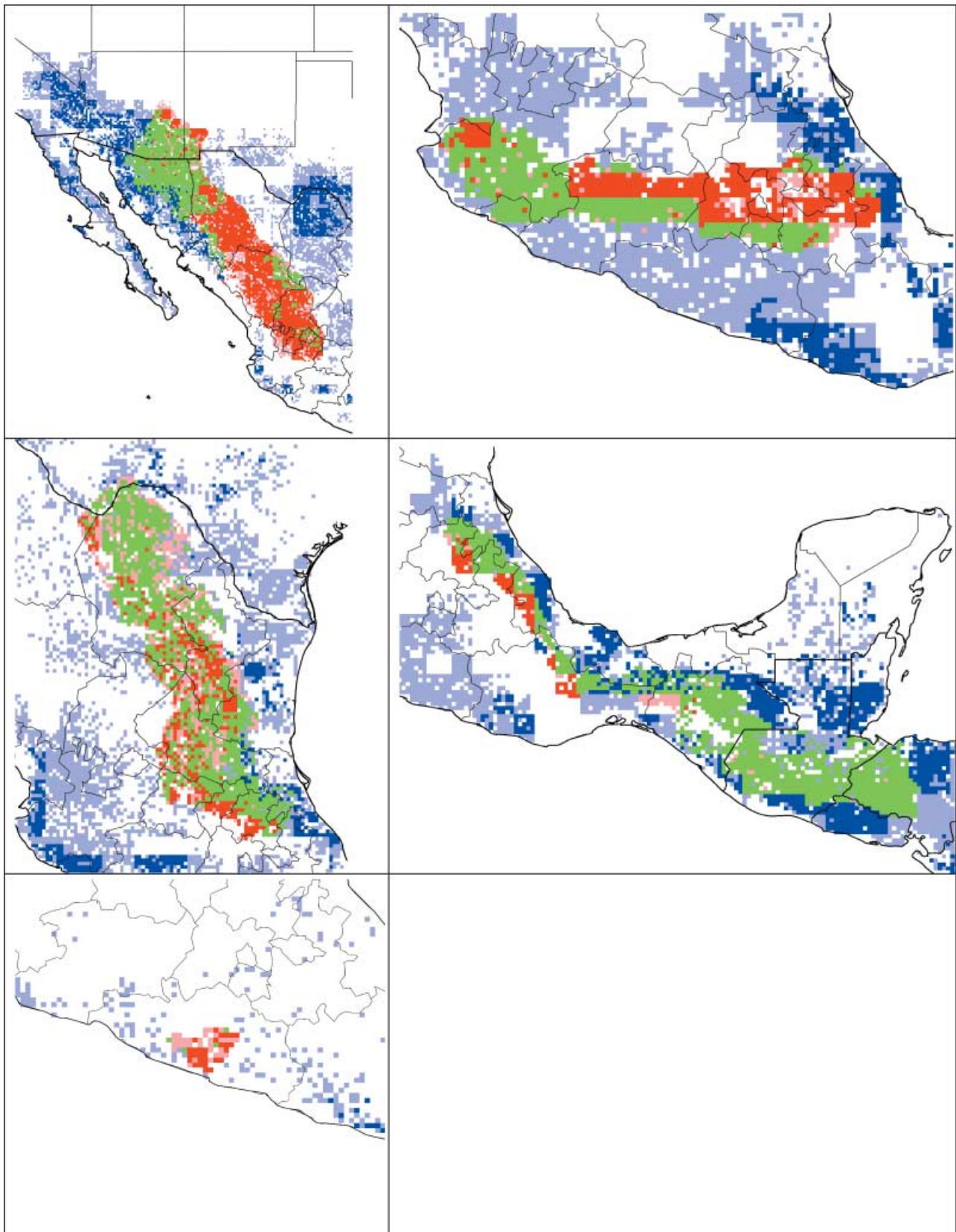


Figure 3 Present and past (21,000 BP) modelled ranges for the remainder of *Aphelocoma*: top left *A. wollweberi*, top right *A. ultramarina*, middle left *A. potosina*, middle right *A. unicolor*, and bottom left *A. guerrerensis*. Green = areas that are stable, being inhabitable in both time periods; red = present distributional areas that are predicted not to have been habitable in the past; and blue = areas predicted to have been habitable in the past that are not presently habitable. Lighter shades of colours indicate prediction at lower levels of confidence.

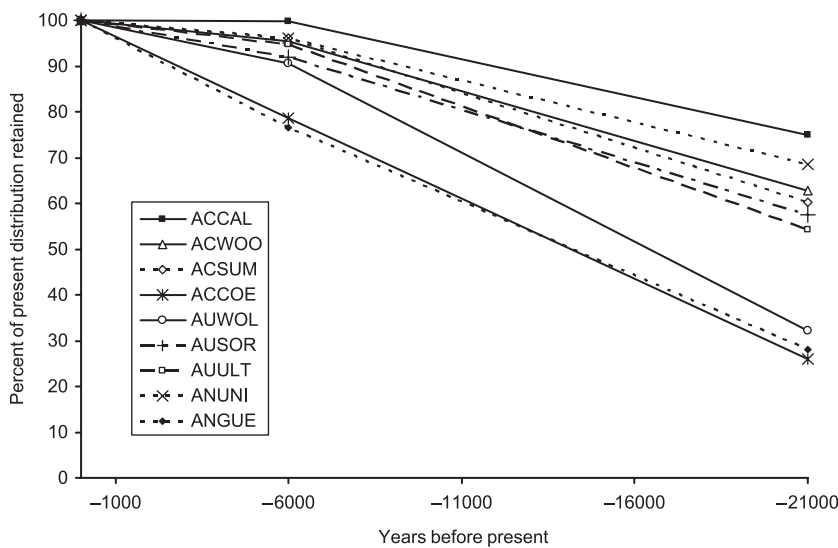


Figure 4 Summary of areas of overlap between modelled present-day and past geographic distributions (predicted by ≥ 5 models out of 10) for *Aphelocoma* jays. See text for taxon abbreviations.

used to develop the model and on the stability of ecological niches as constraints on geographic distributions across time and in different community contexts. The former — ability to *develop* predictive models using the methods that we utilize here — has been explored in a series of sensitivity analyses (Peterson & Cohoon, 1999; Stockwell & Peterson, 2002a,b; Anderson *et al.*, 2003; Stockwell & Peterson, 2003) and tests of model predictivity (Peterson, 2001; Anderson *et al.*, 2002; Peterson *et al.*, 2002a; Peterson *et al.*, 2002c; Peterson & Kluza, 2003). The latter — stability of ecological niches in evolutionary time spans — has been tested now on a variety of fronts, including species' invasions (Peterson & Vieglais, 2001; Peterson, 2003a), Pleistocene-to-recent predictions (Martínez-Meyer, 2002; Martínez-Meyer *et al.*, 2004), predictions between sister species pairs (Huntley *et al.*, 1989; Peterson *et al.*, 1999), and predictions across phylogenies of diverse lineages (Martínez-Meyer, 2002; Rice *et al.*, 2003). Nevertheless, both issues are worthy of consideration — ecological niche *models* may or may not be representative of the ecological requirements and possibilities of species, and niches *may* have evolved (thus changing the species' distributional potential from that reconstructed herein) in particular situations.

Other challenges exist for this approach. Quite important is the crude spatiotemporal resolution of the Pleistocene climate coverage sets — native resolution was of the order of $2\text{--}3^\circ$, which we were able to downscale to $0.5 \times 0.5^\circ$ pixel resolution. Clearly, this crude spatial resolution limits the detail possible for complex distributional phenomena to broad-scale effects. A solution to this limitation consists of development of regional climate models, but these models are quite time-expensive and computation-intensive. Similarly, resolution of shifts in potential distributional areas to just present, 6000 and 21,000 BP limits our ability to discern whether shifting potential distributional areas are continuous when viewed across time. Other complications include (1) that simulated palaeoclimates do not necessarily equal real palaeoclimates (Jackson *et al.*, 2000) (2) that the variables obtained from palaeoclimate simulations may not be the precise

variables that actually control species' distributions and their changes through time (Jackson & Overpeck, 2000), and (3) that climate regimes unrepresented in present-day situations may have been present in the Pleistocene (Jackson & Overpeck, 2000; Jackson & Williams, 2004).

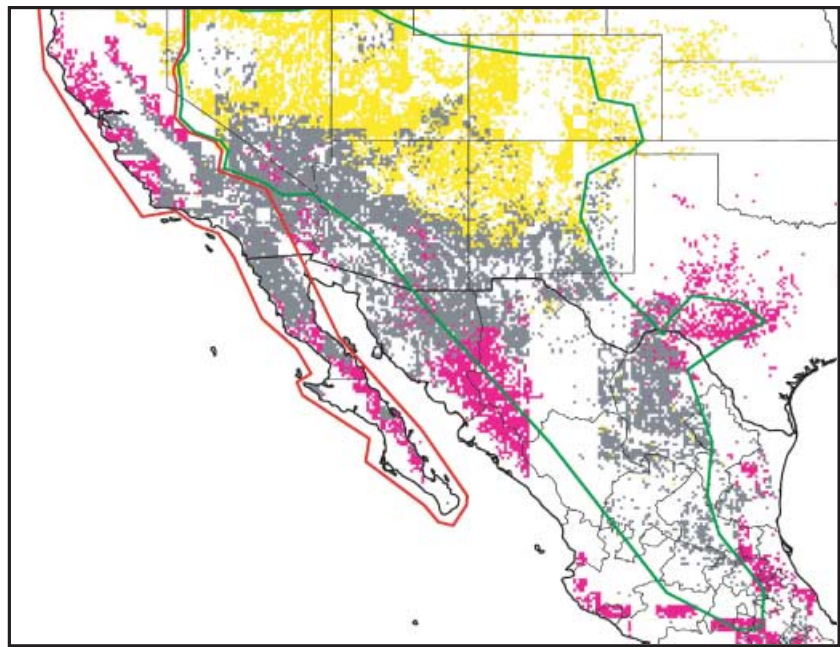
Pleistocene distributional shifts vs. stability

The general result of this analysis was a picture of distributional stability in the *Aphelocoma* jays during the dramatic climate changes across the end of the Pleistocene. This view is unexpected, given that many palaeoclimatic studies suggest fairly dramatic reorganizations of the biota of the south-western United States in that period (Wells, 1983; Prentice *et al.*, 1991; Wright *et al.*, 1993). Nevertheless, inspection of Figs 2 and 3 suggests that most of the distributional areas — particularly for the two northernmost taxa (*A. californica* and *A. woodhouseii*) — were conserved intact and habitable through the past 21,000 years.

These results should prove relatively proof against the limitations discussed above. The ability to develop predictive models depends on the generality of 'causal' connections identified — if the modelling effort has failed in achieving this generality, then past distributional potential should be underestimated rather than overestimated. Similarly, if niches have evolved over the time period examined, the effect would be of broadening the geographic potential of the species involved. Finally, the crude spatiotemporal resolution of results should not detract broadly from the first-level conclusion — that Pleistocene potential distributions of the species involved were broad, much more ample than just the Mojave Desert. As such, our principal results appear to be robust to the limitations that have been recognized in the approach.

The two forms in mainland western North America merit additional comment. In molecular genetic studies (Peterson, 1990b, 1992b), these taxa showed some discrete differences in

Figure 5 Visualization of potential for contact between *A. californica* and *A. woodhouseii* 21,000 BP. Red and green polygons outline present-day distributional limits for the two species, respectively. Areas in pink indicate the predicted Pleistocene range of *A. californica* (≥ 9 models out of 10 predicting), and areas in yellow indicate the predicted Pleistocene range of *A. woodhouseii* (≥ 5 models out of 10 predicting); areas in dark grey are areas predicted to be habitable for *both* species (≥ 5 models out of 10 predicting) in the Pleistocene.



putative allele distributions, which suggested rapid molecular evolution, if one followed the idea of dramatic reorganization of ranges at the Last Glacial Maximum. That is to say, if populations presently constituting *A. californica* and *A. woodhouseii* were intermixed in the pinyon-filled Mojave and Sonoran deserts at the Last Glacial Maximum, then the present genetic differences between the two species would have had to have accumulated just over c. 20,000 years. The results of this paper, however, suggest that the two species may have been able to maintain independent distributional areas, and that the age of the split between them may be older than was previously thought (Peterson, 1993). Similarly, the range of *A. insularis* on Santa Cruz Island was reconstructed as having been habitable even 21,000 BP, suggesting that this taxon, very distinct in molecular characters, may date to still earlier dates. It is worthy of note that these conclusions are robust to variations from an assumption of strict ecological conservatism (Peterson & Holt, 2003), as niche evolution would only serve to broaden the geographic possibilities of each species.

Examining the geography of the contact between *A. californica* and *A. woodhouseii* in more detail (Fig. 5), although present-day ranges are conserved almost intact, an area of potential contact appears in the Pleistocene in the Mojave Desert. The question, of course, is what sort of interactions (complete mixing, narrow contact zone, no mixing) may be expected to have taken place there in the past. Where these two forms come together at present, they hybridize in limited, narrow contact zones (Peterson, 1991a). Nowhere are they known to exist in sympatry, so if contact was established via dispersal into the desert basin, most likely a suture zone with limited hybridization existed. Such limited mixing may be conserved in the isolated 'hybrid' subspecies described as the subspecies *cana* (Pitelka, 1951), which have previously been postulated by one of us to represent cross-desert dispersers that have hybridized (Peterson, 1990a, 1991a).

Potential of the approach

The approach explored herein has enormous promise in illuminating geographic and historical patterns underlying current lineages. The climate coverage scenarios employed are worldwide in scope, and their utility is limited chiefly by the spatiotemporal resolution issues mentioned above. In general, though, this method provides a means of generating spatially explicit geographic hypotheses regarding potential geographic distributions of species for time periods in the past.

When distributional data exist for both past and present, tests of ecological niche conservatism across significant periods of time and drastic climate changes can greatly inform future projections of species' distributional potential in future changing climates (Peterson *et al.*, 2002b; Peterson, 2003b; Thomas *et al.*, 2004). When phylogenetic information is available, these projections can locate particular lineages in space and time, or at least provide falsifiable hypotheses for testing.

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