



Are large-scale distributional shifts of the blue-winged macaw (*Primolius maracana*) related to climate change?

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ABSTRACT

Aim To evaluate whether observed geographical shifts in the distribution of the blue-winged macaw (*Primolius maracana*) are related to ongoing processes of global climate change. This species is vulnerable to extinction and has shown striking range retractions in recent decades, withdrawing broadly from southern portions of its historical distribution. Its range reduction has generally been attributed to the effects of habitat loss; however, as this species has also disappeared from large forested areas, consideration of other factors that may act in concert is merited.

Location Historical distribution of the blue-winged macaw in Brazil, eastern Paraguay and northern Argentina.

Methods We used a correlative approach to test a hypothesis of causation of observed shifts by reduction of habitable areas mediated by climate change. We developed models of the ecological niche requirements of the blue-winged macaw, based on point-occurrence data and climate scenarios for pre-1950 and post-1950 periods, and tested model predictivity for anticipating geographical distributions within time periods. Then we projected each model to the other time period and compared distributions predicted under both climate scenarios to assess shifts of habitable areas across decades and to evaluate an explanation for observed range retractions.

Results Differences between predicted distributions of the blue-winged macaw over the twentieth century were, in general, minor and no change in suitability of landscapes was predicted across large areas of the species' original range in different time periods. No tendency towards range retraction in the south was predicted, rather conditions in the southern part of the species' range tended to show improvement for the species.

Main conclusions Our test permitted elimination of climate change as a likely explanation for the observed shifts in the distribution of the blue-winged macaw, and points rather to other causal explanations (e.g. changing regional land use, emerging diseases).

Keywords

Blue-winged macaw, climate change, ecological niche modelling, geographic distributions, range retraction, South America.

INTRODUCTION

The effects of global climate change on elements of biodiversity have been the subject of considerable discussion (Emanuel *et al.*, 1985; Peters & Darling, 1985; Dobson *et al.*, 1989; Holt, 1990; Peters & Myers, 1991–92; Thomas *et al.*, 2004; Lovejoy &

Hannah, 2005). Numerous efforts have used models of species ecological requirements (ecological niche models; ENMs) in attempts to anticipate the effects of climate change on biodiversity (Carey & Brown, 1994; Huntley *et al.*, 1995; Xia, 1995; Haxeltine & Prentice, 1996; Johnston & Schmitz, 1997; Kadmon & Heller, 1998; Midgley *et al.*, 2003; Pearson & Dawson, 2003;

Peterson *et al.*, 2004; Thomas *et al.*, 2004). Geographical shifts in species distributions consistent with general expectations from climate change effects (Lovejoy & Hannah, 2005) have been documented on global scales – in particular, poleward distributional shifts and phenological shifts towards earlier seasonal activity (Parmesan *et al.*, 1999; Walther *et al.*, 2002). However, the degree to which model predictions translate into real geographical shifts in the distributions of individual species has seen little analysis (Araújo *et al.*, 2005b).

Integration of observations and model predictions into an improved understanding of the effects of global climate change on biodiversity, however, remains incomplete. In particular, the effects of climate change on biodiversity are being suggested as pervasive (Thomas *et al.*, 2004), and the conservation status of species is being re-evaluated, broadly based on climate change considerations (Bomhard *et al.*, 2005). Nonetheless, to avoid the lack of scientific rigour that could result from broad application of generalities regarding the effects of climate change (e.g. insular situations, east–west barriers to dispersal), more rigorous, hypothesis-based analytical tests are needed. Although tests of model predictivity in anticipating

climate-driven range shifts over longer time periods have been presented (Martínez-Meyer, 2002; Martínez-Meyer *et al.*, 2004), only a single example of the testing of model predictions has been developed to date (Araújo *et al.*, 2005a).

In this paper, we provide a detailed example for a species of special conservation concern. Observed range retractions in the blue-winged macaw (*Primolius maracana*, Psittacidae) over the twentieth century were examined in the light of changing climates in the same period. Specifically ENM predictions were used to evaluate climate change as a causative factor in these shifts: spatial shifts in the distribution of environmental conditions modelled as appropriate for this species were examined to assess whether they are consistent with climate change being an explanation for the observed range retractions.

The blue-winged macaw

The blue-winged macaw is a threatened parrot species currently considered vulnerable to extinction (BirdLife-International, 2000). This species was originally common and

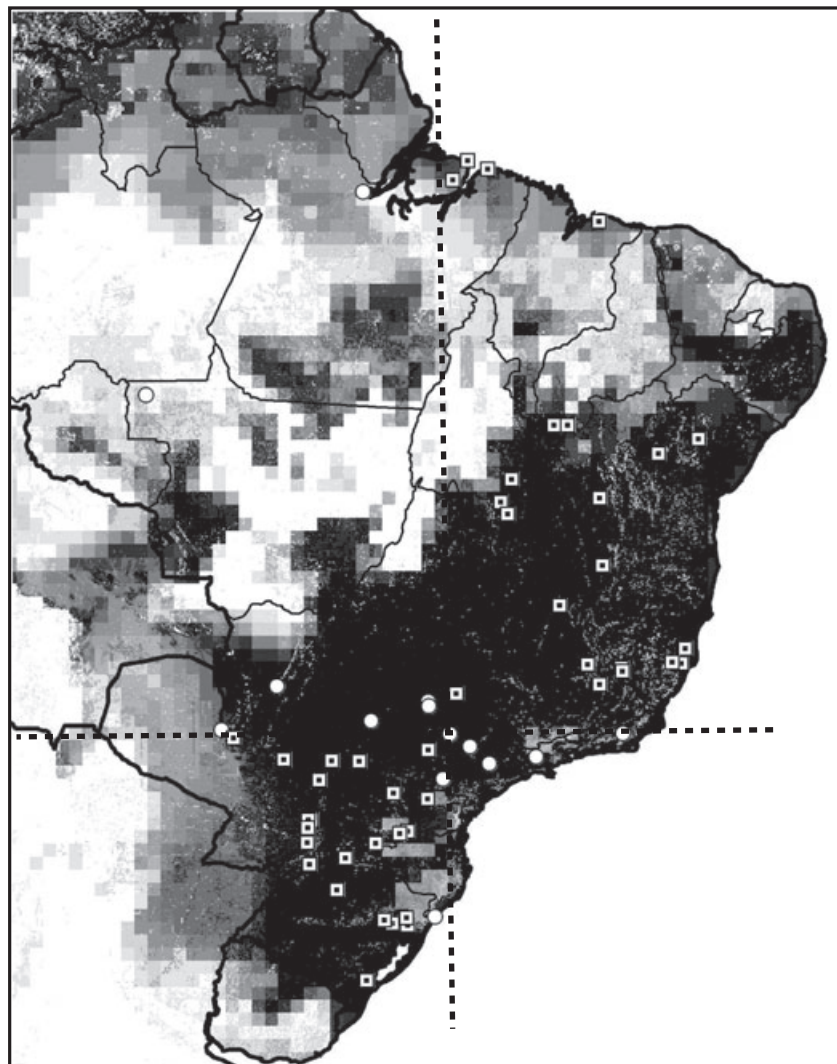


Figure 1 Example results of one quadrant test used to test model predictivity. Shown are data for pre-1950 points, with on-diagonal occurrence points (circles) used to build ecological niche models that predict the spatial distribution of off-diagonal points (dotted squares). Darker shades of grey indicate increasing model coincidence in predicting presence. Dotted lines indicate the median longitude and median latitude used to delimit the quadrants.

widespread across Brazil, eastern Paraguay and northern Argentina; however, in the second half of the twentieth century it showed a marked range retraction (Fig. 1). At present it appears to have been extirpated throughout southern Brazil (Belton, 1994; Rosário, 1996) and Argentina (Chebez, 1996; de la Peña, 1999), and it is rare in Paraguay (Lowen *et al.*, 1996; Clay *et al.*, 1998).

The species' range retraction has been attributed primarily to habitat loss (Olmos, 1993). However, this assertion is not based on a detailed test or in-depth analysis, but rather on logic, since so little forest remains across most of its original distribution (FSOSMA & INPE, 1998). Although other macaw species have also declined without obvious causes (e.g. *Anodorhynchus glaucus*), these cases occurred decades before the present case (Collar *et al.*, 1994). As such, to our knowledge, the broad southern disappearance of *P. maracana* is unique. However, a few points suggest that broader-scale factors may be important in this situation. First, the asymmetry of the observed range contraction does not fit with the idea of habitat loss being totally focused in the southern portion of the species' distribution. Second, the species has apparently disappeared from large southern forests such as the Iguazu Forest (170,000 ha) (Bornschein & Staube, 1991), Serra Geral (17,300 ha) and Aparados da Serra National Parks (10,250 ha) (Forrester, 1993; Belton, 1994), while similar extirpations have not been documented in the north (Novaes & Lima, 1992; Olmos, 1993; Collar *et al.*, 1994). Finally, the species does not appear to be particularly threatened by the pet trade, which is generally one of the main threats to psittacids, and it is not restricted to large forest blocks (Nunes, 2000). Hence, further investigation of possible broader-scale influences on the decline of the blue-winged macaw is warranted.

METHODS

For the purpose of this analysis, the ecological niche of a species or population is defined as the set of environmental conditions within which it is able to maintain populations without immigration (Grinnell, 1917; Holt & Gaines, 1992). Ecological niches and associated potential geographical distributions can be approximated via correlative approaches that relate known point-occurrence data to digital GIS data layers, summarizing spatial variation in relevant environmental dimensions (Guisan & Thuiller, 2005; Soberón & Peterson, 2005). Although this definition differs from other recent conceptualizations (Pulliam, 2000), it coincides in important ways, for example in recognizing the possibility of the absence of species in suitable areas.

Numerous approaches have been used to approximate species ecological niches (Nix, 1986; Austin *et al.*, 1990; Carpenter *et al.*, 1993; Lehmann *et al.*, 2002; Pearson *et al.*, 2002; Phillips *et al.*, 2004). Of these analytical approaches, an option that has seen both detailed sensitivity analyses (Peterson & Cohoon, 1999; Peterson *et al.*, 2002a; Stockwell & Peterson, 2002a,b, 2003) and broad application to questions of climate change (Peterson *et al.*, 2001, 2002b) is the Genetic

Algorithm for Rule-set Prediction (GARP) (Stockwell & Noble, 1992; Stockwell & Peters, 1999; Stockwell, 1999), an evolutionary computing approach for developing ecological niche models (available at <http://www.lifemapper.org/desktopgarp>).

Ecological niche models

In GARP, several steps of subsetting of available occurrence points are used to ensure that the models produced are general (Anderson *et al.*, 2003), i.e. able to anticipate independent sets of occurrence data, rather than being overfitted to a particular sample of occurrences. As a consequence, and given the random-walk nature of the genetic algorithm that GARP employs, we set aside half of the occurrence points for a final validation, and divided the other half evenly into a training data set for model development, and an extrinsic testing data set for selection of the most general models from among 100 replicates, following the recommendations of Anderson *et al.* (2003).

Within the GARP program, several functions occur automatically. As GARP is designed to work based on presence-only data, 'absence' information is included via sampling of pseudo-absence points from the set of pixels where the species has not been detected. GARP works through an iterative process of rule selection, evaluation, testing and incorporation or rejection: a method is chosen from a set of possible tools (e.g. logistic regression, range rules), and is applied to the training data to develop a rule. Rules may then 'evolve' by a number of means (e.g. truncation, point changes, crossing-over among rules) to maximize predictivity. Predictive accuracy is evaluated based on the training data. 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 for either 1000 iterations or until convergence (set at 1% throughout our analyses).

Testing the predictive power of ecological niche models

The projection of ecological niche models onto current landscapes provides an estimate of the present-day geographical distribution of suitable conditions, and allows tests of model predictivity. In general, extrinsic test data were overlaid, and observed correct predictions tallied; we then used simple statistical tests to establish whether the observed degree of coincidence was unexpected, given the proportional coverage of the study area by areas predicted to be habitable. The proportional area predicted present \times the number of extrinsic test data points was used as an estimate of expected successful prediction of points, if prediction and test points were associated at random. A chi-square approach (1 d.f.) was used to test the significance of the departure from random expectations; when expected cell frequencies were < 5 , a binomial probability was used (Anderson *et al.*, 2002).

The nature and difficulty of this test of model predictivity, however, depends critically on how occurrence points are subset into training and testing data sets. We used two

approaches to this step, which simulated distinct phenomena of unknown geographical distribution: (1) the quadrant test – available distributional points were divided into quadrants above and below the median longitude, and above and below the median latitude. Two of the quadrants (above–above, below–below) were used to develop models, and were used to predict the distributions of points in the other two quadrants (above–below, below–above), and vice versa, (2) the random test – available distributional points were divided randomly into two equal parts, one for model development and one for model testing. The quadrant test is probably a more rigorous test of model predictivity, as the model must predict into broad areas from which no input occurrence points are available, whereas the random subsampling perhaps simulates real-life situations more realistically, in which the density of data might vary more commonly than regional representation.

Data on distributions and ecological dimensions

Distributional data representing 174 records (i.e. unique species \times latitude-longitude combinations) for the blue-winged macaw (53 records before 1950, 121 records from 1950 or later) were compiled from the literature (Berlepsch & Ihering, 1885; Ihering, 1899; Sneath, 1914; Sztolcman, 1926; Naumberg, 1928, 1930; Gleish, 1930; Pinto, 1938, 1978; Willis, 1979, 1990; Willis & Oniki, 1981, 1991; Yamashita & Coelho, 1985; Bege & Marterer, 1991; López, 1992; Novaes & Lima, 1992; Forrester, 1993; Hayes, 1995; Lowen *et al.*, 1996; Rosário, 1996; Straube *et al.*, 1996; Anjos *et al.*, 1997; Henriques & Oren, 1997; Parker & Goerck, 1997; Clay *et al.*, 1998; Bauer & Pacheco, 2000; Kirwan *et al.*, 2000; Marsden *et al.*, 2000), data records from natural history museum collections (see museums listed in the Acknowledgements), and correspondence with knowledgeable ornithologists and birdwatchers (see list in Acknowledgements). Ornithological gazetteers (Paynter, 1989, 1995; Paynter & Traylor, 1991) were used to apply geographical coordinates to some historical records.

Environmental data layers included 11 digital maps summarizing aspects of topography (elevation, slope, aspect, topographic index, from the US Geological Survey's Hydro-1K data set, available at <http://edcdaac.usgs.gov/gtopo30/hydro>), and aspects of climate (annual means) including diurnal temperature range, precipitation, maximum, minimum, and mean temperatures, wet days and vapour pressure (from the Intergovernmental Panel on Climate Change, available at <http://www.ipcc.ch>). All environmental data sets were resampled to a pixel resolution of $0.1^\circ \times 0.1^\circ$ (about 10×10 km), for an area including all of central and eastern Brazil and surrounding areas for analysis.

Because global climate models are still quite coarse in spatio-temporal resolution, we per force had to use broader temporal swathes than we would ordinarily wish. In general, we were comparing distributions predicted under IPCC climate scenarios for pre-1950 (climate averages over 1901–30) with scenarios for post-1950 (climate averages over 1961–90). These coarse and crude climate scenarios clearly compromise the

detail possible in our results. Nevertheless, we hoped that these problems would not confound results to the point that broad regional trends would be obscured. We built ecological niche models based on climate data for each period, tested model predictivity within each period, and then projected each model to the other time period.

Developing final distributional predictions

We produced 100 replicate models of the species' ecological niche for each time period. Given the random-walk nature of GARP models, we followed a recent 'best practices' summary (Anderson *et al.*, 2003) for choosing the 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 the true distributional area, here measured as the failure to predict known occurrences as present) and commission (including areas not actually inhabited, here approximated by the proportional area predicted present in the study area); and (3) best models (as judged by experts blind to error statistics) are clustered in a region of minimum omission of independent test points and moderate area predicted (an axis related directly to commission error) (Anderson *et al.*, 2003). Position relative to the two error axes (omission and commission errors) provides an assessment of the relative accuracy of each model – in particular, models failing to predict independent occurrence data sets are discarded for lack of generality. To choose the best subsets of models, we: (1) eliminated all models that had a non-zero omission error based on independent testing points; (2) calculated the median area predicted present among these zero-omission models; and (3) identified the 10 models closest to the overall median area predicted, which were used as the final prediction of the species' potential distribution.

These best-subsets models were then projected among time periods to assess shifts of habitable areas across decades. That is, the rule set for each of the best-subsets models was used to query landscapes for areas fulfilling the species' niche requirements in the 'other' time period. The final prediction was then developed as the sum of the 10 predictions from the best-subsets models – this grid had values ranging from 0–10, representing levels of model agreement, ranging from complete agreement in prediction of absence (0) to complete model agreement in predicting presence (10). These projections require the assumption, here made explicit, that a species' ecological requirements remain constant over change events (Martínez-Meyer, 2002).

To permit visualization of patterns of niche distributions in environmental space, in ArcView, we combined the input environmental grids (e.g. mean annual precipitation, mean annual temperature, elevation) and the final prediction for a particular species to create a new grid with a distinct value for each unique combination of environments. We exported the table associated with this grid in ASCII format. To make visualization more feasible, we reduced data density by

selecting a random 10% of the table for further use; this reduced table was then used as the basis for the development of scatterplots for visualizations.

RESULTS

The developed models showed good predictivity: under both the random test and the quadrant test, the coincidence of independent test points with model predictions was much better than that expected under random models. For random tests, the coincidence of all best-subsets models developed (10 for each time period) with test points was statistically significantly better than random expectations ($P < 0.05$). In the quadrant tests, prediction into the unsampled (testing) areas yielded predictions that were more coincident with the test points from those areas than would be expected by chance (see Fig. 1), with most tests showing statistical significance ($P < 0.05$). The result of statistically significant model predictivity was most pronounced at more restrictive prediction thresholds (Fig. 2), suggesting that areas predicted present with high model agreement are highly likely to hold (at least potentially) populations of this species.

Ecological niche models projected onto geographical landscapes generally matched the known distribution of the species well (Fig. 3). These models also predicted the potential presence of populations in areas from which the species is not known to occur; these sites could be the focus of on-ground field surveys. Viewed in climate space (Fig. 4), the species' distribution is limited to those areas in which temperatures are relatively high, but appears to be quite tolerant of precipitation regimes. At least one of the best-subsets models employed a rule that constituted an absolute cut-off of predicted areas at an annual mean temperature of $\leq 25^\circ\text{C}$.

Predictions between time periods in general reflected the relatively subtle nature of climate changes in the middle part of the twentieth century (Fig. 5): differences between predicted distributions for the two time periods were in general

minor (Fig. 3), and indeed no change in suitability of landscapes was predicted across large areas of the species' original range during the two time periods (Fig. 5). Most relevant to observed shifts in the species' distribution, however, is that no tendency towards range retraction in the south was predicted. Rather, conditions in the southern part of the species' range tended to be improving for the species (Fig. 5).

DISCUSSION

The range retraction observed in the southern part of the range of the blue-winged macaw over the middle part of the twentieth century is dramatic, and should be of considerable conservation concern. However, the causes of this retraction remain unclear. We assessed a hypothesis of climate change as the cause of this retraction, and were able to reject that hypothesis with considerable confidence by simple visual inspection, since climatic conditions have apparently been *improving* for the species in the region of most dramatic range retraction. In spite of that, it is important to consider limitations in the development of climate change projections for species geographical distributions, given the lack of finer-grained climate models.

Several more general limitations, of course, exist for such correlative models. In particular, misidentifications or inaccurate geographical references in the occurrence data can introduce noise into the data used to train or validate models. Similarly, the environmental data sets on which the models are based are not without error – in particular, the coarse resolution of the climate data can cause non-coincidence with actual climates. Finally, the modelling approach used may itself err by including environmental combinations that are actually not used by the species, or by excluding combinations that are actually used. These concerns and others have been evaluated in some papers that argue for caution in the interpretation of 'climate envelope' or niche models (Pearson & Dawson, 2003;

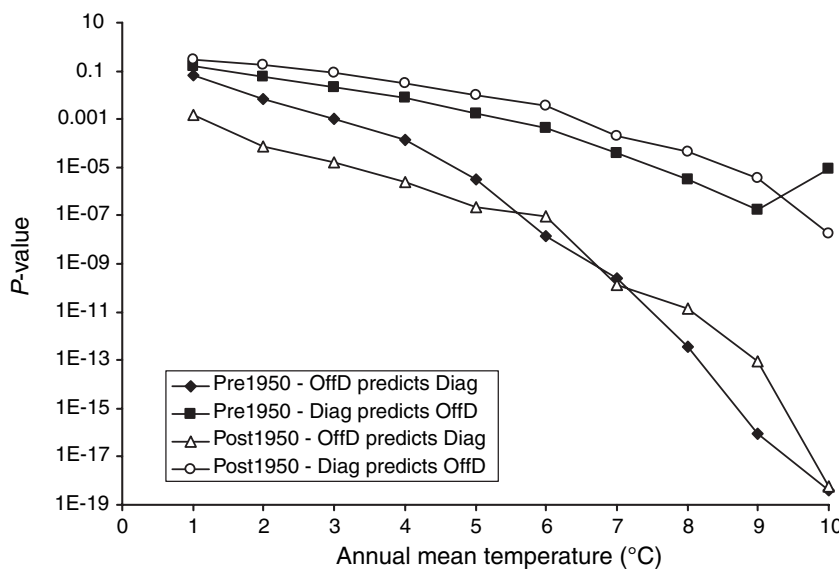


Figure 2 Summary of quadrant tests, in which occurrence points in two quadrants are used to build ecological niche models that predict the spatial distribution of occurrence points in the other two quadrants (on-diagonal quadrants predict off-diagonal quadrants, and vice versa). Curves graphed are significance values of the chi-square tests (see Methods) as a function of level of coincidence of model predictions, from the broad areas predicted by any model or models (value 1) to the more restricted area predicted habitable by all models (value 10).

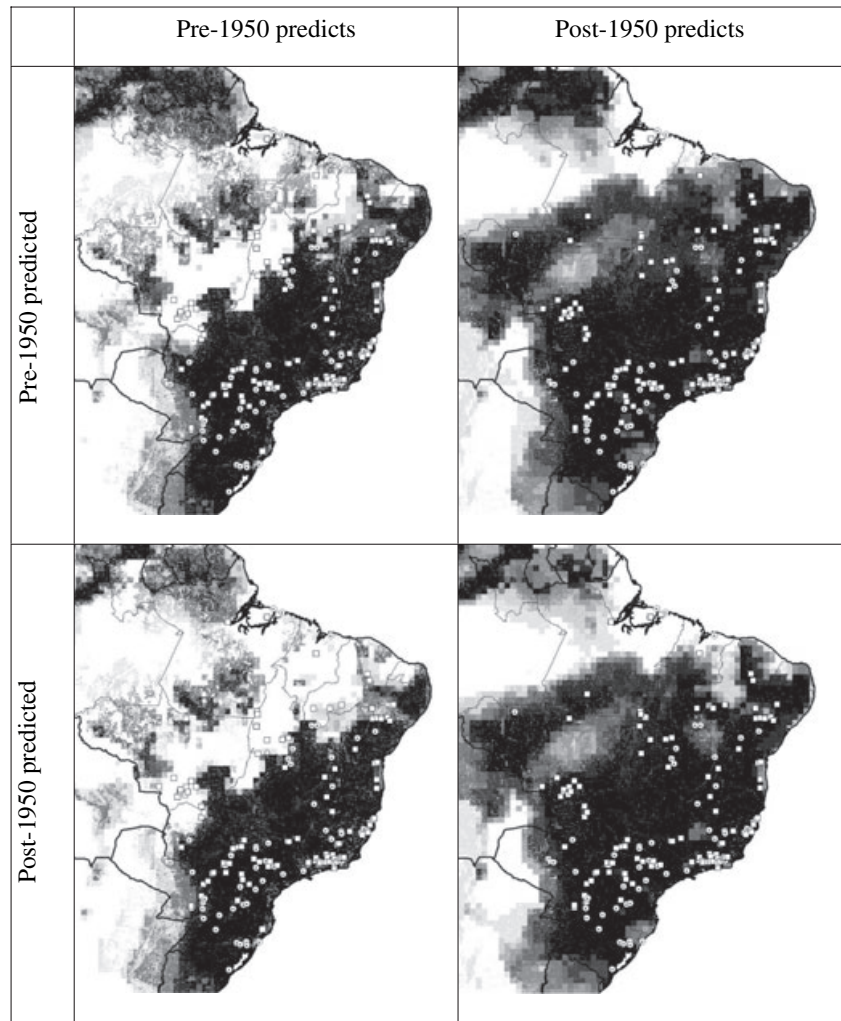


Figure 3 Four predictions among time periods for the potential geographical distribution of blue-winged macaws: pre-1950 predicts pre-1950 and post-1950, and post-1950 predicts pre-1950 and post-1950. Increasingly dark shading indicates greater confidence (model agreement) in the prediction of presence. Dotted circles indicate known pre-1950 occurrences, and squares indicate known post-1950 occurrences.

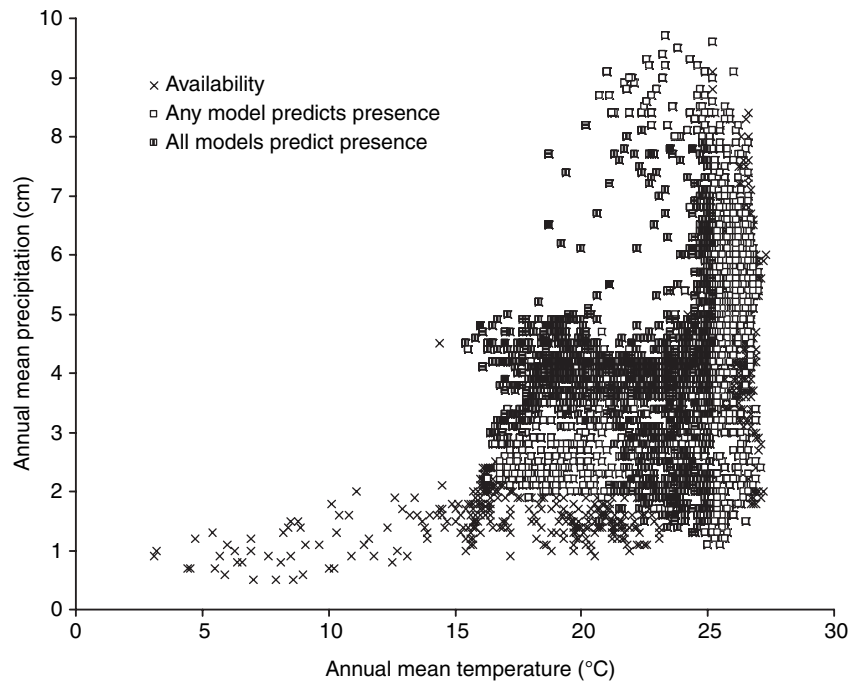


Figure 4 Two-dimensional visualization of modelled ecological niche of blue-winged macaws, in which areas predicted present by all 10 best-subsets models (filled squares), or by any of the 10 best-subsets models (open squares) are compared with those conditions available in the landscape (crosses in terms of annual mean temperature and annual mean precipitation).

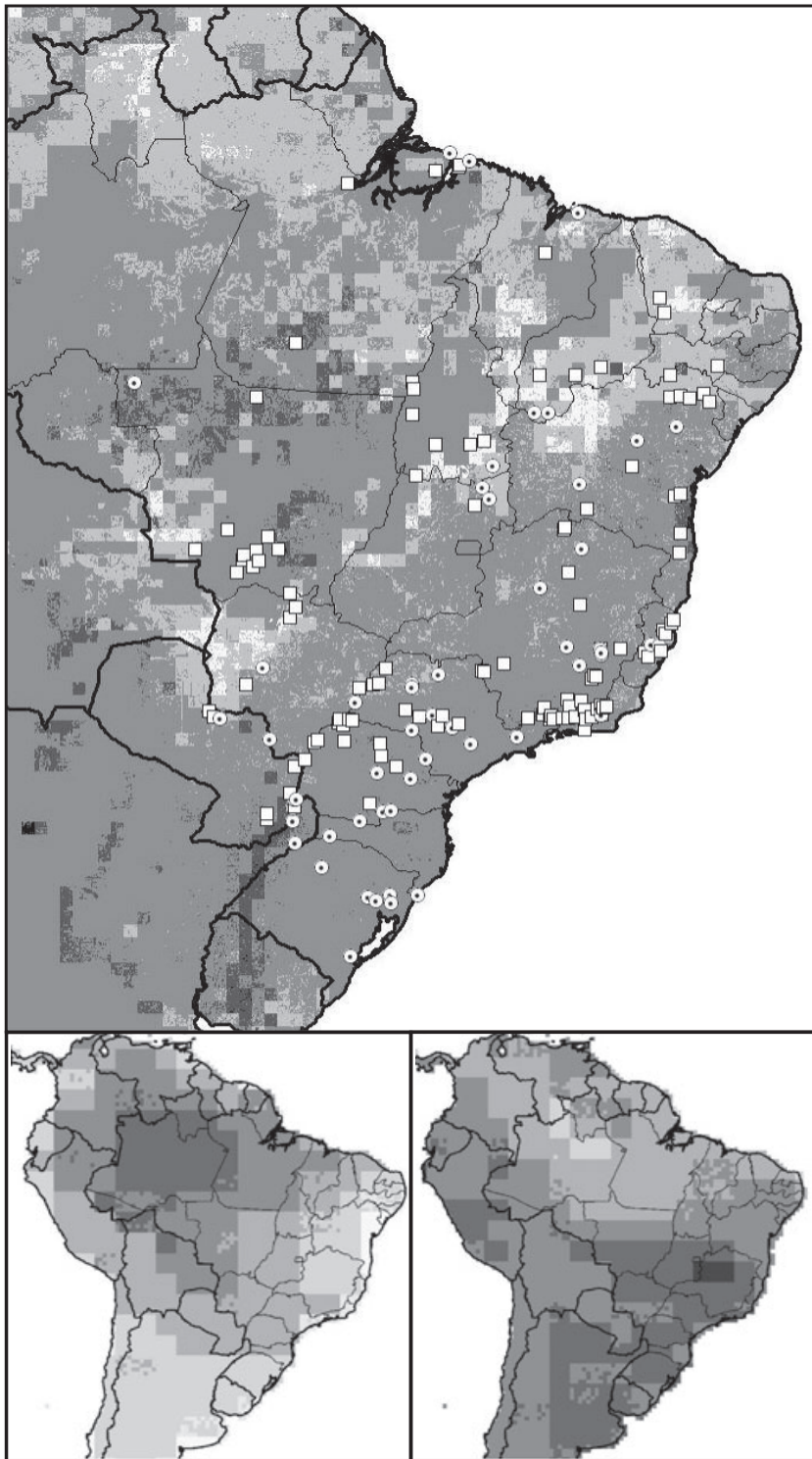


Figure 5 (Top) Difference map indicating changes in the suitability of climate regimes for blue-winged macaws, representing ecological niche models developed based on pre-1950 climates and known pre-1950 occurrences. White and light grey indicate worsening conditions for the species; medium grey indicates no change; and dark grey and black indicates improving conditions for the species. Dotted circles indicate known pre-1950 occurrences, and squares indicate known post-1950 occurrences. (Bottom) Difference maps showing spatial patterns in changes in temperature (left: white = no change, darkest shading = 0.46°C temperature increase, pre- to post-1950) and precipitation (right: white = 20 mm decrease in precipitation pre- to post-1950, darkest shading = 14 mm increase in precipitation, pre- to post-1950).

Hampe, 2004; Thuiller *et al.*, 2004; Thuiller, 2004; Araújo *et al.*, 2005a; Luoto *et al.*, 2005).

This study was developed in terms of broad trends, and our predictions of present-day distributional areas for the species, based only on climate data and topography, were somewhat overestimated. Considerable evidence is accumulating which indicates that ecological niches (as modelled using tools such as GARP) constitute long-term stable constraints on a species'

geographical potential (Peterson *et al.*, 1999; Peterson & Vieglais, 2001; Martínez-Meyer, 2002); these results argue strongly that modelled ecological niches of species would indeed capture the essence of the effects of climate change on species distributions. A small number of studies have now begun to test, and in general so far to validate, the predictive ability of such models across time as climates change (Martínez-Meyer *et al.*, 2004; Araújo *et al.*, 2005a).

So what has caused the decline and disappearance of the blue-winged macaw in the southern parts of its range? If climate change has no role, something has occurred within this geographical area. Our results suggest that other causal explanations (e.g. changing patterns of land use, diseases, the pet trade), should be considered in understanding the conservation status of this species.

Some potential factors at finer scales, such as the degrees of fragmentation of natural habitats, could not be taken into consideration in our models, given the temporally heterogeneous nature of the occurrence information and the lack of data for different periods and regions. Also, our models did not take into account the possibility of shifting interspecific interactions affecting the species' distributional potential. Finally, the precise climatic factors that directly affect the species may not have been captured in the rather simple parameters considered here. For example, heavy rainfall at certain times during the breeding season has been implicated in nesting failure (through cavity inundation) in parrots (e.g. Rowley, 1990) and other hole-nesting birds (Wesolowski *et al.*, 2002), but these local factors would not be expected to act across entire regions.

Additionally, this study was based on presence-based modelling and did not take into account the densities of blue-winged macaw populations across the species' range. Such information is relevant, since it is well known that densities are not constant across a species' range; populations at the periphery of the range tend to occupy less favourable habitats and, as a result, are smaller, more fragmented, and isolated from one another (Gaston, 1996; Brooks, 2000). We have little idea of their original population densities at different sites in the southern part of the range. It may simply be that the species was 'always' rare in the south (although this is not suggested by the ample numbers of historical specimens from the region), making the species more vulnerable to anthropogenic change in that region, notwithstanding the improving climate. Finally, multiple factors may have impacted upon blue-winged macaws across their range, which may act differently in different combinations, intensities and geographical areas.

Climate change, models and observations

Most efforts to link climate change with effects on biodiversity have been correlative and static at best. In many cases, the link is fully correlative, without formal hypothesis testing. In only a few cases has experimental confirmation of climate change as a causal factor for observed shifts been possible (Newton *et al.*, 2000; Ettersson & Shaw, 2001; Nadkarni & Solano, 2002): in most cases (as in the present), we must use correlative approaches, yet even these studies can propose and test hypotheses formally.

To go beyond coarse-scale expectations (e.g. move poleward in latitude and upward in elevation), it is necessary to seek finer-scale coincidence between detailed model predictions and observed shifts. We consider that the testing of hypothesis, as

was done here, is an important step in establishing climate change as a cause, and have found the general approach to be capable of rejecting (e.g. this study) or accepting (Peterson & Shaw, 2003) the effect of climate change as an explanation. Further exploration of these approaches and innovation in developing fine-scale tests (e.g. G. Midgely, personal communication) will be key in identifying causes of the range retraction and thus contributing to the development of a conservation plan for blue-winged macaws.

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